The Whole Fungus

Kananaskis II
The Whole Fungus
The Sexual-Asexual Synthesis

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18
The Teleomorphs of Water-borne Hyphomycetes from Fresh Water

J. Webster & E. Descals

INTRODUCTION

The pioneer studies of Ingold, beginning in 1942 and extending over a third of a century, have alerted mycologists and freshwater biologists to a spectacular flora of micro-fungi on leaves and twigs in freshwater streams and lakes. A characteristic feature of many of these fungi is that their conidia have shapes which seem to be bizarre, but which are presumably adapted to dispersal and anchorage in the aquatic habitat (Webster 1959a). Two basic types of spore morphology recur, the tetraradiate and the sigmoid. Despite the overall similarity in shape, the painstaking and elegant studies of Ingold and others have emphasized that conidial development may take fundamentally different courses, and a basic thesis presented by Ingold is that the tetraradiate propagule has arisen many times in the course of evolution in aquatic habitats (Ingold 1975a).

Over sixty form genera have been erected, and about 150 species have been described. In addition, there are many species, recognized only as spores, still awaiting studies of spore development, and description as new taxa. An admirable guide to identification of the commonly encountered forms is now available (Ingold 1975b). The group has a world-wide distribution (Ingold 1976). Studies from tropical areas would undoubtedly add considerably to the number of species.

In temperate areas with deciduous trees, there is a striking seasonal periodicity in the abundance of spores in streams, largely explicable in terms of availability of leaf and twig substrates, with numbers of spores rising almost to $10^4$ per litre (Iqbal & Webster 1973). In the River Teign, Devon, England, we have encountered spore concentrations of $2-3 \times 10^4$ per litre in October and November following the peak period of leaf fall in 1975 and 1976.

The significance of such fungi in stream ecosystems is now becoming clearer following the studies of Kaushik & Hynes (1968, 1971), Bürlocher & Kendrick (1973a,b, 1976) and Berrie (1976). Colonization of leaf litter by such fungi renders leaves more-palatable and nutritious to invertebrates. The increased nutritive value of colonized leaves is associated with an increase in their protein content (expressed as a percentage of residual dry weight). Presumably the fungi are able to obtain soluble inorganic Nitrogen, available in low concentration but in relatively large amounts from the stream water, and to form microbial protoplasm making use of the carbon available in the leaf tissue. The input of fixed carbon in many streams is allochthonous, and most streams derive the bulk of their carbon input not from attached algae.
or macrophytes, but from litter deposits from adjacent trees. Since the tree leaf litter is initially a relatively poor food source for many aquatic animals, the fungi provide an essential link in a food chain leading from the primary producers (i.e., the deciduous trees) to the consumers (i.e., the aquatic animals).

Although these fungi are commonly known as 'aquatic' Hyphomycetes, evidence is accumulating that many are not exclusively aquatic, but can grow on leaf litter and a variety of other substrata in habitats with no immediate likelihood of contact with flowing water (Bandoni 1972, 1974, Park 1974a,b, Webster 1977a). The idea that such fungi are amphibious rather than aquatic is attractive because it may help to explain why, despite the fact that their conidia are carried passively downstream, these fungi are common close to river sources. Although the number of species encountered tends to increase as leaves are sampled further and further downstream from a river source, there is still the problem of how 'aquatic' fungi with passively dispersed propagules can be distributed against the current. The possibility that some of them may be dispersed by other means is clearly worth examination. One possibility is that spores, which are very effectively trapped by foam in turbulent streams, may be transported upstream, e.g., by waterfowl and other animals. It is also possible that infected leaves, carried out of a stream at the time of flood, may retain these fungi in a viable state (e.g., mycelium, chlamydospores or sclerotia), and be subsequently transported by wind. There is also the possibility that air-borne spores (e.g., ascospores or basidiospores) may occur in their life-cycles, and there is therefore a need to review the teleomorphs of 'aquatic' conidial fungi.

Ingold distinguished between fungi which are primarily aquatic, i.e., those whose entire evolution has taken place in water, and those which are secondarily aquatic, i.e., appear to have become adapted to an aquatic existence, having been derived from terrestrial ancestors. The first group includes zoosporic fungi of varied affinity, now often grouped in the Mastigomycotina (Webster 1977b). The second includes the Ascomycotina, Basidiomycotina and Deuteromycotina. The last group is made up of forms which may well have evolved from the first two, presumably by loss of sexual function, or may represent the unrecognized anamorphs of these two groups.

Evidence linking anamorphs and teleomorphs in aquatic Hyphomycetes is obtained in two ways. Cultures derived from single conidia, incubated under suitable conditions, may give rise to teleomorphs in culture. Alternatively, collections of suspected teleomorphs in nature, e.g., from rotting wood along streams, may be used to start cultures, preferably isolated from a single ascospore, a single ascus, or a single basidiospore. It is useful also to prepare multispore cultures. If ascomata or basidiomata develop in such cultures, but fail to develop in cultures derived from single spores, this may indicate that the fungus in heterothallic. A clue to possible connections can sometimes be obtained when teleomorph and anamorph are constantly found in association.

Table 18.1 lists the known connections between teleomorphic and anamorphic aquatic fungi.
An analysis of these observations shows that, in four of them (*Neatria penicillioides*, *N. lugdunensis*, *Mollisia* sp. and *Leptosporomyces galzinii*), the teleomorph was first described from cultures derived from conidia, and later search on wood in streams or on infected wood incubated in moist chambers has yielded the teleomorphs of some of them on natural substrata. In the remaining three cases, material of ascomata collected in the field has been used to start cultures which developed conidia.

Following these successful demonstrations, extensive collections of Ascomycetes on wood from freshwater streams have been made, and cultures prepared from them (Iqbal 1972), but unfortunately no further connections were established. Since then, Descals has made isolations of a number of anamorphs in Britain, often from spore accumulations in foam, and a number of connections between Ascomycetes and aquatic Hyphomycetes have been established. These are listed in Table 18.2.

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<table>
<thead>
<tr>
<th>Teleomorph</th>
<th>Anamorph</th>
<th>Author</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ascomycotina:</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Neatria penicillioides</em></td>
<td><em>Flagellospora penicillioides</em></td>
<td>Ranzoni 1956</td>
</tr>
<tr>
<td><em>Neatria lugdunensis</em></td>
<td><em>Heliscus lugdunensis</em></td>
<td>Webster 1959b</td>
</tr>
<tr>
<td><em>Mollisia</em> sp.</td>
<td><em>Anguilllospora crassa</em></td>
<td>Webster 1961</td>
</tr>
<tr>
<td><em>Massarina aquatica</em></td>
<td><em>Piricularia aquatica</em></td>
<td>Webster 1965</td>
</tr>
<tr>
<td><em>Hymenoscyphus varicosporoides</em></td>
<td><em>Vartiosporium</em> sp.</td>
<td>Tubaki 1966</td>
</tr>
<tr>
<td><em>Massarina</em> sp.</td>
<td><em>Anguilllospora longissima</em></td>
<td>Willoughby &amp; Archer 1973</td>
</tr>
<tr>
<td>Basidiomycotina:</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Leptosporomyces galzinii</em></td>
<td>Clamped conidium</td>
<td>Nawawi et al. 1977</td>
</tr>
</tbody>
</table>

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</tr>
</thead>
<tbody>
<tr>
<td><em>Rutstroemia</em> sp.1</td>
<td><em>Anguillospora furtiva</em> n.sp. ined.</td>
</tr>
<tr>
<td><em>Orbilia</em> sp.</td>
<td><em>Anguillospora</em> sp.1</td>
</tr>
<tr>
<td><em>Mollista</em> sp.</td>
<td><em>Filosporella</em> n.sp. ined.</td>
</tr>
<tr>
<td><em>Massarina</em> sp.1</td>
<td><em>Clavariopsis aquatica</em></td>
</tr>
<tr>
<td><em>Miladina lechithina</em></td>
<td><em>Actinospora megalospora</em></td>
</tr>
</tbody>
</table>

In view of the evident success of the techniques used, details will now be given, in order to encourage other workers to study the group (see Descals & Webster 1977). River foam is scooped into a screw-topped collecting jar or clean polythene bag. It is returned to the laboratory and, during its transfer there, the sample is preferably kept cool, by placing it either in an insulated box with an ice pack, or in a chilled thermos flask. The use of a mobile
laboratory (a modified trailer) has proved invaluable in working on foam samples remote from a fixed laboratory. If it is not possible to return the foam sample to the laboratory within a few hours, some foam can be smeared, using sterile tissue paper, over the surface of an agar plate carried to the field (details of media are given below). The plates are subsequently scanned in the laboratory. If foam samples are brought to the laboratory, they are poured into glass Petri-dishes and left to stand for a few minutes in order to allow the spores to settle. The dishes are then scanned under a good-quality dissecting microscope (x50-x200 magnification). Spores are then picked up, either with a flamed sewing needle or with a mounted eyelash, from the meniscus of the water formed as the foam collapses, or with a very fine Pasteur pipette operated with a teat bulb or a short length of rubber tubing operated from the mouth. It is advantageous to rinse the pipette, before use, with sterile water. Spores are transferred to filtered 0.1% malt extract agar supplemented with 0.008% Crystamycin (Glaxo Laboratories, Greenford, England). The plates are incubated at 15°C for one to several days, and hyphal tips from germinated spores, when grown free from bacterial contaminants, are transferred to plates of (usually) 2% malt extract agar. Use of a dummy objective with a cutting tool of the pattern described by Keyworth (1959) has been helpful. Prolonged incubation extending over several months may be necessary and, to avoid drying out, about 30 ml of agar is used for each 9 cm Petri-dish. The lids of the dishes are also taped to the bases, using 2.5 cm wide Scotch drafting tape (3M) or Sellotape. This minimizes contamination, but appears to allow satisfactory gas exchange for respiration. The plates are incubated at 10-15°C for several months in a refrigerated cabinet illuminated by daylight, supplemented by continuous NUV from a Phillips Black Light fluorescent tube (TL 40W/08 RS F40 BLB). We use refrigerated display cabinets such as those used in supermarkets for display of dairy products, and modify them by adding sliding glass doors and including a black light tube.

After growth for a suitable period, development of conidia may be encouraged by three methods. Culture strips may be partly submerged in sterile water in Petri-dishes and incubated for one to several days at 10-15°C. Alternatively, culture pieces may be placed in sterile water and forcibly aerated, using a stream of filtered compressed air (Webster & Towfik 1972, Webster 1975). A third method adopted when the two earlier methods have failed is to use a modified microscope slide flow chamber (Descals et al. 1976), in which a small strip of culture is irrigated by a flow of sterile water. This method is particularly valuable when it is desired to produce a series of photographs or drawings illustrating conidium development, or to carry out time-lapse cinematography.

Some of the taxonomic problems raised by the discoveries listed in Table 18.2 will now be discussed.

1. **RUTSTROEMIA SP. 1 AND ANGUILLOSPORA FURRIVA** (FIGS. 18.1-18.3).

This fungus was first isolated from foam samples collected at Becka Falls, near Manaton, Devon, England, and later from Smooth Beck, Esthwaite, Cumbria, England. At the time of isolation, the spores were tentatively identified as *Anguillospora longissima* (Sacc. & Syd.) Ingold (Ingold 1942). However, after culture for several months under the conditions described above, abundant stalked, cream-coloured apothecia with inoperculate asci developed. The
Fig. 18.1. Arbacia angulifera sp. nov., section A, side view. B, side view of condylium. C, section of condylium with 23 septa. D, sketch of apothecium.
Fig. 18.2 *Rutstroemia* sp. 1: Apothecia in culture on 2% malt extract agar.
Fig. 18.3 *Rutstroemia* sp. 1: Asci, ascospores and paraphyses.
fungus was re-isolated from single ascospores and, when these fresh cultures were sufficiently
well-grown, strips were submerged in water and Anguillospora-type conidia developed readily,
showing that the apothecia represented the teleomorph of the Anguillospora and had not arisen
as a contaminant, and also that the fungus is homothallic. The apothecial teleomorph has
been provisionally assigned to the genus Ruststroemia (R.W.G. Dennis, personal communication).
As will be shown later, we have confirmed the findings of Willoughby & Archer (1973) connecting A. longissima with a species of Massarina. Our fungus is critically distinct from A.
longissima, and we propose to call it A. furtiva. A fuller account describing this fungus
will be published elsewhere.

Macroconidial anamorph in culture (Fig. 18.1): Conidiophores mononematous, simple, hya-
line, 45-175 μm long, broadening to a truncate tip up to 3.7 μm diam.; 1-7-septate: conidio-
genous cell integrated, determinate. Conidium development thallic, conidia hyaline, solitary.
The conidium initial is at first straight and eventually becomes curved. The septa are laid
down during development, and before the conidia are released, with the more distinct basal
septum appearing first. Detachment of the conidium is by disarticulation of the basal septum,
leaving a dome-shaped to conical scar at the tip of the conidiophore. Mature, detached coni-
dia measure 130-440 x 5.5-8 μm, widest at the centre, tapering towards the tip, and with a
truncate scar at the base. There are 10-23 septa, and the spore may show constrictions at two
points along its length. Germination takes place through the basal scar, and later from
intercalary cells. In unaerated water, spores may germinate by repetition.

Teleomorph in culture (Figs. 18.2 and 18.3): Apothecia develop only in illuminated cul-
tures (2% malt extract agar, 10-20°C, cool white fluorescent light + NUV, which enhances
apothecial development, in sealed plastic Petri-dishes). They occur singly, mostly near the
margin of the culture, and may arise in concentric circles. They are positively phototropic,
and arise from dark-coloured hyphae on the surface of the agar or on aerial hyphae. They are
shortly-stalked, glabrous, fleshy, with a disk which is creamy-white when mature, turning
brick-red to brown when old. They measure 3-5 mm diam. Ascii narrowly clavate, unitunicate,
short-stalked apex rounded to truncate, not staining with Iodine, 90-120 x 7-9.5 μm. Para-
physes filiform to cylindrical, 1.5-2 μm wide, apex rounded, as long as the ascii, sticky,
thin-walled, staining dark yellow in Iodine. Ascospores obliquely uniseriate or irregularly
arranged, ellipsoidal or shortly clavate, hyaline, non-septate within the ascus, with several
small guttules, 12-15 x 3.5-5 μm. A single median septum may develop later.

2. MASSARINA SP. 1 AND ANGUILLOSPORA LONGISSIMA (FIGS. 18.4 — 18.6).

Willoughby & Archer (1973) have shown that A. longissima has a teleomorph belonging to the
bitunicate Ascomycete genus Massarina. The pseudothecia of their fungus (here referred to as
Massarina sp. 1) developed on twigs of alder, oak, ash and willow submerged in Smooth Beck,
Esthwaite Water, Cumbria, England, for periods of 1-10 months, and subsequently incubated for
3-4 weeks under damp conditions in the laboratory. We have collected their Massarina sp. from
Smooth Beck in May 1976, and have confirmed their findings. A. longissima has a characteris-
tic "marker". In pure culture, in addition to its characteristic sigmoid thalloconidia,
spermogonia develop with minute spores which are thought to function as spermata. Such
spermogonia have been reported by Ranzoni (1953) and Willoughby & Archer (1973), but also occurred in our cultures. We have attempted to germinate the spermatica, but without success. If condensation water drops fall from the lid of a Petri-dish onto a culture of Massarina sp. 1 which has produced spermogonia, it is noticeable that pseudothecia develop at the positions where they have fallen. Undifferentiated, mononematous conidiophores terminating in phialides bearing spermatica have also been found in Massarina sp. (Fig. 18.4 C). These seem not to have been found by other workers, although similar structures have been reported in A. pseudolongissima by Ranzoni (1953).

Teleomorph: Pseudothecia superficial, seated on decorticated wood, globose, flattened at base, black, rough, opening by a circular, non-papillate ostiole; 120-240 μm diam. Ascii cylindrical, shortly-stalked, bitunicate, 8-spored, 96-120 x 9-10 μm. Ascospores biseriate, hyaline, fusoid, constricted at the median transverse septum, tapering towards the ends, and with 4-6 globose guttules; 18-22 x 4.5 μm. Willoughby & Archer describe the ascospores as being 22-28 x 7-9 μm. Possibly the discrepancy is explained by the fact that our measurements were made on specimens stained in cotton-blue lactic acid.

Since Anguillospora longissima is the type species of its form-genus, and since some of the other species which have later been assigned to this form-genus may not, in our opinion, be strictly congeneric, it is important to describe its conidium development critically. Ingold (1942) emphasized the importance of a separating cell at the base of the conidium which, by its breakdown, resulted in conidium separation (aleuric dehiscence). His description of conidium development is as follows: "During development, at the end of a conidiophore, a short cell is cut off which is destined to become the separating cell. When the spore is ripe, this cell breaks down. First, a line of weakness becomes apparent, girdling the cell. Then its contents disappear, the cell wall splits along this line of weakness, and thus the spore is liberated. In a spore which has just escaped from its conidiophore, a little basal collar, representing the remains of the upper half of the separating cell, can be seen, but this is very soon rendered invisible by the bulging of the cross-wall just above it which fills or may exceed the collar. A similar collar is to be seen at the apex of the old conidiophore."

We have confirmed the presence of a separating cell in ascospore isolates of Massarina sp. 1 from Smooth Beck, in a serial study of conidium development carried out using a flow cell. It is of interest that, in some cases, the separating cell seems to burst out some of its oily contents into the medium through a point in the lateral wall. The line of weakness was also detected in some cases. A point not noted by Ingold is that the apex of the old conidiophore may develop percurrently inside the collar representing the remains of the separating cell, to form a second conidium, surrounded at its base by the collar (Figs. 18.5 A, 18.6). Up to three successive collars surrounding the base of the most recently-formed conidium have been seen. The persistence of the basal collar has also been found in detached conidia of A. longissima collected in stream foam. Within the flow cell, the development of a lateral, backwardly-directed appendage has frequently been seen near the base of undetached 'mature' conidia. Possibly such appendages are precocious germ tubes. For a discussion of the taxonomy of other sigmoid aquatic Hyphomycetes with a basal appendage, see Wolfe (1976). The similarity of this type of development to that found in Mycocentrospora Deighton (1972)
Fig. 18.4 *Massarina* sp. 1. A. Bitunicate asci, ascospores and pseudoparaphyses. B. Spermogonium and spermatia. C. Micronematous spermatiophores.
FIG. 18.5. Macrostigma sp.: Macrostigmatid anamorph (Analogiospora longispina) in culture derived from an S. macrosporangia sp. on two colonies. A. Detached condia. Note persistent frill (remains of separating cell) and protrusion of conidial mass and a condium base. B. Developing condium marked by arrow. C. Detached condia. Note persistent frill (remains of separating cell) and protrusion to form new condium. A collar is left near apex of conidiospore. Detached condium.

on two colonies.
Fig. 18.6 Massarina sp. l: Anguillospora anamorph in culture. A. Apex of conidiophore showing percurrent proliferation. Note the two persistent collars (remains of successive separating cells). B. Base of conidium showing persistent collar and a precocious germ tube protruding through it. C. Two mature detached conidia each with persistent basal collar.
is quite striking, and is reminiscent of the type of conidia found in Mycoventrospora aquatica (Iqbal) Iqbal (1971, 1974a,b). When cultures are induced to sporulate by means other than the flow chamber, conidia are readily detached, the sub-basal extension is absent, and germination always takes place through the lowermost septum, as well as from other cells.

If the form-genus Anguillospora is to be retained in the narrow sense for forms with sigmoid thalloconidia released by breakdown of a separating cell, it is clear that the fungus we call A. furtiva (Rutstroemia sp. anamorph) is not referable to Anguillospora. During the development of this fungus (Fig. 18.1 A), no separating cell has been found, and we believe that separation of the conidium is by slow disarticulation of a septum dividing the conidium from its conidiophore.

However, the point we wish to make is that, superficially, the conidia of A. longissima and A. furtiva are very similar, and are difficult to distinguish from each other. These similarities are illustrated in Figs. 18.1 and 18.5, and in Table 18.3.

<table>
<thead>
<tr>
<th>Table 18.3. Comparison of culture and conidium morphology and dimensions in Anguillospora longissima and A. furtiva.</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. longissima (Massarina sp. 1)</td>
</tr>
<tr>
<td>Conidium dimensions * (um)</td>
</tr>
<tr>
<td>Number of cells</td>
</tr>
<tr>
<td>Mean cell length</td>
</tr>
<tr>
<td>Detachment</td>
</tr>
<tr>
<td>Spermogonia</td>
</tr>
</tbody>
</table>

* Data for length of conidia may include that of incipient basal germ tubes.

The overlap in conidium dimensions and septation, plus the possibility that our new species is a widespread organism (it has been isolated in S.W. and N.W. England), make the identification of detached conidia such as are found in foam uncertain, and we would strongly urge caution in interpretation of records based on such determinations. The basal tapered constriction to the conidium of A. longissima (and the frequently conspicuous remains of the separating cell in the form of a delicate frill surrounding the basal germ tube of conidia mounted in lactophenol and observed under high power) may be a reliable guide to identification and, if conidiophores are available, the collar visible at the apex is also a helpful confirmatory feature. The detached conidia of A. furtiva may show constrictions at intervals along their length. Spores with more than thirteen septa should not be assigned to A. longissima without further evidence.

The following species are described as not having a separating cell, with conidium separation brought about by disarticulation of a septum: A. pseudolongissima Ranzoni, A. gigantea Ranzoni (1953), A. orassa Ingold (1958), A. pulchella Wolfe, A. virginiana Wolfe (1976).
In *Pseudoanguillospora prolifera*, Iqbal (1974b) claims that separation may occur either by the formation of a separating cell (seen rarely) or (mostly) by the disintegration of the wall between the conidium and the conidiophore. However, in the type species of this form-genus, *P. stricata*, separation is brought about by disarticulation. The detachment of the conidium leaves a scar, and a new conidium arises from a new apex lateral to the scar.

3. **ORBILIA SP. AND ANGUILOSPORA SP. 1 (FIGS. 18.7 AND 18.8).**

Isolations were made from sigmoid conidium found in foam at Smooth Beck, Esthwaite, Cumbria, England, in April 1976. Seven-month-old cultures on 2% malt extract agar, incubated at 15-18°C under diffuse white light, bore minute apothecia of *Orbilia* sp. after partial submer- sion (see below). Similar conidia isolated from foam collected at Bettws-y-Coed, North Wales, on 25 October 1976, produced cultures which also bore apothecia of the *Orbilia*, also after partial submersion.

**Cultures:** pink or sometimes pale cream in colour, with a superficial mat of monilioid hyphae rich in oil globules; aerial hyphae absent.

**Thalloconidial state in culture** (Fig. 18.7): On 'dry' agar, sporulation was very sparse or absent. When 3-12-month-old slivers were submerged in sterile distilled water for two days at 15°C, abundant thalloconidia developed from submerged or surface hyphae. Conidiophores are single or in clumps, differentiated, acroauxic, hyaline, filamentous, simple, 50-100 μm long, gradually widening to 2-4 μm. **Conidiogenous cells** hyaline, integrated, proliferation typically percurrent through a truncate detachment scar. Conidial development is thallic, each conidium arising by the expansion of the conidiophore. **Conidia** at first straight, but quickly becoming strongly curved, and with septa becoming distinct during development. Release of the conidium is by disarticulation of a septum separating it from the conidiophore. Mature detached conidia are hyaline, strongly curved, helically or bow-shaped, 120-180 μm x 4-6 μm broad at the middle, tapering towards both ends, apex truncate, base truncate, 9-16-septate, not constricted at the septa. Germination in water is by germ tubes which initially develop near the apex and base of the conidium.

**Microconidia:** Some isolates contained abundant, hyaline, usually curved, 2-4-septate 'microconidia,' 22-35 x 3.5-4 μm, which anastomose with hyphal tips in water, and which then develop into apothecium initials within a few days.

**Teleomorph** (see Fig. 18.8): **Apothecia** developed on culture slivers partly submerged in sterile distilled water for 2-4 months at 10-12°C. They are scattered and superficial, minute, 0.3-0.5 mm diam., sessile and borne on a cushion of hyaline hyphae, glabrous, soft and fleshy, translucent, watery. The receptacle tissues are **textura globulosa**, composed of hyaline, thin-walled cells about 12 μm wide, whilst the ectal excipulum is **textura angularis**, composed of smaller cells 3-4 μm wide. Hymenium convex, waxy. **Asci** obconical, with an ill-defined stalk, apex laterally flattened and truncate; 27-32 x 4.5-5 μm, inoperculate, lacking any iodine reaction. **Ascospores** eight, irregularly arranged, shortly club-shaped, inequilateral, curved, 6-9 x 1.5-2.5 μm, smooth-walled, hyaline, eguttulate. **Paraphyses** abundant, frequently branched near the base, slightly exceeding the asci, smooth, cylindrical for much of their length, 21-32 x 0.5-2 μm, expanding at the tip to a thicker-walled knob.
Fig. 18.7. *Angustiispora* sp. I: Conidiophores and conidia from aerated cultures in water.
Fig. 18.8 *Orbilia* sp.: Ascii, ascospores and paraphyses.
or hook up to 6 μm in diam., or sometimes only slightly clavate.

4. **MOLLISIA** SP. 1 AND **FILOSPORELLA** SP. (FIGS. 18.9 AND 18.10).

Skeletonized leaves of *Quercus* collected from Smooth Beck, near Esthwaite, Cumbria, England, on 23 April 1976, bore sigmoid conidia after short submerged incubation. A single-conidium isolate was prepared and transferred to 2% malt extract agar in sealed 9 cm plastic Petri-dishes. Subcultures were incubated for several weeks at 15-20°C, and dark grey to black colonies developed. The cultures were then transferred to 10-12°C. On the dry agar, broad synnemata bearing thalloconidia developed near the centre of the colony. When slivers of culture were submerged in sterile distilled water, thalloconidia developed, some on newly-formed submerged hyphae, and also abundant phialoconidia (Fig. 18.9 A). Incubation of these slivers for several weeks resulted in the development of apothecia. Another culture derived from a single conidium isolated from foam in Smooth Beck, collected on the same date as the *Quercus* leaves, has also produced thallo- and phialoconidia and apothecia.

Thalloconidial anamorph in culture: Conidiophores arising from submerged hyphae are differentiated, mononematous or caespitose, and may be branched several times, irregularly or in a penicillate manner (Fig. 18.9 B). Conidium development is thallic, and the conidigenous cells may be terminal or lateral. After the release of the first conidium by disarticulation of the septum separating it from the conidiophore, the latter may proliferate laterally. Detachment scars may be visible. Mature conidia are hyaline, scolecosporous to narrowly falcate, straight at the base but curved distally. At the base, a flattened, thinned-walled scar is visible, from which a germ tube may appear soon after release. Further germ tubes develop laterally. Thalloconidia measure up to 200 x 6.5 μm, and have usually 6-11 transverse septa.

Phialidic anamorph (Fig. 18.9 A): Conidiophores single or caespitose, simple or sparsely branched, septate, hyaline. Phialides terminal or lateral, 9-35 μm long x 2-3.5 μm at the base, tapering toward the apex and widening into a distinct collarette. Phialoconidia globose to ovoid, 3 x 2 μm.

Teleomorph (Fig. 18.10): In pure culture, apothecia develop singly or in clusters. They are shortly stipitate, but appear hemispherical or pulvinate because their margin is strongly reflexed. They measure 0.5-1.6 mm diam. The base of the stipe is dark greyish-brown, whilst the disk is white, turning reddish-brown to salmon-coloured when old. The asci are clavate, inoperculate, 59-67 x 4.5-10 μm. The tip turns blue in iodine. The ascospores are inequilateral, fusiform or somewhat reniform, hyaline, unicellular, biguttulate, 10-16.5 x 3-4.5 μm. Prior to germination, a single median septum develops, and a germ tube may develop from each cell.

We have so far been unable to identify this apothecial teleomorph fully but, using the keys in Dennis (1968) and Korf (1973), it keys out to the genus *Mollisia*, although darkening of the apothecia only occurs well after ascospore maturation.

The anamorph is referable to the form-genus *Filosporella* Nawawi (1976). This name antedates *Rogersia* Shearer & Crane (1976), but the two names possibly represent the same form-genus. In *F. aquatica*, Nawawi has emphasized the *Penicillium*-like conidiophores. *Rogersia*
Fig. 18.9 Flegoporella sp. A. Phialophores and phialoconidia. B. Conidiophores and macroconidia.
Fig. 18.10 *Mollisia* sp.: Asci, paraphyses and ascospores.
annelidia also has richly-branched conidiophores but, following detachment of a conidium, percurrent development of the conidiogenous cell may result in the formation of a series of the conidia leaving annellations on the walls of the conidiophore. Our fungus appears to be distinct from both these fungi, as indicated by the dimensions in Table 18.4. There is no mention of synnematal conidiomata for the other two fungi.

Table 18.4. Dimensions and morphology of conidia of Filosporella aquatica, Filosporella sp. and Rogersia annelidia.

<table>
<thead>
<tr>
<th></th>
<th>Filosporella aquatica</th>
<th>Filosporella sp.</th>
<th>Rogersia annelidia</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conidium dimensions (μm)</td>
<td>178-245 x 4-5</td>
<td>up to 200 x 6.5</td>
<td>126-208 x 2.0-2.4</td>
</tr>
<tr>
<td>Septa</td>
<td>6-12</td>
<td>4-11</td>
<td>2-10</td>
</tr>
</tbody>
</table>

Several points of interest emerge from this study of the teleomorphs of forms with sigmoid thalloconidia:

1. The diverse relationships of such anamorphs is immediately apparent, reinforcing, for this conidial shape, the idea of convergent evolution, presumably in adaptation to the aquatic environment. The significance of the sigmoid shape in relation to water is still, however, not fully understood. It is of interest that the pollen of some aquatic angiosperms with submerged flowers has a similar shape (Proctor & Yeo 1972).

2. Until further connections between sigmoid thalloconidia and their teleomorphs have been demonstrated, judgment must be suspended on the validity of the criteria on which some of the form-genera are distinguished.

3. The hazards of identifying, to generic and specific levels, detached spores encountered in foam have already been referred to. It is also worth pointing out that links with distinctive teleomorphs are providing reliable evidence of the value of subtle distinctive features which enable accurate identification to be made.

5. CLAVARIOPSIS AQUATICA DE WILDEMAN AND MASSARINA SP. 2 (FIGS. 18.11 AND 18.12)

When studying the teleomorph of Angullospora longissima (Massarina sp. 1), we made a number of isolations from ascospores of Massarina spp. collected on decorticated Fagus sylvatica twigs in Smooth Beck, Esthwaite, Cumbria, England. The twigs were collected in May 1976, and incubated in the laboratory at 10-15°C for three months. Pseudothecia developed, and single- and multi-ascospore cultures were prepared from crushed pseudothecia. Pseudothecial initials and pycnidia were detected four months later in cultures on malt extract agar incubated at 15-18°C. The pseudothecia in culture did not develop asci. When culture strips were placed in sterile distilled water at 15-18°C, abundant conidia of Clavariopsis aquatica developed within two days (Fig. 18.11 A).

Pseudothecial state (Fig. 18.11 B): Pseudothecia superficial or semi-immersed in the wood, globose, mammiform or sub-conical, with a slightly raised, nipple-like, circular ostiole,
Fig. 18.11 Massarina sp. 2, teleomorph of Clavariopsis aquatica: A. Clavariopsis macroconidia which developed in a culture derived from an ascospore of Massarina sp. 2. B. Bitunicate asci and ascospores.
Fig. 18.12 Scanning electron micrograph of *Clavariopsis aquatica*. Note annellations on conidiophore (arrowed) indicating percurrent proliferation.
black, slightly rough in appearance, 140-260 μm diam., seated on a darker, discoloured area of wood by a flattened base. Pseudothecial contents white in colour. Asci bitunicate, cylindrical to clavate, shortly stalked, 62-82 x 11-12 μm, separated by filamentous pseudoparaphyses. Asoospores bi- or tri-seriate, canoe-shaped, hyaline, with one prominent transverse median septum, and 4-6 globose guttules; slightly constricted at the septum, straight or slightly curved, 20-24 x 4-5 μm, surrounded when fresh by a prominent mucilage sheath. Old pseudothecia may contain distorted, brown-walled ascospores.

**Pycnidial anamorph:** The pycnidial anamorph of the fungus was described by Ingold (1942). In our cultures, pycnidia were single or scattered, superficial on the agar or on the aerial mycelium. We have confirmed Ingold's statement that the conidia therein fail to germinate: possibly they are spermata.

**Thalloconidial anamorph:** This anamorph is well-known, and a further description is superfluous. The only point we would wish to add is that the conidiophore apex proliferates percurrently. This is visible with the light microscope and has been confirmed by scanning electron-microscopy (Fig. 18.12) of specimens from another isolate.

The finding that *Clavariopsis aquatica* has a *Masarina* teleomorph is of interest in relation to the fact that the teleomorph of *Clavariopsis bulbosa* (a species found in a salt lake) is *Corollospora pulchella* (Anastasiou 1961, 1963, Kohlmeyer et al. 1967, Shearer & Crane 1971). *Corollospora pulchella* has unitunicate asci with 7-septate ascospores ornamented by peritrichous median and terminal appendages.

6. AQUATIC ANAMORPHS OF *MASARINA* SPP. (FIG. 18.13).

Assuming that the teleomorphs have been correctly assigned to the genus *Masarina* (of which the type species is *M. elurnea* (Tul.) Sacc.), this genus now assumes an important position in the evolution of freshwater aquatic anamorphs. As has been demonstrated, the anamorphs of aquatic forms of *Masarina* represent species of three form-genera of Hyphomycetes, namely *Pyricularia aquatica*, *Anguillospora longissima* and *Clavariopsis aquatica*. It is of interest that all species have dark-coloured mycelium and conidia in 2% malt extract agar, whilst in all of them the conidiophores have percurrent apices (see Fig. 18.13 A). A third common feature is the presence of pycnidia (? spermogonia). Such structures appear not to have been described for *Pyricularia aquatica*, but occurred in some of our cultures (Fig. 18.13 B) as irregular sclerotoid conidiomata containing minute, hyaline, globose, unicellular spores less than 1 μm diam. It would be of interest to know the selective pressures which led to the evolution of such diverse macroconidial shapes in a single genus of Ascomycetes in the aquatic habitat. Amongst terrestrial species of *Masarina*, connections with the following form-genera of pycnidial Fungi Imperfecti have been reported by Bose (1971): *Ceratophoma*, *Microsphaeropsis*, *Coniothyrium* and *Diplodia*. We have several collections of *Masarina* spp. from twigs and wood in water, which form pseudothecia readily in culture, but have failed to develop macroconidia. Ascospores of the *Masarina* type, although rarely abundant, are quite common in foam samples.

Hebert (1971) has shown that the teleomorph of *Pyricularia grisea*, the causal agent of rice blast, is the unitunicate Pyrenomycete *Ceratosphaeria grisea*, and this calls into
Fig. 18.13 Massarina aquatica: A. Pyricularia macroconidial anamorph formed in culture derived from an ascospore. Note percurrent proliferation. B. Spermogonium and spermatia in culture derived from an ascospore.
question whether the conidia of *P. grisea* and *P. aquatica* are correctly assigned to the same form-genus.


*Actinospora megalospora* is a handsome aquatic Hyphomycete with very large conidia which are quite common in foam throughout the year in England. The fungus has rarely been seen attached to its substratum, although Ingold (1952) first described it from a submerged twig of *Crataegus*. We have studied the development of the conidia of this fungus in pure culture, and have shown that conidia develop successively and basipetally from cells at the tips of the dichotomous conidiophore (Fig. 18.15) (Descals et al. 1976). The first-formed conidium is a terminal thalloconidium, and the cell which subtends it may also develop into a conidium. This process may be repeated. In one of our cultures, a single, orange-coloured apothecium developed, but unfortunately the asci failed to form, so that we were unable to identify it or confirm its connection to the anamorph. Recent collections of an orange-coloured Discomycete from logs of *Alnus glutinosa*, which were partially submerged in the River Culvery, near Crediton, Devon, England, a river which has consistently contained conidia of *A. megalospora*, have enabled us to confirm the connection. The teleomorph has been identified as *Miladina lechithina* (Descals & Webster 1978). An unusual and unexpected finding is that the asci are operculate, and this may be the first connection to be demonstrated between an operculate Discomycete (Pezizales) and an aquatic conidial fungus. Since we have recently described the macroconidal anamorph, a further detailed description will not be given here.

**Teleomorph** (Fig. 18.14): *Apothecia* superficial, scattered, single or in small groups, sessile, up to 3 mm diam., discoid, orange in colour, sometimes turning yellow to buff on re-moistening; fleshy, lacking rooting hairs, excipular hairs or setae. Medullary excipulum two-layered, consisting of a basal layer of *textura globulosa* which merges into a hypothecium of *textura angularis*. Ectal excipulum prosenchymatous, ending in loose obovoid or club-shaped cells elongated perpendicular to the surface, rich in orange inclusions. The apothecium is surrounded by a rim which is smooth and paler than the hymenium. Hymenium flat, but with protruding asci visible. *Asci* narrowly clavate or cylindrical, operculate, 220-295 x 13-19 µm Paraphyses abundant, as long as the asci, branched dichotomously or with lateral branches developing beneath a septum. The tips gradually broaden to a club-shaped apical cell, 27-60 x 5-7.5 µm, with smooth walls, contents hyaline at the base but rich in bright orange inclusions near the apex. The paraphyses resemble conidiophores. *Ascospores* eight, uniseriate or loosely-arranged, colourless, ellipsoidal or ovoid, unicellular, protoplasm rich in minute globules, wall smooth or very finely pitted (oil immersion), lacking a gelatinous sheath, 20-22.5 x 10-12.5 µm.

On half-submerged logs of *Alnus glutinosa*, River Culvery, Crediton, Devon, England, July 1977. The River Culvery is a small stream about 2-5 m wide, draining agricultural land. It is well-shaded by various trees and shrubs, and has cut a channel about 1-2 m deep through soil to the stony river bed.

We have recently given detailed descriptions and illustrations of both *Miladina lechithina* and its *Actinospora megalospora* anamorph (Descals & Webster 1978).
Fig. 18.14 *Miladina lechithina*, teleomorph of *Actinospora megalospora*. Operculate asci and paraphyses.
Fig. 18.15 *Actinospora megalospora* conidia in culture derived from a single ascospore. Note basipetal sequence of conidium development.
Single ascospore cultures were prepared by allowing ascospores to be discharged onto the surface of 0.1% malt extract agar. The spores did not germinate immediately, but only after several days' incubation. They produced long, straight, relatively unbranched germ tubes similar to those formed by Actinospora megalospora conidia on germination. The cultures also resembled those derived from conidia. After several days submerged in water, strips of culture derived from ascospores, developed conidia of *A. megalospora*.

**BASIDIOMYCETES WITH BRANCHED, WATER-BORNE CONIDIA.**

A number of conidial types described from freshwater foam, or from leaves, are believed to belong to Basidiomycetes. The evidence for this is the presence of clamp-connections at the septa, indicating the dikaryotic condition, or the presence of dolipore septa. Amongst the forms with clamped conidia is *Leptoeporomyces galzinii* (Bourd.) Jüllich, a member of the Corticiaceae. The conidia of this fungus are abundant in foam in the autumn in certain localities. They resemble a minute *Trioladium*, but there is usually a single clamp-connection on the main axis mid-way between the two laterals. Cultures derived from clamped conidia developed diffuse athelioid basidiomata (Nawawi et al. 1977). Although we have not ourselves collected basidiomata in nature, Jüllich (1972) reports that they occur on bark of conifers, on a moss, and on the fern *Pteridium aquilinum*. We do not know if the teleomorph is formed in water, but we have the intriguing possibility that *L. galzinii* is amphibious, with its anamorph, which we have seen on leaves in water, associated with aquatic habitats and modes of dispersal, whilst the teleomorph is terrestrial, and basidiospore discharge and dispersal take place in air. Whether the basidiospores colonize leaves before they fall into streams is as yet unknown.

Two other clamped, branched, water-borne conidia belong to *Ingoldiella hamata* Shaw (1972) and *I. fibulata* Nawawi (1973). The first of these fungi was originally discovered by Ingold (1959) in foam from a tropical stream. The conidia bear a characteristic, forked, recurved hook at the slender tips of their tapering arms, and clamps are visible at each of the septa. Nawawi recently isolated the teleomorph in Malaysia. It is possibly related to *Sistotrema*, with basidia bearing up to eight basidiospores. Monokaryotic cultures derived from basidiospores develop very similar conidia, but lacking clamp-connections. The teleomorph of *I. fibulata* is as yet unknown.

Amongst forms with water-borne conidia with dolipore septa is *Dendrosporomyces prolifer*. This fungus has conidia which are richly branched, resembling those of the form-genus *Dendrospora*. Ammoniacal Congo-Red staining has revealed the presence of dolipore septa within the conidia, using the light microscope, and the dolipore structure has been confirmed by electron microscopy (Nawawi et al. 1977). Each cell of the mycelium and of the conidia of *Dendrosporomyces prolifer* is binucleate, so we may be dealing with a fungus which does not form clamp-connections in the dikaryotic phase. No teleomorph has yet been discovered. Ammoniacal Congo-Red preparations of the type species of *Dendrospora, D. erecta* Ingold, did not show dolipore septa, and their absence has since been confirmed by electron microscopy (Davey, unpubl.).

The discovery of non-clamped conidia with dolipore septa raises the obvious possibility
that there are other aquatic fungi of basidiomycetous affinity, and a critical examination of the septa of aquatic conidia may be desirable. Nawawi et al. (1977b) have stated that the fungus described as *Trioladium malayesianum* Nawawi (1974) has binucleate cells and doli-pore septa as seen in Ammoniacaal Congo-Red preparations. If it should be shown that the type species of *Trioladium, T. splendens* Ingold, has simple septa, it will be necessary to re-dispose *T. malayesianum*.

ACKNOWLEDGMENTS

We wish to thank Mr. W.D. Graddon and Dr. R.W.G. Dennis for helpful advice on Discomycete identification; Dr. Guy Willoughby for help in showing us the localities in the Lake District in which he collected material, and for valuable discussion; and Dr. A. Nawawi for allowing us to refer to his unpublished results. We are also grateful to Mr. P.F. Sanders and Mr. R.A. Davey for help with scanning electron microscopy, and to Mr. M.A.S. Alexander for assistance with photography.

DIALOGUE FOLLOWING DRs. WEBSTER & DESCALS' PAPER

PIROZYNISKI: How do you explain the worldwide distribution of most of these fungi?

WEBSTER: If they have been around long enough, plate tectonics may explain it. But if they have teleomorphs, that may also give them a contemporary long-range dispersal mechanism. Dr. Talbot told me that there aren't many babbling brooks around Adelaide, but there are crackling creeks, and if you collect dry leaves from these dried up stream beds, and incubate them in water, conidia will often develop on them. So they may not be strictly aquatic, as Bandoni's recent work (1972, 1974) suggests very strongly, and may not be dependent upon aquatic dispersal. We have tried inoculating aquatic Hyphomycetes onto dead leaves, burying them in the soil, and recovering samples at intervals. We know that the so-called aquatic hyphomycetes will survive for at least 4 months like this. So they may be dispersed simply as vegetative mycelium inside leaves (Sanders & Webster 1978).

PIROZYNISKI: Do you think this group is ancient enough to have been present when, for example, Pangaea split up, some 200 million years ago?

WEBSTER: Perhaps; I don't know. Ingold believes that the Ascomycetes are primarily terrestrial and that a few of them have subsequently become aquatic. He may be right, but the evidence needs careful scrutiny. I'd like to ask Dr. Müller a question. Do you think that the teleomorph we have described as *Massarina* is properly disposed in that genus? It is, of course, bitunicate, and it is obviously close to *Massarina*, but I still suspect that *Massarina eburnea* is something different -- the anamorphs that you and Bose have described are pycnidial and don't tie in well with the aquatic Hyphomycetes.

MULLER: These are the kind of observations that say to us, 'Pay attention.' You have shown us that although certain anamorphs -- aquatic Hyphomycetes -- look superficially similar, their teleomorphs belong to such different groups that you must look again at the
anamorphs to see if there are subtle but important differences that we overlooked before. This discovery of such different anamorphs for what appear to be very similar teleomorphs forces us to re-examine *Massarina* very carefully. Of course, everything is possible, and the *Massarina* species may well turn out not to be separable at the generic level.

WEBSTER: These recent discoveries have suggested to us that if we are to maintain the form genus *Arquillospora*, perhaps we should restrict it to those species with separating cells. Some of the other species are only superficially similar to those with separating cells; they have a different kind of conidial dehiscence, and we know that they have different teleomorphs.

KENDRICK: In this context, I'd like to suggest that the anamorph-genus *Ingoldiella* may well turn out to be heterogeneous. In the stauroconidia of the type species, *I. hamata*, all branches arise from clamps, whereas in *I. fibulata* they arise between clamps. This kind of distinction is sometimes important in the taxonomy of basidiomycetous teleomorphs, and it may be equally significant in these anamorphs.

LUTTRELL: These are eminently respectable examples of the cryptic character that I have already mentioned. In this case the reappraisal of the anamorphs is a clear-cut necessity. But I'd like to point out that things aren't always so clear. Ellis maintains the genus *Drechslera*, and refuses to segregate *Bipolaris* from it. And one of his arguments is based on the case of *Podosporiella verticillata* (later described by Drechsler as *Helminthosporium cyclophi*). Shoemaker put this in *Bipolaris*, but when the teleomorph was found to be in *Pyrenophora*, Shoemaker moved the anamorph into *Drechslera*. At this point Ellis (1976, p. 396) says, 'Aha! You are using these characters to distinguish genera, yet you didn't even recognize your own characters until some other evidence prodded you into checking.' My attitude is that regardless of what makes you look for these cryptic characters, if you change the classification, you may be the target of some charges of unfair manipulation of data. I don't think the criticisms are really justified.

WEBSTER: Perhaps I may mention the 'natural' classification that incorporates all the available data. If more data become available, surely we have the right -- possibly even the duty -- to change our opinion.

SUBRAMANIAN: I'd like to ask Dr. Kendrick if he thinks the conidium ontogeny shown by *Actinospora megaloospora* in the film Dr. Webster showed us, is comparable to that in *Basipetospora*.

KENDRICK: In some ways; it is certainly retrogressive. But it is thallic -- each conidium develops from an entire differentiated cell. Although we did not discuss any examples of this kind at Kananaskis-I, we can easily fit it into the scheme of terminology we devised then; it could be described as thallic-retrogressive.

LUTTRELL: Where you mentioned a separating cell that ruptured, and then a subsequent proliferation through that separating cell you avoided using any specific term to designate this.

WEBSTER: The separating cell is long and breaks roughly in the middle, so that half goes with the conidium and half remains behind on the tip of the conidiophore. Then a percurrent proliferation takes place through the lower half of the cell to produce the next conidium. I suppose it might be called an annellide if someone wanted to use the term.
KENDRICK: I don't think it matches anything in our lexicon.

LUTTRELL: Exactly; I was going to congratulate Dr. Webster on not calling it an annellide. Consider the thick-walled brown conidiophores often found in wood-inhabiting hyphomycetes. If they are broken off, they often regenerate from the septum below the break. This process, if repeated, would produce something that looked like an annellide -- but it wouldn't really be an annellide, if you think about it. The regular proliferations in your fungus have as their prerequisite the death of a cell. We can't -- we mustn't -- use the term annellide here, because this phenomenon is not related to what we have defined as an annellide.

CARMICHAEL: It is a conidiogenous cell, or conidiophore, with ring-like scars produced as a result of percurrent proliferations so I don't see why we shouldn't call it an annellide.

KENDRICK: Not if we want, ultimately, to speak of truly homologous structures. This example is comparable to what I was once misguided enough to call a sympodula. I coined the term for sympodially proliferating conidiogenous cells producing blastic conidia, as in Beauveria or Tritirachium, but it was soon used to describe any kind of sympodially proliferating conidiogenous cell, including those producing poroconidia (as in some Helminthosporia) and thallic-arthric conidia (as in Sympodiella). We would do much better to use an adjectival terminology of the kind advocated at Kananaskis-I, and simply describe such conidiogenous cells or conidiophores as 'sympodial', or in the case discussed above, 'percurrent'. A single adjective here represents only a partial description of the whole phenomenon, and is appropriately supplemented by another adjective describing the precise method by which each individual conidium is produced. A good description of Dr. Webster's fungus would be that it has percurrent conidiophores and aleuric dehiscence. Given that kind of description, I think I could probably draw it without ever having seen it!

VON ARX: I have seen these percurrently proliferating conidiophores with separating cells in closely related genera -- Stegnosporium, Prosthemium and others, anamorphs of Splanchnonomema and Pleomassaria. It is a very nice group.

KENDRICK: I would like to know whether the various teleomorphs you have found develop submersed or not.

WEBSTER: They are really half-submerged, but many of them can discharge ascospores under water. I'm coming to the view that these organisms ought to be called, not aquatic Hyphomycetes, but amphibious fungi. [This statement drew a general murmur of approval.]

VON ARX: I have observed that some of these Ascomycetes do not discharge their ascospores violently, but exude them in a drop of slime, which is water dispersal, as in Massaria and Massearina.

WEBSTER: This is true in Neatria lugdunensis. We often find submerged ascomata containing mature asci. Also, if we filter stream water through a millipore filter, we often collect Massearina ascospores. Of course, they may have been shot off into the air and fallen back into the water. But this suggests that they can be released underwater. Many also have a slimy sheath.

KENDRICK: Does this mean that some of these asci may be morphologically bitunicate, but not functionally bitunicate?

VON ARX: Yes, that is typical of many Ascomycetes growing in wet conditions -- on leaves of
Carex, or leaves and stems of rice plants. Some are described as Diaporthaceae, others as Sphaeriales. Many intermediates are present. Luttrell described *Gaumannomyces* as sometimes discharging its ascospores, and sometimes releasing them in a slimy mass. The fungi may retain both options, depending on conditions.

WEBSTER: Our *Pyricularia* is, I know, not typical of the genus since it has septal dissolution at the base of the conidia rather than simple denticles. Can anyone suggest a suitable genus for it?

LUTTRELL: I believe that *Pyricularia grisea* also has separating cells. I don't know what happens in *Pyricularia oryzae*.

WEBSTER: Ingold (1964) maintains that the conidia of *Pyricularia grisea* are violently discharged: I'm not sure how that would affect this issue.

VON ARX: *Pyricularia* and *Nakataea* are close. *Nakataea* has a *Magnaporthe* teleomorph. Further discussion was inconclusive, but served to point out that *Pyricularia* may be heterogeneous, and that a new segregate genus might be required for those species having separating cells. *Hyperparasitic* members of *Pyricularia*-like anamorphs have been segregated into *Trichconis* and *Paratrichioconis* (Deighton & Pirozynski 1972).

WEBSTER: I'd like to know what selection pressures have pushed three species of *Massarina* to evolve anamorphs with, in one case, pear-shaped conidia; in a second, sigmoid conidia; and in the third, tetradiate conidia: all in very similar environments.

WERESUB: You have found some of the ascigerous teleomorphs away from the water. What about the *Leptosporomyces galzinitii*?

WEBSTER: We found masses of conidia, made cultures from them, and the basidiomata developed. Strangely enough, the *Leptosporomyces* was originally described from wood of conifers, and *Pteridium* petioles -- relatively dry habitats. This is one of the reasons I now think in terms of amphibious fungi. But it hasn't been grown from the basidium with the idea of producing conidia. Even if a basidiomycetologist had cultured it in the past, he would not have suspected its aquatic connections, and would not have put it in the kind of conditions that would induce formation of the conidia.

WERESUB: I appreciate that, but I'd still like to compare what you have with a basidiome produced in culture from the germinating basidiospores of an authentic *Leptosporomyces galzinitii* gathered in the field on its usual host.

WEBSTER: We'd be delighted to try it if someone will supply fresh basidiomata. Let's consider another example: *Miladina lechithina*. If a discomycete specialist grew it in culture he would not find the conidia, because he would not think of using the technique that induces them. So he would in all probability report that it had no anamorph.

HENNEBERT: I'd like to offer a little evidence for the concept of amphibious fungi. *Spirosphaera beverwijkiana* usually grows on wet or submerged leaves in a thin film of water. Someone in the United States has just isolated it from dry sand, in the Texas desert.

WEBSTER: At this point I'd like to mention the work of Jack Fisher, an associate of mine, on another group of organisms that we call the aero-aquatic fungi. These grow in stagnant ponds on leaves on the surface of mud. If you bring this black, stinking, most unpromising material into the lab., rinse it and put it in a moist chamber, helicoconidia will appear all over it after about ten days -- *Spirospahaera* among them. We have shown
that many of these fungi will survive for long periods in dead leaf material on a lawn; *Helicodendron triglitzienense* is recoverable from dried leaf powder kept in a desiccator for over a year. So although their prime habitat is probably aquatic, these fungi can survive much drier conditions. Indeed, the dried leaves containing viable mycelium may be an important means of dispersal: when the pond dries up these leaves can be blown considerable distances by the wind.

The basidiomycetous anamorphs mentioned toward the end of that Chapter provide a lead-in (albeit a tenuous one) to the main treatments of Basidiomycetes and their anamorphs, which occupy the next three Chapters....
Most Deuteromycetes, excepting the Mycelia sterilia are, or were once, connected with ascomycetous telemorphs, and so mycologists concerned with the biology of fungi rarely directed their attentions toward the Basidiomycetes. There have been notable exceptions to this gap in our knowledge, although few have dealt with the Agaricales.

For the purpose of this review the circumscription of the Agaricales is that outlined in the 3rd Edition of Singer's monumental work 'Agaricales in modern taxonomy' (1975), although there are some differences of opinion as to the limits of certain taxa. Singer's work is nevertheless the most comprehensive available, and offers a baseline from which to work; in addition it covers a wider range of species than is normally considered agaricaceous, because it deals with some of the polyporaceous fungi normally classified in the Aphyllophorales.

The work described herein is that undertaken as part of a joint study by Bryce Kendrick and myself in 1974, firstly a literature search, and secondarily a dovetailing of this information with my own cultural studies on basidiomycetous anamorphs. This survey was undoubtedly stimulated by Hughes (1971), and is an attempt to create a foundation from which further work can be conducted, because the study of basidiomycetous anamorphs has languished since Brefeld's pioneer work nearly 100 years ago (1877, 1899).

It seemed to Kendrick and myself that the terminology developed at Kananaskis-I should be adopted. Throwing our net as widely as possible, we found examples of most of the major developmental types of conidiogenesis within the Basidiomycetes; some less common, others more frequently encountered than among ascomycetous anamorphs. However, the number is considerably reduced when one restricts the study to the Agaricales alone.

It is therefore hoped that from the details given below, the full range and significance of the morphological and ecological aspects of the anamorphs of the gilled fungi will be appreciated.
The main headings adopted herein follow the compilation by Kendrick and myself (Chapter 20), and are as follows:

- Thallic-arthric conidia
- Chlamydospores
  - Nyctalis-type
  - Solitary terminal
  - Modified clamp-connections
- Solitary holoblastic conidia
- Mycelia sterilia
- Bulbilloid and related structures
- Carpophoroids

**THALLIC-ARTHRIC CONIDIA**

Undoubtedly the commonest conidium in the Agaricales is of the thallic-arthric type. Examples can be found both in nature and in culture, but more particularly the latter. The terms thallic and arthric are accepted as outlined at Kananaskis I (Kendrick 1971). Even within this category, sub-classes can be defined based both on the nature of the separation of the mitospore-units, and the structure on which they are borne.

Conidiophores may be found on large, well-differentiated fruit-bodies at one extreme, or directly in clusters on the vegetative hyphae at the other. The simpler forms are the most frequent and are commonly seen in culture. Long lists of examples could be given ranging over many families, e.g., Polyporaceae, Tricholomataceae, Bolbitiaceae, Coprinaceae and Cortinariaceae, but this would be a pointless duplication: such lists can be found in Chapter 20.

However, three examples, all with form generic names, need special mention: *Notothoclavulina ditopa* Singer, a clavarioid fruit-body, i.e., a giant synnema, the arthroconidial stage of *Arthrosporella ditopa* Singer (Fig. 19.1 D<sub>3</sub>); *Sclerostilbum septentrionale* Povah, the synnematal appendages on the stipe of developed or developing *Collybia racemosa* (Pers. ex Fr.) Quél. (Fig. 19.1 D<sub>4</sub>); and *Antromyopsis broussetiae* Pat. & Trab., the synnematal head produced in cultures and on the stipes of *Pleurotus cystidiosus* O.K. Miller (Fig. 19.1 D<sub>2</sub>). The *Notothoclavulina* anamorph has been called an 'arthrosporocarp' by Singer (1975).

The arthroconidia may be either monokaryotic or dikaryotic; if dikaryotic, they are separated by clamp-connections as in *Collybia racemosa* (Watling & Kendrick 1977) (Fig. 19.1 D). In *P. cystidiosus*, single-celled conidia, formed on a thin denticle, are also produced and these again may be binucleate or uninucleate (see below).

The thallic-arthroconidia almost invariably form on the vegetative mycelium by the multiple septation and later separation of units formed from long hyphae, either directly as branches of the main vegetative mycelium, or as a group of branches formed on the aforementioned branches. They are usually in elongated chains, but may also be sympodial in development, e.g., *P. aurivella* (Batsch ex Fr.) Kummer (Figs. 19.1 H & I). Contraction of the protoplasm is usually absent, and the conidia become detached by the fission of double septa laid down across the full width of the hyphae, or by fracture or lysis of the walls of
adjacent degenerating cells. The first alternative is typical of members of the Tricholomataceae (Fig. 19.1 B), but in members of the Cortinariaceae, Bolbitiaceae and Coprinaceae, i.e., chromosporic agarics, protoplasmic contraction and separation occurs by dissolution of the walls of the emptied parts of the hyphae (Fig. 19.1 C). Some slight thickening of the wall takes place and then it is difficult to distinguish between these arthroconidia and chlamydospores. Swelling usually does not occur, but it can be seen how a possible morphological series runs from thallic-arthic propagules to the chlamydospores of the *Nyatalis*-type. It is interesting here to ponder over Sigler & Carmichael's categorization of the *Malbranchea*-complex in the Hyphomycetes (1976), and even to suggest that the asexual stages of certain agaricoid fungi might be placed in the genus *Maugiinia* Cavara.

The categories based on the location and method of fission can only be determined after cultural studies, indeed, as indicated above, many species are only reported as forming them in culture, although it is suggested that they are commonly found in nature, and then perhaps called *Geotrichum* or *Sporendonema* by the unwary. Heinemann & Thoen (1973) have found arthroconidia at the base of the stipe in *Cystoderma tricholomoides* Heinem. & Thoen and on the pileus in *C.* aff. *longiarorum* (Kühner) Heinem. & Thoen.

Ironically, although the thallic-arthic propagule is the most widespread form of mitospore in the Hymenomycetes, it is apparently rare in the hymenomycetous Heterobasidiidae.

In pure culture it is observed that many species liberally form arthroconidia, either only in young cultures or old cultures, or both. They may only be formed on monokaryotic hyphae, as in most species of *Coprinus* and *Psathyrella* (Coprinaceae), or both in monokaryotic and dikaryotic phases, as in the common lignicolous *Flammulina velutipes* (Curt ex Fr.) Karst. (Tricholomataceae). In *Pholiota gummosa* (Lasch) Singer, Kühner (1946a) has shown that the arthroconidia formed in culture are binucleate and dikaryotic, and serve to multiply the secondary mycelium. In *P. aurivella* (Batsch ex Fr.) Kummer, in contrast, both uni- and bi-nucleate cells are produced; the dikaryotic cells swell and form a terminal conidium, whereas the uninucleate cells are typically arthic.

Arthroconidia are morphologically all very similar, because of the lack of swelling and thickening. However, even a quick scan of Brefeld's plates will indicate that there are some differences from one genus to another, or even between species of a single genus. The conidia formed by members of *Coprinus* subsect. *Lanatuli* are usually casket-shaped or shortly rectangular (Plate 19.1), whilst those in subsect. *Domestici* are often quite elongate, up to ten times as long as wide, and slightly curved.

As indicated in my paper to the Madras Conference (Watling, ined.) a fundamental concept in identifying living organisms is that of correlation of characters, which leads to a reduction of the emphasis which one might wish instinctively to place on a single feature. In agaricology, this has been neglected, perhaps far too frequently, in the past, particularly when new characters have been introduced, but in a group such as the agarics, where fewer characters are available than in a similar-sized group of flowering plants, any additional information is valuable; cultural studies can supply such information. Thus, although it is a simpler process than formation of basidiospores, useful data can be obtained from a simple study of thallic-arthroconidiogenesis. If this is coupled with the physiological characters to be outlined below, new ammunition is available to assist in identification.
In many genera the thallic-arthroconidia act as spermatia, although their activities have often remained relatively obscure because they have simply been dismissed as asexual spores. But although mitotically formed, they are not 'a-sexual' since not only can they fuse with monokaryotic hyphae of their own taxon, but some also produce growth substance(s) which attract the hyphae of their own or closely related taxa. Thus a spermatium can be 'recognized' by the hyphal tips of a growing colony of the same or similar species: Kemp (pers. comm.) has claimed that the "homing response", as he calls it, is not species-specific, and can occur between a hypha and an arthroconidium of closely related species. This homing reaction can frequently be observed within 1-2 hours.

Homing is a very valuable tool for the taxonomic agaricologist, because the response is often found in closely related species, and although a lethal reaction may follow, at least by this means one can ascertain the relative closeness of two taxa. Ecologically, the arthroconidia probably act as 'sterilizing' agents in any microhabitat, suppressing the growth and establishment of any late-comers, or restricting them to other ecological niches.

Undoubtedly there is a stimulatory series in the genus Coprinus (Coprinaceae), for although there are two basic types of arthroconidium, 'wet' and 'dry', the former are frequently poor at germinating although strong attractors, whilst the latter germinate freely but are not usually good at causing the 'homing' effect. Dry and wet conidia are uncommonly found together in a single species.

A range of conidiophores is produced within a single genus such as Coprinus (Fig. 19.1 A & H), and, by screening as many species as possible, work in Edinburgh has shown that the kind of branching of the conidiophore often reflects the infra-generic grouping. Thus Kemp (pers. comm.) has shown that, in the two species of Subsect. Comati he studied, spherical arthroconidia are formed on candelabra-like conidiophores, but those in Subsect. Lanatuli form arthroconidia which coalesce into small 'wet' heads held above the vegetative mycelium.

In the Sect. Hemerobii (s.g. Pseudocoprinus Kühner emend. Orton & Watling, inéd.) the variation in conidiophore morphology is much greater, in my opinion reflecting the greater diversity of the genus, a diversity which is also seen in the range of mating patterns exhibited, i.e., homothallic, 2-spored or 4-spored, bipolar or tetrapolar, and vegetative hyphae with or without clamp-connections. In 2-spored C. sasiti M. lge & A.H. Smith, and 4-spored C. hiasaens (Fr.) Quél., short conidiophores are formed, reduced still further in C. congregatus (Bull. ex St. Amans) Fr., where the arthroconidia are formed in tufts more or less directly on the vegetative hyphae. Species forming wet or dry arthroconidia are found in the Setulosi, and in some species conidiophores are absent altogether. C. pellucidus Karst. and C. stellatus Buller are both homothallic, lack clamp-connections and form dry conidia; in contrast, wet conidia are formed in C. congregatus.

The wet arthroconidia apparently possess a sticky capsule, and although they are formed initially in dry chains, these break up and the individual conidia aggregate in a droplet. Electron microscope studies have shown that in at least two species of the Coprinaceae the sticky capsule is in reality numerous filamentous appendages which are embedded in a layer of mucilage (Jurand & Kemp 1972). Dry conidia do not possess this capsule. It would not be constructive at this point to discuss the use or misuse of the term 'oidia', which has been applied to thallic-arthroconidia inducing hyphal homing. This term is discussed in the introductory section of Chapter 20.
CHLAMYDOSPORES - NYCTALIS TYPE

As mentioned above, the chlamydospores of species of *Nyctalis* are thallic; they are thick-walled resting spores, frequently intercalary, formed by the modification of a pre-existing cell by production of a new, thicker wall, or by thickening of the pre-existing wall and condensation of the protoplasm, often accompanied by swelling. A retraction septum is often found (Fig. 19.1 F & G; Plate 19.2).

The form-genus *Asterophora* Ditmar ex S.F. Gray, adopted by Singer (1975) for a basidiomycetous state, was correctly limited by Donk (1962) to those fungi in which the basidia are more or less replaced by the production of chlamydospores. There are two European species, *A. lycoperdoides* (Bull. ex Merât) S.F. Gray and *A. parasitica* (Bull. ex Fr.) Singer, which correspond to the teleomorphs, *Nyctalis asterophora* Fr. and *N. parasitica* (Bull. ex Fr.) Fr., respectively. The former has irregularly ornamented conidia produced by finger-like projections of the secondary wall pushing through or stretching the original wall of the vegetative hyphae. Only stretching takes place in *A. parasitica*, resulting in a smooth spore. The chlamydospores of *A. lycoperdoides* are binucleate, and after dissemination give rise directly to secondary mycelium (Thomson 1936, Kühner 1977). The stellate chlamydospore of *A. lycoperdoides* has encouraged the erection of several genera, e.g., *Asterotrium* Bon., *Ugola* Adans. and *Stallisera* Leman are considered synonyms by Donk (1962).

Chlamydospores of the *Nyctalis*-type have a characteristic space separating each conidium, which may be because of the condensation and retraction of the cell contents, or because not all cells in a hypha produce chlamydospores. In *Nyctalis asterophora* itself, most of the hyphae in the pileipellis are converted into chlamydospores; parallel conidia may also be found on the stipe, and frequently replace the gills to give an Onygena-like fungus. In *N. parasitica* only the gill tissues possess chlamydospores, the pileus and stipe remaining unchanged.

The similarity between the process of thallic-arthric conidiogenesis and that of chlamydospore formation in the *Nyctalis* pattern is seen in Clemençon's studies on *Lyophyllum* (Tricholomataceae) (1968) where closely spaced septa are laid down before chlamydospore formation (Fig. 19.1 E). This is perhaps an extension of the characteristic development in chrosporic agarics, and resembles that described for *Lentinellus caetoreus* (Fr.) Konrad & Maublanc (Didier-Fichet & Kühner 1967), an agaricoid fungus often classified along with *Auriscalpium vulgarum*. Thick-walled cells in chains with clamp-connections separating the units are found in cultures of *Pleurotus dryinus* (Pers. ex Fr.) Kummer (Plate 19.2); they parallel, except for wall thickness, the thin-walled arthroconidia found in *Collybia racemosa*.

In *Pulveroboletus sulphureus* (Fr.) Singer, *P. lignicola* (Kallenb.) Singer, and related taxa, the chlamydospores formed in culture are brightly coloured and are usually separated from one another by at least one cell; in other agarics they may be separated by two to several cells. The yellow chlamydospores resemble the allocysts described by Kühner (1946a, 1947) from cultures of *Pholiota gummosa*, *P. alnicola* (Fr.) Sing., and *P. conissans* (Fr.) Moser, but it is believed that these are not functional propagules and may act as repositories for unwanted by-products of metabolism. They may be the cultural expression of the chrysocystidia which are so characteristic of members of the Strophariaceae, although they have been found in *Coprinus radians* (Desm.) Fr. (Kühner 1946b), an agaric which, however, lacks the
development of chryso-vessels and related structures. The yellow conidia resemble closely the powdery cells which often adorn the surface of certain species of Pulveroboletus; they do not, however, resemble the pulverulent hyphal pattern found in the type species, P. ravenelli (Berk. & Curt.) Murr.

SOLITARY, TERMINAL CHLAMYDOSPORES

It is certainly an easy morphological step from the Nystalis-type to the Ptyehogaster-type of chlamydospore formation found in various Aphylllophorales. Similarly, from this to the Sporotrichum and/or Allescheriella-types is equally a small step, characterized by the formation of terminal, solitary, often thick-walled conidia which when dispersed possess a broad truncate base, frequently with remnants of the stalk-cell attached. Both types of conidiogenesis are found more frequently in the Aphylllophorales than in the agarics (Fig. 19.1 N). An important exception is Pholiota aurivella (Batsch ex Fr.) Kummer, where a terminal solitary chlamydospore is illustrated by Vandendries & Martens (1932) surrounded by thallic-arthrotic conidia.

In general, the morphology of chlamydospores is quite variable from species to species; wall thickness and shape vary considerably although remaining fairly constant within a particular species. In the agarics, chlamydospores are more frequently found in pure culture than in nature. They are particularly common in lignicolous species, e.g., Polyporaceae, Pleurotoideae, and have been used to assist identification of wood-rotting agarics (Miller 1971).

Chlamydospores either form as the culture ages, or are an integral part of the culture as it develops. In Coprinus trisporus Kemp & Watling the chlamydospores become pigmented and form rows or bunches of cells superficially resembling the external cells of certain sclerotia (Watling 1972).

The allocysts mentioned earlier in some ways resemble the yellow refractive bodies seen by Miller (1971) in many different genera in culture. Their role is not known, and they appear to be less frequent than chlamydospores. Such bodies may be terminal or intercalary. Gloeocystidia and gloeo-chlamydospores (sulpho-chlamydospores) are described for Lentinellus castoreus (Kühner 1947).

MODIFIED CLAMP-CONNECTIONS

The clamp-connected thallic-arthroconidia found in Arthrosporella ditopa (a fungus close to members of the Armillaria mellea (Vahl ex Fr.) Kummer complex), Collybia racemosa and Pleurotus cystidicoum, have been discussed earlier. However, Bas (1965) has demonstrated chlamydospores with clamp-connections in less well differentiated structures in the agarics.

He draws attention to these rather interesting structures, which are found at the base of the basidiomes (or protocarpic tubers) of several species of Squamanita Imbach (Leptotaceae; Tricholomataceae fide Watling). Indeed, he used the morphology of the chlamydospores to help him distinguish species within the genus. The chlamydospores may be quite smooth and irregular in shape as in Discoderma paradoxa (Smith & Sing.) Singer (Watling 1974) (Fig. 19. 1K), or may be subglobose and then with a very complex wall with infra-structure, e.g., Squamanita odorata (Cool) Imbach (Bas 1965) (Fig. 19.1 L). In all the species the conidia arise as a modification of a clamp-connection, just as in Solerostilbum and Antromyopsis.
The original clamp-connection can be seen as a small hook at one end of each cell.

So far this peculiar modification of the clamp-connection, although found in several widely separated groups of Hymenomycetes and hymenomycetous Heterobasidiae, has only been reported in the genera *Squamanita* and *Dissoderma* among the agarics. It is interesting again to speculate as to the similarity between *Squamanita* chlamydospores and the thallic-arthic disarticulating spores of *Pleurotus cystidiosus*, etc., or the sympodially produced arthroconidia of *Pholiota aurivella* (Vandendries & Martens 1932). Perhaps in this way we will obtain some idea of the way they might have evolved. As a footnote, we can report that 'Osteomorpha fragilis' Arnaud has recently been putatively connected with its teleomorph, *Trehispora farinacea* (Watling & Kendrick, in press).

**SOLITARY HOLOBLASTIC CONIDIA**

The final, small category of true conidia found in the Agaricales includes those propagules formed singly at the apex of a long, thin hyphal branch resembling the sterigma of a basidium. Such structures are illustrated by Kaufert (1935) for *Pleurotus saccatus* s. Kauf. (=P. *cystidiosus* O.K. Miller), and by Kühner, Lamoure & Fichet (1962) for *Hohenbuehelia geogina* (DC. ex Fr.) Singer (Tricholomataceae) (Fig. 19.1 O). In the latter fungus they are binucleate and multiply the secondary mycelium, whereas in the former they may be either binucleate or uninucleate depending on whether they are formed on dikaryotic or monokaryotic mycelium respectively. Associated on the same hyphae as the conidiophores are small capitate structures with mucilaginous caps. These resemble in many ways similar structures found in *Nematoctonus*; indeed Barron & Dierkes (1977) have recently figured a basidiome of an unidentified *Hohenbuehelia* which arose spontaneously in a culture of an unnamed species of this Hyphomycete genus. *Nematoctonus* is typified by clamp-connected hyphae; there would appear to be little doubt that several if not all species of this anamorph-genus will ultimately be shown to be related to hymenomycetous teleomorphs, judging from the appearance of the hyphae at the base of herbarium specimens of *Hohenbuehelia*.

These conidia resemble those produced by *Galsinia inornustans* (v. Höhn. & Litsch.) Parm. (Nobles 1937), and similarly formed mitosporus are not infrequent in the Aphyllophorales. However, there are really no parallelisms between Aphyllophorales and Agaricales in the peculiar small, spherical, often quadripartite 'conidia' found in *Coprinus* Sect. *Comati*. Although found commonly both in cultures of *C. comatus* (Müll. ex Fr.) S.F. Gray and *C. sterquilinus* (Fr.) Fr., they neither germinate nor attract hyphae. Their function remains a mystery: they may have lost their former activity; only further work will show this. The wall elongations with apical capitulum in *Schizophyllum commune* Fr., often confused with conidia by some workers, might be similar, but their quadripartite nature draws them closer to *Riessia semiophora* Fres.

**MYCElia STERILIA**

Although they may be rather marginal to the present discussion, I still consider it important to mention the 'Agonomycete' components of some Agaricales, as they often constitute a very impressive part of the life-cycle of certain species; indeed, such anamorphs are often sent to institutes for determination and comments, as if they were teleomorphs.
Probably the most familiar is *Rhizomorpha* (type: *R. fragilis* Roth.) generally considered a vegetative condition of *Armillaria mellea* (Vahl ex Fr.) Kummer (= *Armillariella*). Persoon (1801) included *R. fragilis* as a synonym of the more familiar form-species *R. subaortiaalis* Pers., which undoubtedly belongs to the same agaric species or a close relative. Indeed, experiments are under way in Edinburgh at the moment to elucidate our apparent ignorance of the variability of vegetative state in the *A. mellea* complex. It is probably because of the ease by which the so-called 'boot-laces' of *A. mellea* (= *R. subterranea* Ach.) are identified that many plant deaths are attributed to this species, in cases where it is in fact only a secondary colonizer, and the primary parasite causing the wilt or death has gone undetected.

Fries (1828) was disposed to associate *Rhizomorpha* spp. with the Xylariaceae, possibly influenced by an early treatment of the genus by Acharius (Lichenogr. Univ. 118. 1810), but the consensus of opinion is heavily in favour of connecting Rothman's fungus with *Armillaria*; certainly Persoon's herbarium specimen labelled *R. subaortiaalis* is similar in all ways to that obtainable in culture from mono- or multi-spore, and tissue cultures, of *A. mellea*. An excellent study has been conducted by Snider (1959). It has been possible to repeat Raabe's (1972) work on fruiting *A. mellea* in culture with three other European species, although it still remains an unpredictable event even after efforts have been made to stimulate fructification by cold shocks, etc.

White cords are frequently found in woodland permeating the substrate and often associated with the basidiomes of *Phallus impudicus*. However, another fungus producing similar cords is *Tricholomopsis* (*Megaocalybia* platyphylla (Pers. ex Fr.) Singer; these have been called *Rhizostroma xylostroma* Ach.

Another rather impressive growth is that of *Ozonium auricomum* Link. Whenever the teleomorph is present, it is invariably a species of *Coprinus*. Indeed, the orange brown vegetative growth may be found with a range of *Coprinus* species, but only within the subsect. *Domestici*, although some reports are to the contrary. *C. radians* (Desm.) Fr. is usually associated with *Ozonium*; *C. domesticus* Fr., *C. elliottii* P.D. Orton, and an unnamed species close to *C. micaceus* (Bull. ex Fr.) Fr., with an ornamented hilar plage to the basidiospore, also grow attached to *O. auricomum*. Persoon (1801) referred this species to *O. fulvum* Huds. per Pers., recording *O. auricomum* as a synonym. The *Ozonium* can be produced in pure culture from basidiospores and, as noted above, *C. domesticus* and its allies produce arthric conidia in addition.

An equally conspicuous but entirely sterile mycelial growth is that of *Anthina flamma* (Jungh.) Fr. (= *Ceratoma dilatatum* Roth.; *Himantia flamma* Jungh.). The bright cinnabar red growths with golden yellow tips resemble a coral-fungus, and specimens have been seen up to 30 mm high. It has been suggested as being the mycelium of some Hymenomycete, perhaps 'Peniophora' sanguinea (Fr.) Höhn & Litsch. (Donk 1962). However, although it has not been possible to connect this genetically to any agaric, the mycelium is very close to that of many in the *Dermooyce semisanguineus* complex. There are, however, slight morphological differences, and clamp-connections are not found.

*Rhisostonia* DC is a familiar name to both pathologist and mycologist alike because *R. solani* Kühn, the mycelial state of *Thanatephorus cucumeris* (Frank) Donk, is a widespread plant pathogen. Undoubtedly the name *R. solani* refers to a range of species, perhaps not
all of them having their teleomorphs classifiable in the same genus. They are brought together on the characters of the mycelial growth and branching patterns. The swollen cells found in cultures of *T. cucumeris* are very similar to those found in species of *Psilocybe* (Heim & Wasson 1959), *Conocybe* (Watling 1964), etc. Indeed *Rhizoctonia* should strictly be applied to states of, and forms similar to that of, *Heliothisidium purpureum* Pat. (i.e., *R. croorum* (Pers.) DC), and thus the genus to house these moniliform hyphae would be *Monilopaes* Rutland. The swollen cells found in cultures of agarics resemble in some respects the formation of conidia by some Fungi Imperfecti placed in *Aclidium*. However, they do not apparently act as propagules, and therefore resemble the catenulate hylal segmentation found in *Basidiobolus radula* (Fr. ex Fr.) Nobles (1967). Swollen cells are frequently found in cultures of agarics, e.g., *Tricholomataceae* (Kühner 1947).

**BULBILS, SCLEROTIA AND SIMILAR BODIES**

Eidam (1883) adopted the term bulbil for fungal structures analogous to those found in algae, mosses and phanerogams, i.e., pseudoparenchymatous propagules without internal structural differentiation. Weresub & LeClair (1971) found that this term described admirably the propagules found in the genera *Burgoo* Goidanich and *Minimeda* Weresub & LeClair (both segregates of *Papulaspore* Preuss). Thus the term can neither be used for the aegeritoid growth found in a range of Hymenomycetes nor for the plates of sclerotized cells characterizing the genus *Rhaophyllus* Berk. & Br. Weresub & LeClair clearly delimited the bulbil from the sclerotium, particularly in that the latter differentiates gradually and is probably more of a resting structure than a propagule. True bulbils are not found in the Agaricales.

Eidam also recognized the distinction between the 'bulbillen' and 'sporen knaueln' the latter possessing both central, thin-walled cells which might germinate, and an outer layer composed of thicker-walled and often pigmented cells. Such structures are called sclerotia, developing from an aggregation of hyphae. In some cases the hyphae bind sand-grains or similar soil particles into a mixture of organic and inorganic material; these have long been called pseudosclerotia, but studies of the development of such structures are still urgently required.

True sclerotia are found throughout a whole range of Agaricales, in *Agrocybe arvalis* (Fr.) Singer (Bolbitiaceae), several species of *Coprinus* (Coprinaceae), e.g., *Coprinus tuberosus* Quél. and *C. solerotiger* Watling, and species of *Colybia* (Tricholomataceae), e.g. *C. ookiei* Arnold and *C. tuberosa* (Bull. ex Fr.) Kummer. Normally the sclerotia vary from the size of a pea or small walnut, e.g., *A. arvalis* to the size of an apple pip, e.g., *C. tuberosa*. However, in *Pleurotus tuber-regium* (Fr.) Singer, the sclerotium is very large. It was known to Fries (1822) through its original account, and he associated it with the sterile sclerotium of *Polwa oocose* (Schw.) Fr. in the genus *Paahyma* Fr.

*Scleroma* Fr. has been used for the pseudo-sclerotium of *Panus badius* (Berk.) Sing., and the sclerotium of *Poly porous tuberaster* Jacq. ex Fr., related by Singer (1962, 1975) to the pleurotioid agarics, has been called 'Pietrja fungaija'. A number of polyporaceous fungi possess sclerotia; several examples are given in Chapter 20.
This now leaves those sterile units composed of centripetally developing prosenchymatous tissue, characterised by Aegerita candida Pers. (Sclerotium aegerita Hoffm.; teleomorph Bulbillomyces farinosus (Bres.) Julich). A. duthiei Petch has been related to Tomitomyces (Rajapa) eukhina (Berk.) Heim, a termiotophilous fungus, but several agarics are associated with ant and termite nests, and A. duthiei, as currently used, is undoubtedly a collective term. Such structures have been called Tomtitomphaeria Ciferri. Several species of the Leucocoprineae produce basidiomata associated with ant nests, particularly those of leaf-cutter ants, and it is rather significant that Cocobotrys (Cenococcum) xylophilus (Fr.) Bond. & Pat., another aegeritoid structure, has been associated with the complex around Lepiota meleagris (Sow. ex S.F. Gray) Quél. Attamyces Kreisel (1972), based on A. bromatificus, is according to its author probably the bromatia-forming stage of 'Rosites' gongylophora Müller (Fig. 19.1 M); Singer considers this a Leucaagaricus (Leucocoprineae), and therefore quite clearly related to Lepiota meleagris.

From greenhouse soil one can often isolate small yellow, sclerotoid bodies very similar to those produced in cultures of Coprinus cinereus (Schaeff. ex Fr.) S.F. Gray, although these latter are buff to brownish. Under favourable conditions these yellow structures produce basidiomata of Leucocoprinus bimbaumii (Corda) Singer. Warcup & Talbot (1962) have also isolated this Leucopeprinus from Australia and successfully fruited it along with a Leptogioasum sp., an Omphalina sp. and Coprinus sterquilinus; Warcup & Talbot used helminthological techniques for isolation of the sclerotia, sclerotoid bodies and bulbiloid structures from soil samples.

The mention of Omphalina immediately brings to mind the rather complex structures occurring in Mycena citricolor (Berk. & Curt.) Sacc., more frequently referred to as Omphalia flavida Maublanc & Rangel. The propagule has been termed a gemma and is a rather highly differentiated structure resembling a reduced, sterile, dehiscent pileus hinged at the top of a stipe. Buller (1934) has described this fungus in great detail, and its ability to produce gemmae in pure culture assists in following the various steps in their development. This anamorph, as it must now be viewed, because of its ability to distribute the species and establish secondary mycelium, has been called Stilbum flavidum Cooke. Singer (1951) introduced the term 'stilboid' for these structures, but as Stilbum cannot be upheld for this fungus, its derivative term stilboid is equally inapplicable. They cannot be viewed as gemmae, for they are in no way similar to the gemmae of mosses, etc.; one should always be cautious about the application of botanical terms with very definite circumscription such as cuticle, gemma, etc., to superficially similar structures until developmental studies are completed. A descriptive term is required for these structures and 'cephalosus' might be appropriate.

Similar or parallel structures are not found in any other agaric, although it is interesting to note that several species of Mycena (Tricholomataceae) possess a distinct disjunction between pileus and stipe tissues (Kühner 1926).

Weresub & LeClair (1971) specifically mentioned Rhacophyllum Berk. & Br. in their discussion on Burgoa and Minniecus, because the groups of thick-walled cells in the gills of this fungus have often been referred to as bulbils (Plate 19.3). R. lilacinus B. & Br. has been demonstrated to be an anamorph in the life-history of Coprinus cystalophyllum Maniotis. This was not a chance demonstration by Maniotis (1964), since the same teleomorph has
Plate 19.3  A, D & F, sclerotized cells in hymenophoral trama of *Coprinus clastophyllus.*
B, C & E, thallic-arthric didymoconidia in *Dacrymyces stillatus.*
It subsequently been produced in Edinburgh; in these experiments every possible form, from a typical fertile, deliquescent, coprinoid basidiome, to an entirely asexual form, has been obtained, with intermediates possessing varying numbers of basidia or groups of sclerotized cells. This morphological series is similar to that found in Astorphora, where it is doubtful whether many fruit-bodies are present which are completely in the anamorphic state. It is interesting to note that the chlamydospores in Astorphora parasitica are formed in a parallel way within the gill-tissues, as the lamellar tissue forms pockets of sclerotized cells in Rhacophyllus. It is also tempting to suggest that the sclerotized cells are formed in a similar way to the sclerobasidia known in various members of the Tricholomataceae.

As in Mycena citricolor, no suitable term is available for this kind of structure; Singer (1975) has suggested the term 'bulbillosis', and although he does not wish to convey the notion of a bulbil or bulbil-like structure, nevertheless the term can do nothing but suggest such structures. I propose the term 'Caterva' (pl. caterva) - a crowd, troop or horde. Unlike Mycena citricolor, however, it may be that the rhacophylloid state is common to a number of members of the Coprinaceae.

The Rhacophyllus form of Coprinus aclastophyllus is very similar to the teleomorph, with a pileus, stipe and hymenophoral trama. It could be compared with a carpophoroid, a term used more frequently for the swollen, rather amorphous structures formed by Rhodophyllus (Entoloma) abortivus (Berk. & Curt.) Singer. I mention these structures here, as it is on such fruit-bodies that the genus Acurtis Fries is founded, and this has been taken at times as the correct name for Rhodophyllus. It must, however, be treated as a nomen anamorphosis, because the structures in R. abortivus are gymnocarpic primordia of the teleomorph abnormally expanded following an attack by Armillaria mellea (=Armillariella) (Watling 1974).

Other carpophoroid fruit-bodies include those of Digitellus Paul., considered to be the sterile finger-like growths of Lentinus lepideus (Fr. ex Fr.) Fr. These are frequently found in enclosed dark places in houses (Findlay 1951); Polyporus squamosus (Huds. ex Fr.) Fr. may form similar growths, and the reader is referred to the reinterpretation of Clavicorona dryophila Maas G. (Maas Geesteranus 1976). Lentodium squamulosum Morgan, shown by Lyman (1907) to produce conidia at the actively growing pileus-margin, has been demonstrated by genetical studies to be an enclosed (gastroid) form of Panus tigrinus (Bull. ex Fr.) Singer, unless there are several species within the form-species Lentodium squamulosum (Rosinski & Robertson 1968). The enclosed basidiome often appears at a different time of the year to the typically pleurotioid form, is uniform in a given population, and not evident throughout the range of the hemiangiocarpic form. Miller & Stewart (1971) describe clavarioid (Digitellus) forms in Lentinellus cochleatus (Fr.) Karst. in culture.

CONCLUSIONS

Undoubtedly the commonest and most widespread form of conidiogenesis in the Agaricales is by thallic-arthric means, in which two distinct forms can be observed: those which simply fragment using the parent hyphal wall, and those that produce secondary walls. By swelling and condensation of the proplast, with accompanying wall-thickening, it is easy to imagine how both modified clamp-connections and vegetative hyphae can be converted into thallic chlamydospores.
Single terminal holoblastic conidia borne on denticles are infrequent. Meristem arthrospores, phialospores, tetraradiate and ballistospores have not as yet been seen in members of the Agaricales; nor have the didymospores typical of Daerymyces stillatus Nees (Plate 19.3).

Haplotrichum, Acladium, Spiniger are atypical of the Agaricales although such anamorphs are frequent in various genera within the Aphyllophorales. The complex conidiophores found in the ascomycetous fungi and non-agaricoid Basidiomycetes are replaced in the Agaricales by simple structures, although these may be incorporated in rather complex fruit-bodies; specialized vegetative mycelium classifiable in the Agonomycetes often characterizes certain agarics.

ACKNOWLEDGMENTS
It is with pleasure that I thank Mrs. Norma Gregory for her help in both culturing the fungi and bringing together the experimental data.

DIALOGUE FOLLOWING DR. WATLING'S PAPER
MADELIN: We have grown Asterophora lycoperdoides in culture and its fruit bodies appear to be totally insensitive to gravity when in the chlamydosporic phase. Is this true of Rhacophyllus too?

WATLING: No, Rhacophyllus is always negatively geotropic. But it is interesting that field collections of Nyctalis when growing at an angle and not exhibiting negative geotropism are entirely chlamydosporic, but if there is any negative geotropism the specimens will show some evidence of gills -- of the presence of the teleomorph -- and are often quite agaricoid.

BENJAMIN: I would like to applaud the decision you and Kendrick have taken to avoid the use of the terms 'oidium' and 'gemma' in Basidiomycetes. I'd like to do the same in the Mucorales. These terms have been used so indiscriminately for so many different things that they can be positively misleading. I think that in both groups terms like chlamydospores and thallic-arthric conidia and blastic conidia are entirely appropriate.

WATLING: We certainly won't use 'oidium', because of the confusion with the form-genus Oidium, the anamorph of the powdery mildews. I refer you to the terminological section of our compilation (Chap. 20). I would like to add the adjective 'spermatial' when the thallic-arthric conidia act as gametes. Certainly there is no morphological way of telling whether they are going to act in the sexual context or not.

The term gemma is used in the agarics only for the small cap-like structure found in Mycena citriicolor. It is a modification of a normal pileus, and it would be nice to have a special term for such a unique structure.

WERESUB: We should distinguish between terms coined to describe a form and those which describe a function. To me, gemma is a functional term for anything that is budded off asexually and is detachable. There's no particular implication of a unicellular or multicellular construction -- it's a very general term.

KENDRICK: You could, then, call most conidia, gemmae.
WATLING: They are simply vegetative propagules.

KENDRICK: If it is too broad, it simply comes into competition, at least in our sphere, with better established terms, and we'd be better off without it. I think most biologists know gemmae as those propagules produced in gemma-cups by liverworts, and perhaps this usage should carry the day.

WATLING: I have suggested that the *Mycena citricolor* structure could be called a 'cephalosus'.

MILLER: Our discussion on the use of the term 'oidium' should be included in the book because the term is misused consistently in Swiss laws concerning food hygiene. The law is clearly not aimed at excluding conidia of Erysiphales from food, since these don't hurt anybody. What they are actually trying to control, of course, is the occurrence of the thallic-arthric conidia of *Geotrichum*. The law specifically proscribes 'Hefen, Oidien und Schimmel', and I'm sure it will be very difficult to get it changed. The whole formulation is foolish.

KENDRICK: In our conclusions on the use of this term, Dr. Watling and I were guided by the law of priority, rather than the law of the land.

MADELIN: We shouldn't be too concerned about the legal side of this, because it looks as if it might be a source of remunerative consultancies for mycologists.

WERESUB: Do you know *Oidium morgani*?

WATLING: Only from the literature.

WERESUB: I wonder whether it could be a *Pleurotus* anamorph: it certainly is not a *Botryobasidium* anamorph, and Miller (1971 Plate XI, Fig. 52) published a picture of a *Pleurotus* anamorph that looks like *Oidium morgani*.

WATLING: Linder (1942) described a whole series of *Oidium* species which Dr. Kendrick and I have included in the Tables in Chapter 20 mainly to bring the morphologically similar anamorphs together. The Tricholomataceae in general produce at the ends of hyphae structures which have been called 'refractive bodies'. We don't really know yet whether they germinate or not. In *Lentinellus* those are more differentiated and can be stained with sulphuric aldehyde mixtures, just like gloeocystidia. In *Pholiota*, allocysts that look like *Sporotrichum* are produced; they are filled with yellow material which becomes more intensely coloured in ammoniacal solutions -- but again they don't, so far as we know, function as propagules, but resemble the chrysocystidia found in hymenia. So there is a problem of interpreting the meaning of these phenomena.

LUTTRELL: It seems to me that over much of the agaric spectrum, all the conidia are essentially thallic-arthric. I am surprised that, with so little range in conidial development and morphology, you can make such broad generalizations.

WATLING: Yes. I've been surprised too, as speaker after speaker has shown how relatively limited the correlations between teleomorph and anamorph classification are among the Ascomycetes -- mainly I suppose because evolutionary pressures have produced greater diversity in Ascomycete anamorphs. But in the Basidiomycetes quite large groups are well correlated. The Tricholomataceae always have thallic-arthric conidia of one particular kind, whereas the Bolbitiaceae-Coprinaceae always have thallic-arthric conidia of another kind. Of course, many species remain to be analyzed. But over 50% of European *Coprinus* species have been examined, and the pattern holds.
LUTTRELL: Could this mean that the agaricologists have devised a better classification than the Ascomycete specialists?

WATLING: It may be that there is now a fairly good concept for the genera in the Agaricales, and of relationships between them.

KENDRICK: I think that evolutionary pressure on Basidiomycete anamorphs may have been unidirectional or stabilizing, while that on Ascomycete anamorphs, for some reason we don't yet understand, has been disruptive or multidirectional, forcing diversification on them.

WERESUB: Or perhaps Basidiomycete anamorphs are not sufficiently important to the organism as a whole to be subjected to such pressures.

WATLING: Basidiomycetes spend most of their time in the dikaryophase: you can easily confirm this by observing the repeated fruiting of many agarics in the same place, year after year. It's also interesting to note that although monokaryotic conidia of *Ingoldiella* have been reported in culture, those found in nature are invariably dikaryotic. The survival of dikaryotic mycelia in the natural substrate, with the attendant ongoing potential for sexual reproduction, may be one reason why Basidiomycetes have not been pressured into evolving as many different kinds of conidia -- or conidiogenesis -- as the Ascomycetes. Nevertheless, many collections which look morphologically the same are biologically different, being subjected to heavy selection pressure at the hyphal level because they are sexually of different 'microspecies'.

MULLER: Is there any significant difference in the behaviour of the anamorphs of homothallic and heterothallic species? If they do function as spermatia they should be more essential to the heterothallic species.

WATLING: There is no consistent pattern associated with either.

MULLER: I was thinking of *Neurospora* and *Chaetomium*, where homothallic species usually don't produce anamorphs, and heterothallic species do.

WATLING: That is not the case in *Coprinus*. But remember that in Basidiomycetes there is a dikaryophase that is a reservoir of genetic variability. And here the conidia may be spermatial and can fuse with another thallus just as readily as a basidiospore can -- both can contribute to the genetic mosaic.

LUTTRELL: You distinguished between dry and slimy thallic-arthric conidia. This seems to me similar to the distinction Subramanian wanted to make earlier between dry and slimy blastic-phalidic conidia.

WATLING: I did make that distinction, saying that a few species had both kinds. Here we must consider ecological factors. Those with wet spores are mainly coprophilous, while those with dry conidia are terrestrial or lignicolous. Where both are produced, the wet spores attract but do not germinate; the dry spores, on the other hand, germinate and grow toward the dikaryon or monokaryon of the same species.

VON ARX: During the past six years Dr. Stalpers has cultured many basidiomycetous anamorphs, but many Aphylllophorales that produce fruit bodies on very rotten wood or on soil have consistently refused to grow in pure culture (e.g., Thelephoraceae). A list of these recalcitrant fungi will soon be published. Another problem is that we have never persuaded the conidia of *Sporotrichum* to germinate. New cultures have to be derived from mycelial inoculum. This is a fairly common difficulty with basidiomycetous anamorphs,
raises the question of their function: perhaps many of these propagules are long-term survival mechanisms and require prolonged periods of dormancy, or special and as yet undetermined stimuli to induce germination.

WATLING: Burdsall recently told me that if you allow cultures to dry out slowly over six to nine months, then flood with new medium, they may begin to fruit or the spores to germinate.

MADELIN: I'd like to mention a couple of terms introduced by P.H. Gregory (1966). He categorized spores functionally, into 'memnospores', which stayed put, and 'xenospores', which were primarily for dispersal. He also identified a number of structural and physiological 'tendencies' which went with the basic characters. In Basidiomycetes, the basidiospores must surely be regarded as xenospores. This suggests that there may be a role in the life cycle for a memnospore. Either that, or some of these non-germinable 'conidia' might actually be functionally spermatia, in which case one wouldn't expect them to germinate.

You mentioned that you thought the chlamydospores of Asterophora lyooperdoides had a dispersal function. But they are very difficult to germinate, and the longer they sit, the thicker their walls become. This suggests that they may well be memnospores, rather than xenospores.

WATLING: You are probably right in such cases as Nyatalis and Ptychogaster. The arthric conidia, however, bridge the gap, since they often act as spermatia, particularly in coprophilous species. But there are others which germinate immediately and will seek out hyphae of their own or related species. This may facilitate exchange of nuclear material in nature.

MADELIN: I've often tried to culture Bastridium flavum but never succeeded. I know that it hasn't been connected to a teleomorph, and wonder if it might not be basidiomycetous. The conidia are large, and the septal pores are clearly visible, but I haven't tried staining them to see if they are dolipores.

KENDRICK: Yes, now we have a technique for doing that, we must use it to examine large numbers of fungi.

WATLING: You can see the dolipore in many Basidiomycetes in Melzer's reagent, or in lactophenol cotton blue, but ammoniacal Congo red or ammoniacal erythrosin are better. This is a rapid way of checking for basidiomycetous affinity, but remember that it is only a preliminary test.

KENDRICK: And we must not forget that dolipore-like structures are also found in some yeast-like fungi and in some Zygomycetes -- these are referred to by Drs. von Arx and Benjamin in Chapters 22 and 23.
INTRODUCTION

Most ascomycetous anamorphs occur well separated in time or space from their teleomorphs, and have perforce been given separate 'anamorph'-generic names, a practice legitimized by Article 59 of the International Code of Botanical Nomenclature.

This separation of life forms is less typical of Basidiomycetes (other than Uredinales), and anamorphs, though usually much less conspicuous and frequently overlooked, often appear side by side with the teleomorphs. When perceived, they have generally been treated as an integral part of the teleomorph, and have not been given separate generic names. To some extent this may be because they "are seldom robust, and lack the considerable elegant variations found in the ascomycetous Fungi Imperfecti" (Hughes 1971). Whatever the reason, the absence of recognized generic concepts for many of these basidiomycetous anamorphs has held back our understanding of the group as a whole.

As long ago as the late 19th century Brefeld gave delicate and precise illustrations of many conidial forms produced by a range of Basidiomycetes and, in fact, used his observations of anamorphs as the basis for a hypothesis connecting the major groups of higher fungi. Lyman (1907) recognized three kinds of secondary spore -- conidia, 'oidia' and chlamydospores -- formed by Hymenomycetes, mostly in pure culture, and Nobles (1948), studying cultures of 126 wood-destroying homobasidiomycetes, found the same three kinds of asexual propagule.

But most workers have been primarily concerned with the teleomorphs, and Brefeld's fine pioneer studies were not followed up in detail until recently. Our over-all knowledge of basidiomycetous anamorphs languished for the best part of a century; snippets of information have remained scattered throughout the literature, and the need for a synthesis, such as the one we are attempting here, is unquestionable.

At first sight it might appear that the Basidiomycetes, with the notable exception of the Uredinales, have escaped the relentless evolutionary pressure which produced such a plethora of anamorphs among the Ascomycetes. As we have amassed our data, it has become clear to us that this is only partly true. In outlining an experimental new approach to the classification of conidial fungi, Hughes (1953) mentioned several anamorphs with basidiomycetous
affinities, mainly in his sections IB [holoblastic*] and VII [thallic-arthic]. It was again Hughes (1970b) who expanded the discussion of anamorphs to include the various specialized mitospores of the rusts -- aeciospores, urediniospores and, with some qualifications, pycniospores and teliospores. Subsequently, in a brief survey of 'Phycomycetes, Basidiomycetes and Ascomycetes as Fungi Imperfecti', Hughes (1971a) added to the phenomena he had described earlier, but his compilation was not exhaustive, and it was beyond the scope of his study to provide what Watling (ined.), at the Madras Conference in 1975, suggested was desirable: the sort of finely drawn categories among which the basidiomycetologist might be able to find generic or even specific delimitations.

Nevertheless, the stimulus had been applied, and so a hyphomycetologist (BK) and a basidiomycetologist (RW) have here joined forces in an attempt to lay the groundwork for such potential gains. In any case, the very widespread occurrence, and the ecological importance, of anamorphs in Basidiomycetes are now beginning to be realized. Hence this review.

By casting our net as widely as possible in the literature, and by examining many living cultures of Basidiomycetes, we have tried to provide as inclusive a survey as possible, and as rationally but narrowly drawn categories as seemed feasible.

An acceptable and useful paradigm in taxonomy is "split first, lump later". Analysis must precede synthesis. We are applying this concept to our categories of non-basidiosporous propagules ('mitospores') in an attempt to extract the maximum amount of information from the data available. Weresub & Le Clair (1971) have already set us an example of such fine but rational segregation in their study of bulbils and related structures produced by Basidiomycetes.

TERMINOLOGY

Before we present our scheme we must reassess the terminology currently applied to basidiomycetous anamorphs, because this remains a source of considerable confusion and ambiguity. Although Lyman (1907) recognized only three categories of mitosporic propagule -- conidia, oidia and chlamydospores -- other terms have subsequently been applied to similar non-basidiosporous actual or putative propagules, among them: aeuriospore, allocyst, bulbil, spermatium, sporidiole, and stephanocyst. We will give a brief discussion of these and other relevant terms, in alphabetic order.

ALEURIOSPORE. As defined by Vuillemin (1911), this term refers to an asexual spore that is released by a circumsissile lysis or rupture of its supporting cell. The term is concerned specifically with a distinctive method of spore release, and not with the method by which the spore is formed. This is an important distinction to make, since most of the categories we shall recognize are based initially on the ways in which propagules develop, as advocated

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* Much of the terminology we use to describe anamorphs is that adopted at Kananaskis-I. See Kendrick 1971, Chapter 16.
by Hughes (1953) and elaborated by the participants at Kananaskis-I (see Kendrick 1971). Noting that Aleuriospore has been misapplied many times, we preferred to reject the word, placing aleuriospores sensu stricto under the more broadly defined heading 'chlamydospores'.

Von Arx (1973) wrote that "The genus Sporotrichum is characterized by the formation of basidiomycete-like hyphae which mostly have clamp connections at the septa, and by one-celled conidia with a thick, strikingly pigmented wall. The conidia are separated from the conidiogenous cell by a cross wall without constriction, and have a truncate, broad base. They are liberated by histolysis of the stalk cell, remnants of which often remain attached to the base of the conidia." He was clearly referring to the aleuriosporic phenomenon. This method of dehiscence was beautifully illustrated by Carmichael (1971 Fig. 4.1 F,G; Fig. 4.3 A,B,C) who showed that it is used by some fungi whose conidia have thallic-arthric ontogeny as well as by some which produce chlamydospores. Nevertheless, as far as we can gather, anything called an aleuriospore in Basidiomycete literature would now be included among the chlamydospores. This is a pity. It would clearly be worthwhile to retain a derivative of the term Aleuriospore, perhaps 'aleuric', to describe this specialized mode of dehiscence.

ALLOCYST. A chlamydospore-like structure in Pholiota gummosa (Lasch.) Singer (Kühner 1946, sub Flammula) also in Schizopora paradoxa (Schrad. ex Fr.) Donk. These structures, which according to Kühner do not germinate, are probably just repositories for food or waste products, and in some ways resemble the chrysocystidia of the teleomorph. The term has no relevance to our consideration of basidiomycetous mitospores. There may be some similarities between these structures and the refractive bodies found in various pleurotoid agarics, e.g., Phylloptopis nidulans (Pers. ex Fr.) Singer, and Pleurotus elongatipes Peck (Miller 1971).

BROMATIUM (plural: BROMATIA). The rounded, swollen end of a hypha of a fungus, Attamyces bromatificus Kreisel, cultivated by the Attine ants and used by them for food. Not, strictly speaking, a propagule, though resembling a chlamydospore. When aggregated, bromatia resemble Aegerita Pers. ex Fr.

BULBIL. Eidam (1883) borrowed the term, which was already in use in the algae, mosses and phanerogams, for an analogous fungal structure which he clearly defined as a pseudoparenchymatous propagule without internal structural differentiation. Weresub & Le Clair (1971) found that this original definition very nicely restricted the use of the term to basidiomycetous anamorphs referable to the genera Burgoa Goidânich (Fig. 20.7 G) and Minimedusa Weres. & Le Clair (both segregates from Papulaspora Preuss as treated by Hotson 1912, 1917): they consequently rejected the use of the term for "the firm clusters of apically enlarged and radially disposed hyphae of Aegerita candida [Pers.] Fr. ... and the plates of sclerotized cells which make up the lamellae of agarics which have been classed as Rhaophyllus species." They also carefully delimited the bulbil from the sclerotium on two characters; structural differentiation and origin.

(1) Bulbils are internally undifferentiated; sclerotia are differentiated into rind and medulla. (2) Developing bulbils are immediately distinct from the surrounding mycelium; sclerotia differentiate gradually. In addition, the discrete pseudoparenchymatous nature of the bulbil separates it from the structures produced by Rhizoctonia DC. ex Fr., which always retain their hyphal nature to some extent. The reader is referred to Weresub &
Le Clair (1971) for a fuller and very well illustrated treatment of the subject.

Weresub (pers. comm.) has kindly supplied a definition of the term bulbil as follows: A discrete, compact, multicellular, thallodic propagule initiated in one of several ways but always homogeneous throughout development, with all cells acropetally produced and expanding more or less synchronously to many times (e.g., 4-10x) the diameter of the colourless, thin-walled hyphae from which they arise; pseudoparenchymatous at least at maturity, and lacking internal differentiation.

Bulbils may be readily distinguished from the apparently similar papulaspores both by their ontogeny and by their mature anatomy. Rather than being homogeneous throughout, papulaspores have a larger central cell or cells surrounded by smaller sheath cells (see papulaspore). Nobles (1959) used the term bulbil for small coils of hyphae found in cultures of Phellinus nigrolimitatus (Romell) Bourd. & Galz. (sub Fomes): we consider this an overextension of the term, but only one of many such in the literature.

CHLAMYDOSPORE. This is rather unsatisfactorily defined in the Dictionary of the Fungi, 6th Edition (Ainsworth, James & Hawksworth 1971) as: "a thick-walled, non-deciduous, intercalary or terminal asexual spore made by the rounding up of a cell or cells; a gemma; cf. aleuriospore, conidium." This is a morphological definition with slight functional and developmental overtones.

Barron (1968) defined it as a "thick-walled resting spore, frequently intercalary, which is formed by modification of a pre-existing cell", thus adding another functional element. Both definitions restrict the term to spores with thallic ontogeny. But problems remained. Some cells called chlamydospores are not necessarily particularly long-lived, as a resting spore should be. Carmichael (1971) emphasized that chlamydospores, unlike most of the other spore types under consideration, lack any mechanism for their release, and he characterized them as: "resistant cells, either terminal or intercalary, which are released by mechanical fracture of a non-differentiated cell wall." The Kananaskis-I Conference, aware that the term has been widely used in a variety of senses -- so much so that, as Goos pointed out, it can hardly be restricted to spores distinguished either by their ontogeny or their dehiscence -- finally settled on the following very broad definition: "A thick-walled, thallic, terminal or intercalary spore." Some propagules called chlamydospores are not particularly thick-walled (thick is in any case a relative term), and some structures that have been called chlamydospores have never been observed to germinate (it is assumed that 'spores' will germinate, sooner or later), and may thus merely be repositories for waste products (see also Allocyst).

Since all the evidence has not yet been gathered, we feel unable either to redefine chlamydospore more precisely, or to scrap it altogether. As currently defined, it incorporates most of what were previously called aleuriospores and chlamydospores. Many Basidiomycetes produce structures that fall within the Kananaskis-I definition. They may develop only in pure culture or may be formed on or in various parts of the basidiomata (Fig. 20.5 A-F).

The term chlamydospore has been used in the Ustilaginales as an alternative name for teliospore, but this is inappropriate. If we are to restrict its application to a
particular fungal structure, it should be typified by the *Asterophora* morph of *Nyctalies* (Fig. 20.5 E,F), as originally defined by de Bary (see also aleuriospore, allocyst, gasterosporce, stephanocyst).

CONIDIIUM (plural: CONIDIIUM). Vuillemin (1910a) defined his 'conidia vera' as asexual spores which are cut off from the hypha bearing them as soon as they are formed. This concept of a specific, inbuilt mechanism for secession is now accepted as one good way of delimiting conidia proper from chlamydospores, especially since many conidia are, like most chlamydospores, thick-walled. Note that the participants at Kananaskis-I, in framing the following definition, carefully excluded several other kinds of spore:

"A specialized, non-motile, asexual propagule [mitosporce], usually caducous; not developing by cytoplasmic cleavage or free-cell formation (compare sporangiospores, bacterial spores.)"

A further complication arises when we consider the conidia of the Erysipheales and of certain Basidiomycetes, which have in the past been called 'oidia' (see below). The term 'oidium' has been indiscriminately applied to spermatia, thallic-meristem conidia, and thallic-arthic conidia. Since spermatia, though they may look like conidia, have an exclusively sexual function, we need to differentiate them in our terminology. We can do this for the term conidium by adding to our definition in the following way: "Conidia can always establish a new, independent, vegetative mycelium, but they or the mycelium arising from them may or may not also have a sexual function, fusing with another mycelium. cf. spermatium." So conidia may, potentially at least, have a dual function, as against the purely sexual role of the spermatium.

GASTEROSPORE. As described by Steyaert (1967) this is clearly a very characteristic chlamydospore (of the *Nyctalies-Asterophora* type) which occurs in the pileal trama of many *Ganoderma* species, and has also been recorded in *Hypochnum vellereum* (Ell. & Crag.) Parm. (Eriksson & Ryvarden 1976). Care must be taken, however, concerning the correct interpretation, and site of formation, whenever internal spores are observed: see Reid (1975) on *Oxyporus mollissimus* (Pat.) Reid.

GEMMA (plural: GEMMAE). Several kinds of asexual fungal propagule have been called gemmce, but the term as applied in the algae, bryophytes and pteridophytes is so broad as almost to be synonymous with 'sexual diaspore'. We have accordingly rejected its use in the fungi, and have referred to each so-called 'gemma' under what we consider to be the most appropriate term in our lexicon. The specialized structure found in *Mycoena citriicolor*, and formerly termed a gemma, is better referred to as a cephalosorus (Watling, Chap. 19).

OIDIUM (plural: OIDIIUM). That this term escaped the notice of the Kananaskis-I Conference is indicative of how little the participants were concerned with basidiomycetous anamorphs, since very many Homobasidiomycetes have been found to produce thallic-arthic propagules that have usually been called 'oidia' in the literature, irrespective of whether their function was sexual or asexual. This omission was all the more serious because the term is hopelessly confused, as may be amply and unequivocally demonstrated simply by quoting the three definitions given in the Dictionary of the Fungi, 6th Edition -- appropriately supplemented in square brackets.
"1. Spermatia formed on hyphal branches, esp. in heterothallic hymenomycetes [spermatia];
2. flat-ended asexual spores formed by the breaking up (usually centripetally) of a hypha into cells as in Oospora (Oidium) lactis; arthrospore; [thallic-arthic conidia];
3. a [powdery] mildew [presumably conidia of the Oidium and Ovulariopsis anamorphs of many Erysiphales: thallic-meristem conidia]."

The term is thus being applied to purely sexual spermatia, to thallic-arthic conidia, and to thallic-meristem conidia, respectively.

The name Oidium is now an officially conserved generic name for many anamorphs of Erysiphales (Ascomycetes) (see Weresub 1973, Petersen 1975) and should be used only in that sense. The morphological elements listed in the Dictionary of the Fungi are better referred to by their currently accepted functionally or ontogenetically based names.

PAPULASPORE. Weresub (in litt.) has supplied the following definition: "A discrete, compact, multicellular, thallodic propagule initiated when one or a few hyphal cells (central cells) are encircled by branches arising from the same hypha, producing an early and continuing differentiation into a core of large, central, germinable cells, and a sheath of cells usually abruptly smaller and purportedly sterile. In very large mature papulaspores, the distinction between core and sheath is not always recognizable. Note that papulaspores are ascomycetous mitotic propagules, and are defined here only for comparison with the similar bulbil (q.v.)."

PYCNIOSPORE. This is an unusual kind of mitospore which is actually the agent of dikaryotization in Uredinales (cf. the thallic-arthic spores of many Agaricales). Pycniospores are produced from phialides (Fig. 20.3 C) in usually flask-shaped structures called pycnia or spermogonia (stage 0 in the complex life history of Uredinales), and they are basically non-motile male gametes, or spermatia, although their fusion with receptive hyphae leads in the short term only to a restoration of the dikaryophase. It is entirely inappropriate to refer to pycniospores as 'oidia'. See discussion by Savile, Chap. 21.

SCLEROTIUM (plural: SCLEROTIA). As in the case of the bulbil, it seems appropriate in the interests of the precision for which Weresub & Le Clair (1971) pleaded so eloquently, to give the term sclerotium a fairly narrow definition. Otherwise the term tends to lose its clarity and become extremely blurred around the edges by the inclusion of a welter of vaguely similar resting structures. We propose the following definition: 'A discrete, multicellular structure, microscopic or macroscopic, presumably functioning in a survival capacity during conditions inimical to vegetative growth, and often requiring a dormant period before becoming capable of germination. Arising by aggregation of many hyphae, sclerotia are essentially plectenchymatous, and are at maturity differentiated into a frequently darkly pigmented, thick-walled, outer rind layer, and a thinner-walled, internal medulla.' Pending detailed studies of the whole range of multicellular resting structures, some of which cannot at present be categorized as bulbils, papulaspores or sclerotia, we shall list them as 'sclerotoid bodies'. Willetts (1972) has reviewed the literature on sclerotia, and the reader is referred to his account.
SPERMATIUM (plural: SPERMATIA). The Dictionary of the Fungi defines this as: "a sex cell, e.g., pycniospore or oidium [sic]; a microconidium in the discomycetes and pyrenomycetes; a non-motile gamete as in Laboulbeniales."

However named, it is obviously a cell with an exclusively sexual function -- a non-motile fungal gametic cell. In the Basidiomycetes, therefore, we can apply the term definitely to: 'A haploid spore which has a specifically sexual function, and is incapable of giving rise to a new, independent vegetative mycelium -- that is, it cannot act as a means of vegetative or asexual reproduction.' Thus, though a spermatium may resemble a conidium ontogenetically and morphologically, the two are clearly differentiated at the functional level. We note that Cain (1952), discussing Phialophora, suggested that the conidia were originally derived from spermata by such a switch in function. There is obviously room for some condensation of terms here: microconidium should not be used in this sense, since it has, etymologically, only a morphological meaning; and oidium (q.v.) we have rejected elsewhere.

SPORIDIOLE (plural: SPORIDIOLA). This term is simply defined in the Dictionary of the Fungi as "a small spore", but was used in a more specific sense by Rea (1922) for his initial separation of the Basidiomycetes into 'Homobasidiae' and 'Heterobasidiae' as follows:

"I Basidia simple; spores giving rise to a mycelium on germination ......................................... Homobasidiae

II Basidia longitudinally divided, transversely septate, or simple; spores producing sporidiola on germination ............. Heterobasidiae" [germination by repetition' and budding?]

Rea's sporidiola are produced on structures that resemble sterigmata, but whether they are or are not, in fact, shot off (ballistospores -- secondary basidiospores), we consider them to be conidia, and therefore regard sporidiola, in the sense in which it has been specifically applied to Heterobasidiomycetes, as a synonym of conidium. Although nothing is yet known about the karyological status of these cells (Bandoni, pers. comm.), Tu, Kimbrough & Aldrich (1977) have broached this subject with their investigations of Thanatephorus cucumeris (Frank) Donk and similar taxa.

Sporidiola have also been considered to be a feature of the Ustilaginales, but since there is doubt about the true systematic position of the group (Kreisel 1969) we do not consider this aspect any further.

SPORIDIUM (plural: SPORIDIA). The Dictionary of the Fungi defines this term as:

"1. a basidiospore of the Uredinales and Ustilaginales or, in the latter, any spore other than a chlamydospore;

2. ascospore (obsol.)."

This term is probably best reserved for the outgrowths of the promycelium in the Ustilaginales which on anastomosing produce holoblastic conidia -- see Kreisel (1969) and Donk (1973). The genus Crotalia Liro was erected for the 'sporidia' of certain sedge smuts: thirty years later, Kukkonen & Vatanen (1960) demonstrated experimentally that these 'sporidia' represented the anamorph of Anthracoidea. In morphology and development they are unlike anything in the Deuteromycota.
is unclear, we do not consider sporidia any further.

**STEPHANOCYST.** Boidin (1950) originally gave this name to the two-celled structure produced on the hyphae of *Hyphoderma tenue* (Pat.) Donk, the upper cell hemispherical and girdled at its base by a row of 10-14 short, upwardly directed spines (Fig. 20.5 G1). Later, Boidin (1958), apparently influenced by structures he found in *Hyphoderma puberum* (Fr.) Wallr. (Fig. 20.5 G2), came to consider the stephanocyst as fundamentally a single, spini-ferous cell. Neither Boidin nor subsequent workers (Dearden unpubl., Burdsall 1969) have been able to assign a clear function to the stephanocyst, although Burdsall (1969) reports germination and suggests that the upper cell of a two-celled stephanocyst may be forcibly shot off.

The crown-like ring of spines, which gives the structure its name, is certainly unique, and its origin puzzling. Lentz's drawing (1971, plate IV, Fig. 30) makes it appear that the crown arises as a result of the bursting out of the stephanocyst initial through the hyphal wall, but Boidin's (1958) observation of scattered spines on stephanocysts of *Hyphoderma pallidum* (Bres.) Donk, a phenomenon also seen by Dearden (unpubl.) in *Hyphoderma gutuliferum* (Karst.) Donk, *H. pallidum*, and *H. tsugae* (Burt) J. Erikss. & Skrid, and rows of spines not situated at septa (as in 'Corticia' No. 364 of Boidin 1958), seem to contradict this suggestion.

Galericina badipes (Fr.) Kühner (Agaricales) in culture produces vesiculose diverticula which in many ways resemble stephanocysts of *Hyphoderma* (Lamoure 1960).

Echinocysts, thin-walled, rounded bladders with blunt projections and dense cytoplasm, are in some ways similar to stephanocysts, and have been recorded in *Hyphoderma comuptum* (H.S. Jacks.) Jülich, *H. echinocystis* J. Erikss. & Skrid, and *H. pallidum*. The reader is referred to Jülich (1976).

**SYSTEMATIC ARRANGEMENT**

We have recognized a fairly large number of categories, often subdivided, perhaps arbitrarily, as we saw fit. Some of them are certainly heterogeneous; some may overlap. We have used any defining feature that seemed of potential taxonomic value, and although there is a clear over-all ontogenetic bias, functional or morphological peculiarities have also been used where appropriate. What we have produced is not a classification -- it is an analysis or dissection -- but it undoubtedly contains elements from which a useful taxonomic scheme may ultimately be derived. That happy day will arrive when the sexual and asexual phases of the Basidiomy-cetes have both received the attention they deserve, and we achieve the necessary level of understanding to perform the synthesis.

For the present, our aims are much less ambitious. We hope that our aggregations will be of some value in pointing out possible relationships, and in suggesting, to those who dis-cover basidiomycetous anamorphs, where in the existing classification they may seek the telemo-morphs. Our groups are listed below. Illustrations representative of most sections are presented in Figs. 20.1-20.7.
(1) Blastic solitary conidia:
   (A) on hyphae
   (B) on basidiospores.

(2) Blastic solitary conidia forcibly discharged -- ballistospores.

(3) Blastic conidia on discrete conidiophores -- Haplotrichum-type:
   (A) formed singly on pegs or denticles
   (B) formed in unbranched or branched acropetal chains.

(4) Blastic synchronous conidia formed on an ampulliform conidiophore apex -- Spiniger-type.

(5) Blastic conidia formed in unbranched or branched acropetal chains in the absence of discrete conidiophores -- yeast-like budding.

(6) Blastic-sympodial conidia.

(7) Blastic-annellidic conidia.

(8) Blastic-phialidic conidia.

(9) Thallic-meristem conidia.

(10) Thallic-arthric conidia.

(11) Chlamydospores:
    (A) Solitary terminal chlamydospores: no discrete conidiophore
    (B) Terminal chlamydospores on branches of a discrete conidiophore -- Allescheriella-type
    (C) Terminal and lateral chlamydospores on branches of a discrete conidiophore -- Sporotrichum-type.
    (D) Terminal and intercalary chlamydospores, often forming in chains -- Asterophora-type
    (E) Miscellaneous chlamydospores
    (F) Stephanocysts.

(12) Modified clamp connections:
    (A) Disarticulated clamp connections
    (B) Modified hyphal systems
    (C) Complex clamp connections
    (D) Chlamydospores and Stephanocysts.

(13) Stauroconidia:
    (A) Modified hyphal systems
    (B) Aggregations of propagules
    (C) 'Tetraradiate' propagules.

(14) Bulbils and similar propagules:
    (A) True bulbils
    (B) Bulbilloid bodies
    (C) Centripetally developing prosenchymata
    (D) 'Bulbilloid' bodies in splash cups
    (E) 'Bulbilloid' bodies on stalks
    (F) Bromatia.
(15) Sclerotia and sclerotoid bodies:
   (A) True sclerotia
   (B) Pseudosclerotia
(16) Conidia in pycnidioi'd conidiomata
(17) Blastic-retrogressive conidia.

Within each of the categories given above, we have usually listed the anamorph-teleomorph connections in the following taxonomic sequence:

Unknown Basidiomycetes
Hymenomycetes
   Agaricales
   Aphyllophorales
Gasteromycetes
Hymenomycetous Heterobasidiae
   Auriculariales
   Brachybasidiales
   Dacrymycetales
   Exobasidiales
   Septobasidiales
   Tremellales
Basidiomycetous yeasts
Uredinales

BLASTIC CONIDIA

Blastic conidium ontogeny is defined as: 'one of the two basic modes of conidium development; there is a marked enlargement of a recognizable conidium initial before the initial is delimited by a septum. The conidium differentiates from part of the cell' (Kendrick 1971).

The usual pattern is for a limited area of the wall of the conidiogenous cell to be replasticized and 'blown out'. The archetype of this is simple budding in the yeast, *Saccharomyces cerevisiae* Meyer ex Hansen (though it should be noted here that Streiblová, Beran & Pokorny (1964) and Streiblová & Beran (1965) have shown that proliferation in many other yeasts is far from being a simple budding process). The blastic mode is characteristic of our sections 1-8, 16 and 17.

The several groups which follow are separated by such characters as the timing of conidio genesis (serial or synchronous), whether or not conidia are forcibly discharged, the orientation of conidia on the conidiophore or in relation to one another (solitary, botryose, catenate) and the configuration of the conidiogenous cell and/or conidiophores. These groups are illustrated in Figs. 20.1-20.3 C.
Fig. 20.1 A, unnamed anamorph of *Galzinia incrustans* (group 1A); B, conidial ballistospores of *Daerymyces stillatus* (group 2); C, conidial ballistospores of *Achroomyces disciformis* (group 2); D, *Haplotrichum rubiginosum* anamorph of *Botryobasidium robustior* (group 3A); E, *Haplotrichum similis* anamorph of *Botryobasidium similis* (group 3B); F, *Spiniger* anamorph of *Resinicium furfuraceum* (group 4); G, *Strobodidium magnum* (group 5).
Fig. 20.3 A, unnamed anamorph of *Typhula micans* (group 7): B, *Tuberculina* anamorph of *Helicobasidium brebissonii* (group 8): C, pycnial anamorph of *Gymnosporangium olavipes* (group 8): D, aecial anamorph of *Uromyces erythronii* (group 9): E, aecial anamorph of *Peridermium pini* (group 9).
Fig. 20.4  A, unnamed anamorph of Phlebia sp. (group 10):  B, unnamed anamorph of Coniophora puteana (group 10):  C, Sclerostilbum septentrionale anamorph of Collybia raemosa (groups 10, 12A)  (1) teleomorph bearing synnematal anamorph along stipe, (2) a synnematal conidioma, (3) clamped hyphae disarticulating to form conidia:  D, Antromycopsis broussetiae anamorph of Pleurotus cystidiosus (groups 10, 12A):  E, unnamed anamorph of Dacrymyces stillatus (group 10).
Fig. 20.5  A, Pagidospora amoebophila anamorph of unknown Basidiomycete (group II A): B, Allescheriella anamorph of Leucogaster floccosus (group II B): C, Sporotrichum aureum anamorph of Polyporus metamorphosus (group II C): D, Ptychogaster rubescens anamorph of Punctularia atropurpurascens (group II D): E, Asterophora parasitica anamorph of Nyctalis parasitica (group II D): F, Asterophora lycoperdoides anamorph of Nyctalis asterophora (group II D): G, stephanocysts of (1) Hyphoderma tenue, (2) H. puberum (group II F).
Fig. 20.6 A, unnamed anamorph of Dissoderma paradoxa (groups 11D, 12A, 12D); B, 'Osteomorpha fragilis' anamorph of Trechispora farinacea (groups 10, 12A); C, Syzygospora anamorph of Christiansenia mycophaga (group 12C); D, Taeniospora gracilis anamorph of Leptosporormyces galzinii (groups 12B, 13A); E, Ingoldiella hamata anamorph of Sistotrema sp. vel aff. (groups 12B, 13A); F, Thyrsidina carneo-miniata anamorph of unknown Basidiomycete (group 12C); G, unnamed anamorph of Tremella polyporina (group 12C).
Fig. 20.7 A, *Digitispora marina* (group 13C); B, *Nia vibrissa* (group 13C); C, *Riessia semiophora* anamorph of unknown Basidiomycete (group 13B); D, *Glomospora empetri* anamorph of unknown Basidiomycete (group 13B); E, *Glomopsis corni* anamorph of unknown Basidiomycete (group 13B); F, *Aegerita candida* anamorph of *Bulbillumycetes farinosus* (group 14C); G, *Burgoa versuoliana* anamorph of *Bistotrema* sp. (group 14A).
### Table: SOLITARY BLASTIC CONIDIA ON HYphae (Fig. 20.1 A)

<table>
<thead>
<tr>
<th>Teleomorph</th>
<th>Anamorph</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>HYMENOMYCETES</strong></td>
<td>Sporotrichum dimorphosorum Arx</td>
<td></td>
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<tr>
<td>Agaricales</td>
<td></td>
<td></td>
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<tr>
<td>Pleurotus cystidiosus O.K. Miller*</td>
<td></td>
<td>Vandendries 1934b: probably a species of Hohenbuehelia; 'pinsitus' is usually used for a species of Clitopilus.</td>
</tr>
<tr>
<td>'Pleurotus' pinsitus Fr.</td>
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<tr>
<td>Aphyllumorphales</td>
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<tr>
<td>Amylocystis lapponicus (Rom.) Bond. § Sing.</td>
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<tr>
<td>Christiansenia effibulata Ginns &amp; Sunheide</td>
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<tr>
<td>C. mycetophila (Peck) Ginns &amp; Sunheide</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. tumefaciens Ginns &amp; Sunheide</td>
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<tr>
<td>Galzinia incrustans (Höhnh. &amp; Litsch.) Parm.</td>
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<tr>
<td>Hapalopilus rutilans (Pers. ex Fr.) Karst.</td>
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<tr>
<td>H. salmonicolor (B. &amp; C.) Pouz.</td>
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<td></td>
<td></td>
<td>Stalpers 1978.</td>
</tr>
</tbody>
</table>

* Ghosh, Pathak & Singh (1977) have recorded Antromyoops broussonetiae for Pleurotus ostreatus Jacq. ex Fr. This is almost certainly an error. The teleomorph was not deposited under accession no. IMI 196786 at Commonwealth Myc. Institute, Kew, as stated by the authors.
Teleomorph  Anamorph  References

Hyphodontia alutacea (Fr.) J.-Erikss.*
H. floccosa (Bourd. & Galz.) J.-Erikss.

Laeticorticium simplicisubsidium
Linds. & Gilb.

Laricifomes officinale (Vill. ex Fr.) Donk
'Leucogyrophana' subillaqueata

Poria carbonica Overh.
Spongipellis sp.
Spongipellis sp.
Spongipellis sp.

Tyromyces amarus (Hedgc.) Lowe
T. fissilis (B. & C.) Donk

HYMENOMYCETOUS HETEROBASIDIAE

Tremellales
Tremella translucens Gordon

Gordon 1938: segregated by Donk (1966) into a section of uncertain position, and called 'Microtremella'.

HYMENOMYCETES

Aphyllophorales

Christiansenia effibulata Ginns & Sunhede
C. mycetophila (Peck) Ginns & Sunhede
C. mycophaga (Christians.) Boid.
C. tumefaciens Ginns & Sunhede

Paullicorticium pearsonii (Bourd.) J. Erikss.

HYMENOMYCETOUS HETEROBASIDIAE

Auriculariales

Platygloea sebacina (B. & Br.) McNabb

McNabb 1965e.

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* The type-species of this genus, H. pallidula (Bres.) J. Erikss., was originally described as a species of Gonatobotrys (Hyphomycetes) by Bresadola (1903).

** The production of blastic conidia made these species atypical of the Ceratobasidium spp. recorded by Christiansen.
### Teleomorph

**Brachybasidiales**

- Ceraceosorus bombacis (Bakshi) Bakshi
- Proliferobasidium heliconiae Cunn.

**Dacrymycetales**

- Calocera furcata (Fries) Fries
- C. glossoides Pers.
- C. pallido-spathulata Reid
- Dacrymyces adpressus Kobay.
  - D. capitatus Schw.
  - D. estonicus Raitv.
  - D. intermedius Olive
  - D. minor Peck
  - D. paraphysatus Olive
  - D. san-augustinii Kobay.
  - D. stillatus Nees ex Fr.
- Dacryonema rufum (Fr. ex Fr.) Nannf.
- Dicellomyces scirpi Raitv. apud Parm.
- Ditiola pezizaformis (Lév.) Karst.
- Heterotextus alpinus (Tracy & Earle) Martin
- H. luteus (Bres.) McNabb

**Exobasidiales**

- Exobasidium camelliae Shirai
- E. gaultheriae Sawada
- Muribasidiospora indica Kamat & Rajend.

**Septobasidiales**

- Septobasidium burtii Lloyd
- S. grandisporum Couch

**Tremellales**

- Tulasnella lactea Bourd. & Galz.
- T. pinicola Bres.
- T. pruinosa Bourd. & Galz.
- T. violae (Quél.) Bourd. & Galz.

### Anamorph

### References

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- Olive 1958b.
- Olive 1958b.
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- Christiansen 1959: 'microconidia' and presumed ballistospores also formed.
- Christiansen 1959: 'microconidia' and presumed ballistospores also formed.
- Patouillard 1900, Rogers 1932.

At the end of the blastic-symposial listing (group 6) are mentioned a number of genera which were reported by Kobayasi & Tubaki (1965) to form conidia "in clusters [probably sympodial] or singly on short ..... germ-tubes from basidiospores or sections of them." Any of these genera which produce only single conidia would belong in the foregoing section.
(2) SOLITARY BLASTIC CONIDIA FORCIBLY DISCHARGED -- BALLISTOSPORES
(Figs. 20.1 B,C)

A large category of Basidiomycetes produces solitary holoblastic conidia on small lateral outgrowths (pegs or denticles), or short hyphae, arising from basidiospores (and occasionally from hyphae). These are the hymenomycetous Heterobasidiae which were long characterized by the production of so-called 'repeating basidiospores' (Patouillard 1900) or 'sporidiola' (Rea 1922) used as a primary taxonomic character in the delimitation of the Heterobasidiomycetes from the Homobasidiomycetes (see Donk 1964, 1972b). Lohwag (1926) regarded them as conidia. Buller (1933) and Donk (1972b) considered them to be basidiospores, but we conclude that, whatever they are, they are not basidiospores (i.e., meiospores). Since they are not formed on basidia, their formation is not preceded by the appropriate karyological events, and we insist on treating them as holoblastic conidia which are forcibly discharged by the methods originally evolved for the basidiospore. We can immediately compile about 500 fungi in this category. A representative selection, for which illustrations exist, is given in the list which follows. In many cases these propagules are borne asymmetrically, in the same manner as many basidiospores, and are thus clearly forcibly discharged. But some of the illustrations we have seen do not show asymmetry, and it is possible that the shooting mechanism has been lost (cf. the attachment of basidiospores in many Gasteromycetes). The extent of this loss will only become known when detailed studies of the fungi concerned have been made. At present the literature is confused, so we listed in the preceding section (1) only species which definitely produce single blastic conidia that are not forcibly discharged.

Some Hymenomycetes are also known to produce solitary holoblastic conidia, but in the Homobasidiomycetidae these usually arise from vegetative hyphae rather than from basidiospores.

In the so-called basidiomycetous yeasts, it will be impossible to say, until detailed karyological and life-history studies have been done, whether all ballistospores produced are basidiospores, or whether some of them are conidia, as has been shown in Tillettiaria anomala Bandoni & Johri (1972). Studies on the morphology of Iteronilia perplexans Derx (Olive 1952) show that the ballistospore produced from the basidiospore is asymmetrically placed on a sterigma and is supplied with the nucleus from the original basidiospore, i.e., no nuclear division or genetic recombination are involved. The same appears to be true in the initial studies on Thanatephorus cucumeris (Frank) Donk made by Tu, Kimbrough & Aldrich (1977).
Telemorph

HYMENOMYCETOUS HETEROBASIDIAE

Auriculariales

Achroomyces disciformis (Fr.) Donk
A. effusus (J. Schroet) Mig.

Auricularia mesenterica (Dicks ex S.F. Gray) Pers.
A. velutina Lév.

Cystobasidium sebaceum Martin & Couch

Helicobasidium anomalum Olive
H. brebissonii (Desm.) Donk

Helicogloea lagerheimii Pat. apud Pat. & Lag.

Herpobasidium filicinum (Rostr.) Lind

Hirneola auricula-judae (Bull. ex St. Amans) Berk.

Mycogloea tahitiensis Olive

Platygloea javanica Pat.
P. opalina Talbot

Exobasidiales

Muribasidiospora indica Rajendren

Tremellales

Basidiodendron cinereum (Bres.) Luck-Allen

Eichleriella deglubens (B. & Br.) Lloyd

Exidia guttata Bref.
E. rolleyi Olive

Exidiopsis effusa (Bref. ex Sacc.) E. glaira (Lloyd) Wells

Heterochaete delicata (Kl. ex Berk.) Bres.
H. shearii (Burt) Burt

Patouillardina cinerea Bres.

Protodontia uda Höhn.

Anamorph

References

Brefeld 1888 (Tafel IV:12-15): sub Tachaphantium tiliae Bref.
Christiansen 1959: sub Platygloea; illus. difficult to interpret.

Brefeld 1888 (Tafel IV:10-11).
Patouillard 1900.

Martin 1939b.

Olive 1958a.
Donk 1966: also forms phialoconidia.

Christiansen 1959: but compare fig. in McNabb 1964.

Christiansen 1959, Jackson 1935.

Brefeld 1888 (Tafel IV:3-9): sub Auricularia sambucina Mart.; formed on hyphae.

Olive 1958b.

Patouillard 1900: illus. difficult to interpret.
Talbot 1958.

Rajendren 1968: called ballistospores, but the figs. suggest holoblastic conidia.

Christiansen 1959.

Christiansen 1959.

Brefeld 1888 (Tafel V:12-13).
Olive 1958b.

Reid 1970.
Christiansen 1959.

Olive 1958b.
Olive 1958b.

Olive 1958a.

Martin 1932.
<table>
<thead>
<tr>
<th>Teleomorph</th>
<th>Anamorph</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Sebacina calcea</strong> (Pers. ex St. Amans) Bres.</td>
<td>S. effusa (Bref. ex Sacc.) Pat.</td>
<td>Wittlake 1934.</td>
</tr>
<tr>
<td>S. pulverulenta Hauers.</td>
<td>S. punaeuiae Olive</td>
<td>Patouillard 1900.</td>
</tr>
<tr>
<td>S. subfarinacea Hauers.</td>
<td>S. sublilacina Martin</td>
<td>Martin 1936.</td>
</tr>
<tr>
<td><strong>Sebacina sp.</strong></td>
<td>S. citrinospora Hauers.</td>
<td>Olive 1958b.</td>
</tr>
<tr>
<td><strong>Seismosarca hydrophora</strong> Cooke</td>
<td>S. subvelutina Hauers.</td>
<td>Hauerslev 1976.</td>
</tr>
<tr>
<td><strong>Tremella acaciae</strong> Olive</td>
<td>S. subvelutina Hauers.</td>
<td>Olive 1958b: yeast-like budding also seen.</td>
</tr>
<tr>
<td>T. boraborensis Olive</td>
<td>S. subvelutina Hauers.</td>
<td>Brefeld 1888 (Tafel VI:27): sub <strong>Gyrocephalus</strong> rufus</td>
</tr>
<tr>
<td><strong>Tulasnellaceae and related groups</strong></td>
<td>S. subvelutina Hauers.</td>
<td>Talbot 1965: see also Rhizoctonia sp.</td>
</tr>
<tr>
<td><strong>Ceratobasidium anceps</strong> (Bres. &amp; Syd.) Jacks.</td>
<td>S. subvelutina Hauers.</td>
<td>Talbot 1965: see also Rhizoctonia sp.</td>
</tr>
<tr>
<td>C. cornigerum (Bourd.) Rogers</td>
<td>S. subvelutina Hauers.</td>
<td>Martin 1939.</td>
</tr>
<tr>
<td>C. obscurum Rogers</td>
<td>C. sublilacina Martin</td>
<td>Christiansen 1959: illus. difficult to interpret.</td>
</tr>
<tr>
<td>C. plumbeum Martin</td>
<td>C. pseudocornigerum Christians.</td>
<td>Warcup &amp; Talbot 1971: see also Rhizoctonia sp.</td>
</tr>
<tr>
<td>C. pseudocornigerum Christians.</td>
<td><strong>Ceratobasidium sp.</strong></td>
<td>Talbot 1965: illus. difficult to interpret.</td>
</tr>
<tr>
<td>Oliveonia fribillosa (Burt) Donk</td>
<td>Oliveonia pauxilla (Jacks.) Donk</td>
<td>Talbot 1965: illus. difficult to interpret.</td>
</tr>
<tr>
<td>Oliveonia pauxilla (Jacks.) Donk</td>
<td><strong>Tulasnella allantospora</strong> Wakef. &amp; Pearson</td>
<td>Christiansen 1959, Rogers 1933, Warcup &amp; Talbot 1971: see also Rhizoctonia sp.</td>
</tr>
<tr>
<td><strong>T. calospora</strong> (Boud.) Juel</td>
<td><strong>T. fusciolaceae</strong> Bres.</td>
<td>Warcup &amp; Talbot 1967: see also Rhizoctonia sp.</td>
</tr>
<tr>
<td>T. griseorubella Litsch.</td>
<td><strong>T. inclusa</strong> (M.P. Christ.) Donk</td>
<td>Rogers 1933.</td>
</tr>
<tr>
<td>T. sphaerospora Martin</td>
<td>T. sphaerospora Martin</td>
<td>Christiansen 1959: illus. difficult to interpret.</td>
</tr>
<tr>
<td>T. violea (Quél.) Bourd. &amp; Galz.</td>
<td>Rogers 1933.</td>
<td></td>
</tr>
<tr>
<td>Rogers 1932: sub T. tulasnei (Pat.) Juel.</td>
<td>Rogers 1933.</td>
<td></td>
</tr>
</tbody>
</table>
Teleomorph | Anamorph | References
--- | --- | ---
Uthatobasidium sp. | Sporobolomyces salmonicolor (Fisch.) & Brebak Kuyver & van Neel | Christiansen 1959.

**BASIDIOMYCETOUS YEASTS**

Aessosporon salmonicolor van der Walt | Sporobolomyces salmonicolor (Fisch.) & Brebak Kuyver & van Neel | van der Walt 1970, von Arx 1974: see also Bandoni, Johri & Reid 1975.
A. dendrophilum van der Walt | Bullera dendrophila van der Walt & Scott | von Arx 1974.

Kobayasi & Tubaki (1965) list the following additional genera as producing conidial ballistospores:

- Bourdotia
- Ductifera
- Eocronartiura
- Heterochaetella
- Heteromyces
- Metaboordotia
- Phyllogloea
- Platycarpa
- Pseudohydnum
- Stypella
- Tremellodendron
- Uredinella
- Xenogloea
- Xenolachne

**Blastic Conidia Arising Singly or in Chains, Often from Pegs on Conidiogenous Cells Borne on Discrete Conidiophores -- Haplotrichum-Type.**

(Figs. 20.1 D,E)

This group is based on known or suspected anamorphs of Botryobasidium species. Many of these anamorphs were treated by Linder (1942) as part of the anamorph-genus Oidium. Unfortunately, many of the taxa placed in Oidium by Linder were not conidial Basidiomycetes, and the anamorph-generic name Oidium has also been applied to the obligately leaf-parasitic anamorphs of Erysiphe and some other powdery mildews. The confusion has been analyzed by Weresub (1973), whose proposal to conserve the name Oidium for anamorphs of the Erysiphales was accepted by the Leningrad Congress (Petersen 1975). Holubová-Jechová (1976) pointed out that this necessitates the adoption of another generic name for the anamorphs of Botryobasidium, and she provided new combinations in Haplotrichum for all such anamorph-species.

Hughes (1953) discriminated two main groups of species within this group: "(1) those in which the conidiophores (often merely repent hyphae) produce vesicles bearing solitary conidia or conidiophores with chains of conidia produced directly upon them, and (2) those in which the conidiophores bear a number of conidia solitary on conspicuous denticles which are not usually restricted to any one cell of the conidiophore, and those cells bearing the denticles are not at all or only slightly swollen." Hughes placed 22 of the species treated
by Linder in the first group, and six in the second group, though he considered that there was no clear line separating the groups. This is a reasonable point of view, because intermediate forms exist, and because both groups, after all, contain anamorphs of the same basidiomycete genus. While noting the morphological heterogeneity of the anamorphs, we will for the present accept Holubová-Jechová's disposition of all the species in one genus, though we have informally grouped the anamorphs into Haplotrichum type (A) and type (B), under appropriately descriptive headings which are similar to, though not congruent with, Hughes's earlier groupings.

Not all species of Botryobasidium have proven anamorphs: B. angustifolium Boidin, B. danicum Erikss. & Hjortst., B. laeve (Erikss.) Parm., B. obtusisporum Erikss., B. pruinatum (Bres.) Erikss. and B. subcoronatum (Höhn. & Litsch.) Donk have not been found with Haplotrichum morphs. See Eriksson & Ryvarden 1973. Holubová-Jechová did not think that Oidium lanosum (Cooke) Linder, O. pulvaceum (Ellis) Linder, and O. ramosum (Fuckel) Hughes, were likely to have teleomorphs in Botryobasidium or related genera.

Some of the species included in Oidium by Linder have rather swollen, almost vesiculose conidiogenous cells, and are transitional to the recently described Spiniger Stalpers. These are listed under the Spiniger-type anamorphs.

The chains of swollen cells found in several quite different groups of Basidiomycetes, e.g., Peilocybe spp. (Agaricales: Heim & Wasson 1959); Basidiomycetum radula (Fr.) Nobles and Cryptosporum volvatus (Peck) Shear (Aphyllophorales: Nobles 1948, 1967); Tulasnella spp., Sebacina vermiculosa Oberwinkler and Ceratobasidium sphaerosporum Warcup & Talbot (Hymenomycetous Heterobasidiae: Warcup & Talbot 1967, 1971; also see Watling, Chapter 19), although superficially similar to Haplotrichum spp., have not been shown to be diasporic and therefore lie outside the scope of this account.

Graphiola thaxteri E. Fisch. superficially resembles a 'Haplotrichum' and has been termed 'Cladosporium-like' by Tubaki (1958), but since it is not clear whether this fungus is a Hyphomycete (fide Hughes 1953, Kendrick & Carmichael 1973) or one of the Ustomycota (Endomycetes fide Kreisel 1969) we do not consider it here: see Donk (1973).

(3A) HOLOBLASTIC CONIDIA USUALLY ARISING SINGLY ON PEGS OR DENTICLES AT VARIOUS POINTS ON CONIDIogenous CELLS - HAPLOTrichum-TYPE (A)

**Teleomorph**

**Anamorph**


* Linder gave Olpitrichum Atk. as a synonym of Oidium Link ex. Fr., but we consider Olpitrichum a good genus; Oidium macrosporum (Farlow) Linder = Olpitrichum macrosporum (Farlow) Sumstine 1911. Holubová-Jechová (1974) has revised the genus Olpitrichum on the unusual configuration of the denticles; Oidium tenellum (B. & C.) Linder is considered to belong to Olpitrichum. Botrytis moniliformis Penz. & Sacc. (Icones Fung. Javanicum 1904) would appear to belong to this group.

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<table>
<thead>
<tr>
<th>Teleomorph</th>
<th>Anamorph</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Haplotrichum linderi Hol.-Jech.</td>
<td>Haplotrichum linderi Hol.-Jech.</td>
<td>Linder 1942: this is Oidium elongatum Link non Haplotrichum elongatum (Fr.) Bon.</td>
</tr>
<tr>
<td>Haplotrichum tenerum (Sumst.) Hol.-Jech.</td>
<td>Haplotrichum tenerum (Sumst.) Hol.-Jech.</td>
<td>Linder 1942.</td>
</tr>
</tbody>
</table>

**HYMENOMYCETES**

**Aphyllophorales**

**Botryobasidium conspersum Erikss.**


**Botryobasidium ellipsosporum Hol.-Jech.**


**Botryobasidium robustior Pouzar & Hol.-Jech.**

| Haplotrichum rubiginosum (Fr.) Hol.-Jech. | Haplotrichum rubiginosum (Fr.) Hol.-Jech. | Pouzar & Holubová-Jechová 1967: type species of Physospora Fr.: also known as Sporotrichum rubiginosum Fr. |

**Botryobasidium vagum (B. & C.) Rogers**


**Botryobasidium sp.**

(3B) HOLOBLASTIC CONIDIA IN UNBRANCHED OR BRANCHED ACROPETAL CHAINS -- HAPLOTRICHUM-TYPE (B)

<table>
<thead>
<tr>
<th>Teleomorph</th>
<th>Anamorph</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>UNKNOWN BASIDIOMYCETES</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Haplotrichum pulchrum (Berk.)</td>
<td>Linder</td>
<td>Linder 1942; Linder compares this with O. vesiculosum (see below).</td>
</tr>
</tbody>
</table>

HYMENOMYCETES

Aphyllophorales

<table>
<thead>
<tr>
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</thead>
<tbody>
<tr>
<td>Botryobasidium sp.</td>
<td>'Oidium' sp. (cf. capitatum (Link) Link)</td>
<td>Eriksson &amp; Ryvarden 1973: (=Christiansen No. 52).</td>
</tr>
<tr>
<td>Flagelloscypha abruptiflagellata Agerer</td>
<td></td>
<td>Agerer 1975: also forms conidia sympodially.</td>
</tr>
</tbody>
</table>

(4) BLASTIC-SYNCHRONOUS CONIDIA FORMED ON AMPULLIFORM CONIDIOPHORE APICES -- SPINIGER-TYPE (Fig. 20.1 F)

The hyphomycete genus Oedoeaeohalum is easily recognized by its simple, determinate, hyaline, septate conidiophores producing many single, more or less synchronous, blastic, hyaline, amoenoconidia on denticles distributed more or less evenly over the surface of a single swollen, terminal vesicle or ampulla. The type species of the genus, O. glomerulosum (Bull.) Sacc., has no known teleomorph, but several species have been connected with discomycetes, including Pyronema omphalodes (Bull. ex St. Amans) Fuckel, Peziza praetervisa Bres., and Peziza anthraeaphila Dennis (= P. echinospora Karst.). Hughes (1971) believed that the homobasidiomycetous anamorphs reported herein could be differentiated from the ascomycetous
Fig. 20.8 A conidiophore apex of the *Spiniger meineckellus* anamorph of *Heterobasidion annosum* (Courtesy J. Stalpers)
analogues by their longer, tapering conidiogenous denticles. The generic name *Spiniger* has recently been proposed for these basidiomycetous anamorphs by Stalpers (1974).

Cook (1977) has recently compared the oedocephaloid conidiophore and the development of conidia in *Cunninghamella echinulata* Thaxter (Zygomycetes) and *Heterobasidion annosum* (Fr.) Bref. (Basidiomycetes). Bakshi (1952) considered *Oedocephalum lineatum* Bakshi to be the anamorph of *H. annosum*, though Findlay (1952), and not Bakshi, established the connection. Earlier, the conidial anamorph of *H. annosum* had been named *Cunninghamella meinekellia* by Olson (1941) according to Donk (1971), and Stalpers (1974) found that the type material did indeed consist of a fungus similar in all ways to *Oedocephalum lineatum*. *Vararia* spp. with globose to ellipsoid basidiospores appear to be typified by an oedocephaloid anamorph best situated in *Spiniger*.

*Bondarzewia* is an isolated genus within its own family Bondarzewiaceae in the Aphyllophorales, but it, too, has an oedocephaloid anamorph (Nobles 1965).

The production of conidia in the genus *Jacobia* Arnaud nomen nudum (1951) has some similarity with the *Spiniger*-type. Blastic-synchronous conidia appear to be recorded among the Basidiomycetes only in members of the Aphyllophorales.

### (4) BLASTIC SYNCHRONOUS CONIDIA - SPINIGER-TYPE

<table>
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<tr>
<td><strong>UNKNOWN BASIDIOMYCETES?</strong></td>
<td>Oidium lanosum (Cke.) Linder</td>
</tr>
<tr>
<td></td>
<td>Oidium tenellum (B. &amp; C.) Linder</td>
</tr>
<tr>
<td><strong>HYMENOMYCETES</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Aphyllophorales</strong></td>
<td></td>
</tr>
<tr>
<td>Asterostromella dura Bourd. &amp; Galz.</td>
<td><em>Spiniger</em> sp.</td>
</tr>
<tr>
<td>Bondarzewia berkeleyi (Fr.) Bond. &amp; Sing.</td>
<td><em>Spiniger</em> sp.</td>
</tr>
<tr>
<td><em>Heterobasidion annosum</em> (Fr.) Bref.</td>
<td><em>Spiniger</em> meinekellum (Olson) Stalpers</td>
</tr>
<tr>
<td>H. insulare (Murr.) Ryv.</td>
<td><em>Spiniger</em> sp.</td>
</tr>
<tr>
<td>Laurilia sulcata (Burt) Pouz.</td>
<td><em>Spiniger</em> sp.</td>
</tr>
<tr>
<td>Mutatoderma brunneocortexum Gomez</td>
<td><em>Spiniger</em> sp.</td>
</tr>
<tr>
<td>M. heterocystidium (Burt) Gomez</td>
<td><em>Spiniger</em> sp.</td>
</tr>
<tr>
<td>M. mutatum (Peck) Gomez</td>
<td><em>Spiniger</em> sp.</td>
</tr>
<tr>
<td>Resinicium furfuraceum (Bres.) Parm.</td>
<td><em>Spiniger</em> sp.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stalpers 1974.</td>
</tr>
<tr>
<td>Stalpers 1974.</td>
</tr>
<tr>
<td>Stalpers 1978.</td>
</tr>
</tbody>
</table>
Teleomorph | Anamorph | References
---|---|---
V. granulosa (Fr.) Laurila | Spiniger sp. |  
V. pallescens (Schw.) Rog. & Jacks. | Spiniger sp. |  
V. ramulosa Boid. & Lanqu. | Spiniger sp. |  
V. rhodospora (Wakef.) Cunn. | Spiniger sp. |  

(BLASTIC * SYNCHRONOUS CONIDIA -- CHROMEOSPORIUM-TYPE)

Brefeld (1889) reported 'connections' between Botryohypochnus isabellinus (Fr.) J. Erikss. (sub Tomentella flava) and Chromelosporium carneum (Pers.) Henneb. (sub Botrytis argillacea), and between 'Hypochnus' brefeldii Sacc. (sub Tomentella granulata) and Chromelosporium tuberculatum (Pers.) Henneb. (sub Botrytis epigaea), because they were closely associated on the natural substrate, and because their spores were morphologically similar. This connection has not subsequently been confirmed. Litschauer (1928) doubted its accuracy, and Donk (1962b) concluded that Brefeld had been mistaken; Brefeld did not see the connection himself, but the illustrations for Tafel I were taken from his student Johan-Olsen. Although von Höhnel (1907) also connected Botryohypochnus isabellinus with C. ochraceum Corda (as Botrysis isabellinus Pers.) and Tomentella fusca with C. carneum (as Botrytis carneum Schum.) it is now thought that the known telemorphs of Chromelosporium species are all operculate discomycetes of the genus Peziza sensu lato (Hennebert 1973). Thus the only holoblastic-synchronous conidiogenesis known in Basidiomycetes is that classified in the anamorph-genus Spiniger, and dealt with in the preceding section.

Baniecki & Bloss (1969) claim to have connected Stiatotrema brinomannii (Bres.) Erikss. with Phymatotrichum omnivorum (Shear) Duggar, but this is questionable.

Zygoceassus Corda (type species, Z. hypochmoideis Corda) has been applied to very different fungi, especially several Tomentella spp. which have been confused because of a superficial similarity, with Z. fusus Corda, an epithet published some years after 1837 (Z. fusus = Tomentella biennis (Fr.) A.M. Rog. & D.P. Rog.). This confusion has extended the problem outlined under Chromelosporium.

We conclude that Chromelosporium-type conidiophores have not yet been recorded among the Basidiomycetes.

(5) BLASTIC CONIDIA IN UNBRANCHED OR BRANCED ACROPETAL CHAINS IN THE ABSENCE OF DISCRETE CONIDIOPHORES -- YEAST-LIKE BUDDING (Fig. 20.1 G)

This method of producing a multiplicity of conidia is really a pulsed modification of normal hyphal growth, in which Kendrick (1971) has postulated that as extension growth proceeds, the rate of wall setting accelerates and decelerates in a regular sequence: it may temporarily cease altogether during the blowing out of each spherical bud. This method of conidiogenesis is common among the hymenomycetous Heterobasidiae, and is, of course, regular procedure in
the basidiomycetous yeasts, where the difference between a normal vegetative cell and a mitospore has become blurred to the point of irrelevance.

Species of Tremella seem to be very uniform in their conidial anamorphs. Some Cryptococcus spp. may possibly be derived from Tremella (Aitken, Nielands & Phaff 1970). Bandoni & Bisalputra (1970) have carried out electron-microscope studies on budding in T. mesenterica. Several micro-Tremella spp. (see Donk 1966) are characterized by conidial anamorphs involving a modified clamp-connection, but the true position of these is somewhat in doubt.

Laetiiortiaium simplioibasidium Lindsey & Gilbertson is unique in that the basidium is considerably reduced, and the basidiospores germinate by repetition. The result is almost yeast-like and in some ways resembles the monilioid hyphae of Moniliopsis (Lindsey & Gilbertson 1977).

Aitken, Nielands & Phaff (1970) have carried out analyses of ferrochromes and rhodotorulic acids in various yeasts, and suggested connections between certain yeasts and various Heterobasidiae based on these clinical studies.

(5) HOLOBLASTIC CONIDIA IN BRANCHED OR UNBRANCHED ACROPETAL CHAINS - YEAST-LIKE BUDDING

<table>
<thead>
<tr>
<th>Teleomorph</th>
<th>Anamorph</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>HYMENOMYCETOUS HETEROBASIDIAE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Auriculariales</td>
<td></td>
<td></td>
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<tr>
<td>Mycogloea carnosa Olive</td>
<td></td>
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</tr>
<tr>
<td>Tjibodasia Holterm. (=Platygloea Schroet. fide Martin)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Septobasidiales</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Septobasidium westonii Couch</td>
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<td></td>
</tr>
<tr>
<td>Tremellales</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Holtermannia corniformis Sacc.</td>
<td></td>
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<tr>
<td>S. magnum Boed.</td>
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<tr>
<td>S. sanguineum Lag. &amp; Pat.</td>
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<tr>
<td>Sirobasidium brefeldianum Møller</td>
<td>Cryptococcus diffluens (Zach)</td>
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<tr>
<td></td>
<td>Lodder &amp; Kreger-van Rij</td>
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<tr>
<td>Tremella boraborensis Olive</td>
<td>Hormomycoses aurantiacus Bon.</td>
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<tr>
<td></td>
<td>(=Sphaerocolla aurantiaca Karst.)</td>
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</tbody>
</table>

Olive 1950, Kobayasi & Tubaki 1965.
Kobayasi & Tubaki 1965, Bandoni 1956.
Couch 1938.
Kobayasi & Tubaki 1965.
Olive 1947.
Kobayasi 1962.
Flegel 1976: the anamorph is compared with Bullera and Cryptococcus.
Martin 1936.
Olive 1958b.
Brefeld 1888 (Tafel VIII:20-24); Donk 1966.
Kobayasi & Tubaki 1965.
Brefeld 1888 (Tafel VIII:14-19); Donk 1966.

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Teleomorph | Anamorph | References
---|---|---
T. virescens (Schum. ex Fr.) Bref. | | Brefeld 1888 (Tafel VIII:25-28); Donk 1966.
Xenolachne Rogers | | Rogers 1947; Kobayasi & Tubaki 1965.

BASIDIOMYCETOUS YEASTS

Chionosphaera apobasidialis Cox
Filobasidiella neoformans Kwon-Chung
Filobasidium floriforme Olive
F. capsuligenum (Fell et al.) Rod. de Miranda

Cryptococcus neoformans (Sanf.) Buill.
Torulopsis capsuligenum van der Walt & van Kerken
Sterigmatomyces halophilus Fell
Trichosporon beigelii (Küh. & Rabenh.) Buill.
Trichosporonoides oedocephalis Haskins & Spencer

Cox 1976.
Olive 1968.
Rod. de Miranda 1972.
Fell 1966: possibly not a basidiomycete.
de Carmo Sousa 1970: Aciculoconidium and Sarcinosporon are segregate genera of unknown affinity.
Haskins & Spencer 1967.

The following are better placed in the Ustilaginales:

Leuocosporidium scottii Fell et al. (anamorph: Candida scottii Diddens & Lodder): Rhodosporidium toruloides Banno (anamorph: Rhodotorula glutinis (Fres.) Harrison), R. sphaericarpum Newell & Fell (anamorph: Rhodotorula glutinis (Fres.) Harrison 'marine strains'). Rhodosporidium has been studied at some length by Fell, Hunter & Tallman (1973) who accepted seven species.
(6) BLASTIC-SYMPODIAL CONIDIA (Fig. 20.2 A-F)

Each individual blastic-sympodial conidium develops by a 'blowing out' of all wall layers of the parent cell. The feature that separates this ontogenetic grouping from other blastic types is the serial formation of a plurality of conidia during sympodial proliferation of the conidiogenous cell.

In the Basidiomycetes, this kind of conidium ontogeny is found among the Uredinales and both the hymenomycetous Heterobasidiae and hymenomycetous Homobasidiae. The manner in which the phenomenon is displayed ranges from the highly characteristic, branched conidiogenous apparatus borne at the apex of an upright conidiophore stipe in the Ditangium anamorph of Craterocolla cerasi (Tul.) Bref. (Fig. 20.2 D) to the clusters of conidia formed on short outgrowths from basidiospore cells in Exidia saccharina Alb. & Schw. ex Fr. (Fig. 20.2 B) and many other Heterobasidiomycetes.

In the first section of the table which follows, the key numbers given designate the kinds of structure on which conidia are borne.

1 = conidia on sympodially proliferating outgrowths from basidiospores.
2 = conidia on sympodially proliferating vegetative hyphae.
3 = conidia on sympodially proliferating cells borne on recognizable conidiophores.

The examples of sympodial conidia in the Uredinales illustrated in the literature have been discussed by Hughes (1970) and include Chaconia butleri (Syd.) Mains, Cystopeora oleae Butler, Gymnosporangium sabinæ (Dicks.) Wint. and Puccinia helianthi Schw. in teliospores; Cronartium ribicola J.C. Fisch., Gymnosporangium gaumannii Zagg, Hyalopectora aspidiotus (Peck.) Magn. and Melampsora lini (Schum) Lév. in urediniospores; and Phragmidium rubi (Pers.) Wint. in both uredinio- and telio-spores. There is no doubt that the list could be expanded considerably, and recent authors have found sympodial development in Cronartium fusiforme Cunn. (Eleuterius 1967), Hyalopectora polyopii (Diet.) Magn. (McGinnis 1977), Puccinia coronata Corda (f. sp. avenae: Harder 1976), P. graminis Pers. (Bole & Parsons 1973) and P. penniseti Zimm. (Kulkarni 1958), Uromyces appendiculatus (Pers.) Unger (Müller et al. 1974) and U. phaseoli Wint. (Bole & Parsons 1973) in urediniospores; and Gymnosporangium juniperi-virginianæ Schw. (Mims 1977), Kuhneola japonica (Diet.) Dietel (Kohno et al. 1977), Puccinia coronata Corda (f. sp. avenae: Harder 1977), P. malvacearum Mont. (Allen 1933), P. penniseti Zimm. (Kulkarni 1958) and P. sorgii Schw. (Rijkenberg 1977) in teliospores. For these references we are grateful to A.P. Bennell, Edinburgh, who from his own observations has added Puccinia emyrtii Biv-Bernh. and Transschelica anemones (Pers.) Nannf. to the list.

The anamorph-genus Costantinella has been suggested to have basidiomycetous affinities (Eriksson & Hjortstam 1969), but conflicting claims have been made for the Ascomycetes, especially the Morchellaceae (Molliard 1904a,b, Costantin 1936). For Costantinella athrix Nannf. & Erikss. and C. tilletei (Desm.) Mason & Hughes, see Nannfeldt & Eriksson (1952); and for C. terrestris (Link ex Fr.) Hughes and C. micheneri (B. & C.) Hughes, see Eriksson & Hjortstam (1969).

Rhinitrichum decipiens Cke. was considered to have basidiomycetous affinity by Bisby (1944).
Fig. 20.9 The blastic-sympodial anamorph of *Sistotrema raduloides* (Courtesy J. Stalpers)
Phleogena faginea (Fr. ex Fr.) Link has been accepted as a member of the Heterobasidiomycetes for almost a century (Brefeld 1888) but lacks repeating basidiospores (ballistospores); Shear & Dodge (1925) compare the anamorph with Rhinotrichum, and it is interesting to note that Linder (1942) also discussed this taxon in his paper on Oidium. The anamorph of *P. faginea* is certainly very different from that of any other member of the hymenomycetous Heterobasidiae so far studied, and has been compared by Shear & Dodge (1925) with the Protogasteromycetes. To us it has some morphological similarities with *Nodulisporium*, a form-genus usually connected with the ascomycetous family Xylariaceae. Barr & Bigelow (1968) have shown that *Martindalia epironema* is nothing more than *Phleogena faginea*.

Brefeld (1888) illustrated a conidial fungus which he thought was the anamorph of *Sebacina inarustans*. Arnaud (1951) gave this anamorph the (invalid) name *Flahaultia hyalina*, but considered that it was probably a separate fungus parasitic on the *Sebacina*. Several parasitic hymenomycetous Heterobasidiae are now known to grow in the hymenium of other Basidiomycetes; a careful reappraisal is required.

In *Exobasidium* the primary conidial bud apically and mimic holoblastic acropetal chains (q.v.). Sundström (1964) was able to indicate the presence of a contaminant fungus by discrepancies in morphology of the conidial products. The name *Fusidium vaqoinii* Fuckel has been incorrectly applied to several species of *Exobasidium* (see Donk 1966).

*Sistotrema* is close to some of the fungi placed in the hymenomycetous Heterobasidiae (Donk 1966) and might be expected to have similar anamorphs as shown in the tables (see Talbot 1965).

*Eohinodia* is a strange, pseudosympodial form in which each conidium arises from just below the apex of the last. The resulting chains are in some ways reminiscent of the disarticulating clamped hyphae found in *Collybia racemosa* (Pers. ex Fr.) Quéi. and *Pleurotus cystidiosus* O.K. Miller, and of the acropetal chains produced by some *Haplotrichum* anamorphs of *Botryobasidium*.

(6) BLASTIC-SYMPODIAL CONIDIA

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<thead>
<tr>
<th>Teleomorph</th>
<th>Anamorph</th>
<th>References</th>
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<tbody>
<tr>
<td><strong>HYMENOMYCETES</strong></td>
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<tr>
<td>Agaricales</td>
<td></td>
<td></td>
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<tr>
<td>Baeospora myosura (Fr.) Sing.</td>
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<td></td>
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<tr>
<td>Aphyllophorales</td>
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<tr>
<td>Flagelloscypha abruptiflagellata Agerer</td>
<td></td>
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</tr>
<tr>
<td>Hyphodontia alutacea (Fr.) J. Erikss.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paullicorticium niveo-cremeum (Höhn. &amp; Litsch.) Oberw.</td>
<td></td>
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<td></td>
<td></td>
<td>Redhead pers. comm.: in culture only</td>
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<tr>
<td></td>
<td></td>
<td>Agerer 1975: conidia develop on apical extensions of marginal hairs &amp; may be 1-septate: also forms blastic conidia in acropetal chains</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lyman 1907: sub Corticium.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Boidin 1958: sub Corticium: also forms thallic-arthric conidia.</td>
</tr>
</tbody>
</table>
Teleomorph                                      Anamorph                                      References
Polyporus hydrophorus B. & Br.                2 Echinodia theobromae Pat.                   Patouillard 1918, Donk 1962: an earlier name for this fungus would appear to be Ceriomyces borgoriensis Holterm.

Ramaria? flaccida (Fr.) Ricken.
Sistotrema brinkmannii (Bres.)                 3                                             Talbot pers. comm.
J. Erikss.
S. raduloides (Karst.) Donk                    3                                             Biggs 1937: sub Corticium coronilla.

Typhula athryii Remsb.
T. culmigena (Mont. & Fr.) Berth.              2                                             Maxwell 1954: sub Trechispora; also forms thalic-arthric conidia and sclerotia.
T. itoana Imai
T. lutescens Boud.
T. micans (Pers. ex Fr.) Berth.
T. quisquiliaris (Fr.) Corner
T. trifolii Rostr.
T. uncialis (Grev.) Berth.
T. variabilis Riess

HYMENOMYCETOUS HETEROBASIDIAE

Auriculariales

Auricularia mesenterica (Dicks. ex S.F. Gray) Pers. 1
Cystobasidium sebaceum Martin & Couch 1
Hirneola auricula-judae (Bull. ex St. Amans) Berk. 1,2,3
Phleogena faginea (Fr. ex Fr.) Link 2
Platygloea abdita Band. 3

Dacrymycetales

Calocera cornea (Batsch ex Fr.) Fr. 1
C. glossoides (Pers. ex Fr.) Fr. 1
C. pallido-spathulata Reid 1
C. viscosa (Pers. ex Fr.) Fr. 1,2
Dacrymyces estonicus Raitvir 1
D. lacrymalis (Pers. ex S.F. Gray) Sommerf. 1,2
D. ovisporus Bref. 1,2

References

Brefeld 1888 (Tafel IV:10-11): also forms solitary holoblastic conidia on denticles.
Martin 1939b.
Brefeld 1888 (Tafel IV:3-9): sub Auricularia sambucina; also forms solitary holoblastic conidia on denticles.
Brefeld 1888 (Tafel I-III): sub Pilacre petersii.
Bandoni 1959.
Brefeld 1888 (Tafel XI:14-17): also forms blastic solitary conidia on denticles.
Brefeld 1888 (Tafel XI:1-2): sub Dacrymyctra: also forms blastic solitary conidia on denticles.
Reid 1974a: also forms blastic solitary conidia on denticles.
Brefeld 1888 (Tafel XII:6-13): also forms blastic solitary conidia on denticles.
Brefeld 1888 (Tafel X:2-17): sub Dacrymyces chrysocomus; also forms blastic solitary conidia on denticles.
Brefeld 1888 (Tafel X:4-8): sub Dacrymyces cerebriformis & D. lutescens; also forms blastic solitary conidia on denticles.
Brefeld 1888 (Tafel X:20-21) : also forms blastic solitary conidia on denticles.
<table>
<thead>
<tr>
<th>Teleomorph</th>
<th>Anamorph</th>
<th>References</th>
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</thead>
<tbody>
<tr>
<td>D. stillatus Nees ex Fr.</td>
<td>1,2</td>
<td>Reid 1974: see also Brefeld 1888 (Tafel IX): thalic-arthric conidia also formed.</td>
</tr>
<tr>
<td>Dicelomyces scirpi Raitv. apud Parm.</td>
<td>1</td>
<td>Reid 1976.</td>
</tr>
<tr>
<td>Ditiola pezizaemis (Lév.) Reid</td>
<td>1,2</td>
<td>Brefeld 1888 (Tafel X:3-5): sub Guepinia femsjoniana; also forms blastic solitary conidia on denticles.</td>
</tr>
<tr>
<td>Guepinopsis chrysocoma (Bull. ex St. Amans) Brasf.</td>
<td>1,2</td>
<td>Brefeld 1888 (Tafel X:18-19): sub Dacrymyces longisporus Bref.</td>
</tr>
</tbody>
</table>

### Exobasidiales

| Exobasidium camelliae Shir.                    | 2        | Reid 1969.                                                               |
| Exobasidium scirpi Peck                        | 2        | Sundström 1964.                                                         |
| E. japonicum Shir.                             | 2        | Sundström 1964.                                                         |
| E. karstenii Sacc. & Trott.                    | 1        | Sundström 1964.                                                         |
| E. myrtilli Siegm.                             | 2        | Sundström 1964.                                                         |
| E. oxycocci Rostr.                             | 1        | Sundström 1964.                                                         |
| E. uvae ursi (Maire) Juel                      | 1        | Sundström 1964.                                                         |
| E. vaccinii (Fuckel) Woron.                    | 1,2      | Sundström 1964.                                                         |
| E. vaccinii-uliginosi Boud. apud Boud.          | 1        | |
| & E. Fisch.                                    |          |                                                                           |

### Tremellales

| Craterocolla cerasi (Tul.) Bref.                | 3        | Brefeld 1888 (Tafel XI:9-21): also known as D. cerasi (Schum. s. Tul.) Const. Nag Raj 1978. |
| Exidia glandulosa (Bull. ex St. Amans) Fr.      | 1        | Brefeld 1888 (Tafel IV:2-4).                                             |
| E. guttata Bref.                                |          | Brefeld 1888 (Tafel V:12-13):; not accepted as a true Exidia by Donk 1966. |
| E. plana (Wigg. ex Schleich.) Donk              | 1        | Brefeld 1888 (Tafel V:5): sub E. plicata.                                |
| E. saccharina Alb. & Schw. ex Fr.               | 1,2      | Brefeld 1888 (Tafel VI:1-8): sub Tremella [Ulocolla] foliacea.           |
| Myxarium hyalinum (Pers.) Donk                  | 1        | Brefeld 1888 (Tafel V:14): sub Exidia albida.                            |
| Sebacina effusa (Bref. ex Sacc.) Pat.           | 1        | Brefeld 1888 (Tafel V:20-22): sub Exidiopsis.                            |
| S. incarnatus (Pers. ex Fr.) Tul.               |          | Brefeld 1888 (Tafel VI:22-26): also forms blastic solitary conidia on denticles. |
| T. polyporina Reid                              | 2        | Koske 1972.                                                              |
| T. translucens Gordon                           | 2        | Gordon 1938.                                                            |
| Tulasnella violea (Quél.) Bourd.                |          | Rogers 1932.                                                            |
| § Galz.                                        |          |                                                                           |

In addition to the hymenomycetous Heterobasidiae in the above table, Kobayasi & Tubaki (1965) list the following genera with blastic-symposial conidiogenesis: Arrhytidia, Bourdotia, Daomyoterra, Daorygina, Daorypinax, Ezidiopsis, Helioogloea, Herpobasidium, Holtermannia, Myoogloea, Sirobasidium, Tremellodendron. These authors also suggest that blastic-symposial conidia may be found in the Septobasidiales.
Many Hyphomycetes and Coelomycetes produce annellidic conidia, but only five examples of this kind of conidiogenesis have been discovered among the Basidiomycetes; they are so far restricted to the vegetative phases of members of the Clavariaceae, have been found only in culture, and have not been named. Rijkenberg & Truter (1974) have recently re-examined the production of spermatia in rusts, and suggested that these are annellidic in at least two species, Gymnosporangium clavatiforme Rees and Puacinia sorghi Schw. We find their illustrations ambiguous and unconvincing. See Phialoconidia.

### References

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<th>Teleomorph</th>
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<td>HYMENOMYCETES</td>
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<tr>
<td>Aphyllophorales</td>
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<tr>
<td>Macrotypula fistulosa (Fr.) Petersen</td>
<td>Berthier 1976.</td>
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<tr>
<td>M. tremula Berthier</td>
<td>Berthier 1976.</td>
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<tr>
<td>T. micans (Fr.) Berthier</td>
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<td>Berthier 1976.</td>
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<tr>
<td>T. (groupe) setipes (Grev.) Berthier</td>
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### (8) BLASTIC-PHIALIDIC CONIDIA (PHIALOCONIDIA) (Fig. 20.3 B,C)

PHIALIDIC - A mode of blastic conidium ontogeny in which the conidia are clad in an entirely new wall, which is not derived from any existing layers of the wall of the conidiogenous cell. A basipetal succession of conidia is formed from a fixed conidiogenous locus (Kendrick 1971).

Hughes (1970b, 1971a), using his opinion on observations by Olive (1944), concluded that the spermatia (pycniospores) of Gymnosporangium clavipes (Cke. & Peck) Cke. & Peck are phialoconidia, and that rust spermatia are probably the only examples of phialidic ontogeny found among the Basidiomycetes. Rijkenberg & Truter (1974) made transmission electron microscope studies of spermatium formation in Puacinia sorghi Schw. and considered it to be basically annellidic rather than phialidic. Unfortunately, their electron micrographs are not particularly informative, and we cannot confirm their claim. They adduce other 'evidence' from the literature in favour of their conclusion: they mention the account of spermatium formation in Gymnosporangium clavatiforme Rees by Blackman (1904) which mentions a 'curious ring of thickening' and a 'collar' on the spermatiophores. They claim that these are probably 'annellation zones'. But since they concede that the spermatia all secede at the same level, and since we know that wall material builds up inside the neck of many small phialides (Subramanian 1971, Figs. 7.2, 7.3, 7.4) we are inclined to doubt whether the matter has been settled as conclusively as Rijkenberg & Truter seem to think, particularly as more recent work by Mims, Seabury & Thurston (1976) clearly indicates phialides in G. juniperi-virginiana Schw. In any case, there is considerable developmental similarity between certain phialides and certain annellides, and the question of the degree to which they differ...
has still to be resolved (see Morgan-Jones, Nag Raj & Kendrick 1972).

We have found a number of additional reports of what we take to be phialides in the Hymenomycetous Heterobasidiae. The conidial anamorph of *Helicobasidium brebissonii* (Desm.) Donk, a *Tuberculina* species, is at present interpreted as being phialidic, and Olive (1958b) reported several other taxa in the same group with suspiciously phialide-like conidiogenous cells. These observations should now be carefully repeated.

Coles & Talbot (1977) have clearly shown the presence of mono- and poly-phialidic conidia in *Septobasidium*.

It is interesting to note that within the Basidiomycetes the phialidic conidium has as yet been recorded only from those fungi producing either a septate basidium or a typical 'Daarymyces' tuning-fork basidium.

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<th>Teleomorph</th>
<th>Anamorph</th>
<th>References</th>
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<tr>
<td><strong>HYMENOMYCETOUS HETEROBASIDIAE</strong></td>
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<tr>
<td>Auriculariales</td>
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</tr>
<tr>
<td><em>Helicobasidium brebissonii</em> (Desm.) Donk</td>
<td><em>Tuberculina sp.</em></td>
<td>Buddin &amp; Wakefield 1927: also produces sclerotoid hyphal aggregates (Rhizoctonia crocorum): see Donk 1966.</td>
</tr>
<tr>
<td>Dacrymycetales</td>
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<tr>
<td>Arrhytidia lagerhei (Pat.) Olive</td>
<td><em>Harpographium corynelioides</em></td>
<td>Coles &amp; Talbot 1977.</td>
</tr>
<tr>
<td>Septobasidiales</td>
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<td></td>
</tr>
<tr>
<td><em>Septobasidium clelandii</em> Couch</td>
<td><em>Harpographium corynelioides</em></td>
<td>Coles &amp; Talbot 1977.</td>
</tr>
<tr>
<td>Tremellales</td>
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<tr>
<td><em>Tremella carnealba</em> Coker</td>
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<tr>
<td>T. rubromaculata Lowy</td>
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<tr>
<td><strong>UREDINALES</strong></td>
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<td></td>
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<tr>
<td><em>G. juniperi-virginianae</em> Schw.</td>
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</table>
Meristem conidiogenesis was defined by the Kananaskis-I Conference as a mode of thallic ontogeny in which there is a continuous retrogressive conversion of an indeterminate conidiophore whose apical region is continuously extending. There is a linear series of cytoplasmically connected conidia maturing concurrently, the distal conidium being the most mature, the proximal conidium hardly yet differentiated from the cells of the conidiophore (Kendrick 1971).

This phenomenon apparently occurs in the aecia of Uredinales -- Hughes (1970b) re-draws figures of five rusts to illustrate this -- but is almost entirely absent elsewhere in the Basidiomycetes as far as we can tell. If the data presented here may be extrapolated to include all Coleosporium, Cronartium and Peridermium species, we can add about 125 species to our list. If the aecia of all species of Puccinia and Uromyces are also included, the total rises by several hundred.

Wright (1960), in his observations on Phaeotrametes decipiens (Berk.) Wright, described: "chlamydospores formed in a manner reminiscent of aeciospore production", but his illustrations cannot be regarded as convincing evidence for this conclusion. One of us (RW) has examined Australian material of this species and considers the propagules in question to be routine chlamydospores. If these spores were in fact thallic-meristem conidia, they would be unique among the Aphyllophorales. This anamorph is of interest chiefly because of the splash-cup fructification in which the spores form (see also section 14D of this chapter). The splash-cup, although found in such diverse groups as Marchantiales (Hepaticae), Tetraphidales (Musci), and Nidulariales (Gasteromycetes) (see also Minniea cannea), is nevertheless rare and noteworthy. Within the Aphyllophorales compare the genus Poronidutus Murrill, based on Polyporus conchifer (Schw.) Fr., although the cups in that case apparently remain sterile.

### (9) THALLIC-MERISTEM CONIDIA

<table>
<thead>
<tr>
<th>Teleomorph</th>
<th>Aeciospores</th>
<th>Teliospores</th>
<th>Chlamydospores</th>
<th>References</th>
</tr>
</thead>
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<tr>
<td>HYMENOMYCETES</td>
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<tr>
<td>Aphyllophorales</td>
<td></td>
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</tr>
<tr>
<td>Phaeotrametes decipiens (Berk.) Wright</td>
<td>x</td>
<td></td>
<td></td>
<td>Wright 1966: in specialized cups: may be chlamydospores.</td>
</tr>
<tr>
<td>UREDINALES</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Cronartium ribicola J.C. Fisch.</td>
<td>x</td>
<td></td>
<td></td>
<td>Hughes 1970b: redrawn from Colley 1918.</td>
</tr>
<tr>
<td>Didymopsora paraguayensis (Speg.) Cunn.</td>
<td></td>
<td>x</td>
<td></td>
<td>Hughes 1970b: redrawn from Cunningham 1968.</td>
</tr>
<tr>
<td>Peridermium pini (Willd.) Kleb.</td>
<td>x</td>
<td></td>
<td></td>
<td>Hughes 1970b: redrawn from Sappin-Trouffy 1896.</td>
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</tbody>
</table>
At least in theory, this is one of the simplest ways to produce conidia -- an existing hypha disarticulating at the septa. This assumes that the septa are of double-walled construction and that an abscission layer between the two walls lyses to liberate the conidia. This basic pattern is exhibited by *Geotrichum candidum* and by many agarics. Of course, the phenomenon is not always present in the simplest form, and several variations on the theme were explored by Cole & Kendrick (1969), Kendrick (1971:160-168), Kendrick & Chang (1971), Hashmi, Morgan-Jones & Kendrick (1972), and Cole (1976).

The definitions accepted by the Kananaskis-I Conference are as follows:

**THALLIC:** one of the two basic modes of conidium ontogeny; if there is any enlargement of the recognizable conidium initial, it occurs only after the initial has been delimited by a septum or septa. The conidium differentiates from a whole cell.

**arthric:** a form of thallic conidium ontogeny characterized by conversion and disarticulation of a pre-existing determinate hyphal element (i.e., one whose extension growth has ceased). Secession of conidia may be by fission of double septa laid down across the full width of the hypha, or by fracture or lysis of the walls of adjacent, degenerated cells.

We note, however, that these last two methods of release could qualify their propagules for inclusion among the chlamydospores, especially if they were thick-walled.

Basidiomycetous thallic-arthric propagules have often been called oidia, but 'oidium' is a confused term, which we have rejected elsewhere. Such propagules usually function as conidia, but in some cases they are clearly spermatia, though these two different functions are not reflected in differing morphologies. The problem has already been discussed under the appropriate headings in the terminological section of this chapter.

This is one of the most widespread forms of non-basidiosporous propagule in the hymenomycetous Homobasidiaceae, but is apparently rare among hymenomycetous Heterobasidiaceae. Arthroconidia are particularly characteristic of the lignicolous members of the Cortinariaceae and Tricholomataceae.

Thallic-arthric conidia may be dry or slimy, in short or long chains, in fairly complex branched arrangements, or simple disarticulating hyphae. Although it would be very difficult to subdivide this large assemblage into watertight compartments at present, we have noted, wherever our data permitted, the following dichotomies, which may have varying degrees of biological or taxonomic significance: (1) whether the conidia are formed from morphologically undifferentiated vegetative hyphae, or on well-defined fruiting structures such as the conspicuous coremia found in the *Sclerostilbum* state of *Collybia racemosa* (Pers. ex Fr.) Quéıl. (Watling & Kendrick 1977), conidial *Pleurotus cystidiosus*, and the *Nothoclavulina* state of *Arthroporella ditopa* (see Chap. 19); (2) whether the arthroconidia are formed and released simply by the splitting apart of the two layers of a double septum as in *Phlebia*, or as a result of the laying down of retraction septa which often leave empty hyphal segments between the differentiating conidia as in *Coniophora* and *Punctularia strigosossonata* (Schw.) Talbot. Kühner (1977) suggests that these two somewhat different ontogenies may be associated respectively with white- and dark-spored agarics. This suggestion has been fully supported by our own observations (RW) and is worthy of serious investigation;
(3) whether the conidia have been observed on naturally occurring fruit-bodies, or in culture; and (4) whether the conidia are dikaryotic and incorporate part of a disarticulated clamp-connection. Watling (Chap. 19) has already discussed the biological significance, morphology and development of thallic-arthric conidia in the Agaricales.

The reader is referred to Sigler & Carmichael's (1976) article on the Malbranchea complex in which arthroconidial anamorphs of various Hymenomycetes are tentatively referred to the genus Mauginiella. In fact the authors describe as group 1, isolates resembling Geotrichum in development but differing in the production of dry arthroconidia. In most respects these strains resemble the type of Mauginiella; M. saettae Cavara. However, in M. saettae the fertile hyphae are wider than the vegetative mycelium and break up reluctantly. There is little doubt that some anamorphs of Hymenomycetes have previously been placed in Scytalidium and related genera.

Sigler & Carmichael (1976) compare the conidial apparatus in their Mauginiella Group 4, with Collybia 'conigena' (Pers.) Karst. as their example, with Oidiocendron and Sporendonema. The partly mature arthroconidia of this group resemble the alternate arthroconidia of Sporendonema until the walls of the separating cells collapse, when the chains of arthroconidia resemble strings of sausages.

Arnould (1952) describes Geotrichum cyphellae Arnould on Lachnellula alboviolascens (Alb. & Schw. ex Pers.) Fr.; although cyphellloid, the genus Lachnellula is now regarded as containing reduced members of the Marasmius-group of agarics. It is therefore possible that Arnould's fungus is in fact an anamorph. In the same paper Arnould also described Sporendonema roseum var. album nov. var. This may also turn out to be a basidiomycetous anamorph.

(10) THALLIC-ARTHRIC CONIDIA (ARTHROCONIDIA)

<table>
<thead>
<tr>
<th>Teleomorph</th>
<th>Anamorph</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>UNKNOWN BASIDIOMYCETES</strong></td>
<td>Moniliophthora roteri (Cif.)</td>
<td>Evans, Stalpers, Samson &amp; Benny</td>
</tr>
<tr>
<td></td>
<td>Evans, Stalpers, Samson &amp; Benny</td>
<td></td>
</tr>
<tr>
<td></td>
<td>'Oidium' morgani Linder</td>
<td>Linder 1942, Weresub pers. comm.</td>
</tr>
<tr>
<td><strong>HYMENOMYCETES</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agaricales*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agrocybe semiornicularis (Bull. ex St. Amans) Fayod</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Armillaria albolanaripes</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arthosporella ditopa (Sing.)</td>
<td>Nothoclavulina ditopa Sing.</td>
<td></td>
</tr>
<tr>
<td>Sing.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Collybia 'conigena' (Pers.) Karst.</td>
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</table>

* anamorph reported in culture except where otherwise indicated.
<table>
<thead>
<tr>
<th>Teleomorph</th>
<th>Anamorph</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. metachroa (Fr.) Kumm.</td>
<td>Sclerotostilbum septentrionale</td>
<td>Brefeld 1889 (Tafel III:26-27): we cannot</td>
</tr>
<tr>
<td>C. maculata (Alb. &amp; Schw. ex Fr.) Kumm.</td>
<td></td>
<td>determine to what interpretation of C.</td>
</tr>
<tr>
<td>C. racemosa (Pers. ex Fr.) Québec</td>
<td></td>
<td>metachroa Brefeld refers.</td>
</tr>
<tr>
<td>Conocybe farinacea Watling</td>
<td></td>
<td>Watling &amp; Kendrick 1977, Lutjeharms 1934:</td>
</tr>
<tr>
<td>C. pubescens (Gillet) Kühner</td>
<td></td>
<td>conidia formed on numerous large synnematal</td>
</tr>
<tr>
<td>C. tenera (Schaeff. ex Fr.) Fayod</td>
<td></td>
<td>conidomata arising along the stipe of</td>
</tr>
<tr>
<td>Coprinus cinereus (Schaeff. ex Fr.)</td>
<td></td>
<td>the basidiome.</td>
</tr>
<tr>
<td>S.F. Gray</td>
<td></td>
<td>Watling pers. obs.</td>
</tr>
<tr>
<td>C. congestatus (Bull. ex St. Amans) Fr.</td>
<td></td>
<td>Brefeld 1889 (Tafel III:1-6): sub Galera:</td>
</tr>
<tr>
<td>C. macrocephalus (Berk.) Berk.</td>
<td></td>
<td>conf. Watling.</td>
</tr>
<tr>
<td>C. aff. patouillardi Quéél.</td>
<td></td>
<td>Anderson 1971: this species has been called</td>
</tr>
<tr>
<td>C. aff. plicatilis (Curt. ex Fr.) Fr.</td>
<td></td>
<td>Coprinus lagopus in the genetical</td>
</tr>
<tr>
<td>C. radiatus (Bolt. ex Fr.) S.F. Gray</td>
<td></td>
<td>literature.</td>
</tr>
<tr>
<td>C. kimurae Hongo &amp; Aoki</td>
<td></td>
<td>Kemp &amp; Watling pers. obs.: very short chains</td>
</tr>
<tr>
<td>C. stellatus Buller</td>
<td></td>
<td>and bulbiloid bodies.</td>
</tr>
<tr>
<td>C. sterilcoreus Fr.</td>
<td></td>
<td>Kemp pers. comm.: slimy heads produced.</td>
</tr>
<tr>
<td>C. sterquilinus (Fr.) Fr.</td>
<td></td>
<td>Watling pers. obs.</td>
</tr>
<tr>
<td>C. trisporus Watling</td>
<td></td>
<td>Kemp pers. comm.: slimy heads produced.</td>
</tr>
<tr>
<td>Crinipellis perniciosus (Stahl) Sing.</td>
<td></td>
<td>Kemp pers. comm.</td>
</tr>
<tr>
<td>Cystoderma amianthinum (Fr.) Fayod</td>
<td></td>
<td>Kemp pers. comm.</td>
</tr>
<tr>
<td>C. carcharias (Pers. ex Secr.) Fayod</td>
<td></td>
<td>Kemp pers. comm.: slimy heads produced.</td>
</tr>
<tr>
<td>C. aff. longisporum Heinem. &amp; Thoen</td>
<td></td>
<td>Kemp pers. comm.</td>
</tr>
<tr>
<td>C. tricholomoides Heinem. &amp; Thoen</td>
<td></td>
<td>Kemp pers. comm.</td>
</tr>
<tr>
<td>Flagelloscypha abruptiflagellata Agerer</td>
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<td>Kemp pers. comm.</td>
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<tr>
<td>Flammulina velutipes (Curt. ex Fr.) Karst.</td>
<td></td>
<td>Brefeld 1877 (Tafel VI:1-13): a misinterpreted</td>
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<tr>
<td></td>
<td></td>
<td>species: see Watling &amp; Kits van Waveren 1968.</td>
</tr>
<tr>
<td>Galerina mutabilis (Schaeff. ex Fr.) Orton</td>
<td></td>
<td>Kemp pers. comm.</td>
</tr>
<tr>
<td>G. myriadophylla Orton</td>
<td></td>
<td>Kemp pers. comm.: conf. Watling.</td>
</tr>
<tr>
<td>Gymnopilus hybridus (Fr. ex Fr.) Sing.</td>
<td></td>
<td>Kühner 1969.</td>
</tr>
<tr>
<td>G. penetrans (Fr. ex Fr.) Murr.</td>
<td></td>
<td>Heinemann &amp; Thoen 1973: on pileus.</td>
</tr>
<tr>
<td>Hypholoma capnoides (Fr. ex Fr.) Kumm.</td>
<td></td>
<td>Heinemann &amp; Thoen 1973: on base of stipe.</td>
</tr>
<tr>
<td>Marasmius limosus Quéél.</td>
<td></td>
<td>Watling pers. obs.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Watling pers. obs.</td>
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<tr>
<td></td>
<td></td>
<td>Brefeld 1889 (Tafel IV:6-8): sub Pholiota</td>
</tr>
<tr>
<td></td>
<td></td>
<td>marginata (Batsch ex Secr.) Quéél.</td>
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<tr>
<td></td>
<td></td>
<td>Watling pers. obs.</td>
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<td></td>
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<td>Watling pers. obs.</td>
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<td></td>
<td></td>
<td>Watling pers. obs.</td>
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<tr>
<td></td>
<td></td>
<td>Vandendries 1934c.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lamoure 1960.</td>
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<tr>
<td>Teleomorph</td>
<td>Anamorph</td>
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<tr>
<td>Mycena inclinata (Fr.) Quél.</td>
<td>Antromycopsis broussonetiae</td>
<td>Watling pers. obs.</td>
</tr>
<tr>
<td>P. semiovatus (Sow. ex Fr.) Lund.</td>
<td></td>
<td>Watling pers. obs.</td>
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<tr>
<td>P. sphinctrinus (Fr.) Quél.</td>
<td></td>
<td>Watling pers. obs.</td>
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<td>Pholiota aurivella (Batsch ex Fr.) Kumm.</td>
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<td>Vandendries &amp; Martens 1932.</td>
</tr>
<tr>
<td>P. elongatipes Peck</td>
<td></td>
<td>Malloch pers. comm.</td>
</tr>
<tr>
<td>Psathyrella candolleana (Fr.) Smith</td>
<td></td>
<td>Watling pers. obs.: slimy heads.</td>
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<tr>
<td>P. coprophila Watling</td>
<td></td>
<td>Brefeld 1889 (Tafel III:22): sub Psathyra.</td>
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<tr>
<td>P. spadicea (Schaeff. ex Fr.) Sing.</td>
<td></td>
<td>Heim &amp; Wasson 1959.</td>
</tr>
<tr>
<td>P. spadiceo-grisea (Fr.) Maire</td>
<td></td>
<td>Heim &amp; Wasson 1959.</td>
</tr>
<tr>
<td>Psilocybe acutissima Heim</td>
<td></td>
<td>Heim &amp; Wasson 1959.</td>
</tr>
<tr>
<td>P. hoogshagenii Heim</td>
<td></td>
<td>Heim &amp; Wasson 1959.</td>
</tr>
<tr>
<td>P. mexicana Heim</td>
<td></td>
<td>Heim &amp; Wasson 1959.</td>
</tr>
<tr>
<td>P. mixaensis Heim</td>
<td></td>
<td>Heim &amp; Wasson 1959.</td>
</tr>
<tr>
<td>P. yungensis Sing. &amp; A.H. Smith</td>
<td></td>
<td>Heim &amp; Wasson 1959.</td>
</tr>
<tr>
<td>P. zapotecorum Heim</td>
<td></td>
<td>Heim &amp; Wasson 1959.</td>
</tr>
<tr>
<td>Strobilurus stephanocystis (Kühn. &amp; Romagn. ex Hora) Sing.</td>
<td></td>
<td>Watling pers. obs.: Brefeld vol. 8, Tafel IV:23-25, sub Collybia conigenus (Fr.) Karst., probably refers to this species: see also Sigler &amp; Carmichael 1976.</td>
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<tr>
<td>Stropharia melanosperma (Bull. ex Fr.) Gillet</td>
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<td>Brefeld 1889 (Tafel III:32-34).</td>
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<td>Aphyllorophales</td>
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<td>Amylostereum areolatum (Fr.) Boidin</td>
<td></td>
<td>Boidin 1958b, Talbot 1964.</td>
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<tr>
<td>Amylostereum sp.</td>
<td></td>
<td>Talbot pers. comm.: fungus identified with Sirex.</td>
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<tr>
<td>Antrodia serialis (Fr.) Donk</td>
<td></td>
<td>Brefeld 1889 (Tafel II:28): sub Polyporus.</td>
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<tr>
<td>Athelia sp.</td>
<td></td>
<td>Butler 1930: sub Corticium centrifugum.</td>
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<tr>
<td>Teleomorph</td>
<td>Anamorph</td>
<td>References</td>
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<tr>
<td>Basidiomycetes radula (Fr.) Nobles</td>
<td></td>
<td>Brefeld 1889 (Tafel II:3-4): illus. difficult to interpret: cf. also blastic conidia Haplotrichum-type sub Radulum orbiculare Fr.</td>
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<tr>
<td>Buglossosorus quercinus (Schrad. ex Fr.)Kotl. &amp; Pouz.</td>
<td></td>
<td>Lyman 1907.</td>
</tr>
<tr>
<td>Ceraceomyces serpens (Fr.) Ginns</td>
<td>Cerrena unicolor (Bull.) Murr.</td>
<td>Brefeld 1889 (Tafel II:34-36): sub Polyporus.</td>
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<tr>
<td>Coniophora arida (Fr.) Karst.</td>
<td>C. puteana (Schum. ex Fr.) Karst.</td>
<td>Ginns &amp; Sunhede 1978: but illus. appears blastic.</td>
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<tr>
<td>Coriolus ambiguus (Berk.) Cunn.</td>
<td>C. versicolor (L. ex Fr.) Quéél.</td>
<td>Ginns &amp; Sunhede 1978: but illus. appears blastic.</td>
</tr>
<tr>
<td>C. zonatus (Nees ex Fr.) Quéél.</td>
<td>D. squalens (Karst.) Reid</td>
<td>Stalpers 1978.</td>
</tr>
<tr>
<td>Dichomitus albidofuscus (Doman.) Doman.</td>
<td></td>
<td>Boidin 1958, McDonald 1939: conidia delimited by retraction septa.</td>
</tr>
<tr>
<td>Lagaricipites officinalis (Vuill. ex Fr.)Donk</td>
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<td>Brefeld 1889 (Tafel II:17-20): sub Lenzites.</td>
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<tr>
<td>Mycoacia fuscoatra (Fr.) Donk</td>
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<td>Stalpers 1978.</td>
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<td></td>
<td></td>
<td>Brefeld 1889 (Tafel II:23-25): sub Trametes.</td>
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<tr>
<td>Teleomorph</td>
<td>Anamorph</td>
<td>References</td>
</tr>
<tr>
<td>------------------------------------------------</td>
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<td>------------------------------------------------</td>
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<tr>
<td>Perenniporia elongata (Overh.) Doman.</td>
<td></td>
<td>Stalpers 1978.</td>
</tr>
<tr>
<td>Phellinus lamaensis (Murr.) Heim</td>
<td></td>
<td>Stalpers 1978.</td>
</tr>
<tr>
<td>P. pachyphloeus (Pat.) Pat.</td>
<td></td>
<td>Brefeld 1889 (Tafel II:14-16): sub Lenzites.</td>
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<tr>
<td>Phlebia gigantea (Fr. ex Fr.) Donk</td>
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<td>Brefeld 1889 (Tafel II:6-8): often synonymized with P. radiata.</td>
</tr>
<tr>
<td>P. radiata Fr.</td>
<td></td>
<td>Stalpers 1978.</td>
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<tr>
<td>P. squamosus Hud.s. ex Fr.</td>
<td></td>
<td>Nobles 1948.</td>
</tr>
<tr>
<td>Poria albipellucida Baxter</td>
<td></td>
<td>Lindsey &amp; Gilbertson 1977.</td>
</tr>
<tr>
<td>P. cocos (Schw.) Wolf</td>
<td></td>
<td>Wright &amp; Deschamps 1972.</td>
</tr>
<tr>
<td>Punctularia strigosozonata (Schw.) Talbot</td>
<td></td>
<td>Stalpers 1978.</td>
</tr>
<tr>
<td>P. coccineus (Fr.) Bond. &amp; Sing.</td>
<td></td>
<td>Brefeld 1889 (Tafel II:3-4): illus. difficult to interpret: cf. also blastic conidia, Haplotrichum-type.</td>
</tr>
<tr>
<td>Radulum fagineum Fr.</td>
<td></td>
<td>Stalpers 1978.</td>
</tr>
<tr>
<td>Resinicum bicolor (Alb. &amp; Schw. ex Fr.) Parm.</td>
<td></td>
<td>Brefeld 1889 (Tafel II:11-13): sub Irpex obliquus.</td>
</tr>
<tr>
<td>Schizopora paradoxa (Schrad. ex Fr.) Donk</td>
<td></td>
<td>Biggs 1937: sub Corticium coronilla; Weresub &amp; Le Clair 1971: also forms bulbils.</td>
</tr>
<tr>
<td>Serpula lacrymans (Wulf. ex Fr.) Karst.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sistotrema brinkmannii (Bres.) J. Erikss.</td>
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<td></td>
</tr>
</tbody>
</table>
Teleomorph  Anamorph  References
Spongipellis delectans (Peck) Murr. 'Osteomorpha fragilis' Arnaud
T. cingulata Berk. apud Hook.
T. gibbosa (Pers. ex Fr.) Fr.
T. hirsuta (Wulf. ex Fr.) Pilát
T. meyenii (Klotz.) Lloyd
T. suaveolens (L. ex Fr.) Fr.
Trechispora farinacea (Fr.) Liberta
Typhula athyrii Remsb.
T. betae Rostr.
T. culmigena (Mont. & Fr.) Berthier
T. quisquiliaris (Fr.) Corner
T. trifolii Rostr.
T. uncialis (Grev.) Berthier

HYMENOMYCETOUS HETEROBASIDIAE

Dacrymycetales
Dacrymyces capitatus Schw.
Dacrymyces stillatus Nees ex Fr.  'Dacrymyces stillatus'

The name *Dacrymyces stillatus* gradually, though of course incorrectly, became delimitated for the thallic-arthic anamorph, while *D. deliquescent* (Bull. ex Fr.) Duby has been widely applied to the teleomorph: see Donk 1966.

Septobasidiales

Septobasidium accumbens (B. & Br.) Couch
S. lanosum Pat.
S. paulense P. Henn.
S. pilosum Boed. & Stein.
S. sinense Couch

*Septobasidium theae* Boud. & Stein and *S. oonidiophorum* Couch are reported to have both dark and light hyphae (Couch 1938) and the sections he took from specimens on wood may well have contained extraneous fungi. His plate 48, Fig. 7, strongly resembles *Aureobasidium pullulans* (de Bary) Arnaud.

(11) CHLAMYDOSPORES (Figs. 20.5 A-G, 20.6 A)

Much has been written concerning the nature of the chlamydospore. A modest review is presented in the terminological section of this paper. Having arrived at the rather unsatisfactory compromise of a broad, inclusive definition of the chlamydospore, we must now try to redeem the situation, at least in part, by segregating groups of chlamydosporic anamorphs on the manner in which these propagules are borne. Accordingly, we have recognized five such categories, with a sixth of uncertain relationship (stephanocysts); three of the groups are based on existing generic concepts.
(A) Solitary terminal chlamydospores; no discrete conidiophore.
(B) Terminal chlamydospores on branches of a discrete conidiophore --
*Allescheriella*-type.
(C) Terminal and lateral chlamydospores on branches of a discrete conidiophore --
*Sporotrichum*-type.
(D) Terminal and intercalary chlamydospores, often forming in chains --
*Asterophora*-type.
(E) Miscellaneous chlamydospores.
(F) Stephanocysts.

Chlamydospores are widespread throughout the Basidiomycetes, especially in culture. At
the present time no strict relationship between any one category above and a particular
group of fungi has been formulated, except for the rather specialized stephanocysts which
are confined to *Mutatoderma* Gomez and *Hyphoderma* Wallr. Chlamydospores are probably common-
est in the Aphyllorophales.

Chlamydosporic fructifications of *Nyatalis asterophora* and *N. parasitica* are much more
commonly encountered than basidiomata. In *N. asterophora* the upper pileus and gills are
transformed into a mass of dry, wind-dispersed (?) chlamydospores. In *N. parasitica* only the
gills become largely converted into chlamydospores.

Several species of *Nyatalis* were described in Saccardo's *Sylloge Fungorum*, but authentic
material no longer exists or the descriptions are based on single collections. It is doubt-
ful whether all these can be assumed to be congeneric or even assignable to the Tricholomataceae:
Lyophylleae. Pegler (1977) records *N. caniculata* Pers. ex Fr. and *N. cappearena* Eichelb. from
Tanzania, the latter with a short description. The mode of formation of chlamydospores in
these additional species of *Nyatalis* is unknown.

*Bometina* is the chlamydosporic anamorph of *Diacanthodes*. In this fungus the anamorph
forms encrusting sheaths around the roots of coffee and vines, causing a condition known as
phthiriosis. In a manner perhaps atypical of the Basidiomycetes, the teleomorph arises from
the anamorph, rather than vice versa.

Corner (1972) records that similar structures to those found in cultures of *Buchwaldoboletus*
are found on the stipe tissue of *Boletus chlamydosporus* Corner. This is unique; no develop-
mental information is given, but it is considered that these spores are splashed into the
soil by rain, or consumed by unknown members of the fauna and so distributed. It must always
be remembered that even in the field extraneous fungi may frequently use the agaricoid basi-
diome as a structure in/on which to fruit (Watling 1971).

(11A) **SOLITARY TERMINAL CHLAMYDOSPORES**

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<thead>
<tr>
<th>Teleomorph</th>
<th>Anamorph</th>
<th>References</th>
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<tbody>
<tr>
<td>UNKNOWN BASIDIOMYCETES</td>
<td>'Myxodochium hyalinum' Arnaud</td>
<td>Arnaud 1951: Myxodochium is invalid because it lacks a Latin diagnosis.</td>
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<td></td>
<td>Pagidospora amoebophila Drehsl</td>
<td>Drehsl 1960.</td>
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<td></td>
<td>Riessia semiophora Fres.</td>
<td>Goos 1967: also listed under <em>Stauroconidia</em>.</td>
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<td><strong>HYMENOMYCETES</strong></td>
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<td><strong>Agaricales</strong></td>
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<td></td>
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<tr>
<td>Coprinus cinereus (Schaeff. ex Fr.)</td>
<td>S.F. Gray</td>
<td>Day 1959: sub Coprinus lagopus; redet. Watling.</td>
</tr>
<tr>
<td>Pholiota aurivella (Batsch ex Fr.)</td>
<td>Kumm.</td>
<td>Vandendries &amp; Martens 1952: also produces arthroconidia.</td>
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<td><strong>Aphyllophorales</strong></td>
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<tr>
<td>Botryobasidium croceum Lentz</td>
<td>Allescheriella crocea (Mont.) Hughes</td>
<td>Lentz 1967: also listed under Allescheriella-type.</td>
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<td>Coriolus zonatus (Nees) Quél.</td>
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<td>Nosbes 1948: sub Polystictus.</td>
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<td>Diacanthodes philippinensis (Pat.)</td>
<td>Sing.</td>
<td>Donk 1948, Mangin &amp; Viala 1903, Viala &amp; Marsais 1930: also listed under Allescheriella-type.</td>
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<td>Funalia gallica (Fr.) Bond. &amp; Sing.</td>
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<td>Vandendries 1934a: sub Trametes hispida.</td>
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<td>Hericium coralloides (Scop. ex Fr.)</td>
<td>S.F. Gray</td>
<td>Stalpers 1978.</td>
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<td>H. erinaceus (Bull. ex Fr.) Pers.</td>
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<td>Patouillard 1900: his Fig. 4 also showed gloeocystidia.</td>
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<tr>
<td>Oxyporus obducens (Pers.) Donk</td>
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<td>Vandendries 1934a: also produces arthroconidia.</td>
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<tr>
<td>Phaeolus schweinitzii (Fr.) Pat.</td>
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<td>Corner 1976.</td>
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Teleomorph | Anamorph | References
---|---|---
Phlebia radiata Fr. |  | Nobles 1948.
Podoscypha bolleana (Mont.) Bold. |  | Corner 1976.
Pycnoporus cinnabarinus (Jacq. ex Fr.) Karst. |  | Boidin 1958: also produces arthroconidia.
Tyromyces galactinus (Berk.) Bond. |  | Nobles 1948: sub Polyporus.
Vararia effuscata (Cke. & Ell.) Rog. & Jacks. |  | Lyman 1907: see also blastic conidia, Spiniger-type.

HYMENOMYCETOUS HETEROBASIDIAE

Dacrymycetales
Calocera viscosa (Pers. ex Fr.) Fr. |  | Reid 1974a.

Tremellales

(11B) CHLAMYDOSPORES: ALLESCHERIELLA-TYPE

Teleomorph | Anamorph | References
---|---|---
UNKNOWN BASIDIOMYCETES
UNKONWN BASIDIOMYCETES | Oidium simile sensu Linder | Linder 1942.
Sporotrichum azureum Wright & Arx non S. azureum Link - see Hughes 1958 | von Arx 1973: we consider that this anamorph would be better disposed in Allescheriella.

HYMENOMYCETES

Aphyllophorales
Botryobasidium croceum Lentz | Allescheriella crocea (Mont.) Hughes | Lentz 1967: also listed under solitary terminal chlamydospores: see Baker & Dale 1951 for synonymy.
Diachanthodes novo-guineensis (Henn.) Fidalgo | Bornetina sp. | Fidalgo 1962, Wakefield 1917: sub Polyporus coffeae Wakef.: also listed under solitary terminal chlamydospores.
Inonotus rickii (Pat.) Reid | Psychogaster cubensis Pat. | Roy 1971.
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<td>Leucogaster floccosus Hesse</td>
<td>Leucophlebs sp.</td>
<td>Zeller &amp; Dodge 1924.</td>
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<td>Aphyllophorales</td>
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<td>Bjerkandera fumosa (Pers. ex Fr.) Karst.</td>
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<td>Dichomitus campestris (Quél.) Dom. &amp; Orlicz</td>
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<td>Fistulina hepatica Schaeff. ex Fr.</td>
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<td>Hyphodontia arguta (Fr.) J. Erikss. H. crustosa (Pers. ex Fr.) J. Erikss.</td>
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<td>Phanerochaete chrysosporium Burds. apud Burds. &amp; Eslyn Phanerochaete sp.</td>
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<td>Podoscypha venustula (Spec.) Reid</td>
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<td>Polyporus metamorphosus Fuckel</td>
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<td>Punctularia tuberculosa (Pat.) Pat.</td>
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<td>Schizopora paradoxo (Schrad. ex Fr.) Donk</td>
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*Trichosporium curtisi is also known as Reticularia affinis B. & C., R. atrorufa B. & C., and R. venulosa B. & Br. Talbot (1974) also indicates that R. pyrrothoraeas B. & C. is similar.
Hughes (1958) lists many species of Sporotrichum as being conidial Basidiomycetes; some are simply Hyphomycete names for what are really resupinate teleomorphs. We can at present do no more than record this conclusion, and list the taxa concerned. The following is a summary:

Sporotrichum badium Link = Tomentella atroviolacea Litsch. (= T. badia (Link ex Steud.) Stalp.)
S. bryophilum Pers.
S. candidum Link (= Byssocladium)
S. chlorinum Link
S. cinnamomeum Link
S. fusca Link = Tomentella rubiginosa (Bres.) Maire. This is taken as the type of Alytosporium (Stalpers 1975) and becomes a synonym of Tomentella
S. intertextum Schw.
S. isabellinum Karst.
S. lapidum Pers.
S. muscorum Link = Acrotamnium violaceum Nees. This has basidiomycetous mycelium (Hughes 1958). Donk (1962a) tentatively suggests Helicobasidium
S. obducens Pers.
S. stuporum Link
S. subvinosum Schw.
S. vitellinum Link

(11D) CHLAMYDOSPORES: ASTEROPHORA-TYPE

### Teleomorph

**HYMENOMYCETES**

**Agaricales**

Boletus lignicola Kallenb.
B. sulphureus Fr.

Coprinus cinereus (Schaeff. ex Fr.) S.F. Gray
C. sclerotiger Watl.

Dissoderma paradoxa (A.H. Smith & Sing.) Sing.

Flammulina velutipes (Curt. ex Fr.) Fr.
Lentinus lepideus (Fr. ex Fr.) Fr.
L. sajor-caju (Fr.) Sing.
L. tigrinus (Bull. ex Fr.) Fr.

Lyophyllum leucopaxilloides (Bigel. & A.H. Smith) Clem.
L. suburens Clem.

### Anamorph

**References**

Pantidou 1962: sub Phlebopus: currently referred to Buchwaldoboletus Pilát.
Pantidou 1961: sub Phlebopus: currently referred to Buchwaldoboletus.

Day 1959: see also terminal chlamydospores: also forms thallic-arthric conidia and hyphal aggregates.
Watling 1972: see also sclerotia: cells become heavily pigmented and ultimately aggregated.

Bas 1965: sub Squamanita.

Miller 1971.

Nobles 1948.
Westhuizen 1958.
Lyman 1907, Nobles 1948.
Clemençon 1968.

Clemençon 1968.
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<tr>
<th>Teleomorph</th>
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<tbody>
<tr>
<td>N. parasitica (Bull. ex Fr.) Fr.</td>
<td>Asterophora parasitica (Bull. ex Fr.) Sing.</td>
<td>Miller 1971.</td>
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<tr>
<td>P. elongatipes Peck</td>
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<td>P. sapidus (Schulz. apud Kalchbr.) Sacc.</td>
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<td>Squamanita odorata (Cool.) Bas</td>
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<td>S. pearsonii Bas.</td>
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<td>Athelia macrospora (Bres.) Christ.</td>
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<td>Bondarzewia montana (Quél.) Sing.</td>
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<td>Buglossoporus pulvinus (Pers.) Donk</td>
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<td>Ceraceomyces borealis (Rom.) Erikss. &amp; Ryv.</td>
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<td>Climacodon septentrionalis (Fr.) Karst.</td>
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<td>Climatoxystis borealis (Fr.) Kotl. &amp; Pouz.</td>
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<td>C. sinuosus (Fr.) Sarkar</td>
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<td>Corticium 'subcostatum' (Karst.) Bourd. &amp; Galz.</td>
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<td>D. quercina L. ex Fr.</td>
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<td>D. stereoides Fr. s. Lloyd</td>
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<td>Dichomitus albidosfuscus (Doman.) Doman.</td>
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<th>Teleomorph</th>
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<td>D. squalens (Karst.) Reid</td>
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<td>Stalpers 1978: arthroconidia occasionally formed.</td>
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<td>Fistulinia hepatica Schaeff. ex Fr.</td>
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<td>Stalpers 1978.</td>
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<td>Fomes hemitephrus (Berk.) Cke. F. rufolaccatus Bose</td>
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<td>Grifola frondosa (Dicks. ex Fr.) S.F. Gray</td>
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<td>Stalpers 1978: arthroconidia formed on haploid mycelia.</td>
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<td>Hapalopilus croceus (Pers. ex Fr.) Donk</td>
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<td>Stalpers 1978.</td>
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<td>Haploporus cytisinus (Berk.) Doman.</td>
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<td>Stalpers 1978: arthroconidia also formed.</td>
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<td>Hexagonia sulcata Berk.</td>
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<td>Stalpers 1978: arthroconidia also formed.</td>
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<td>Hymenochaete rubiginosa (Dicks. ex Fr.) Lév.</td>
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<td>Nobles 1948: sub Fomes fraxineus.</td>
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- Stalpers 1978
- Boidin 1958b
- Boidin 1958b
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<td>Inonotus nidus-pici Pilát</td>
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<td>Benkert 1971.</td>
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<td>Boidin 1958b: sub Stereum; Stalpers 1978.</td>
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<td>Lentinellus castoreus (Fr.) Romagn. L. pilatii Herink</td>
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<td>Kühner 1946.</td>
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<td>Lenzites palisotii (Fr.) Fr.</td>
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<td>Miller 1971.</td>
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<td>Loweporus lividus (Kalch.) Wright</td>
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<td>Stalpers 1978: arthroconidia sometimes formed.</td>
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<td>Merulius tremellosus (Schrad.) Fr.</td>
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<td>Wright 1976.</td>
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<td>Mycoacia fuscoatra (Fr.) Donk</td>
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<td>Donk 1974a, Falck &amp; Falck 1937.</td>
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<td>Mycoleptodonoides aitchisonii (Berk.) Maas G.</td>
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<td>Odontia corrugata (Fr.) Bres.</td>
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<td>Osteina obducta (Berk.) Donk</td>
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<td>P. sordida (Karst.) Burt</td>
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<td>Phaeotrametes decipiens (Berk.) Wright</td>
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<td>Wright 1966: see discussion of thallic-meristem conidia.</td>
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<td>Phellinus bambusinus Pat.</td>
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<td>Patouillard 1900: illus. difficult to interpret.</td>
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<td><em>Podoscypha venustula</em> (Speg.) Reid</td>
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<td>Martin 1937b.</td>
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<td>P. alveolarius Bosc. ex Fr.</td>
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<td>P. brumalis (Pers. ex Fr.) Fr.</td>
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<td>P. eucalyptorum Fr.</td>
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<td>P. roliniophilus (Murr.) Lloyd</td>
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<td>P. rubidus Berk.</td>
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<td>Lombard &amp; Gilbertson 1965.</td>
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<td>P. oleracea Davids. &amp; Lomb.</td>
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<td>P. placenta (Fr.) Cke.</td>
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<td><em>Pycnoporus coccineus</em> (Fr.) Bond. &amp; Sing.</td>
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<td>Westhuizen 1958: sub Polyporus: arthroconidia also formed.</td>
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<td><em>Schizophyllum commune</em> Fr.</td>
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<td><em>Sparassis crispa</em> (Wulf. ex Fr.) Fr.</td>
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<td><em>Spongipellis delectans</em> (Peck) Murr.</td>
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<td>Wright, Deschamps &amp; Rovetta 1973: conidia on denticles also formed on vegetative hyphae.</td>
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<td><em>S. stramineus</em> Pat.</td>
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<td>Trametella extenuata (Dur. &amp; Mont.)</td>
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<td>Wright, Deschamps &amp; Rovetta 1973</td>
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<td>Sing.</td>
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<td>Bondarzew 1953, Bourdot &amp; Galzin 1927.</td>
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<td>T. albidos (Schaeff.) Donk</td>
<td>Ptychogaster rubescens Boud.</td>
<td>Wright &amp; Deschamps 1972.</td>
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<td>T. apalus (Lév.) Bond.</td>
<td>Ptychogaster sp.</td>
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<td>Fidalgo 1958, Davidson, Christensen &amp; Darley 1946.</td>
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<td>T. kymatodes (Rostk.) Donk</td>
<td>(Pers. ex Steud.) Donk</td>
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<td>T. suaveolens (L. ex Fr.) Fr.</td>
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<td>Stalpers 1978.</td>
</tr>
<tr>
<td>T. versicolor (L. ex Fr.) Pilát</td>
<td></td>
<td>Stalpers 1978.</td>
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<tr>
<td>Trametes sp.</td>
<td></td>
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<tr>
<td>T. borealis (Fr.) Imaz.</td>
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<td>Stalpers 1978.</td>
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<tr>
<td>T. chioneus (Fr.) Karst.</td>
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<td>Stalpers 1978.</td>
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<tr>
<td>T. tephroleucus (Fr.) Donk</td>
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<td>Stalpers 1978.</td>
</tr>
<tr>
<td>Vararia effuscata (Cke. &amp; Ell.) Rog.</td>
<td></td>
<td>Lyman 1907: sub Corticium.</td>
</tr>
</tbody>
</table>

Note that Stalpers (1978) uses *Trametes* in such a way as to include *Pseudotremaetes* and *Coriolus* spp., as is very recent practice. Also note the multiple connections reported for *Ptychogaster rubescens*, indicating either conflicting taxonomic conclusions, or heterogeneity of the taxon.
Fig. 20.10 The Ptychogaster citrinus anamorph of Trametes rennyi (Courtesy J. Stalpers)
<table>
<thead>
<tr>
<th>Teleomorph</th>
<th>Anamorph</th>
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<td>Broomeia congregata Lév.</td>
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<tr>
<td>Tilletiopsis minor Nyland</td>
<td></td>
<td>Nyland 1950.</td>
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<tr>
<td><strong>Agaricales</strong></td>
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<tr>
<td>ex Fr.) Fr.</td>
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</tr>
<tr>
<td>Oudemansiella radicata (Relhan</td>
<td></td>
<td>Miller 1971.</td>
</tr>
<tr>
<td>ex Fr.) Sing.</td>
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<tr>
<td>Rhodotus palmatus (Bull. ex Fr.)</td>
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<td>Miller 1971.</td>
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<tr>
<td>Maire</td>
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<td>Miller 1971.</td>
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<tr>
<td>Tricholoma portentosum (Fr.)</td>
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<td>Miller 1971.</td>
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<tr>
<td>Cunn.</td>
<td>Mass.</td>
<td></td>
</tr>
<tr>
<td>Hyphoderma sambuci (Fr.) Júlich</td>
<td></td>
<td>Boidin 1958.</td>
</tr>
<tr>
<td><strong>Laeticorticium polygonioideis</strong></td>
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</tr>
<tr>
<td>(Karst.) Donk</td>
<td></td>
<td>Boidin 1958.</td>
</tr>
<tr>
<td>L. ursinus (Fr.) Kühn.</td>
<td></td>
<td>Miller 1971.</td>
</tr>
<tr>
<td>Phaeotrametes decipiens (Berk.)</td>
<td></td>
<td>Wright 1966: see discussion under thallic-meristem conidia.</td>
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<tr>
<td>Wright</td>
<td></td>
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<tr>
<td>Xenasma tulasnelloideum (Höhn. &amp; Litsch.) Donk</td>
<td></td>
<td>Boidin 1958: sub Corticium.</td>
</tr>
</tbody>
</table>

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**References**

Wright & Gamundi 1973.

Nyland 1950.

Nyland 1950.

Kühner, Lamoure & Fichet 1962.

Miller 1971.

Miller 1971.

Miller 1971.

Miller 1971.

Cunningham 1956, Donk 1962, Massee 1888.

Boidin 1958.

Boidin 1958.

Boidin 1958.

Boidin 1958.

Boidin 1958.

Boidin 1958.

Boidin 1958.

Boidin 1958.

Boidin 1958.
Teleomorph | Anamorph | References
---|---|---
HYMENOMYCETOUS HETEROBASIDIAE
Cystobasidium sebaceum Martin & Couch | | Martin 1939a.

BASIDIOMYCETOUS YEASTS

HYMENOMYCETES

Aphyllophorales

Hyphoderma echinocystis Erikss. & Strid
H. guttuliferum (Karst.) Donk
H. pallidum (Bres.) Donk (?)
H. praetermissum (Karst.) Erikss. & Strid
H. puberum (Fr.) Wallr.
H. tenue (Pat.) Donk
H. tsugae (Burt.) Erikss. & Strid | | Eriksson & Ryvarden 1975.
Bardon & Ryvarden 1975.
Burdsall 1958, Dearden unpubl.
Boidin 1950.
Boidin 1950.
Boidin unpubl.

Hyphoderma sp. (aff. gemmiferum) (Bourd. & Galz.) Erikss. & Ryv.) | | Boidin 1958.

(12) CONIDIA ARISING AS MODIFICATIONS OF CLAMP-CONNECTIONS (Fig. 20.6 A-G)

The unique mode of origin of many of the propagules listed below is often obscured once they are liberated. The propagules of Syzygospora must be seen during development for their bizarre nature to be fully appreciated. The conidia of Tremella polyporina Reid would draw little comment from anyone unaware of their unique ontogeny. The strangely shaped thallic-arthric spores of Osteomorpha, seen in isolation, might puzzle the uninitiated (though this particular jig-saw is easily pieced together). Yet these and the other mitospores compiled here all spring ultimately from that definitively dikaryotic diverticulum, the clamp-connection.

Although the clamps are modified in a number of different ways, and the conidia fall into a number of different ontogenetic groups, we felt that it was worthwhile to bring the various examples together under a single heading. The idea of the clamp-connection is well rooted in every mycologist's mind, and the clamp component of the phenomena listed here will be recognized at once if they are seen in situ.

In Collybia racemosa (Pers. ex Fr.) Quél., Pleurotus cystidiosus O.K. Miller, and 'Osteomorpha fragilis' Arnaud, hyphae with regular, closely spaced clamps may disarticulate across each clamp, as shown in Fig. 20.6 B, to produce highly irregular thallic-arthric mitospores. In Tremella polyporina Reid a succession of contiguous clamps may form by very...
short sympodial proliferations of the conidiogenous hypha (Fig. 20.6 G), the outer cell of each clamp in turn becoming swollen and seceding as a propagule. In Syzygospora, the two short outgrowths from the same hypha fuse to form a clamp-like conidium which is subsequently liberated (Fig. 20.6 C). In Squamanita, the clamps become swollen, thick-walled chlamydospores (Fig. 20.6 A). Some staurosporous aquatic propagules may be considered as branched hyphal systems in which the branches always arise from a clamp, and every cell is clamped, e.g., the Ingoldiella hamata anamorph of Sistotrema sp. (vel aff.) (Fig. 20.6 E). In Thyroidina carneominiata HÖhn., a succession of clamps builds a 'dictyospore' (Fig. 20.6 F).

(12A) DISARTICULATED CLAMPS

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<th>Spore category</th>
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<tr>
<td>Agaricales</td>
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<tr>
<td>Squamanita odorata (Cool.) Bas S. pearsonii Bas</td>
<td></td>
<td>Chlamydospores</td>
<td>Bas 1965.</td>
</tr>
<tr>
<td>Aphyllophorales</td>
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<td></td>
<td>Bas 1965.</td>
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</table>

(12B) MODIFIED HYPHAL SYSTEMS

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<td>Bas 1965.</td>
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HYMENOMYCETES

Aphyllophorales

### (12C) COMPLEX CLAMP CONNECTIONS

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<tr>
<th>Teleomorph</th>
<th>Anamorph</th>
<th>spore category</th>
<th>References</th>
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</thead>
</table>

**HYMENOMYCETES**

**Aphyllorales**


* Martin (1937) thought that the bizarre spore formation of *Syzygospora* indicated an auriculariaceous basidium, but Kao (1956) found holobasidia on the same mycelium (Fig. 20.6 C), so the *Syzygospora* 'basidiospores' are now regarded as conidia. Kao showed up to three fusing pairs arising at one point. There is resemblance between this behaviour and the formation of multiple clamp-connections by such fungi as *Stereum sanguinolentum* (A. & S.) Fr. and *Coniophora puteana* (Schum. ex Fr.) Karst. (see Nobles 1959), and also some similarity with the paarige branching found in some cultures of the Boletaceae (Pantidou & Groves 1966), particularly the genus *Suillus* (Pantidou & Watling 1970).

**HYMENOMYCETOUS HETEROBASIDIAE**

**Auriculariales**

<table>
<thead>
<tr>
<th>Cystobasidium sebaceum</th>
<th>Martin &amp; Couch</th>
</tr>
</thead>
</table>

**Agaricales**

| Dissoderma paradoxa (A.H. Smith & Sing.) Sing. | Chlamydospores | Bas 1965: sub Squamanita: see also disarticulating clamps. |
| Squamanita odorata (Cool.) Bas                  | Chlamydospores | Bas 1965: see also disarticulating clamps. |
| S. pearsonii Bas                                 | Chlamydospores | Bas 1965: see also disarticulating clamps. |

**Aphyllorales**


| Hyphoderma guttuliferum (Karst.) Donk. | 'Stephanocyst' | Boidin 1950, 1958b. |
| H. puberum (Fr.) Wallr. | 'Stephanocyst' | Boidin 1950, 1958b. |

**HYMENOMYCETOUS HETEROBASIDIAE**

| Tremella mycophaga Martin | Sympodial | Torkelsen 1968. |
| T. polyoporina Reid        | | Koske 1972. |
This Saccardoan category covers a wide range of morphological expressions (see Chap. 5), and is therefore highly heterogeneous; nevertheless it is a useful, easily recognized grouping, and its members are extremely characteristic and readily distinguishable. Sixty-seven of the genera illustrated by Kendrick & Carmichael (1973) produce stauroconidia sensu lato. If we attempt to analyze the evolutionary patterns underlying the stauroconidium, three lines seem to emerge:

(A) propagules which are basically a branched hyphal system. Here we may draw an analogy with the 'paarige' branching found in the Boletaceae, and illustrated by Pantidou & Groves (1966).

(B) propagules arising from a fusion or aggregation of originally separate components. For example, if a tightly knit group of amerococonidia fail to dehisce individually, they may then come to be shed as a group which is an easily recognized entity.

(C) propagules with specialized appendages; often tetraradiate in configuration.

We have thus listed our basidiomycetous stauroconidia under these three headings.

Modified hyphal systems often bear clamps, as in Ingoldiella, and thus betray their affinities even if no teleomorphic connection is yet known; but in other such cases, no clamps may be present, and the presumed basidiomycetous connection is based on the presence of dolipore septa and binucleate cells, as in 'Trioladium' malaysianum Nawawi. As Webster & Descals point out in Chap. 18 of this book, if Trioladium splendens Ingold is found to have simple septa, T. malaysianum will need to be redispaced (cf. Oedoecephalum-Spninger). And, of course, there may be as yet unrecognized basidiomycetous anamorphs which do not display clamp connections.

In Glomopsis oorni (Peck) Henderson and G. lonicerae (Peck ex Gould) Henderson the conidio- phores have appendages which are presumed to be homologous with clamp-connections (see modified clamp-connections). The conidial head in both species is completely fused and secedes as a unit. Glomospina empetri Henderson is similar in many ways, the conidial head being liberated as a unit by the fracture of the uppermost cell of the stipe. Squashing the pustules releases individual conidia.
Teleomorph

UNKNOWN BASIDIOMYCETES

- Ingoldiella fibulata Nawawi (Nawawi 1973: all cells with clamps.
- 'Titaeella capnophila' Arnaud nomen nudum (Arnaud 1951: only subtending hyphae have clamps, conidia more or less tetraradiate.

HYMENOMYCETES

Aphyllophorales

- Leptosporomyces galzinii (Bourd.) Julich
- Sistotrema sp. vel aff.

HYMENOMYCETOUS HETEROBASIDIAE

Auriculariales

- Herpobasidium deformans Gould

Anamorph

<table>
<thead>
<tr>
<th>Teleomorph</th>
<th>Anamorph</th>
<th>References</th>
</tr>
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<tbody>
<tr>
<td>Ingoldiella fibulata</td>
<td>Ingoldiella fibulata Nawawi</td>
<td>Nawawi 1973: all cells with clamps.</td>
</tr>
<tr>
<td>'Titaeella capnophila'</td>
<td>'Titaeella capnophila' Arnaud nomen nudum</td>
<td>Arnaud 1951: only subtending hyphae have clamps, conidia more or less tetraradiate.</td>
</tr>
</tbody>
</table>

References


Ingoldiella fibulata Nawawi 1973: all cells with clamps.

'Titaeella capnophila' Arnaud nomen nudum Arnaud 1951: only subtending hyphae have clamps, conidia more or less tetraradiate.


Ingoldiella hamata Shaw Ingold 1961, Shaw 1972, Nawawi 1973, Webster & Descals Chap. 18: all cells clamped; branches arise from clamps -- see modified clamp connections.


*Riessia is marginal, but may have arisen from the failure of four amoerconidia to secede. Syzygospora alba Martin is one possible type of precursor; Dechowardi tetraspora or Sporotrichum aureum represent others. Goos (1967) wrote: 'The compound conidium of R. semiophora Pres. appears to consist of several cells, usually four of which have fused during development into a single morphological unit. Each cell possesses the ability to germinate, and germ-tubes emerging from single cells bear clamp-connections.' The account of Skirgiello & Gesicka (1970) does not clarify the ontogeny of the stauroconidia.
(13C) 'TETRARADIATE' PROPAGULES

<table>
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<tr>
<th>Teleomorph</th>
<th>Anamorph</th>
<th>References</th>
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<tr>
<td>Aphyllorhales</td>
<td></td>
<td></td>
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<tr>
<td>Digitatispora marina Doguet</td>
<td></td>
<td>Doguet 1962, Kohlmeyer 1971: Doguet considers the tetraradiate propagules to be basidiospores, but Donk (1964) doubts this.</td>
</tr>
<tr>
<td>GASTEROMYCETES</td>
<td></td>
<td></td>
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<tr>
<td>Nia vibrissa Moore &amp; Meyers</td>
<td></td>
<td>Moore &amp; Meyers 1959, Kohlmeyer 1971: the quinqueradiate propagules are considered by some to be basidiospores.</td>
</tr>
</tbody>
</table>

(14) BULBILS AND SIMILAR PROPAGULES (Fig. 20.7 F,G)

The subject of bulbils and similar propagules has been covered in the section on terminology. Little remains for us except to list the various examples we have located and to mention that much remains to be done before mycologists will either fully understand the development of the various propagules that have been called bulbils, or arrive at an entirely satisfactory classification for them. We have accepted the definition given by Weresub & Le Clair (1971), which does not include the swellings with enveloping narrow branches so termed by Nobles and Stalpers in such taxa as *Phellinus nigrolimitatus* (Rom.) Bourd. & Galz., *Peniophora pithya* (Pers.) J. Erikss., and *P. septentrionalis* Laurila.

The fused heads of teliospores in *Nothoravenelia japonica* Diet. as discussed by Lohwag (1941) could well be considered in this section, as bulbiloid bodies. Comparison with *Daotutiophora* Leakey (1964) should also be made.

Eriksson & Ryvarden (1976) suggest that the *Aegerita* state of *Bulbillomyces farinosus* (Bres.) Jülich, found on wood on shores of lakes and by streams, is a means by which the fungus is dispersed by water; the diaspore is a floating unit in much the same way as conidia of *Helicium* (see discussions of aero-aquatic fungi in Chaps. 18, 24). The same authors (1976) also suggest that the soredia-like aggregations found in the *Laeticorticium roseum* complex should be termed hyphelia.

The condition in which basidiospore production in *Coprinus clastophyllus* is suppressed in favour of the formation of bulbiloid bodies (the *Rhaeoophyllus* anamorph) has been termed 'bulbillosis' by Singer (1962).
### (14A) TRUE BULBILS

<table>
<thead>
<tr>
<th>Teleomorphs</th>
<th>Anamorph</th>
<th>References</th>
</tr>
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<tr>
<td><strong>UNKNOW</strong>N BASIDIOMYCETES</td>
<td>Minimedusa polyspora (Huts.) Weresub &amp; Le Clair</td>
<td>Weresub &amp; Le Clair 1971.</td>
</tr>
<tr>
<td><strong>HYMENOMYCETES</strong></td>
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<tr>
<td><strong>Aphyllophorales</strong></td>
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### (14B) BULBILLOID BODIES

| **HYMENOMYCETES** | | |
| **Agaricales** | | |
| Coprinus clastophyllus Maniotis | Rhacophyllus lilacinus Berk. | Reijnders & Malencon 1969, Maniotis 1964, Watling pers. obs.: breaking up easily into unicellular chlamydospores, each capable of germinating: such anamorphs will probably be found in some other Coprinaceae. |
| | | Bondarzew 1953: chlamydospores in receptacles: this species also known as Heteroporus biennis (Bull.) Laz. Stalpers 1978. |
| Abortiporus biennis (Bull. ex Fr.) Sing. | | |
| Phellinus nigrolimitatus (Rom.) Bourd. & Galz. | | |

### (14C) CENTRIPETALLY DEVELOPING PROSENCYMATA

| **HYMENOMYCETES** | | |
| **Agaricales** | | |
| Coprinus cinereus (Schaeff. ex Fr.) S.F. Gray | Coccobotrys (Cenococcum) xylophilus (Fr.) Boud. & Pat. | Watling pers. obs.: microsclerotia free of the substrate in culture. Lohwag 1941: mycelial aggregates: may also be present in other Lepiota spp., esp. those associated with ant & termite nests. |
| Lepiota aff. meleagris (Sow. ex S.F. Gray) Quéhl. | | |

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* Baniecki & Bloss (1969) suggested that *S. brinkmannii* is the teleomorph of *Phyuratrichum omnivorum* (Shear) Duggar, but Weresub & Le Clair considered this most unlikely. Biggs (1937) reported bulbils in *Corticium coronilla*, which was synonymized with *Sistotrema brinkmannii* by Warcup & Talbot (1962); Rogers & Jackson (1943) dealt with this species under the genus *Trechispora.*
<table>
<thead>
<tr>
<th>Teleomorph</th>
<th>Anamorph</th>
<th>References</th>
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<tbody>
<tr>
<td>Rajapa eurhiza (Berk.) Sing.</td>
<td>Aegerita duthei Berk.</td>
<td>Petch 1913; this is what Ciferri (1935) called Termitosphaeria.</td>
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<tr>
<td>Aphyllorales</td>
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<td>Erikss. &amp; Ryv.</td>
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<tr>
<td>Bulbillomyces farinosus (Bres.)</td>
<td>Aegerita candida Pers. ex Fr. (=Sclerotium aegerita Hoffm. = Crocyporium aegerita Corda)</td>
<td>Lyman 1907: sub Peniophora candida: stalked bodies composed of radially arranged, branched, clamped hyphae with a palisade of swollen hyphal tips at the surface; placed in Metulodontia by Parmasto 1968a.</td>
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<tr>
<td>Jülich</td>
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<td>Hymenomycetes</td>
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<tr>
<td>Agaricales</td>
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<tr>
<td>Mycena citriicolor (B. &amp; C.) Sacc.</td>
<td>'Stilbum' flavidum Cke.*</td>
<td>Buller 1934, Salas &amp; Hancock 1972: better known as Omphalia flavida Maubl. &amp; Rangl.: this propagule was termed a gemma, and resembles a reduced, sterile, dehiscent cap: we propose the term 'cephalosus'.</td>
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<td>(14D) BULBILLOID BODIES IN SPLASH-CUPS</td>
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<td>(14E) BULBILLOID BODIES ON STALKS</td>
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<td>(14F) BROMATIA</td>
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* This use of the name *Stilbum* is incorrect, because it should be applied to a hymenomycetous Heterobasidiomycete (Donk 1958) or a stilbaceous ameroconidial Hyphomycete (Kendrick & Carmichael 1973).
Werexub & LeClair (1971) noted a clear differentiation of true sclerotia into rind and medulla, and also their development from an aggregation of hyphae. Anything which is not bulbil-like, and does not fall within the above circumscription of sclerotium, we have called a sclerotioid body: usually such a structure will be recognizably hyphal rather than pseudo-parenchymatous, and will lack tissue differentiation.

The best known examples of sclerotium-forming Basidiomycetes are some members of the genus *Typhula*, and the structure of the sclerotium is of considerable value in identifying species or species-groups (Remsberg 1940, Corner 1950). Until Berthier's work (1976) the presence of a sclerotium was thought to be diagnostic for *Typhula*. In contrast to true sclerotia, the microsclerotia formed by many fungi in culture, and undoubtedly in nature (cf. Warcup & Talbot 1962), are anatomically heterogeneous. Willetts (1971, 1972) has reviewed many aspects of the formation, germination, and survival of sclerotia.

We have given only a representative selection of those Basidiomycetes which produce sclerotia or sclerotioid bodies, since these propagules are really peripheral to our main theme. Nevertheless, it is the lot of the 'Deuteromycetologist' to cope with such non-conidial propagules, since few other people seem willing to look at them. Werexub is a notable exception to this, and we have based our arrangement of the various propagular hyphal aggregations on her work.

Watling (Chap. 19) has discussed the sclerotium-forming members of the Agaricales, and also mentioned the monilioid hyphae, constricted and septate to a greater or lesser degree, sometimes found in culture; these hyphae have been compared with *Moniliopsis* Ruhl (type: *M. aderholdii* Ruhl.). Similar hyphae are found in *Cryptopus volvatus* (Peck) Schum.

We have divided our records into three groups:

(A) True sclerotia
(B) Pseudosclerotia
(C) Sclerotioid hyphal aggregations (incl. *Rhizoctonia*; compare with *Orcheomyces* Burgeff)

Category C is not discussed further because it is doubtful whether such hyphal aggregations ever act as diaspores. They include the *Rhizoctonia globularis* anamorph of a *Sebacina* sp., (Warcup & Talbot 1966), the *R. goodyerae-repentis* Cost. anamorph of *Ceratobasidium cornigerum* (Bourd.) Rog. (Talbot 1965), and the *R. crocorum* (Pers.) DC. anamorph of *Helico-basidium brebissonii* (Desm.) Donk (Donk 1966), the type species of *Rhizoctonia*. Talbot (1965) and Warcup & Talbot (1967, 1971) give several teleomorphs of unnamed *Rhizoctonia* spp. in the genera *Ceratobasidium*, *Sebacina*, and *Tulasnella*.
<table>
<thead>
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<th>Anamorph</th>
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<td></td>
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<tr>
<td>Agaricales</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agrocybe arvalis (Fr.) Sing.</td>
<td>A. tuberosa (Henn.) Sing.</td>
<td>Lange 1938, Singer 1962.</td>
</tr>
<tr>
<td>C. sterquilinus (Fr.) Fr.</td>
<td></td>
<td>Warcup &amp; Talbot 1962.</td>
</tr>
<tr>
<td>Leucocoprinus birnbaumii (Corda) Sing.</td>
<td></td>
<td>Warcup &amp; Talbot 1962.</td>
</tr>
<tr>
<td>Omphalina sp.</td>
<td></td>
<td>Singer 1962: see also Murray 1886.</td>
</tr>
<tr>
<td>Pleurotus tuber-regium (Fr.) Sing.</td>
<td>Pachyma Fr.</td>
<td></td>
</tr>
<tr>
<td><strong>Aphyllophorales</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Athelia arachnoidea (Berk.) Júlich</td>
<td></td>
<td>Stalpers 1978.</td>
</tr>
<tr>
<td>A. neuhoffii (Bres.) Donk</td>
<td></td>
<td>Stalpers 1978.</td>
</tr>
<tr>
<td>A. rolfssii (Curzi) Tu &amp; Kimbr.</td>
<td>Sclerotium rolfssii Sacc.</td>
<td>Venkatarayan 1950: considerable dispute concerning the teleomorph - until recently referred to Botryobasidium</td>
</tr>
<tr>
<td>Cristella sphaerospora (Maire) Donk</td>
<td></td>
<td>Warcup &amp; Talbot 1962: see Trechispora, considered by many to be an earlier name for Cristella.</td>
</tr>
<tr>
<td>P. myliattae Cke. &amp; Mass.</td>
<td></td>
<td>Willis 1963: the large sclerotium is known as 'Black-fellow's bread'.</td>
</tr>
<tr>
<td>P. rhinoceros Cke.</td>
<td></td>
<td>Lohwag 1941.</td>
</tr>
<tr>
<td>P. sacer Fr.</td>
<td></td>
<td>Lohwag 1941.</td>
</tr>
<tr>
<td>Typhula gyrans Batsch ex Fr.</td>
<td>Sclerotium complanatum Tode ex Fr.</td>
<td>Donk 1962.</td>
</tr>
</tbody>
</table>
Teleomorph | Anamorph | References
---|---|---
Waitea circinata Warc. & Talb. | | Warcup & Talbot 1962.

HYMENOMYCETOUS HETEROBASIDIAE

Auriculariales


Tremellales


(15B) PSEUDOSCLEROTIA

HYMENOMYCETES

Agaricales


L. similis B. & Br.
L. velutinus Fr.

Panus badius (Berk.) Sing. | Sclerotoma Fr. | Pegler 1972.

P. fasciatus (Berk.) Sing. ex Pegler

Phlebopus colossus (Heim) Sing. | | Singer 1962.

Aphyllophorales

Polyporus aremosobasus Lloyd
P. basilapiloides (McAlp. & Tepp) Clel. & Cheel.

P. hartmanni Cke.
P. tuberaster Jacq. ex Fr. | 'Piedra fungaia' | Reid 1974b.

P. tumulosus Cke. & Mass.

Reid 1974b.
Willis 1963: rounded, rock-like mass of cemented fungal mycelium and sand grains: originally described as Laccocephalum McAlp. & Tepp.
Cunningham 1965.
Singer 1962: 'Stone fungus': incorporates vegetable and/or mineral material.
Cunningham 1965.

(16) CONIDIA IN PYCNIDIOID CONIDIOMATA (Fig. 12.9)

Only in the last few years have we become aware that a few coelomycetous anamorphs have basidiomycetous affinities. The only clear cut example so far published is Fibulocoeela indica Nag Raj (Nag Raj 1978), in which the hyphae bear numerous unmistakable clamp connections, and aggregate to form pycnidiod conidiomata within which holoblastic ameroconidia with an apical appendage are formed at the ends of branched fertile hyphae. Other coelomycetous basidiomycetous anamorphs are known but have not yet entered the literature. For a detailed discussion of F. indica see Chap. 12.
(17) BLASTIC-RETROGRESSIVE CONIDIA

The blastic-retrogressive mode of conidiogenesis was first recognized and demonstrated by Cole & Kendrick (1968), and was descriptively named at Kananaskis-I (Kendrick 1971). It may be defined as follows: A form of blastic conidiogenesis in which serial, retrogressive conidiogenous loci gradually convert a determinate conidiogenous cell or hypha into a basipetal chain of conidia.

Until very recently there was no suggestion that this kind of conidiogenesis was to be found among the Basidiomycetes. But as this book was in the final stages of preparation, just such a suggestion entered the literature. Evans, Stalpers, Samson & Benny (1978) have demonstrated that Monilia roreri Cif., an important pathogen of Cocoa in South America, has dolipore septa, and is thus a basidiomycetous anamorph. They also state that its conidiogenesis is basipetal, apparently resembling that of the Basipetospora rubra Cole & Kendr. anamorph of Monascus ruber van Tiegh. Since Monilia fructigena Pers., the type species of Monilia, is the anamorph of Monilinia fructigena (Aderh. & Ruhl.) Honey, an inoperculate discomycete, and forms conidia in acropetal chains, Evans et al. have proposed a new generic name, Moniliophthora, for their basidiomycetous, basipetal, cocoa pathogen. Moniliophthora roreri may be the first example of blastic-retrogressive conidiogenesis to be recorded among the Basidiomycetes. However, we have hedged our bets by also listing this species in section 10, thallic-arthric conidia.

DISCUSSION

The current preoccupation of many mycologists with pleomorphy in fungi is more in the nature of a renaissance than a new idea. Brefeld, a mycologist who was in many ways ahead of his time, believed in 1888 that an understanding of the processes of differentiation, both in the sexual state and during the formation of conidia in the vegetative phase, was essential for the elucidation of the true affinity and descent of the basidiomycetous fungi. Thus he derived the 'jelly fungi', herein catalogued as the hymenomycetous Heterobasidiae, from the smuts (Ustomycota) through replacement of the transversely septate basidium by a vertically divided basidium, intermediate stages being represented by the Uredinales and relatives of Hirneola (Auriculariales). He considered the 'Autobasidiomycetes' (Gasteromycetes and Hymenomycetes -- typified by a single-celled holobasidium) to have been derived from these 'Protobasidiomycetes' by the loss of the basidial septa. But at no time except at the generic level did he directly incorporate in this scheme the vast amount of information he had accumulated on conidial anamorphs. Brefeld was an authoritative spokesman, but it must be pointed out that not all of his contemporaries agreed with him: for instance Möller (1895) postulated separate origins for the Proto- and Auto-basidiomycetes.

Juel (1898) demonstrated that the fungus known as Stilbum vulgare Tode, at that time placed in the Hyphomycetes, really possessed a transversely septate basidium: in other words, it
was a Protobasidiomycete, though other species placed in *Stilbum* did not have this feature. This revelation led Massee (1900) to hypothesize on the origin of the Basidiomycetes, and on connections within the group, in his arguments leaning heavily on the structure of the conidiogenous hyphae. Strongly maintaining the homogeneity of *Stilbum*, as it was then defined, and basing his conclusions on Juel's observations, he suggested that *Stilbum microsporum* Cke. & Mass. and *Tuberularia volutella* Corda were also auriculariaceous. On the same grounds, he constructed a morphological series between *S. vulgare* and *Tuberularia vulgare* Tode (conidial *Neotria cinnabarina* (Tode) Fr.), which we now recognize as a synnematal Hyphomycete producing phialoconidia. Massee cited intermediate forms such as *T. volutella* and *T. subpedicellata* Schw., and concluded that the conidial phase of *Sphaerostilbe gracilipes* Tul. (*Stilbum fasciculatum* Berk. & Br.) was identical to that of *Himeola*. Massee also figured basidia for *Isaria pulcherrima* Berk. & Br., and drew parallels between it and *Pilocrella detectans* Møller, cementing his idea of a connection between Ascomycetes and Basidiomycetes by deriving the latter from the anamorphs of the former. Massee also tried to exemplify Brefeld's connection of the Autobasidiomycetes and Protobasidiomycetes by *Tulostoma*, with its basidium "agreeing in all essentials with the so-called conidiophore that passes directly into a typical Autobasidiomycete basidium." He compares his idea with the observations of *Matruchotia* (which, incidentally, he relates to *Stilbum* and *Isaria*) by Boulanger (1893), who reported the conidiophores as being cylindric-clavate and bearing 3-5 conidia at different levels. He used this to postulate that from the same basic anamorph one may derive the *Tulostoma* basidium, and thence the Autobasidiomycetes.

Massee also drew attention to the similarity, superficial though it now appears, between the conidial apparatus found in *Botrytis* sensu lato (*Cristularia* especially) and the basidia of a typical Autobasidiomycete, and illustrated basidia of *Coniophora ochracea* Mass. (= *Uthatobasidium ochraceum* (Mass.) Donk) as a species now considered intermediate between the 'jelly fungi' and the resupinate Hymenomycetes. Finally he considered that *Isaria umbrina* Pers. (conidial *Hypoxylon*), and *Triehoderma viride* Pers. (conidial *Hypoarea* *Pufa* (Pers. ex Fr.) Fr.), were comparable to Autobasidiomycetes.

From what we now know about the development and karyology of these fungi, it is easy to find Massee and Brefeld's theories in error, and to be condescending toward their seemingly wild ideas. Yet it is also now easier for us to recognize the parallels that exist between the anamorphs of Ascomycetes and Basidiomycetes. We have long known that *Oedosaphalum*-like anamorphs are produced by members of both classes: only recently have they been segregated at the generic level. The anamorph of *Phleospora faginea*, although frequently referred to *Rhinotrichum* (Shear & Dodge 1925), resembles a *Nodulisporium*, though that form-genus is usually associated with *Xylariaceous* Ascomycetes. Whether such parallels imply deep-rooted relationships between the major groups is a question we are not yet qualified to answer (though we are inclined to suspect convergent evolution -- different groups coming up with the same or similar solutions to problems associated with the formation and dispersal of mitospores).

Although our temerity does not, perhaps, equal that of a Massee or a Brefeld, we do believe that in the foregoing compilation many interesting connections and relationships await recognition. We hope that, by making it available, we have done something to hasten the process.
We wish to acknowledge the award of a fellowship to B.K. by the Royal Society of London, which permitted him to study in Edinburgh during the summer of 1974 while on sabbatical leave. Without this assistance, it is doubtful whether the vast amount of time required to scan the literature could have been made available. We also extend sincere thanks to Dr. L.K. Weresub, who provided invaluable information and insightful comments throughout the preparation of this chapter.
The Evolution of Anamorphs in the Uredinales

D.B.O. Savile

INTRODUCTION

Hughes (1970) discussed and illustrated the ontogeny of spore formation in Uredinales. Savile (1976) discussed the elaboration of the various spore states from the viewpoint of evolution and the combatting of ecological problems. The evolutionary approach helps us to recognize homologies. We cannot hope to reach a phyletic and permanently useful classification if we neglect the ecological aspects; for, in doing so, we blind ourselves to the immense frequency of ecologically stimulated convergent evolution in these fungi. In the context of the fungi in general, all the spore states in the rusts provide examples of convergence; for they employ patterns of spore formation found in other conidial fungi (Hughes 1970), but all the accessory spore states certainly arose de novo in the rusts, and the first rusts produced only simple teliospores, by the rounding up of mycelial cells in the host tissues, and the basidiospores that are the products of their meiotic divisions. We should not be surprised at such convergences, for there are only a limited number of mechanisms by which the critical processes of the formation and release of spores can be achieved.

This paper attempts briefly to place the rusts in context with other conidial fungi, but for some details and documentation the reader is referred to Hughes (1970) and Savile (1976).

The first anamorph to evolve was surely the uredinium, although it may have been closely followed by the pycnium. The aecium was the last spore state to evolve, having been modified from the uredinium after adoption of heterospermism.

UREDINIA AND UREDINIOSPORES

Urediniospores are dikaryotic conidia that allow extensive dispersal as well as great population increase. Effective dispersal must have been strongly adaptive, because the small and delicate basidiospores are short-lived. Urediniospores are pedicellate, the spore mother-cells being produced successively round the apices of meristematic basal cells (Figure 21.1) (sympodial, Hughes 1970). Urediniospores are always one-celled except for occasional two-celled ones in Gymnosporangium gaeumannii, found in mixed sori with the normally two-celled teliospores, through a slight relaxation of epigenetic control. Urediniospores routinely separate from their pedicels at the middle lamella of the septum between spore and pedicel.

Even in Uredinopsis, which host relationship and comparative morphology indicate to be the most ancient extant genus, spore formation and release are essentially as in more modern
Figure 21.1 Uredinal basal cell of *Uromyces viciae-fabae*; mature spore and pedicel (centre); spore mother-cell dividing into spore and pedicel (right); initial lobe of mother-cell (left) with premitotic nuclei distorted by streaming.

Figure 21.2 Pycnium types, adapted from Hiratsuka & Cummins (1963). Types are defined by position in host tissue, lateral extent and shape of hymenium, and presence or absence of bounding hyphae. Type 2 is probably most primitive.

Figure 21.3 Aeciospore column in *Uromyces viciae-fabae*, showing two immature spores with intercalary cells cut out of lower corner, nearly mature and young spore mother-cells, and a meristematic basal cell in conjugate telophase. (all printed, with permission, from Savile 1976, Evol. Biol. 9:137-207)
genera. There have been claims of sessile urediniospores in a few inadequately studied genera; but the delicate pedicels in many of the older genera shrivel beyond recognition in herbarium material (Moss 1926). No such claims can be accepted unless based on cytological preparations from fresh material.

The uredinia of Uredinopsis possess a very delicate peridium (a structure greatly elaborated in some more advanced Pucciniastraceae). The maturing urediniospores point into the central ostiole of the peridium. As each spore bears a sharp apical spine, the sorus is substantially protected from very small arthropods. Shed spores may be eaten, but the meristematic basal cells are protected as long as sporulation is active. The Devonian springtail Rhynia-la is now assigned to a group of families whose modern members are all spore and pollen eaters (Kevan et al. 1975). Thus Uredinopsis, or something very close to it, may have appeared well before the end of the Devonian. Such an unspecialized peridium was presumably the starting point for the functionally and structurally distinct peridium of the aecium.

PYCNIA AND PYCNIOSPORES

In the first rusts the dikaryon was presumably established by hyphal fusions between compatible monokaryons, as still occurs in self-sterile species of the phylogenetically related simple ascomycete, Taphrina. When urediniospores allowed increasingly sparse infections at the periphery of the range, gene flow between populations, as distinct from recombination within the offspring of a single teliospore, may have caused strong selection for the formation of monokaryotic conidia. Such conidia would decrease the average distance between monokaryons. Modern pycniospores are regularly cut off in basipetal succession from the apices of cylindrical sporogenous hyphae. Whether the sporogenous cells are always true phialides, as Hughes (1970) suggested, is a moot question. In detailed cytological examination of several Puccinia, Uromyces and Melampsora species (Savile 1939), employing various fixation, mordanting and staining techniques, I saw no indication of a collarette. The apex of the sporogenous cell seemed to be so thin as to be essentially fluid, with its form maintained by forces within the cell. With such thin walls the presence or absence of a collarette is perhaps a somewhat arbitrary distinction. It should be noted that as soon as a pycniospore is released, its base becomes rounded, indicating that the wall is still not rigid.

Mycelial tips, both monokaryotic and dikaryotic, project occasionally through stomata and rarely between epidermal cells in many temperate rusts; but they are usually short-lived, those in the stomata sometimes being pinched off by the closing guard cells. They seem to serve no function, for they are much too rare and erratic in occurrence to serve as receptive hyphae even if their protoplasm were not quickly disorganized. In a tropical fern swamp, however, such emergent hyphae may well have persisted and cut off small conidia. As evolution progressed, these simple conidiophores became grouped together and associated with nectar that attracted insects. Specialized receptive hyphae allowed direct transfer of spore nuclei into a compatible mycelium; and the pycnia, as we may now call them, became associated with the fundamentals of primary uredinia. Eventually the pycniospores lost the ability to form germ tubes, their nuclei passing through slightly papillate pores into receptive hyphae; and they now contain minimal cytoplasm and lipids.

The pycnium, with sperm cells, receptive hyphae and insect-attracting nectar, is an organ
that evolved within, and is unique to, the rusts. It is analogous to an entomophilous perfect flower. To term it a spermogonium is to obscure two of its three functions and can only confuse students. To do so is equivalent to calling the flower an anther.

Hiratsuka and Cummins (1963) set up eleven pycnium types, based on the form and position of the layer of sporogenous cells and the presence or absence of bounding hyphae or periphyses (Fig. 21.2). Hiratsuka & Hiratsuka (1977 and in preparation) have recently added a type 12, somewhat intermediate between types 1 and 4. Pycnium morphology is relatively stable, largely at least because the organ is protected from the external environment by the host tissues and its own nectar drop. Position (subcuticular, intraepidermal or subepidermal) is somewhat variable; but structure is unusually constant, and is a good guide to relationships in the higher rusts, in which convergent similarity in the teliospores can be very misleading (Savile 1976). Pycniospore production seems to be essentially the same in all types.

In Pucciniastreaceae, pycnium type is 1, 2 or 3. In Melampsoraceae, a complex whose internal relationships are still far from clear (Savile 1976), we find types 2, 3, 4, 5, 7, 8, 9 and 12. In Pucciniaceae sensu stricto we find only type 4. In Raveneliaceae we find types 5 and 7. In Phragmidiaceae we find types 6, 8, and especially 10 and 11. The types (6, 10 and 11) confined to Phragmidiaceae probably evolved in the Tertiary, for all the hosts of this family are decidedly modern. Most of the other types must date back to early or mid Cretaceous, and types 1, 2 and 3 may be much older than Cretaceous. It is possible that type 2 evolved in the late Devonian.

AECIA AND AECIOSPORES

The aecium was plainly the last state to evolve, and resulted from the initiation of heteroecism. Heteroecism involves a severe population decrease twice each year; and it could only have been selected for after the establishment of uredinia and pycnia, and then only in response to a drastic need (Savile 1976). Apparently a changing climatic regime involving a dry season caused the fern fronds to die down. With the resumption of rain, basidiospores presumably germinated promptly, before the rising water table allowed new fern fronds to expand. Until a teliospore dormancy mechanism could evolve, the only alternative to extinction was to infect an adjacent progymnosperm, which had a deep enough root system to remain active through the dry weather. As we approach arctic or alpine tree line, obligately heteroecious rusts occur only with increasingly close proximity of the two hosts until they are in intimate contact just inside tree line, where few uredinia can be formed before they give way to telia. Clearly the initiation of heteroecism, with at first imperfect adaptation to a new host, could not succeed without several uredinial generations per annum to offset the population loss. Similarly, pycniospores (or their predecessors) would have to be available to aid dikaryotization of the increasingly scattered monokaryons that resulted from longer mean travel of basidiospores. Thus the other accessory states clearly preceded the aecium.

Both cytology and morphology indicate that the aecium is derived from the uredinium (Savile 1959, 1955). In particular, the intercalary cell, which invaginates a lower corner of the aeciospore above it, is plainly homologous with the pedicel of the urediniospore. The morphological changes involved in the evolution of the aecium reflect the mechanical problems involved in rupturing the presumptively heavy epidermis of a progymnosperm leaf. The delicate
uredinial peridium, probably much like that of *Uredinopsis*, evolved into a domed structure of thick-walled, nearly isodiametric cells, analogous to an Eskimo snow-house. As so often happens, a structure that evolved in response to one problem was modified to perform a new function. Further upthrust results from the meristematic basal cells cutting off the spore mother-cells one above the next in cylindrical columns, with little or no intervening space. The final division into spore and intercalary cell takes place with oblique spindles. The rules of the partitioning of space tell us that, when a cell is to be cut off that is a small proportion of the total volume of a cylinder (Thompson 1948, Savile 1954), it must be cut off in the corner of the cylinder with a curved septum that meets the end and side walls of the cylinder at right angles (Figure 21.3). A familiar example of this principle is a bubble in the corner of a drinking glass. Although growth forces may slightly distort it, this form of intercalary cell survives in all aecia whose spores are forcibly discharged, for the excellent reason that it serves as a fulcrum for the spore above it. In the aecidioid aecium that we see in most *Puccinia* and *Uromyces*, the whole structure is coordinated to facilitate spore discharge. The peridial cells have thick outer and thin inner walls, so that under turgor they curve outward, away from the paths of ejected spores. The inner walls have slender digitate warts that serve as compression springs to maintain lateral pressure on the spores. The aeciospores are finely and closely verrucose, so that few will fall out until turgor and upthrust from the column are sufficient to ensure vigorous propulsion. When lateral friction is finally overcome, the invaginated lower wall snaps outward against the intercalary cell, and the spore is thrown outward, often for 10 mm or more (Savile 1954). The thin-walled intercalary cell is turgid to the moment of spore ejection. At that time it probably swells and bursts, adding to the thrust on the spore; for we never see recognizable intercalary cells either on the slide in spore discharge tests or above the uppermost spore of a chain in cytological sections.

If aeciospores are regularly formed in dry weather, when adequate turgor may not be achieved, as in the repeating aecia of *Puccinia palmeri* or *P. rufescens* (Savile 1968), or in most species of *Gymnosporangium*, we may see several correlated changes. The peridial cells become nearly symmetrical; their digital warts become shortened; the peridia do not recurve but are cylindric to cornute with narrow marginal slits, through which the spores sift when wind is adequate to ensure dispersal; and the spore walls are pigmented as a protection from desiccation (Savile 1976).

There is great morphological variation in aecia, which can be assigned to four form genera: *Peridermium*, found in many conifer rusts, has a stout cylindric peridium that does not recurve; *Caeoma* has no peridium and is best known in *Melampsora* and *Phragmidium*; *Aecidium*, with a recurving peridium as described above, occurs in most *Puccinia* and *Uromyces*; and *Roestelia*, with a cornute peridium, is seen principally in *Gymnosporangium*. Yet the basic pattern of spore formation is common to all rusts that possess a true aecial state.

**TELIA AND TELIOSPORES**

In *Pucciniastraceae*, which includes the fern rusts (*Uredinopsis*, *Milesina* and *Hyalopsora*) and several genera predominantly on old woody dicotyledons, the teliospores are simply rounded up cells or groups of cells within the host tissues; and in most genera they are so scattered that we can hardly speak of them as forming sori. Only when we reach *Melampsoraceae*, with
variously erumpent telia, does increased exposure to the environment allow rapid evolution of the telia. Finally, as we reach the families Pucciniaceae, Raveneliaceae and Phragmidiaceae, the teliospores become individually pedicellate and start to take on a new function, that of diasporic conidia. Ancestrally the teliospore housed nuclear fusion and meiosis, bore the basidiospores, and often served as a resting spore. From studies of several genera in each of these advanced families it appears that pedicellate teliospores are invariably formed successively from a meristematic basal cell, in exactly the same way as urediniospores are produced; but the method has arisen de novo at least once in each family, probably through a displacement of the epigenetic control system that is uniformly present in uredinia.

Apparently even firm-pedicelled teliospores are occasionally broken free by the upthrust of younger spores in the sorus. This spasmodic release of the spores as extra diasporas was enough to stimulate selection for any means by which spore release could be facilitated. With the advanced teliospores taking on the added role of diasporas, we have an anomalous situation with the spores that are defined as representing the sexual state being also functioning conidia. They therefore come within the scope of this paper.

In a substantial, but far from complete, study of teliospores and their pedicels, I found (Savile 1976) that effective teliospore release has evolved in 15 genera of the three families, by nine mechanisms, for a total of 49 separate initiations of spore release. The findings are summarized in Table 21.1, which shows that four methods have evolved independently in two families, and that one has evolved in all three families.

Passive separation at the middle lamella between spore and pedicel (universal in urediniospores) is very rare, being known to me only in two closely related Uromyces. We are thus reminded that, although urediniospore release was established, once and for all, very early in the evolution of the rusts, teliospore release is a modern phenomenon, still evolving in three families. Localized weakening of the pedicel, near the apex, middle or base, through thinning, perforation or gelatinization of its wall, sometimes assisted through lifting by the swelling of sterile cells or the pedicel base, have evolved repeatedly. Separation at the middle lamella does occur in Trachyspora (Phragmidiaceae), but this is a forcible discharge, powered by turgor in the upper cell of a septate pedicel extending the thin apex until the ring of thin primary wall is ruptured.

The perfection of spore release is usually accompanied by morphological changes that reflect new functions: spore walls are of nearly equal thickness throughout, rather than very thick at the apex as in spores held in the sorus; the germ pores tend to drift from the apical and septal positions; and the walls become sculptured, which adds buoyancy to a diaspare.

The multiple evolution of methods of teliospore release emphasizes the importance of adding another diaspare to the life cycle. The importance is particularly great in highly evolved rusts with a strong tendency to eliminate the aecia or uredinia or both. Clearly we must not be too surprised (or unduly disappointed) if a method of spore formation or spore release known in other fungi proves to have evolved more than once. With a limited number of possible means for achieving an important function, convergent similarities turn up repeatedly in all organisms.

Finally, we must recognize, after this brief summary of teliospore evolution, that it is not possible to define teliospores by precise homology: during evolution of these spores more
and more cell divisions have been intercalated between the functioning teliospore cell and the hyphae from which it originated. A teliospore may be a rounded up mycelial cell that may or may not become septate; one of a palisade of united or free modified hyphal tip cells; one of two or more tip cells cut off from a meristematic basal cell; the upper part of such a cell that has divided into spore and pedicel; a spore such as the last, divided into two to many cells; or finally (in Ravenelina) an elaborately compound spore of many cells, subtended by a circle of swelling sterile cells and supported by a compound pedicel. The most practical definition is perhaps a pragmatic one that states it to be a cell or permanently united group of cells within the soralus, any of which houses a fusion nucleus, and produces a basidium in which meiosis occurs and which normally bears basidiospores.

### TABLE 21.1. MULTIPLE EVOLUTION OF TELIOSPORE RELEASE MECHANISM.

<table>
<thead>
<tr>
<th>Device</th>
<th>Occurrence</th>
<th>Number of origins</th>
<th>Family</th>
</tr>
</thead>
<tbody>
<tr>
<td>Separation at middle lamella of hilum by upthrust of young spores</td>
<td>Uromyces</td>
<td>1</td>
<td>Pu</td>
</tr>
<tr>
<td>Separation at middle lamella of hilum by evagination of pedicel apex</td>
<td>Trachyspora</td>
<td>1</td>
<td>Ph</td>
</tr>
<tr>
<td>Rupture of pedicel below apical thickening by upthrust of young spores</td>
<td>Puccinia-Uromyces (20+), Ravenelina, Prospodium, Sphaerophragmium, Triphragmium, Xenodochus, Cleptomyces</td>
<td>25</td>
<td>Pu, Ra, Ph</td>
</tr>
<tr>
<td>As last but by pressure of gelatinous sterile cells</td>
<td>Uromycladium, Ravenelina</td>
<td>2</td>
<td>Ra</td>
</tr>
<tr>
<td>Separation of pedicel base, without swelling</td>
<td>Puccinia (3), Prospodium, Ravenelina, Uropyxis, Phragmopyxis, Dipyxis, Cumminsiella</td>
<td>7</td>
<td>Pu, Ra</td>
</tr>
<tr>
<td>Separation at lysed fracture zone in pedicel</td>
<td>Phragmidium, Uropyxis, Ravenelina</td>
<td>3</td>
<td>Ph, Ra</td>
</tr>
<tr>
<td>Separation by localized gelatinization of pedicel</td>
<td>Uropyxis (3 types), Phragmopyxis (2 types), Puccinia (2)</td>
<td>7</td>
<td>Ra, Pu</td>
</tr>
<tr>
<td>Swelling and bursting of pedicel</td>
<td>Puccinia</td>
<td>1</td>
<td>Pu</td>
</tr>
<tr>
<td>Swelling causing lifting and basal rupture</td>
<td>Puccinia, Phragmidium</td>
<td>2</td>
<td>Pu, Ph</td>
</tr>
<tr>
<td>Total probable origins</td>
<td>49</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Ph = Phragmidiaceae, Pu = Pucciniaceae, Ra = Raveneliaceae
Most of this book has been concerned with fungi whose teleomorphs could be described as undoubted Ascomycetes or Basidiomycetes. But we can hardly afford to neglect that great category, the 'yeasts'. Though they are clearly fungi, it did not become clear until very recently to which of the major taxa they belonged. And now we have this information, we discover that the 'yeasts' are indeed phyletically heterogeneous. The next chapter will reveal the full spectrum of organisms now grouped under the rather misleading 'yeast' label, and the concept of anamorph and teleomorph will be shown to apply just as well to 'yeasts' as it does to other fungi....
Propagation in the Yeasts and Yeast-Like Fungi

J.A. Von Arx

The yeasts in general are characterized by the absence of hyphae, either coenocytic or septate. Their thalli usually consist of small cells which propagate by budding or fission (Lodder 1970, von Arx et al. 1977).

Research workers who concern themselves with yeasts are referred to as zymologists. These specialists are often quite removed and distinct from mycologists who work with filamentous fungi. This is at least partly because the methods used in taxonomy of filamentous fungi and yeasts have developed along different lines. The characterization and identification of yeasts involves fermentation and assimilation patterns of carbohydrates, and additional characters such as utilization of nitrate, inositol and other substances, or growth on vitamin-free media.

Type specimens are unknown in yeast taxonomy: zymologists designate a living strain as the type. Usually only one name is used for a species; there are no separate names for teleomorphs and anamorphs. When the teleomorph is discovered in a species hitherto only known as an anamorph, the name of the latter is no longer used. Many yeasts, however, generally develop only the anamorph. The formation of the teleomorph requires special cultural conditions, such as poor, acid media (containing sodium acetate) (van der Walt in Lodder 1970). In heterothallic yeasts the teleomorph develops only in mating experiments on appropriate media.

The position of the yeasts in the fungal system is still problematic. A great number of yeasts form endogenous spores in asci following meiosis, that is, in addition to their blasto- or arthroconidia. These yeasts have been accordingly placed in the Ascomycetes, usually in a separate subclass, the Hemiascomycetes. Small groups of yeasts have been placed in the Aphyllorphorales of the Basidiomycetes.

The yeasts are, indeed, phylogenetically heterogeneous. This is shown, not only by morphological characters visible under the light microscope, but also by submicroscopical, chemical, physiological and serological characters. It has been shown, mainly by such characters, that the yeasts with asci are not closely related to the true Ascomycetes. In this respect Heller & Smith (1966) wrote: "Nearly as many differences exist between the composition of the nucleic acids of Neurospora and Saccharomyces as there do between Neurospora and man" (Demoulin 1970). Some arguments for the exclusion of the ascus-producing yeasts from the Ascomycetes, and their segregation as Endomycetes, are summar-
Fig. 22.1  A, Dipodascus australiensis Arx & Barker, gametangial branches, young asci and arthroconidia; B, Ascoidea africana Batra & Francke-Grosmann, ascophore with many-spored asci and a young, proliferating ascus; C, Saccharomycopsis vini (van Rij) van der Walt & Scott, ascogenous hypha with asci and ascospores; D, Hyphopichia burtonii (Boidin et al.) Arx & van der Walt, conidiogenous hyphal cells forming blastoconidia on denticles, and conjugating conidia becoming asci. ca. x1100.
Fig. 22.2  A, Ambrosiozyma monospora (Saito) van der Walt; B, Ambrosiozyma cicatricosa (Scott & van der Walt) van der Walt; C, Botryoascus synnedendrus (van der Walt & Scott) Arx; D, Saccharomyces vini (van Rij) van der Walt & Scott, conidiogenous structures and conidia. ca. x1200.
Fig. 22.3 *Hormoascus platypodis* (Baker & Kreger-van Rij) Arx, ascophores with catenate asci. x1500.
ized in Table 22.1.

Table 22.1.

<table>
<thead>
<tr>
<th>% GC of DNA</th>
<th>Endomyctes</th>
<th>Ascomycetes</th>
<th>Ustomycetes</th>
<th>Basidiomycetes</th>
</tr>
</thead>
<tbody>
<tr>
<td>% chitin in the cell wall</td>
<td>&lt; 50</td>
<td>&gt; 50</td>
<td>&gt; 50</td>
<td>&gt; 50</td>
</tr>
<tr>
<td>% mannann in the cell wall</td>
<td>&gt; 5</td>
<td>&lt; 5</td>
<td>&lt; 5</td>
<td>&lt; 5</td>
</tr>
<tr>
<td>simple septal pores</td>
<td>-</td>
<td>+</td>
<td>(+)</td>
<td>-</td>
</tr>
<tr>
<td>dolipores</td>
<td>-(-)</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>micropores (plasmodesmata)</td>
<td>(+)</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>diploid vegetative cells</td>
<td>(+)</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>fruit bodies/hymenia</td>
<td>-</td>
<td>+(-)</td>
<td>-</td>
<td>+(-)</td>
</tr>
<tr>
<td>&lt; less than</td>
<td>&gt; more than</td>
<td>absent</td>
<td>+ present</td>
<td></td>
</tr>
</tbody>
</table>

In general, the yeast cell can be considered to be a conidium. This may be a blastoconidium or an arthroconidium. In yeast text books (e.g., Lodder 1970), three types of asexual reproduction are considered:

1. fission cells, comparable with arthroconidia.
2. bipolar budding, comparable with formation of blastic conidia in basipetal succession on percurrently elongating cells.
3. multilateral budding, comparable with formation of synchronous or sympodial blastoconidia, with a very narrow or relatively narrow base.

There are generic names for conidial yeasts, e.g., Candida, 'Torulopsis', Cryptococcus, Trichosporon or Rhodotorula. Some connections between the teleomorphic and anamorphic names are given in Table 22.2:

Table 22.2:

<table>
<thead>
<tr>
<th>Endomycetales</th>
<th>Teleomorph</th>
<th>Anamorph</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dipodascaceae</td>
<td>Dipodascus Fig. 22.1a</td>
<td>Geotrichum Figs. 22.1a, 22.4a</td>
</tr>
<tr>
<td>Ascoideaceae</td>
<td>Saccharomyces Fig. 22.1c</td>
<td>Candida Fig. 22.2d</td>
</tr>
<tr>
<td></td>
<td>Stephanosacous</td>
<td>Candida</td>
</tr>
<tr>
<td></td>
<td>Rhypophichia Fig. 22.1d</td>
<td>Candida, Trichosporon Figs. 22.1d, 22.4b</td>
</tr>
<tr>
<td>Saccharomycodaceae</td>
<td>Botryosacous</td>
<td>Raffaelea Fig. 22.2c</td>
</tr>
<tr>
<td>Saccharomycetaceae</td>
<td>Hanseniaspora</td>
<td>Kloeckera</td>
</tr>
<tr>
<td>'Debaryomyces'</td>
<td>Saccharomyces</td>
<td>Torulopsis</td>
</tr>
<tr>
<td>Torulaspora</td>
<td>Torulaspora</td>
<td>Torulopsis</td>
</tr>
<tr>
<td>Dekkera</td>
<td>Brettanomyces</td>
<td></td>
</tr>
<tr>
<td>Issatchenkia</td>
<td>Candida</td>
<td></td>
</tr>
<tr>
<td>Metschnikowiacaeae</td>
<td>Metschnikovia</td>
<td>Candida</td>
</tr>
<tr>
<td>Sporobolomyctaceae</td>
<td>Aessosporon</td>
<td>Sporobolomyces Fig. 22.6a</td>
</tr>
</tbody>
</table>
Table 22.2 clearly shows that the large form genera Candida and Torulopsis must be heterogeneous. The genus Candida comprises species which are anamorphs of Ascoideaceae, Saccharomyces, Metschnikowiaceae, and the ustilaginaceous genus Leucomonomosporidium. Some Torulopsis species belong to Saccharomyces and similar genera, some to Basidiomycetes.

The Dipodascaceae contains only one genus, Dipodascus (Fig. 22.1a), all species of which have Geotrichum anamorphs (Figs. 22.1a, 22.4a). The asci develop singly from conjugating gametangial tips and are 1- to many-spored. The hyphae are septate, and the cells are connected by few or many small pores, described by Wilsenach & Kessel (1965) as micropores (see also Cole 1975). Kreger-van Rij & Veenhuis (1972) again observed these pores in several species and called them plasmodesmata. The conidiogenous hyphae form new inner walls, the cross-walls are often thicker than the new lateral walls and become double at maturity, at which time the old, outer wall breaks open (Fig. 22.4a).

A further genus usually classified in the imperfect yeasts, and which has hyphae forming fission cells, is Trichosporon. In its type species, T. beigelli (Küchenmeister & Raben.) Vuill., the septa have dolipores without pore caps, indicating a relationship to the Basidiomycetes. The formation of the fission cells is similar to that in Geotrichum. Besides fission cells, blastoconidia with a broad, truncate base are often formed sympodially or singly (Fig. 22.4b). Teleomorphs are unknown. The genus Trichosporon must be restricted to species with dolipores.

The yeasts classified in Schizosaccharomyces are also unrelated to Geotrichum-Dipodascus. They have no septate hyphae, only fission-cells being produced. In elongated cells, a double crosswall is formed which splits at maturity (Fig. 22.4c). The cells are haploid; conjugating cells become asci containing 4 to 8 thin-walled spores.

The Ascoideaceae (or Endomycetaceae, see Redhead & Malloch 1977) comprise yeast-like fungi with multi-nucleate, septate hyphae. In general the asci are formed on the hyphae, often in a catenulate or botryose manner, and the ascospores are hat-shaped or saturnoid. In the typical species of the genera Ascoidea (Fig. 22.1b) and Saccharomyces (Figs. 22.1c, 22.2d) the hyphal septa are provided with micropores, and this indicates a relationship to Dipodascus. However, they form blastoconidia with a usually broad, truncate base, leaving indistinct scars after release. These blastoconidia are often formed sympodially or in acropetal chains. Similar hyphae and conidia which leave scars are observed in the genera Ambrosiozyma (Figs. 22.2a, 22.2b) and Hormoascus. Sometimes the conidiogenous cells are phialide-like, but elongate during formation, leaving annellations, or lateral scars when elongating sympodially at a later stage (von Arx 1972, 1973). In both genera the septa of the hyphae have centrally plugged dolipore-like structures, as observed with the electron microscope by Kreger-van Rij & Veenhuis (1969). Both genera exclusively comprise ambrosia fungi from bark beetles. The
Fig. 22.4  A, Geotrichum candidum; B, Trichosporon beigelii; C, Schizosaccharomyces octosporus, formation of conidia.
Fig. 22.5  A, Saccharomyces ludwigii, bipolar budding; B, Hansenula anomala, multilateral and acropetal budding and 3 ascospores.
Fig. 22.6 A, Sporobolomyces sp., formation of conidia and ballistospores, B, Filobasidium oapsuligenum, formation of blastoconidia, conjugating blastoconidia, erect hyphae with clamp connections and forming an acropetal whorl of "sporidia".
asci develop on erect hyphae; catenate in Hormoascus (Fig. 22.3) and clustered in Ambrosiosis.

The hyphae are haploid in Stephanoascus eiferrii Smith et al., Hyphopichia burtonii (Boidin et al.) v. Arx & van der Walt, and in Saccharomycopsis lipolytica (Wickerham et al.) Yarrow. The latter species may represent an as yet undescribed genus. As far as is known, the septa of these fungi have no pores. Kreger-van Rij & Veenhuis (1973) observed a single, central, dark line in the wall between adjacent cells; either a micropore or the line of contact of the centripetally developing septum. The blastoconidia develop sympodially or synchronously, and have a rather narrow, often denticulate base or leave denticles after release (Sporothrix-like). In Stephanoascus eiferrii a persistent ascus develops in a cell arising from two conjugating hyphal tips as a lateral outgrowth (Smith et al. 1976). In Hyphopichia burtonii (Fig. 22.1d) two conjugating yeast cells form a non-persistent ascus containing 2-4 small, hat-shaped ascospores (von Arx & van der Walt 1976).

Cephaloascus fragrans is the only known filamentous yeast-like fungus which has septa with a simple, central pore (Kurtzman 1977), indicating a relationship to the Ascomycetes (Cain 1972). A clamp-like, lateral branch conjugates with the adjacent hyphal cell. From the resulting cell, upright ascophores develop on which the asc i form in a whorl of long chains. Acropetal, branched chains of conidia are formed on the haploid hyphae (Hyalodendron-like).

Some more genera of filamentous yeast-like fungi have been keyed out by von Arx et al. (1977). Some of them form only hyphae and asci, and no conidia.

The so-called apiculate, bipolar yeasts are classified in the family Saccharomycodaceae. Septate hyphae are absent. The yeast cells are elongate and the daughter-cells are formed in basipetal succession at the ends of the biapiculate mother-cell, leaving broad scars; some indistinct annellations can often be observed (Fig. 22.5a). The yeast cells are usually diploid, e.g., in Saccharomycodes and Hanseniaspora. The apiculate yeasts are not closely related to the multilateral yeasts classified in the Saccharomycetaceae.

In the Saccharomycetaceae the bud can develop on any part of the yeast cell. The daughter cells are formed singly or in acropetal chains. Several buds may develop at different places on a single yeast cell, and this budding is called multilateral. The daughter cells are connected by a narrow base to the mother cell, and leave a small, inconspicuous scar after release. An old mother cell may be covered with numerous small scars (Fig. 22.5b).

In typical Saccharomyces species, such as S. cerevisiae, the yeast cells are diploid and each cell may become a persistent ascus containing 2-4 spherical ascospores. In the species of the genus Zygosaccharomyces, the yeast cells are haploid and two conjugating yeast cells become an ascus. Some other genera also have haploid yeast cells, e.g., Torulaspora and 'Debaryomyces', in which asc i are formed without conjugation of separate cells. In some cases 'conjugation' of mother-cell and unreleased daughter-cell has been observed. The distinction of the genera is difficult and cannot be based on morphological characters alone. Important additional characters are the chitin content of the cell wall, the co-enzyme Q, the ability to ferment certain sugars, to assimilate inositol, or to utilize nitrate. Some genera such as Hansenula and Piowia are characterized mainly by the shape of the ascospores, which are hemispherical or hat-shaped. The cell walls of the Saccharomycetaceae in general contain less than 1% chitin, and this is also the case in some mycelial yeasts, for example
in the species of the genera Ambrosiozyma and Hormoascus or in Nematospora, Ashbya, Eremothecium and Crebrothecium. In the last four genera, hyphal cells become 'asci' which usually contain a large number of acicular ascospores. Budding cells are present only in the genus Nematospora. The budding is synchronous or sympodial with a narrow base, the budding cells often forming acropetal chains.

In the red yeasts, which are classified in the Sporobolomycetales of the Ustomycetes (Moore 1972), conidiogenesis is only imperfectly understood, but it differs from that of the Saccharomycetales. Budding may take place at random, but there is usually a single conidigenous locus, and the conidia are formed in basipetal succession. The yeast cell can be compared with a phialide, an inconspicuous collarette occasionally being observed. In Sporobolomyces, ballistospores are formed in addition to the yeast cells. These spores develop superficially on erect, sterigma-like outgrowths, singly or sympodially, and are discharged in the same manner as the basidiospores of many Basidiomycetes (Fig. 22.6a).

In Sporidiobolus and other genera, thick-walled, diploid resting spores are formed after conjugation. Septate hyphae can also be observed and these may be provided with clamp connections; but only simple pores have been observed in the septa.

Clamp connections and septal dolipores are known in the species of the genera Filobasidium and Filobasidiella. These genera, therefore, have been classified in the Aphylllophorales of the Basidiomycetes (von Arx et al. 1977). All species are heterothallic, and the haploid states are yeast-like, forming only roundish, rather thick-walled budding cells (form-genus Cryptococcus). The budding takes place in sympodial succession; the base is rather broad, and a septum is formed between the mother-cell and its bud. In old mother-cells several adjacent scars can be observed. In mating experiments, two yeast cells conjugate. They develop thick-walled, often erect, branched hyphae with clamp connections at the septa. In the apical part of these basidium-like hyphae, meiosis occurs and a cluster of aerial blastospores is formed (Fig. 22.6b). Single-spore cultures of Filobasidium capsuligenum (Fell et al.) Rodrigues de Miranda showed that this species is 'bipolar', but about 30% of the cultures failed to react as mating partners.

CONCLUSIONS

It may be concluded that the existing taxonomic groups within the yeasts and the yeast-like fungi can also be recognized by their kind of conidium formation.

In the yeasts with asci, five groups can be distinguished:
1. Saccharomycetales, Metschnikowiaceae (and some Ascoideaceae): The yeast cells are formed sympodially or synchronously as blastoconidia with a narrow or rather narrow base.
2. Saccharomycodaceae: The budding is bipolar, the conidia have a broad base and are formed in basipetal succession leaving 'multiple scars', often with annellations.
3. Ascoideaceae: Mycelial yeast forming sympodial or percurrent blastoconidia with a broad, truncate base.
5. Schizosaccharomycetales: The yeast cells are formed by fission of new crosswalls.

The genera Guilliermondella, Arthroascus, Eremothecium, Ashbya and Crebrothecium usually form only asci, and hyphae which may disarticulate into separate cells. Conidia are not produced.
Two groups can be distinguished within the so-called basidiomycetous yeasts.
1. Sporobolomycetaceae (sensu von Arx et al. 1977): The yeast cells are usually formed in basipetal succession, with a narrow base, from a determinate conidiogenous cell with a fixed conidiogenous locus (phialide, unipolar) (e.g., form genera Rhodotorula, Sporobolomyces, Symbiotaphrina).
2. Filobasidiaceae: The usually spherical yeast cells are formed sympodially and have a broad base (form genus Cryptococcus).

DIALOGUE FOLLOWING DR. VON ARX'S PAPER
KENDRICK: I feel that I have just learned a lot about the yeasts. Imagine yeasts with only hyphae and no budding cells! There's bound to be some discussion of that. Dr. von Arx in one of his tables used Ordinal names to indicate the three main groups of yeasts -- Endomycetales, Sporobolomycetales and Aphyllophorales. I presume that these imply the next level up in the taxonomic hierarchy -- the classes Ascomycetes, Ustomycetes, and Basidiomycetes.
WEBSTER: Do you regard the Sporobolomycetales as a homogeneous group?
VON ARX: Yes, they do form a natural group, the Ustilaginales-like 'red' yeasts. In the teleomorphs, which I did not discuss, they produce dark resting spores -- Leucosporidium, Rhodosporidium, Sporidiobolus and Tilletiaria.
CARMICHAEL: As a medical mycologist, I try to keep abreast of developments in the yeasts, and I was aware of the recent discoveries in the basidiomycetous yeasts and the Sporobolomycetaceae. But if you hadn't shown those photomicrographs of the ascomycetous yeasts, I wouldn't believe you. This is an astounding enlargement of what we know about yeasts.
VON ARX: That is why I brought the pictures.
MALLOCH: What is the principal biochemical difference between the Ascomycetes and the Endomycetes?
VON ARX: Mainly the content of fungal chitin. Ascomycetes have 10-20% chitin. The Endomycetes with micropores have about 5% chitin. The typical non-hyphal yeasts, and also those which produce only hyphae, have 1% chitin or less.
MALLOCH: What is the rest of the wall made of?
MADELIN: Bartnicki-Garcia has established these correlations. The principal pairs of polysaccharides in the different taxa are as follows: basidiomycetous yeasts have chitin and mannann. The ascomycetous yeasts have glucan and mannann. The filamentous Ascomycetes have glucan and chitin. The typical 'yeast' morphology tends to be associated with high mannann content.
LUTTRELL: You described yeasts with no budding cells. Are these also low in chitin?
VON ARX: Yes. The genera Eremothecium, Crebrothecium and Ashbya have only hyphae, and yet have little or no chitin.
MADELIN: If the organism doesn't have budding cells, and is entirely mycelial, how can you define it as a yeast?
VON ARX: It has no fruit body. Asci just form on the hyphae in mycelial forms.
MÜLLER: Equally important is that yeasts never have a dikaryophase. Those 'yeasts' which do have a dikaryophase and form clamps, are really Basidiomycetes, not yeasts.

VON ARX: Yeast-like fungi with hyphae with clamp connections belong to such genera as Sporidiobolus, Filobasidium and Itersonilia. The last two genera we classified in the Aphyllolophorales of the Basidiomycetes. However, Sporidiobolus is close to Sporobolomyces, a genus of the 'red yeasts' (von Arx et al. 1977).

PIROZYNSKI: Could Dr. von Arx tell me whether the heterobasidiomycetous yeast Symbiotaphrina was so named to indicate a relationship to Taphrina?

VON ARX: In pure culture, Taphrina is rather similar to the heterobasidiomycetous yeasts. The colonies are pink, the multiplication (conidiogenesis) is basipetal, as it is in Rhodotorula, Sporobolomyces, Rhodosporidium or Symbiotaphrina. I would prefer to classify the Taphrinales next to the Sporobolomycetales and the Ustilaginales in the Ustomycetes (The Tilletiaceae may represent true Basidiomycetes).

MALLOCH: Is the switch from chitin-glucan to glucan-mannan very basic, or is it just a minor or change associated with the conversion from hyphal to yeast form? Does a similar chemical change occur in, for example, some medical fungi which are yeast-like in the host, but mycelial in culture, or yeast-like at 37°C but mycelial at lower temperatures?

VON ARX: We did not find any difference when we compared the yeast cells with the hyphae, though some authors have found differences. But I have, as I said, studied some yeasts that produce only hyphae, and they had no chitin. You can only recognize these as yeasts chemically, or by the absence of fruit bodies.

MADELIN: There is a good review of this by Bartnicki-Garcia & McMurrough (1971). I believe that the medically important Blastomyces dermatitidis and Histoplasma capsulatum don't conform to this pattern of increased mannan in the yeast form. So the pattern is not ubiquitous. Interest was focussed on this area by investigations of dimorphism in Mucoa rouxii by Bartnicki-Garcia & Nickerson (1962) and Bartnicki-Garcia (1963). If you reduce oxygen and increase carbon dioxide, the fungus changes from its mycelial form to its yeast form, and the mannann content concomitantly increases roughly five-fold. This kind of shift is often associated with the change in growth form.

MALLOCH: That is why I have not used the occurrence of a yeast form as a taxonomic character -- I felt it had probably happened over and over again throughout the fungi.

LUTTRELL: Surely it would be of great interest to study this shift in fungi like Taphrina, Exobasidium and Ustilago.

WATLING: But this is also a very common phenomenon in many Tremellales and Auriculariales. When the basidiospores are germinated on agar, they will produce small blastic sympodial conidia.

VON ARX: Cain (1972) suggested that Cephalosporus is closely related to Ophiostoma and Ceratoctys. It was a very interesting idea but de Hoog rejected it, after studying both. I think Ophiostoma is a member of the Sphaeriaceae, related to Chaetosphaeria but adapted to spore dispersal by insects. It is quite distinct from Ceratoctys.

CARMICHAEL: We now have a major terminological problem. In the past the term 'yeast' has had a morphological connotation. We obviously need a new name for what you are calling 'the yeasts'.
VON ARX: Yes, but yeast specialists are conservative. I have suggested to them that they use the term 'conidium' which they have never previously adopted. Nor do they use 'phialide' or 'basipetal' or 'acropetal' or many other appropriate terms. They don't like to be influenced by true mycologists. Most of them don't even give measurements for the ascospores of yeast teleomorphs.

MÜLLER: I think the term yeast ('Hefe' in German) is understandable in a popular sense. But it should not be used in a scientific or taxonomic sense. For example, de Hoog (1977) has recently published a study of the 'black yeasts'. These are not yeasts at all, they are Ascomycetes.

CARMICHAEL: But they are yeasts if 'yeast' is a morphological term like 'tree' or 'shrub'. We need a new term for this group which includes both filamentous and 'yeast'-like forms.

MALLOCH: But this is just a heterogeneous assemblage.

KENDRICK: Like the Plectomycetes, which are also of diverse ancestry: I certainly don't use it as a taxon in the classification I give my students. In fact I try not to mention it at all for fear they will think it is a real entity. So I think we should use the proper Class, Order and Family names, as appropriate.

VON ARX: I would like to use the Class name Saccharomycetes instead of the name we now use, Endomycetes. Apart from anything else, the type species of Endomycetes is not yet known in pure culture.

LUTTRELL: I feel sure that the Sporabolomycetaceae are heterogeneous, but it is almost impossible to tell from the yeast literature because the illustrations are drawn on too small a scale to show the differences between, for example, Bullera and Sporabolomyces. One ballistospore is borne symmetrically on the 'sterigma,' the other, asymmetrically (Fig. 22.7).

WATLING: When Bryce Kendrick and I were looking through all the illustrations of Heterobasidiomycetes we found whole series both of asymmetrically borne ballistospores and symmetrically borne ballistospores, but we couldn't decide from the illustrations exactly what was going on. Even in the same publication one may see both kinds illustrated, for example in Christiansen (1959), and full cytological explanations of these structures are rare or absent. It seems likely that there is no preceding meiosis in the case of the symmetrically borne spores, so these are not basidiospores, but conidia. Dr. Luttrell's point is very important because the classification of the Tremellales and Auriculariales depends on the occurrence of 'sporidola', secondary ballistospores, the nature of which is not exactly clear. Some people call them 'secondary basidiospores'. Dr. Kendrick and I prefer to call them conidia.

VON ARX: Sterigmatomyces is also supposed to be a Basidiomycete -- there is a stalk on which a new yeast cell is formed. The yeast specialists call that stalk a sterigma, but I have not yet studied the genus so I cannot say whether it is or not.

MADELIN: Does the prevalence of flanged, hat-shaped or saturn-shaped ascospores imply a common origin for many yeasts? Or is it just an adaptive effect?

VON ARX: This phenomenon occurs in several different groups of fungi; Eurotiaceae, Onygenaceae, yeasts and some Ophiostoma species, but I don't think it indicates relationship by descent, but rather convergence.

MALLOCH: This is where Dr. von Arx and I disagree. I believe that the reduced forms with
Fig. 22.7 Repetitive formation of ballistospores in (A) *Bullera alba* (Hanna) Derx (ATCC-18568) and in (B) *Sporobolomyces* sp. In addition to being symmetrical, the ballisto- 
spore of *Bullera* is broadly attached to the tip of a short conidiophore and is separated 
by a distinct septum in the conidiophore. The hilum is a conspicuous, short-cylindrical 
protrusion. *Bullera* differs morphologically from other genera of the *Sporobolomyceta-
ceae* and probably should be removed from this family. -- E.S. Luttrell.
hat-shaped ascospores are related by descent. If we decide that the 'yeast' character is
not particularly important, taxonomically (and we appear to agree on that), then the ascospores are all we have left to use. I think they do indicate relationships.

VON ARX: Saturn-shaped ascospores are found in Eurotiaceae and Onygenaceae, which are a long way from what I've just been discussing.

MALLOCH: But they are quite different from the bowler hat-shaped ones.

KENDRICK: What about the hat-shaped and nearly hat-shaped ascospores in Ceratoctyctis. They may indicate affinities with some of the yeasts Dr. von Arx has mentioned.

VON ARX: Only Ceratoctyctis fimбриata has hat-shaped ascospores. Some other species have more or less kidney-shaped spores with a brim, but are not really hat-shaped.

KENDRICK: Oh, I think they are pretty close. The idea is the same, the hat has just been bent or squashed a little.

PIROZYSNISKI: What is the function of the flange?

MADELIN: Whitney & Blauel (1972) found that the slime surrounding the spores of some species of Ceratoctyctis would disperse only in some organic solvents or conifer resin, not in water; so there is some basis for the idea of ascospores whose affinities might be for lipid rather than aqueous materials.

VON ARX: Yeast ascospores are often released in slime, but they are usually water- or insect-dispersed.

WERESUB: Do you consider the typical yeasts to be related to any of the other Ascomycetes?

VON ARX: I don't know. If they are related, it must be a long way back. They obviously diverged a long time ago.

MALLOCH: But what about Cleistothelæbolus, which is a yeast in liquid culture, but forms regular cleistothecia on solid media?

VON ARX: I always find it difficult or impossible to decide whether one fungus is more primitive or more highly evolved than another. So I don't construct phylogenies.

HENNEBERT: Is there a yeast phase in every species of Trichosporon?

VON ARX: We have studied most species described in Trichosporon. Some have proved to be the anamorphs of Hypophysciæ; three we have already transferred to Geotrichum; we don't have a generic name for four or five others; and two new genera have recently been proposed for two others. We now recognize only three species in Trichosporon proper. Trichosporon is an anamorphic yeast with true hyphae; it forms arthric conidia and blastic conidia, and it has dolipores. It is an anamorphic basidiomycetous yeast. Trichosporonoides also has dolipores.

LUTTRELL: You mentioned that Candida species were anamorphs of fungi belonging to very different groups. Could you not separate these by wall chemistry?

COOKE: In Lodder's yeast text, some genera are being separated on the basis of whether species utilize nitrate N or not.

VON ARX: This generic character is, in my opinion, a very bad one, and should not be used. For example, Píchia doesn't use nitrate, Hansenula does. Newer and better characters are now available, such as which group of Coenzyme Q each produces. We have found that many yeast genera are heterogeneous -- Píchia, Hansenula, and Saccharomyces, for example -- and yeast taxonomy is currently in a state of flux.
MADELIN: You seem to be emphasizing the idea that in a natural group all members share at least one determining feature (a monothetic group). This may not always be the case (as in polythetic groupings). How does one decide that a character is 'good' -- because it is easy to apply, or because it reflects what one believes to be phylogenetic relationships?

VON ARX: Characters such as fermentative abilities, that have long been used in yeast taxonomy, are very easy to apply, very nice for identification purposes, but they are not natural and not stable. And we would like at least to have natural genera.

CARMICHAEL: If we find a new character that seems to change our classification we usually decide whether it is 'good' or not by seeking out other characters correlated with it. In other words we are using, not a single, isolated character, but a cluster of characters.

KENDRICK: And what may be regarded as a single character may actually be a whole set, since we often use one word to describe a very complex phenomenon. One synthetic pathway resulting in a single end-product may involve ten or twenty enzymes. Some people speak of an ascus as if it were a single character, when we know it represents a whole bushel basket of characters.

The next chapter concerns another group which lies outside the mainstream of the Conference, but in which the matter of anamorph and teleomorph is still of vital concern. In fact, the classification of the group is largely based on characters of the anamorphs, as you will see....
INTRODUCTION

On the occasion of the first Kananaskis conference held in 1969, Hughes (1971a) presented a general account of the kinds of asexual spores formed by most of the major groups of fungi. Of the Zygomycotina, he discussed only the Zygomycetes where he stressed especially the kinds of spores that resemble those of anamorphs associated with members of the other subdivisions, Mastigomycotina, Ascomycotina, Basidiomycotina, and Deuteromycotina (Ainsworth, Sparrow & Sussman 1973). Because he covered in a limited amount of space several large and diverse groups of fungi, Hughes made no attempt to treat any one of these in detail. Therefore, it shall be my purpose in this synopsis to dwell only on the Zygomycetes, where I shall try to characterize the orders of this class as I interpret them. This will involve not only a discussion of their asexual spores—the primary theme of the present Conference—but also a characterization of their sexual spores on which the ultimate natural classification of these fungi doubtless will be based. For the purposes of this discussion, the Zygomycetes will include also the Harpellales, an order usually treated in a separate class, Trichomycetes, of the Zygomycotina.

SPORES OF ZYGOMYCETES

Spores of Zygomycetes may be formed by four fundamentally different processes. The first is known to be sexual in many instances, and the resulting zygospores are formed in a variety of ways following the union of morphologically differentiated or undifferentiated cells or hyphae. The other three processes are asexual. Two of these result in the delimitation of endogenous spores (sporangiospores and chlamydospores) whereas in the other, the spores (arthrospores, yeast- or bud-cells) are formed exogenously and are the analogues of the conidia of members of the Ascomycotina, Basidiomycotina, and Deuteromycotina.

Zygospores are not known in all forms that by other criteria may be included in the Zygomycetes. They are regularly found only in homothallic members of the class and have yet to be demonstrated for a great many, presumably heterothallic, species. When the zygospore is produced, its characteristics, in terms of our present understanding of it, are such that it cannot yet form the basis of a workable taxonomy, at least not at the species level. Nevertheless, zygospore characteristics are an important adjunct to classification, especially at the ordinal level.
As sexual states (teleomorphs) of more and more species are discovered and studied in detail the zygospore might eventually form the basis of a more natural classification at the family and even the genus level, especially in the Mucorales (O'Donnell, Hooper & Fields 1976, O'Donnell, Ellis, Hesseltine and Hooper 1977a; O'Donnell, Flegler, Ellis and Hesseltine 1978, Schipper, Samson & Stalpers 1975).

It occasionally happens that a zygospore-like spore develops from a single gametangium without any evidence of sexual fusion. Such azygospores are not uncommon in the Mucorales (Benjamin & Mehrotra 1963; O'Donnell, Ellis, Hesseltine & Hooper 1977b,c), and they also are known in the Zoopagales (Drechsler 1946), Endogonales (Gerdemann & Trappe 1974), and Entomophthorales (Gustafsson 1965, Waterhouse 1973b). Many of the so-called resting spores of members of the latter two orders may be azygospores.

Because the sexual, or zygosporic, state alone cannot be used for establishing botanical taxa in Zygomycetes, the predominant asexual, i.e., anamorphic (Hennebert & Weresub 1977), state—that producing sporangia and sporangiospores—is the one on which the names of species are based and taxa classified in all members of this class. The whole organism, or holomorph of Hennebert & Weresub (1977), is encountered in nature or the laboratory mostly in homothallic species in which a single thallus can bear both sporangia and zygospores. The zygosporic state of heterothallic species develops in nature or the laboratory only by the fortuitous or willful bringing together of sexually compatible strains.

Defined simply, the sporangiospore is a spore formed in a sporangium (Ainsworth 1971), and in the Euymycota it is the characteristic asexual spore of the Mastigomycotina and Zygomycotina (Ainsworth, Sparrow & Sussman 1973). Sporangiospores are distinguished from other asexual spores formed by members of these subdivisions in being cleaved out of the cytoplasmic contents of the sporangium (Bracker 1966, 1968, Dick 1973a,b, Fletcher 1972, Gay & Greenwood 1966, Sparrow 1960, 1973a,b, Waterhouse 1973a) without the wall of the sporangium being directly involved in the formation of the spore wall, i.e., they are enterothallic (Kendrick 1971b). In the mostly aquatic Mastigomycotina, with a few exceptions among parasites of terrestrial plants, sporangia delimit sporangiospores that bear one or two flagella at some stage of their existence and are actively motile, whereas in the mostly terrestrial Zygomycotina sporangiospores are nonflagellate and nonmotile. In the Zygomycotina, as in the Mastigomycotina, which are not being considered further here, the sporangium often has undergone extreme modification and diversification in the course of evolution, doubtless to satisfy particular needs for dispersal or survival under extreme environmental conditions (Ingold 1953, Ingold & Zoberi 1963).

In many Zygomycetes the primary asexual spores, i.e., sporangiospores, develop on specialized, simple or branched, usually aerial sporophores, and are formed singly or in rows of few to many units rather than in well-defined, more or less globose sporangia or sporangiola as in the majority of Mucorales. The sporangial nature of the spore-forming structure in such instances may only be inferred by presumed homology with other multisспорed sporogenous structures on the basis of development. In some forms the presence of a readily separable, more or less persistent sporangial wall that is continuous with the subtending supporting structure is easily discerned by the usual light-microscopic techniques.
In others, however, the sporangial origin of the spore is not easily detected, the sporangial wall being either ephemeral or so closely appressed to the spore wall that it cannot be readily observed by the usual methods. Fine structural evidence of sporangial development of only a few of the latter kinds of spores is available (Benney & Aldrich 1975, Khan 1975, Moss & Lichtwardt 1976). The arbitrary use of the term conidium for these kinds of primary asexual spores of Zygomycetes should be avoided; such spores, in my opinion--perhaps just as arbitrary--should be called sporangiola or, if preferred, simply spores.

In 1859, de Bary introduced the term chlamydospore (fide de Bary 1866:129) to describe the thick-walled spores formed in abundance in hyphal cells on and in the carpophores of Nyctalis asterophora Fr. and N. parasitica Bull. ex Fr. (=Asterophora lycoperdoides (Bull.) Ditmar ex Fr. and A. parasitica (Bull. ex Fr.) Singer (fide Singer 1962)). Van Tieghem & Le Monnier (1873) adopted de Bary's term to designate one of the two forms of asexual spores they recognized in the Mucorales (their Mucorinées), i.e., 'forme sporangale' and 'forme chlamydiée'. They defined the chlamydospore as a spore (1) formed by the same mycelium giving rise to sporangia but developing endogenously by the local condensation and walling off of protoplasm and (2) liberated by the breakdown of the enveloping hyphal membrane. Van Tieghem & Le Monnier recognized two types of chlamydospores in the Mucorales. The first, called sessile mycelial chlamydospores, were characterized as being smooth walled, terminal or intercalary, single or in chains, and formed in the vegetative hyphae or in the sporangiophores after maturation of the sporangia. The second, called aerial pedicellate chlamydospores, were characterized as being rough walled and formed terminally in slender branches arising from the aerial mycelium. They found this spore type commonly in species of Mortierella Coemans and for it van Tieghem (1875) adopted the name 'stylospore', a term proposed by the Tulasnes (1861) for certain kinds of spores formed acrogenously on simple conidiophores inside pycnidia.

The concept of the chlamydospore has been expanded from that originally implied by de Bary and van Tieghem & Le Monnier to encompass a variety of thick-walled, terminal or intercalary spores. Ainsworth (1971) defined it as "a thick-walled, non-deciduous, intercalary or terminal asexual spore made by the rounding up of a cell or cells; a gemma." Kendrick (1971b), following the first Kananaskis conference, defined it broadly as "a thick-walled, thallic, terminal or intercalary spore." And Griffiths (1974), following his extensive review of the chlamydospore, redefined it as "a viable, asexually produced, accessory spore resulting from the structural modification of a vegetative hyphal segment(s) possessing an inner secondary wall, usually impregnated with hydrophobic material, and whose function is primarily perennation and not dissemination." Griffiths suggested "that in the Mucorales the term chlamydospore should be restricted to those thick-walled spores formed within the vegetative mycelium." This is the concept of the chlamydospore, actually the same as that of van Tieghem & Le Monnier (1873), that I have adopted for the Zygomycetes.

Whereas the formation of endogenous chlamydospores is common in many Zygomycetes, formation of truly exogenous spores, i.e., conidia, is rarely encountered and may be represented only by the production of chains of variably elongate, ovoid, or globose spores (Fig. 23.2 G,R) commonly formed by the submerged hyphae of several species of Mucor Micheli ex Fr. (Mucorales) growing in culture (Bartnicki-Garcia 1972, Benjamin & Mehrotra 1963, Hesseltine 1954, Lendner 1908).
Such spores have been called oidia or gemmae (Hesseltine 1954, 1955, Hesseltine & Ellis 1973, Lendner 1908). They appear to be formed in basipetal succession, may disarticulate readily, and then may proliferate by yeastlike budding. The term oidium is derived from the form genus Oidium Link emend. Sacc. (=Aerosporium Nees, fide Hughes 1958) and suggests that these spores have a basocatenulate origin, that they are "meristem arthrospores" (Kendrick 1971a). The exact method of their formation has yet to be determined, but the term arthroconidium (or arthrospore) probably is more descriptive of such spores than oidium. The term gemma has a long history of usage in botany and mycology (Hughes 1971b) and finds its best use as a general term for any budlike asexual reproductive structure of fungi, algae, bryophytes, and pteridophytes. Its use as a synonym for chlamydospore (Fischer 1892, Gäumann 1926, Zycha, Siepmann & Linnemann 1969) in the Zygomycetes should be avoided.

Gemmae in the Zygomycetes are best represented by the yeast- or bud-cells formed in culture by arthrospores and especially sporangiospores of species of several genera of Mucorales (Actinomucor Schost., Cokeromyces Shanor, Mucor, Myaotypha Fenner). Except for the occasional formation of yeast-cells along with typical hyphae in ordinary aerobic cultures of Myaotypha (Fig. 23.2 S) (Benny & Benjamin 1975, Hall & Kolankaya 1974), yeast-cell formation and the phenomenon of yeast-mold dimorphism in species of Mucor and Myaotypha reflects special adjustments that can be made in the cultural environment, especially anaerobiosis with or without high $p$CO₂, high glucose concentrations, etc. (Bartnicki-Garcia 1968, Bartnicki-Garcia & Nickerson 1962, Hall & Kolankaya 1974, Jeffries & Kirk 1976, Price, Storck & Gleason 1973, Schultz, Kraepelin & Hinkelmann 1974, Terenzi & Storck 1969a,b). Fisher (1977) induced yeastlike growth in Mucor pusillus Lindt and Actinomucor elegans (Eidam) C.R. Benjamin & Hesseltine in aerobic cultures to which had been added a number of antibiotics, fungicides, or metabolic inhibitors. Yeast production occurred only in the presence of fermentable substrates. In a fine-structural study of the budding process in yeast-cells of Mucor rouxii (Calmette) Wehmer, Lara & Bartnicki-Garcia (1974) described typical yeastlike blastic development of the yeast phase in which the emergent daughter cell ruptures the parent spore wall, forms its own wall de novo, and then is separated from the parent cell by a centripetally formed septum.

SYNOPSIS OF THE ORDERS AND FAMILIES OF ZYGOMYCETES
The following list gives a summary of the orders and families of Zygomycetes as treated in this review:

MUCORALES

Choanephoraceae
Cunninghamellaceae
Mortierellaceae
Mucoraceae
Piloblaceae
Radiomycetaceae
Saksenaeaceae
Syncephalastraceae
Thamnidiaceae

576
ZOOPAGALES
  Cochlonemataceae
  Helicocephalidaceae
  Piptocephalidaceae
  Zoopagaceae

ENGOGONALES
  Endogonaceae

ENTOMOPHTHORALES
  Basidiobolaceae
  Entomophthoraceae

DIMARGARITALES
  Dimargaritaceae

KICKXELLALES
  Kickxellaceae

HARPELLALES
  Harpellaceae
  Legeriomycetaceae

MUCORALES

The ordinal name Mucorales was adopted as early as 1899 by the American L.M. Underwood and a few years later by Sumstine (1910), but for many years the terms Mucorineen and Mucorinées, which were long used by most European workers, continued in general use until the appearance of Fitzpatrick's text in 1930. Although systems of classification vary in details, most recent concepts of Mucorales (Arx 1967, 1970, Benjamin 1959, 1966, Fitzpatrick 1930, Hesseltine 1955, Hesseltine & Ellis 1973, Milko 1974, Moreau 1953, Muller & Loeffler 1968, Naumov 1935, 1939, Zycha 1935, Zycha et al. 1969) have followed more or less traditional lines established in the latter part of the last century and early in this century (Berlese & de Toni 1888, Fischer 1892, Lendner 1908, Schröter 1886, 1893, van Tieghem 1875, 1876, van Tieghem & Le Monnier 1873) regarding the included taxa. Kreisel (1969) removed the Kickxellaceae Linder and Dimargaritaceae Benjamin to a new order, Kickxellales, and transferred the Piptocephalidaceae to the Zoopagales. These families are excluded from the Mucorales as treated here. Except for the above families and Helicocephalidaceae Boedijn, Endogonaceae Fr., and Mortierellaceae Fischer, the remaining families of Mucorales treated by Hesseltine & Ellis (1973) in their survey of the order (i.e., Choanephoraceae Brefeld, Cunninghamellaceae Naumov ex Benjamin, Mucoraceae Bonorden, Pilobolaceae Corda, Radiomycetaceae Hesseltine & Ellis, Saksenaeaceae Hesseltine & Ellis, Syncephalastraceae Naumov ex Benjamin, and Thamnidaceae Brefeld) appear to form a phylogenetically closely related group of fungi.

Helicocephalidaceae, proposed by Boedijn (1958) for two genera whose species are known to parasitize nematode eggs, are here provisionally included in the Zoopagales (Milko 1974). Endogonaceae (Gerdemann & Trappe 1974, 1975), are a heterogeneous assemblage of soil-inhabiting fungi, many mycorrhizal, of which only a few are known to form zygospores. It seems best to treat the family as a separate order, Endogonales, pending better understanding of the possible affinities of its genera, and not imply close relationship of its members to Mucorales.
Figure 23.1. A-L. Sporangiospores of representative Mucorales. A. Utharomyces pallocaulis Boedijn, x1300; B. Mucor petrinsularis Naumov, x1300; C. Phycomyces blakesleeanus Burgeff, x1300; D. Mucor hiemalis Wehmer, x1300; E. Rhizopus stolonifer (Ehrenb.) Ehrenb., x1300; F. Absidia corylophora Hagem, x1300; G. Mucor bacilliformis Hesseltine, x1300; H. Absidia cuneoapora Orr & Plunkett, x1300; I. Hesseltinella vesiculosa, x1300; J. Gilbertella peritocaria, x1300; K. Choanephora trispora (Thaxt.) Sinha, x1000; L. Radiomyces spectabilis, x1300. — M. Radiomyces embreei. Unispored sporangiola, x1300. — N-P. Cunninghamamella echinulata (Thaxt.) Thaxt. N. Living sporangiola mounted in water on agar film showing intact sporangiolar wall with calcium oxalate spicules intact, x2100; O. Calcium oxalate spicules dislodged from sporangiolar wall in water mount on agar film, x1300; P. Sporangiola mounted in NHC1; spicules are soluble in this acid, x1300. — Q-W. Sporangiola of representative Mucorales. Q. Backusella ciroina Ellis & Hesseltine, x600; R. Chaetoozadium jonesii, x1300 (from Benny and Benjamin 1976); S-T. Backusella atenidia (Durrell & Fleming) Pidopl. & Milko ex Benny & Benjamin, x700; U. Thamnostylum piriforme (Bainier) Arx & Upadhyay, x560; V. Choanephora cucurbitarum (Berk. & Rav.) Thaxt., x1000; W. Choanephora trispora, x1000. — X. Choanephora trispora. Sporangiolar pedicel showing slightly developed columella and basal remnant of sporangiolar wall, x2100. — Y-Z. Backusella lamprospora (Lendner) Benny & Benjamin. Y. Water mount of living immature sporangium showing calcium oxalate spicules, x2100; Z. Dislodged spicules in water mount on agar film, x2100.
Mortierellaceae are here retained in the Mucorales, but their species possess such distinctive vegetative, asexual, and sexual characteristics that they must surely represent a line of evolution that long ago diverged from that leading to the development of the other families of the order.

Zygospores still are unknown for many Mucorales, but they have been demonstrated for representatives of all but one family (Saksenaceae). Species of Radiomyces Embree (Radiomycetaceae) (Benjamin 1969, Embree 1959) and Mortierella Mortierellaceae) (Gams, Chien & Domsch 1972, Kuhlman 1972, 1975) have a thin, nearly hyaline zygosporangium enclosing a smooth, hyaline, thick-walled zygospore. The zygosporangium of members of the Choanephora ceae (Hesseltine 1953, Kirk 1977, Mehrotra & Mehrotra 1964, Poitras 1955) also is thin-walled and smooth whereas the zygospore proper has a thick, finely striate, dark-colored wall. The zygosporangium of other members of the order typically is bright or dark colored to nearly black, thick, apparently three-layered, and more or less coarsely roughened (O'Donnell, Hooper & Fields 1976, O'Donnell, Ellis, Hesseltine & Hooper 1977, Schipper et al. 1975) and encloses a thick-walled, hyaline zygospore. The wall of the zygospore may be nearly smooth, but in some instances it is distinctly and characteristically sculptured (O'Donnell, Flegler, Ellis & Hesseltine 1978). In Mucorales the zygosporangium is typically formed by the fusion of more or less equal gametangia delimited by often enlarged and highly differentiated hyphal suspensors formed below, on, or above the surface of the substrate. Suspensors formed within, near, or at the surface of the substrate tend to be more or less apposed during early stages of development, becoming tonglike as they mature (Fig. 23.3 D,F), and often the zygospore develops more above than between the opposed suspensor tips (Fig. 23.3 E). Suspensors developed from hyphae projecting well above the surface of the substrate typically are opposed during all stages of development, and the zygospore matures between the suspensor tips (Fig. 23.3 A-C). Suspensors are nearly smooth in most species, but a few, i.e., some species of Absidia van Tiegh., Phycomyces Kunze ex Fr., and Radiomyces, bear simple or branched appendages (Fig. 23.3 B,F).

Sporangiospores vary in size and shape in the Mucorales and are mostly globose (Fig. 23.1 A,B,N, Q-T), ovoid (Fig. 23.1 C-E,J,K,P,U-W), or somewhat cylindrical (Fig. 23.1 F), although other shapes occasionally are found (Fig. 23.1 G,H,L). Most appear smooth-walled by light microscopy, but a few may be slightly roughened (Fig. 23.1 B) or even striate (Fig. 23.1 E-K). They are formed in sporangia that typically develop terminally on simple or branched, aerial sporangiophores arising directly from substrate or aerial hyphae. Sporangia vary in size from large, multisporous, columnellate or noncolumnellate (as in most Mortierellaceae), more or less globose or pyriform cells containing hundreds or thousands of spores, to columnellate or noncolumnellate one-, few-, or many-spored sporangiola. The sporangial wall may be persistent, but is usually readily fragmenting, or diffluent, and it may or may not bear needlelike, broad-based spicules of calcium oxalate (Fig. 23.1 N,O,Y,Z).

Chlamydospores are very common in the vegetative hyphae of many Mucorales and they occur regularly in sporangiophores of a few species, especially in the section Racemosus of Mucor (Fig. 23.2 A,B). They typically are smooth, thick- or thin-walled, terminal or intercalary (Fig. 23.2 D,E,I-O), and occur singly or in chains of few to several spores. They vary greatly in size and conformation, but are mostly more or less globoid, ovoid, or elongate,
and may be nearly equal in diameter to the hypha in which they are formed, or greatly enlarged. In most instances, chlamydospores are morphologically identical in taxa of the several families and have little or no taxonomic usefulness. In some species, however, they are so distinctive that they may have considerable taxonomic significance as in *Chlamydoabsidia* padenii Hesseltine & Ellis (Fig. 23.2 C), and members of the *Absidia oxyribifera* (Cohn) Sacc. & Trotter complex (Fig. 23.2 F-H). In *Mortierella*, especially, chlamydospores have attained a state of development wherein for some species they probably play an important role in dispersal. In many species of this genus, smooth-walled chlamydospores like those occurring in other Mucorales are formed in the substrate or aerial hyphae (Fig. 23.2 P). These often are accompanied by ovoid or globose intercalary or terminal (i.e., stylospores) chlamydospores in which the spore itself is spiny or the hyphal wall enveloping the spore may form more or less slender, hyaline projections that give the mature chlamydospore a spinose or echinulate appearance (Fig. 23.2 M-O). These readily detached spiny or fimbriate chlamydospores thus have a greatly increased surface area and the resulting increase in buoyancy undoubtedly enhances dispersibility in air currents.

Species of genera assigned to the Mucoraceae sensu Hesseltine & Ellis (1973) (but including *Dioranophora* Schröter, *Gilbertella* (Eddy) Hesseltine, and *Halateromyces* Shipton & Schipper (1975), and excluding *Backusella* Hesseltine & Ellis (Thamniidae), *Firella* Bainier (Thamniidae), and *Amygosygnum* Chesters (= *Mortierella: Mortierellaceae*), vary greatly in the characteristics of their sporangia which may be produced singly or simple, elongate sporangiophores, or, more commonly, on sympodially, umbellately, verticillately, or dichotomously branched structures. Sporangia may vary considerably in size in members of the family and are usually nearly globose or occasionally pyriform, but they always have the same basic structure and wall characteristics in any given species.

Two other families of Mucorales are characterized by the production only of multispored sporangia. The Pilobolaceae, with three genera, *Pilobolus* Tode ex Fr., *Pilaiva* van Tiegh., and *Utharomyces* Boedijin, are commonly found on dung. All members of these genera form large, black, persistent-walled, cutinized sporangia. In *Pilobolus* spp. the sporangium is forcibly discharged by the rupture of a pronounced subsporangial swelling, whereas in species of the other genera the sporangiophore elongates greatly and the sporangium becomes detached and adheres to any contacted surface. The family Saksenaceae was proposed (Ellis & Hesseltine 1974) for two anomalous, monotypic genera, *Saksenaea* Sakse and *Echinosporangium* Malloch. The sporangium of *Saksenaea vasiformis* Sakse has the shape of a stalked, round-bottomed, long-necked flask, is columellate, and opens by dissolution of the sporangial apex. *Echinosporangium transversalis* Malloch has a transversely lobate, somewhat divaricate sporangium bearing several spinelike projections at each extremity, and is noncolumellate. Zycha et al. (1969) placed *Echinosporangium* in the Mortierellaceae. As noted by Ellis & Hesseltine (1974), *Echinosporangium* and *Saksenaea* do not appear to be closely related, and their alliance in the same family can only be regarded as provisional.

The Thamniidae, sensu Benny & Benjamin (1975, 1976) is, like the Mucoraceae, undoubtedly polyphyletic, and much additional information is needed before the genera of these families can be realigned into possibly several families or, perhaps subfamilies, that will realistically reflect their relationships. Thamniidae, as treated here, have in common the
Figure 23.2. A-O. Chlamydospores of representative Mucorales. A-B. Mucor racemosus Fres. A. Chlamydospores formed in sporangiophore and columella, x600; B. Chlamydospore in sporangiophore, x800. — C. Chlamydoabsidia padenii Hesseltine & Ellis. Chlamydospores formed terminally on aerial hyphae, x80. — D. Phascolomyces articulous Boedijn ex Benny & Benjamin. Intercalary chlamydospore formed in substrate hypha, x175. — E. Baakusella lamprospora. Intercalary chlamydospore formed in substrate hypha, x175. — F-H. Absidia corymbifera (Cohn) Sacc. & Trotter. F-G. Highly lobate chlamydospores formed in aerial hyphae, x175; H. Chlamydospore type common to other strains showing lobate, hyaline remnants of evacuated cell, x175. — I. Zygorhynchus californicus Hesseltine, C.R. Benjamin & Mehrotra, x800. — J-L. Ellisomyces anomalus (Hesseltine & Anderson) Benny & Benjamin. J-K. Terminal and intercalary single chlamydospores, x800; L. Intercalary chain of chlamydospores, x800. — M-O. Mortierella indohii Chien. Intercalary chlamydospores showing spinelike projections formed by hypha enveloping the smooth-walled spores; note that these projections may at times develop on the hypha not associated with the spores, N, x800; N, x600; O, x700. — P. Mortierella sp. Smooth-walled chlamydospore common to many species of this genus, x700. — Q-R. Arthrospores formed by submerged vegetative hyphae. Q. Mucor azygosporus Benjamin. Note budding cell (bottom) derived from an arthrospore, x250; R. Mucor bainieri Mehrotra & Baijal, x400. — S. Mycocypha microspera Fenner. Vegetative hyphae and budding cells ('gemmae') from surface growth of 2-day-old colony, x600.
production of small one- or several-spored, columellate or noncolumellate sporangiola having persistent, separable sporangiolar walls (Fig. 23.1 Q-U). The sporangiola are borne on sporangiophores that often also bear large, columellate but diffusely-walled sporangia. Columellate sporangia accompanied by few-spored or occasionally one-spored sporangiola occur in six genera: Baeckeaella Hesseltine & Ellis (Fig. 23.1 Q,S,T), Helicostyllum Corda, Fennelomyces Benny & Benjamin, Pirella, Thamidiidu Link ex Gray, and Thamostiilum Arx & Upadhya (Fig. 23.1 U). Species of Cokeromyces, Ellisomyces Benny & Benjamin, and Zychaeae Benny & Benjamin (all monotypic) form only few-spored sporangiola. Unispored sporangiola are characteristic of all species of Chaetocladium Fresenius (Fig. 23.1 R), Dichotomooladium Benny & Benjamin, Mycootypha, and Phasoolomyces Boedijn ex Benny & Benjamin.

Mortierellaceae (Hesseltine & Ellis 1973, Zycha et al. 1969), include perhaps four genera, Mortierella, Haplosporangium Thaxter, Dissophora Thaxter, and Aquamortierella Embree & Indoh. Linnemann (in Zycha et al. 1969), included Echinosporangium in the family but excluded Aquamortierella, and Gams (1969, 1977) treated Haplosporangium as a section of Mortierella. Aquamortierella elegans Embree & Indoh (1967) is known only from its original description from liquid-preserved material. The species, found in New Zealand, possibly parasitizing a midge larva in water, is unique in the Mucorales in having sporangiospores that bear apical, hyaline appendages—apparently an adaptation for water dispersal. Its relationships still are obscure. Little is known of Dissophora save for Thaxter's (1914) description of its type species, D. decumbens, in which an elongate axis gives rise laterally to divergent, simple, somewhat medianly swollen branches bearing small, terminal, multispored sporangia. Mortierella is one of the largest genera of Mucorales and many of its species are among the most common of soil-inhabiting fungi. In his recent key to the species, Gams (1977) recognized two subgenera. Subgenus Micromucor Gams includes several species having distinctly Mucor-like characteristics. They form low-growing, velvety colonies, lack a distinctive odor, and have sporangia that are usually pigmented and possess an often well-developed columella. Subgenus Mortierella comprises the bulk of the species of the genus and is subdivided into nine sections. Species of this subgenus typically develop delicate, white, cottony or arachnoid, freely anastomosed aerial hyphae forming simple or racemously or cymosely branched sporangiophores bearing colourless sporangia. Columellae are absent or only rudimentary, and the diffusely sporangial wall lacks calcium oxalate spicules. Most species of the subgenus possess a distinctive garlic-like odour, and though usually growing readily in culture often form sporangia only on nutrient-poor media. Benjamin (1978) has added a third subgenus, Gamieilla, the type species of which, G. multidi varicata, differs from all other species of the genus in forming large numbers of sporangiola simultaneously on a several-times divaricate sporangiophore. Special features of the chlamydospores in some members of the family already have been mentioned.

The Choaneophoraceae probably should be limited in scope to a single genus, Choaneophora Currey (Arx 1970, Benjamin 1959, Poitras 1955, Sinha 1940) although there still is much sentiment in favor of retaining Blakeslea Thaxter as distinct from the former (Hesseltine & C.R. Benjamin 1957, Hesseltine & Ellis 1973, Mehrotra & Mehrotra 1964, Naumov 1935, 1939, Zycha et al. 1969). Choaneophora spp. produce columellate, many-spored sporangia terminally on simple sporangiophores separate from other distally branched sporangiophores that bear uni- (i.e., Choaneophora) or few-spored (i.e., Blakeslea) sporangiola on apical enlargements.
Sporangiospores typically are longitudinally striate and bear apical, hairlike appendages (Fig. 23.1 K). Spores in unispored sporangiola lack appendages and may be striate or smooth-walled (C. conjuncta Couch). Smooth-walled chlamydospores are commonly formed in the submerged and aerial vegetative hyphae of all species of Choanephoraceae that have been studied in culture (Mehrotra & Mehrotra 1964). Gilbertella persiciaria (Eddy) Hesseltine is the only other member of the Mucorales in which the sporangiospores also bear hairlike appendages (Fig. 23.1 I), and the species is sometimes included in the Choanephoraceae (Hesseltine & Ellis 1973). Its zygospores are mucoraceous, however, and on this basis it is best allied with the Mucoraceae (Zycha et al. 1969).

The family Radiomycetaceae was established by Hesseltine & Ellis (1974) for two genera, Radiomyces and Hesseltinetla Upadhyay (1970) in which sporangiola are borne on stalked, secondary ampullae arising from intercalary or terminal primary ampullae borne on simple or branched, often stoloniferous sporangiophores. The stalks bearing the secondary ampullae always are once-septate. Both species of Radiomyces, R. spectabilis Embree and R. embreei Benjamin, are homothallic and form smooth, thick-walled zygospores enclosed in smooth, thin-walled zygosporangia flanked by suspensors bearing elongate, branched appendages (Fig. 23.3 B). The sporangiola of R. spectabilis are borne on globose secondary ampullae and contain small, often slightly reniform spores (Fig. 23.1 L), whereas sporangiola of R. embreei are unispored (Fig. 23.1 M) and are borne on elongate secondary ampullae. In both species, the sporangial wall bears capitate, spinose processes. Zygospores still are unknown in Hesseltinetla vesticulosa Upadhyay, and each secondary ampulla of the sporangiophore bears only one relatively large multispored sporangiole containing small, asymmetrical, acicular spores (Fig. 23.1 I); the sporangial wall bears numerous elongate calcium oxalate spicules. Chlamydospores, arthrospores, and gemmae have not been observed in species of Radiomycetaceae.

Cunninghamellaceae produce only unispored sporangiola, and in 1973 Hesseltine & Ellis included four genera in the family: Cunninghamella Matruchot, Myaotypha, Phascolomyces, and Thamnocephalis Blakeslee. Benjamin (1959) also assigned Myaotypha to Cunninghamellaceae, but more recently this genus, as suggested by Young (1969), and Phascolomyces have been placed in the Thamniaceae by Benny & Benjamin (1976). The familial relationships of Thamnocephalis await further study, but this genus probably is not closely related to Cunninghamella. Nor perhaps is Sigmaeomycetes Thaxter which was described originally (Thaxter 1891a) as a genus of Hyphomycetes; it bears some resemblance to Thamnocephalis. No representative of Sigmaeomycetes (Thaxter 1891a; Bayliss-Elliott 1913, McLean 1923) or Thamnocephalis (Blakeslee 1905, Mehrotra & Mehrotra 1963, Ou 1940) has as yet received definitive study in pure culture.

Cunninghamella spp. have long been regarded by many mycologists as being truly conidial members of the Mucorales (Cook 1977, Dykstra 1974, Hawker, Thomas & Beckett 1970, Hesseltine 1955, Hesseltine & Ellis 1973, Lendner 1908, Naumov 1935, 1939, Samson 1969, Young 1968 a). A few students have argued in favor of their sporangial nature (Benjamin 1959, Khan 1975, Khan & Talbot 1975). All but one of the described species of Cunninghamella (Caretta & Piorelli 1977, Samson 1969) form what are usually regarded as echinulate or spinose spores. Although the "spore spines" have been compared with those formed on the sporangial wall of many other Mucorales (Hawker 1971, Hawker et al. 1970), it is commonly assumed that the spines
form a part of the spore wall proper. If, however, one compares the living cunninghamamel-
laceous sporangial wall with that of many other mucoralean sporangia it is found to be
simply fragile and readily fugacious as in many species of Mucoraceae and Thamnidaceae.
The spines are composed of calcium oxalate. If spinose sporangiola of Cunninghamaella spp.
are mounted with minimum disturbance in water on an agar film, the sporangial wall and its
spicules remain essentially intact (Fig. 23.1 N). Even a moderate amount of pressure
together with a slight lateral displacement of the cover glass will dislodge the spicules
from the sporangial wall (Fig. 23.1 O) as in similarly treated sporangia of other Mucorales
(Fig. 23.1 Y, Z). Sporangiola of Cunninghamaella spp. mounted in acetic acid retain their
spines, whereas the spines are dissolved without liberation of gas (CO₂) when mounted in
hydrochloric or sulphuric acids (Fig. 23.1 P). The easily disrupted sporangial wall in mem-
bers of this genus may account for the difficulty that has been experienced in preparing spor-
angiola for transmission electron microscopy, whereas the sporangial wall and its spicules
remain intact during preparation for scanning electron microscopy.

Chlamydospores have not been observed in species of Cunninghamaella (Samson 1969).
The family Syncephalastraceae is monogenic and includes possibly only two species, the
common and widely distributed Syncephalastrum racemosum Cohn ex Schröter, and the recently
described S. verruculosum Misra (1975). In their vegetative and sexual characteristics
(zygosporides are known only in S. racemosum), species of Syncephalastrum Schröter are like
typical members of the Mucoraceae. They are saprobic and grow and sporulate readily on simple
culture media. Unlike all other Mucorales, however, they produce sporangiospores in elon-
gate sporangiola (merosporangia) (Fig. 23.4 A) arising on terminal ampullae formed on simple
or branched sporangiophores. In the past, the merosporangium of Syncephalastrum has been
likened to those of Piptocephalis de Bary and Syncephalis van Tiegh. & Le Monnier (Benjamin
1959, 1966), but it undoubtedly has arisen independently in this genus and has no phylogenetic
relationship with the merosporangia of the other two genera. The fine-structural study by
Fletcher (1972) has shown that development of spores in the merosporangium of S. racemosum
is comparable in all respects to that of spore development in the mucoraceous Gilbertella
persicaria (Bracker 1968). Developmental and karyological studies at the light-microscopic
level of several species of Piptocephalis and Syncephalis by Benjamin (1966) and the fine-
structural study of merosporangial ontogeny in Syncephalis sphaerica van Tiegh. by Baker,
Hooper & Beneke (1977) indicate developmental processes differing somewhat from those
observed in Syncephalastrum racemosum.
Figure 23.4. A. *Synoephalastrum racemosum*. Two merosporangia, one intact the other broken, x2100 (from Benjamin 1966).—B-D. *Synoephalis tenuis*. B. Two immature sporophores showing early stages of acropetal development of the two-spored sporangiola, x145; C. Distal part of sporophore showing maturing merosporangia, x290; D. Mature merosporangia disarticulating; note sporangiolar wall and slightly apiculate spores, x600.—E. *Synoephalis cornu* van Tiegh. & Le Monn. Single immature merosporangium mounted in KOH-phloxine showing isthmus-like connections between developing spores and hyaline intermediary zones with separation discs (arrows), x2100 (from Benjamin 1966).—F. *Synoephalis asymmetrica* van Tiegh. & Le Monn. KOH-phloxine preparation again showing well-defined intermediary zones with separation discs (arrows), x2100.—G-I. *Piptocephalis indica*. Three late stages of merosporangium development (orcein preparations). G. Spore primordia showing hyaline intermediary zones, x2100; H. Later stage showing developing transverse spore walls, x2100; I. Mature merosporangium disarticulating; note lowermost spores formed in base of branched merosporangia, x2100 (from Benjamin 1966).—J-L. *Piptocephalis tieghemiana* Matruchot. Three stages in development of two-spored merosporangia in which spores are delimited after sporangium reaches definitive size by uniform elongation (orcein), x2100 (from Benjamin 1966).—M-N. *Piptocephalis lepidula*. Two stages in development of two-spored merosporangia in which the upper part of the sporangium arises by budding from the lower part (orcein), x2100 (from Benjamin 1966).
ZOOPAGALES

The order Zoopagales was tentatively proposed by Bessey (1950)* for three families, Zoopagaceae Drechsler ex Drechsler, Harpellaceae Léger & Duboscq, and Genistellaceae Léger & Gauthier (=Legeriomycetaceae Pouzar); members of the first are either parasitic or predacious on soil-inhabiting microanimals, whereas those of the latter two live attached to the digestive tract of aquatic larvae of insects. The Harpellaceae and Legeriomycetaceae now are generally placed in a separate class, Trichomycetes, and order, Harpellales, and will be discussed in a later section.

Drechsler proposed the family Zoopagaceae in 1935(a) but did not validate the name until 1938 when he provided a Latin diagnosis of it. Duddington emended the family in 1973 when he separated the parasitic from the predacious forms and placed them in a second family Cochlonemataceae (as Cochlonemateae). Kreisel (1969) transferred the Piptocephalidaceae into the order, and when one considers the many parallelisms between members of this family and the other two, it appears likely that all share commonly ancestry and a pattern of evolutionary development on soil-inhabiting organisms divergent from the probably related Mucorales. All known Piptocephalidaceae are obligately parasitic on other fungi, and with few exceptions (Piptocephalis xenophila Dobbs & English and Syncephalis synneae Thaxt.) are known only on hosts belonging to Mucorales. Because of their production of merosporangia, it has been presumed that Syncephalastrum, Syncephalis, and Piptocephalis are related (Benjamin 1959, 1966) and even that the first genus may be ancestral to the other two (Hesselhine & Ellis 1973). The mucoralean characteristics of spore development in Syncephalastrum (Benjamin 1959, 1966, Fletcher 1972) are very unlike the more or less arthric mode of spore formation.

* ZOOPAGALES Bessey, ord. nov.


Fungi endo- vel ectoparasitici microanimalium vel fungorum. Corpus vegetativa ex thallo simplici ramoso vel nonramoso aut mycelio nonseptato plus minusve extense ramoso constans. Ectoparasitae haustoria intra hospitem formantes. Reproductio asexualis a chlamydosporis aut sporangiolitis uni- vel multisporis; sporangiosporae sporangiolorum multispororum in catenas (merosporangii) simplicibus vel ramosis productae. Reproductio sexualis a zygosporis paene globosis; hyphae sexuales hypis vegetativis similibus vel plus minueve amplitate.

Fungi endo- or ectoparasites of microanimals or fungi. Vegetative body consisting of a simple, branched or unbranched thallus or more or less extensively branched mycelium. Ectoparasites forming haustoria inside the host. Asexual reproduction by chlamydospores or uni- or multi-spored sporangia; sporangiospores of multispored sporangiola produced in simple or branched chains (merosporangia). Sexual reproduction by nearly globose zygospores; sexual hyphae similar to the vegetative hyphae or more or less enlarged.
in *Piptocephalis*, *Syncehalis* (Benjamin 1959, 1966, Baker et al. 1977) and many other Zoopagales, especially those forming catenulate spores (Drechsler 1935a,b, 1937, 1938, 1939a,b, 1941, 1942, 1946, 1947b, 1951a, 1955b, 1959, Jones 1959, 1962). Superficial resemblance between the merosporangium of *Syncehalastrum* spp. (Fig. 23.4 A) and the merosporangia of species of *Piptocephalis* and *Syncehalis* (Fig. 23.4 B-N) may best be interpreted as resulting from convergence rather than reflecting close common ancestry.

Members of the Zoopagaceae and Piptocephalidaceae develop extensive mycelia; the hyphae are delicate, more or less highly branched, nonseptate -- except in age or when delimiting reproductive structures -- and upon contacting a suitable host become attached to it and form usually branched, internal haustoria. In Zoopagaceae capture of the usually motile host is effected by secretion of a sticky substance by the fungus hypha. The host is held fast during haustorial formation. Jeffries & Young (1976) have described "mucilage-like material" between the appressorium of *Piptocephalis unispora* Benjamin and the hypha of its host, *Cokeromyces recurvatus* Poitras, which may be homologous with the adhesive secretion of other Zoopagales. In *Piptocephalis* spp. and the species of several genera of Zoopagaceae (*Acaulopage* Drechsler, *Stylopage* Drechsler, *Zoopage* Drechsler) (Fig. 23.5 B,N) the haustoria are of limited extent and consist of a small number of relatively short branchlets. In *Syncehalis* and nematode-infecting *Cystopage* Drechsler spp. the infective hyphae are robust and may form a rather extensive, highly branched haustorial system.

In Cochlomenataceae the spores either become attached to the surface of the host, also apparently by secretion of adhesive material, or are ingested prior to becoming infective. *Amoebophillus sicuosporus* Drechsler (Fig. 23.6 M) and *Bdellospora helicoides* Drechsler (Fig. 23.5 L,M), representing monotypic genera, are ectoparasitic, and the attached spore itself forms the thallus after sending small, lobate or branched haustoria into the amoebal host. In the other genera of the family the internally developed thallus is cushion-shaped in *Apleatosoma microsporum* Drechsler, more or less coiled and branched or unbranched in species of *Cochlomena* Drechsler and *Endocochlus* Drechsler, or mycelial in species of *Euryancale* Drechsler.

Asexual spores of members of Zoopagaceae and Cochlomenataceae are formed either singly or in chains of few to many elements and superficially bear a striking resemblance to the conidia of Hyphomycetes. In his many contributions to the Zoopagaceae s.l., Drechsler (1935a,b,c, 1936a,b, 1937, 1938, 1939a,b, 1941, 1942, 1945, 1946, 1947a,b, 1948, 1949, 1951a, 1955b, 1957a, 1959; 1962) often considered the question of the possible sporangial nature of the asexual structures of these fungi and even of their possible homology with those of the Piptocephalidaceae (Drechsler 1938). He apparently never satisfied himself that this is so. Bessey (1950), on the other hand, assumed that the spores of Zoopagaceae are the homologues of the sporangiospores of Zygomyces. Hughes (1971a) also pondered the question of the sporangial nature of the spore-bearing structures of Zoopagaceae and concluded only that the idea deserved further serious consideration. The reality of the sporangial nature of the asexual structures of the zooparasitic Zoopagales must, of course, be subject only to speculation until representatives of these fungi are grown in cultures that will provide for detailed developmental studies, especially at the fine-structural level. Hopefully, methods like those being employed by Barron (Barron 1969, 1970, 1977, Barron & Davidson 1972, Barron...
& Perry 1975, Davidson & Barron 1973b) for studying nematophagous fungi belonging to other groups will be adapted to these fungi.

The pattern of spore development in the Zoopagales is unlike that of Mucorales and in many instances may actually best be considered as a specialized type of chlamydospore or arthrospore formation. In many forms of Zoopagaceae and Cochlonemataceae whose fertile hyphae give rise to unispored structures either singly or in succession (Acaulopage, Amoebophilus Dangeard, Endoocoolius, Euryanoa, Stylopage) the contents of the mature spore accumulate as the result of the partial evacuation of the parent hypha or spore initial (Fig. 23.5 A,C,I, J,N). The resulting spore, which must be regarded as endogenously formed, may bear one or more hyaline appendages representing evacuated parts of what may logically be regarded as the homologue of a sporangium (Fig. 23.5 C,J). As regards its formation, the "chlamydospore" of Cystopage spp. (Fig. 23.5 G) is no different, except for shape and location relative to its parent hypha, from the spores of forms like Endoocoolius gigas Drechsler (Fig. 23.5 I,J).

It is in those Zoopagaceae and Cochlonemataceae that form catenate spores (Aplectosoma Drechsler, Bdellospora Drechsler, Cochlonema, Zoopage) that the most marked correspondence with piptocephalidaceous merosporangia is found. The simple or branched fertile hyphae of the former (Fig. 23.5 D,E,F,H,K,M) bear no great similarity to the simple or branched merosporangia of species of Piptocephalis and Synoeaphalis. In all instances where spore formation has been reasonably well studied, the spores are delimited simultaneously, and as they mature are separated from one another by hyaline zones enclosed laterally by the remains of the wall of the original fertile hypha up to the time of maturation and disarticulation. Such intermediary zones were described and figured often by Drechsler and in some instances the spores bear apical apiculi (Fig. 23.5 D) comparable to those of some species of Synoeaphalis (Fig. 23.4 D). Spore development in Zoopagaceae and Cochlonemataceae having catenate spores appears to be more like that found in Synoeaphalis than in Piptocephalis, and suggests that the former genus may be less closely related to the latter than it is to some members of the other families.

Up to now, fine-structural studies of the zoopagalean sporangiolute have been confined to the unispored Piptocephalis unispora (Jeffries & Young 1975) and Synoeaphalis sphaerica (Baker et al. 1977). The distinctive characteristics of spore formation in species of Piptocephalis and Synoeaphalis are suggested mostly by the light-microscopic studies of Thaxter (1897) and Benjamin (1959, 1966). Spore formation in the multispored, branched merosporangia of Piptocephalis indica Mehrotra & Baijal (Benjamin 1966) involves the progressive elongation of the sporangial branches with the concomitant sequential division of the progeny of an originally single nucleus. Spore formation is simultaneous, as is the development of adjacent end walls of the spores themselves (Fig. 23.4 G,H). Sporangial disarticulation follows by the rupture of the sporangial wall adjacent to the hyaline intermediary zones (Fig. 23.4 I). A similar process of merosporangial elongation followed by the simultaneous formation of spores apparently is characteristic of most species of Piptocephalis (Fig. 23.4 J-L). However, in P. lepidula (Marchal) Benjamin, P. curvata Baijal & Mehrotra (1968), and at least two other species, as yet understood, the merosporangium is two-spored and its development is acropetal. The distal part of the sporangium arises as a bud-like outgrowth from the lower part. The nucleus in the lower half, in P. lepidula, divides and one daughter nucleus migrates into
the upper half following which the two spores mature simultaneously (Fig. 23.4 M,N). Spore germination in members of this genus always is lateral, never through the polar regions of the spore (Benjamin 1959).

Spore formation in the simple or branched merosporangia of Synoephalis spp. is accomplished by the simultaneous cleavage of the sporangial contents and involves the development of a cytoplasmic isthmus between each presumptive spore, together with a distinctive "intermediary zone" consisting of stainable and nonstainable regions (Thaxter 1897, Benjamin 1966) (Fig. 23.4 E,F) not found up to now in developing merosporangia of other merosporangiferous forms. In S. sphaerica, the only species studied thus far by electron microscopy (Baker et al. 1977), isthmus formation and spore cleavage are shown to be accomplished by invaginations of the merosporangial plasmalemma accompanied by the development of a distinctive cleavage zone which forms centripetally and eventually separates the spores. The side walls of each spore of S. sphaerica develop in advance of the end walls and represent a distinct wall lining layer formed during the precleavage stage of merosporangial development. The end walls of each spore develop later on each side of the intervening abscission zones. In some species of Synoephalis the mature spores appear apiculate, even the distal end of the terminal spore (Fig. 23.4 D,E). Apiculate spores have been illustrated by Drechsler in several catenulate species of Zoopagaceae s.l., which suggests that the mechanism of spore formation in these species may be like that in Synoephalis. Synoephalis tenuis Thaxter resembles Piptocephalis lepidula in having a two-spored merosporangium with an acropetal mode of development (Fig. 23.4 B-D). The nuclear cycle accompanying spore development in S. tenuis has not been determined. Spore germination in Synoephalis spp., where it has been observed, always is polar (Benjamin 1959), and doubtless reflects the manner in which spores are developed.

Branched spores are formed in the basal part of the branched merosporangia of several species of Piptocephalis (Fig. 23.4 I) and Synoephalis. These are comparable to similar branched spores formed by branched fertile hyphae of some Cochlonemataceae (Fig. 23.5 K).

Stylospores (i.e., terminal chlamydospores) were reported by van Tieghem (1875) for Synoephalis nodosa van Tiegh. and S. reflexa van Tiegh. and by Bainier (1882) for S. curvata Bainier. I have never observed such spores in any of the species, including S. nodosa, that I have studied in culture, nor, as far as I am aware, has any other student of these fungi (Indoh 1962). I question the occurrence of stylospores in the genus, and suspect that their earlier description was based on cultures contaminated with Mortierella spp.

Zygospores are known for representatives of all genera of Zoopagales except Aplectosoma, Cystopage, and Euryancale. These spores are relatively small in the minute parasitic or predaceous Zoopagaceae and Cochlonemataceae, and the sexual hyphae are usually relatively undifferentiated (Fig. 23.6 I,J-M) and may be spirally wound around one another (Fig. 23.6 C,E,H). The zygosporangium may form between the conjugating sexual branches or, more commonly, develop from a budlike enlargement arising from one of the gametangia. In several species of Cochlonema the coiled or apposed sexual hyphae delimit gametangia that may become more or less enlarged (Fig. 23.6 D,E,G,H) and often bear a striking resemblance to those of some species of Synoephalis (Fig. 23.6 B). The zygospores may be smooth and more or less undulate or papillate, or may bear conspicuous, truncate or somewhat capitate knobs or warts. Zygospores of species of Piptocephalis (Fig. 23.3 I,J) and Synoephalis (Fig. 23.6 A,B) are
Figure 23.6. Representative zygospores of Zoopagales. A. *Synoephalis cornu*. Mature zygospore formed above point of fusion of gametangia, x880 (from Benjamin 1959).—B. *Synoephalis nodosa*. Mature zygospore formed in globose outgrowth of one gametangium, x880 (from Benjamin 1959).—C. *Bdellospora helicoides*. Shows origin of spirally wound sexual hyphae from two thalli (centre), nearly mature (right) and mature (left) zygospores, x665 (after Drechsler 1935a).—D. *Coahlonema odontosperma* Drechs. Three stages in development of zygospore, x665 (after Drechsler 1937).—E. *Coahlonema megasporum* Drechs. Zygospore arising in globose outgrowth of one of two enlarged, apposed suspensors, x665 (after Drechsler 1939a).—G. *Coahlonema agamum* Drechs. Mature azygospore (below) and immature azygospore developing from a single hypha, x665 (after Drechsler 1946).—H. *Coahlonema symplochum* Drechs. Spirally wound sexual hyphae (left) and mature zygospore (right), x665 (after Drechsler 1941).—I. *Endooclus asteroides* Drechs. Three stages in development of zygospore in budlike outgrowth from one of two undifferentiated sexual hyphae, x665 (after Drechsler 1935a).—J. *Acaulopage aeratospora* Drechs. Two stages in development of zygospore from undifferentiated sexual hyphae, x665 (after Drechsler 1935b).—K. *Stylopage rhynchospora* Drechs. The same, x665 (after Drechsler 1939b).—L. *Zoopage phanera* Drechs. The same; one sexual hypha has arisen from a germinated spore, x665 (after Drechsler 1935a).—M. *Amoebophilus stacysporus*. Development of zygospores from thalli derived from primary and secondary spores attached to host amoeba, x665 (after Drechsler 1959).
much larger than those of the other genera of the order. Their sexual hyphae (suspensors) are typically apposed or coiled during early stages of development (Fig. 23.3 G,H) and the zygosporangia usually develop mostly above the point of fusion of the gametangia (Fig. 23.3 I,J) or, as in some species of Synocephalis, may arise as a budlike enlargement from one gametangium (Fig. 23.6 B).

The family Helicocephalidaeae was established by Boedijn (1958) for two genera of nematophagous fungi. Species of Rhopalomyces Corda (Barron 1973, Ellis 1963, Ellis & Hesseltine 1962) form numerous single spores simultaneously over the surface of ampullae arising terminally on elongate, robust sporophores, whereas species of Helicocephalum Thaxter give rise to a single chain of spores formed simultaneously from the usually coiled termination of the sporophore (Barron 1975, Drechsler 1934, 1943, 1954, Thaxter 1891b). The vegetative mycelium of species of these genera is delicate, highly branched, coenocytic, and has been shown to parasitize nematode eggs (Barron 1973, 1975, Drechsler 1943, Ellis & Hesseltine 1962), and in Rhopalomyces elegans Corda even living nematodes (Barron 1973) by the formation of extensive, branched haustoria arising from appressoria that can adhere to and hold the living host body while haustorial penetration takes place. Ellis & Hesseltine (1962) succeeded in culturing R. elegans on a complex medium of relatively high pH containing baby beef liver and various animal fats or vegetable oils, after having germinated the spores on a separate medium containing nutrients derived from killed cells of Bacillus cereus Frankland & Frankland.

The sporangial nature of the spore-forming structures of Rhopalomyces and Helicocephalum spp. has not been established, but the resemblance of these structures to merosporangia of Synocephalis, especially, and other Zoopagales suggests that they may be homologous. It is interesting to note that Ellis (1966) succeeded in growing several species of Synocephalis in pure culture employing a tryptone-potassium phosphate agar supplemented with sterile cubes of baby beef liver. The spores of several species of Piptocephalis have been germinated in the absence of a host (Benjamin 1959, Berry & Barnett 1957, Leadbeater & Mercer 1957), and a limited mycelium develops that may produce depauperate sporophores bearing spores. In the absence of a suitable host, however, such axenic-culture spores (Manocha 1975) fail to germinate, or if they do, they will not develop hyphae. No species of Piptocephalis has yet been induced to grow and sporulate normally in axenic culture.

Globose, smooth, relatively thick-walled, slightly pigmented chlamydospores have been observed in cultures of Rhopalomyces elegans (Barron 1973, Ellis 1963, Ellis & Hesseltine 1962). These are produced terminally or laterally on short branches, and are the only presumably resistant structures that have been observed in these fungi. Whether or not they are chlamydospores, azygospores, or some type of true zygospore remains to be determined.

For the present, Helicocephalidaeae seem best allied with the Zoopagales, as suggested by Milko (1974), rather than with the more generalized, typically saprobic Mucorales where only a few species are known to be weak facultative parasites of other Mucorales, i.e., Abelia parricida Renner & Muskat, Chaetocladium brefeldii van Tiegh. & Le Monn., C. jonesii (Berk. & Br.) Fres., and Parasitella simplex Bainier. These all form distinctive galls where they contact their hosts, never true haustoria like all but the endoparasitic members of the Zoopagales.
ENDOGONALES

The order Endogonales was proposed by Moreau (1953)* for fungi that traditionally have been regarded as an anomalous family, Endogonaceae, of Mucorales. Until recently (Hesseltine & Ellis 1973, Moreau 1953) only three genera, Endogone Link ex. Fr., Glaziella Berk., and Soleroystis Berk. & Br., have been recognized from among the several genera that had been proposed earlier. Species of these genera typically form their spores in more or less well-defined sporocarps, i.e., small or large, solid or hollow, mostly hypogeous hyphal aggregates within which the spores may be randomly distributed or regularly arranged side-by-side in discrete clusters. What appear to be true zygospores are known only in species of Endogone. These form following fusion of equal or subequal gametangia delimited by usually apposed sexual hyphae, and the zygosporangium arises as a budlike outgrowth that may develop above the point of fusion of the gametangia or wholly from one of the gametangia. Many species formerly assigned to Endogone, including Sphaeroareas Sacc. & Ellis, and all species of Soleroystis and Glaziella (Thaxter 1922) produce only relatively large, thick-walled, terminal chlamydoospores, or what may be interpreted as azygospores. Only two species, now placed in Modicella Kanouse (1936) form what appear to be sporangia containing endogenous spores.

*ENDOGONALES Moreau, ord. nov.

Endogone Moreau, nomen nudum, Les Champignons, Tome II. Systématique.


Fungi plerumque hypogaei, raro epigaei, saprobii et viventes liberi vel vulgo endomycorrhizae vesiculis et arbusculis in radicibus plantarum viventium formantes; ectomycorrhizae rarissimae. Hyphae mycelii vegetativi nonseptatae. Reproduatio asexualis a sporangiosporis, chlamydoisporis terminalibus, aut azygosporis terminalibus vel lateralibus. Reproducuntio sexualis a sygosporis paene globosae vel ovoidae; hyphae sexuales plerumque hyphis vegetativis similibus; gametangia eaequalis vel inaequalis. Sporae solitariae et liberae vel in sporocarpiis formantes.

Fungi mostly hypogeous, rarely epigeous, saprobic and free living or commonly forming endomycorrhizae with vesicles and arbuscules in roots of living plants; ectomycorrhizae very rare. Hyphae of vegetative mycelium nonseptate. Asexual reproduction by sporangiospores, terminal chlamydoospores, or terminal or lateral azygospores. Sexual reproduction by nearly globose or ovoid zygospores; sexual hyphae similar to the vegetative hyphae; gametangia equal or unequal. Spores solitary and free or formed in sporocarps.

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Kanouse (1936) described mortierellaceous-type sporangia and chlamydospores in what she believed to be pure cultures of *Endogone sphagnophila* Atkinson and *E. occidentalis* Kanouse (Both =*E. pisiformis* Link ex Fr. fide Gerdemann & Trappe 1974), and for the first species she even described and illustrated what she believed to be zygospore formation. Kanouse was unable to repeat her initial presumed successful cultures of surface-sterilized sporocarps of *E. sphagnicola* and her observations have not been confirmed. The abundance of *Mortierella* spp. in soil and the predilection many species of this genus have for forming chlamydospores in culture suggest that her cultures may have consisted of one or more species of *Mortierella*.

The capacity of many species assigned to *Endogone* to form endotrophic mycorrhizae and their possible significance in the development of crop plants has led to intensive study of these fungi for many years (see Gerdemann 1971 for references). Except for Kanouse's claim, no one has succeeded in growing any of these fungi in pure culture. However, several techniques have been devised for isolating the spores of *Endogone* and related forms from soil and inducing vesicular-arbuscular (VA) endomycorrhizal infections in the roots of susceptible plants growing in the laboratory (Barrett 1961, Gerdemann & Nicolson 1963, Mason 1964, Mosse 1953, 1956, Mosse & Bowen 1968a,b). These studies, which have shown that many *Endogone*-like spores associated with endomycorrhizae are not necessarily formed in sporocarps, have led recently to a revision of the generic concepts in the Endogonaceae by Gerdemann & Trappe (1974).

Only those species of Endogonaceae forming what may be regarded as true zygospores (Fig. 23.3 M) are assigned to *Endogone*. All species of this genus develop hypogeous or epigeous sporocarps and are not known to form endomycorrhizae. One species, *E. flammicorona* Trappe & Gerdemann has been implicated in the formation of ectomycorrhizae (Fassi & Palenzona 1969). Three genera have been segregated from *Endogone* as previously recognized. *Glomus* Tulasne & Tulasne includes both sporocarpic and nonsporocarpic species forming large, thick-walled, terminal chlamydospores (Fig. 23.3 L), and all species of the genus may eventually prove to be endomycorrhizal (Gerdemann & Trappe 1974). *Modicella*, with two species, forms mostly epigeous sporocarps consisting of numerous presumed sporangia containing chlamydospores (Fig. 23.3 K) and is not known to be mycorrhizal. Species of *Gigaspora* Gerdemann & Trappe are endomycorrhizal, lack sporocarps, and form large, terminal (?)zygospores subtended by a small, somewhat swollen enlargement that usually bears a short, slender hypha attached to the spore. Species of *Acaulospora* Gerdemann & Trappe form VA mycorrhizae, are nonsporocarpic, and develop large, thick-walled, globose chlamydospores that form laterally on the stalk of a large, thin-walled vesicle which eventually collapses. *Solerocystis* spp., all of which are probably VA mycorrhizal, resemble *Glomus* spp., but form their chlamydospores side by side in solid, single or aggregated sporocarps. *Glaziella aurantiaca* (Berk. & Br.) Cook, the sole member of the genus, forms chlamydospores scattered in the thin walls of a large, hollow sporocarp. Its mycorrhizal propensities, if any, have not been demonstrated.
ENTOMOPHTHORALES

A separate position within the Zygomycetes has long been accorded the fungi placed here (Schröter 1893, Thaxter 1888) and one of the first to adopt the ordinal name Entomophthorales was Underwood (1899). Many members of the order have developed parasitic tendencies, especially on insects (Entomophthora Fres., Mesospora Peck, Stronguellea Batko & Weiser) or on minute soil-inhabiting animals (Baliocephala Drechsler, Entomophthora, Macrobrotophthora Reukauf, Meristaorum Drechsler, Zygnemomyces Miura) and may be relatively virulent pathogens. Others are soil-inhabiting saprobes (Basidiobolus Eidam, Comidiobolus Brefeld) that are only facultatively parasitic on insects or animals, including man, and a few are known only as parasites of green plants (Anaylistes Pfitzer, Completoria Lohde). The vegetative mycelium of Entomophthorales is coenocytic but usually the hyphae become septate and form uni- or multi-nucleate segments. In species of Entomophthora, especially, the segments may separate readily, forming so-called hyphal bodies that then multiply by fission. In all but two genera (Mesospora, Zygnemomyces) the primary means of asexual reproduction is by the production of single, terminal, uni- or multi-nucleate sporangiola that are forcibly ejected at maturity. Three distinct mechanisms for forcible discharge have evolved in the order. (1) In several species usually placed in Entomophthora, of which E. muscae (Cohn) Fres. is representative (MacLeod, Müller-Kügler & Wilding 1976), the sporangiola is broadly attached to the somewhat swollen tip of the sporangiophore and at maturity is shot away following rupture of the sporophore apex. Cytoplasm from the collapsing sporophore accompanies the discharged sporangiola and may help it adhere to any contacted surface. Von Arx (1970) proposed retaining the generic name Myiophyton Lebert for E. muscae and related species. (2) In Basidiobolus spp. the terminally formed sporangiola is subtended by a turgid, distal enlargement of the sporophore (Fig. 23.7 B-E). This subsporangial swelling develops a subbasal, circumscissile line of weakness which ruptures and, jetlike, the upper portion of the swelling flies off carrying the sporangiola with it. The detached part of the sporophore, which projects into the base of the sporangiola as a minute columella, usually separates from the sporangiola during flight. A similar mechanism of discharge has been proposed, but not yet proven, for Baliocephala spheerospora Drechsler (1951b) in which each of the many sporangiola arising from the sporophore is subtended by a small, turgid enlargement, a part of which accompanies the sporangiola when it is released and propelled at least a short distance outward from its point of origin. Pohlad & Bernard's (1978) observations regarding forcible discharge of the sporangiola of their tardigrade parasite, B. pedicellata, were inconclusive. (3) In many species assigned to Entomophthora s.l. (Sawyer 1931), Anaylistes (Couch 1949), Completoria (Leitgeb 1881), Comidiobolus (Couch 1939), Meristaorum (Davidson & Barron 1973a, Drechsler 1960), and Strongwellsea (Humber 1976), forcible discharge of the sporangiola is effected by the rounding off of turgid cells (Ingold 1934, 1953). Couch (1939) beautifully illustrated and described this mechanism when he characterized Comidiobolus brefeldianus Couch. As the sporangiola develops, cytoplasm from the subtending sporophore flows into the enlarging sporangiola, and as the latter reaches definitive size a rounded to conical columella is formed against which the base of the developing spore is appressed (Fig. 23.7 A). A vacuole develops in the spore adjacent to the columella. With increased turgor inside the spore, sufficient pressure is exerted against the columella so that the sporangiolar wall is ruptured near the base of the
Figure 23.7. A. Conidiobolus sp. Optical section of sporangiole and part of subtending stalk showing rounded columella and hyaline zone developing at base of spore. Projecting laterally into the picture at upper right is tip of a sporangiophore from which the sporangiole has been discharged, x600—B-E. Basidiobolus microsporus. Four stages of development of sporangiole and subsporangial swelling, x340 (from Benjamin 1962).—F. Basidiobolus ranarum. Elongate adhesive spore, x465.—G-J. Basidiobolus microsporus. G-I. Three stages of development of the zygospore, x310; J. Mature zygospore, x620 (I, J, from Benjamin 1962).—K. Basidiobolus microsporus. Chlamydospores in submerged vegetative hyphae, x340 (from Benjamin 1962). L-O. Conidiobolus coronatus. L. Primary sporangiole that has given rise to a secondary sporangiole borne on a short secondary sporangiophore, x800.—M. Primary-type sporangiole bearing numerous microspores on short microsporangiophores, x550.—N. The same after discharge of microspores, x550.—O. Villose resting spore, x600.
columella.

In the above brief commentary, I have regarded the primary asexual spore of Entomophthorales as a unispored sporangiola. Its formation from a primordium into which all or part of the cytoplasm of its subtending cell or hypha moves suggests its homology with the sporangia or sporangiola of many other Zygomycetes, especially Mucorales and Zoopagales. And it has long been regarded as a derived sporangium by many students of these fungi (Bessey 1950, Thaxter 1888), although it still is commonly referred to as a conidium. In several species of Entomophthora (examples: E. aquatica Anderson & Ringo, E. creatonotus Yen, E. gloeospora Vuill., E. montana (Thaxt.) Gustafsson (MacLeod & Müller-Köger 1973), E. aphidis Hoff., E. ovispora Nowak. (Gustafsson 1965)) and in the two known species of Strongwellesa, S. castrana Batko & Weiser and S. magna Humber (Humber 1976) the sporangiolar wall readily separates from the spore wall above the papillate basal extension of the spore. In most species of Entomophthorales, the thin sporangiolar wall remains firmly in contact with the spore wall above the protruding papilla. In their fine-structural study of Conidiobolus coronatus (Cost.) Batko (as Entomophthora coronata (Cost.) Kevorkian), Garrison, Mariat, Boyd & Tally (1975) interpreted the spore wall as consisting of three layers (their Figs. 4,6): a thick inner layer (ca. 110 nm), a less thick median layer (ca. 60 nm), and a thin outer layer (ca. 10nm) which ends at its juncture with the spore papilla. This thin outer layer undoubtedly represents the original wall of the developing sporangiola initial that was continuous with the sporophore wall prior to sporangiolar discharge, and it is easily interpreted as the homologue of the separable wall of forms like the species of Entomophthora and Strongwellesa named above.

The primary sporangiola of many Entomophthorales has a remarkable capacity for forming secondary accessory types of asexual spores for short-term survival in the event a suitable substratum is not immediately available. Whether or not all of these secondary spores may be regarded as secondary sporangiola or as true exogenously formed conidia, as may be the case in Basidiobolus microsporus Benjamin (1962), remains to be determined. When implanted on a substratum suitable for growth, the primary spores of all species that have been studied in any detail apparently are capable of immediate germination by the formation of germ tubes. If, however, the primary sporangiola falls on a nonnutritive substratum (i.e., a dry surface, water, water agar, etc.) it may give rise to a short sporophore bearing a single, similar, but smaller, sporangiola (spp. of Basidiobolus, Complectoria, Conidiobolus, Entomophthora) (Fig. 23.7 L). Such secondary (and tertiary, etc.) sporangiola appear to be morphologically and developmentally identical to the primary sporangiola. In several species of Conidiobolus, under similar circumstances (see especially King 1976a,b, 1977, Page & Humber 1973, Prasertphon 1963), the primary sporangiola develops a multitude of short sporophores each forming a terminal multiplicative spore (microspore) similar to the primary sporangiola in structure and manner of discharge (Fig. 23.7 M,N). Also, the primary sporangiola of several species of Entomophthora (Thaxter 1888), Conidiobolus (King 1976a,b, 1977), and Basidiobolus Benjamin 1962, Drechsler 1947c, 1955a, 1956, 1958, 1964) form single, more or less elongate, often strobiliform secondary spores terminally on slender, elongate stalks that, except for two species of Conidiobolus (King 1977), are passively detached rather than being forcibly ejected.
In Basidiobolus (B. haptosporus Drechsler, B. magnus Drechsler, B. meristosporus Drechsler, and B. vonarum Eidam) (Benjamin 1962, Drechsler 1947, 1955a, 1956, 1964) these elongate spores produce adhesive material terminally on a short protuberance (Fig. 23.7 F) that enables them to attach to surfaces with which they may come into contact. In B. microsporus (Benjamin 1962), the primary sporangiole gives rise to numerous long-beaked microspores each arising from an internally formed cell. The microspores of this species, unlike those of Conidio-
obolus spp., are morphologically unlike the parental sporangiole and are not forcibly ejected at maturity. They are conidial in appearance, and only a fine-structural study is likely to elucidate their true structure and origin relative to the subtending cell. Primary sporangiole and elongate secondary adhesive spores of Basidiobolus spp. are also known to form endogenous spore-like bodies (Drechsler 1947c, 1955a, 1956, 1958, 1964, Levison 1927) that have been likened to the sporangiospores of Mucorales, and their production has been suggested as evidence of the sporangial nature of the primary and secondary spores of members of the genus. Basidiobolus is the only genus of Entomophthorales in which the contents of the primary or secondary spores may form two or more endogenous spore-like bodies that may germinate directly, give rise to stalked microspores, or form zygospores in a manner identical to that proceeding in vegetative hyphae (Benjamin 1962, Drechsler 1955a). In an unnamed species of Basidiobolus from Indonesia, Drechsler (1958) described the formation of spore-like bodies, inside ordinary vegetative hyphal cells, that appear identical to those formed in primary spores and elongate adhesive spores. Homology of such endogenous "spores" with the sporangiospores of Mucorales is doubtful, and it seems logical to regard such "spores" as a kind of internal vegetative proliferation comparable to ordinary hyphal development.

An alternative interpretation of the nature of the entomophthoralean sporangium has been proposed in which those sporangiole having a basally discontinuous, nonseparable outer wall are regarded as prosporangia, whereas those having a separable outer wall are regarded as true monosporous sporangia. Thus, Batko (1964a,b,c) in dividing Entomophthora into five genera, attributed true monosporic sporangiola to Zoophthora Batko, whereas the other four segregates, Entomophthora s.s., Triplosporium (Thaxt.) Batko, Culicicola Nieuwland, and Entomophaga Batko, included species having so-called asporic sporangia (prosporangia). By the same token, the sporangiola of Basidiobolus and Conidiobolus were regarded as prosporangia by Langeron & Vanbreuseghem (1952). The separability or nonseparability of a probably identically derived outer wall of the sporangiola of otherwise related forms hardly seems sufficient reason for distinguishing a true sporangium from a "prosporangium."

Thick-walled resting spores are known for most species of Entomophthorales and their formation undoubtedly is necessary for the survival of many parasitic species for which a suitable host may not be immediately available. In some species of Entomophthora (i.e., the provisional genus Tarichium Cohn of MacLeod & Müller-Kögler 1970), they are the only kind of spore known. In many species the resting spore may be regarded as a true zygospore because of its development from the apparent sexual union of the contents of contiguous cells of the same or adjacent hyphae, or copulating hyphal bodies (Fig. 23.7 G-J) (Benjamin 1962, Couch 1939, Drechsler 1954, 1957b, 1961, Gustafsson 1965, Miura 1973, Thaxter 1888), whereas in others its sexual development has not been observed, or its parthenogenetic development is suspected and it is regarded as an azygospore (Gustafsson 1956, MacLeod & Müller-Kögler 1970, 1973,
MacLeod et al. 1976). The wall of zygospores and azygospores appears to be two- or three-layered (Thaxter 1888, Waterhouse 1973b) and it may be smooth or variously sculptured with warts, ridges, echinulations, striae, undulations, etc.

Smooth, thick-walled chlamydospores (Fig. 23.7 K) morphologically like those of many Mucorales are formed in the vegetative hyphae of several species of Conidiobolus (King 1976a, b, 1977), Entomophthora (Gustafsson 1965), and Basidiobolus (Benjamin 1962, Drechsler 1958). Conidiobolus coronatus is unique in that its primary sporangiola or subsequently formed secondary, tertiary, etc., sporangiola may form villose resting spores (Fig. 23.7 0) when they are discharged onto water or a moist surface such as the wall of the culture chamber or the surface of the parent colony, where they cannot contact the nutritive substratum (Prasertphon 1963). Villosity of this type of resting spore results from the development of numerous short, slender outgrowths from the spore wall.

Entomophthorales long have been regarded as a natural taxon or order of related fungi separate from the Mucorales (de Bary 1887, Bessey 1950, Fitzpatrick 1930, Schröter 1893, Underwood 1899, Waterhouse 1973b), but their classification into families and genera still has not been stabilized. In her summary of the order, Waterhouse (1973b), like Fitzpatrick (1930) and Bessey (1950), recognized only the Entomophthoraceae Warming with six genera, Ancylistes, Completoriella, Masseospora, Entomophthora, Basidiobolus, and Conidiobolus. She did, however, give a fairly complete list of the generic names that have been proposed in the order -- except for Ballocephala (Drechsler 1951b), Meristacrum (Drechsler 1940), Macrobiosphoruthora (Reukauf 1912), and Zygnemomyces (Miura 1973) -- and evaluated the recent proposals by Batko (1964a,b, 1966) to fragment Entomophthora into no less than five separate genera as listed earlier. She (see also Waterhouse 1975), like Gustafsson (1965), MacLeod & Müller-Kögler (1970, 1973), and MacLeod et al. (1976) who have made recent contributions to taxonomy of Entomophthora s.l., feels that many of the described taxa still are too imperfectly known both morphologically and cytologically to divide the genus as proposed by Batko. Humber's (1976) recent work on Strongwellsea argues strongly in favor of distinguishing this genus from Entomophthora.

Many mycologists recognize at least two families, Entomophthoraceae and Basidiobolaceae Claussen in Engler & Gilg (Alexopoulos 1962, Claussen in Engler & Gilg 1924, Chadeauf 1970, Couch 1939, Langeron & Vanbreuseghem 1952, Moreau 1953). Ubirzy & Vörös (1966) placed Ancylistes in a separate, perhaps superfluous family, Ancylistaceae. Some would include the Zoopagaceae s.l. in the Entomophthorales (Arx 1970, Webster 1970), but I cannot see evidence of a close relationship of Zoopagales (see above) with Entomophthorales. Kreisel's (1969) inclusion of Pilobolaceae (Mucorales) in the order cannot be taken seriously. Couch (1939) claimed to have demonstrated cellulose in the cell walls of Basidiobolus ranarum and he, followed by Langeron & Vanbreuseghem (1952), stressed this as an important reason for maintaining the genus in a separate family. Frey (1950), however, using X-ray analysis, could not detect cellulose in B. ranarum, and the histochemical studies of Hoddinott & Olsen (1972) likewise confirmed the absence of cellulose in the cell walls of this species. This is in line with the results of studies on the distribution of cellulose in the cell walls of fungi (Bartnicki-Garcia 1968). Other arguments that can be made for maintaining family status for Basidiobolus include its usually uninucleate cells, the tendency for its hyphae not to break
up into hyphal bodies, and its presumably unequal gametangia -- characteristics found occasionally in members of other genera of the order (Waterhouse 1973b). Also, although *Basidiobolus* spp. may be facultative parasites of animals, including man, they are not known to parasitize insects or other microanimals. None of these features would seem to be sufficiently important to maintain the genus in a separate family. However, stronger arguments for such recognition include the unique manner of sporangial discharge, the tendency for certain of its spores and even vegetative hyphal segments to form endogenous spore-like bodies, and especially the unique accessory cells accompanying gametangial delimitation (Fig. 23.7 G-J). It is my opinion that *Basidiobolus* should be retained in a separate family, Basidiobolaceae.

**DIMARGARITALES**

When the family Dimargaritaceae was established by Benjamin in 1959 it was included in the Mucorales along with the Kickxellaceae Linder, and both families were regarded as derived offshoots of a line of evolution within this order which also included two other families of so-called merosporangiferous forms, i.e., Piptocephalidaceae and Syncpephalastraceae. Unlike typical Mucorales (including Syncpephalastraceae), Zoopagales (including Piptocephalidaceae), Endogonales, and Entomophthorales, all members of Dimargaritaceae and Kickxellaceae have vegetative hyphae possessing distinctive cross walls that are formed during the earliest stages of development. These characteristic septa, which also occur in the spore-bearing structures (Fig. 23.8 C,G) (Benjamin 1958, 1959, Benny 1972, Benny & Aldrich 1975, Young 1969), set these fungi apart from all other fungi except Harpellales and Asellariales of the Trichomycetes.

The close alliance of Dimargaritaceae and Kickxellaceae has been presumed primarily on the basis of their similar septa and the characteristics of their globose, thick-walled zygospores formed in thin-walled zygosporangia derived from morphologically undifferentiated hyphae (Benjamin 1958, 1959, 1961, 1963, 1965). When other characteristics are considered, the two families are very distinct. A fundamental distinction between the two families is shown by differences in the plug formed in the septal cavity (Benjamin 1959, Moss & Young 1978). In Dimargaritaceae the biconvex plug has distinctive polar protuberances, especially conspicuous in the cross-walls of the sporangiophores, and is readily soluble in dilute alkali (2-3% KOH), whereas in the Kickxellaceae the biconvex or biumbonate plug lacks polar protuberances and is insoluble in dilute alkali. All Dimargaritaceae grow readily as haustorial mycoparasites of other fungi (Mucorales and *Chaetomium* spp. are known hosts), whereas Kickxellaceae are saprobes or in a few, as yet unproven, instances appear to be capable of growing as weak nonhaustorial parasites of other fungi. The sporangiola of Dimargaritaceae are uniformly two spored, whereas those of all Kickxellaceae are one spored. Each family comprises a well-defined and seemingly very natural group of fungi.

Kreisel, in 1969, proposed separation of the Kickxellaceae and Dimargaritaceae from the Mucorales as a distinct order, Kickxellales, which he also removed from the Zygomycetes and placed in Arx's Endomycetes (Arx 1967). Kreisel rightly recognized the need to separate these families from the Mucorales, where they generally have been treated (Arx 1967, Benjamin 1958, 1959, 1961, 1963, 1965, 1966, Hesseltine 1955, Hesseltine & Ellis 1973, Milko 1974,
Müller & Loeffler 1968, Zycha et al. 1969), but I cannot accept their removal from the Zygomycetes. A number of studies carried out during the past decade (Farr & Lichtwardt 1967, Manier 1973, Manier & Coste-Mathiez 1968, Moss 1975, 1976, Moss & Lichtwardt 1976, Moss & Young 1977, 1978, Sangar, Lichtwardt, Kirsch & Lester 1972) have presented strong evidence that the Kickxellaceae are more closely allied with Harpellales and Asellariales than with other Zygomycetes, even Dimargaritaceae which appear to occupy an isolated position within the class. Their superficially similar cross-walls and zygospores notwithstanding, it seems best to separate Dimargaritaceae and Kickxellaceae at the ordinal level, retaining Kickxellales for the latter family and placing the former in a new order, Dimargaritales.

DIMARGARITALES Benjamin, ord. nov.

Parasites haustoria in fungi alii facientes. Corpus vegetativa hypharum septatarum ramosarum sporangiophora septata ramosa vel nonramosa produens. Septa cum cavitatibus medians disciformibus; cavitates obturamenta incolorata plus minusve biconvexa continentes; obturamenta processibus polaribus in alkalino diluto dissolventia. Reproduction asexualis a sporangiolia bioporis; sporangiola in ampullis terminalibus aut in cellulis ramulorum fertilium simplicium vel ramosorum vel in ampullis terminalibus vel in fasciculis terminalibus exorientibus genita. Reproduction sexualis a zygosporis paene globosis; hyphae sexuales hyphis vegetativis similibus.

Parasites forming haustoria in other fungi. Vegetative body of septate, branched hyphae, producing septate branched or unbranches sporangiophores. Septa with median disciform cavities containing colourless, more or less biconvex plugs; plugs with polar protuberances, dissolving in dilute alkali. Asexual reproduction by 2-spored sporangiola; sporangiola formed on terminal ampullae or on cells of simple or branched fertile branchlets arising from terminal ampullae or in terminal fascicles. Sexual reproduction by nearly globose zygospores; sexual hyphae simple, similar to the vegetative hyphae.

There are three genera of Dimargaritaceae in which species have been grown in culture, Dimargaris van Tiegh., Dispira van Tiegh., and Tieghemomyces Benjamin. A fourth genus, Spinalia Vuillemin (1904), was provisionally assigned to the family by Benjamin (1959), but the type species, S. radians Vuill., still is known only from the original description based on scanty preserved material. All Dimargaritaceae that have been discovered thus far (Benjamin 1959, 1961, 1963, 1965, Mehrrotra & Baijal 1963, 1964) are haustorium-producing mycoparasites, being found in nature mostly on Mucorales or, occasionally, Chaetomium Kunze ex Fr. spp. (Brunk & Barnett 1966, Mandelbrot & Erb 1972).

Parasitism of these fungi apparently is not obligate. Several species have been grown in axenic culture, though weakly, on ordinary media containing starch or glucose as the carbon source (Benjamin 1959, Brunk & Barnett 1966), but vigorous growth and sporulation on such media will not occur in the absence of a suitable host. Physiological studies bearing on nutritional requirements for axenic growth of Dimargaritaceae have been carried out primarily by H.L. Barnett and his students at the University of West Virginia (Barnett 1970, Barker & Barnett 1973, Binder & Barnett 1973, 1974, Kurtzman 1968). Their studies have involved five species, Dispira corvuta van Tiegh., D. simplex Benjamin, Tieghemomyces parasiticus Benjamin, Dimargaris baasilispora Benjamin, and D. verticillata Benjamin, and they have shown that
excellent, though slow, axenic growth and sporulation of these species will take place on complex or defined media utilizing glycerol, but not simple sugars, as the carbon source in combination with various nitrogen sources, especially moderate or high concentrations (2-4%) of casein hydrolysate or various combinations of certain amino acids.

Sporangiophores of Dimargaritaceae arise more or less vertically from the substrate hyphae and in culture on a proper host are unaccompanied by sterile aerial growth. More or less restricted, branched haustoria develop inside the host hyphae from a short infection peg arising from a slightly swollen appressorium. Sporangiophores may be cymosely or irregularly verticillately branched.

Sporangioles of all members of the family delimit only two spores. Van Tieghem's (1875) implication of multisporous merosporangia in his original descriptions and illustrations of Dimargaris cristalligena van Tiegh., and Dispira cornuta undoubtedly was based on erroneous observations (Bainier 1906). The sporangiola arise successively in distal whorls from the uninucleate cells of simple or ramified branchlets (Fig. 23.8 K) which I have (Benjamin 1959) termed sporiferous branchlets to distinguish them from the sporocladia of Kickxellaceae. The sporiferous branchlets arise in relatively large numbers on terminal ampullae or form terminal fascicles or intercalary verticils of few to many elements, and they usually disarticulate readily in age. Two distinct mechanisms of sporangial development occur in Dimargaritaceae (Benjamin 1959, 1966). In two species, Dimargaris bacilliispora and D. oblongispora Mehrrotra & Baijal, the uninucleate sporangiola initial elongates to its definitive size, following which the nucleus divides and the two uninucleate sporangiospores form simultaneously. In all other known species of the family, development of the merosporangium is acropetal, the distal half of the sporangium arising as a bud-like outgrowth from the lower half. Again, the sporangial initial is uninucleate. The nucleus divides in the lower part and one daughter nucleus migrates into the upper part, as in Piptocephalis lepidula (Zoogales). The two spores then mature simultaneously. All known species of Dispira and Tieghemiomyces are dry-spored at maturity, whereas both wet- and dry-spored species are known in Dimargaris. Young (1968a, and unpublished), who has carried out electron-microscopic studies of the surface characteristics of the spores of several species of all three genera, has found that the spores of dry-spored forms examined (Dispira cornuta, D. parvispora Benjamin, Tieghemiomyces californicus Benjamin, T. parasiticus, and Dimargaris arida Benjamin) have walls bearing ridges or warts, whereas those of wet-spored forms examined (Dimargaris bacilliispora and D. vertiicillata) have smooth walls. He observed a similar correspondence between smooth- and rough-walled spores in wet- and dry-spored species of Piptocephalis (Zoogales) and several members of the Mucorales (Young 1968a).

Zygospores of Dimargaritaceae (Fig. 23.8 L,N) are remarkably like those of Kickxellaceae (Fig. 23.8 J), being formed in thin-walled, hyaline zygosporangia developed following the union of morphologically undifferentiated vegetative hyphae (Fig. 23.8 N). Zygospores or presumed zygospores have been observed in all described species of Dispira (3) and Tieghemiomyces (2) and in six of the seven species of Dimargaris. The usually thick, typically hyaline zygospore wall is smooth in a few species, but more often it is uniformly sculptured with punctae or shallow circular depressions. In Dispira spp. the zygosporangium is not formed from an enlargement developed at the juncture of the anastomosed sexual hyphae, as in most species of Dimargaris (Benjamin 1959, 1965) and Tieghemiomyces (Benjamin 1959, 1961),
Figure 23.8. A. *Kickxella alabastrina*. Sporocladia in lateral view, x560 (from Benjamin 1958).—B. *Coemansia spiralis*. Sporocladium (orcein preparation) showing uninucleate cells of sporocladium, pseudophialides, and spores, x2100 (from Benjamin 1966).—C. *Kickxella alabastrina*. Cross wall, x1300 (from Benjamin 1959).—D-E. *Spiromyces* sp. D. Young sporocladium showing development of first sporangiola, x1400; E. Sporocladium showing progressive development of sporangiola; one has become detached, x1400.—F. *Linderina pennispora*. Immature and mature sporocladia, x340.—G. *Dispira cornuta*. Cross wall, x1300 (from Benjamin 1959).—H-J. *Coemansia crassicaulis*. H. Copulating sexual hyphae, x1300; I. Young zygosporangium, x1300; J. Mature zygospore, x1300.—K. *Dimargaris cristalligena*. Fertile cells of sporiferous branchlets showing distal whorls of two-spored merozpgorangia (orcein), x1300 (from Benjamin 1959).—L. *Dispira cornuta*. Pedicellate zygospore, x475 (from Benjamin 1959).—M-N. *Dimargaris bacillipespora*. M. Early stage of development of zygosporangium, x1300; N. Mature zygospor, x560 (from Benjamin 1959).
but develops terminally on a more or less elongate stalk projecting well above the point of fusion of the sexual hyphae (Fig. 23.8 L) (Benjamin 1959, 1961, 1966). Mehrotra & Baijal (1963) described and illustrated the same type of zygospore development in *Dimargaris oblong-ispora*.

Chlamydomospores or other kinds of accessory asexual spores are unknown in *Dimargaritaceae*.

**KICKXELLALES**

With the separation of *Dimargaritaceae* to a separate order, only the Kickxellaceae, with eight known genera, are retained in Kriesel's Kickxellales.* With two exceptions Kickxellaceae are saprobes and most commonly occur in soil or dung. *Martensella pectinata* Coemans, known only from its original description (Coemans 1863), was thought to be parasitic on *Mucoraceae* or *Saprolegniaceae*, and *M. corticii* Thaxt. ex Linder has been found associated only with the Basidiomycete *Corticium radiatum* Fr. (Jackson & Dearden 1948) on which it may be a nonhaustorial parasite. When Linde established the family in 1943, only three genera were recognized, *Coemansia* van Tiegh. & Le Monn., *Kickxella* Coemans, and *Martensella* Coemans. Subsequently, five additional genera were added: *Linderina* Raper & Fennell, *Martensiomyces* Meyer, *Spirodaylon* Benjamin, *Dipsacomyces* Benjamin, and *Spromyces* Benjamin. All Kickxellaceae produce an extensively branched, delicate, septate, vegetative mycelium from which arise simple or ramified sporophores bearing unispored sporangiola on specialized septate or nonseptate branchlets termed sporocladia (Fig. 23.8 A,B,D-F) (Linder 1943, Benjamin 1958, 1959, 1966).

In representatives of all genera except *Spromyces* each sporangiola is subtended by a smallish, phialide-like cell which I earlier (Benjamin 1958) dubbed pseudophialide. The nearly globose sporocladium of *Linderina* spp. (Fig. 23.8 F) is multinucleate and provides a single nucleus to each pseudophialide.

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*KICKXELLALES* Kreisel, ord. nov.


Fungi pleurope saprobii vel leniter parasiticci, sine haustoriis. Corpus vegetativa hyph- arum ramosarum septatorum sporangiophora septatae ramosa vel nonramosa producens. Septa cum cavitatebus medianis disciformibus; cavitates obturamenta incolorata biconveca vel biumbonata continentes; obturamenta in alkalino diluto persistentia. Reproductio asexualis a sporangioliis unisporis; sporangiola in pseudophialidibus ex ramulis fertilibus (sporocladia globosis vel elongatis, septatis vel nonseptatis exormentibus genita. Reproductio sexualis a zygosporis paene globosis; hyphae sexuales hyphis vegetativis similibus.

Fungi mostly saprobic or weakly parasitic, nonhaustorial. Vegetative body of branched, septate hyphae giving rise to septate, branched or unbranched sporangiophores. Septa with median disciform cavities containing colorless biconvex or biumbonate plugs that are persistent in dilute alkali. Asexual reproduction by unispored sporangiola borne on pseudophialides arising from globid to elongate, septate or nonseptate fertile branchlets (sporocladia). Sexual reproduction by nearly globose zygospores; sexual hyphae similar to the vegetative hyphae.
Each cell of the septate sporocladium of *Coemansia* spp. (Fig. 23.8 B) (and presumably species of *Dipsacozymes*, *Martensella*, *Martensiomyces*, and *Spirodactylon* which have similar sporocladias) is uninucleate and by successive nuclear divisions provides a single nucleus to each of its several pseudophaeides as they are delimited (Benjamin 1959, 1966). The sporocladium of *Kickxella alabastrina* Coemans (Fig. 23.8 A) usually has only two fertile cells that form a succession of uninucleate pseudophaeides. In *Spiromyces minutus* Benjamin the sporocladium consists of a single basal uninucleate cell that develops a single terminal uninucleate cell which undoubtedly is the homologue of the pseudophaeide in the other genera except that it forms a succession of uninucleate sporangioles (Benjamin 1963). In an as yet undescribed species of *Spiromyces* (Fig. 23.8 D, E), the terminal, sporangiole-bearing cell is cut off from the basal cell by a septum, whereas in *S. minutus* it is not. The nuclear condition of the sporangiospore of only a few species has been determined. Spores of *Linderina pennispora* Raper & Fennell may contain 1-3 nuclei (Benjamin 1966, Benny & Aldrich 1975) whereas those of *Coemansia majovensis* Benjamin and *C. spiralis* Eidam (Fig. 23.8 B) (Benjamin 1959, 1966) and *Spiromyces minutus* (Benjamin 1963) have a single nucleus. One-nucleate spores probably are the rule in members of the family.

When mature, the sporangiole of species of *Spiromyces* and *Spirodactylon*, which are sub-globose to ellipsoidal, remain dry. Those of the other genera which are more or less elongate, often somewhat acicular, become engulfed in a liquid droplet. When viewed by light microscopy, the sporangiole of most *Kickxellaceae* appear smooth. However, in a series of electron-microscopic studies, Young (1968a,b, 1970, 1971, 1973a,b) demonstrated that the spore wall of several wet-spored species (*Linderina macrospora* Chang, *L. pennispora*, *Coemansia majovensis*, *C. aciculifera* Linder, *C. spiralis*, *Martensiomyces pterosporus* Meyer, *Kickxella alabastrina*, and *Dipsacozymes acuminosporus* Benjamin) bear small spines arranged randomly or in more or less transverse rows. These spore spines are embedded in the wall in *Linderina pennispora* and *L. macrospora* (Young 1968b), arising from the inner of two well-defined layers (see also Benny & Aldrich 1975). Young also showed that the sporangiole of *Spirodactylon aureum* Benjamin and *Spiromyces minutus*, both dry-spored species, are spinose (Young 1968b), but the spines appear to arise from the surface of the spore rather than being embedded within the wall.

The sporangial nature of the sporangiole of *Kickxellaceae* is not readily apparent by light microscopy. In only a few instances has the sporangial wall been demonstrated in the living sporangiole, i.e., *Dipsacozymes acuminosporus* (Benjamin 1961) and *Coemansia majovensis* and *C. aciculifera* (Young 1968b). In the undescribed species of *Spiromyces*, already mentioned, which has a sculptured spore (Fig. 23.8 E), the sporangial membrane can just be discerned under the light microscope. The sporangial wall has been demonstrated in a few other species by electron microscopy (Young 1968b, Benny & Aldrich 1975).

Zygospore formation in the *Kickxellaceae* was first suggested by Linder (1943) for *Coemansia aciculifera* and confirmed by Benjamin (1958) not only for this species but also for *C. majovensis*, *C. braziliensis* Thaxt. ex Linder, and *Kickxella alabastrina*. Zygospores subsequently have been described for *Spirodactylon aureum* (Benjamin 1959) and *Spiromyces minutus* (Benjamin 1963). Zygospores are thick-walled, hyaline or bright coloured, and develop within a thin-walled zygosporangium arising from a cell formed at the junction of two copulating.
undifferentiated hyphae as in *Coemansia aciculifera* (Fig. 23.8 H-J) and *Kickxella alabastrina* (Benjamin 1958), or from a cell delimited by an undifferentiated hypha near its point of anastomosis with another hypha as in *Coemansia mojavensis* and *C. brasiliensis* (Benjamin 1958). The zygospore wall usually remains smooth, but, as in *Spiromyces minutus*, the surface may be ornamented with shallow circular pits. No cytological or fine-structural studies have as yet been carried out on the kickxellaceous zygospore.

Asexual spores other than sporangiospores have not been observed in any of the Kickxellaceae.

**HARPELLALES**

The Harpellales*, along with the Asellariales, Amoebidiales, and Ecrininales are usually included in a separate class of Zygomycotina, Trichomycetes (Lichtwardt 1973a,b, 1976, Manier & Lichtwardt 1968). With the exception of *Amoebidium parasiticium* Cienk., which grows on the outer surface of its host, all trichomycetes are obligate endosymbionts or endocommensals of arthropods and live attached by a more or less simple holdfast to the chitinous lining of the digestive tract of their hosts, mostly crustaceans, diplopods, and insects.

Harpellales are the only trichomycetes in which a number of species produce what may be interpreted as true zygospores, and for this reason they are being discussed here. All members of this order are restricted to the larvae of insects that undergo development in water, mostly rapidly flowing freshwater streams, occasionally the still waters of ponds or lakes. Two families are distinguished on the basis of thallus complexity. The Harpellaceae Léger & Duboscq, with three genera, *Harpella* Léger & Duboscq, *Stachyiina* Léger & Gauthier, and *Carouzella* Manier, Rioux & Whisler ex Manier & Lichtwardt, form simple, unbranched thalli (Fig. 23.9 B) that become septate and form uninucleate reproductive cells. They develop and reproduce only in the midgut of their hosts attached to the peritrophic membrane. In the Legeriomycetaceae Pouzar (1972) (=Genistellaceae Léger & Gauthier ex Manier), the thallus becomes septate, forming uninucleate cells, is branched (Fig. 23.9 A), and usually develops and sporulates wholly within the hindgut of the host. Only occasionally does the thallus project through the anus of the host and develop spores outside the body of the animal (*Zygopolaris ephemeralum* Moss, Lichtwardt & Manier; *Pteromaktron protrudens* Whisler). Thirteen genera of Legeriomycetaceae are currently recognized and are separated mostly on the characteristics of their sporangia and, to a lesser extent, on zygospore and holdfast characteristics (Lichtwardt 1973b, 1976): *Legeriomyces* Pouzar (=Genistella Léger & Gauthier); *Genistellospora* Lichtwardt, Glotzia Gauthier ex Manier & Lichtwardt, *Graminella* Léger & Gauthier ex Manier, *Orphella* Léger & Gauthier, *Pennisella* Manier, *Pteromaktron* Whisler, *Simulomyces* Lichtwardt, *Smittium* Poisson, *Spartiella* Tuzet & Manier ex Manier, *Stipella* Léger & Gauthier, *Trichosygospora* Lichtwardt, and *Zygopolaris* Moss, Lichtwardt & Manier.

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*The ordinal names Harpellales and Asellariales are being validated elsewhere by Lichtwardt & Manier (1978).*
Figure 23.9. A. Smittium culisetae Lichtwardt. Part of living thallus showing trichospores developing in basipetal succession from generative cells formed by a terminal branch, x1000.—B. Stachylina grandispora Lichtwardt. Trichospores which have broken loose from their generative cells; each spore bears a single, elongate appendage, x1500.—C. Smittium sp. Trichospore showing collar and single appendage, x1500.—D-E. Trichozygospora chironomidarum Lichtwardt. D. Maturing zygospore attached to a zygophore, x1500; E. Released mature zygospore showing collar within which are attached a bundle of many fine appendages that trail from the spore, x1500. (All photographs courtesy R.W. Lichtwardt.)
The only asexual structures formed by members of the Harpellales are usually elongate, unisporated sporangiola (Fig. 23.9 A-C) (Moss 1976, Moss & Lichtwardt 1976) formed in basipetal succession and singly by each cell of the unbranched thallus in Harpellaceae (Fig. 23.9 B), or by the distal several cells of the thalloid branches in Legeriomycetaceae (Fig. 23.9 A). The cell giving rise to the sporangiola, termed the generative cell, is actively involved in the formation and often the release of the sporangiola. Its wall is continuous with that of the sporangiola and within it are often formed one or more appendages that are attached to the cross-wall separating the generative cell from the sporangiola. Appendages are known for species of all genera except Carouxella and Zygopolaris, and because of them the term trichospore, introduced by Manier & Lichtwardt (1968), has become the accepted appellation for the sporangiola of members of the order. Trichospore appendages are thought to serve a passive but important function in dissemination by perhaps becoming entangled with algal filaments or impaled on other debris in the immediate environment of the host. Rapid movement of the sporangiola downstream then is less likely and it may be more readily available for ingestion by feeding hosts (Williams & Lichtwardt 1971). Once ingested, the sporangiospore is released from the sporangial (trichospore) wall. The spore becomes attached to the gut wall of the host by means of a holdfast usually secreted from the apical pole of the spore, which then becomes the morphological base of the thallus. Fine-structural studies of the development of trichospore appendages have been carried out by Moss & Lichtwardt (1976) for Genistellospora homothallica Lichtwardt, and for Stachylina grandispora Lichtwardt by Moss (1976). The appendages of these species, and others for which data are known (Moss & Lichtwardt 1976), are formed within sac-like invaginations of the plasmalemma of the generative cell's proplast, and two basic patterns of appendage development are recognized on the basis of studies made thus far (Moss & Lichtwardt 1976). (1) The appendage or appendages develop after septal formation, may be attached at any point on the cross wall, and each is enclosed by its own pendulous plasmalemmal invagination (appendage sac) (Stachylina grandispora (Moss 1976), Smittium spp., Trichozygospora chironomidarum Lichtwardt). (2) The appendages form early in sporangial development, are attached at the periphery of the cross-wall, and are enclosed by a plasmalemmal invagination that is continuous and lies adjacent to the longitudinal wall of the generative cell. In the species of a few genera, when the appendaged trichospore, containing its uninucleate sporangiospore, is released from the generative cell, the upper part of the latter may remain attached to the sporangiola as a more or less well-defined collar. Trichospores of Carouxella spp. remain attached to their generative cells and are dispersed by the disarticulation of the thallus.

Distinctive, smooth, thick-walled, nearly hyaline zygospores (Fig. 23.9 D-E) have been described for members of all but four genera of Harpellales. They still are unknown in Stachylina (Harpellaceae), Graminella, Orphella, and Pteromaktron (Legeriomycetaceae). In two genera, Carouxella (Harpellaceae) and Zygopolaris (Legeriomycetaceae), the spores are basally attached, rounded below, and pointed distally; in all other genera the Zygospores are biconical and medianly or submedianly attached to their supporting cell. Except for Genistellospora homothallica, zygospores typically arise following conjugation of two cells, often cells of different thalli, suggesting heterothallism, but this cannot always be determined accurately in species having branched thalli (Lichtwardt 1976).
The cell subtending the zygospore is more or less elongate and arises directly from one of the conjugating cells or from a short branch developed by a conjugating cell. The supporting cell, the suspensor cell (Lichtwardt 1967) or zygosphorophore (Lichtwardt 1972, Moss, Lichtwardt & Manier 1975), is separated from the zygosphorophore by a cross-wall. When the zygospore is released, it may be accompanied by the contents as well as the upper portion of the wall of the zygosphorophore. This remnant, like that formed by part of the generative cell of some trichospores, is termed the collar. In representatives of three genera of Legeriomyctaceae (Legeriomyces, Smittium, and Trichozygospora), the detached zygospore bears appendages (Fig. 23.9 E) which resemble those borne by the trichospores and which also originate within the collar. Based on their attachment to the zygosphorophore, four distinct types of zygospores can be recognized (Moss et al. 1975): (1) zygospore medianly attached and perpendicular to zygosphorophore (Harpella, Simuliomyces, Spartiella, Stipella); (2) zygospore submedianly attached and oblique to zygosphorophore (Legeriomyces, Glotzia, Smittium, Trichozygospora); (3) zygospore medianly attached but positioned parallel to zygosphorophore (Genistellospora, Pennella); and (4) zygospore basally attached and in line with the long axis of zygosphorophore (Carouwella, Zygodiplosis).

Whether or not all the forms placed in Trichomycetes are phylogenetically related has been debated for some time (Lichtwardt 1973a,b, 1976, Whisler 1963). Studies carried out on cell wall chemistry, comparative serology, and ultrastructure of selected members of the four orders placed in the class have recently been summarized by Moss (1975) who concludes that while Harpellales and Asellariales appear definitely related, there is no evidence that they are allied to the Amoebidiales and Eccrinales or should even be included in the same class with the latter. Furthermore, concludes Moss, there is little evidence that Amoebidiales and Eccrinales are related. Whisler (1963) expressed doubt that Amoebidiales are true fungi.

On the other hand, evidence has accumulated that Harpellales, and perhaps Asellariales, may be allied with Kickxellales. The similarity of the peculiarly flared septal pore with its median plug, common to members of both trichomycetous orders (Farr & Lichtwardt 1967, Manier 1973, Manier & Coste-Mathiez 1968, Moss 1975, 1976, Moss & Lichtwardt 1976, Reichle & Lichtwardt 1972) as well as to all known members of Kickxellales (see previous section) suggests affinity of these fungi. Also, positive immunological reactions have been obtained by Sangar et al. (1972) between antisera of several species of Smittium (Legeriomyctaceae) and antigens of Dipsoraomyces acuminosporus and Linderina pennispora (Kickxellaceae). Comparisons of the pseudophialide-sporangiole complex of the Kickxellaceae with the generative cell-sporangiole complex of the Harpellales (Benny & Aldrich 1975, Moss & Lichtwardt 1976, Moss & Young 1977) strongly support the notion that these groups are related. Moss & Young (1978), in further reviewing existing evidence, conclude that the Kickxellaceae are indeed closely allied with Harpellales and Asellariales, and suggest that they may have evolved from a common ancestral archetype.

The trichospore of Harpellales has undergone extreme modifications that have adapted it for dispersal and growth in a very specialized environment (the gut of living insects) whereas the sporangiole of Kickxellaceae, species of which are saprobes and free living or at the most weakly parasitic, have less exacting requirements for dispersal. Several Kickxellaceae, i.e., species of Spirodactylon and Spiromyces, are dry spored and probably wind dispersed; members
of the other genera are wet spored and probably dispersed mostly by small animals or water (Ingold & Zoberi 1963). Within the pseudohialide, attached to the lower surface of the septum separating it from the sporangiole, Young (1974) described a "labyrinthiform organelle" in Kickxella alabastrina. Benny & Aldrich (1975) have called a similar organelle in Linderina pennispora an "abscession vacuole." These organelles resemble somewhat the plasmalemmal invagination within which the trichosporangial appendages of many Harpellales are formed (Moss & Young 1977). Sporangiola of Kickxellales, however, do not bear appendages. Benny & Aldrich (1975) also have observed "abscession vacuoles" in the pseudohialides of Dipsacomyces acuminosporus and Martensiomyces pterosporus, and speculate that the structure may in some way be directly involved with spore liberation in wet-spored species of Kickxellaceae; they suggest further that the organelle may provide hygroscopic material that upon hydration contributes to formation of the spore drop.

The zygospore of Harpellales, with its specialized zygosporophore and, in some instances, attached appendages, appears, like the trichosporangia, to be well adapted for dispersal and subsequent germination in its insect host. It has little resemblance to the mostly globose zygospores of other Zygomycetes, even Kickxellales or Dimargaritales. Only in species of Dispira and one species of Dinargaris is the zygospore formed on a pedicel that superficially resembles the zygosporophore subtending the harpellalean zygospore. Moss & Lichtwardt (1977) succeeded in studying at the fine-structural level a representative of each of the four types of harpellalean zygospore. The lack of similar studies on the zygospores of Kickxellales and Dimargaritales precludes any comparison of these spores for evidence of relationship between these orders, or with Harpellales, at this time.

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DIALOGUE FOLLOWING DR. BENJAMIN'S PAPER

'Dolipore'

PIROZYNSKI: You said that some Zygomycetes have a central septal pore of the dolipore type. Could you expand on that, and also tell us what happens in other Zygomycetes -- is there a single central pore, or a number of smaller, scattered plasmodesmata or micropores?

BENJAMIN: Plasmodesmata or micropores have been seen in some Mucorales. The central pore with the flared ring and a plug is only found in the Kickxellales and in two related
orders of Trichomycetes, the Harpellales and Asellariales, which should go into the Zygomycetes -- I don't recognize the Trichomycetes because I think it's an artificial assemblage of three unrelated groups of organisms.

WATLING: I'm a little unhappy that you are calling this structure in the Zygomycetes a 'dolipore', because there is evidence that in the Basidiomycetes these structures are mechanisms which control nuclear migration. The dolipores can apparently distinguish between the different nuclei of the dikaryon -- one kind will be allowed to pass through much more rapidly than another, while some may not be allowed through at all. Is there any evidence that the so-called 'dolipore' in the Zygomycetes has any such regulatory function?

BENJAMIN: No. I used the term dolipore in this context simply because during the second International Mycological Congress at Tampa, 1977, several people adopted it, apparently because the structure physically resembles that in the Basidiomycetes.

VON ARX: Some yeasts have dolipore-like structures which we call 'plugged dolipores' -- perhaps this term could also be used in the Zygomycetes.

KENDRICK: But there's a plug in the Basidiomycete dolipore, too.

BENJAMIN: When the chemical nature of these plugs is worked out, some differences may emerge. I'm sure this will be the case in the Kickxellales, because I suspect that the Kickxellaceae and the Dimargaritaceae will eventually be shown to be very different from one another.

Sporangium vs. sporangiole

VON ARX: You use the terms sporangium and sporangiole: how do they differ? Is the presence or absence of a columella a good differentiating character?

BENJAMIN: A sporangiole is just a small sporangium: there's no sharp dividing line. Basically a sporangium is the same kind of structure no matter how many or how few spores it contains. I don't think a columella is important, although there is a tendency for the columella to be lost as sporangium size decreases.

LUTTRELL: If a species produces both large and small sporangia (for example, Thamnidium elegans), you need to distinguish the smaller ones in some way, perhaps by calling them sporangiola. If there is a series of similar organisms, and some members of the series lack the large sporangia, it is reasonable to extrapolate and apply the term sporangiole to their small sporangia.

BENJAMIN: Yes, that's right. The Thamnidiaeae is a hodge-podge and will need to be split up later -- some members of this family, for example Backusella and Themnostylum, have large, deliquescent sporangia, but all of them (at least according to the definition Benny and I have applied) produce sporangiola with a persistent but separable wall.

VON ARX: We have some difficulty in separating Backusella and Mucor.

BENJAMIN: Well, the Mucoraceae is a mess, and we decided to take out some fungi that have dimorphic sporangia and put them in the Thamnidiaeae. But I agree that we have a long way to go in our characterization of these families. Many intermediates need to be studied, and I'm sure we will eventually come up with better criteria than these sporangial differences. But we have made a start.

VON ARX: I was thinking of introducing a new genus for the Mortierella isabellina group -- what do you think of this?
BENJAMIN: I believe *Mortierella isabellina* and *M. rammanniana* belong in *Mucor*, but we can't make a really rational decision unless we find zygospores. This group is abundant in soil, and I still think that if someone isolated 100 strains and paired them all, the zygospores might turn up.

SUBRAMANIAN: While we are discussing affinities, could you comment on the genus *Gonimochaete* described by Drechsler?

BENJAMIN: Drechsler put it in the Entomophthorales, but I don't believe it belongs here. Barron (1977) has recently suggested that *Gonimochaete horridula* may prove to be an oomycete, though he didn't give reasons. It needs to be grown in culture.

SUBRAMANIAN: I thought the spores looked like endoconidia.

BENJAMIN: To me they look like oomycete sporangiospores.

**Stylospores**

WEBSTER: I'd like your interpretation of the stylospore in *Mortierella*. Do you think it evolved from a chlamydospore or from a monosporous sporangium?

BENJAMIN: Gams no longer recognizes the term 'stylospore' in the Mortierellaceae: to him they are just a special kind of chlamydospore. I agree with him.

**Chlamydospores**

PIROZYNSKI: What is the function of chlamydospores in the Zygomycetes -- is it survival or disposal of waste material?

BENJAMIN: Many chlamydospores germinate, so they must serve for survival. Griffiths (1974) did an extensive study of chlamydospores and concluded that in the Mucorales they did not function in dissemination. But that isn't true in the Mortierellaceae, where they are dry, blow around easily, and germinate readily. In fact, they may be produced almost to the exclusion of any other propagules.

**Yeast phase**

MADELIN: A number of Zygomycetes can turn into a yeast-like form in the laboratory (for example, *Mycotypha*, *Cokeromyces* and some *Mucor* species), but there is, as far as I know, no naturally occurring yeast with zygomycetous affinities. Do you think you could recognize such a yeast?

BENJAMIN: Not unless it reverted to the hyphal form. I doubt if such things exist.

MADELIN: We invoke an ascomycetous or basidiomycetous ancestry for many yeasts, but generally speaking those groups don't change into yeasts in culture as readily as some Zygomycetes. I'm a little puzzled that the Zygomycetes should have foregone this ecological niche, especially since there are some stable Zygomycete mutants that remain in the yeast form: there must be the potential for evolution in that direction.

WATLING: Doesn't *Basidiobolus ranarum* exist in a yeast form when it attacks horses?

BENJAMIN: Yes, when they are adventitious parasites these fungi do many strange things inside their hosts. Many Mucorales can also be adventitiously parasitic.

WATLING: So they can exist in the yeast phase?

BENJAMIN: Yes, inside the living organism, and perhaps more often than we are aware of.

VON ARX: Speaking of yeasts: when Kreisel introduced the Order Kickxellales he classified it in the Endomycetes. I disagree with him, but what do you think of the idea?
BENJAMIN: I don't like it. Did he do it because of the few cases in the Dimargaritaceae where one spore buds from another? There certainly aren't any vegetative budding cells in that group. Kreisel also put the Pilobolaceae into the Entomophthorales, and I can't accept that, either. Was it simply because both groups shoot off their spores? Forcible discharge mechanisms have been evolved separately by many very different groups, and hardly constitute overriding similarities.

VON ARX: We screened both Zygomycetes and yeasts, looking for intermediate forms, but we didn't find any. Zygomycetes and yeasts are seen to be very different, chemically, if their sugars are examined by gas chromatography. But then, the Mucorales and the Entomophthorales are also chemically very different.

MADELIN: We've spoken of mycelial and yeast-like forms, but when Tyrrell & MacLeod (1972) grew Entomophthora in Grace's insect tissue culture medium, they obtained a free-living amoeboid phase, and subsequently they have also found this in the parasitized host. So there are actually three possible forms -- mycelial, yeast-like and naked protoplast.

BENJAMIN: In the Entomophthorales several kinds of spores are produced. Basidiobolus, for example, produces primary spores (which I consider to be unispored sporangia) and secondary spores: even vegetative hyphae can produce endogenous spore-like bodies.

KENDRICK: They might even be conidia.

BENJAMIN: They might.

**Conidia vs. sporangiospores**

SUBRAMANIAN: Do I understand that conidia sensu stricto are rare or absent in Zygomycetes?

BENJAMIN: I never use the term conidium for the primary spore: this is a sporangiospore, whether it is produced in a many-spored or a one-spored sporangium. Perhaps you can apply the term conidium to the chlamydospores or the yeast-like cells, but you certainly wouldn't give them a form-generic name.

KENDRICK: The definition of a conidium that we produced at Kananaskis-I specifically excluded sporangiospores because these are formed in a different way -- by cytoplasmic cleavage, in multispored sporangia at least.

SUBRAMANIAN: What about Conioscypha, where the conidium develops its own separate wall within something that looks like a sporangium, and the production of subsequent conidia involves precurrent proliferation within the 'sporangium'?

KENDRICK: We regard Conioscypha as an example -- perhaps the only one in the Hyphomycetes -- of the percurrently proliferating phialide that is so often found in Coelomycetes. But I admit that there are resemblances to sporangiospore development.

BENJAMIN: That is rather like the endochlamydospore in Mucor racemosus, which forms inside a hypha.

KENDRICK: I was a little surprised to see that you don't consider the chains of spores formed by some Zoopagales to be conidia, but rather merosporangia.

BENJAMIN: If I may speculate for a few moments, I believe that the development of these spores in the Zoopagaceae and Cochlonemataceae will prove to be very similar to that of the merosporangia in Piptocephalis and Syncephalis. I consider the Mucorales and Zoopagales to be fairly closely related. The zygospores of some Cochlonemataceae are very similar to those of Syncephalis.
The Zoopagales have evolved into very specialized niches -- they are haustorial parasites on soil-inhabiting organisms -- and this may explain why they appear so different from the Mucorales, which are never haustorial parasites. I think *Piptocephalia* sits out by itself, just as in the Kickxellales the Dimargaritaceae are outsiders. I think the Kickxellaceae are allied to the Harpellales. We might as well forget about the Endogonales for the present, because we just don't know enough about them (despite their importance as endomycorrhizal partners of higher plants). The Entomophthorales also constitute a very distinct group.

So within the Zygomycetes as I define them, there are four very different aggregations: (1) Mucorales and Zoopagales, (2) Kickxellales and Harpellales, (3) Endogonales, and (4) Entomophthorales.

**Madelin:** Could I pick up this theme of speculation, apropos of whether to call the primary spores of Zygomycetes sporangiospores or conidia? In his talk, Dr. Benjamin mentioned the striking resemblance between the structures at the base of the spores in the Harpellales and in the pseudophialides of the Kickxellaceae. From recently published electron-micrographs it seems clear that the structure in the Kickxellaceae has little function, and can only be explained as a relic or a vestigial organ. Now if there is a connection between the Kickxellaceae and the Harpellales, the evolutionary progression may have been from the Trichomycetes toward the Mucorales. Just as Pirozynski & Malloch (1975) advance the idea of algae and oomycetes emerging from the water jointly and giving rise to the land plants, I might suggest that the arthropods and the Trichomycetes emerged together, and the Trichomycetes gave rise to the Kickxellaceae. If that is the case, then the Trichomycete 'conidium' is the primary structure, and the sporangium of the Zygomycetes is derived from it. Perhaps because we were conditioned for so long to think of the 'Phycomycetes' -- to lump the Zygomycetes with the Mastigomycotina -- we accepted their sporangia as homologous. But the Zygomycete sporangium may be a highly derived structure, and we may have been reading the series in the wrong direction. We might now try starting with the Trichomycetes, moving to the Kickxellaceae, then to two- or few-spored sporangia, then to many-spored sporangia. If all this is true, then we could consider a *Mucor* sporangium as a conidium that has undergone internal cleavage.

It would be interesting if a palaeontologist could turn up a fossil arthropod, with a Trichomycete in its hind-gut, dating from a time before the earliest terrestrial record of a Zygomycete, which I gather from Dr. Pirozynski is Carboniferous.

**Kendrick:** That was a real tour de force, and it continues a trend I noticed last week at the Mycological Congress in Florida. Several prominent mycologists, either from real conviction or from a desire to stir up their audience, made extremely inflammatory, iconoclastic statements, suggesting that evolution in many groups had taken place in a direction opposite to that which has long been accepted. Our ultimate triumph may be to establish that the red algae evolved from the Ascomycetes.

Perhaps I can round off this discussion by asking Dr. Benjamin a very general question. What role do the anamorphs play in the classification of the Zygomycetes?
BENJAMIN: They play the prime role at present. You couldn't produce reasonable subdivisions of the group without using the anamorphs. Orders, families and genera are all delineated on characters of the anamorph. The teleomorph (zygospores) at present has little importance in the lower levels of the hierarchy within the Zygomycetes.

KENDRICK: And yet yesterday you were asking me why you had been invited to this Conference. Why, you are the best example we have of a mycologist to whom the anamorph is the principal source of taxonomic characters.
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Dialogue on the Ecology of Anamorphs and Teleomorphs

The Conference

ANAMORPHTELEOMORPH ALTERNATION

KENDRICK: In this segment of our discussions it seems to me that our basic approach should be to place on record what we consider to be the biological and ecological roles played by the teleomorph and the anamorph(s) of our fungi. These obviously vary from one group to another, and are much more obvious in some groups than in others, but perhaps we can come up with a broad survey.

MÜLLER: We should start from a very general point of view. Hyphomycetous anamorphs, being relatively small and simple structures, can often be produced more quickly and easily than the corresponding teleomorphs, and may thus serve for rapid propagation and spread of the species.

The teleomorph also serves as a means of propagation, but it has the additional function of bringing about genetic recombination, which allows the species to respond to the 'fine-tuning' selective pressures exerted by the environment. Of course there are also many autogamic Ascomycetes in which genetic recombination does not occur. In these cases the teleomorph may in fact function simply as a long-term survival propagule.

WEBSTER: Perhaps I should qualify your remarks about autogamous, homothallic species by adding that gene recombination is possible in some cases because heterokaryosis permits a degree of outcrossing. This certainly occurs in Sordaria.

I'd like to add another general point. The teleomorph is often linked with seasonality. Many Ascomycetes parasitize the leaves and stems of herbs, or leaves of deciduous trees, and the release of ascospores is timed to coincide with the onset of vegetative growth or flowering of the host in the following season. The unitunicate Rhytisna acerinum is one excellent example. Its ascomata ripen during the winter and ascospores are released in spring to infect the new leaves of the sycamore tree. The bitunicate Venturia inaequalis operates in the same way, its ascomata ripen in the dead apple leaves, and the spores infect the young apple leaves in spring. Inoperculate discomycetes of the Sclerotinia-ceae behave similarly. This is a very common phenomenon.

MADELIN: Is there any intrinsic reason why the system adopted in these cases must be sexual reproduction once a year? Why has the teleomorph, rather than an anamorph, adopted this role?
KENDRICK: In the cases Dr. Webster just mentioned, one of the prime reasons, surely, is that the teleomorph has evolved an effective spore-shooting mechanism whose ripening and discharge can be timed to coincide precisely with, for example, the flowering period of the host, which may be very short. The concentration of ascospore discharge into a correspondingly short period may greatly increase the efficiency of the infection process. And this may be the only time in the year when the host is especially susceptible to infection.

LUTTRELL: This phenomenon of sexual reproduction once a year also occurs in the migratory aphids. A number of parthenogenetic generations is followed in the fall by sexual reproduction -- and it is generally the eggs which overwinter.

In Phacidium there is an annual cycle in which only the ascospores effectively disperse the fungus. For the rest of the year the fungus grows vegetatively and often almost invisibly in the leaves of its evergreen host.

In many Ascomycetes there is considerable dispersal during the growing season by means of conidia, and a similar pattern applies to the Oomycetes. Basidiomycetes and Zygomycetes may well behave rather differently.

In the Oomycetes, sexual reproduction results in the production of a resting spore. The alternative to this in the Ascomycetes is often a longer period of development -- a gradual ripening of the ascomata during the winter.

I would consider this slow development process as being equivalent to a resting spore. If an alternative method of survival becomes available, the whole sexual phase may be short-circuited. If the fungus can survive as mycelium inside the host, or if the conidia are tough enough, sexual reproduction may be suppressed.

WEBSTER: But we must consider heterothallism here. Many fungi can survive perfectly well in the short term by asexual reproduction and dispersal. But they occasionally need the opportunity to reproduce sexually, by means of an encounter between compatible mating types, which provides the genetic recombination that will take care of long-term evolutionary trends. This may be the reason we don't find the teleomorph very often in some species -- the meeting of compatible strains under conditions suitable for the development of the teleomorph may be a rare event.

KENDRICK: In this respect, the Basidiomycetes have an advantage over the Ascomycetes in that once compatible mycelia have met and established a dikaryophase, that phase can continue living vegetatively until it finds conditions suitable for the formation of the basidioma. The Ascomycetes require these two conditions to be fulfilled more or less simultaneously.

BENJAMIN: The Zygomycetes have the same problem as the Ascomycetes. How many people who work on Zygomycetes have ever found zygosporae in nature? We have to identify many Zygomycetes in culture from their anamorphs, because we don't have the appropriate mating types in hand. But they may meet more often in nature than we know. One of the problems is that zygosporae are so small and inconspicuous. We simply don't know how important sexuality is to many of the fungi, because we work on them only in culture.

LUTTRELL: We've been talking about the rarity or total suppression of sexuality, but some
Ascomycetes have gone to the opposite extreme and suppressed the anamorph. In some of the groups I reported on earlier (see Bitunicate Committee report) it is not simply that conidial states have not been found: we are fairly sure that they do not exist. *Leptosphaerulina* ascomata mature within a week, and you can get repeated cycles of this -- the sexual phase is clearly a dispersal phase as well as a survival phase, and here plays the role commonly associated with the anamorph.

MULLER: We tend to think of fungi as being parasitic or saprophytic or periphytic, but the ecology of many Ascomycetes shows that they infect a host plant in spring, then survive or grow in it without producing symptoms until it dies, when they proceed to fruit. This kind of lifestyle doesn't exactly fit our existing terms.

WEBSTER: *Leptosphaeria acuta* is a good example of that. This bitunicate Ascomycete can be isolated from practically all nettle stems (*Urtica dioica*), even when these are alive, healthy and apparently symptomless. This fungus is a good example of a species which will produce ascomata only when a high level of moisture is present. It fruits normally only on the few basal internodes of the dead, standing nettle stem. But if the stems are cut down and laid on the ground, ascomata will develop all along them. This is also true of *Heterosphaeria*, and *Neatvria cinnabarinata*. The wetter parts of the host bear the teleomorph, while the drier parts often give rise to conidiomata of the anamorph.

CARMICHAEL: Before we leave the subject of plant parasitic fungi, we should note a very excellent and readable book by E.C. Large, 'The Advance of the Fungi' (1940), in which he gives some fine discussions of this topic, and he was certainly ahead of his time in his treatment of the respective roles played by the teleomorph and the anamorph.

**AMPHIBIOUS FUNGI**

WEBSTER: When Ingold described the tetraradiate spore he pointed out that the common occurrence of the shape was due to convergent evolution. This has now been demonstrated conclusively, such spores being produced by various groups of Ascomycetes, Basidiomycetes, and even by completely unrelated organisms like the brown alga *Sphaelaria*. Experimental evidence shows that one of the important features of this kind of propagule is that it is more effectively trapped by underwater substrates, because it makes a stable three-point landing. Bandoni (1974) also suggests that these conidia are more effectively dispersed in surface films, but this is a little difficult to test experimentally.

BENJAMIN: There is one lonely member of the Mucorales that may show adaptation for water dispersal. *Aquamortierella elegans*, which is known only from preserved material from New Zealand, is thought to be aquatic, and has sporangiospores with gelatinous appendages.

WEBSTER: There are two interesting marine Basidiomycetes: *Digitatispora marina* which has tetraradiate basidiospores, and the gasteromycete, *Nia vibrissa*, in which the basidiospores within the global mass are also appended.

KENDRICK: Ms. Shannon Berch, one of my graduate students, recently found a good collection of *Tylospora asterophora* (Bonord.) Donk, a terrestrial resupinate hymenomycete with basidiospores that have suspiciously tetraradiate tendencies: they are at least as tetraradiate as the conidia of the aquatic hyphomycete *Heliscus lugdunensis*.

WEBSTER: Another puzzle that confronts us at present is the common evolution of sigmoid propagules. We do not know the ecological significance of the sigmoid shape, and I would
welcome any suggestions for experiments to investigate this phenomenon. Sigmoid conidia often have a sticky pad at one end, and if you let them sediment in a dish, they become attached by this terminal pad and sit on the bottom waving at you.

KENDRICK: That suggests to me that they are aquatic corkscrews, which will always strike a substrate with one or other of their sticky ends, and the impact will help anchor them.

CARMICHAEL: Neither of these forms can make any appreciable area of contact with a flat surface, and both may provide a strong point-stimulus to hasten germination and anchorage.

WEBSTER: True tetraradiate conidia will always land as a tripod, and do in fact germinate very quickly from the tips of the three arms which are touching the substrate. Since a tripod is the most stable configuration, that is most probably the significance of the tetraradiate propagule. This leads to the question: If the tetraradiate configuration is so efficient, why produce more than four arms? This happens in such fungi as Dendrospora, Dendrosporomyces, and Varicosporium.

Ingold also had the idea that the tetraradiate propagule sank more slowly in the aquatic environment than spores of more conventional shapes. This is true, but experiments have shown that the rate of sedimentation of these spores is extremely low compared to their probable horizontal translocation in streams. They settle at about 0.1 mm/sec., whereas the flow rate in streams is commonly of the order of 1 m/sec. to 5 m/sec. So even if you increased the sedimentation rate by a factor of ten, it would make a negligible difference. And of course, streams are not simple systems -- there are eddy currents. So flotation is hardly a problem.

There is an attractive yeast-like fungus called Candida aquatica which is common in foam on mountain lakes. Its habitat appears to be the hollow internodes of aquatic plants such as Equisetum. If you grow it in culture on moderately rich media, say 1% liquid malt extract, its cells are short, with dense cytoplasm. On dilute medium, or in water, the cells become very attenuated. The well-fed cells have a high sedimentation rate, while the starved cells bud to form a tetraradiate configuration, and become virtually planktonic -- a nice adaptation for dispersal at the appropriate time.

The ascospores of amphibious fungi undoubtedly play the role of long-distance dispersal mechanisms, while the passively dispersed conidia may move only downstream. If Bandoni's observations, that tetraradiate conidia are common on leaves well away from water, are correct, one explanation of that could be that these leaves have been initially colonized by ascospores. On the other hand, the bursting of air bubbles is probably quite an efficient mechanism for flipping tetraradiate conidia from the surface film into the air, and I think this is a credible way in which these amphibious fungi may be dispersed into habitats away from the stream.

AERO-AQUATIC FUNGI

WEBSTER: The other group with which we work, the aero-aquatic fungi, which inhabit ponds rather than streams -- stagnant or standing rather than flowing water -- all seem to sporulate at an air-water interface. As their three-dimensional conidia develop, they entrap air. If the water rises, the conidia will float away. This flotation effect is achieved by diverse configurations: barrel-shaped coils, as in Helicoon; repeated dichotomous branching, as in Clathrosphaerina; complex coiling, as in Spirosphaera and
Helicodendron; semi-solid hyphal masses, as in Aegerita. These conidia are also very hydrofuge -- difficult to wet.

These strategems appear to have been adopted independently by various groups of fungi (again both ascomycetous and basidiomycetous anamorphs are represented) but the large, three-dimensionally coiled helicosporous anamorphic fungi do not as yet appear to have any known teleomorphs.

KENDRICK: Many of the other helicosporous fungi have, of course, been connected with their teleomorphs, and I suspect that the helicosporous fungi probably do not comprise a related group, but rather the various products of convergent trends in anamorphs.

**APPENDAGED PROPAGULES**

WEBSTER: Another curious example of convergent evolution is in the branched or appendaged spores formed by freshwater fungi and marine fungi. In the freshwater forms, this configuration has been adopted by the conidia. In marine Ascomycetes, it has been the ascospore that has tended to become branched. They must represent two quite separate lines of evolution, because in the freshwater conidia, the arms are cellular extensions of the spore, while in the marine ascospores, the appendages are often mere outgrowths of the epispore. It has not been conclusively proved that these two types of tetraradiate spore function in exactly the same way.

NAG RAJ: At least 100 genera of Coelomycetes have conidia that bear appendages, which vary in number, in configuration, and in their nature.

WEBSTER: The type of spore with one appendage at each end appears to have evolved many times. I came across it first in the Dinemasporium anamorph of Phomatospora, but it is also found in many Hyphomycetes, such as Menispora, and other fungi. The appendage isn't always mucilaginous.

NAG RAJ: No, in Dinemasporium and many others the appendages are tubular extensions of the cells.

KENDRICK: It is fascinating though not, perhaps, surprising that there are five or six ways in which an effective appendage can be developed. These have been explored by Cunnell (1958), Sutton & Sellar (1966) & Shoemaker (1971), Nag Raj & Kendrick (1970, 1971) and Nag Raj (1973, 1976).

I'd like to ask Dr. Benjamin if he thinks the appendages found on mature zygospores of some species of Phycomyces, Absidia and Radiomycetospora are adaptations for dispersal by small animals?

BENJAMIN: These appendages are found on so few species in the Mucorales, and apparently nowhere else in the Zygomycetes, that I must answer: we simply don't know.

WEBSTER: In Dinemasporium is the fructification a splash cup?

NAG RAJ: Yes, almost certainly, as it probably is in many other coelomycetous genera such as Pseudolachnea, Chaetopatella, Hymenopsis and Polynema.

WEBSTER: I've noticed that the Septoria and Phaeoseptoria anamorphs of graminicolous Leptosphaeria species commonly form elongate phragmoconidia in pycnidial conidiomata. I wonder why this pattern is so common? These conidia must be splash-dispersed, because I have often seen the ascospores in Hirst spore traps, but never the phragmoconidia.
ECOLOGY OF HUMAN PATHOGENS

KENDRICK: Can I now ask Dr. Carmichael about the roles of the anamorph and teleomorph in the Gymnoascaceae.

CARMICHAEL: There are two general groups of parasitic Gymnoascaceae. The dermatophytes are restricted to the keratinaceous tissues of the host and can also decompose keratin in the soil. In the parasitic growth form they have a reduced morphology. They are hyphal, and produce only arthroconidia. Growing on shed keratin they produce conidia in abundance. The teleomorph may appear in old cultures, producing tiny but resistant ascospores. *Histoplasma* and *Blastomyces* are yeast-like in host tissue, and have conidia similar to dermatophytes in culture. With appropriate mating you may get ascomata in cultures. In the human pathogens, the arthric conidia are probably the infective agent, the ascosporic state probably having little importance in this context. Most filamentous fungi parasitic to Man and animals belong to the Gymnoascaceae. The teleomorph is rarely found in nature, but will often develop on hair bait kept in contact with moist soil for long periods -- but then, who goes around collecting old hairs from soil? They also occur on owl pellets.

DUNG AND OTHER SPECIALIZED HABITATS

MALLOWCH: I think a lot of the pathogenic forms are normally associated with rodents. People often act like rodents, and so similar fungi turn up in our habitat -- *Penicillium cyclopium*, *Aspergillus flavus*, *Eurotium*, Gymnoascaceae. Rodents store food, are creatures of habit, have bathrooms and bedrooms. Groundhogs build a many-layered bed of grass, and I have found Gymnoascaceae scattered throughout this bed. *Apinisia graminis* has large hyphal coils emerging from the peridium of the ascoma, and some species have hooks and barbs which probably hook right onto the hair of the rodent as it goes by. Birds' feathers and nests are also rich sources of Gymnoascaceae.

Some cleistothecial forms have long necks, as in *Sphaeronaemella* and *Ceratoaystis*, and the ascospores are exuded in a slimy droplet at the top. In such forms, the anamorph also tends to form a stalked spore drop at the top of a tall mononematous or synnematous conidia. In a few, like *Microascus*, the ascospores are produced in a dry mass at the top of the neck. In these, the anamorphs are also elevated and dry-spored. Most cleistocarpous forms have no neck, and the ascoma splits open to reveal a dry mass of ascospores. A few members of the Onygenaceae have irregularly thickened hyphae in the centrum which twist when exposed to changes in temperature or humidity -- a form of capitillium to facilitate spore dispersal. Some cleistocarpous forms have sutures built into the ascoma wall -- preformed lines of dehiscence which have evolved over and over again in different groups.

Most of these organisms grow in covered situations which would be quite unsuitable for organisms with forcible spore discharge.

Many fungi are encountered on dung and it is perhaps appropriate to make a few generalizations here.

In my experience there are three basic dispersal types among coprophilous fungi; 1) those with forcible spore discharge (*Pilobolus*, *Sordaria*, *Coprinus*) having the
well-known dung-grass-gut-dung cycle, 2) those with exposed spore masses (Dictyostelium, Muco, Penicillum, Graphium, Sphaeronaemella) that are probably transmitted by arthropods and 3) those having mechanisms associated with transmission by vertebrates; involving the transport of spores in hooked or barbed enclosures (Onygenaceae, Phaeotrichum, Lophotrichus, Chaetomium). Members of the first group are found mainly on the dung of migratory herbivores, those of the second group on dung of migratory and sedentary herbivores and dung of carnivores, and those of the third group on dung of sedentary herbivores and carnivores. Only in the first group is forcible spore discharge the rule. In my opinion, no coprophilous fungus is anemophilous (wind-dispersed); those with forcible discharge have heavy spores with only a very short trajectory.

SEWAGE FUNGI

COOKE: I have isolated many fungi from sewage and polluted water over a period of 17 years, and am still searching for a good way of classifying them. Most of the time I find conidial states -- anamorphs -- and I'd like to know if this has ecological significance. Of a total of 23,316 isolates I recorded:

544 Sphaeropsidales -- 2.3%
1617 Mucorales -- 7%
3384 Imperfect yeasts -- 14.5% (this figure is low, because I didn't record yeasts for the first 6 years)

17771 Moniliales -- 77.2% made up as follows:
2015 thallic-arthic (Geotrichum candidum, etc.) -- 11.3%
15756 blastic -- 89% -- subdivided as follows:
12397 phialidic -- 20% of genera produce 70% of isolates
  684 tretic -- Alternaria -- 4%
2672 other types -- Cladosporium and Rhinoladiella mansonii -- 15%

So phialidic conidia were the most numerous category, but the most important single genera were Geotrichum and Rhinoladiella. 35 or 40 species are dominant. These will be catalogued and published by the Environmental Protection Agency. 930 species are on the list. Anamorphs and teleomorphs will be cross-indexed.

WEBSTER: Is there any evidence that these fungi reproduce in sewage, or do they really represent the remains of a population that was actively growing and reproducing at some time before it entered the sewage?

COOKE: I can only speak about trickling filters, and perhaps activated sludge. With the notable exception of Geotrichum, the fungi in these substrates do not sporulate at all, but there is a great deal of vegetative growth. My own belief is that the largest functioning biomass in sewage treatment plants is that of the fungi. Bacteria are present in high numbers, but fungi are doing the work. One thing I can say: all trickling filters I have sampled have essentially similar mycofloras; all activated sludge tanks I have sampled have similar floras; all heavily sewage polluted streams have similar floras, whether they are in Utah, Colorado or Ohio. In temperate North America populations are very uniform.
SPORE GERMINATION REQUIREMENTS

MULLER: It is interesting that the ascospores of some members of Erysiphales (e.g., Podosphaera leucotricha on apple, Blumer 1967) have never been seen to germinate. This may mean that the fungus overwinters as conidia or mycelium.

KENDRICK: In New Zealand, where the Erysiphales are also economically important, they must be classified on the basis of their anamorphs, because the teleomorph rarely develops (Hammert 1977). This is a strange and dramatic contrast with the situation in Canada, where the teleomorphs develop abundantly every year.

WATLING: For many years the basidiospores of many gasteromycetes resisted all attempts to germinate them. However, the basidiospores of Calvatia and Lycoperdon have been germinated by using the yeast, Rhodotorula, as an inducer (Bulmer & Beneke 1964). Fries, following up his earlier studies (Fries 1941, 1966) has now succeeded in germinating many basidiospores, particularly those of mycorrhizal fungi, in the presence of Rhodotorula and activated charcoal (Fries 1977). He has recently been successful with such fungi as Paxillus, Laccinum scabrum, Suillus, Russula and Lactarius. Many chemicals apparently can trigger basidiospore germination, and are documented in the literature. For example, Petersen (1960) increased the germination of basidiospores of Coprinus ephemerus from 40% to 91% by using furfural. The problem, of course, is that we have no idea whether it is these or other substances that trigger germination in nature. Lösel (1964, 1967) has worked on germination-stimulating substances in Agarious bisporus, but this is just a beginning.

NUTRITIONAL REQUIREMENTS

PIROZYNSKI: Nutritional divergences between anamorph and teleomorph may account for some of our difficulties. Many Hyphomycetes are ubiquitous on properly rotted leaves, while their teleomorphs may be both host-specific and parasitic on leaves. In the tropics these fungi may well survive the dry season in the anamorphic condition -- in dead leaves in hidden, damp places, reinfecting the host by means of conidia at the beginning of the wet season. [This of course is exactly the reverse of what we see so often in the temperate zone] One specific example is the anamorph Beltraniella portoricensis which is common on many kinds of leaf litter in the tropics, while its teleomorph, Pseudomassaria carolinensis (Barr & Hodges 1971) is parasitic and appears to be host-specific to Persea.

KENDRICK: Do the anamorph and teleomorph of the amphibious fungi have differing nutritional requirements? This seems likely because the anamorph inhabits leaves, and the teleomorph, woody substrates.

ENTOMOGENOUS AND NEMATOPHAGOUS FUNGI

MADELIN: We can make similar observations about some of the entomogenous fungi. Cordyceps militaris seems to require an insect substrate in order to produce the teleomorph, while the Paecilomyces anamorph can live in the soil. We don't know whether in nature there is direct insect-to-insect transmission via the teleomorph. We worked out a technique for producing perithecial stromata in vitro (Basith & Madelin 1968), but the best selective medium in nature is still an insect.

WEBSTER: One large assemblage of fungi which appears to be almost devoid of teleomorphs is the nematophagous fungi. These 60 or more species include both ascomycetous and
basidiomycetous anamorphs.

MALLOCH: Barron & Dierkes (1977) recently produced a teleomorph for one of these fungi -- a *Nematootonus* culture developed a basidioma of *Hohenbuehelia*. When I went and checked out the *Hohenbuehelia* collections in our herbarium, I found that if I dug down in the wood or at the base of the stipe, they all have nematode-catching knobs on the hyphae. So here is a whole genus of mushrooms that seems to supplement its diet with nematodes.

KENDRICK: Barron & Dierkes (1977) noted this for *Hohenbuehelia longipes*, and suggested that of the 26 known species of *Hohenbuehelia*, some will have anamorphs identical to described species of *Nematotoonus*, other may have as-yet-undescribed *Nematotoonus* anamorphs, and some, especially the endoparasitic species of *Nematotoonus*, may have lost the teleomorph. Barron & Dierkes suggested that the logical thing to do now is germinate basidiospores of all known *Hohenbuehelia* species in the presence of nematodes, and compare the resultant anamorphs with the known species of *Nematotoonus*.

BENJAMIN: *Ballocephala* and *Meristaorun* of the Entomophthorales are also predaceous, and Drechsler (1940, 1951) described zygospores for both of them.

EDITOR: Pohlad & Bernard (1978) give an excellent photomicrograph of the zygospores of a new species of *Ballocephala*.

DICOSMO: While working on the list of connections, I noticed that none of the Laboulbeniales appears to have an anamorph.

BENJAMIN: That is probably true. It has been speculated that some of the insecticolous conidial fungi which have pigmentation and anchoring devices rather like those of the Laboulbeniales might be their anamorphs, but there is no real evidence for this supposition.

KENDRICK: You mean that things like *Muiaria* and *Muiogone* are just Hyphomycetes?

BENJAMIN: As far as we know, yes.

MALLOCH: But many Laboulbeniales bear a spermatial state: could you call those anamorphs?

BENJAMIN: I don't think so. They are very tiny phialidic spores which are purely sexual in function.

WERESUB: This is analogous to the pycniospores in rusts, which are given a state number, but are never named.

**SPORAS FROM SPORES**

WEBSTER: If you germinate ascospores of some species of *Pleospora* on water agar, they will produce conidia of their *Alternaria* or *Stemphylium* anamorph directly or on a very short germ tube. (If you germinate the ascospores on nutritive agar, they will give rise to vegetative mycelium, and conidiation will be delayed.) This is probably a widespread phenomenon in the Ascomycetes, and very useful in proving connections directly.

KENDRICK: As Dr. Muller pointed out earlier, starvation will often have the effect of inducing reproduction; and since the ascospore does not have the resources to produce another ascma, it will follow the only other route open to it, the production of a conidium. Some of the sooty molds habitually produce conidiogenous cells right on the ascospore, as do some *Leptosphaeria* and *Tympanis* species.

MULLER: This is also a way of multiplying the number of propagules. *Taphrina* does the same
thing. Another way of doing this is the arthric dissociation of the cells of phragmosporous ascospores. This is a widespread phenomenon: *Sporormia, Clavicipitales, Epiclados, Hypocrea, Ophiobolus* and *Geoglossum* species.

PIROZYNSKI: Should these fragments be called ascospores or conidia?

MULLER: Part-spores, I believe. They are actually parts of ascospores, and are not budded off or otherwise secondarily derived from them.

KENDRICK: This multiplication of propagules can be ecologically very important in genera like *Claviceps* and *Cordyceps* which have very specific targets that may be available only for a short time.

MALLOCH: How would you define the situation in the smuts or in *Filobasidiella* (Kwon-Chung 1975) where the basidium keeps on budding off spores. These aren't exactly basidiospores, they are just multiplying the results of a meiosis.

MADELIN: They could be described nicely by Subramanian's term 'synechidic', which implies the property of being able to produce an indefinite number of spores in a basipetal succession. This is a very clever mechanism, found in annellides and phialides -- and now in a basidium.

LUTTRELL: On a glass slide (and that is surely an unfavourable substrate) the conidia of *Claviceps paspali* will germinate but will quickly produce another spore. I don't know if they will do it more than once.

MULLER: The straightforward multiplication of propagules is well exemplified by the many Ascomycetes that have more than eight spores in each ascus. This is not usually due to spore fragmentation or budding, but to repeated mitosis before the spores are delimited.

KENDRICK: *Podospora* is a good example in which a series of steps in the multiplication can be found -- 16, 32, 64, 128, 256, 512, or even 1024 spores per ascus in different species (Mirza & Cain 1969).

**WHAT IS A BASIDIOSPORE?**

MULLER: We can call the spores of *Filobasidiella* secondary basidiospores, since such things help to characterize the Heterobasidiomycetes.

KENDRICK: But Roy Watling and I were not convinced that the products of 'germination by repetition' should be called basidiospores at all. We tended to call them conidia. Perhaps the term should be restricted to spores containing the direct products of meiosis.

WERESUB: In species of *Sistotrema* with 8-spored basidia, each spore receives a product of the mitosis that follows the original meiosis. In many species of the Aphyllophorales with 4-spored basidia, the diploid nucleus in the basidium divides meiotically to produce 4 haploid nuclei. Each of these then divides mitotically to give 8 nuclei. Four of these degenerate when each spore receives a single nucleus. You can't tell me these aren't basidiospores.

KENDRICK: If you extrapolate from that position, any spore arising after any mitosis that follows the meiosis could be called a basidiospore.

WERESUB: You are going to have a tough time defining them precisely.

KENDRICK: Perhaps only the first spore to arise from a particular sterigma or locus following meiosis should be called a basidiospore sensu stricto. If you open the time-slot any wider than that, I think you're in trouble.
MALLOCH: This isn't a problem in most Basidiomycetes, but in *Filobasidiella* there is a basipetal succession of spores, each of which arises directly from the basidium -- not by budding from an existing basidiospore.

KENDRICK: Then perhaps 'basidiospore' could be used for spores arising directly from the basidium, even if they are formed well after the original meiosis, and even several or many mitoses later. If these *Filobasidiella* spores were all formed inside the meiosporangium, as in polysporous asci, they wouldn't bother us at all. It's only when a temporal succession is involved that we get excited about imposing limitations -- it says something about how we look at the world. We may not have resolved the basidiospore issue, but we certainly gave it a good airing. We must now invite the participation of other mycologists in the debate, and await the emergence of some consensus.

ANAMORPH-TELEOMORPH ECOLOGY IN BASIDIOMYCETES

WATLING: The Basidiomycetes are unique in that they are often free-living, wide-ranging dikaryons. Barron's connection of a nematode-trapping fungus and an agaric does not greatly surprise me, because although we appear to have a lot of ecological information about the teleomorph in the Basidiomycetes, our observations have been relatively superficial. There is, for example, some indication that a certain group of *Hebeloma* species, although they grow under trees, are in fact associated with the urine or droppings of rodents. The agaric teleomorph is seasonal, ephemeral, and almost certainly represents the long-range dispersal mechanism. The anamorph may be a short-range mechanism. Perhaps I could just run through the Orders and make some remarks on their ecology.

The Exobasidiales are systemic parasites, or at least they perennate in parts of the host -- a pattern found nowhere else in the Basidiomycetes except in the Uredinales and the very atypical Ustilaginales. They produce their anamorphs freely on the galls both when these are on the ericaceous hosts and after they have been shed. The basidiospores often produce conidia by budding, and may develop a yeast-like phase. Sundström (1964) has described this for several species in culture, but it is common in nature also. There is no doubt that the anamorph plays an important role in reinfecting the host buds, which are developing (in *Rhododendron* at least) in June-July, when the conidia are being liberated.

The Aphyllorhales: in some Polyporaceae the anamorph can replace the teleomorph entirely or partially, so that a structure that looks like a basidioma can sometimes be a conidioma. In the various *Ptychogaster* anamorphs of *Tyromyces*, and in *Laetiporus sulphureus*, part or all of the basidioma is converted into chlamydospires. The connections established between *Sporotrichum* and various Aphyllorhales are mainly based on field observations, since neither the *Sporotrichum* chlamydospires nor the basidiospores have yet been germinated in vitro.

I don't know of any anamorphs in the Hydnaceae, but this is probably because no one has looked for them. If other Basidiomycetes are anything to go by, these anamorphs exist. Annellidic and sympodial blastic conidia have been observed in *Typhula* (Clavariaceae), and the single observation in Gomphaceae (*Ramaria*) has shown conidiophores to be formed there also.
In the Corticiaceae and related groups, some free-living anamorphs are known: *Haplotrichum*, *Acladium*, etc., which can often be found on woody debris either alone or in association with the teleomorph. Talbot (1952) has suggested that insects are involved in dispersing basidiospores of resupinate fungi: it is equally likely that they disperse the conidia.

Among the Gasteromycetes, only the rather atypical *Broomeia* is known to produce an anamorph. Unfortunately I haven't seen it and so cannot comment on it.

Tremellales and Auriculariales, as we have noted earlier, produce yeast-like anamorphs in culture, but I have seen nothing in the literature about any ecological role these may play: perhaps they exist free-living in nature in nooks and crannies in bark on dead and living trees.

We have already dealt with the agarics, and I pointed out the ecological significance of the arthric conidia. Kemp suggests that they could act as sterilizing agents in a particular environment, by means of a lethal reaction. Mycelia of the Agaricales and Aphyllophorales are often long-lived, and the areas colonized by such mycelia are obviously catchment areas for basidiospores and conidia of the same species. We know that the conidia may sometimes fuse with existing mycelia and thus contribute to their heterokaryotic nature. Burnett (1956), analyzing the genetics of *Piptoporus betulinus*, showed that mycelia and basidiomata from different parts of the same tree were genetically heterogeneous. The tree represented a genetic mosaic, which conferred increased flexibility on the fungus. Rayner & Todd (1977) have, however, shown that in some species, diaspor germinating and colonizing woody substrates frequently remain quite independent of each other.

The chlamydospores of *Abortiporus* and *Nyotalis* are produced in such large numbers that they must surely have some short-range dispersal function, as well as a possible long-term survival value.

Many basidiospores will germinate only in the presence of red yeasts such as *Rhodorula mucilaginosa*, and this has been a very useful discovery, because it permits us to do cultural studies of fungi such as *Laccaria laccata*, *Laccinum*, *Suillus* and *Paxillus* (Fries 1977).
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Techniques for Establishing Connections Between Anamorph and Teleomorph

B. Kendrick with G.J. Samuels, J. Webster & E.S. Luttrell

This chapter has been compiled by the Editor, with major contributions from Drs. Samuels, Webster, and Luttrell, and notes from Drs. von Arx, Madelin and Watling. Since there is no immediately obvious logical sequence for these diverse data, I have chosen to begin with the enunciation of one or two general principles, to continue with more specialized but still widely applicable techniques, then focus on some highly specific procedures which have been developed for particular organisms, and finally to review a few relevant publications. There may appear to be some repetition in the several descriptions of techniques, but I have left each author's narrative untouched, because subtle differences may render one of these methods easier or more successful than the others in the hands of a particular investigator.

During the discussion of techniques, several speakers mentioned problems arising from the use of pure cultures in systematics. The most important of these concerned radical changes in, or loss of, features when many fungi are repeatedly transferred on standard laboratory media. In some cases loss of fruiting ability is noticeable at the first transfer, and this loss may all too often be apparently irreversible. Dr. Luttrell suggested that 'old' cultures not be used, and advocated the laying down of many cultures derived from the original isolate on silica gel. This would make possible extended series of experiments, since each could begin with a culture just one transfer removed from the original isolate. Multiple freeze-dried cultures are another option. It was generally agreed that to base taxonomic conclusions on isolates that had been repeatedly transferred was extremely undesirable. Dr. Luttrell pointed out that in order to do serious research on a particular species it is almost obligatory to see the fungus in nature and to make your own isolations. Several other members of the Conference felt that for much taxonomic work only material on the natural substrate was satisfactory, and pointed out that on standard laboratory media many fungi either will not grow at all, or do not produce characteristic reproductive structures. It was recommended that if the natural substrate was known, an attempt should always be made to grow the fungus on it.

During the Conference there was considerable discussion of the various ways in which anamorph-teleomorph connections are established. It appears that there is a probability gradient running from the least reliable kind of connection, a single report of the physical proximity of an anamorphic and a teleomorphic fungus on a natural substrate, all the way to the
connection proven by repeated cultural experiments. Drs. Carmichael, Weresub and Pirozynski formalized this gradient in a numbering scheme which we have applied to many of the connections listed in Chapter 17. It will be immediately apparent to anyone scanning our lists of 'connections' that many of them are of less than perfect authenticity, and that even if they are in many cases probably correct, this fact remains to be proven. The only way to establish unequivocal anamorph-teleomorph relationship is to observe the transition from one phase to the other under conditions of axenic culture. Some groups of fungi, well exemplified by the Trichocomaceae (see Chap. 10), perform this metamorphosis in cultures derived from any part of the life cycle, anamorphic or teleomorphic. But many other Ascomycetes will not develop the teleomorph in a culture derived from the anamorph. This is often, but not by any means always, because the fungus is heterothallic. In such cases painstaking matings of many anamorphic strains may eventually produce the desired teleomorph. Fortunately, cultures derived from the teleomorph (usually from single ascospores or the contents of single asci) are not so reticent, and will frequently give rise to the proper conidial anamorph. The importance of this culture technique is underscored by the three sections of this chapter that follow, contributed by Drs. Samuels, Webster, and Luttrell. Dr. Samuels discusses techniques for handling collections, and for the derivation of single-ascospore isolations in the field, and favours the use of a micromanipulator. Dr. Luttrell offers manual (and hence less expensive) alternatives to the micromanipulator; and Dr. Webster writes with particular reference to the amphibious fungi, both Ascomycetes and Basidiomycetes.

NOTES ON ISOLATION OF SOLITARY ASCOSPORES -- A FIELD GUIDE: Gary J. Samuels

Many Fungi Imperfecti (anamorphs) are parts of life cycles that also include sexual states (teleomorphs): this is inescapable fact. The problem lies in knowing just which conidial fungus belongs to which life-cycle. Mycologists before, including, and after Fries have noted the constant association of specific anamorphs with specific teleomorphs. Such observations made over many years are one kind of evidence for relationship. The Tulasne brothers (1861), while gently chiding the Master of Uppsala for eschewing use of the newly discovered microscope, actually followed individual hyphae from chlamydoospores to conidiophores, and from conidiophores to ascomata. Their magnificent illustrations and detailed observations (Fig. 25.1) leave no doubt as to the association of teleomorphs and anamorphs. Brefeld & Tavel (1891) observed ascospores germinating in water or in a nutrient solution, and recorded the resultant anamorphs for many Ascomycetes. Klebahn (1918) germinated ascospores and conidia on nutrient agar and followed development, not only of anamorphs, but also of teleomorphs, in artificial culture, thus elucidating the entire life-cycle.

In order to confirm a teleomorph-anamorph relationship, one may start with spores of either state and hope to observe development of the other. Gordon (see Booth 1971a), for example, induced perithecium formation in thirteen species of Fusarium. Nine of these were heterothallic, and perithecia formed only when isolates from widely separated geographical areas
Figure 25.1. One way of proving the connection between a teleomorph and its anamorph; taken from Tulasne & Tulasne (1861).
were mated. Gordon was lucky as well as diligent. Sexual fruit-bodies do not often form in artificial culture.

It is usually far easier, and more direct, to isolate ascospores into cultures, and to induce conidium formation. The only way of being absolutely certain that a given teleomorphic fungus has produced an observed anamorph is to begin with one sexual spore (or a single ascus). There are, however, reservations concerning the use of cultures derived from single spores. Firstly, the anamorph formed in culture does not necessarily reflect the degree of complexity found in nature. Cultural studies must always be made in connection with observations of the species in nature. Secondly, an isolate derived from a single spore may not be genetically representative of the species as a whole. It is best to compare several single-spore cultures from several collections of a species. The most obvious case is heterothallism, with compatible mating-type factors being carried in different spores. Just as mating-type alleles are segregated into different spores, so, sometimes, are alleles governing the production of metabolites, and if one is studying fungal biochemistry or physiology, it is necessary to know whether a colony is ultimately derived from one, or more than one, nucleus.

The following notes were prepared to assist individuals who have never worked with solitary ascospores. The technique described is one that has been successful in quick handling of several hundred collections made on expeditions of one or two months' duration in the neotropics. It is only one method among many possibilities, and the reader is referred especially to Tuite (1969) for a very good description of several techniques of single spore isolation. Other descriptions are found in the CMI Plant Pathologist's Handbook and in Booth (1971b).

Collection of Specimens for Isolation

In order to isolate fungi into pure culture they must be collected and subsequently treated prior to isolation in such a way as to reduce contamination and to retain essential features for identification. This first section is intended for the mycologist who plans to spend periods of a month or more in the field. These suggestions are based on experience gained in the wet tropics where rapid deterioration of specimens is a very real hazard.

Collections are made in paper bags, but paper packets are almost as good. Although plastic bags, especially the kind packaged in rolls, are at first glance tempting, the advantages of paper bags are overwhelming. Field data and notes can be written directly on paper and are not easily obliterated. Paper bags can be firmly and quickly closed in the field and easily opened in the laboratory. Opening a knotted plastic bag can be positively diabolical. Paper bags can go directly onto the drier, where they allow for efficient circulation of air. For obvious reasons, plastic bags cannot go onto a hot-air drier. Finally, specimens -- especially those collected under wet conditions -- cannot be kept in closed plastic bags for any length of time or they will become moldy.

The biggest disadvantage of paper bags is that under wet conditions, either of weather or of specimens, the glue at the seams of the bags may loosen, or the paper itself may disintegrate. This can be anticipated, and to some extent prevented, by using two bags, by trimming specimens, and by protecting the specimens while they are being carried. A further drawback is that the Xylariaceae discharge their ascospores in paper bags.
Specimens should be processed the day they are collected. It is eminently worthwhile to make field determinations, and to divide specimens as soon as possible, if they are to be distributed to other mycologists or other herbaria. Specimens must be dried soon after collecting, and it is very easy to make a portable drier (Fig. 25.2). Some important factors to remember are that the drier must be light enough and compact enough to carry on your back for long distances, but large enough to hold 100 or more collections (of Ascomycetes), and it must allow for free circulation of hot air. Heating elements may be electric bulbs connected in series, or heating cones of 500w or 1000w (please remember that the electrical systems of some villages are fragile!), or any of a variety of natural gas or liquid fuel stoves.

If a collector intends to isolate from his specimens, he must divide each into two portions, making certain that each portion bears the same species. The larger portion is dried with heat and killed. The smaller portion, often bearing only a few fruit bodies, is air dried. Specimens to be air dried are left in their bags or paper packets in an area that has good air circulation. Twenty or more air-dried portions in small paper packets may be air-mailed in a first-class envelope to a laboratory, where they may be studied immediately or refrigerated for future study. A number system must obviously be devised so that the portions may eventually be reunited. It is necessary to kill one portion soon after it is collected, because the ascii of air dried specimens may dissolve, or the spores may begin to germinate in the interval between collection and study. Germinating ascospores can be easily isolated, but are not very useful for identification of the species.

Fungi that shoot their spores -- Discomycetes are good examples -- may be isolated in the field by inverting fruit-bodies over agar and securing them to the top of a petri dish lid with a gel or grease (Vaseline, for example). Ascospores may then shoot onto the agar and germinate. It is possible to carry tubes of agar and empty sterile plastic petri dishes into the field. The agar can be easily melted and poured into the petri dishes, and cultures can either be sealed by taping the lid, or by transferring to a culture tube using an alcohol- and flame-sterilized needle. Sealed plastic petri dishes containing agar may also be carried into the field.

Some Mechanisms of Isolating Ascospores

Several ways of isolating single spores have been reviewed by Booth (1971b), Tuite (1969) and Hildebrand (1938,1950). Two basic methods involve streaking a suspension of spores onto a solid medium and then locating individual spores, or removing spores one by one with a micromanipulator from a mass of spores at a point. The streak method is easier and quicker. Its disadvantages are that it can be difficult to obtain spores free of bacterial contaminants; spores must be widely separated if they are to be removed by hand from the agar without including other germinating spores; a streak does not always free the number of spores desired for study; there may not be enough material to allow for a streak; there is no certainty that a smaller spore, adhering to a larger spore, is not germinating rather than the desired spore. These are not great disadvantages, and they can be overcome either by using antibiotics in the medium to retard bacterial growth, or through practice in streaking, locating and removing spores.

The advantage of using a micromanipulator lies in the absolute certainty that only one spore has been isolated. This is not true of any other method. The three greatest
Figure 25.2. A field dryer that is easily transported can be made from an aluminum mailing case that measures approximately 90 cm long x 45 cm wide x 15 cm deep (A). Holes measuring 4-5 mm in diam. are drilled in all the surfaces of the box at intervals of approximately 2 cm (B). Legs are approximately 1 meter long and are made of aluminum "bracket-shelving" supports, i.e. pieces of aluminum that have three sides at right angles, each side approximately 8 mm wide, and with holes measuring 4-5 mm spaced at short, regular intervals along the length. The legs are secured to the top and bottom of the box (B) with wing nuts whose slotted heads are on the leg side (C-b) and whose nut is on the inside of the box (C-a). Heat is retained within the dryer through the use of a flame-proofed cloth (B-a) that wraps around the dryer and reaches the floor. It is secured to the dryer using clips such as clothes pins (B-b). Heat is provided by a variety of sources such as a natural gas-propane or butane-stove (D-a), a liquid fuel stove ("Primus", "Svea", D-b), 2-3 electric light bulbs (60-75W) connected in series (D-c) or electric heating cones (500-1000W, D-d).
disadvantages of the micromanipulator, apart from its expense, are the time involved in its use, the difficulty in transporting it, and the necessity of having an instrument for making finely tipped glass needles.

In order to prepare a specimen for isolation, a single ascoma is removed from the substrate and placed in a drop of clean (but not necessarily sterile) water on a glass slide. The ascoma is then observed through a stereomicroscope and crushed with a blunt glass needle. Sometimes a second needle may be needed to hold the ascoma in place. The exuded spores are then taken up in a capillary tube having an internal diameter of 0.7 mm or less, and blown into a drop of water at a marked spot on an agar surface. The spore suspension may now be streaked using a wire loop or blunt glass rod. If a micromanipulator is to be used, a drop of spore suspension can be blown onto each of three marked spots (Fig. 25.3 A) that are more or less equally spaced from each other and about 1 cm in from the edge of the petri dish. Enough room must be left so that the needle and its holder will fit within the dish without hitting the edge (Fig. 25.3 A). Petri dishes with spores to be micromanipulated are then allowed to stand, with their lids partially removed, until the drops of water have evaporated. Contamination is not a problem at this stage.

The medium to be used for either the streak or micromanipulation methods must be clear, and should be hardened with the equivalent of about 5% (w/v) agar. I use Difco cornmeal-dextrose agar almost exclusively. The agar surface must be smooth, level and dry. A dry surface is obtained by cooling the agar before pouring, and by pouring plates a day ahead of time. An antibiotic, to reduce bacterial contamination, and chemicals needed to stimulate germination, may be added to the agar. Stimulatory chemicals may also be added to the solution in which the ascomata are crushed.

A special microscope is not required for micromanipulation. Focussing may be accomplished by moving either the stage or the objective, but it is more convenient to use a microscope with a movable objective. Bausch & Lomb make a particularly convenient microscope on which both stage and objective are movable. With this microscope the petri dish can first be adjusted to the height of the micromanipulator needle, and focussing can then be done by moving the objective. With most other microscopes, the needle carrier of the micromanipulator must be raised to the level of the stage with books or blocks. It is easiest to use the micromanipulator in an area free of vibration. Ideally, the job should be performed on a concrete, energy absorbing table, such as is used for balances and other delicate instruments, but it can also be used on any solid base made of concrete or steel. I use a 13 cm-thick concrete building block in times of need.

Spores measuring 10 μm or more in length can be readily seen and manipulated at a magnification of about 100 diameters, and additional magnification can be obtained with 20x eye-pieces. Thus, using a low power objective of up to 10x, and 10-20x eye-pieces, most ascospores can easily be moved with a micromanipulator. The working distance of most higher-powered objectives is usually too small (less than 3 mm) for easy operation of the micromanipulator. Special objectives having long working distances are available, but they are very expensive. When a fungus, such as a species of Hypocrea, has ascospores measuring only about 5 μm in diameter, I usually wait for a day to see whether they will germinate before trying to isolate them.
Figure 25.3. Steps in the isolation of solitary ascospores. For explanation see text.

Figure 25.4. An example of a device used to couple 9 cm diam petri dishes to a mechanical stage. This petri dish holder is made of 2 mm thick clear plastic. A= topview. B= side view. The petri dish is held in place by four bolts and nuts (A-b) while tension is held on the petri dish by a spring (A-a). The plastic must be cut to allow it to clear the stage controls (A-d). The microscope condenser lens is indicated at A-c. A schematic representation of the holder in place on a microscope stage is shown in C.
The first step in isolating spores with a micromanipulator is to centre the mass of spores in the low-power field of view. Because the spores will be moved either up or down, position the dish so that movement in those directions does not immediately lead into the side of the petri dish (Fig. 25.3 A, B). The microscope stage is then lowered, or the objective raised, depending on the method of operation of the microscope; this gets the petri dish out of the way, thus protecting the needle while it is being positioned.

After the mass of spores is centered, but before the needle is put under the objective, the micromanipulator controls, both the fine horizontal and fine vertical, must be centered. If focussing of the microscope is controlled by moving the stage, then the objective should be in position to focus on the surface of the petri dish. The needle is put under the objective and the tip is brought into focus using the coarse vertical control of the micromanipulator. The needle is then raised with this control until its tip is visible but out of focus. The petri dish can then be brought into focus again and the needle should be slightly above the surface of the agar. If focussing of the microscope is controlled by moving the objective, the needle should be placed over the mass of spores, centering its tip roughly on the light coming through the substage condenser, and then is lowered until it is about 1 mm above the surface of the agar. The objective is then lowered until the spores come into focus. The needle, whose tip will be out of focus and off center, is then centered by hand and by coarse horizontal control, and is positioned slightly above the plane of focus.

The easiest and quickest way to move spores with a micromanipulator is to pick them up from the surface of the agar singly and remove them to a marked spot. This is usually done with spores measuring 30 μm or more in length, or with germinating spores. If they cannot be picked up, they must be pushed to marked places. About ten mature-looking spores are selected and brought to a spot at either the top or the bottom of the microscope field (Fig. 25.3 C). They are then pushed toward for a distance of one 100x field away from the mass of spores (Fig. 25.3 D). Continuing in a straight line, a single spore is left behind at intervals of one microscope field until all the spores have been isolated (Fig. 25.3 E). With the needle, a small mark is made in the agar behind each spore to mark its position (Fig. 25.3 F). The resultant line of marks is usually visible to the unaided eye, but it is convenient to mark on a piece of paper the location of each line relative to the mass of spores. Each time the petri dish is moved, the needle is raised above the surface of the agar.

The process of pushing spores over the surface of the agar cleanses them of adherent bacteria or any small fungal spores, but it can be extremely tedious if the needle is too sharp or if its angle is too great relative to the surface of the agar. The needle should move smoothly along the surface of the agar without penetrating it. It is necessary to use hard-en media to prevent penetration. Although it is possible to place the petri dish on the microscope stage and move it by hand, it is far easier to make a device that will hold the petri dish, and that is coupled to the mechanical stage of the microscope. Such a device, made of clear plastic, is illustrated in Fig. 25.4.

In most of the Ascomycetes that I have tried to isolate, the spores germinate within twelve hours. If they have not germinated within thirty-six hours they are either not going to germinate or they may require stimulation. For reviews of techniques used in stimulating spore
germination see Sussman & Halvorson (1966) and Sussman (1976). Often, isolated ascospores do not germinate, whereas those left in the mass of spores do germinate. If their germ tubes have not grown too deeply into the agar, those spores can be picked up from the mass with the micromanipulator. It is important that the collection not be killed until all attempts at spore germination are ended.

One should not assume, on the basis of only a few unsuccessful attempts, that a species will not grow in pure culture, nor should one draw too many conclusions when only one ascospore germinates. The ability of the spores of a species to germinate varies from collection to collection, and may also vary with the season. If only one spore germinates, it is possible that it does not belong to the fungus you wish to culture.

The process of removing germinated ascospores from agar is the same regardless of whether the streak or the micromanipulation method has been used. The germinating spores are examined first under the compound microscope to note any peculiarities of germination. Such peculiarities may be taxonomically useful and should be recorded. The petri dish is then examined using a stereomicroscope equipped with transmitted light. Around each spore a block of agar measuring 1-2 mm² is cut from the plate using a sterile, very sharp, pointed (No. 11) scalpel (Fig. 25.3 G) and transferred to a new petri dish with the normal concentration of agar. Although it is possible to put up to ten isolated ascospores onto a 9 cm diam. petri dish, it is best to put fewer spores onto each plate, thus avoiding the possibility of a rapidly growing contaminant ruining your hard work, or of isolated, rapidly growing colonies growing into each other. Sphaeriaceous Ascomycetes are generally slow growing, and may be easily overrun by contaminants. A well-sporulating dried culture, preferably from the original isolation, should be retained in the herbarium with the specimen. The medium should be noted on the herbarium packet.

Many brands of micromanipulators are available (Brinkmann, de Fonbrun, Leitz, Singer, Zeiss, to name a few), and there are models that can be used only for coarse work, and models for extremely fine work. Skerman (1968) has described a small instrument said to be accurate enough to isolate individual bacterial cells, yet simple and inexpensive enough to be used by undergraduate students.

I am familiar with only two instruments, the de Fonbrun (Etablissements Beaudouin, Paris) and the Singer Mk. III (Singer Instrument Company Ltd., Somerset, England). Both are very fine instruments, capable of moving spores under high magnifications, and of microsurgery. The de Fonbrun is pneumatic and works on a system of three pumps for vertical and horizontal movement. Movement is controlled by a single 'joy-stick'. This instrument is light and is supplied in a wooden carrying case. The instrument is in two pieces, the receptor and the manipulator. Two instruments can be used in tandem, and more than one tool may be used on a single instrument at one time. In my experience, the instrument is fragile. The system must be absolutely air-tight, and the slightest leak makes it inoperable.

The Singer Mk. III is typical of mechanical macromanipulators. It consists of a single unit, and is of all-metal construction, which makes it rugged. The details of operation of this instrument are nearly identical to those of the pneumatic micromanipulator.

Micromanipulator needles are made from soft glass rods measuring about 5 mm in diameter. A needle about 1 mm in diameter is pulled by hand using an alcohol flame. The tip is then
produced using a special needle-puller or microforge. In isolating ascospores, the only micro-tool needed is a straight needle with a fine tip; loops and hooks are unnecessary. An effective and easily used device for making microneedles is the 'Livingston Micro Pipette Puller' (F.S. Hockman, 638 Flagler Blvd., Lake Park, Florida, U.S.A. 33403).

**SINGLE ASCOSPORE ISOLATION: E.S. Luttrell**

The first principle to remember in making single ascospore isolations is that it is usually unnecessary. For special purposes, such as analyzing progeny from crosses in genetic studies or determining the range of potential biotypes in the field, single spore isolations are essential. For routine isolation of representative cultures or establishment of genetic connections among states of a species isolations from several spores, as, for example, from all eight spores from an ascus, are better. This is especially true of heterothallic species. The simplest approach to determining genetic connections is to isolate from ascospores and produce conidia in culture. Whenever possible, however, it is desirable to complete the cycle in culture. In attempting to produce ascocmata in culture it is pointless to add to the question of what environmental conditions may be appropriate the question of whether compatible mating types are present by using single spore isolates. The procedures for ensuring pure cultures from single spores will ensure pure cultures from several spores.

Allow any spores that are capable of being discharged forcibly to be discharged onto agar. This applies to Basidiomycetes and some Deuteromycetes as well as to Ascomycetes. Generally, ascospores are forcibly discharged. Under drying conditions ascospores may collect in masses at the tips of ascoma beaks in many species. This by no means indicates that the ascospores are not normally discharged forcibly under suitable conditions. Place a wet fragment of leaf or stem sliver bearing the ascoma, or a single ascus selected under the dissecting scope, on a wet square of No. 3 filter paper in the lid of a Petri dish. Replace the bottom of the dish and mark on the bottom the outline of the area covering the filter paper square in the lid. Turn the dish right side up and let the spores fall onto the agar below. Surface tension of the water is sufficient to hold the material to the lid. Check for spore discharge by inverting the Petri dish, rotating the bottom over a clear area in the lid, and scanning the surface of the agar through the thin layer in the bottom of the dish with the 10x microscope objective. Any reasonably clear agar such as malt-extract agar is satisfactory without filtration. When spores are being discharged, rotate the lid frequently to new areas to scatter the spores. The location of selected spores may be marked with an arrow on the bottom of the dish. The lid may be removed from the dish for direct examination of the spores under both 10x and 40x microscope objectives.

Permitting downward discharge of spores obviates the need for determining the force of ejection, and usually causes no serious problems with contaminants if the desired spores are ready for immediate ejection and the dish lids are rotated frequently to scatter the spores. Upward discharge, unless it is very weak, may be obtained in inverted Petri dishes by
building a stack of wet filter paper squares in the lid of the dish to bring the ascomata within a few millimetres of the agar surface above them. Upward discharge may be much better from large pieces of stroma or entire stromata of fungi such as Xylariaceae than downward discharge from small fragments attached to the lids.

Observe the spores throughout germination. Small hyaline spores may swell during germination and, after production of germ tubes, may be visible under the dissecting scope. Small-spored contaminants also may become apparent. Isolated spores or groups of identified spores may be removed by cutting out a square of agar with the flattened tip of a dissecting needle. Rest your hand on the microscope stage and make short, parallel cuts or jabs on either side of the selected spore. Rotate the plate 90° and complete the square with two more cuts. Examine the block under the 10x and 40x microscope objectives before lifting it out. The blocks may be cut out under the 10x microscope objective, but inversion of the image requires practice to coordinate hand and eye. The agar blocks may be transferred to a fresh agar plate face down, for continuing observation of the germinating spores through the bottom of the Petri dish, or face up for more critical observation of the surface with the lid removed from the dish.

If spore streaking must be resorted to, avoid the use of water. Plates should be poured long enough in advance for surface films of water to dry. Use the dissecting scope for picking up and depositing spores. Touch the dry tip of a dissecting needle to dried masses of conidia and streak the needle lightly across the agar surface between two points previously marked on the bottom of the Petri dish. If necessary, take up a tiny triangular block of agar on the tip of the needle, touch it to the spores, and push the block over the surface of the plate. Dark conidia may be tapped onto the surface of a filing card. Individual conidia may be picked up by touching them with the dry tip of a needle. They are then deposited on the surface of the agar over small circles previously marked on the bottom of the dish. Blocks cut from sporulating colonies in agar cultures dry quickly on paper. The dry conidia may then be dislodged onto a filing card for pick-up of single spores. If spores ooze in masses from acervuli, pycnidia, or ascomata, pick up tiny masses of dried spores, deposit them on the agar plate, and prod the spore ball across the plate. Attempt to leave single spores scattered along the way. If spores are not extruded from pycnidia or ascomata, pick out the dry sporoma and place it on the agar plate. Force it below the surface and push it through the agar to remove surface contaminants. Bring it to the surface and prod it across the plate. If spores do not ooze out and the wall is too sturdy to rupture against the agar, crack the wall between the tips of two needles, and continue prodding. Leave the sporoma on the surface at the end of the trail. It may produce mycelium even if no mature spores are present. Isolations may be made from sclerotia by the same procedure.

The most important point with all methods is to keep identified spores under microscopic observation until germination is completed and colonies are well established.
TELEOMORPHS

The teleomorphs of a number of conidial aquatic fungi are known (See Chap. 18). Evidence linking teleomorph and anamorph can be obtained in two ways: either by the development of teleomorphs in cultures derived from conidia, or by the development of conidia in cultures derived from ascospores or basidiospores. Teleomorphs occur in nature mostly on twigs and branches of threes half-submerged in streams, or on previously submerged wood on the banks of streams and rivers. Collection of ascomata or basidiomata on these substrata is simple, but it may be necessary to carry a saw or an axe to remove conveniently-sized pieces of wood. These may be transported to the laboratory in suitable containers. Pieces of wood not bearing teleomorphs may, if incubated in the laboratory under moist conditions, develop such structures.

The isolation of fungi from ascomata can be done in two ways, either by allowing the ascoma to project ascospores onto an agar surface, or by crushing an ascoma in sterile water to obtain a suspension of ascospores which are then streaked or spotted out onto an agar agar plate. Single and multi-ascospore cultures should be prepared. These different cultures will provide information as to whether a fungus is homothallic or heterothallic.

(a) Shooting off ascospores: A small piece of substratum bearing one or a few ripe ascomata is placed eccentrically in the lid of a Petri-dish on a small piece of moist filter paper. The lid of the dish is kept on the lower side, and the base of the dish, containing 10 ml of filtered 0.1% malt extract agar (or other suitable medium), with or without antibiotic, is placed above it. It may be helpful to prepare the lid of the dish first, using an empty dish, and then to transfer a base containing medium over it. The dish should be placed near a window because asci are often phototropic. After a few hours, it may be possible to see ascospore deposits on the underside of the agar. The lid may be rotated a few degrees at intervals and, in this way, several spore deposits may be obtained. A fresh lid is then placed over the base containing the ascospore deposit. Well-separated ascospores can then be marked and the dish set aside at about 15°C to allow germination. Transfer to fresh media of single germinated ascospores can be made after 1-2 days.

(b) Ascospore suspensions: A single ascoma is crushed in a drop of sterile water on a sterile microscope slide, using a flattened needle. The density of the ascospore deposit can be adjusted by the degree of crushing of the ascoma, or by diluting the suspension by transferring to further drops of sterile water. Using a fine Pasteur pipette or a loop, the ascospore suspension is streaked or spotted onto marked areas in a Petri-dish containing 0.1% malt extract agar. Single spores are marked and, after germination has taken place, are transferred to suitable media. We have no evidence that ascospores of aquatic fungi need any special stimulus to germinate, although some may take several days before germinating.

(c) Isolation from basidiomata: Although the number of aquatic conidial forms with known basidiomycetous affinity is small, some spores are known with dolipore septa or clamp connections (characteristic of Basidiomycetes), so that it is presumed that they may have
basidiomycetous teleomorphs. The known distance of basidiospore discharge is insufficient to allow the spores to be projected upwards from the lid of a Petri-dish to an agar surface above it, but it should be possible to allow basidiospores to fall from the lid to the base. Slivers of substratum bearing basidiomata should be fastened to the lid by an adhesive (petroleum jelly, Araldite) and the hymenial surface should face downwards. Rotation of the lid relative to the base should ensure that the basidiospore deposit is not too dense. Since at least one form, Ingoldiella hamata, is known to have monokaryotic unclamped conidia and dikaryotic clamped conidia, it is important that single- and multispor cultures be prepared. Matings between monokaryotic cultures derived from single basidiospores will yield information on mating-type behaviour.

ANAMORPHS

Many aquatic (amphibious) Hyphomycetes will grow on 2% malt extract agar. The optimum temperature for growth and sporulation of many species from temperate areas is about 15°C, but the optimum temperatures for fungi from other areas, such as the tropics and arctic-alpine areas, need investigation. After growth for about ten days at 15-20°C, many common aquatic Hyphomycetes are able to fruit. Most do not fruit on the dry agar surface, but there are exceptions to this. In order to induce fruiting, pieces of the culture should be placed in sterile water, and conidiophores and conidia may develop within 1-2 days, although for some species up to several weeks may be needed. Sporulation in most species is enhanced if culture pieces in water are vigorously aerated by compressed air (Towfik & Webster 1973, Webster 1975). This can be done in a flask or bottle, and the air may be introduced through a fine jet, a sintered glass bulb or an aquarium aerator. The stream of air bubbles sweeps many of the spores from the water and, after 1-2 days, a scum composed of an almost pure suspension of spores can be seen as a tide mark on the walls of the vessel above the point where the bubbles break. If this operation is carried out aseptically, and the entering air is filtered through a sterile cotton-wool filter, the resulting spore suspension can be used to inoculate fresh cultures. This helps to maintain the ability of the fungi to sporulate, which may be lost after repeated vegetative transfer.

A useful technique for producing a large amount of culture material for experimental purposes is to spread about 1 ml of a concentrated spore suspension over an agar plate and incubate it for ten days. Alternatively, macerated culture fragments prepared by homogenizing pieces of culture aseptically can be spread over a plate or added to a Petri dish to which cool molten agar (about 45°C) is then added.

A number of conidial aquatic fungi can be induced to form their teleomorphs in pure culture (Webster & Descals Chap. 18), but this may take several weeks or months. In such cases, it is best to grow the fungus in a plastic Petri dish containing extra medium (say 30-40 ml) to delay drying out, and to tape the lid to the base of the dish with adhesive tape. Low temperature incubation (10-15°C) is advantageous. Exposure to light from a white fluorescent tube, and especially to "black-light" (near UV) sometimes stimulates the development of the teleomorph. Prolonged incubation (for several weeks) of strips of agar well-colonized by aquatic Hyphomycete mycelia, in sterile water, so that the surface of the culture strip just protrudes above the water surface, may be effective in inducing teleomorphs, especially
apothecial ascomata.

SPECIAL CASES

*Ceratozystis ips, C. minor, C. capillifera:* teleomorph -- ascoma development is stimulated by some unsaturated fatty acids, especially linoleic acid, and by one saturated fatty acid, arachidic acid (Dalpé & Neumann 1976).

*Ceratozystis piceae, C. ulmi:* teleomorph -- ascoma development is stimulated by the presence of alphacel in the medium; anamorph -- development of synnematal conidiomata is stimulated by the unsaturated fatty acids, oleic acid and linoleic acid, as well as by terpenes (Neumann & Hubbes 1972, Hubbes 1975 and pers. comm.).

*Ceroespora:* many strains will sporulate only on potato-carrot agar (von Arx pers. comm.).

*Cordyeeps militaris:* teleomorph -- medium as follows: 10g long grain polished rice in 25 ml distilled water. Leave for 1 day before autoclaving. Inoculate and incubate at 16-22°C with illumination at 1000 lux or more for about 2 months. (Other species of Cordyceps might form teleomorphs under these conditions -- *C. ophioglossoides* forms large but sterile 'fructifications' under them. Low incubation temperatures and bright light probably facilitate fruiting in Cordyceps.) (Basith & Madelin 1968).

Plant parasitic fungi: often sporulate better on very poor media, and can sometimes be induced to sporulate by exposure to long wavelength UV for 3-4 days, followed by darkness (von Arx pers. comm.).

Yeast: sporulation media are detailed by van der Walt in Lodder (1970). Of the media mentioned on pp. 56-58 of that book, CBS prefers:

1. McClary's acetate agar for *Saccharomyces, Kluyveromyces, Zygosaccharomyces, Pichia, Torulaespora,* etc.
2. V8 agar for *Hansenula, Pichia*
3. malt-agar for *Hansenula, Hanseniaspora, Schizosaccharomyces*
4. YM agar for nearly all yeasts:

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<td>1 g</td>
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<tr>
<td>Malt extract, powdered</td>
<td>0.3 g</td>
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<tr>
<td>Yeast extract, powdered</td>
<td>0.3 g</td>
</tr>
<tr>
<td>Peptone</td>
<td>0.5 g</td>
</tr>
<tr>
<td>distilled water</td>
<td>100 g</td>
</tr>
<tr>
<td>agar</td>
<td>1.5-2 g</td>
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(von Arx pers. comm.).
MAJOR REFERENCES

The Mycology Guidebook, compiled by a special committee of the Mycological Society of America, contains a great deal of information relevant to this section. A selection of topics and page references follows.

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There is also an extensive appendix of culture media for general and specific purposes on pages 657-692.

Methods in Microbiology, Volume 4, edited by C. Booth and published by Academic Press, is a mine of information and appropriate references on methods of isolating and culturing fungi, and persuading them to sporulate. A list of topics and page references follows.
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<td>Light induction of sporulation</td>
<td>625 - 635</td>
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The Classification and Nomenclature of Fossil Fungi

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Although many of the fossil fungi we mentioned earlier (Chap. 8) can be recognized or at least matched with living forms, few of the names we used for them seem to be referable to anything familiar in the taxonomy of fungi. Most of the names are somehow reminiscent of structural chemical formulae, sounding alien to mycology, even to taxonomy in general. Their occurrence among more traditional names reflects the variety of kinds of classification in use by palaeontologists, for although -- as almost everyone knows -- classification and nomenclature should not be confused, they are closely linked. And some classificatory schemes are so completely dissociated from a biological rationale, their categories characterized so simply, that their names can serve as diagnoses.

A quick scan of the literature on fossil fungi gives us the following picture. Some of the fossils are identified with, and bear the name of, botanical* species (Hypoxylon truncatu-

wm) or anatomical* anamorph-species (Tetraploa aristata). Others are named separately as fossil species within extant genera, botanical (Vizella memorabilis) or anatomical (Sporides-
mium henryense). Some authors use the names of extant botanical or anatomical genera, but with an -ites suffix (Chaetosphaerites polenisimilis, Cladosporites bipartitus). And then there are the still recognizably biological names that have been created especially for genera of fossil holomorphs** (Cryptocolax clamensis), teleomorphs** (Martustia andegavensis) or anamorphs** (Morosporium lignitum), without reference to names of living genera. So far, this variety of names provides a comprehensible nomenclature for the insertion of fossils into the current taxonomy of fungi, in a series indicating a progressively increasing distance in the relationship between fossil and living.

In addition, an altogether different set of names has appeared in literature particularly since the 1950's. These are names so graphically expressive that each name is itself an instant reflection of the characteristics of the category and its position in the classification -- names such as Fusiformisporites*** (F. rugosus), Lacrimasporonites (L. levis), and Pluri-
cellaesporites (P. psilatus). They are taken from special classifications devised for micro-

* & ** Terms: * as in Hennebert (1971); ** as in Hennebert & Weresub (Chap. 3). Especially to be noted is the use here of "botanical", not in contrast to "zoological", but as opposed to "anatomical" or, more broadly, "artificial".

*** In order to emphasize the independence from ICBN control originally intended for these names, they are not italicized in this paper.
fossils of all kinds (not all originally including fungal forms). The arrangements are such that the microfossils can be catalogued according to pre-established architectural criteria in what amounts to a multiple-choice key, usually for single characters. Most of these classifications were proposed as informal systems, largely intended to be taxonomically non-committal, with their basic units assigned "supra-generic binomials". As we have seen, the names from these systems have been picked up and treated by one author or another as form-generics, with the originally non-taxonomic morphographic categories accepted as taxa.

In short, the systems of classification adopted by palaeobotanists are either botanical or, in varying degree, artificial; if artificial, they may be anatomical (as for Fungi Imperfecti), morphographically "half-natural" (see Potonié 1951), or mechanical (as in a catalogue, see Lange & Smith 1971). And these systems are expressed by a variety of nomenclatural schemes, some of them achieving legal status by chance rather than design, none of them outlawed per se by the International Code of Botanical Nomenclature (ICBN).

**APPROACHES TO FOSSIL PLANTS**

To understand the situation, it is necessary to review briefly the evolution of palaeobotanical classification and nomenclature, with special reference to palaeopalynology. Basic palaeontological approaches were formulated by Adolphe Brongniart (1828), one of his principles being that descriptions of fossils should be drawn from direct observation of the features of the fossils themselves rather than via speculative correlation of these features with those of living organisms. At the same time (as Stafleu 1966 expressed it), "in his opinion a profound knowledge of the anatomy of living pteridophytes and gymnosperms would be of immense use for the recognition of taxonomic relationships in fossil plants". Clearly, although Brongniart stressed that it was better to base an artificial system of classification on the limited characteristics available in fossils, than to speculate prematurely on "natural relationship", he had no doubt that finding a "natural system" should remain the ultimate goal of the taxonomist. By this qualification of his basic principle of unfettered objectivity, Brongniart invited workers in different disciplines to choose an approach that best suited their background: geologists generally opted for the artificial, biologists for an attempt at the "natural". Brongniart's use of the term "natural" was non-evolutionary, ours has a phyletic connotation; but a difference between artificial and "natural" classificatory approaches remains.

During the 19th century, the geologist and botanist were frequently one person. And so the split between artificial and "natural" systems did not arise, the palaeobotanist being comfortable enough in the world of plant life to appreciate the usefulness of taxonomically uncommitted designations for some fossil forms without allowing the label to interfere with a botanical understanding of these fossils. For example, Seward (1898:11) wrote: "Brongniart and other authors... instituted several convenient generic terms of a purely artificial and provisional nature, which are still in general use", and (1898:112) "...Sphenopteris being one of those extremely useful provisional generic terms which are used in cases where we have no satisfactory proof of precise botanical affinity... the purely artificial form-genus..." (the emphasis is ours). How skilfully these palaeobotanists were able to overcome the difficulties of interpreting the fossil remains of plants is described briefly by Delevoryas (1969).
With the development and growth of palaeopalynology, "...haphazardly," N.F. Hughes & Moody-Stuart (1967) have said, "rather more from geology than from botany", vast amounts of data on fossil pollen, spores and other microfossils accumulated in a short period. Organizing them became a problem of dimensions unforeseen by early palaeontologists. The only solution for those who were faced with the pressing need of processing the data for rapid retrieval was some practical classification with this limited purpose, demanding no time-consuming taxonomic investigation. Little else was possible for those who had to concern themselves with, for example, all miospores -- these being (as defined by Guennel and quoted by Kosanke 1969:223) "all fossil spores and spore-like bodies smaller than 0.20 mm, including homosporous, true microspores, small megaspores, pollen grains, and prepollen", not to mention fungus spores as well. Few botanists today have sufficient experience with widely different biologic groups to be able to deal competently with so heterogeneous an assemblage of biological material. Most of us are satisfied if we know enough about diverse groups to be able to sort material into sets for different experts. But the palynologist, probably frustrated by a lack of interest among experts on living forms, has chosen to become an expert himself on all miospores. This he manages to do by following Brongniart's prescription more literally than it was intended, describing and sorting microfossils along purely architectural lines (with or without wings or lobes, openings or marks of various kinds, sculpturing, etc.) as objects observed to have a particular form and construction, avoiding the taxonomist's obligation to view their morphology as a biological manifestation.

According to Brideaux (1968:183), in a most useful review of this history (see also, e.g., Rouse 1957), "Potonié (1931) began the modern phase of miospore nomenclature by defining a second extremely broad fossil miospore genus Pollenites, in addition to ... Sporites H. Potonié 1893", the former for all pollen, the latter for all presumed sporomorphs (except megaspores), whether phanerogamic or cryptogamic or even non-sporic. It is noteworthy that Brideaux wrote that the "genus" was "defined" (rather than described or circumscribed), for in fact the classification became a catalogue of terms and definitions (see Stafleu 1967). Apparently, the definitions for Pollenites and Sporites were so broad that the categories soon lost their "generic" connotation ("except in an informal sense"), and their names became, for some, "names of informal ranks" within which various other categories (paratax, see Schopf 1969:71) were established, such as Potonié's hierarchical turmae. Pant (1954:47), however, used the taxonomically formal rank "phylum" for the categories called Pollenites, Sporites and his own Prepollenites, although he did make clear that he used terms such as "phylum", "class" and "genus" differently from the way in which they are used in taxonomy. He wrote: "If the characters are well preserved in specimens ... the names of the subgroups [e.g. Punctatissporites Ibr.] ... should be used as 'generic' names ... If, however, the characters are ill defined ... the name of the next identifiable higher category [e.g. Division Azonalessporites] may be used as the 'generic' name ... Even ... Sporites may have to be used..." In fact, Pant's scheme was "meant only for scattered spores and pollen grains about whose affinities...it is difficult to say more than what their remaining form and characters merely indicate". In other words, Pant proposed an inventory of microfossils too poorly characterized to be incorporated in a botanically understandable taxonomy. Yet he did weigh the possibility of some phylectic distinctions being reflected in his frankly artificial classification.
And he did refer to the priority of some of the names, and recognize taxonomic levels (phyla, classes and subclasses) that have become fixed in a sequence prescribed by the ICBN. Thus the scheme and the names in it appear to be on a par with classifications and names established for botanically based fossil-genera. And the fact that a Latin diagnosis is not required for validation of the names of fossils would have put Pant's "subgroup" names in competition with the names of fossil genera, were it not that Art. 35 requires a "clear indication of rank" (in terms of Art. 4), and the requirement is unfulfilled for the "subgroups" in his publication.

Erdtman (1947) tried to avoid this problem by being even more explicit about the names he introduced in a proposed artificial classification: "It should be borne in mind...that the names mentioned...are...not to be codified in nomenclature". His scheme is precisely organized: In "'Hexorites oblata n.spm.' (...nomen imaginatum), 'Hexorites' provides information as to the morphology of the spore and corresponds, as a 'nomen typicum abstractum', to the generic name in ordinary nomenclature, whilst 'oblata', as a 'nomen differentiale', corresponds to the specific name...In 'nomina typica concreta'...Fagidites...the letters 'id'...stress similarity, and nothing is said or assumed concerning any possible relationship".

The use of individual letters in a descriptive coding of diagnostic features pervades palynological nomenclature. In Laevigato-sporites, for example, Ibrahim (1953) gave an abbreviated characterization of a fossil spore (-sporites) that is smooth (laevigat-) and with a mark that may be a scar or a pore (-o-), in this instance mono-lete, i.e., single. The connective was changed to -a- if the spore was a-lete, lacking a scar, or to -i- if the mark was tri-lete, three-pronged. Other ingenious codes have been devised, nonverbal (Tschudy 1957) as well as verbal with prefixes and suffixes describing not only the minutiae of structure but also indicating whether the interpretation of a character is well founded or uncertain, and in what time zone the find was made. It seems to be an inspired solution for the often irritating problem of the inapplicability of so many biological names.

Many of these schemes are based on penetrating architectural analyses (e.g., Erdtman 1954, Walker 1976) of the pollen grains of living plants. And in fact, van der Hammen's (1954) fossil form-genera, such as Monoporites, Monocolpites, etc., were nomenclaturally typified by living species, respectively Zea mays, Iris pseudacorus, etc. As it happens, this action made the names of most of these genera superfluous under Art. 63. Only his form-genera for fungus'spores bear legitimate names, and this only because he knew (and cared) so little about living fungi that he typified his fungus-spore form-genera, e.g., Monoporispores, Diorisporites, by fossil form-species. Aside from his disregard for the ICBN and fungi, van der Hammen, like Erdtman and others, laid stress on the fact that microfossils are relic plants, to be understood only in the light of experience with living forms, though best organized in artificial classifications with highly descriptive terminological names as their basic classificatory device. The expressiveness of the names, pinpointing a position in the organizational plan, seems to be of supreme importance.

Other classifications hover between total artificiality and a sometimes diffident recognition of the botanical affinity of the dispersed entities under study. But some schemes are clearly one or the other. Norem (1958), for example, produced a set of keys for the classification of fossil spores and pollen into the same kind of predetermined morphographic cate-
gories others were using, but wisely eschewed taxonomic designations and names with "Greek or Latin endings imitating official nomenclature". "The use of the official categories" of the ICN, he stated, "in an artificial classification system will be confusing". Norem's scheme was frankly without taxonomic pretensions. On the other hand, Bharadwaj & Venkatachala (1968) objected that morphographic systems, though convenient, ignored the fact that "the significance of any characteristic is not the same for every plant group in which it occurs"; and they attempted to make taxonomic sense out of some of the artificial groups to "furnish a foundation for...a morphographical system based on phylogenetical considerations" without, however, revising the nomenclature already in use.

Additional classificatory schemes and terminological names have been proposed. N.F. Hughes & Moody-Stuart (1967), for example, contemplated "the open use of a stratigraphical prefix on generic names", the possibility that "the genus...fundamentally of the same nature as the higher taxa...might well become unnecessary", and that "the retention of the word 'species' is questionable". N.F. Hughes (1976a) has also remarked that "probably all angiosperm fossils from the whole of the Cretaceous should be grouped in newly defined taxa based on fossil evidence alone...free of extrapolations from...standard comparisons with living plants". And more recently, N.F. Hughes (1976b) has proposed the rejection of "the Linnaean system" of nomenclature as inappropriate for palaeontology. This would seem to achieve a most desirable end, in that the terminological labels now being used for fossils slotted in morphographic categories would cease to burden formal nomenclature (Stafleu 1967). We are certainly not angered (as Doyle 1976 feared) by N.F. Hughes's rejection of the "Linnean system of data handling" when all he wants is a "code for recording and stratigraphic use of material". But, by further isolating the palaeontologist, might there be less desirable consequences?

As it is, the palynologist is faced with a dilemma. His data about microfossils must be recorded, ordered and reported, so that the information gathered is quickly available for the stratigraphic and other uses he may find for it. Convenience dictates that the arrangements made should be taxonomically uncommitted. "Clarity", as Schopf (1969) points out, "requires that terms denoting...[these artificial]...systems of classification be differentiated from formal names denoting the taxa of plants". And with a clear nomenclatural division between artificial and taxonomic systems, it should be possible to keep their applications separate. But as matters stand, whether the morphographic categories are informally designated or dressed up with Latinized names as if they were botanical taxa, and however reluctant the palynologist may be to make a taxonomic decision tying the fossil to the living, he nevertheless cannot help but be aware that fossils are permanent records of the course of biological evolution. And by this awareness, he is often seduced into treating the artificial categories of organs as if they were steps in an evolutionary pattern.

Determined to have "an artificial system within which all spores and pollen can be methodically classified regardless of their botanical affinity" (Pierce 1961), insisting on an "analysis of...fossil remains...not prejudiced by comparative...studies of living plants" (Doyle 1977), the palynologist cannot yet resist thinking in terms of evolution. He forgets that microfossils divorced from botanical foundations are simply pieces of architecture, and that they have been classified artificially on the basis of more or less arbitrarily selected characters, many of them analogous at best, homologous only by chance. Under these conditions, the palynologist's daring visions of "character phylogenies" are such as would not be possible
if he accepted the discipline imposed by biological "prejudices". For example, while Doyle & Hickey (1976:178) were able to suggest that the stratigraphic layering of pollen grains could be interpreted as evidence for "evolutionary transformation" of pollen, the same kind of evidence (though "more sporadic") for leaf forms led to no more than postulating "extensions of morphological complexes". Behind the relative caution of the latter statement was the fact that conclusions regarding fossil leaves were influenced by Hickey's (1971) "comparative morphological analysis of modern leaves", etc., whereas there appeared to be no similar restriction on hinting at (Doyle & Hickey 1976:146) the evolution of "tricolpate" to "tricolporoid" to "tricolporate" pollen.

The "benefit of phyletic reasoning" (Schopf 1969), when applied to the study of organisms in their living or fossil state, is that a relationship is postulated and the organisms incorporated in a formal taxonomic treatment, to some degree reflecting a hypothesis regarding their phylogeny. What benefit accrues from evolutionary reasoning applied to entities that are deliberately excluded from recognizable taxa (and from the commitment to homology they represent) is not obvious, in spite of the erudite use to which, e.g., Doyle (1977) puts it. But let us be fair. Unlike some followers of morphographic systems, palaeobotanists like Pierce and Doyle have not surrendered their botanical knowledge to the sterility of total artificiality. References to the characteristics of known groups, as by Doyle & Hickey (1976) to "monosulcate pollen...found...in modern monocots and magnoliid dicots", etc., testify to an understanding of living plants that guides their use of morphographic analyses. Nevertheless, Doyle (1977) insists, "Although some of the pollen types involved may be relatable to high-rank Recent taxa, it should be noted that this analysis itself is independent of any such relationships".

The celebration of the triumph of objectivity over prejudice is unjustifiable. Complete objectivity is possible only through total ignorance; and the authors we have quoted as seeking this objectivity are too much lacking in ignorance to be able even to approach such independence in their observations. The "prejudices" of a background of knowledge enter at every point. Objects discovered in geologic deposits are referred to the category of "fossils" on the basis of a familiarity with biological forms. Fossils are divided into zoological and botanical on the basis of what we have learned from living organisms, the criteria perhaps arbitrary, but a distinction possible only by reference to previous studies. Even extinct groups, like Acritarcha or Chitinozoa, which are not known to have living relatives, cannot be interpreted except in the light of the characteristics that appear in extant biota. We cannot pretend to see fossilized organisms as they were, but only as they appear to us today, our minds steeped in preformed concepts. The situation may have disadvantages, but ignoring its existence will not remove them. In fact, we are convinced that, in dealing with fossils, what we know about living groups is not disadvantageous; it is our not knowing enough that leads us astray.

We have, in this review, come to appreciate the problems of the palaeontologist, and especially the palynologist, when faced with fossil forms not easily classifiable in a taxon at some level in the hierarchy of plant taxonomy. With Schopf (1969) and others, we accept the usefulness -- however limited -- of informal, special classifications including morphographic systems, to those who must concentrate on practical data-retrieval and prefer to ignore, or
postpone, consideration of the botanical links of these fossils. We understand, but deplore, the confusion that has resulted from a lack of appreciation of the limitations of special classifications. We share, with many others (including palaeo-botanists and -palynologists, neo-botanists and -mycologists), a concern for the way in which terminological concepts (Stafleu 1967) are being treated as form-genera, when nothing is gained thereby, and only a bewildering proliferation of formal names for heterogeneous taxa results.

To Schopf's (1969:54) admonition that "perhaps of all the opportunities of exercising taxonomic judgment, the decision to identify or not to identify is most important", we might add: "particularly by the use of a name regulated by the ICBN", for we should like to see such a name reserved for use by those prepared to make a taxonomic statement, i.e., with "phyletic implications" (Schopf 1969), however tentative and unprovable.

Now the question arises of why palaeopalynologists often prefer to hide, behind morphographic labels, whatever taxonomic judgements they are prepared to make. Is it because they agree with N.F. Hughes (1963) that early events are obscured "by a mass of assumptions implicit in the backward-looking practice of assigning very incomplete fossils of single organs to well understood and studied Recent genera of complete plants"? Or because (Doyle pers. comm.) even a "perfect match" may lead to wrong conclusions, warped by the likelihood of convergence, the mixture of primitive and derived characters in modern groups, etc.? Or is it in large part, perhaps, because the palaeontologist assumes that only he is faced with the problem of "taking the part for the whole" (Stafleu 1967), forgetting that the neobotanist's (and, yes, the neomycologist's) material is also fragmentary. "Taxonomy is almost always a question of evaluation of incomplete material". Undoubtedly the degree of incompleteness is greater when only fossil pollen or spores are available, and the evaluation thereby more difficult and undeniably more uncertain. But the uncertainty, too, is a matter of degree. It is apparent, throughout palaeopalynological literature (as well as in comments by some neomycologists) that a misconception exists regarding taxonomic statements: there seems to be an assumption that these are absolute statements, either absolute fact in themselves or made with absolute confidence of fact. When N.F. Hughes & Moody-Stuart (1967) recommend "that all attributions of new specimens from a new horizon or new locality should bear the prefix 'cf.' before the species name", they must imagine that when a neobotanist identifies a specimen of recent plant with a known species, the determination is unquestionably correct and accepted as such; else why designate these particular identifications as necessarily less dependable than others? Brideaux (1968:185) refers to a proposal for a "half-natural system whereby a possible botanical affinity could be indicated...; and a natural system wherein material would be placed if it could be positively identified with a living taxon". It may be shattering to the faith possessed by palaeopalynologists in neontological determinations and dispositions, but they should know that even the most positive taxonomic statement -- the simple identification of a living plant -- can frequently be challenged, sometimes with justification, for, under any and all circumstances, it is no more than a hypothesis.

Notwithstanding this lack of certainty, the neotaxonomist who wants to communicate with his colleagues by means of the nomenclature that is the common language of taxonomy is required to make a decision regarding the relationship of the organism under study. It can only be hoped that he does so with care, cognizant of his responsibility as a scientist (see Schopf
1969). The same hope and expectation are extended to the palaeobotanist. And if he is not ready to make a decision regarding kinship with living plants at some level of taxonomy, it is understood that he is not ready to use taxonomic classification and nomenclature.

In view of the kind of material he has to study, the palynologist's unreadiness to leap to taxonomic conclusions is understandable and often commendable. He is entitled to whatever kind of classification satisfies his needs, and the ICBN also provides for the naming of artificial genera (see later) as a nomenclatural reflection of whatever taxonomic decisions he feels able to make. But the palynologist has treated evolutionary botany and botanical taxonomy unfairly, both by disguising as taxa the morphographic categories that make no taxonomic demands on him, and concealing his taxonomic conclusions under the cloak of terminological names. Both actions serve to re-inter the vast store of discovered information on the plants that inhabited this earth in earlier times. It is this double camouflage, rather than the domination by "theorists", as N.F. Hughes (1976a:12) has it, that "devalue[s] the study of the fossils, which can be entirely dismissed from consideration in an otherwise serious work (e.g., Davis and Heywood 1966)"

Only when the student of microfossils ventures a taxonomic opinion in terms understandable to a taxonomist can there be communication between them. For example, Bharadwaj & Venkatachala (1968) have divided Laevigatosporites ibr. among the Sphenopsida and Pteropsida. Now there is at least some common ground, some basis for consideration of the material by a taxonomist who may be able to evaluate the taxonomic decision and weigh the implications of the finds, whereas Laevigatosporites, as one of the heterogeneous units of a conglomerate group of mechanically sorted forms, was hardly likely to catch the attention of a taxonomist/evolutionist.

**APPROACHES TO FOSSIL FUNGI**

These matters of the classification and nomenclature of microfossils concern the mycologist not only because fossil fungi are involved and frequently buried in morphographic terminology, but for other reasons as well, to be discussed later.

First, let us look briefly at the history of palaeomycology, a study that developed in the 19th century through the efforts of palaeobotanists (see also Pirozynski 1976a) whose interest in fungi was usually only marginal. Lindley & Hutton (1833) described *Polyporites bowmanni* with the comment that, "if it is a fungus, it is perhaps the first that has been discovered in the Coal Flora". Göppert (1836) encountered a fossil which, apparently with the help of Nees, he connected with *Exotipula sphaerioides* Fr. and described as *Exotipulas neasti* gen. et sp. nov. Various authors such as Engelhardt, Ludwig and others in Germany, Heer in Switzerland, Saporta in Portugal and Lesquereux in the United States (to name only a few) included, among their discourses on fossil plants, descriptions also of leaf spots that were sometimes dotted with black specks referred to as "perithecia"; and they classified most of them in recent genera of leaf-spotting fungi, frequently *Sphaeria* Haller.

Mycologists of the time were apparently too much involved in the excitement of discovering new living fungi to take much note of fossils. There seems to have been little exchange and cooperation between them and mycologically inclined palaeobotanists. This lack of interest on the part of mycologists of the 19th century is especially surprising in view of their broad
training, sometimes even in palaeontology. Corda, for instance, enjoyed a reputation as a palaeobotanist (Corda 1845) and as a world authority on trilobites (Hawle & Corda 1847); yet he ignored fossil fungi. Perhaps it was his neglect that influenced other mycologists, for Berkeley (1848), in describing three new species of fossil fungi, one in what he called a new genus (Brachycladium Berk. non Corda 1838 = Brachycarpium Berk. 1849), commented: "The actual occurrence of fungi in a fossil state has hitherto been very problematical... I do not find any notice of the occurrence of fungi in any shape in the magnificent work of Dr. Corda on fossil remains of vegetables". Fresenius (1861; and Fresenius & Meyer 1856) seems to have been one of the few other mycologists of this period to acknowledge the existence of fossil fungi. He published the new species Sphaeria areolata and Phelonites (sic!) lignitum, along with the transfer of Licea stroblina Alb. & Schw. into Phelonites. This was undoubtedly meant to be the genus Phelonites Chev. ex Fr., the change from -itis to -ites perhaps an attempt to modify its name for fossil members, but more likely a lapsus.

The products of the first 80 years of palaeomycology were compiled by Meschinelli (1902). His lists included 357 species classified in 63 genera. In many cases, the disposition of these fossil "fungi" was inferred from an association of particular symptoms with a particular host, or from superficial macroscopic characters of little use to us today. And so, most of the fossils in Meschinelli's lists are unimportant mycologically, of primary interest only historically and nomenclaturally.

The record shows that, as soon as a fossil was judged to be fungal (however mistakenly), it was described as far as possible in mycological terms, classified among other fungi, and compared with known living fungi that were similar in structure and regarded as relatives. A few completely new names were introduced for fossil genera, such as Grilletia, Palaeomyces and Oochoytrim, Renault's (1885, 1896) names for Carboniferous finds. Many authors (e.g., Heer 1855, 1874, Ludwig 1857, 1859, Engelhardt 1885, 1891) almost consistently simply described new species in extant genera, only occasionally (e.g., Engelhardt 1895) accepting an -ites modification of the names of these genera; whereas authors such as Göppert (1836, 1852, 1854), Unger (1845, 1850), Massalongo & Scarabelli (1859), Felix (1894), Meschinelli (1892, 1902), and Meschinelli & Squinabol (1893) almost exclusively used the -itis suffix. The modified names were attributed, by some, to the author who first added the suffix to the known name, e.g., Hysterites Ung., Sphaerites Ung., Polystigmites Mass., Phacidites Mesch., etc.; by others, to the author of the root name, e.g., Hysterites Tode, Sphaerites Hall., Polystigmites Pers., Phacidites Fr. Meschinelli himself vacillated at first but, in his final comprehensive work in 1902, settled on, e.g., "Gen. Sphaerites Hall. (Sphaeria) sensu latissimo", though species names originally published in Sphaeria are shown as transfers, e.g., Sphaerites deperditus (Heer) Mesch., and the suffixed generic name, as well, is usually shown in the index as a transfer from the root-name, e.g., "Sphaerites (Hall.)".

In the 20th century, fossil fungi continued under study mainly by palaeobotanists using the same approach, some (e.g., Engelhardt & Kinkel 1908) accepting fossils as new species of extant genera with their names unmodified, others (e.g., Fritel 1910, Piá 1927, Fiore 1931) adding the conventional suffix, sometimes with an implicit or even explicit acceptance of the extant genus as simply broadened in circumscription (e.g., Fritel used "Sphaerites Hall. (Sphaeria sens large)"); even when the suffixed name is attributed to a later author (e.g., again from Fritel: "Phomites n. gen. (Phoma Fries, sens large)"). Cookson (1947), in her
pioneer work on fossil thyriothecia, also proposed genera as new when she added the -ites suffix; and Singer & Archangelsky (1957, 1958) presented Phellinites as a new genus, with P. degiustoi sp. nov., a fossil species, as its type. Dilcher (1965) has employed all three methods of naming fossil finds -- assigning some to species in extant genera with unmodified names, others to genera with names modified by the -ites suffix, and the rest to fossil genera with totally new names -- to signify his assessment of the taxonomic proximity of fossil to extant taxon. And in all this work, fossil forms were integrated into the classification of living fungi, and were therefore accessible to the mycological taxonomist, who, admittedly, paid little attention to them.

Then, as happened in the study of fossil plants, a shift away from this integration of fossils in the normal classification began in the 1930's with the development of palynology. Two factors guided the new direction; palynological techniques yielded enormous numbers of dispersed spores and fragments, and the new field attracted mainly geologically oriented rather than botanically oriented students of fossils -- and still, few mycologists. Consequently, although the percentage of fungus material among "miospores" is probably very high, few micropalaeontologists pay any attention to them; and of those who do, most do not attempt to treat them as the remains of once-living fungi. The result is, predictably, that fossilized spores and fragments of fungi are re-buried in several of the existing morphographic systems of classification and nomenclature.

In one of the systems mentioned earlier, Ibrahim (1933) restricted the use of the name Sporonites R. Potonié (1931) for spores of Palaeozoic fungi. Ibrahim did not formally use this category, and the Sporonites system has expanded little beyond the addition of a few form-species, except for the treatment by Rueda-Gaviola (1969). He extended the use of Sporonites, at the level of "superdivision", to geological periods more recent than the Palaeozoic and therefore, having so many more and different kinds of fungus spores to contend with, split the "superdivision" into "divisions", "subdivisions" and "subgroups".

Meanwhile, Palaeozoic coal petrologists, employing petrological (thin and polished sectioning) techniques, also discovered the presence of fungi, and some declared them to be the commonest microfossils encountered in coals. During the Third Congress of Coal Petrology held in 1951, an international committee adopted the term "sclerotinites" for the fossils in these finds. Independently of schemes proposed for classifying Palaeozoic pollen and spores recovered by maceration, a separate system for cataloguing sclerotinites was developed by Stach & Pickhardt (1957), and then expanded to include fungus finds in Tertiary coals. The system, as reviewed by Benes (1969), is based on morphographic categories of the same kind as in other such systems, bearing the same kind of descriptive terminological names, the spelling of which differentiates between Palaeozoic and Tertiary finds. Tertiary fossils are sorted into Sclerotites and Sclerosporis, and Palaeozoic into groups whose names end in -sclerotes, -ascina and -sporina, e.g., Striatosclerotes, Clavascina, and Rosasporina.

From these independent schemes, there results, for instance, Pluricellaesporites (P. psilatrus Clarke) for a grouping of Palaeozoic phragmospores with hyphal fragments recovered by palynological (maceration) techniques, and Cellulasclerotes (C. abnormis Pickh.) for similar objects recovered by petrological (polished section) methods. As in all morphographic schemes the names are highly expressive, indeed diagnostic, the systems constructed in such a way that
slots exist for practically any combination of the features used, whether or not they have been encountered in convincingly fungal material.

The features around which various morphographic schemes are built are those that have emerged from the analysis of pollen grains, many of them, in fact, "phylogenetically useful pollen characters" (Walker 1976). The same characters and combination of characters were used in establishing categories for all fossil miospores, whether these were judged to be relics of phanerogamic or cryptogamic plants, of algae or fungi; a pollen grain, spore, or bit of hypha.

In van der Hammen's system, fossil spores of fungi are classified in categories whose names bear the suffix "-sporites". These "form-genera" for fungal ("or algal") spores (Monoporosporites, Triporisporites, Polyadosporites) parallel those for pollen (Monoporites, Triparites, Polyadites), with less detail but on the basis of the same kinds of character: number of cells, number and position of "apertures" or "pores". Van der Hammen's system is the most widely used among palynologists interested in fossil fungi (Elsik 1968, Elsik & Jansonius 1974, Elsik & Dilcher 1974, Sheffy & Dilcher 1971, Ramanujam & Rao 1978), although the -sporites suffix continued to be used as well in names for spores of vascular plants, and Clarke (1965) has proposed -sporites for fungus names.

Elsik (1976), to whom we are indebted for his persistent emphasis on the mycota in fossil remains, has ventured to propose the formal classification of fungi among fungi, i.e., a new "Form Order", Fungi Sporae Dispersae, within the "Class" Fungi Imperfecti, for fungus spores to be divided among the new "Form Families" Sporae Monocellae, Monodicellae, Dicellae, etc., with the "Form Order" Mycelia Sterilia expanded to include the new "Form Families" Cellae, Hyphae, Peltae, Indeterminae. No change is made in the morphographic features used for categories of fungus spores from those used for pollen grains, the "character of apertures and septation" distinguishing "suprageneric" categories, while "genera and species are definable on morphologic character including overall shape or symmetry, apertures, septation and ornament". To Elsik, "the phylogeny of fungal spore types is readily apparent from a study of detailed stratigraphic occurrences"; and he is undeterred from postulating that "distinctive offshoots of the Fusiformisporites line are 1) diporate, aseptate spores and 2) diporate, monoseptate spores, both possessing prominent longitudinal ribs".

Regarding the questionable basis for such character phylogenies, we need say no more than we have already said. Regarding the practice of retaining pollen features as criteria for classifying fungus spores, we feel impelled to comment further on what is undoubtedly an admirable allegiance to objectivity. It is a goal not only unattainable but also deluding unless recognized as imaginary. "Objectivity" is already transgressed by the designation of the fossil material as fungal. Once identified as a fungus, a fossil ceases to be an isolated entity. It has become a member of a known group of organisms to which it is biologically related at some taxonomic level. Its characteristics can be viewed with understanding only by the fullest use of the accumulated knowledge of 200 years of mycology. The use of palynological jargon in place of mycological jargon is not a sign of objectivity, but only of unfamiliarity with more applicable characters, terms, names and groupings. If the students of living and of fossil fungi are to meet for the advancement of mycology (of which palaeomycology is a necessary part), they must understand each other. Their common ground, the basis of
their science, is a synthesized classification of all fungi, fossil and modern; their common language, mycological terminology and nomenclature.

TERMINOLOGY

Broadly defined, terminology is the science of the proper use of terms, which are the words or phrases that are peculiar to a field of study. Our concern is mycological terminology. Unquestionably, many terms are used in mycology in the same way as in other sciences, in other fields or even lay language. But certain terms have been coined especially for our need, or defined anew in conjunction with the study of living fungi and purified by long usage in a mycological context. Where these apply, particularly in descriptions of fungi, the use of non-technical terms will, for obvious reasons, be less precise and accurate; the borrowing of terms that have evolved within a different discipline will usually result in their misapplication; and the consequence of misusing terms that have mycological meaning can only be confusion.

In palaeontological literature, mycological terms are more often ignored than misused, and, in view of the history of palaeomycology, this is not unexpected. Both of the departures from mycological terms that are referred to above (into lay and palynological terms) can be demonstrated in numerous examples.

The description of fossil fungal components in non-technical, lay language: "A thin-walled sac-like body containing rounded, smooth-walled and dark spores of varying forms. Some of them look as though they are multicellular, others appear to be unicellular". This may accurately describe what was seen, but it is obvious from the language used that the observer's eyes were unaccustomed to looking at fungi, and his mind untrained to interpreting what was seen. The description, with its broadly applicable and ambiguous terms (how many forms can a "sac-like body" take?), has neither diagnostic value nor any clue to the disposition of the purported fungus. Is there any assistance in the name the author applied to this microfossil? Not if it was a morphographic name, from which no taxonomic guidance can be expected. Or is this perhaps one of the finds to which a name is better not applied at all until a mycological interpretation can be made of the observed characters?

Dispersed fossil propagules and fragments identified as fungi but described in palynological terms: "Diporate spores of oval to fusiform ambitus; apertures apical, small and may be obscure; exine reticulate with slight tendency of muri and lumina to be parallel to the axis". OR "Spores dicellate, capsular, diporate, pores pouting, atrium present; wedge-shaped thickenings on septa". Or "Spores melanin-coloured, inaperturate, tetrads 25-35 μ in diam."

First, realizing that these descriptions have been drawn up by palynologists, an interested mycologist might be expected to look up unfamiliar or non-mycological terms in a palynological glossary. "Ambitus" would cause no problem; it has no peculiarly mycological meaning, mycologists being satisfied with "outline" or "shape", but they can accept the latinization. "Muri" may be something of a hurdle, though we can associate it with the familiar term "muricate" and arrive at an understanding of its use here to describe wall markings, while trying to avoid thinking of the use of the root in the term "muriform" (synonymous with "dicytosporous", see Chap. 5).

"Tetrad" is familiar to anyone with a botanical background. It correctly describes the group of four cells that result from meiotic division of, e.g., the pollen mother cell. It is
so familiar in that context that a mycologist might well wonder at its loose application in the description above of what appears to be a four-celled conidium of *Isthmospora* or *Spegazzinia*.

"Exine", according to Kremp (1956), is "the wall of fresh pollen grains", either simple, consisting "of structureless endexine", or complex, composed of two parts "which are strongly chemically differentiated", "structureless endexine (inner) and more or less structured ek- texine (outer)". Here is an elaborately defined term for a unique feature of a pollen grain. An analogous mycological term might be "exospore", if the spore wall is layered. But the use of either term would be incorrect in the description given, since all that is referred to is the wall-surface. And the application of so specialized a palynological term as "exine" to the wall of a spore presumed to be fungal is not only inaccurate but also grossly misleading.

We come now to the problem of terms which have a specialized and different meaning in the two disciplines. No mycologist needs to look up the term "lumen" in a glossary, until he realizes that the palynologist must be referring to lumina of a quite different kind from those in fungi if they occur alongside "muri" in the reticulation of wall markings. This use of a familiar mycological term in an unfamiliar way can be seriously confusing, though here it may be merely an irritant, one that can be overcome through patience and goodwill. Not so, however, with terms such as "capsular", "atrium", "aperture" and "pore".

In mycology, "capsule" refers to the hyaline gelatinous sheath that may surround a yeast cell. In the description of a fungus spore, it could be taken to mean a similar encapsulation, there being no other meaning possible with reference to a spore. How does one discover what the author intended?

In describing pollen grains, the use of the term "atrium" is closely tied to the concept of the "exine", an atrium being formed "if the endexine is largely dissolved in the pore region so that an endopore forms that is more than three times as large as the exopore" (Kremp 1956). Not only is the term "atrium" being used in the above quoted description in a sense different from its mycological sense (invasion court, infection court: Snell & Dick 1957), but also it is being applied to a fungus spore structure that cannot possibly be comparable to a pollen grain's atrium. So, too, with apertures and pores. The form and arrangement of these structures are highly characteristic in pollen and perhaps spores of plants, often diagnostic of major groups. In fungi, too, what palynologists call apertures, pores and atria may be characteristic and taxonomically useful. Fungus spores have germ pores and slits that may be called pores or apertures without perversion. But in many descriptions of fossil spores, there is no knowing what those terms may be referring to, for they are applied indiscriminately to germ pores and slits, to marks on conidia which are scars of attachment to a conidiophore or to other conidia in a chain, to openings that result from the disintegration of delicate end-cells or appendages, even to broken ends of propagules or hyphae.

So far, we have dealt with terms that have palynological significance and are incorrectly applied to features of fungus spores. Some of these terms also have a mycological meaning that is different, and therefore their use can be doubly deceptive, since there is always the possibility (though rare) that the term is being used appropriately. And that brings us to the snare in the use of strictly mycological terms.

Take the following description of a type specimen for the name of a new fossil Ascomycete;
"Pseudoperithecia large, measuring 100-125 μ in size. Central part of most specimens ruptured. Ascomata hardly represented by 1 or 2 club-shaped tiny structures. Stroma are characterized by non-cellular massive disc with dark brown part and translucent part". A similar case has been discussed by Korf (1977). The terms are mycological. The structures may perhaps be fungal. But undoubtedly they have been misrepresented by the mycological terms used. Behind this misuse is, probably, an unfamiliarity with all fungi, and certainly, a misconception of the terms. Claims of the discovery, in Palaeozoic and Tertiary coals, of isolated ascogenous hyphae and asci in all likelihood stem from the investigator's lack of appreciation of the specificity of these terms. And a lack of experience with living fungi can lead to the creation of new terms to describe striking phenomena that turn out to be understandable "artifacts" brought on by the processes of fossilization itself. For instance, the various kinds of "septal thickenings" which are assigned much diagnostic significance are most likely to be merely flaps of collapsed perforate septa.

This is not meant to imply that mistakes in the use of terms -- errors of all these kinds -- are never made in descriptions of extant fungi. The difference in significance lies in the fact that the neomycologist knows that he must give his attention to living fungi, no matter how poorly described or interpreted, whereas he has not yet realized that he may not ignore what is written about fossil fungi. Therefore, faced with perverted or non-mycological language in palynological literature, the neomycologist concludes that the message is not intended for him.

It is obvious that, in order to observe fossils and identify them as fungal, to interpret the observations with some comprehension, a basic knowledge of living fungi is necessary, even if the fossil forms are extinct. Then, to express intelligibly the information acquired, terms must be used that have mycological meaning -- and in their mycological sense. There is no escape from the full set of these prerequisites to the study of fossil fungi, for only familiarity with the living can cast light on the fossil, and only by unambiguous communication can the fossil elucidate the early history of the living. Misinformation becomes worse than no information at all; discussing fungus spores in terms of pollen turns both palynologist and mycologist away: neither can be reached with inapplicable language.

CLASSIFICATION

"Classification is the arrangement of entities into systems, either for convenience, or to illustrate principles of relationship" (Traverse 1961). The relative merits of phyletic and "convenient" classifications have been discussed by Schopf (1969) as by many others; but Schopf's discourse is particularly relevant to our cause, since he gives what we view as proper weight to each. What may be considered our own bias is revealed in the following ways: Classifications devised for special purposes (i.e., other than phyletic), for a convenience of one kind or another, we refer to as "artificial", though acknowledging the fairness of Schopf's comment that all classificatory systems are to some degree artificial. Furthermore, we do not use the term "taxonomy" for the classification of organs or forms or morphs or any incomplete plants, accepting Stafleu's (1967) definition of a taxon as "ultimately...an assemblage of individual plants...brought together by the systematist because he considers them to be related." We reject the last part of Stafleu's definition of a taxon, "...related in one way or
another", because we prefer here to restrict the term "relationship" to what Schopf (1969) calls "phylectic (genetic or 'blood')" kinship. Therefore, from our point of view, a taxon is ultimately an assemblage of whole organisms postulated [explicitly or implicitly] as phyletically connected (see also Schopf 1978). When a systematist brings together a group of, e.g., spores, or of individual organisms but on the basis of similarities which disregard such a relationship, that group is to us not a taxon but simply a "group", or an informal "category" or, at most, a "parataxon", "pseudo-taxon," or "form-taxon". This is the language that we have been using throughout this discussion; its nuances are of particular import to what we have to say on classification.

There are special aspects to the current taxonomy of living fungi that have been ignored by palynologists. A synoptic reminder of these aspects is therefore in order.

In the classification of the heterogeneous groups we call slime moulds and "phycomycetes", characteristics of the thallus, teleomorphic and anamorphic organs, and spores of various kinds play a variety of classificatory roles. Structures that are often ephemeral must be known to occur before many of these organisms (not all of them Fungi) can at present be placed within a class, order or family. Although spores within sporangia or attached to sporangiophores may be diagnostic of a taxon at some level of the hierarchy, many, when dispersed, are too undistinguished in morphology to be of taxonomic value. However, highly distinctive propagules do occur in some of these groups -- zygospores, oospores, resting spores, sometimes even meio- or mito-spores, that are relatively resistant. These, when among dispersed micro-fossils, can sometimes be identified (cf. Pirozynski 1976b) by being matched with the spores of a modern species or genus. Failing spores that are so directly diagnostic of lower-level taxa, only the preservation of distinctive but usually very delicate portions of thallus, etc., within plant or animal tissues or in a matrix such as amber, can lead to the disposition of fossils in higher-level taxa of "phycomycetes" and slime moulds.

The taxonomy of hymenomycetes and gasteromycetes also places primary stress on the characteristics of delicate and evanescent organs, in this case basidia. Lower levels of the taxonomic hierarchy are, in turn, characterized by morphogenetic and sometimes biochemical features of basidiomata, basidia and basidiospores. But the correlation of these characters is frequently high enough, and individual characters distinctive enough, that the presence of one or other set of features can sometimes place an isolated part of one of these fungi in a family or genus, perhaps a species. Fossilized basidiomata, even when sterile, have been identified (cf. Pirozynski 1976a) with closely related species or genera of living fungi. But basidiospores of many hymenomycetes, though instantly recognizable as such by reason of the possession of an apiculus, bear few morphological markers. They are in any case unlikely to turn up among dispersed fossil spores, since most of them are perhaps too delicate to withstand not only the rigours of fossilization but also subsequent processing in the laboratory. Still, basidiospores with resistant walls (thickened or pigmented) may be recoverable from fossil deposits, and among them will be spores that are distinctive enough to characterize some families, some genera or individual species. As for gasteromycetes, the identification of Saleroderma spores in amber (D.M. Dring pers. comm.) shows that even basidiospores unequipped with an apiculus can be recognized by a unique combination of characters. These are shape, size, colour and ornamentation of the spore, the same sort of cri-
teria that may help in distinguishing pollen grains as well as ascospores, and yet with differences in the quality of each character and its application as a criterion, differences perhaps too subtle to make their mark on current keys but nonetheless obvious to the experienced.

The importance of spore morphology rises to explicit prominence in rusts, smuts, and -- especially -- Ascomycetes and the mainly ascomycetous anamorphs that are classed in Fungi Imperfecti. Their systematic arrangement rests largely on the morphology of their propagules. It is true that, since the 1930's, the previous artificial groups in the Ascomycetes, based on spores and on environmentally influenced features of ascomata, have become more phylogenetically coherent through the introduction of genetically more stable though more transitory characters of centrum organization and spore ontogeny. But this change in emphasis has resulted in the reassessment of higher taxonomic categories; characters of spores still play a major role in the delimitation of genera and species. There is even some correlation between ascopore morphology and centrum characteristics; in bitunicates, it is seen in the inequality of cell-size in two- to many-celled ascospores, and in the likelihood that muriform (dictyosporous) ascospores belong to the Pleosporales.

Conidia are often readily distinguishable from ascospores, because the difference in ontogeny is betrayed by the presence or absence of attachment scars. And usually, both ascospores and conidia can be easily distinguished from the propagules of rusts and smuts, by those with the experience to detect what are frequently undescribed differences.

As we are discovering during this meeting, more and more correspondence is showing up between method of conidium ontogeny and present-day groupings of affiliated teleomorphic phases. The features of conidium ontogeny are very likely, therefore, to help in the refinement of systems of classification devised for Fungi Imperfecti, and to bring about reassessment of anamorphic pseudo-taxa formerly based on conidium morphology alone. Nevertheless, conidia remain the most distinctive organs within ontogenetic categories, and the ontogenetic pattern can often be deduced from the morphological features of the conidia, especially the position and appearance of attachment scars.

Thus, in Ascomycetes, rusts and smuts, the most resistant organs are their propagules, and these account for most of the fossil record of fungi generally. Fortunately, they are also the source of characters that are often the most important diagnostic criteria in current taxonomy. In this respect, the palaeomycologist is in a more fortunate position than either the palaeobotanist or -palynologist. Palaeobotanists must usually work with fossilized organs whose characteristics are accessory to those by which most taxa of modern vascular plants are discriminated -- subsidiary characters painstakingly revealed (see Sporne 1976) as correlated with primary taxonomic features. Palaeopalynologists have to work with pollen grains and spores of plants, whose features have only rarely entered into characterizing even the lowest taxa in the classificatory schemes devised for living plants (see N.F. Hughes 1976b: 20) and which, in some groups, are only now being investigated. But when the palaeomycologist is faced with dispersed spores, he can be sure that, if their living relatives are known, the spores are likely to have been illustrated along with the most recent descriptions of those fungi.

Yet, in spite of the high diagnostic value of spore morphology in the taxonomy of Asco-
mycetes, rusts and smuts, identifying a fossilized entity still usually depends on a first-hand knowledge of its modern equivalent. The uniquely distinctive conidia of *Grallomyces portoricensis* and *Hoeipira hendrickxii*, and ascospores of *Pleospora farlowiana*, have already been spotted in the fossil record (Ramanujam & Rao 1978, pers. comm.). The identification of many others is almost literally at hand. But more general success will depend on the neomycolologist's taking to heart a lesson from the palynologist and such rare neomycologists as Malençon (e.g., 1958): that morphological features of diagnostic value deserve a thorough analysis. When all who understand the ontogeny and biology of distinctive fungus spores disclose what their first-hand knowledge depends on, we shall have the means to treat spores as the characteristic representatives of fungus taxa that they are. From sophisticated analyses of spore morphology can arise what may be artificial keys to *sporae dispersae*, but they will lead to the identification of taxa in a phyletic classification. And then the palaeomycologist and the neomycolologist will be talking to, rather than at, each other.

They will both find that neither is helpless when confronted with a mass of dispersed propagules such as zygospores, etc., from "phycomycetes"; teleospores and resting spores, etc., from rusts and smuts; basidiospores, ascospores and conidia. Some of these spores will prove to be unique to living species, many of them to known genera, a few even to families (e.g., Xylariaceae, Thelephoraceae s.s., Coniophoraceae). Indeed, relatively few higher-level taxa in our current classification of fungi, e.g., families such as the Meliolaceae, Microthyriaceae, Micropeltaceae, are recognizable by the characteristics of non-sporic, easily fossilizable organs. This may be one of the reasons for the mistaken approach to fossil fungi by geological and botanical palaeopalynologists: accustomed to fossilized elements of vascular plants which are more likely to be identifiable to a family or higher taxon, many micropalaeontologists have been misled into assuming that, if fungus spores are unassignable to families, there is little likelihood of their being correlated with lower-level taxa. This is not so, as we have tried to show earlier (Pirozynski & Wereub, Chap. 8), and as L. Frederick is quoted by Elsik (1976:856-7) as saying: "...identification should be possible, in many instances, from isolated [conidia and asco-] spores. Fossilization should result in excellent preservation of ...distinctive and stable morphologic...features...Fossilized spores...should be readily identifiable to genus and in large measure to species..."

Despite this encouraging assessment by Frederick, Elsik presented a plan for the formal artificial classification of fossil fungus spores in the Fungi Imperfecti, undoubtably to provide accommodation for fungus finds while they await correlation with modern taxa. However, whereas (Schopf 1969:66) "there is ... no established classificatory tradition to fall back on among palynomorphs" of other groups, there is already a well established informal, artificial, morphographic scheme for fungus spores. Since the latter part of the last century, mycologists have been using the Saccardoan system (Table 26.1) with a good chance of identifying their fungi that way. Drs. Kendrick and Nag Raj present a detailed reexamination and clarification of the Saccardoan spore terminology in Chap. 5 of this book. Some herbaria, even now, classify undetermined Ascomycetes, etc. in Saccardoan spore- and other categories, and have found the scheme most serviceable for cataloguing and information retrieval. The advantage of the palaeontologist's using the Saccardoan system does not lie only in the fact that fossils identified as the spores of fungi will be filed in a plan familiar to mycologists
and devised especially for the classification of fungus spores. It will also mean that these fossils will have to be examined as fungus propagules, on the basis of characteristics known to be of diagnostic value among fungi, even if the classification is artificial. Undetermined fossil spores placed alongside spores of similar morphology but from living fungi will have the best possible chance of being identified or judged as belonging to an extinct taxon. Or if not, if they are so poorly preserved or so lacking in distinctive characters that the fossil entity cannot be given taxonomic standing, need it be identified further? As Lange & Smith (1971) point out, "not much is achieved by calling featureless little amerospores anything different".

Table 26.1. SACCARDO’S SPORE GROUPS*

<table>
<thead>
<tr>
<th>Spores</th>
<th>Name covering 1 and 2</th>
<th>1 Spores hyaline or bright (Hyalo-)</th>
<th>2 Spores dark (Phaeo-)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A 1-celled (and not E, F or G)</td>
<td>Amerosporae</td>
<td>Hyalosporae</td>
<td>Phaeosporae</td>
</tr>
<tr>
<td>B 2-celled</td>
<td>Didymosporae</td>
<td>Hyaloididymae</td>
<td>Phaeoididymae</td>
</tr>
<tr>
<td>C 2 or more cross septa</td>
<td>Phragmosporae</td>
<td>Hyalophragmae</td>
<td>Phaeophragmae</td>
</tr>
<tr>
<td>D Muriform</td>
<td>Dictyosporae</td>
<td>Hyalodictyae</td>
<td>Phaeodictyae</td>
</tr>
<tr>
<td>E Filiform</td>
<td>Scolecosporae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F Spirally coiled</td>
<td>Helicosporae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>G Star-like in form</td>
<td>Staurosporae</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* From Ainsworth et al. (1971)

We have already seen (Chap. 8, Plates I & II) that palaeomycologists are faced with fragments of hyphae, etc., which they feel called upon to identify. In using the Saccardoan scheme for spores, the palynologist will learn the basis for distinguishing, not only the different kinds of propagule that occur in fungi, but also the difference between an organized propagule and a casual fragment of thallus. Non-sporic propagules (such as papulaspores, bulbils, sclerotia, etc.), mycelial mats (such as those of Rhizoctonia), and bits of hyphae can all find their place in the Mycelia Sterilia. There, among recognizable equivalents from living fungi, non-sporic entities can meet their match, whereas they are alien elements among spores that are superficially similar (as in the morphographic fossil category Pluristicellaeasporites which Lange & Smith (1975), in a tactful understatement, describe as "at risk of becoming a terminological catch-all"). For many years, sterile mycelia of sooty moulds were referred in different herbaria to informal categories such as "Capnodiaceae indet.", "Capnodiaceous mycelia" or "sooty moulds". We can now sort them into taxonomic families (Hughes 1976) on the characteristics of the hyphae alone. Fossil mycelia among living mycelia, perhaps sterile fruitbodies of fossil origin among living equivalents, may eventually be sortable in the same way. And meanwhile, we will have avoided the formalizing of ter-
minological names for taxonomically heterogeneous morphographic categories.

Undoubtedly it will amuse non-mycologists that we, as mycologists, dare to criticize the morphographic classifications produced by palynologists. After all, the classification of the Fungi Imperfecti is always used as an example of an artificial classification when discussion turns to the form-genera of fossil plants (Faegri 1963, Schopf 1969, Stafleu 1967). In fact, it sometimes seems that the continuing existence of our anamorphic pseudo-taxa is used to support all kinds of artificiality in classification. The time has come to analyze the differences as well as the similarities.

Artificiality in classification can appear at various levels and in a variety of ways. There is, first, the fact that even a taxonomic classification (i.e., of whole organisms postulated as phylogenetically connected) may be based on non-homologous characters. Most of our taxonomies suffer to some degree or other from this kind of artificiality. Our hope is that every bit of additional knowledge about the organisms classified helps to eradicate a bit of that artificiality, helps to turn "poor" taxonomy into "good" taxonomy. All we can ask of a taxonomic classification is that it bear the stamp of at least implicit phyletic reasoning, whether or not we agree with the reasoning itself. If there is an attempt to group on the basis of relationship, the classification must be accepted as a taxonomic one and thereby, in our terms, not artificial. Incidentally, most phenetic studies, which shun an avowal of phyletic postulation, are nevertheless committed to the homology of the characters they compare; their classifications are thereby taxonomic in our terms (though pheneticists will undoubtedly not thank us for this judgement).

A classification that groups organisms but without regard for their relationships, openly on the basis of arbitrary or convenient characters, is artificial, the degree of its artificiality depending on the phyletic heterogeneity of the components. A common example might be a phenetic classification that is undisciplined by an appreciation of biological, phylogenetic processes (see Kendrick & Weresub 1966).

When questions of homology are not ignored, when phyletic reasoning is indeed applied, but in a special classification for only parts, or morphs or organs of whole organisms, the classification is non-taxonomic by reason of our definition of a taxon as composed of whole organisms. As Faegri (1963) says, "The 'artificiality' is not dependent on how good is our guess as to which plant we shall hang our leaf on, but upon the fact that we give a name to a detached leaf without taking into account the rest of the plant". If homologous criteria are used in the classification, the categories or parataxa may be homogeneously phyletic; but as long as their components are hands or larvae or roots or spores, rather than individual people or insects or plants or fungi, the classification is, to us, artificial. This lowest level of artificiality (or near-taxonomy) is perhaps of the kind visualized for the organ-genus of palaeobotany (see Faegri 1963, Jansonius 1974, Traverse 1975a), now discarded (compare Art. 3, Note 1 in ICBN 1972 with Traverse 1975b).

It follows from our definition of taxonomy that classifications of parts of organisms on a non-phyletic basis are most completely artificial. The fossil form-genus, as defined in the ICBN of 1952 ("maintained for classifying fossil specimens...[of detached organs]...that lack diagnostic characteristics indicative of natural affinity...[and which] may...include species belonging to different families or even groups of higher rank...") would seem to be
the appropriate example. So, too, is the form-species (see Faegri et al. in Appendix to Stafleu 1967). The most extreme condition is the terminological (Stafleu 1967) form-taxon of morphographic systems for miospores. Saccardoan categories for fungus spores provide another example of a terminological classification of this kind, but they, at least, are not necessarily embossed with official ICBN names.

Somewhat different is the form-genus when used as a category for fossils such as dinoflagellate cysts (see Evitt 1969). Brideaux (1968:181) makes a most pertinent comment, contrasting the miospore, which represents only one or some of "the sporogenous cells of a complex...plant body", with a dinoflagellate cyst which "comprise[s] the complete stage of one part of the life cycle of an acellular (unicellular) organism" (the emphasis is ours). It seems somehow less artificial to classify forms that are a complete stage of a life cycle than to create categories for nothing but, e.g., leaves, which have no existence in nature on their own, or, e.g., spores, which are merely the link between one growth phase and another in the life cycle of an organism. But as long as only parts, rather than whole organisms, are the units of a classification, it is artificial.

Stress must be laid on the fact that classifying detached portions (or organs, or stages of a life cycle) or organisms is not the same as having fragmentary types for the names of whole organisms (see Stafleu 1967, Hennebert & Weresub, Chap. 3). Most botanical types are fragmentary. All descriptions are incomplete. But taxa are assemblages of whole plants. Botanists seem to have no restriction against describing a modern taxon on the basis of leaves or even pollen alone, it being understood that the taxon comprises the whole plants of which the leaves or pollen are merely a part. Indeed, since the elimination of, e.g., Recommendation PB 6B (as of the Montreal Code of 1961), there is no hint of ICBN disapproval of the same being done with fossil finds, for the same assumption can be made, that the taxon being introduced is not confined to leaves or pollen, but is established for the whole plants of which the fragments described are merely the first parts discovered. Hence, whether a fossil entity is to be classified taxonomically (in a genus or species) or artificially (in a form-genus or -species) depends not on the type but solely on the taxonomic daring or expertise of the botanist. Only if postponement of a taxonomic decision is preferred, while a "binomial label" (Traverse 1961) seems convenient, is fossil material to be described formally as a form-taxon encompassing only the detached organs or parts at hand. A neobotanist, on the other hand, is denied this escape into an artificial category.

Now we come to the artificiality of classifying the anamorphic phases of fungi as Fungi Imperfecti. Here we deal with a fungus in what is generally an independent phase of its growth, in a self-replicating cycle that may or may not be part of a holomorph with a more complex lifecycle. Many of the groups in the Fungi Imperfecti were established as taxa for anamorphs when they were thought to be autonomous fungi. Under ordinary circumstances in taxonomy, the discovery of affiliated forms or an additional growth phase, judged to be genetically linked with the phase first discovered, requires simply an emended circumscription of a taxon. So it is for all zoological, botanical and mycological groups except pleomorphic Ascomycetes and Basidiomycetes. It is only the mycologist working with the last two groups named who may not exercise his taxonomic daring and expertise by describing a holomorphic taxon from whatever material he has at hand. If all that he has is its anamorphic phase, it
must be described in an artificial category. Indeed, even if the anamorph is, as far as is known, completely autonomous -- the "whole plant" in fact -- it is still denied official holomorphic status, no matter how ready the mycologist may be to postulate its relationship among holomorphs.

The classification of anamorphs of Ascomycetes and Basidiomycetes is, by definition, artificial, on the basis of its restriction to only a particular kind of reproductive phase, whether or not it is known to be part of the long life-cycle of a pleomorphic holomorph. But the creation of the Fungi Imperfecti as a unit is largely a historical accident (see Weresub & Pirozynski Chap. 2). And the maintenance of this pseudo-class now stems increasingly from a nomenclatural imposition. Although the anamorph-genus is considered a form-genus and, like the fossil form-genus, has often been "known to contain species which are unrelated according to the ordinary systems of taxonomy" (see Faegri 1963), it is currently more likely to approach the phyletic soundness of the now-defunct organ-genus of palaeobotany, or, in fact, any holomorphic genus. In many cases, the continuing use of the artificial classification for a newly discovered anamorph is more a nomenclatural formality than the expression of a need for a "provisional and taxonomically non-committal designation" (Faegri 1963).

This has been an attempt to demonstrate the several differences in kind of artificiality that exist between the classification of Fungi Imperfecti and classifications for fossils. And it may be that our experience with the relatively limited artificiality of anamorph-genera gives us the right to warn against the delusion of convenience that lies in the extremely artificial systems devised for fossil pollen and spores. There is little preparatory value for taxonomy in a failure to understand what is being classified: in the case of morphographic systems, the failure to appreciate that the objects under study are biological entities; in both anamorphic and morphographic systems, the failure to avoid fixity of categories and their names until there is at least a modicum of comprehension of the relationship with other biological entities.

It is our contention that, with a fossil record for fungi largely composed of the single most diagnostic organ that fungi produce, palaeomycologists can best serve mycology by classifying recognizable fungus spores among the modern fungi that produce similar spores. As we have seen, those with a taxonomic background (from the early nineteenth century to the present day, e.g., Dilcher, Singer) have tended to give graphic evidence of their conclusions regarding the affinity of fossil to living forms by the nomenclature they use, particularly by use of the name of a modern genus, with or without an -ites suffix. "By so doing", wrote Wolf (1969), "it is implied that the given fossil is closely related morphologically to a given contemporary genus". Inasmuch as most of our taxonomy is based on the hypothesis that phyletic relationship is reflected in the morphology of fungi, we can accept "implied... closely related morphologically" to mean "postulated as phyletically connected".

That this is what is postulated by these authors is clear from comments such as the statement of Felix (1894): "Unter dem Namen Chaetosphaerites fasse ich diejenigen fossilen Pyrenomyceten-Reste zusammen, welche mit der lebendem Gattung Chaetosphaeria so Übereinstimmen dass sie möglicherweise zu ihr gerechnet werden können", and the footnote in Meschinelli (1892) quoted by Holm (1959), which can be loosely translated as follows: "In the case of all these names by which the genera of fungi are designated, I thought it appropriate that the ending -ites be added for the purpose of distinguishing from those that are living and
with which they can be linked for very basic reasons, yet cannot be equated absolutely".
In discussing the status of the names in Meschinelli, Holm argues soundly that, e.g., "Agaricites L. (Agaricus) sensu latissimo" (as Meschinelli cited it) could be interpreted as "an extension of Agaricus L., including also those fossil fungi which resemble Agaricus". This, to our mind is the best way to make the fossil record intelligible to mycologists.

Of course, Doyle's (1976) warning against "uncritical matching" is justified, as is his concern (Doyle 1977) that the identification of fossil with living is an approach which is incapable of recognizing extinct groups intermediate between major groups of extant forms. Nevertheless, he must realize that this recognition will be possible only after the attention of those who know living fungi has been focused on fossil fungi. But, asks N.F Hughes (1976b), "how can the details of descent of a living plant taxon from some Cretaceous fossils be determined, when the latter have already been identified with the former?" How? By an understanding of the meaning of a taxonomic (in contradistinction to a morphographic) identification. The observation that a fossil spore has the characteristics of Staphlosporonites places the spore permanently in a morphographic slot with, usually, unrelated spores -- a grouping impossible to work with in evolutionary terms. The identification of a fossil spore as Pleosporites (if regarded as "Pleospora sensu fossile") is a hypothesis of relationship with Pleospora, and is treated by mycologists as no more binding than any other hypothesis. But it is, at least, an invitation to look into the background of Pleospora. And in the hands of a monographer, information about the scattering of Pleospora-like spores in the fossil record can begin to elucidate the picture of the history of the Pleosporales. "Extrapolation backwards" is more rewarding than the construction of phylogenies "upwards" without a proper understanding of the significance of various morphological expressions. Probably a sound taxonomist can make sense of either technique. But it is more logical to start with a living potential descendant than with an arbitrary, hypothetical ancestor.

The procedure open to those working with fossil fungi can take various forms. A teleomorph, whether fertile or sterile, is legal basis (whether or not taxonomically satisfying) for description of a taxon of holomorphic Ascomycetes or Basidiomycetes. Any portion of a teleomorph therefore, such as an ascospore, whether living or fossil, should fulfil the minimum legal requirement for description of a taxon of holomorphic fungi, as long as the author is prepared to make the taxonomic commitment of taking the ascospore to represent the holomorph that is the ultimate unit of the taxon, modern or extinct. Should he be unwilling or unable to make a taxonomic commitment, he need only refer the ascospores to their place in the informal Saccardoan system.

An ascomycetous or basidiomycetous anamorph, complete or partial, fertile or sterile, is legal basis for description of an anamorph-taxon, but (by nomenclatural edict) not for a holomorphic taxon, however ready the mycologist may be to make the necessary taxonomic commitment. It follows that any portion of an anamorph, such as a conidium, whether living or fossil, fulfils the legal prerequisite for description of an anamorph-taxon, but again a taxonomic forecast must be made -- the author's acceptance of the conidium as representative of the entire anamorphic phase, whether fossil or living, modern or extinct. Lacking sufficient information to go that far, the mycologist must exercise his discretion to decide whether to use Saccardoan spore categories available to him for the informal filing of his find, or ignore
it completely.

And finally, if the fossil spores are such that they can be presumed to belong to an extinct fungus, but do not provide enough evidence for any assurance of the likely structure of the whole fungus, the palaeobotanist's artificial device of form-taxa is available. Thus a category is created for these spores and their like, with a binary name covering only spores. If they are distinctive enough to be recognizable when found again, there will be at least stratigraphic value in the grouping, and perhaps eventually, in the light of an understanding of other fossilized fungi, some evolutionary value as well.

To summarize: whatever the needs of the palaeobotanist or palynologist may be for such special categories as fossil form-taxa, whether in morphological or morphographic special classifications, "half-natural" or mechanical, the palaeomycologist's need for this device is relatively minimal until he enters pre-Tertiary geological periods. Having taken the leap into the mycological world by deciding that the material under study is fungal, a mycologist has the informal Saccardian system (with modifications that can be introduced -- see Chap. 5) for describing and classifying "during early phases of ... exploration when announcement of formal taxonomic results probably would be premature" (Schopf 1969). A formal taxonomic statement can follow only after a number of decisions have been made, on whether the find is distinctive enough to be judged extant or extinct and placed in a taxon, known or new, holomorphic, anamorphic or form. Unless such taxonomic judgments are made, there seems to be no value in formal designation of the fossil find, its position in the Saccardian system providing as useful a non-taxonomic repository as is possible.

NOMENCLATURE

We have repeatedly stressed that, if a fossil is identifiable with a taxon of living organisms, at any level whatsoever in the hierarchy of their taxonomy, it can no longer be treated in isolation, as though it had no biological history in common with them. Yet, many palaeontologists treat their finds in such isolation and are under the impression that support for this approach to the classification of fossils is supplied by the special rules in the ICBN for the nomenclature of fossils. By making allowances for the sometimes special needs of palaeontologists, needs not recognized by the Zoological Code (see Evitt 1969:459), the ICBN is seen to be fostering the isolation of fossils, as if becoming fossilized has united them biologically into a group separate from their acknowledged relatives: plants, photosynthetic protists, monerans and fungi.

Recognizing that nomenclatural rules neither support nor repudiate classificatory systems or philosophies of any kind, let us examine the ICBN's special provisions for fossils. We present them here, as revised at the Leningrad Congress (see Traverse 1975a,b), with our comments.

Art. 3, Note 1. Since the names of species, and consequently of many higher taxa, of fossil plants are based on fragmentary specimens, and since the connection between these specimens can only rarely be proved, form-genera are distinguished as taxa within which species may be recognized and given names according to the Code. A form-genus may be unassignable to a family, but may be referable to a taxon of higher rank (see Art. 59). Examples...
Comment: First, we must point out again that the names of species in all groups are usually based on fragmentary specimens (see Stafleu 1967), and that "proof" of connections is possible only under ideal conditions even with living material, though undoubtedly the identification of a fossil with a living species is more chancy than that of a living plant with a "herbarium... sub-fossil" (Stafleu 1967).

Secondly, it is of particular interest to mycologists that the term "form-genus" applies in the ICBN to fossils alone, in spite of its long-time mycological meaning. Indeed, it was first proposed for use in the International Code by Atkinson et al. (1909) to refer, of course, to what we are now calling the anamorph-genus. But the term "form-genus" did not enter the Code then, in either its mycological or palaeobotanical sense. It turned up again in 1935 at the Amsterdam Congress, but this time among proposals for the nomenclature of fossils, by Jongmans et al. (in Sprague 1935). And "form-genus" made its first official appearance in the Stockholm Code (1952), among the special provisions for fossil plants in Appendix IV. There has been some activity in behalf of reclaiming "form-taxon" (for form-genus, form-species etc.) as a mycological term and using it in Art. 59. But in view of what appear to us to be significant differences between the fossil form-taxon and the current fungus form-taxon, and because of the official recognition accorded by the ICBN to the palaeobotanical rather than mycological meaning of the term, we propose that mycologists relinquish their historical hold on "form-genus" and substitute "anamorph-genus" as a more precise and unambiguous term. In this way, if a mycologist finds a need to give formal nomenclatural recognition to a fossil fragment that he judges to represent an extinct fungus, he can use the palaeobotanical form-taxon as an artificial category, without fear that it will be confused with an anamorph-taxon, whose name is much more rigidly controlled by Art. 59.

Finally, let us be reminded that, because the ICBN provides a mechanism for formally naming fossilized fragments of plants and fungi as separate form-taxa if necessary, the provision is not to be taken as an invitation to use this mechanism casually, any more than the concession in Art. 59 for the naming of anamorph-taxa is to be taken as a recommendation to give several names to a single fungus.

Art. 7, par. 14. The type of the name of a taxon of fossil plants of the rank of species or below is the specimen whose figure accompanies or is cited in the valid publication of the name (see Art. 38). If figures of more than one specimen were given or cited when the name was validly published, one of those specimens must be chosen as type.

Note 2. The typification of names of genera based on plant megafossils and plant microfossils (form- and organ-genera), genera of imperfect fungi, and any other analogous genera or lower taxa does not differ from that indicated above.

Comment: these two paragraphs merely emphasize that the typification of the names of fossils (and of "imperfect fungi") follows the same rules as that of names for living plants as well as fungi that are not "imperfect", except for the tie-in with Art. 38, which requires the illustration of a fossil (see also comment on Art. 9). The presence of this emphasis is due to the removal (after the Montreal Congress) of the Appendix on fossil nomenclature into eventual integration in the body of the Code. The reason for the insertion of the reference to "imperfect fungi" must have been due to someone's remembering that they, too, were in cat-
egories somewhat similar to fossil form-taxa.

Art. 9, Note 1. If it is impossible to preserve a specimen as the type of a name of a species or infraspecific taxon of recent plants, or if such a name is without a type specimen, the type may be a description or figure.

Note 2. One whole specimen used in establishing a taxon of fossil plants is to be considered the nomenclatural type. If this specimen is cut into pieces (sections of fossil wood, pieces of coalball plants, etc.), all parts originally used in establishing the diagnosis ought to be clearly marked.

Comment: The point here is that, although Art. 34 requires an illustration for validation of the name of a fossil species, palaeontologists do not accept that illustration as type specimen for its name; whereas the name of a modern species, which can be validly published without an illustration, may nevertheless be typified by means of a figure or description.

It is not clear from Note 2 whether the "one whole specimen" cut into sections is to be considered a holotype with isotypes, or all sections holotypic. The same problem, of course, arises with the fleshy or woody fruitbody of a fungus -- another instance of the fact that the problems of palaeobotany are not unique to the field.

Art 13. (Valid publication of names for plants of the different groups is treated as beginning at the following dates...)

Fossil plants

j. All groups, 31 Dec. 1820 (Sternberg, Flora der Vorwelt...)

Comment: Here, fossils are certainly treated as though they are not be integrated with related modern plants and fungi. But what does Sternberg's work mean to the palaeomycologist? Meschinelli (1902) refers to only two names of Sternberg's, Carpolithes umbonatus, which Meschinelli places in synonymy with Polyporites bowmani Lindl. & Hutton (see Pirozynski 1976a) and Agaricites intertextus, which is transferred to Rhizomorphites. Since Meschinelli treated Agaricites as a Linnean name, and Polyporites a Friesian name, Sternberg's names were of no particular significance to him. And indeed, Sternberg's entire work holds no more interest for palaeomycology than his names. Therefore, since there already seem to be more than enough that is keeping neomycologist and palaeomycologist apart, the integration of starting points may be considered the very least we can do to bring together all the students of fungi, fossil and modern.

It may be pointed out that some fossil remains that are almost certainly fungal may not show characters sufficient to indicate whether they are lichen or slime mould (1 May 1753), rust, smut or gasteromycete (31 Dec. 1801), or belong to one or other of the remaining groups of fungi (1 Jan. 1821). The obvious answer is that such fungi may be better left in an informal Saccardoan grouping until their relationships are clarified. Or, if they are distinctive enough, but unassignable to these groups, they are unlikely to have previously published names (unless morphographic ones), and so may be named with little worry about valid prior synonyms.

Art. 13, Note 2. Whether a name applies to a taxon of fossil plants or of recent plants is decided by reference to the specimen that serves directly or indirectly as its nomenclatural type. The name of a species or infraspecific taxon is treated as pertaining to a recent taxon unless its type specimen is fossil in origin. Fossil material is distinguished from recent material by stratigraphic relations at the site of original occurrence. In
cases of doubtful stratigraphic relations, regulations for recent taxa shall apply.

Comment: This reinforcement of the type method shows how Art. 13 Note 1 ("The group to which a name is assigned for the purposes of this Article is determined by the accepted taxonomic position of the type of the name") applies to names for fossil material. The guidance regarding "cases of doubtful stratigraphic relations" is particularly helpful in view of the possibility, pointed out to us by Prof. Schopf, that more ancient fossil plant material can be invaded by later fungi.

Art. 36. In order to be validly published, a name of a new taxon of plants, ... algae and all fossils excepted, published on or after 1 Jan. 1935 must be accompanied by a Latin description or diagnosis of the taxon...[and] of recent algae published on or after 1 Jan. 1958...

Comment: Whether or not valid publication of the name of a fossil that falls under jurisdiction of the ICBN should be contingent on the use of Latin, as are all other names regulated by the Code, has been a continuing controversy: "palaeobotanists have on more than one occasion managed to avoid being forced to write their diagnoses in Latin simply because other botanists do" (N.F. Hughes 1976b:24). The most persuasive argument in behalf of Latin was put forth by Fosberg at the Montreal Congress (see Bureau of Nomenclature 1960:97), when he pointed out that "the matter of Latin diagnoses is a matter of international courtesy, not of palaeobotany". We agree wholeheartedly.

Our concern is with the fungi as an integrated group comprising fossil and modern forms. Therefore, it is only logical that the validation of their names be under as many of the same rules as possible, most certainly including the requirement for a Latin description or diagnosis. What will it mean to palaeomycological nomenclature to re-insert fossil fungi among extant fungi for compulsory Latin validation of their names?

Considering that most of the fossils published as fungi were treated before 1935 (when Latin became mandatory), we are in the unusually fortunate position of not having many post-1935 names that would need to be validated by the publication of a few words of Latin. Considering that most of these relatively few post-1935 names are of the terminological kind that are better rejected in favour of informal Saccardoan terms, we are fortunate to have the Latin requirement as a means of denying these names any formal validity. We are aware that the work of Cookson, Dilcher, Selkirk, and a handful of others, is worth saving. They took the trouble to describe and identify fossil fungi correctly; they omitted a Latin diagnosis only because it was not demanded of them. But because of the meagre amount of mycological work that has been done with fossil fungi ("comparatively little attention has been paid to them" -- Tschudy 1969), the names proposed in these scrupulous studies are unlikely to be in jeopardy and can be validated without difficulty. Meanwhile, an opportunity will be provided from a reassessment of the taxonomic conclusions of these authors, a review of other forms that were published under invalid names, a sorting out of fragments of little or no diagnostic value and therefore unlikely to be recognized even if found again, and a proper redescription (in mycological terms) and redisposition (among other fungi) of adequately diagnosable and identifiable material. All this can be achieved before chaos descends on palaeomycology (see also Kremp 1959) in the form of hundreds of useless but indestructible morphographic names. It is a simple device that can save us: requiring a Latin description for fossil fungi as for modern fungi,
retroactive to the same date, 1 Jan. 1935.

Art. 38. In order to be validly published, a name of a new taxon of fossil plants of specific or lower rank published on or after 1 Jan. 1912 must be accompanied by an illustration or figure showing the essential characters, in addition to the description or diagnosis, or by a reference to a previously and effectively published illustration or figure.

Comment: Oh! that mycologists had had the wisdom to join palaeontologists in this requirement as far back as 1912, or at least to join the algologists, who (in Art. 39) require illustrations as of 1 Jan. 1958. But Subcommittee C of the Nomenclatural Secretariat of the International Mycological Association submitted their report to the meetings at Tampa, in September 1977, with rejection of the proposal that illustrations be required to validate the names of modern fungi. In this instance, we are fortunate that palaeomycology has been a part of palaeobotany instead of neomycology. And we recommend that, as far as this article is concerned, no distinction be made between fossil fungi and other fossils, though we are left with no requirement for the illustration of modern fungi.

Art 42. Comment: The sentence referring specifically to a palaeobotanical ruling on the publication of a monotypic new genus was deleted at Leningrad (see Traverse 1975a).

Art. 58. When a taxon of recent plants, algae excepted, and a taxon of the same rank of fossil or subfossil plants are united, the correct name or epithet of the recent taxon takes precedence.

Comment: This ruling came into effect in the Stockholm Code (1952). There are probably very few names that need this kind of protection. The consequences of the Article are twofold. First, and unfortunate, is the fact that neomycologists are reinforced in their disregard of palaeomycological literature, having no need at least to assure themselves that no earlier name exists for a fossil fungus, which might be applicable to a living fungus. Second, and providentially, this ruling retains the taxonomic synonym that is likely to have the more useful type specimen, a "herbarium sub-fossil" from a living fungus. The value of the second consequence (Just et al. 1949:3) outweighs the disadvantage of the first — though arguably.

Art. 59. As in the case of pleomorphic fungi, the provisions of the Code shall not be construed as preventing the use of names of form-genera in works referring to such taxa.

Comment: As we have already noted, the form-genera of fossils and the anamorph-genus of pleomorphic Ascomycetes and Basidiomycetes are not of the same nature. This addition to Art. 59 does not actually violate this understanding, for apparently it intends only to legalize the continued use of the names of form-genera for parts of fossil plants even when these parts have been postulated as affiliated with whole plants in botanical taxa, whether fossil or extant. This is the same permission afforded in the body of Art. 59 to the use of the names of anamorph-taxa ("of imperfect states").

Rec. 75A. Generic names ending in -ites to be considered masculine, no matter what gender was ascribed to them by the original author (passed at Leningrad, see Traverse 1975a).

So much for the International Code of Botanical Nomenclature and its special rules for the names of fossil plants. In our attempt to bring the neomycologist and palaeomycologist closer together, we have suggested a couple of relatively simple changes in these rules. One other controversial matter remains for discussion: the application of the names of extant taxa to fossil material. Some palaeobotanists stress the pitfalls of identifying fossils with
living organisms, and would prefer that the names of modern taxa never be applied to fossils, or at least never to those older than the Tertiary period. Others insist that, since an identification is a hypothesis of relationship, a taxonomist should be free to use the normal nomenclatural means to express his hypothesis that a fossil is conspecific or congeneric with a modern taxon. We here propose a compromise between these opposing camps, the one most often used in palaeomycological literature for signifying this relationship but without merging fossil with living: the addition of the -ites suffix to the name of a modern genus, best interpreted as a broadening of the circumscription of the modern genus to include fossil members.

As we have already mentioned, Holm (1959) gave good reasons for so interpreting the use of the -ites names by authors such as Meschinelli. But Holm then rejected his own logic, and denounced these names as nomina nuda, having been published without a generic diagnosis. He pointed out that if, for example, "Sphaerites Haller (Sphaeria sens large)" (as Fritel 1910 had it) is "an extension" of Sphaeria Hall "including also those fossil fungi which resemble" Sphaeria (whatever that may be) -- as the Code stands, Sphaerites would be illegitimate as a later synonym of Sphaeria "based on the same type". And of course, Holm is right.

Therefore, we recommend a change in the Code. Since it is not impossible that any genus of modern fungi may have close relatives turn up in a fossilized condition, all genera should be hospitably prepared to accommodate fossil members by a system of autonyms. The fossil autonym of a modern genus is the name of the genus with an -ites suffix. Typification of a fossil autonym is, like that of a subgeneric or other autonym, automatically identical with that of the root name. The decision that a fossil spore is likely to be a Pleospora spore does not require creation of a new genus, only a recognition of its place either in a modern or fossil species, under the automatically available name Pleosporites. The use of -ites endings for the names of genera of living fungi will have to be prohibited. The few that already exist create a minor problem. As we see it, they will, at least eventually, have to be replaced if they are homonyms of the fossil autonyms for other living genera. For example, if Cordiera A. Rich. ex DC. had been a fungus name, Cordierites Mont. would fall when fossil members of Cordiera were discovered. As matters stand, unless the rule is extended to the generic names of plants, Cordierites is in no jeopardy, and Cordieritesites (tongue-twister though it is) can serve as its fossil autonym. Macowanites Kalchbr. is in a similar position, being a replacement for Macowania Kalchbr., non Oliver (of the Compositae). Muellerites Holm (with autonym Muelleritesites) is also safe, there being, as far as we know, no Muelleria in the literature. But certainly, closure should be imposed on the further publication of -ites-suffixed names for genera of extant fungi. On the rare occasion when such a name for a genus of plants coincides with a fossil autonym for a genus of fungi, the name of the latter will have to be suffixed with -ites or some other appropriate version of the ending. We shall certainly avoid disturbing the nomenclature of plants, unless palaeobotanists choose to associate themselves with this proposal.

**CONSEQUENCES OF SUGGESTED APPROACH**

A. Examples:

1. Identification of a fossil with modern species: a) A spore matching in all respects a distinctive spore identified as the ascospore of Pleospora farlowiana Rehm (Farr & Horner 1968) (Fig. 26.8) was found in Miocene clays of western India (C.G.K. Ramanujam pers. comm.)
(Fig. 26.9). Because the ascospore is fossilized, it is identified as *Pleosporites farlowianus* Rehm, in accordance with the postulation that the fossil ascospore belongs in the same species with the type specimen of the name of *Pleospora farlowiana*. Should the identification prove to be a misdetermination, an appropriate redispersion of the fossil ascospore can be made without any nomenclatural side effects.

b) A fossil conidium resembling in all aspects of its morphology the unique conidium of *Grallomyces portoricensis* F.L. Stev. (Fig. 26.4) was identified in the fossil record (Fig. 26.5), but described as Allopeysporonites scabatus Ramanujam & Rao (1978). This name may be useful for a specially programmed data-retrieval system, but it is taxonomically, ecologically, phylogenetically and probably even stratigraphically useless, because Allopeysporonites is "defined" with a fixed morphology that is likely to be either too narrow to accommodate the normal variability of fossil spore morphology, or broad enough to encompass the architecture of a number of unrelated spores. In any case, with validation requiring a Latin diagnosis or description, *A. scabatus*, although published as a "gen. et sp. nov." is outlawed as *nom. nudum*. The fossil conidium needs no new name; it is simply identified as the anamorph-species bearing the name of *Grallomyces portoricensis* F.L. Stev.

c) A distinctive conidium of *Hiospira hendrickxii* (Hansf.) R.T. Moore (Fig. 26.6), which is known to be the anamorphic expression of *Brooksea tropicalis* Hansf., has been identified in the fossil state as the *Hiospira* state of *Brooksea tropicalis*, but described as Rethelicosporonites elskii Ramanujam & Rao (1978) (Fig. 26.7). The name *Hiospirites hendrickxii* (Hansf.) R.T. Moore applies only to the anamorphic fossil, but it can be taken to represent *Brooksea* as the *Hiospirites hendrickxii* anamorph of *Brooksea tropicalis*. It seems a biologically logical assumption to make, more plausible than to imagine that so distinctive an anamorph could have been linked with a different teleomorph in an earlier phase of its evolution.

d) A foliicolous Ascomycete bearing both teleomorphic and anamorphic organs was found fossilized and described as a fossil taxon, *Shortensia memorabilis* Dilcher (1965) n. gen., n. sp. It was subsequently recognized as a member of recent genera: first as *Manginula* and transferred to this genus as *M. memorabilis* (Dilcher) R.T. Lange (1969), then as *Vizella*, *V. memorabilis* (Dilcher) Selkirk (1972). Pirozynski (1976a) tentatively considered it conspecific with *V. oleariae* Swart. If this opinion is sustained, the fossil can be identified as *Vissellites oleariae* Swart, using the holomorphic name for the fungus in both sexual and asexual expression.

2. Disposition of a fossil as a new taxon in a recent genus. An ascospore resembling that of fungi classified in the modern *Chaetosphaeria*, but not recognizable as representing a known species, was described as a new species *Chaetosphaerites bilyahnis* Felix (1894), on the basis of two fossil ascospores, which are thereby its type (Fig. 26.2). There is undoubtedly some difficulty in accepting an isolated ascospore as type for a holomorphic name. Yet, a spore is frequently sufficiently distinctive to be identified as teleomorphic, and often diagnostic of a species. If the Code does not disallow the acceptance of an immature ascoma, devoid of asci, as legitimate representative of a teleomorph, it cannot deny acceptance to an ascospore. After all, in practice, few teleomorphs can be identified unless mature ascospores are present.

If the forthcoming revision of Art. 59 (to be proposed by a Subcommittee of the I.M.A.
Fig. 26.1 *Passeriniella dichroa*: ascospores, from Berlese (1894).

Fig. 26.2 *Chaetosphaerites bilychnis*: spores, from Felix (1894).

Fig. 26.3 *Chaetosphaerella phaeostroma*: ascospore, from Berlese (1894).

Fig. 26.4 *Grallomyces portoricensis*: conidium, from Deighton & Pirozynski (1966).

Fig. 26.5 Alleppeysporonites scabratus: spore, from Ramanujam & Rao (1978).

Fig. 26.6 *Hiospora hendrickxii*: conidium, modified from Deighton & Pirozynski (1966).

Fig. 26.7 Retihelicosporonites elskii: spore, from Ramanujam & Rao (1978).

Fig. 26.8 *Pleospora farlowiana*: ascospores, from Farr & Horner (1968).

Fig. 26.9 Unnamed fossil fungus: spores, from Ramanujam (pers. comm.).

Fig. 26.10 *Pesavis tagluensis*: spore, from Elsik & Jansonius (1974).

Figs. 26.11 - 19 Unnamed fossil fungi. 11,13,19, Mycelia sterilia: 11, fructification; 13 & 19, chlamydospore-like aggregations of cells; 12, 14-18, spores representative of Saccardoan categories; 12, Phragmosporae; 14, Scolecosporae; 15, Helicosporae; 16, Didymosporae; 17, Dictyosporae; 18, Amerosporae. (11, 16 & 17 from Ramanujam, pers. comm.; 12 from Ramanujam & Rao 1978 as "Cannanorosporonites raoi gen. et sp. nov."; 14 from Lange 1971).
Nomenclatural Secretariat) adopts the terms proposed by Hennebert & Weresub (1977 and Chap. 3), the requirement that the type specimen of a holomorphic name give evidence of sexuality (in the Current Code: "the perfect state ... characterized by the presence of the asci ... basidia ..." etc.) will be expressed as teleomorphic evidence. In other words, the type will have to be what can, in the judgment of the author, serve to characterize the teleomorphic phase of the fungus (i.e., "an ascocarp [ascoma] or its equivalent, at maturity producing asci and ascospores; ... a basidiocarp [basidioma] ... etc.").

This is not intended to open the door to the novel practice of describing new taxa of modern fungi from a single spore. Such practice will remain "bad" taxonomy, as it is today. But the ICBN is not meant to protect taxonomists against themselves or the carelessness of their colleagues: only the integrity of a scientist can do so. In describing a new species of living fungi, more is expected of the type specimen than simply an ascospore, however characteristic it may be. In spora dispersa, there are only spores to be seen.

Let us consider our example further. An ascospore has been judged distinctive enough to characterize a new fossil species of the modern genus Chaetosphaeria, and described as Chaetosphaerites bilychnis. What can happen to it?

a) A later author judges the spore to be better disposed in a genus segregated from Chaetosphaeria, the modern genus Passeriniella. A normal transfer results in Passeriniellites bilychnis (Felix) comb. nov. imag*, the type, of course, remaining the same, the fossil ascospore.

b) Chaetosphaerites bilychnis Felix (1894) is judged to be conspecific with Chaetosphaerella phaeostroma (Dur. & Mont. 1846) Müller & Booth (1972) (Fig. 26.3); and Ch. bilychnis becomes a facultative synonym of Chaetosphaerellites phaeostroma (Dur. & Mont.) Müller & Booth, the type of which is the modern material typifying the name of the species in its living expression, Chaetosphaerella phaeostroma.

c) Ch. bilychnis Felix (1894) is judged conspecific with Passeriniella diohroa (Pass.) Berl. (1894, arbitrarily taken to be later) (Fig. 26.1). If -- as is more likely -- fossil fungi are retained under the force of Art. 58, priority being given to the names of modern fungi even if published later, Chaetosphaerites bilychnis Felix will become a facultative synonym of Passeriniellites diohroa (Pass.) Berl. (typified by modern material, but with the suffixed form of the generic name applicable to fossil members).

d) Previously undescribed living material is discovered and judged to be the same as Chaetosphaerites bilychnis Felix. What follows again depends on whether or not fossil fungi are excepted from Art. 58. If not, the living material is described on the basis of a living type that provides the full complement of the teleomorphic phase, and is given a new binomial -- Chaetosphaeria felixiana sp. nov. imag.; and Chaetosphaerites bilychnis becomes a facultative synonym of Chaetosphaerites felixianus.

3. Fossil material not identifiable with modern species or genus.

a) Pesavis tagluensis Elsik & Jansonius (1974) (Fig. 26.10) is a highly distinctive propagule, apparently a conidium, of a fungus unknown in present-day mycota, and therefore judged to be extinct. If unassignable to modern fungi, it is best presented as a form-species in a

* as in Erdtman (1947), imag. (imaginatum) is added to all combinations introduced in this paper to indicate that they are not being made seriously, are not here accepted by us, and are thereby (Art. 34) invalid.
form-genus for spores alone, in line with the palaeobotanical use of form-taxa.

b) If it had been diagnostic of, for example, the kind of anamorphs that are produced in a family of rusts, it could have been presented as a fossil anamorph-genus.

4. The disposition of fossil entities potentially identifiable with modern fungi but not assignable (at the present state of mycological knowledge) to any but the highest taxonomic levels; and the temporary cataloguing of spores not immediately identifiable as modern or extinct; or preserved too poorly or in insufficient numbers to permit identification: Saccardo's spore groups and Mycelia Sterilia, the latter expanded, perhaps, to include sterile fruit-bodies, etc. (somewhat as proposed by Elsik 1976), provide informal categories for storing and retrieving such data as are shown in Figs. 26.11-26.19.

5. The establishment of autonymic status for the ites-suffixed names of modern genera will have consequences of the following kind: *Asterothyrites* Cookson (1947:209) and *Meliolinitea* Selkirk (1974:70) were proposed for the fossil forms of *Asterina* and *Meliola* respectively, but are unavailable for that purpose, being pre-occupied as autonyms for *Asterothyrium* and *Meliolina*; the fossil forms of *Asterina* and *Meliola* automatically bear the generic names *Asterinites* and *Meliolites*. *Triahopeltinitea* will not need to be validated by the publication of a Latin description because, when introduced by Cookson, it already existed as an autonym for fossil members of *Triahopeltina*. However, from Cookson's reference to the possible identity of *Triahopeltinites* pulaher Cookson with *Triahopeltis reptans* Speg., the fossil may be better placed in *Triahopeltisites* or *Triahothyrites*.

These, then, are our suggestions for procedures to be adopted by students of fossil fungi (not to be confused with the authoritative list of suggestions for students of plant micro-fossils, adopted by Faegri et al. in 1950; see Appendix to Stafleu 1967).

1) All modern genera, on publication, to be automatically prepared for fossil members, the generic name modified by means of an -ites suffix and treated as an autonym. The autonym requires no separate validation, being typified by the type species of the root name.

All modern species, on publication, to be similarly prepared, the epithet requiring no change (except perhaps in gender), the generic name indicating the autonomic fossil member by its -ites modification.

2) The starting-point date for the names of fossil fungi to coincide with the starting-point dates for the names of modern fungi.

3) Validation of the names of fossil fungi to be re-incorporated in Art. 36, which rules on the names of modern fungi, requiring the publication of a description or diagnosis in Latin, as of 1 Jan. 1935.

4) If a fossil shows characters diagnostic of one species of the modern mycota, identification to be made with the modern species, under the modified name of the modern genus, as in 1) above.

5) If a fossil shows characters diagnostic of a modern genus, but not of any known species therein, the fossil to be described as a new species in the modern genus (its name modified as in 1) above); if the fossil is teleomorphic (or both teleomorphic and anamorphic), in a holomorphic genus; if anamorphic alone, in an anamorph-genus.

6) If a fossil shows characters diagnostic of a modern family, but inadequate for distinguishing among its genera, a new species to be described in the type genus, its name modified as in 1) above.

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7) If a fossil is not immediately recognizable as referable to a modern species, genus or family, or not distinctive enough to be judged extinct without further study, formal taxonomic naming is not recommended, the fossil to be given informal designation within a Saccardoan group.

8) If the fossil represents only part of a phase of a fungus (e.g., spores), and is distinctive enough to be judged extinct but not referable to a modern genus or family, it is to be published as a fossil form-species restricted to, e.g., spores alone, in a fossil form-genus for spores. It is recommended that indication be given of the lowest-level taxon (among higher categories) to which the form-genus can be referred.

9) If the fossil comprises enough of (a) a teleomorphic phase, and is distinctive enough to be judged extinct but not referable to a modern genus or family, it is to be published as a fossil holomorphic species in a fossil holomorphic genus; or (b) an anamorphic phase and is distinctive enough to be judged extinct but not referable to a modern anamorph-genus or -family, it is to be published as a fossil anamorph-species in a fossil anamorph-genus.

10) Names for new genera of living or fossil fungi are to be formed as for other botanical groups (Art. 20) except that (a) the -ites suffix is to be reserved for the fossil autonyms of the names of living genera; and (b) a construction of the name such that it can be confused with the names of informal morphographic categories is to be abjured. These suggestions we present for the consideration of mycologists, both neo- and palaeo-, in the hope that a full discussion among us can bring about consensus on ways in which we can avoid the obvious dissatisfaction and chaos that prevails in other botanical studies that try to make taxonomic and evolutionary sense out of inadequately integrated information about living and fossil forms.

ACKNOWLEDGMENTS

We are indebted to several colleagues, especially Professor James M. Schopf (Ohio State University) and Dr. J. McNeill (Biosystematics Research Institute, Agriculture Canada), for their thoughtful reviews of the pre-final form of this paper. They exerted every effort to reform us, and are not to be blamed for any errors or heterodox ideas that have remained for publication.

DIALOGUE FOLLOWING DR. PIROZYNKI & WERESUB'S PAPER

MÜLLER: I have been looking at fossil fungi from the Tertiary for some time. I can find Meliola. There is no question that it is Meliola. We find the same kind of ascospores, some germinating and beginning to form hyphopodia. We find portions of mycelia with the two kinds of hyphopodia. In such cases I don't see the need even for Meliolites. These fossils are exactly what we see today. They match some of the illustrations in Hansford (1961) down to the last detail. Of course, we don't know the host, but this doesn't matter too much. We also have forms that fit perfectly into Sporidesmium, and ascomata which fit Asterina or Microthyrium, but lack ascospores. Here is a difficulty. We can tell the
group from the morphology of the ascoma, but we can't tell the genus, because these genera are based on ascospores.

PIROZYSKI: In the Tertiary, we have an essentially modern mycota that is very extensive and diversified.

WATLING: The difficulties Emil raises are no more severe than those faced by people working with flowering plants. In the Tertiary you can often give a generic name simply from a truly recognizable leaf, but when you move back toward the Triassic and Jurassic, differences are sufficient to force the use of an '-ites' suffix. Tertiary Araucaria fossils are easily referable to that name, but Jurassic fossils have slight differences and so the name Araucarites is adopted. This seems inevitable.

KENDRICK: This problem is all tied up with difficult questions such as: What is the life-span of a taxon? and: What constitutes extinction?

PIROZYSKI: The reason I would prefer not to use the modern generic name, even for those beautiful Meliola fossils, is that we can never be entirely sure. Even an apparently perfect match indicates only morphological congruence, which is all we can claim for it. The '-ites' suffix is a sign warning us to proceed with caution by being aware of the fossil's often fragmentary state, of modifications induced by the process of fossilization, and of only circumstantial evidence at best providing clues to its former habit and habitat.

Some palaeobotanists and palaeopalynologists shun identification of fossils with their living counterparts, claiming that the present state of palaeobotany, to them less than satisfactory, is the hangover from prematurely postulated correlations. Others insist that the logical way of dealing with fossil members of extant taxa is by incorporating them into botanical classification and nomenclature. Our sympathies clearly lie in the latter camp, but to go all the way with them would be to enter the existing impasse. Palaeomycology is not yet weighted down with accumulated penalties of amendments. We can make a fresh start and we favour the compromise of the '-ites' names.

MÜLLER: The genus Muellerites has already been established -- but for a living fungus.

PIROZYSKI: I suppose that makes you a 'living fossil'.

MALLOCH: Would you comment on Palaeosolerotium.

PIROZYSKI: This is a strange fossil. The name Palaeosolerotium pusillum gen. & sp. nov. was given by Rothwell (1972) to sclerotium-like bodies found in Carboniferous wood about 300 million years old. Dennis reexamined the specimen and, after consulting Prof. Singer, published a claim (Dennis 1976) that P. pusillum was a teleomorphic fungus bearing asci which contain ascospores. Further, he noted that the hyphae forming walls of the fructifications have "dolipore-like septa", and those emerging to form vegetative mycelium bear clamp-connections. He therefore concluded that the fossil represents an extinct group of fungi intermediate between Ascomycetes and Basidiomycetes. Notwithstanding scepticism expressed by McLaughlin (1976), Singer (1977) reiterated Dennis's conclusions and suggested a possible affinity of Palaeosolerotium to both cleistothecial Ascomycetes and gasterocarpic Basidiomycetes.

I have not seen the fossil material, but from the descriptions, and especially from Dennis's published photographs (1976), it seems clear to me that the purported asci are simply cavities in the stroma, and the 'ascospores' look suspiciously like tetraspores,
complete with trilete markings. I do not think that *Palaeosclerotium* is an Ascomycete, but the question remains: What are tetrasporangia doing inside a mass of fungal cells connected to clamped hyphae? Tetrasporangial conceptacles occur in some fleshy thallophytes from the early Palaeozoic (Niklas & Phillips 1976). Some of these contain fungal elements, sometimes as septate hyphae (Pratt et al. 1978) or filaments with thickened septal pore margins (Schmid 1976). I agree with Dennis and Singer that *Palaeosclerotium* provides a glimpse of an early dikaryomycete. Not an Asco-Basidiomycete, in my opinion, but a representative of a group linking Basidiomycota with extinct, possibly symbiotic, lichen-like thallophytes.

In the preceding chapter, the authors have made an invaluable interdisciplinary contribution, which must be taken seriously by neo- and palaeo-mycologist alike. Their proposals, if and when accepted and incorporated into the ICBN, must surely lead to more reasoned exchanges between those dealing with the past and the present of fungi. The nomenclatural insights presented by the authors lead fairly naturally into an over-all review of the naming of what they so appropriately dub 'anamorph-taza'.

Early in Kananaskis-II, a 'non-Committee' of three was set up to examine the nomenclatural matters raised by Dr. Carmichael in Chapter 4. The members of this non-committee, true to their avowed intentions, did not meet as a committee. Instead, they conjugated in pairs, in all possible combinations. Each pair exchanged information, apparently without the knowledge of the third. It seems that in nomenclature, three's a crowd. Despite this, and to everyone's surprise, they managed to agree on certain things, although as you will read in the next chapter, some important areas of disagreement remain.

Ultimately it was left to Dr. Weresub to write the report which follows. In my judgment, it is a breathtaking tour de force, for which not only her fellow committee members, but all concerned with the ICBN, must be in her debt. Surely she has explored every angle, every quirk that could arise from any possible expression or interpretation of the rules. She has given those of us who are not so well versed in nomenclature a unique opportunity to follow, step by step, the intricacies implicit in apparently simple, straightforward statements. Every potential booby-trap has been skilfully detected, unearthed and its workings exposed for our edification.

Do not abandon hope, all ye who enter the next chapter: it may be a harbinger of change, and of a more rational approach to the nomenclature of pleomorphic Ascomycetes, Basidiomycetes, and truly anamorphic fungi.....
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On the Question of Naming Pleomorphic Anamorphic Fungi

L.K. Weresub for the Nomenclatural Committee of Kananaskis - II

I OUR LANGUAGE

Life cycle terms: To avoid the variety of subjective connotations now borne by terms such as "imperfect" and "state" with reference to pleomorphic fungi, we join the other members of this conference in adopting the terms introduced by Hennebert & Weresub (Chapter 3), as follows: for an asexual form or morph of a fungus, anamorph; for the sexual form or morph, teleomorph; and for the whole fungus, in all its morphs and phases, holomorph. Most pleomorphic fungi include a teleomorph along with one or more anamorphs in their complete, holomorphic life cycle. But, for all we know, some holomorphs may be composed of only one or several anamorphs and lack a teleomorph altogether.

Nomenclatural terms: By the authority of Art. 59 of the ICBN (International Code of Botanical Nomenclature 1972), a name that is typified by a teleomorph becomes a nomen holomorphosia, applicable to a whole pleomorphic Ascomycete or Basidiomycete, whereas, "in the case of imperfect states" of presumed Ascomycetes and Basidiomycetes, a nomen anamorphosis "refers only to the state represented by its type". For the purpose of this discussion, in which we consider the possibility that a fungus may have irrevocably dropped the teleomorph from its life-cycle, we shall use the term ana-holomorph for a wholly anamorphic fungus that is postulated to be totally autonomous, its name a nomen ana-holomorphosis.

Traditionally, the units covered by nomina anamorphosia have been referred to by mycologists as form-genera and form-species, in spite of the fact that the ICBN ignores the mycological use of these terms and uses "form-genus" only with reference to fossils. As Pirozynski & Weresub (Chap. 26) have pointed out, there are sufficient differences between the mycological and palaeontological uses of form-taxa for a distinction in terminology to be necessary. They propose that mycologists renounce their claim to these terms in favour of "anamorph-genus" and "anamorph-species". We accept this change for the purpose of this discussion.

Lay terms: Some words with broad general meaning are to be used herein with restricted definition. "Related", as we use it here, refers only to organisms of postulated, presumed or accepted kinship -- genetic, phyletic, evolutionary. "Formal" is applied to nomenclatural systems that are under the jurisdiction of the ICBN, all other systems being treated here as "informal".
II OUR PROBLEM AND POSSIBLE SOLUTIONS

This committee has been convened to attempt to arrive at a solution to the problem enunciated and analyzed by Hennebert (1971): that Art. 59 provides no guidance or rule for the choice of a name that covers the whole pleomorphy of a fungus known only in an anamorphic condition. Nor does Art. 59 distinguish between a monomorphic and a pleomorphic "imperfect state". Carmichael's (Chap. 4) proposed solution has revived our concern and prompted this analysis.

In the discussion that follows on the various ways in which the matter can be treated, the present system will be referred to as Scheme (1). Hennebert (1971) presented us with three other possible procedures, as follows: scheme (2), the strictly anatomical, whereby paramount emphasis is laid on the fact that the system for anamorph-taxa was designed for the convenience of those who find it necessary to use binary names for disjunct anamorphs, and that any attempt to adapt this purely artificial approach by giving formal recognition to a postulated anamorphic holomorphy distorts the original purpose; scheme (3), the fully botanical, treating pleo-anamorphic fungi as we do teleomorphic holomorphs (but separately, so as not to intrude on the priority of teleomorphically typified names), whereby primary emphasis is placed on the need to give formal expression to postulating a relationship among anamorphs, over the need that led to the creation of the conventional artificial system for anamorphs; and scheme (4), the botanico-anatomical, a compromise between the other two outlined here, whereby the anamorph-genus is restricted to an anatomical monomorphy, whilst the pleo-anamorphic species is treated botanically as an ana-holomorph (but only up to the point where an affiliated teleomorph is discovered, when the priority of the teleomorphically typified botanical name takes precedence). Finally, we have scheme (5), Carmichael's (Chap. 4) refinement of this botanico-anatomical system, whereby the cross-reference trinomial, which is an informal part of schemes 1, 2 and 4, becomes the dominating formal nomenclatural device to express the postulated ana-holomorphy of a pleo-anamorphic species.

III APPLICATION OF SCHEMES TO PARTICULAR CASES

In undertaking the consideration of this matter, let us first emphasize that, when a taxonomist deals with an anamorphic fungus as a Fungus Imperfectus, it is presumed to be an anamorph of either ascomycetous or basidiomycetous affinity, since the conventional anatomical system for anamorphs involves no other organisms. At least to that extent, the anamorphic fungi under discussion here are botanically disposed. Beyond that, anamorph-genera may be as phyletically sound as uredo or as heterogeneous as Selerotium. An anamorph-species may group monomorphic elements universally accepted as the morph of a known teleomorphic holomorph (such as the Spilocaea pomi anamorph of Venturia inaequalis); it may comprise all elements of an apparently autonomous, monomorphic or pleo-anamorphic fungus (such as Tricho-sporonoides oedoeaphalis Haskins & Spencer), or be an aggregate of still inadequately distinguishable anamorphs with several different teleomorphic or anamorphic affiliations (such as the Botrytis cinerea complex).

Our examination of the various approaches to the nomenclature of these anamorphs will take the form of illustrating how they work in the following cases:

CASE A. Cronartium ribicola J.C. Fischer ex Rabh. (1872) is a teleomorph-typified name covering a holomorphic fungus that is postulated to include a Peridermium anamorph. This morph
was separately described under the separately typified name, *P. strobi* Kleb. (1887).

CASE B. *Strigopodia batistae* Hughes (1968) is a teleomorph-typified name for a holomorphic fungus described originally as including *Hormisiella* phragmoconidia and *Capnophialophora* pialides. *Helminthosporium pseudotenuis* W.B. Cke (1952) had been previously (Hughes 1958) considered synonymous with *Hyphosoma resinacea* (M.C. Cke) Hughes, the phragmoconidial morph of *S. resiniae* (Sacc. & Bres.) Hughes, but was later (Hughes 1968) identified with the *Hormisiella* morph of *S. batistae*.

CASE C. *Lasioseaoria elinorae* and *Helioseporium elinorae* were published simultaneously by Linder (1929), with the postulation that *H. elinorae* is an anamorphic phase of *L. elinorae*. According to Pirozynski (1972), the purported affiliation is mistaken.

CASE D. The yeast described under the name of *Histoplasma capsulatum* Darling (see Carmichael 1962), when grown outside of infected tissue, produces a conidial anamorph considered to be either a *Chrysosporium* or a *Sepeidium*. For the purpose of this discussion, we shall ignore the fact that the teleomorph of this fungus is now known.

CASE E. The acervular fungus, *Ceroosporella antirrhini* Wakef. (1918), was transferred to *Pseudodiscosia* as *P. antirrhini* (Wakef.) Budd & Wakef. (1929), at the same time as its pycnidial morph was described as a separate anamorph-species under the name of *Heteropatella antirrhini* Budd. & Wakef.

CASE F. A di-anamorphic fungus was first named *Verticillium chlamydocephorum* Goddard (1913), its type bearing both phialidic and chlamydosporic morphs. What is considered to be the same fungus is later described under the name *Stemphyliopsis ovorum* Petch (1939), its type also bearing both morphs, and then under *Diheterospora heterospora* Kamyschko (1962), in a new anamorph-genus that was explicitly dimorphic. The original circumscription of *Diheterospora* included another new species, *D. catenulata* Kamyschko.

Each of these cases will now be treated as dictated by each of the schemes outlined in section II above.

CASE A

CASE A, SCHEME 1. *Cronartium ribicola* may refer only to the teleomorph on which it is based, but, under Art. 59, it also covers the holomorphic fungus, including any and all anamorphic phases known or as yet unforeseen. When *Peridermium strobi* was postulated to be a morph of *C. ribicola*, the use of the holomorphic name came to be understood as covering this anamorph as well as the teleomorph, although *P. strobi* is explicitly permitted to continue in use for exclusive reference to the anamorph.

Informally (i.e., without ICBN jurisdiction), a cross-reference trinomial, the *Peridermium* morph (or state, or form, or phase) of *C. ribicola*, is frequently substituted for the binary name of the anamorph-species. And sometimes, if exclusive reference to the teleomorph is desired, it is referred to as the *Cronartium* phase of *C. ribicola*. It is obvious that the binomial, *C. ribicola*, and the cross-reference name for its teleomorph, the *Cronartium* phase of *C. ribicola*, are obligate synonyms, sharing a type; but the status of *C. ribicola* anam. *Peridermium* is different.

Although the separately described and typified *P. strobi* may be universally accepted as the *Peridermium* morph of *C. ribicola*, the type specimen of the name *P. strobi* is no more than facultatively assigned to *C. ribicola* anam. *Peridermium*. It is not impossible
that P. strobi may some day be shown to be affiliated with another teleomorph, but that
realization leaves the name C. ribicola anam. Peridermium untouched. Its application to
a particular specimen may always be in doubt, but its accuracy, as referable to the
Peridermium anamorph that is actually affiliated with the teleomorph of C. ribicola, is
inviolable.

The Code gives formal recognition to C. ribicola as holomorphic and P. strobi as ana-
morphic; it neither recognizes nor repudiates the use of cross-reference names.

CASE A, SCHEMES 2, 3, and 4. The approaches discussed by Hennebert refer only to pleo-
anamorphic fungi, and therefore have no direct bearing on this case. But if scheme 3
(the botanical system) were adopted, the monomorphic application of many generic names
would be lost, making the use of the informal trinomial frequently too ambiguous for the
kind of purpose that it currently serves.

CASE A, SCHEME 5. Carmichael's approach, if formalized in Art. 59, would directly affect
cases of this kind. The acceptance of the purported affiliation would make C. ribicola
anam. Peridermium the only fully legitimate way to refer to P. strobi.

CASE A: Summary of Nomenclators

1. Formal: Cronartium ribicola
   incl. anam. Peridermium strobi (legit. for separate ref. to anam.).
   Informal: C. ribicola
   ≡ C. ribicola teleo. Cronartium
   plus C. ribicola anam. Peridermium
   = P. strobi.


3. Formal: Cronartium ribicola (with no separate designation of the anamorph).
   No formal system.


5. Formal: C. ribicola
   ≡ C. ribicola teleo. Cronartium
   plus C. ribicola anam. Peridermium
   = P. strobi.
   No informal system.

CASE B

CASE B, SCHEME 1. In accordance with the ICBN, which tolerates but does not require binary
names for anamorphs affiliated with a teleomorphic phase, Hughes did not transfer the
epithet of Helminthosporium pseudotsugae W.B. Cke. to Hormisciella when he stated that
the Hormisciella phragmoconidia of Strigopodia batistae had previously been described
under W.B. Cooke's binomial. In effect, he adopted the informal trinomial to designate
the phragmoconidal and phialidic anamorphs of S. batistae. And he changed Helmintho-
sporium pseudotsugae to a facultative synonymy with S. batistae anam. Hormisciella, from
facultative synonymy with both Helminthosporium resinaceum (q.e. = S. resinæ anam.
Hormisoiella), and Coccodinium laricis W.B. Cke. & C.G. Shaw anam. Helminthosporium.

As far as Art. 59 is concerned, Hughes could have assigned binary names to both anamorphic species of S. batistae, by transferring pseudotsugae to Hormisoiella and describing a new anamorphic species of Capnophialophora; but he chose not to do so.

CASE B, SCHEME 2. In the purely anatomical system, emphasis is on the monomorphic typification and application of names for anamorph-species. Therefore, assigning non-synonymous binomials to individual though affiliated anamorphs might become more customary even if not compulsory. Hughes's treatment, however, would still be formally acceptable.

CASE B, SCHEME 3. The botanical system of naming pleomorphic anamorphs would interfere with the kind of informal nomenclature used by Hughes, in that monomorphic anamorph-genera such as Hormisoiella and Capnophialophora might disappear into synonymy with botanically characterized pleo-anamorphic genera. And a fully botanical system might be less tolerant (than our current permissive legislation) of a separate nomenclatural designation for the individual morphs of a holomorph, even if only by means of the cross-reference name.

CASE B, SCHEME 4. Under Hennebert's botanico-anatomical system, stress would be laid on the possibility of encountering the Hormisoiella and Capnophialophora morphs separately from the teleomorph. The tendency would be to make the new combination in Hormisoiella from Helminthosporium pseudotsugae, monomorphically typified by the phragmoconidia but covering the dimorphic anamorphic phase that includes both phragmoconidia and phialides. Then the two anamorphs, when independent of the teleomorph, could be referred, informally, to Hormisoiella pseudotsugae anam. Hormisoiella and anam. Capnophialophora. And these trinomials would be in facultative synonymy with Strigopodia batistae anam. Hormisoiella and anam. Capnophialophora.

CASE B, SCHEME 5. Under Carmichael's botanico-anatomical system, Hughes's procedure would be the only legitimate way to name a holomorph fungus while simultaneously postulating that a teleomorph and two anamorphs are affiliated.

CASE B: Summary of Nomenclators

1. Formal: Strigopodia batistae
   incl. anam. Hormisoiella pseudotsugae comb. nov. imag.*
   (Legit. for separate ref. to anam.).
   plus anam. Capnophialophora anam. sp.

   Informal: S. batistae
   ≡ S. batistae teleo. Strigopodia
   plus S. batistae anam. Hormisoiella
   = Helminthosporium pseudotsugae.
   and S. batistae anam. Capnophialophora.

2. Formal and Informal as in Bl.

*imag. - imaginatum: comb. nov. not to be taken as accepted by the authors of this report.
3. Formal: *S. batistae*.
   No informal system.

4. Formal: *S. batistae*
   incl. anam. phase, *Hormisciella pseudotsugae* (Legit. for separate
   ref. to anam.).

   \[ \equiv \text{Helminthosporium pseudotsugae} \]
   and anam. Capnophialophora

Informal: *S. batistae*

   \[ \equiv S. batistae \text{ teleo. Strigopodia} \]
   plus *S. batistae* anam. *Hormisciella*

   \[ = H. pseudotsugae \text{ anam. } *Hormisciella* \]
   \[ \equiv \text{Helminthosporium pseudotsugae} \]
   and *S. batistae* anam. Capnophialophora

   \[ = H. pseudotsugae \text{ anam. } \text{Capnophialophora}. \]

5. Formal: *S. batistae*

   \[ \equiv S. batistae \text{ teleo. Strigopodia} \]
   plus *S. batistae* anam. *Hormisciella*

   \[ = \text{Helminthosporium pseudotsugae} \]
   and *S. batistae* anam. Capnophialophora.

CASE C

CASE C, SCHEME 1. Art. 59, as it stands today, explicitly authorizes Linder's publication
of a binomial for *Helicosporium elinorae* at the same time as he postulated its affiliation
with *Lasiosphaeria elinorae*, in effect placing the name of this newly proposed ana-
morph-species in facultative synonymy with the informal cross-reference name, *L. elinorae*
anam. *Helicosporium*. When Pirozynski (1972) denied the affiliation, he was able to
transfer *H. elinorae* into facultative synonymy with *H. pannosum*, which he judged to be
the *Helicosporium* morph of *Tubeufia helicoma*.

CASE C, SCHEMES 2, 3, and 4. As noted under Case A, Hennebert's systems would influence this
case only if the botanical scheme (3) was adopted, with the possible unavailability of a
monomorphic value for the anamorph-genus *Helicosporium*.

CASE C, SCHEME 5. Publication of the binomial, *Helicosporium elinorae*, along with a postu-
lation of the anamorph's affiliation with the teleomorph of *Lasiosphaeria elinorae* would
be considered invalid under Art. 34 (because interpretable as the simultaneous proposal
of alternative names) or illegitimate under Art. 63 (because superfluous). The anamorph
described by Linder would not typify the trinomial to which it was referred; it would
simply constitute the description of anamorphic material identified as the *Helicosporium*
morph of *L. elinorae*. Then, Pirozynski's removal of the anamorph from *L. elinorae* would
not be made explicit in any nomenclatural way; it would simply record Pirozynski's opinion
that Linder's determination of a specimen was incorrect, with Pirozynski's redetermination
of that specimen as *Tubeufia helicoma* anam. *Helicosporium*.
CASE C: Summary of Nomenclators

1. Linder: Formal: Lasiosphaeria elinorae incl. anam. Helicosporium elinorae (Legit. for separate ref. to anam.).
   Informal: L. elinorae
   \[\equiv L. elinorae \text{ teleo. Lasiosphaeria} \]
   plus L. elinorae anam. Helicosporium
   \[= H. elinorae.\]

   Pirozynski: Formal: L. elinorae (without ref. to anamorph).
   Tubeufia helicoma incl. anam. Helicosporium pannosum (Legit. for separate ref. to anam.).
   \[= H. elinorae.\]
   Informal: L. elinorae
   \[\equiv L. elinorae \text{ teleo. Lasiosphaeria.}\]
   T. helicoma
   \[\equiv T. helicoma \text{ teleo. Tubeufia} \]
   plus T. helicoma anam. Helicosporium
   \[= H. pannosum\]
   \[= H. elinorae.\]

2. Formal and Informal as in Cl.
   T. helicoma.
   No informal system.
4. Formal and Informal as in Cl.
5. Linder: Formal: L. elinorae
   \[\equiv L. elinorae \text{ teleo. Lasiosphaeria} \]
   plus L. elinorae anam. Helicosporium.
   Pirozynski: Formal: L. elinorae
   \[\equiv L. elinorae \text{ teleo. Lasiosphaeria.}\]
   T. helicoma
   \[\equiv T. helicoma \text{ teleo. Tubeufia} \]
   plus T. helicoma anam. Helicosporium
   \[= H. pannosum\]
   (= L. elinorae anam. Helicosporium sensu Linder non verit.).

CASE D, SCHEME 1. According to the present Art. 59, the Chrysosporium anamorph of Histoplasma capsulatum could legitimately have received a binomial of its own, separate from the binary name typified by the yeast phase. In the absence of a second binomial for
the second anamorph of this di-anamorphic fungus, although the formally approved application of the name, *H. capsulatum*, extends no further than the yeast phase of the fungus, it is informally understood to cover the fungus in both phases, each being referred to by the appropriate cross-reference trinomial, the *Histoplasma* and *Chrysosporium* anamorphs of *H. capsulatum*. These cross-reference names have no standing under the ICBN, but neither does the Code rule them illegitimate.

CASE D, SCHEME 2. With a restrictedly monomorphic anatomical system, the application of *H. capsulatum* to more than the yeast phase of the di-anamorphic fungus would be in obvious violation of the rules. But again, unless ruled explicitly illegitimate, cross-reference trinomials could continue to give informal expression to an assertion that the yeast and the conidial morph comprise one fungus.

CASE D, SCHEME 3. A fully botanical system for anamorphic fungi would accept *H. capsulatum* as the name for the ana-holomorphic fungus, without separate designation of the individual anamorphs that comprise the fungus. And if the fungus is considered botanically congeneric with the type species of *Chrysosporium*, the epithet *capsulatum* would be transferred from *Histoplasma* (1906) to *Chrysosporium* (1833).

CASE D, SCHEME 4. The botanico-anatomical system of Hennebert would also accept *H. capsulatum* as applicable to the di-anamorphic fungus, and with the epithet transferable to *Chrysosporium*, if the conidial anamorph is judged to be the more diagnostic morph. Here, the cross-reference trinomial, although still informal, would be more logically applicable.

CASE D, SCHEME 5. Carmichael's botanico-anatomical system would designate *H. capsulatum* as uniquely applicable to the di-anamorphic fungus, its epithet not transferable to *Chrysosporium* (although it could be transferred to another anamorph-genus whose name is typified by a yeast-phase). No other binomial would be legitimate either for the di-anamorphic fungus or for the *Chrysosporium* morph. Separate reference to the latter would be legitimately made only by the cross-reference trinomial, *H. capsulatum* anam. *Chrysosporium*, or the *Chrysosporium* morph of *H. capsulatum*.

CASE D: Summary of Nomenclators

1. Formal: *Histoplasma capsulatum*
   Informal: *H. capsulatum*
   
   = *H. capsulatum* anam. *Histoplasma*
   plus *H. capsulatum* anam. *Chrysosporium*

2. Formal: *Histoplasma capsulatum*
   and *Chrysosporium* sp.
   Informal: *H. capsulatum*
   
   = *H. capsulatum* anam. *Histoplasma*
   plus *H. capsulatum* anam. *Chrysosporium*

3. Formal: *C. capsulatum* (Darl.) comb. nov. imag.
   No informal system.

4. Formal: *H. capsulatum* Darl. OR *C. capsulatum* (Darl.) comb. nov. imag.
   Informal: as in D1; OR
C. capsulatum
≡ C. capsulatum anam. Histoplasma
≡ H. capsulatum
plus C. capsulatum anam. Chrysosporium
5. Formal: H. capsulatum
≡ H. capsulatum anam. Histoplasma
plus H. capsulatum anam. Chrysosporium

CASE E

CASE E, SCHEMES 1 & 2. The Buddin & Wakefield approach is strictly in accordance with both the Code as it stands and a restrictedly monomorphic nomenclature for anamorphs. Ceroosporella antirrhini Wakef. and Pseudodiscosia antirrhini (Wakef.) Budd & Wakef. apply to the acervular morph, and Heteropatella antirrhini Budd & Wakef. to the pycnidial morph. And in both systems, although not formally acceptable, cross-reference trinomials (P. antirrhini anam. Pseudodiscosia and anam. Heteropatella; or H. antirrhini anam. Heteropatella and anam. Pseudodiscosia or Ceroosporella) could continue in informal use.

CASE E, SCHEME 3. The botanical system would accept Ceroosporella antirrhini Wakef. as covering not only the acervular fungus first described under that name but also any and all anamorphs to be discovered and postulated as affiliated. The discovery of a pycnidial morph classifiable in Heteropatella would call for the transfer of the epithet antirrhini Wakef. from Ceroosporella (1880) to Heteropatella (1869). The publication of H. antirrhini Budd. & Wakef. as a new species would be illegitimate under the circumstances outlined.

CASE E, SCHEME 4. Hennebert's botanico-anatomical system would also deny legitimacy to the publication of Heteropatella antirrhini Budd. & Wakef. sp. nov. under the conditions given. However, the authors would have the choice of transferring the epithet from Ceroosporella antirrhini Wakef. to Heteropatella if they considered the newly discovered pycnidial morph more satisfactorily diagnostic. And, whether transfer was made to Pseudodiscosia or to Heteropatella, cross-reference names would serve appropriately to give informal nomenclatural expression to the affiliation of the two morphs.

CASE E, SCHEME 5. The difference between scheme 4 and Carmichael's botanico-anatomical system here is the restriction in transferability of the epithet first published for the anamorphic fungus, the transfer from the acervulus-typified C. antirrhini being permitted to the acervulus-typified Pseudodiscosia but not to the pycnidium-typified Heteropatella. Under the conditions stated, the only legitimate binomials for the fungus as a whole are C. antirrhini and P. antirrhini, and the only legitimate way to refer to the Heteropatella while indicating that there is an affiliation of the two morphs in the one fungus is by means of the cross-reference trinomial.

CASE E: Summary of Nomenclators
1 & 2 Formal: Pseudodiscosia antirrhini (Wakef.) Budd. & Wakef.
≡ Ceroosporella antirrhini Wakef.
and Heteropatella antirrhini Budd. & Wakef.
Informal: \( P. \text{antirrhini}, \) sensu ana-holomorphic sp.
\[ \equiv P. \text{antirrhini anam. Pseudodiscosia} \]
plus \( P. \text{antirrhini anam. Heteropatella} \)
\[ = H. \text{antirrhini B. \\& W.} \]

3. Formal: \( H. \text{antirrhini} \) (Wakef.) comb. nov. imag. (Note: \( H. \text{antirrhini} \)
B. \\& W. disallowed.)
\[ \equiv C. \text{antirrhini} \]
No informal system.

4. Formal: \( P. \text{antirrhini} \)
\[ \equiv C. \text{antirrhini} \]
OR
\( H. \text{antirrhini} \) (Wakef.) (Note: \( H. \text{antirrhini} \) B. \\& W. disallowed)
\[ \equiv C. \text{antirrhini} \]

Informal: \( P. \text{antirrhini} \)
\[ \equiv P. \text{antirrhini anam. Pseudodiscosia} \]
plus \( P. \text{antirrhini anam. Heteropatella} \)
OR
\( H. \text{antirrhini} \) (Wakef.)
\[ \equiv H. \text{antirrhini anam. Cercosporella} \]
plus \( H. \text{antirrhini anam. Heteropatella} \)

5. Formal: \( P. \text{antirrhini} \) (Note: \( H. \text{antirrhini} \) B. \\& W. disallowed)
\[ \equiv C. \text{antirrhini} \]
\[ \equiv P. \text{antirrhini anam. Pseudodiscosia} \]
plus \( P. \text{antirrhini anam. Heteropatella} \).

CASE F

CASE F, SCHEME 1. As Art. 59 stands at present, no distinction is made between a monomorphic
and a pleomorphic "imperfect state" (anamorphic phase). Two interpretations of this case
are therefore possible.

(a) Since both morphs are present in the material designated as type, and \textit{Verticilliium}
\textit{ahlamydosporium} was originally described as comprising both morphs, the Code apparently
allows this binary name to be di-anamorphically typified and applied. The same holds for
\textit{Stemphyliopsis ovorum} and \textit{Diheterospora heterospora}. The three names are therefore fully
synonymous, \textit{ahlamydosporium} the prior epithet, and the choice of generic name for the
binary combination applicable to the ana-holomorph depends on the taxonomist's decision on
the advantage of stressing the \textit{Verticilliium} phialides, the \textit{Stemphyliopsis} chlamydosporas
or the \textit{Diheterospora} dimorphy.

(b) Art. 59 has also been interpreted (perhaps arguably) as placing a monomorphic
restriction on the typification of the name of anamorph-species that are disposed in mono-
morphic anamorph-genera. Therefore, the following approach may be as legitimate as that
in (a) above: The name \textit{Verticilliium} being typified by a phialidic anamorph-species, the
disposition of \textit{V. chlamydosporium} in \textit{Verticilliium} is taken as indication that the name of
the anamorph-species, if monomorphically typified, should be considered based on the phialidic part of its type material (although it might well be argued that the epithet chosen indicates typification by the chlamydosporic morph instead). The name *Stemphyliopsis* being typified by a chlamydosporic anamorph-species, the disposition of *S. ovorum* is taken as indication that its name, if restricted to monomorphic typification, is to be considered based on the chlamydosporic part of its type material. With such a narrowing of typification, Art. 59 rules that application of the name is also narrowed, *V. chlamydosporiun* restricted to the phialidic anamorph, *S. ovorum* to the chlamydosporic anamorph, their names thereby non-synonymous, being differently typified and applied to exclusively circumscribed anamorph-taxon. And since *Diheterospora* was published as dimorphic, *D. heterospora* also stands as potentially correct and independently non-synonymous, a name for the di-anamorphic species, encompassing but not equivalent to the other two mono-anamorph-species.

In addition, nothing in the current Code totally outlaws the use of additional names for this one fungus. Informal cross-reference names are available (the *Verticillium* state, or morph, or anam. of *V. chlamydosporiun* for the phialidic morph, and the *Stemphyliopsis* morph of *V. chlamydosporiun* for the chlamydosporic morph, OR, if preferred, *S. ovorum* anam. *Verticillium* and *S. ovorum* anam. *Stemphyliopsis*) to make explicit the affiliation of the two anamorphs. The dimorphically typified third name is therefore unnecessary, but not thereby illegitimate or even formally synonymous. And in fact, *D. heterospora* anam. *Verticillium* and anam. *Stemphyliopsis* can also be used to replace the previously published binomials without causing any confusion or incurring any legal penalty.

**CASE F, SCHEME 2.** In the fully anatomical monomorphic system, as in 1(b) directly above, the transfer of *chlamydosporiun* is possible only to another anamorph-genus whose name is typified by a phialidic morph; it is not transferable to *Stemphyliopsis* or to *Diheterospora*. This scheme differs from 1(b) above by what happens to *Diheterospora*. Neither *Diheterospora* nor the name of its type species is allowed to remain dimorphically typified and applied. They must both be lectotypified by one of the two anamorphs. And since, in the original description of *Diheterospora*, there was a second species, *D. catenulata*, with the same kind of chlamydosporic morph as in the type species but with a phialidic morph not referable to *Verticillium*, it seems reasonable to lectotypify the generic name by the chlamydosporic morph. *D. heterospora*, then, lectotypified by this morph, becomes a facultative synonym of *S. ovorum*. And, unless the type chlamydosporic morph of *Stemphyliopsis* is judged to be generically distinct from that of *Diheterospora*, the generic names also become facultative synonyms. Thus, *V. chlamydosporiun* is the correct name for the phialidic morph of the di-anamorphic fungus, but correct only for that morph. *S. ovorum* is correct for the chlamydosporic morph (with *D. heterospora* in synonymy) as long as this morph is considered a *Stemphyliopsis*; or, if judged distinguishable from *Stemphyliopsis* chlamydospores, this anamorph is transferred to *Diheterospora* as *S. ovorum*. None of these names is formally applicable to the ana-holomorphic fungus. But informal use of cross-reference names bears an implicit broader application of the binomials.

**CASE F, SCHEME 3.** This case fits naturally into a botanical system, because the two morphs of this fungus are consistently associated. *Verticillium chlamydosporiun* is the first
published name for the ana-holomorph, with *S. ovorum* and *D. heterospora* in full facultative synonymy. The di-anamorphic fungus is called *V. chlamydosporium* if it is judged to be related to the type species of *Verticillium*, the genus being given a full botanical value for all related anamorphic species whether mono- or pleomorphic. If not considered a *Verticillium* in that sense, the *chlamydosporium* fungus is transferred to *Stemphyliopsis*, when, in the judgement of the taxonomist, it is more closely related to the type species of *Stemphyliopsis*. Only if the taxonomist excludes it from a botanical relationship with the type species of the names of these two prior genera may the species be called *Diheterospora chlamydosporia*. As long as the generic names are not synonyms, any one of the three combinations with *chlamydosporium* may be correct, depending on taxonomic judgement.

CASE F, SCHEME 4. In Hennebert's botanico-anatomical system, *Diheterospora* is restricted to a monomorphic typification as in scheme 2, and becomes applicable only to the kind of chlamydosporic morph found in its type species, *D. heterospora*. No synonymy is possible between *Verticillium* and *Stemphyliopsis*, because of the obvious difference between phialidic and chlamydosporic morphs. Whether *Stemphyliopsis* and *Diheterospora* are considered synonyms depends on whether or not the chlamydosporic morphs that are their respective types are considered of the same kind or generically distinguishable. As for the di-anamorphic fungus itself, *chlamydosporium* is the epithet for the ana-holomorphic species and transferable to any anamorph-genus that is taxonomically acceptable. The species is *V. chlamydosporium* if its phialidic morph is considered most distinctive, *S. chlamydosporium* if its chlamydosporic morph is judged diagnostic and of the same kind as the chlamydosporic morph that typifies *Stemphyliopsis*, or *D. chlamydosporia* if a distinction is made between the *Stemphyliopsis* and *Diheterospora* chlamydosporic morphs. Under this scheme, as in the botanical system, any one of the three combinations can be correct for the di-anamorphic holomorph, depending on taxonomic judgement. But here, when the choice of the binomial has been made, the two morphs can be separately designated in the informal cross-reference system.

CASE F, SCHEME 5. As in schemes 2 and 4, *Diheterospora* becomes monomorphically lectotypified by the chlamydosporic morph of *D. heterospora*, and falls into synonymy with *Stemphyliopsis* if this morph is judged to be of the same kind as that which typifies *Stemphyliopsis*. Again as in schemes 2 and 4, no synonymy is possible between *Verticillium* and *Stemphyliopsis*, because their type morphs are phialidic and chlamydosporic respectively.

One significant difference in scheme 5 is that the sole legitimate binomial for the di-anamorphic fungus is *V. chlamydosporium*. The phialidic morph is specified as *V. chlamydosporium* anam. *Verticillium*. The chlamydosporic morph is *V. chlamydosporium* anam. *Stemphyliopsis*, with *S. ovorum* and *D. heterospora* as facultative synonyms. No change in the binomial is permitted, unless a name earlier than *V. chlamydosporium* is discovered, or the phialides of this fungus are judged to belong to a phialidic anamorph-genus other than *Verticillium*.

Another noteworthy point in this scheme is the following. Had Kamyschko known of the existence of *V. chlamydosporium* as a name for the fungus he had at hand, but considered the chlamydosporic morph to be worthy of distinction from *Stemphyliopsis*, this scheme
would sanction his publication of *Diheterospora* as a new anamorph-genus, typified by the chlamydosporic morph of *D. heterospora* anam.-sp. nov. But the binomial would have been published only to validate the name of the new anamorph-genus, not to serve as a name for the di-anamorphic species (already covered by *V. chlamydosporium*) or for the chlamydosporic anamorph, which was automatically covered by *V. chlamydosporium* anam. *Diheterospora*.

It must be further noted that, in this scheme, although *V. chlamydosporium*, *S. ovorum* and *D. heterospora* are theoretically *nomina ana-holomorphosium* for one fungus, they are not to be considered full synonyms unless the names of the anamorph-genera to which they are assigned are potentially synonyms; i.e., *Verticillium* being phialidic and both *Stemphyliopsis* and *Diheterospora* chlamydosporic, the only possible synonymy is between *S. ovorum* and *D. heterospora*. In other words, although these names are *nomina ana-holomorphosium* in application, they are *nomina anamorphosium* in typification, and their synonymy depends on the identity of their type morphs.

Finally, Carmichael proposes that, to be validly published, a binary *nomen anamorphosis* must be typified by the kind of anamorph specified by the name of the anamorph-genus used; e.g. (i) *V. catenulata* (Kamyschko) comb. nov. imag. (a transfer from *Diheterospora* to *Verticillium* as a taxonomic statement that *D. catenulata* and *V. chlamydosporium* are related) would be ruled invalid because it is agreed that the phialidic morph of *D. catenulata* is a *Paeaeilomyes* rather than a *Verticillium*; (ii) describing a new species in *Verticillium* because the fungus bears the same kind of chlamydospores as does *V. chlamydosporium* would be ruled invalid unless the type of the name of the new species bears a phialidic morph disposable in *Verticillium*.

**CASE F: Summary of Nomenclators**

= *Stemphyliopsis ovorum*, di-anam.-sp.  
= *Diheterospora heterospora*, di-anam.-sp.

OR

*S. chlamydosporium*

≡ *V. chlamydosporium*

= *S. ovorum*

= *D. heterospora*

OR, if D. ≠ S.

*D. chlamydosporis*

≡ *V. chlamydosporium*

= *S. ovorum*

= *D. heterospora*

Informal: e.g. *V. chlamydosporium* (or *S. or D.)*

≡ *V. chlamydosporium* anam. *Verticillium*

plus *V. chlamydosporium* anam. *Stemphyliopsis*
(b). Formal: \( D. \) heterospora, di-anam.-sp.
   incl. \( V. \) chlamydosporium, anam.-sp. (Legit. for separate ref.)
   and \( S. \) ovorum, anam.-sp. (Legit. for separate ref.)
Informal: \( D. \) heterospora, sensu ana-hol.-sp.
   incl. \( D. \) heterospora anam. Stemphyliopsis
      \( = S. \) ovorum
   and \( D. \) heterospora anam. Verticillium
      \( = V. \) chlamydosporium

2. Formal: \( V. \) chlamydosporium, anam.-sp.
   and \( S. \) ovorum, anam.-sp.
      \( = D. \) heterospora, anam.-sp.
   OR, if \( D. \) \( \neq S. \)
\( V. \) chlamydosporium, anam.-sp.
   and \( D. \) ovorum, anam.-sp.
\( \equiv S. \) ovorum
\( = D. \) heterospora
Informal: e.g. \( V. \) chlamydosporium, sensu ana-hol.-sp.
   incl. \( V. \) chlamydosporium, anam. Verticillium
      \( \equiv V. \) chlamydosporium, anam.-sp.
   plus \( V. \) chlamydosporium anam. Stemphyliopsis
      \( = S. \) ovorum, anam.-sp.
      \( = D. \) heterospora, ana-hol.-sp.
   (OR using \( S. \) or \( D. \) ovorum sensu ana-hol.-sp.)

3. Formal: (If congeneric with the type sp. of Verticillium):
\( V. \) chlamydosporium ana-hol.-sp.
   \( \equiv S. \) ovorum ana-hol.-sp.
   \( = D. \) heterospora ana-hol.-sp.
   OR
(If congeneric with type sp. of Stemphyliopsis but not Verticillium):
\( S. \) chlamydosporium ana-hol.-sp.
   \( \equiv V. \) chlamydosporium
   \( = S. \) ovorum
   \( = D. \) heterospora
   OR
(If not congeneric with type sp. of either Verticillium or Stemphyliopsis):
\( D. \) chlamydosporis ana-hol.-sp.
   \( \equiv V. \) chlamydosporium
   \( = S. \) ovorum
   \( = D. \) heterospora

No informal system.

4. Formal: as in F3 [but without considering priority of the generic name].
Informal: e.g. *V. chlamydosporium*, ana-hol.-sp.
incl. *V. chlamydosporium* anam. *Verticillium*
plus *V. chlamydosporium* anam. *Stemphyliopsis*
   = *S. ovorum*
   = *D. heterospora*

(OR using *S.* or *D. chlamydosporium*)

5. Formal: If *D.* = *S.*, *V. chlamydosporium*, ana-hol.-sp.

   ≡ *V. chlamydosporium* anam. *Verticillium*
   plus *V. chlamydosporium* anam. *Stemphyliopsis*
      = *S. ovorum*
   = *D. heterospora*

If *D.* ≠ *S.*, *V. chlamydosporium*

   ≡ *V. chlamydosporium* anam. *Verticillium*
   plus *V. chlamydosporium* anam. *Diheterospora*
      = *S. ovorum*
   = *D. heterospora*

IV ASPECTS OF THE VARIOUS SOLUTIONS

(i) The cross-reference name

This trinomial combination is always automatic, because it exists as the natural expression of any proposed affiliation, however impossible. It is often anticipatory, for it need not, and frequently can not, be fixed to an actual specimen. It is most certainly an autonym, but usually unlike the autonyms treated in Arts. 19, 22 and 26 of the ICBN.

Case E provides an illustration of how the cross-reference trinomial operates. *Cerco*
sporella antirrhini Wakef. anam. *Cercosporella*, like the ICBN-authorized autonym *C. antirrhini* var. *antirrhini*, is obligately tied to the binomial and to the type specimen of the binomial. But the cross-reference name for the non-type anamorph, *C. antirrhini* anam. *Heteropatella*, although also obligately tied to the binomial, is not typified at all -- unless the type specimen of *C. antirrhini* happened to bear both the *Cercosporella* acervulus and the *Heteropatella* pycnidium in an undeniable oneness. In fact, without indisputable evidence of this affiliation in the type of *C. antirrhini*, there can never be a type for *C. antirrhini* anam. *Heteropatella*, the name uniquely applicable to the *Heteropatella* anamorph that actually belongs in *C. antirrhini*. The postulation that *H. antirrhini* Budd. & Wakef. is that anamorph is unprovable. Even though a fungus identified as *C. antirrhini* was grown in culture and seen to produce the anamorph that was named *H. antirrhini*, no obligate linkage exists either between the cultured fungus and the type specimen of *C. antirrhini*, or between the names *C. antirrhini* anam. *Heteropatella* and *H. antirrhini*. It is not possible to fix *C. antirrhini* anam. *Heteropatella* to a specimen that is only postulated to be the *Heteropatella* affiliate of *C. antirrhini* anam. *Cercosporella*, because the combination *C. antirrhini* anam. *Heteropatella* cannot be jeopardized by the possibility of a faulty typification. Whether or not a *Heteropatella* anamorph actually exists in the life cycle of *C. antirrhini*, *C. antirrhini* anam. *Heteropatella* remains indestructibly available for it, always correctly applicable to it.
Here, therefore, in the cross-reference name, is an automatic version of an anticipatory, provisional name which is not, and may not be, covered by Art. 34 (2). When (see Case C) Pirozynski (1972) denied Linder's (1929) postulation that Helicosporium elinorae was an anamorph of a Lasiosphaeria, he could remove H. elinorae from synonymy with L. elinorae anam. Helicosporium, but the cross-reference name remained, automatically prepared for the discovery of a Helicosporium morph actually affiliated with L. elinorae. Indeed, although Pirozynski asserted that the association of Helicosporium anamorph with a Lasiosphaeria teleomorph was only accidental, that their affiliation was unlikely, and even if positive proof (if such were possible) existed in support of his assertion, L. elinorae anam. Helicosporium would stand as the automatic and ever correct way to refer to the anticipated affiliation. In other words, perhaps Lasiosphaeria does not produce a Helicosporium morph; but if it did, the morph would unquestionably be "the Helicosporium morph of Lasiosphaeria". Describing another Helicosporium as affiliated with the teleomorph of L. elinorae would be taxonomically helpful, but it would do nothing to re-establish the anamorph's already automatically established name; and the specimen described would bear no more than a facultative link to the cross-reference trinomial.

These are the inherent and essential characteristics of the cross-reference name. It is instantly recognizable for what it is, and immediately applicable in only one way. It is invariable and without competition. Cross-reference names neither need regulation nor can they be manipulated by rules of any kind. Undoubtedly, although they are automatic, anticipatory and usually untypifiable, cross-reference names might be made obligatory or recommended for use; but they certainly fall outside the normal prescriptions of the law. If their use was made obligatory, a requirement for formal introduction might also be legislated. But it is difficult to visualize any other way in which cross-reference names could be regulated by the ICBN.

The use of cross-reference names remains informally available in schemes 1, 2 and 4. It becomes mandatory in scheme 5. In view of the long, hard fight to establish typification as the basis for botanical nomenclature, we are faced with the question of whether the ICBN should even recommend, much less require, the use of mainly untypifiable autonyms. From the point of view of Hennebert and Weresub, it seems of surpassing significance that "the application of names of taxonomic groups is determined by means of nomenclatural types" (Principle II, ICBN). Carmichael agrees that names of taxa must be typified. But morphs, he points out, are not taxa in themselves (see also Pirozynski & Weresub, Chap. 26) but only morphs of taxa. Cross-reference names are not names of taxa; they are names for morphs of taxa. Consequently, in the view of Carmichael, the Code's requirement for a type to determine the application of the name of a taxon has no bearing on the cross-reference name for a morph. Since postulating an affiliation automatically brings forth a trinomial cross-reference name for the affiliate, it should be entrenched in the Code as the only legitimate name for the anamorph, which is no longer an independent taxon and thereby undeserving of a typified binary name.

(ii) Applying either Art. 34 or Art. 68 to outlaw the publication of a new binomial for an anamorph while postulating its affiliation with an already known and named anamorphic fungus (see Examples C and E above).
The last paragraph of Art. 34 rules against the simultaneous publication of alternative names. Currently, it refers to Art. 59 as allowing an exception to the rule. However (see Weresub et al. 1974:570), the publication of a name typified by a teleomorph (and thereby applicable to a holomorph) simultaneously with a name typified by an anamorph (and thereby applicable to the anamorph alone) cannot be construed as the publication of alternative names for the same taxon. Taking Example C above: *Lasiosphaeria elinorae* and *Helicosporium elinorae* were simultaneously published as affiliated, but they are different names for different taxa, the latter an anamorph species that is postulated to be encompassed by, but not identical with, the holomorphic species that is *L. elinorae*. If, however, trinomial cross-reference names were made obligatory for ana-holomorphs (as proposed by Carmichael), it would be logical to require their use also for pleomorphic holomorphs that include teleomorphs. Then, the postulation of the affiliation in this case would mean the instantaneous availability of *L. elinorae* anam. *Helicosporium*, with *H. elinorae* obviously an alternative to the trinomial.

So, too, with Case E: when *Heteropatella antirrhini* was postulated as a morph of *Cercosporella antirrhini*, the former name was clearly an alternative name for the available *C. antirrhini* anam. *Heteropatella*. Therefore, if cross-reference names were given ICBN status (whether obligatory or recommended), it would be logical to outlaw the simultaneous publication of a competing binomial. It might, of course, be argued that, the cross-reference name being automatic, it did not need to be proposed; and that, therefore, it would not be considered to have been "proposed simultaneously" with the binary name. But certainly it is clear that the spirit of Art. 34 would be transgressed by the publication of *H. antirrhini*, if ICBN official and formal recognition were granted to the trinomial autonym. And if the binomial somehow escaped Art. 34, it might be ruled illegitimate as a superfluous name under Art. 63 -- except that Art. 63 is based on the inclusion of "the type of a name or epithet which ought to have been adopted under the rules", and no type can exist for *C. antirrhini* anam. *Heteropatella*. But this escape, too, would violate the spirit of the Code.

The crux of this aspect of Carmichael's proposal is therefore the same as that discussed under IV (i) above: the question of formalizing the use of the currently informal cross-reference names.

If we concede, as does Art. 59, that we still need to retain an anatomical system of nomenclature for anamorphs, separate from the botanical nomenclature for teleomorphic Ascomycetes and Basidiomycetes; and if we concede, as does Art. 59, that an anamorph may legitimately bear a binary name even when its affiliation to a teleomorph is accepted; then it follows that we must concede that an affiliation to other anamorphs should also not prevent an anamorph from legitimately bearing a binomial. Although Carmichael concedes the first, he makes neither of the last two concessions, insisting on the self-evident logic that if a name already exists, none needs to be proposed.

This logic has bearing on all automatic cross-reference trinomials, combinations with not only names for anamorphs but also teleomorphically typified names for holomorphs. Yet, Art. 59 explicitly tolerates the use of a binary name for an affiliated anamorph, in spite of the fact that the *nomen holomorphosis* applies also to this affiliate. It may not be logical, but
mycologists have found it useful. And the ICBN permits it for its practical value. To propose now that an untypifiable autonym be granted a formal precedence that has been denied even to a *nomen holomorphosis* is to annul one of the provisions steadfastly maintained in the Code for the use of students of Fungi Imperfecti. Perhaps mycologists are prepared to surrender their use of binary names for affiliated anamorphs in a separate anatomical system. If so, they may be ready to discard Art. 59 altogether. Meanwhile, as far as Hennebert and Wereub are concerned, outlawing binary names for anamorphs affiliated with other anamorphs, while condoning the use of binomials for anamorphs affiliated with teleomorphs, is even less logical than the present system. Carmichael would outlaw both.

(iii) While retaining a monomorphic typification for the names of all anamorph-taxes, assigning priority and holomorphic application to the first legitimate binary combination published for any one of the anamorphs of a pleo-anamorphic fungus.

In order to achieve their end of providing for a single binomial to cover all anamorphs of a presumed pleo-ana-holomorph, both Hennebert's (1971) and Carmichael's (Chap. 4) botanico-anatomical schemes have had to make a distinction between the typification and the potential application of the first binary name published for an anamorph-species. This kind of distinction, of course, is common practice in all botanical nomenclature, wherein it is implicit that, however fragmentary the type, the name is applied to the whole individual (see Hennebert & Wereub, Chap. 3). In the somewhat modified botanical system for pleomorphic Ascomycetes and Basidiomycetes, as regulated by Art. 59, the distinction is of a particular kind: there is the restrictive anatomical requirement that a teleomorph is needed in order to typify the more broadly applicable holomorphic name. And so, it would seem that imposing a similar distinction (between typification and application) on the binomials for pleo-anamorphic fungi would introduce no serious new distortion of nomenclatural philosophy.

But let us not forget that this introduction of a botanical approach would be within the framework of an anatomical scheme that was originally devised to avoid the uncertainties of tentatively proposed affiliations. The simplest form of this approach is seen in scheme 2, in which the basic unit is monomorphic, and its name monomorphic in typification and application. Having been conceived for the purpose of providing obligately applicable names for isolated anamorphic phases, the strictly anatomical scheme ignores both pleo-anamorphy and possible ana-holomorphy, leaving the expression of postulated affiliations among anamorphs to whatever informal system may be found convenient.

Carmichael points out that this permissiveness gives no guidance to the choice of a single name to cover a pleo-anamorphic fungus, and that, by ignoring the problem, the ICBN does not fulfill its function of legislating a uniform means of expressing a particular taxonomic opinion, in this instance that two or more anamorphs are affiliated in a single fungus. Let us look further, therefore, at the procedures proposed.

In both of the botanico-anatomical schemes under discussion here, the simplicity of the monomorphic anatomical system is retained for the naming of anamorph-genera. It is in their botanical approach to anamorph-species that the schemes differ somewhat (see section II and III above), but both surrender to that approach the very characteristics of the anatomical system for which it was created -- the simple directness and convenience of a binary name for
an anamorph, now explicitly tolerated by the ICBN, whether the anamorph is affiliated or autonomous. It must be pointed out that a cross-reference trinomial (informal in scheme 4, formalized in scheme 5) does not fully replace the certainty of a binary name; for example, if *Histoplasma capsulatum* is to be understood as either monomorphic or dimorphic or both, *H. capsulatum* anam. *Histoplasma* pinpoints its monomorphic application with an obligate typification, but *H. capsulatum* anam. *Chryosporium* has no comparable anchor. Thus, in spite of being introduced into the botanical nomenclature of these fungi as a concession to the practical need for naming the separate morphs of holomorphs, the cross-reference name does not wholly fill that need.

Furthermore, cross-reference names aside, schemes 4 and 5 differ in how fully they satisfy those who want a botanical approach to ana-holomorphs. Two characteristics are basic to a botanical treatment: a single name applicable to a holomorphic species, and the grouping of related holomorphic species in a genus. Both schemes provide for the first. In addition, scheme 4 serves the second, making possible a nomenclatural reflection of the taxonomic decision that the ana-holomorphic species are related, by allowing the transfer of the prior epithet into combination with the earliest name of whatever anamorph-genus a taxonomist judges to be appropriate. In other words (see Case F4), if *Verticillium chlamydosporium* is judged to be phyletically unrelated to the type species of *Verticillium* (though they share a similar phialidic morph), but more closely related to *Diheterospora catenulata* (whose phialidic morph is different, a *Paecilomyces*), the presumed relationship is reflected by their classification in *Diheterospora* as *D. chlamydosporis* and *D. catenulata*. In scheme 5, on the other hand, the botanical approach does not go that far. On the basis of the same anatomical criteria that are used in the strictly anatomical system, scheme 5 restricts the transfer of *chlamydosporium* to anamorph-genera whose names are typified by phialidic morphs. Therefore, *V. chlamydosporium* is retained in *Verticillium*, and *D. catenulata* in *Diheterospora*. The fact that they share a *Diheterospora* chlamydosporic morph is shown by the use of the cross-reference name; but a taxonomist's judgement that they are related cannot be reflected in the binomials borne by the two fungi.

Hennebert's scheme 4 anticipates that eventually anamorph-genera will comprise only related anamorphic fungi, becoming as phyletically sound as any teleomorph-containing holomorphic genera. Carmichael's scheme 5 emphasizes that anamorph-genera are only para-taxa, and that phyletic reasoning applied to them and the disposition of their anamorph-species (even if ana-holomorphic) confuses the anatomical system for anamorph-genera with the botanical system for "true" genera. In other words, scheme 5 makes a precisely limited demand on the ICBN's injection of a botanical approach into the anatomical system: the need that a taxonomist may have to indicate a relationship among anamorph-species is to be denied fulfilment by the Code.

(iv) Legislated an additional exclusive criterion for the valid publication of the names of anamorph-species.

Scheme 5 proposes that, to be validly published, the name of an anamorph-species must be typified by the kind of morph that is specified by the name of the anamorph-genus used in the binomial for the species. In essence, the name of an anamorph-species has both a type anamorph specified by the name of the anamorph-genus and a type specimen; and for valid
publication of the binomial, the type specimen must include that type anamorph.

A ruling of this kind is not unprecedented. Art. 59 as it stands today has several exclusive specifications, on the legitimacy of particular combinations for new species and the valid publication of certain kinds of new combinations for known species. But mycologists are rebels against the proliferation of special rules for restricted groups. In the report of the Subcommittee on Art. 59 that was delivered at the 1977 Congress of the International Mycological Association, it was stressed that the members of the subcommittee had agreed on a central issue: as long as names were applied in accordance with their types, nomenclatural problems could be solved without the need for exclusive rules for the validity and legitimacy of the names of particular groups. If Art. 59 is reformulated in accordance with this thesis, removing the current penalties for the choice of an unauthorized generic name, it would be a regressive step now to introduce penalties for the infraction of a new set of exclusive rulings in behalf of the names of anamorph-species.

(v) The synchronous legitimacy and illegitimacy of a binary name that is proposed for a new anamorph-species which, while typifying the name of a new anamorph-genus, is postulated as applying to an already known and named pleo-morphic species.

As was noted under F5, if Kamyschko had been aware of the existence of *Verticillium chlamydosporium* and Stemphyliopsis ovorum as both applying to the anamorphic fungus he had at hand, and if he judged that its chlamydosporic morph differed sufficiently from the one typifying *Stemphyliopsis* to be worthy of segregation in a new anamorph-genus, he could have legitimately published *Diheterospora* as a new anamorph-genus for this kind of chlamydosporic morph, and typified its name by a new anamorph-species, *D. heterospora*. But, under scheme 5, it would be illegitimate for him to use this binomial for what should be referred to as *V. chlamydosporium anam. Diheterospora*.

To Carmichael, this is a necessary evil to ensure that even pseudo-taxa such as anamorph-genera have a nomenclatural type species and hence are tied to a type specimen to fix the application of their name. To Hennebert and Weresub, this part of scheme 5, which would enforce the publication ofa binomial only to prohibit its use, would be another illogicality unnecessarily introduced into the ICBN.

V CONCLUSION

It must be obvious that this committee did not come to any agreement on a proposal for change in the ICBN to accommodate those who seek naming pleo-anamorphic fungi.

After this review of what we hope are all possible aspects of the botanico-anatomical systems proposed to deal with this problem, Hennebert and Weresub have only been reinforced in their earlier (see Chap. 3, footnote) assessment of Hennebert's (1971) approach, and judge it even more applicable to Carmichael's (Chap. 4) proposal: the complexities involved in these schemes override any small advantage that might be gained by the few who could comprehend and apply the new rules to the handful of fungi involved. As long as Art. 59 exists for the protection of teleomorphically typified names for holomorphous Ascomycetes and Basidiomycetes over anamorphically typified names for their anamorphic phases, anamorph-species (whether affiliated or ana-holomorph) will remain outside the fully botanical system for the nomenclature of fungi. Burdening us with formal rules for postulating affiliation among
morphs, while excluding these presumed ana-holomorphs from botanical status in other ways, solves only the one small problem, but at the expense of the current simplicity of the purely anatomical system, without moving any closer to the integration of the two nomenclatural systems. To Hennebert and Weresub, it is better to leave the whole idea of ana-holomorphy to be dealt with on an informal level by cross-reference names totally ignored by the ICBN.

When affiliations among anamorphs as well as between anamorphs and teleomorphs are so well known that the unaffiliated need no special nomenclatural concessions, and when most of the anamorph-taxa have become narrowed to phyletically acceptable circumscriptions, then will be the time to reconsider ana-holomorphy and the integration of autonomous pleo-anamorphic fungi in the botanical system that is now, among non-lichenized Ascomycetes and Basidiomycetes, the exclusive domain of the teleomorph-endowed.

To Carmichael (and here we quote verbatim to avoid misinterpretation), "it is important that binomials should designate only whole species (holomorphs), not phases or states of species, and that the ICBN should ensure that only one binomial can be correct for any one species. Species that occur as different morphs at different seasons, or when on different substrates, present special difficulties in identification, but they do not require the ICBN to abandon the principle of one name per species. Cross-reference names, whether used formally or informally, provide an alternative".

The members of this committee agree on the usefulness of cross-reference names. Most of our disagreement centres on the recognition of these names by the ICBN. Carmichael does not insist on their formalization in the Code, though he would consider the principles of the ICBN strengthened thereby. Hennebert and Weresub reject any additional involvement of the Code in regulating the conventional, anatomical system of nomenclature for anamorph-taxa. This report of our discussions is presented here so that all aspects of the problem can be weighed by the mycological community in preparation for whatever proposals may eventually be made for a change in the ICBN.
28
Postscript

B. Kendrick

As I sat before the fire on a chilly evening in late Autumn, reflecting on the tome nearing completion, it occurred to me that a brief postscript might be useful -- to give a distillation of some of the ideas and information presented in the preceding several hundred pages, and to recount a little of the folklore of Kananaskis-II. The Conference was a distillation in itself, a very concentrated experience. One morning Dr. Luttrell was heard to ask his wife what day it was, and on repeating the question in the evening, was amazed to receive the same reply. Dr. Weresub claimed to have spent most of her life in the Conference room.

Neither of these incidents did anything to dispel the rumours about the slave-driving propensities of the Chairman. "Why," said one despairing member of the Conference, "do you think he gets us out here, so far from civilization? There's no escape unless you want to live on roots and berries and wild mushrooms." This might not have been too difficult, because the fungi of the Kananaskis Valley fruited profusely during our stay, and our many impromptu forays were always productive.

I have heard a Conference defined as a gathering where conversation is substituted for the dreariness of labour and the loneliness of thought. I do not think this is applicable to Kananaskis-II, but the reader will doubtless have formed his own judgment. I hold a firm conviction that scientists who reach a high level of achievement, and accumulate a rich store of experience, need a different kind of outlet from that provided by most scientific journals. They should be enabled, once in a while, to speculate, to share their hunches, to speak out about that which normally reverberates only within the chambers of their mind, or is mumbled into their beer. During the Conference, Dr. Luttrell claimed to have found a quotation in the library at Kananaskis (though I would not be surprised to find that he had authored it himself), which expresses this philosophy very well. "It is perhaps, then, rather a duty than a piece of presumption for those who have had experience to take opportunity of helping things on by irresponsible expressions of opinion." In thus abandoning Appollonian orthodoxy for a brief Dionysian season, their free-ranging imaginations may spawn valuable ideas or hypotheses, and enliven the literature with an infusion of personality. Certainly the character of the various people can be discerned in many of the chapters -- and perhaps even more in the ensuing dialogues.

There is a certain irony in the fact that this treatise on 'the whole fungus' grew to such a size that it had to be divided into two parts. Fortunately, the logistical necessity
for doing this presented me with a solution to at least one small problem. When there was to be just a single volume, I was discussing the cover design with Luella Weresub, and mentioned that I planned to use a Tulasne illustration of an ascomycetous teleomorph plus anamorph on the front cover, and a Brefeld illustration of a basidiomycetous teleomorph plus anamorph on the back cover. She liked the idea, but questioned the positioning. I noted that there were more Ascomycete than Basidiomycete chapters and connections in the book. Her rejoinder: "More isn't necessarily better." End of conversation. As it happened, the logical break between volumes came at a point which placed almost all the Ascomycete material in Volume 1, and almost all the Basidiomycete material in Volume 2. Brefeld and his basidiomycetous holo-morph now appear, significantly and a little serendipitously, on the front cover of Volume 2.

Although many of these chapters and discussions are inevitably aimed at the cognoscenti, repeated attempts can be found throughout the book to make the terms and concepts we discussed accessible to students. I have not delineated these passages or comments in red, but the interested and enterprising student will find them. These student-oriented explications are part of the over-all plan behind the book. My chief concern in having it published was not that it be on glossy paper between hard covers, and insulated from most of its potential readership by the kind of ridiculously high price that seems to be the hallmark of academic books today. No: I wanted the price to be kept as low as possible, so that even students could afford to own a copy. The National Museum of Natural Sciences has proved an invaluable ally in this endeavour.

Although I have spent a year putting this book together, I have not grasped the full significance of any part of it. That remains to be realized by its readers.

What gains do I already see as being embodied in 'The Whole Fungus'?

In Chapter 2, a perceptive and timely overview of the historical separation of anamorph and teleomorph, showing how understandable, if deplorable, it was.

In Chapter 3, the consolidation of valuable new terms for the different morphs, or morphological expressions, of a fungus -- and for the whole fungus.

In Chapter 4, the formal introduction of the cross-reference names for fungi already adopted by some authors, and an extended discussion of the (to the uninitiated) unexpectedly complex and often baffling ramifications of seemingly simple nomenclatural decisions -- all this leading up to Chapter 27 in which the alternatives are superbly dissected and their inner workings exposed to the public gaze for the first time, complete with fully-worked examples. If you have a logical turn of thought, this is for you.

In Chapter 5, the rationalization of some time-honoured terms which, in their new and, we hope, more logical incarnation, are needed to describe the conidia and conidiomata of anamorphs. As a bonus, most of the mitospore terminology is equally applicable to the meio-spores of the teleomorphs!
In Chapter 6, the formulation of a convincing theory to explain the developmental plasticity that can convert one kind of conidiogenesis into another; and in Chapter 7 the documentation of the phenomenon of simultaneous 'plecoconidiogenesis'!* within a single taxon. Both of these chapters imply a retreat of conidium ontogeny from its central position in anamorph systematics, and help to clear the way for the recognition and exploration of the new characters we need -- or at least for a more balanced approach to the information now accessible to us.

In Chapter 8, the first serious attempt to explain the current distribution of certain groups of Ascomycetes and their anamorphs in the light of plate tectonics and the fossil record. This pioneering paper is bound to be only the first of many in this rapidly developing area.

In Chapters 9 to 15 there is encouraging evidence of increasing two-way communication across the gap between anamorph specialists and teleomorph specialists, and of attempts to consider all available information when taxonomic decisions have to be made.

Chapter 16 lucidly summarizes what we know about the factors which induce (or suppress) sporulation of anamorph and teleomorph. It becomes clear that experimental work in this area is difficult and often frustrating, since suitable experiments may be difficult to design, and since the same factor may have diametrically opposite effects on very closely related fungi. We obviously have much to learn before we will be able to engineer phase change at will, and it seems that the ecological requirements of individual species, rather than any underlying genetic pattern, usually dictate the responses of the organism to the various stimuli.

Chapters 17 and 20 consist mainly of extensive lists of teleomorph-anamorph connections. Since I have been deeply involved in the compilation of these very lists, I am just as deeply concerned with their fate. 'Garbage in - garbage out' is an apopthegm among computer specialists. Any data-bank is only as useful as its contents are accurate. It is almost inevitable that many of the 'connections' in our lists existed only in the minds of their authors, and not between the morphs thus wishfully yoked together. It is obvious that the coming generation of holomycologists will have to devote a great deal of time and energy to sifting these connections, and weeding out the errors. Even now an inspection of the two 'digests' in Chapter 17 (lists arranged by Ascomycete order and family) may reveal inconsistencies. Today, we know enough to say that if, to take a hypothetical example, one of the Erysiphales were listed as having a Botrytis or Alternaria anamorph, we would suspect the authenticity of the connection. (We already know that Botrytis anamorphs are characteristic of some inoperculate discomycetes; Alternaria of some bitunicates.) When we approach a similar level of sophistication in other groups, the anomalies in our lists will become

* verb. imag. -- imaginary word, not being introduced seriously, not here accepted by me, and thereby invalid.
just as obvious. The actual case of the anamorph-genus Chrysosporium may help to make my point. This genus is cited as having teleomorphs in sixteen unitunicate ascomycetous genera (mostly Gymnoascaceae and Omygenaceae) and one basidiomycetous genus (Phanerochaete). I think one of our basic assumptions must be that there are bound to be profound (though not always obvious) genetic differences between ascomycetous and basidiomycetous anamorphs. The most reasonable approach in this case is surely to consider the possibility of an inappropriate generic disposition for the Phanerochaete anamorph. My suggestion is that it be compared with the anamorph-genera Allescheriella or Sporotrichum, both morphologically reminiscent of Chrysosporium, but both with established basidiomycetous affinities.

The reader may have noted that Chapter 20 (Basidiomycete connections) is set up very differently from Chapter 17 (Ascomycete connections). This is not, as some might suspect, entirely a matter of editorial perversity, but rather one of necessity. The Basidiomycete lists are given in three columns: teleomorph on the left, anamorph in the centre, reference(s) on the right. The reader can hardly fail to be aware of the gaping hole down the middle of many pages. This blank column is a graphic and deliberate demonstration of the inadequacy of our knowledge. Although Basidiomycetes commonly possess anamorphs, it is very uncommon for those anamorphs to be dignified with a name. Thus, since we had so few anamorph names, we had to rely on other characters to group the anamorphs. We chose developmental characters, partly because in 1974, when we began work on Chapter 20, such characters were still regarded as pivotal. We have seen in Chapters 6 and 7 how these characters have now been brought into a more realistic perspective, and further evidence for this view can be adduced from such listings as the 'blastic-sympodial' (group 6) in Chapter 20, since the taxa compiled therein represent an undeniably heterogeneous assemblage. Nevertheless, a beginning has been made. I am sure the new generation of holomycologists will not let things rest, but will refine and synthesize the data in a way we can only dream of at present.

Returning to the subject of Chapter 17 for a moment, I would like to issue a nomenclatural caution. Many of the Aspergillus and Penicillium binomials in our lists are not acceptable according to Article 59 of the Code, since they are based on ascomycetous types (D. Malloch, pers. comm.). Most of the names for anamorphs sharing a basionym with the teleomorphs (such as Aspergillus amstelodami (Mangin) Thom & Church, with Burotium amstelodami Mangin as basionym) are incorrect, and in most such cases there is probably no legitimate binomial available for the anamorph (this is not, of course, to suggest that these anamorphs don't belong to the genera Penicillium and Aspergillus -- they most certainly do).

Picking up the thread again at Chapter 18, we find aquatic anamorphs with stauro- and scoleco-spores unequivocally connected with teleomorphs from several different groups, both Ascomycetes and Basidiomycetes. Here are some of the best demonstrations we could possibly ask for of convergent evolution in anamorphs. Once again it is clear that when we know the nature of the teleomorphs, we may have to reassess the taxonomy of the anamorphs, inconspicuous characters often assuming unwonted significance. It seems to me that this process is bound to bring about an increase in the number of anamorph generic names, and that in future, more and more critical observations of anamorphs will be needed if they are to be properly identified.
Chapter 19 seems to indicate that those agaricologists who take anamorphs into consideration (a small but growing band) have already made a number of highly significant correlations between anamorph and teleomorph taxonomy -- and this largely in the absence of anamorph names. It is apparent to me that when they grant those anamorphs formal status, and provide them with handles in the form of anamorphic names, progress should be even more rapid as they benefit from the hard-won conceptual constructs of the specialists in Fungi Imperfecti.

Chapter 21 places the rust fungi beautifully in context, as producing a most diversified and functionally refined collection of anamorphs. The view of rust evolution presented here is convincing, and a model to those of us who worry about the evolutionary and functional patterns of the anamorphs we work with.

Chapter 22 should be required reading for all mycologists -- and microbiologists -- illuminating, as it does, an area of fungal taxonomy that has been historically murky. Again, the statement, breathtaking in its simplicity, that most yeast cells can be regarded as conidia, and the careful exposition of the anamorph-teleomorph correlations among that most heterogeneous of groups, have strengthened my faith in the new terminology, and in the almost universal applicability of the underlying biological pattern.

Chapter 23 does nothing to dispel this belief. Here is a reassessment of Zygomycete classification with a rationalization and realignment of some major groups. It ultimately stresses the dependence of the classificatory structure on data derived from both teleomorph and anamorph. In fact, zygospores tend toward uniformity of form and function, so although zygomycetous generic names are always regarded as holomorphic (and hence, circumscribing the teleomorph), and no anamorphic names have been provided, many generic concepts actually rest on features of the highly diversified and often elaborate anamorphs.

Chapters 24 and 25 are drawn from the collective experience of the participants at Kananaskis-II. I have already enunciated elsewhere my belief that ecological information may well be the next major addition to our taxonomic armament, so I will content myself with the suggestion that students of the fungi may find in these chapters some nuggets of new information, some subtle stimuli to their thinking.

Chapter 26 is an eye-opening discussion of how it is possible to go about the business of classification in many different ways, and an exploration of the logic of some of those ways as they have been applied to fossil fungi. It should be read by all serious students of fungal taxonomy, since it will occasion them some heart-searching concerning their own attitudes. But it is primarily aimed at the palaeontologists and their sometime conceptual identification of morphographic categories with the processes of biological classification. A cohesive and fascinating story, and an object lesson.

And that, for what it's worth, is my initial response to 'The Whole Fungus'. Erasmus, in 1501, wrote "Although it is sheer madness to publish bad books, it is extremely difficult to publish good ones". Perhaps the madness can be avoided, and the difficulty overcome, by choosing one's fellow authors from among people such as those who kindly agreed to join me in producing 'The Whole Fungus'.

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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