CHAPTER 26. The Fossil Record

It seems unlikely that the saprolegniaceous fungi have evolved so recently as to have escaped some form of compression or infiltration, or so fragile as to have left no imprint whatever in the Earth's crust. To be sure, suggestively shaped, obviously fossilized remnants have been uncovered and are thought to have recognizable counterparts among present day zoosporic fungi (E. W. Berry, 1916; Bradley, 1967; Fry and McLaren, 1959; R. Harvey *et al.,* 1969, and Pampaloni, 1902, for example). But of the watermolds themselves? What were the ancient ones like? The published record is sparse indeed, and equivocal (von Pia, 1937). One would not today presume to apply a familial or ordinal name to mere hyphal fragments found in association with organic matter, yet little more than aseptate fossilized filamentous accumulations have been named as saprolegnians.

In their summary account of the fossil record, B. H. Tiffney and Barghoorn (1974: 13, fig. 5) accept four genera of fossil Saprolegniaceae: *Palaeachlya, Achlyites*, *Paleomyces*, and *Paleoperone*. The earliest record seems to be from the Silurian (430-395 million years), and the most recent from the Miocene (26-5 million years). Various configurations of filaments or tubules have also been reported from fossil deposits and compared with the Saprolegniaceae (or in a broader sense with Oomycetes). Among these accounts are ones suggesting that the respective investigators had little familiarity with the nature of these fungi.

ASSOCIATIONS WITH CALCIFIED AND CORALLINE MATRICES

Kölliker (1859) and Wedl (1859) found tubular cavities in calcified remains of some marine animals, and the latter also described filamentous structures in Devonian shell fragments. These authors proposed that the specimens were remnants of "Confervae" identical to Kützing's *Saprolegnia ferax*. There is nothing in either account to suggest that the tubules were impressions or infiltrations of fungal filaments, and certainly none of the illustrations bear any resemblance to *S. ferax*. Moseley (1876:116, 117) referred to "parasites" (his term) of coralline substrates as distinctly green filaments "... though they appear to be fungi..." which, when dissolved out with acid, had the appearance of a "...ramifying mycelium..."

The presence of tubules and filamentous cavities in Silurian and Tertiary corals (and in some present day ones as well) was recorded by Duncan (1876a, b). Duncan (1876a:210) interpreted one such collection of tubules as a remnant of an alga which he named *Palaeachlya perforans* and classified " ... amongst the unicellular types in the neighbourhood of *Achlya*..." He also described (from extant corals) *Achlya penetrans* with oospores (1876b: pl. 7, figs. 48, 49) and zoospores (1876b: pl. 7, figs. 53, 55, 61), and an alga that he identified as *Achlya ferax* Kützing. The fragmentary structures linked to *A. penetrans* had counterparts in fossil corals, according to Duncan (1874b). Humphrey (1893) thought that *A. penetrans* was a siphonaceous alga, and Kawaguchi (1942:105) considered it to be a parasitic green alga. Moseley (1881) reported finding in specimens of *Millepora* filaments like those which Duncan referred to as *Achlya* and *Saprolegnia*. Nadson (1932) believed that the *S. ferax* [*sic*] and *A. penetrans* of Duncan were merely specimens of a boring alga belonging to the genus *Ostreobium*. In a review of accounts of fungal filaments in calcareous matrices, Duerden (1902) concluded that the organisms which were described were simply green algae that infested such materials. After an analysis of the literature to that time, Topsent (1887) concluded that the filaments such as Duncan had described were indeed parasitic Thallophytes.

The illustrations of *Achlya penetrans* and *Palaeachlya perforans* (Duncan, 1876a, b) are of elements bearing -- provided a liberal dose of imagination is applied -- a superficial resemblance to coenocytic hyphae. The figures of oospores and zoospores illustrate nothing that can be found in a watermold of this day. Duncan made some unjustifiable taxonomic changes: he simply put the genus *Saprolegnia* into *Achlya* evidently because he saw no differences between the two taxa. James (1893b) commented on Duncan's *A. penetrans* noting that the name was applied to "growths" on existing corals, yet resembled ones on corals of the remote past. James (1893b: 272) wrote that if "… the parasitic *Achlya penetrans* of modern seas is identical with the parasite of Silurian seas, the case is without a parallel in the organic world."

The genus *Achlyites* (as *Achylites*) is listed by B. H. Tiffney and Barghoorn (1974) as an endozoic form of Silurian and Tertiary origin, and references to the genus are attributed to Duncan (1876b) and James (1893a, b). None of these papers, however, mentions this generic name. *Achlyites* appears to have been coined by Meschinelli (1902) -- although erroneously attributed to Nees von Esenbeck as the author of the genus -- and applied to Duncan's *Achlya penetrans.* The only fossil "phycomycetes" listed by Meschinelli (1892) were *Peronsporites* of W. G. Smith (1877) and *Protomycites*, but in his account of 1902 he includes references also to *Palaeachlya perforans* and *P. tortuosa*.

Two "fungi" believed to resemble achlyoid species were described in 1891 by Etheridge. Various tubular borings in a coral from the Permo-Carboniferous periods were named *Palaeachlya tortuosa*, and filamentous tracings in *Stenopora crinata* from the same deposits were identified as *Palaeoperone endophytica*. The comparisons to living specimens of *Achlya* are indeed tenuous, and only the most imaginative eye would see a correlation between the spores allegedly produced by these ancient forms and those of species of *Achlya*.

The *Palaeomyces* (alpha) described by D. Ellis (1914-15) from calcareous oolithic sediment of the Jurassic and Cretaceous consisted of filaments of two sizes, some being about 2 μm in diameter, and others 4-5 μm. The illustrations seem to suggest coenocytic hyphal tips, but the fossilized remnants could certainly not be allied to the Saprolegniaceae. In 1971 B. J. Taylor called attention to the similarity of vermiform tubules in Lower Cretaceous macrurous decapod cuticles and discinid brachiopod shells to the thallus of *Leptolegnia marina* (no longer included in the Saprolegniaceae).

ASSOCIATIONS WITH FOSSIL BRYOZOANS

Elias (1965) has suggested that marine entoprocts from the Ordovician to the present harbored true fungi. He established the family Ordovicimyceae, and a new genus and species *Ordovicimyces gallowayi*, to accommodate fossil specimens showing a coenocytic hypha traversed by a subcentral cytoplasmic strand. Elias compared the fossil structures with Coker's (1923) illustrations of early stages in the internal proliferation of sporangia of *Saprolegnia monoica* var. *glomerata* (=*glomerata*). The fossil fungus, however, consisted of sporangium-like structures that were attached to the substratum by simple haustoria. The relationship of Elias' specimens to existing saprolegniaceous fungi is very distant indeed.

As to the taxonomy of the Saprolegniales, Elias (1965: 8) emended G. M. Smith's (1938) description of the order to include the "Monoblephariaceae"”[*sic*] and to accommodate, tentatively, a single fossil representative, "*Monoblepharis*? *thalassinosus*" In this emended order Elias placed "symbiotic forms" which had lost their cytoplasmic content, and ones which occasionally had septa positioned in the filaments in no relation to reproductive cells. This septate condition, Elias thought, was probably inherited from ancestral algae.

ASSOCIATIONS WITH PLANT REMAINS

Although he was aware of the resemblance of his *Peronosporites antiquarius* (found in the scalariform tracheary elements of *Lepidodendron*) to certain Saprolegniaceae, W. G. Smith (1877) did not assign his fossil fungus to this group. Smith was not particularly careful in his observations, and described, as zoospores, spore-like bodies in spherical cells that he called oogonia. He obviously chose to ignore reality in the decision to relate the specimens to the Peronosporas, and this is a failure that generates little confidence in his findings. Williamson (1881) reexamined W. G. Smith's material, confirmed that it was indeed a fungus, and decided that its affinities were to the saprolegnians. The illustrations of the material that Williamson provided (1881: pl. 54, figs. 28, 31; pl. 48, figs. 36, 37) are quite suggestive of gemmae.

In the parenchymatous cells of the leaf bases of *Lepidodendron* (*fuliginosus*?) D. Ellis (1918:142) found fossilized, branched filaments which he named *Palaeomyces bacilloides*. The *Oidium*-like filaments of this fossil certainly are without a living counterpart in the Saprolegniaceae, although Ellis felt that the nearest allies were to be seen in members of this family, perhaps finding "... their analogue among certain species of *Achlya*." This conclusion is curious since he believed (Ellis, 1918:143) that the reproductive cells associated with the filaments in the *Lepidodendron* did not "...point conclusively to the Saprolegniaceae."

OTHER ASSOCIATIONS

Fossilized material of a presumed fungal origin and resembling W. G. Smith's species of *Peronosporites* was described from shale by Hancock and Atthey (1869) as *Archagaricon bulbosum*. Because some of the filaments had bulbous swellings at intervals and also were papillate, it is doubtful that these specimens were fossilized watermolds. Although some of the 15 fossil fungi (from early Devonian) described and illustrated by Kidston and Lang (1921) certainly were vaguely oomycetous, the likenesses fade under close examination. Some of the vesicular elements they described suggest gemmae or immature sporangium-like bodies, but the resemblance is too superficial to be taken seriously. Boullard and Lemmoigne (1971) reexamined the fossilized remnants reported by Kidston and Lang, but, like the latter two authors, could not be certain of the nature of the structures. Some of the elements illustrated by Boullard and Lemoigne resemble hyphae and perhaps gemmae.

The genus *Eomycetopsis* and its two species described by Schopf (1968, 1970) from Late Precambrian deposits (bedded carboniferous chert) were thought by Pirozynski and Malloch (1965) to be oomycetous fungi. Pirozinski repeated this view in 1976(a), and on the basis of this conclusion suggested (1976b) that the microfossil found by Schopf and Barghoorn pointed to a Proterozoic origin of the Oomycota. Awramik *et al.* (1976) thought that *Eomycetopsis* represented preserved sheaths of some cyanophyceous organism. Priozynski and Malloch (1965) also saw in the ascus-like fossil element (in silicified dolomites and black chert of Late Precambrian) illustrated by Schopf and Barghoorn (1969) a resemblance to an intercalary oogonium of some extant member of the Saprolegniaceae.

Tyler and Barghoorn (1954) found in the roughly two billion-year-old Gunflint chert, a branched, coenocytic form with associated free, spore-like bodies. Perhaps the form was phycomycetous (by current definition), but there is nothing beyond the aseptate nature of the filaments to suggest a saprolegniaceous affinity.

Protoascon missouriensis was described by Batra *et al*. (1964) as a fossilized, perithecium-like ascocarp with attendant, septate appendages arising from the base of the fructification and enveloping it. Baxter (1975:2) redescribed the material of Batra and his associates, and concluded that the specimens could not be thought of as remnants of an Ascomycete. He suggested that the fossil was "...similar in some ways to the oogonia and surrounding antheridia..." of certain members of the Saprolegniales. It is difficult to equate the so-called septate appendages described by Batra *et al*. with the antheridial apparatus of any existing watermold. The fructification of Kohlmeyer's *Spathulospora adelpha*, an Ascomycete, seem to us reminiscent of the *Protoascon*. The fructification appendages in the former (Kohlmeyer, 1973: fig. 1) have the same noticeable configuration (and seemingly the same origin) as those of the fossil form (Batra *et al.*, 1964: figs. 1-11). There is a less obvious (but nonetheless very suggestive) similarity between the antheridia of *S. adelpha* (Kohlmeyer, 1973: fig. 6) and some of the appendages of *P. missouriensis* figured by Batra and his associates (1964: fig. 8). The ostiolate ascocarp of the *Protoascon* (Batra *et al.*, 1964: fig. 7) also resembles the mature ascocarpic fructification of Kohlmeyer's species (1973: fig. 3).