LIVING AND FOSSIL ALGAE AND FUNGI, FORMERLY KNOWN AS STRUCTURAL PARTS OF MARINE BRYOZOANS

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ABSTRACT

Some bryozoans (Ectoprocta) appear to be infested by symbiotic to parasitic algae and fungi. Filamentous Red alga boring into the recent *Heteropora pelliculata* has been apparently previously considered as "denticles" and "prolongations" (in cyclostome *Entalophora proboscidea:* Canu & Bassler, 1920, after Pergens). It is described as conchocelis phase of *Porphyra drewae,* sp. nov (of Bangiales).

Rare blue-green colored fungus infests zooecia in the recent *Heteropora neozelanica,* and is described as *Monoblepharis* (?) *thalassinosus* sp. nov. A more abundant fungus in this same bryozoan is described as *Heterosporimyces spinosa,* gen. et sp. nov., and still another, rare fungus in it, is tentatively classified as *Ordovicimyces recensis,* sp. nov. The genus *Ordovicimyces* is introduced for the transitional algo-fungus *O. gallowayi,* gen. et sp. nov., abundant in the ordovician trepostomatous bryozoan *Nicholsonella cornula.* In this same bryozoan occurs also a rare Blue-Green colonial alga named *Prochamaesiphon cumingsi,* gen. et sp. nov.

A fairly abundant fungus *Propythium carbonarium,* gen. et sp. nov. occurs in the upper Carboniferous bryozoan "*Batostomella*" *polyspinosa,* where also occurs rare *Prochamaesiphon geitleri,* gen. et sp. nov., and *Prochamaesiphon* (?) sp.

INTRODUCTION AND ACKNOWLEDGEMENTS

WHEN studying the literature on fossil and living bryozoans, I became interested in the enigmatic microstructures which have been repeatedly described as parts of the bryozoan's own structure, even if their function remained unexplained. Through the kind cooperation of Dr. Anna Hastings, British Museum (Natural History) and particularly of Dr. D. A. Brown, University of Otego, New Zealand, I was fortunate to obtain from him good zoaria of *Heteropora neozelanica* and *H. pelliculata*, both with the well preserved, above-mentioned microstructures. The late Dr. J. J. Galloway, University of Indiana, has loaned me the thin sections of the Ordovician *Nicholsonella cornula*, in which he has discovered the peculiar "spines" (described in Cumings & Galloway, 1915, p. 358). My student Don Slama, University of Nebraska, forwarded for my study his slides with well preserved foreign microstructures detected by him in the Pennsylvanian "*Batostomella*" *polyspinosa*.

All these microstructures are described here as endozoic marine algae and fungi.

All sketches have been originally prepared by me in 1952-54 in pencil, and although the sketched structures were recognized at that time as marine crytogams, I was not in a position to make their detailed comparison with the particular algae and fungi, as now discussed in the descriptive text. The presently published inked sketches are fairly accurate copies of the original pencil sketches, with no attempt of any additions or elaborations in the light of the present understanding and classification of these microorganisms.

Class RHODOPHYCEAE

Order BANGIALES

Genus *Porphyra*

Kathleen Drew (1954, and earlier shorter contributions) has proved by laboratory cultures that the boring alga, known as *Conchocelis rosea* Batters, is but a "conchocelis-phase" in the life cycle of *Porphyra umbilicalis* (L.) Kutz. var. *laciniata* (Lightf.) J. Ag. In view of this the below described new boring alga, which in many respects is similar to *Conchocelis rosea*, is classified here as a conchocelis-phase of *Porphyra drewae*, whose foliate, non-boring phase, is at the present unknown.

Porphyra drewae sp. nov.

Pl. 1, Figs. 1 (?), 2, 3

? 1889. "Denticles circavité" in *Entalophora proboscidea* Milne-Edw. Pergens: *Mém. Soc. belge Géol.*, v. 3, p. 309, fig. 1 (*see* pl. 1, fig. 1).

? 1920. Same "denticles" in *Mecynoecia* (*Entalophora*) *proboscidea* (Milne-Edw.), Canu & Bassler: *Bull. U.S. nat. Mus.*, 106, Fig. 238-F, reproduced from Pergens, 1889.

? 1933. "Small formations" in *Heteropora pelliculata*. Borg: *Zool. Bidr. Uppsala*, Bd. 14, p. 292.

Description — Straight to gently curving principal (primary) boring filaments, mostly of fairly uniform 2μ diameter (PL. 1, FIG. 1); occasionally bifurcating, but more frequently laterally branching at 50 to 80 degree angle, into secondary filaments of 1-1·5μ diameter. Principal filaments start from filamentous loops, which border the 11μ wide circular communicating pores in interzooecial walls of *Heteropora pelliculata* Waters. Broad connections, measuring 3-4 μ in length, between a principal and a secondary filament, growing parallel to each other (FIG. 2, left part), could be a result of gradual enlargement in the course of growth, as observed by Drew in her cultures (1954, p. 199, PL. 11, FIGS. 3, 5, also TEXT-FIG. 2). The single, apparently fertile cell-row of this same species consists of cells 10 to 15 μ long and 2 to 3·5 μ wide, and a transversely developed flask-like vesicle resembling plant initial in Drew (1954, FIG. 5). Small subcircular bodies in the apical cell of the row resemble the dark gray granules filling the cells in the similar cells of the conchocelis-phase illustrated by Drew (1954; PL. 12, FIG. 7). Transverse walls in the cells of the row are as thick as the lateral ones, and thicken with the growth of cells from 0·5 to 1·2 μ.

Comparison — Differs from the similar conchocelis-phase of *Porphyra umbilicalis* var. *laciniata* by the more than twice thinner primary and secondary filaments, linear instead of irregularly branching fertile cell-rows, and considerably more elongated cells of the rows.

Loop-like encirclement by filaments around the borders of communicating pores between zooecial chambers is similar to the encirclement by the filaments of *Solenopora texana* of the zooecial walls in the algal-bryozoan consortium *Acanthocladia guadalupensis* (RIGBY, 1957, TEXT-FIGS. 1, 2; PL. 69).

The above mentioned (in the synonymy-like list) published illustration of "denticles circavité" by Pergens undoubtedly belongs to a similar or even identical conchocelis-phase of *Porphyra*.

Occurrence — As a boring conchocelis-phase in walls of *Heteropora pelliculata* Waters collected in Tatarskii Gulf near Sakhalin and Yezo islands, lat. 41°-46° N., long. 141°-143° E., at depths of 25-67 m. (75-201 feet) (after Borg, 1933, p. 285).

Class MYXOPHYCEAE (CYANOPHYTA)

Order CHAMAESIPHONALES

Genus *Prochamaesiphon* gen. nov.

The new genus is proposed for two endozoic marine fossil forms, which are nearer to each other than to the modern fresh water epiphyte *Chamaesiphon*.

Diagnosis — Individual thalli elongate, goblet-shaped, with a slight terminal flare. Wall thickens distally. Attenuated base immersed in the substratum (zooecial wall of bryozoan). Rudimentary colony formation is apparently formed by germination of a single conidium (exospore) within an individual goblet.

Comparison — Many Green and Yellow-Green algae have similar goblet-like shape and somewhat similar, although far more extensively developed, colonial habit, just as in some species of the Blue-Green alga *Chamaesiphon*. Such are *Echalocystis* and *Ankistrodesmus* of Chlorophyceae (FRITSCH, 1935/48, FIGS. 36 and 46), and *Dynobryon* and *Hyalobryon* of Chrysophyceae (*Ibid.*, FIGS. 171-M and 174). All these living forms differ from *Prochamaesiphon* by much thiner walls, quite different manner of multiplication, and are attached to the substratum by the secretion of mucilage. Besides, they are either planctonic or (mostly) epiphytic freshwater forms.

Prochamaesiphon differs from the nearest to it *Chamaesiphon* by the apparent production of only one conidium (exospore), and its apparent germination at point with no definite location relative to "pseudovagina"; the latter is developed inside the second generation goblet in genotype of *Prochamaesiphon*. The apparent development of a single gonidium and its role in the colonial development, are the most striking characters of *Prochamaesiphon*, and indicate its belonging with Myxophyceae.

Genotype: *Prochamaesiphon cumingsi* sp. nov.

Prochamaesiphon cumingsi sp. nov.

Pl. 1, Fig. 7

Description — Besides the generic characters mentioned, the only specimen of the species contains two (or three ?) successive individual generations, rising out of each other in a colony-like chain. The first generation is a wide goblet, whose base is deeply rooted in the substratum; its middle part is subcylindrical; and upper part is widely expanded, but the expansion is mechanically exaggerated on the right side by the apparent pressure from the slanted second goblet. This same pressure could have also caused the healed fractures in the middle-upper part of the first goblet. The bulbous base of the second goblet appears to be the membrane of a germinated spherical conidium, from which has apparently risen the third goblet: it is tightly inserted in the second one, and is broken into three parts. The basal and middle parts are solid and narrowly cylindrical; the upper, which has a narrow central lumen, resembles the " empty pseudovagina" of *Chamaesiphon polymorphus*, Fig. 10. The whole combination of 2nd and 3rd goblets in *P. cumingsi* is much like " single cell with pseudovagina " of *Chamaesiphon fuscus* (FRITSCH, 1945/52, FIG. 315A),— see Fig. 9. The 1st generation fossil goblet is distinctly yellowish; the next goblets are practically colourless.

Comparison — Differs from *Prochamaesiphon geitleri* Elias by the uniformly thick wall in the 1st and 2nd goblets, by gradual tapering of the immersed basal part of the 1st goblet, and by the presence of the thick-walled pseudovagina in the 3rd goblet; but the size and shape of the 2nd goblet and that of *P. geitleri* are quite alike. The particular resemblances to the modern species of *Chamaesiphon* were already mentioned.

Occurrence — Together with *Ordovicimyces gallowayi* Elias in zooecia of the Ordovician *Nicholsonella cornula*,— for details see the occurrence in the description of the latter.

Prochamaesiphon geitleri sp. nov.

Pl. 1, Fig. 8

Description — The only known individual is a goblet with a sharply differentiated, narrowly cylindrical base, immersed in the substratum; and with a lumen as wide as the thickness of the wall, Goblet expands sharply directly above substratum, but the thickness of its walls remains the same to its middle, above which the walls begin to thicken gradually, up to twice as thick at flaring rim. Basal inner part of goblet above substratum is occupied by pseudovagina with a narrow, but upwardly expanding lumen. Dark band above its oblique terminal edge could be a thickened undifferentiated cytoplasm.

Comparison — Differs from *Prochamaesiphon cumingsi* Elias by substantially greater thickness of wall in distal half of goblet, and by differentiation of its immersed basal part into a straight thick-walled tube.

Occurrence — Single individual in zooecium of *" Batostomella " polyspinosa* (CONDRA) Girty, in South Bend limestone, Missouri series, Upper Pensylvanian, at South Bend, Nebraska. Thin section 29-14-3-52 (DON SLAMA).

Prochamaesiphon sp.

Pl. 1, Fig. 12b (b in 12)

Empty, thin-walled, gently curved goblet, gradually tapering upwards. Basal part obscure, terminal slightly contracted. Wall very gradually thickening upwards. Small cluster of spherical aplanospores (?) above the distal edge apparently escaped from the goblet.

Comparison — Resembles *Chamaesiphon sideriphilus* in general shape and curvature of goblet (GEITLER, 1932, FIG. 251),— Fig. 11.

Occurrence — Together with *Propythium carbonicum* and *Prochamaesiphon geitleri* — see the occurrence of these species.

Class PHYCOMYCETAE

From time to time the mycologists have advanced various theories on origin and evolution of fungi. All these theories were based on comparative study of the recent forms only, because no fossil fungi of any phylogenetical significance have ever been discovered. The present description of several genera of true fungi in a few marine bryozoans (Ectoprocta), extant and fossil, constistute by far more complete information on the marine " algal fungi " than previously recorded. This information includes microscopic details pertaining to asexual and sexual reproduction of both extant and extinct fungi, in as far as can be judged by the various mummified stages of their life-cycles. Good preservation of these has been provided by their entombment within the sealed zooecial chambers (filled with calcite in fossils) of the bryozoan colonies, ranging in age from Ordovician to Present.

In my opinion, the new evidence gives qualified support to the views by DeBary (1887), Atkinson (1909), Gäumann (1952), and others, who suggested that more than one major group of algae, rather than protozoa, gave rise to the Phycomycetae (" algal fungi "). All of the presently described marine endobryozoic fungi belong to this class; and the comparative study tends to indicate their origin from certain filamentous Green algae,— as discussed below. Furthermore, this evidence tends to support the elevation of the oögamous fungi into an order (GÄUMANN). This is indicated particularly by an apparent existence of a transitional, algo-fungi group, in Ordovician time, from which the oögamous fungi apparently originated.

Order SAPROLEGNIALES *sensu* SMITH (1938), em. ELIAS

The order is close to " Oomycetes " (OOMYCETALES) *sensu* Gäumann Wynd (1952), who include in it, however, the family Peronosporaceae *sensu lato*, that embraces the " subfamily Pythiaceae " (1952, p. 61); whereas Smith (1938, p. 399) placed Pythiaceae in his Saprolegniales (accepted here), and has elevated the remaining Peronosporaceae to the rank of a separate order Peronosporales, whose genera are all parasites on land plants.

Pythiaceae, on the contrary, are largely aquatic; but among them, as well as among other Saprolegniales, many species are saprophytic, adapted to moist terrestrial habitat (such as soil).

The principal present emendation to Smith's 1938 understanding of Saprolegniales is the addition to the order of the aquatic family Monoblephariaceae. DeBary has already accorded it the most primitive position within his " *Ascomycetous series* or *Main series of Fungi* composed of Phycomycetes, Ascomycetes, and Uredineae " (DEBARY, 1887, p. 120). Becuase DeBary has not included in his " Main Series " the Chytridiales, the Monoblephariaceae became the lowest family in it; and DeBary justified his placement of this family in the " Main Series " by pointing out that the species of *Monoblepharis* (still the principal genus of the very small family) " resembles the Pythiaceae in their vegetative structure and in their mode of life " (DEBARY, 1887, p. 140).

No flagellae have been found preserved in the fossil fungal spores described here; hence, it is impossible to consider the presence of one or two flagellae in their taxonomy and phylogeny. This omission may not be particularly important in view of the opinion by the mycologist Atkinson (1909, p. 457), that even in the case of the extant Chitriales, the appearance of both uniciliate and biciliate zoospores in its species " need not . . . militate against the idea of regarding them as forming a phylogenetic series. The uniciliate ones may have arisen from the biciliate ones by the division of the biciliate ones being carried one step further."

All the observed spores in the presently described fungi appear to be encysted, or aplanospores; but there are many other morphological peculiarities in them, which are useful in the determination of their relationships to the previously known fungi.

Characteristics — The following characteristics of the Saprolegniales are restricted to those peculiarities which is possible to recognize or comprehend from the study of the described new genera *Heteroporimyces* (Recent), *Propythium* (Pennsylvanian), and *Ordovicimyces* (Ordovician). Their mycelia are attached to the inner walls of some Cyclostomata (Stenostomata) and Trepostomata, and were studied in thin sections prepared from the containing bryozoans, and viewed under high magnification (up to ×1400).

The wording of the characteristics is largely that of Bessey (1950), and partly of Coker (1923), with a few additions based on personal comparative analysis and observations — these are italicized.

Mycelia stiff, in general not provided with true septa, except to fence off its sporangia and gametangia, or portions of the mycelium that have exhausted their *cytoplasmic* contents, or *occasionally in no relation to reproduction*; *occasional presence of septa in vegetative hyphae is apparently inherited from ancestral algae.* Reproductive organs mostly terminal or subterminal on the external (above substratum) hyphae and their branches. Saprophytic, parasitic, *or symbiotic*, spoken of usually as *water molds.*

The zoosporangia are of the same diameter as the hyphae or somewhat enlarged, elongated, subspherical or spherical, smooth or spinose. At their inception the cytoplasm from the lower portion of the hyphae flows and concentrates into the terminal portions destined to become zoosporangia until these are filled with dense cytoplasm. It is eventually transformed into zoospores. Escape of the zoospores occurs through the softened tip or through a lateral papilla. In some cases the primary zoospores apparently produce no flagellae (*as in the new* *genera here described*), but creep to the opening or papilla of the zoosporangium, and there encist within it as separate round cells (*aplanospores*). In some species the encysted zoospores do not escape at all, but germinate directly by germ tubes within zoosporangium (*such as in the described Heteroporimyces*).

Coker observes (1923, p. 92-93) that " in the primitive *Protoachlya paradoxa* (COKER) a sporangium emptied and all the spores were expelled to some distance from the opening, all remaining in a group as if held lightly together, and all coming to rest at once in group . . . [thus indicating] that spores are expelled by sporangial turgor in this family and not by their own power."

In *Saprolegnia* (*and also in Ordovicimyces*) new sproangia may be formed within the empty ones. *In some species the upwardly flowing cytoplasm forms a narrow, apparently dense subcentral strand*, as shown by Coker (1923, PL. 21, FIG. 5; PL. 22, FIGS. 5, 7) in some proliferating zoosporangia; see also in Bessey (1950, FIG. 35-A, after COKER). Similar strands traverse subcentrally some hyphae in *Ordovicimyces*.

Marine and estuarian Saprolegniales. Only a few of these have been recently diagnosed briefly and illustrated scantily by Johnson & Sparrow (1961, p. 328-338; FIGS. 118-125): three species of *Leptolegnia*, four of *Thraustochytrium*, and one of *Japonochytrium*; also four species of *Pythium*, family Pythiaceae.

The first occurrence in trepostomatous bryozoans of a fungus-like coenocytic tube, containing spherical spore-like bodies, was recorded by Etheridge (1892, p. 95, PL. 3). He discovered it in *Stenopora crinita* Lonsdale from the " Permo-Carboniferous of New South Wales and Queensland," Australia. He named the spore-bearing tube *Palaeoperone endophytica*, and compared its spores with those of *Saprolegnia*. When summarizing this and other occurrences of " tubular cavities " in fossil invertebrates, Seward (1898, p. 215) commented: ". . . it is almost impossible to decide how far these tubes in shells and corals "... where at that time Nicholson classified the paleozoic bryozoan *Stenopora* ... " should be attributed to fungi, and how far to algae."

The presently described *Monoblepharis thalassinosus* and *Heteroporimyces spinosus* is the first recognition of Saprolegniales in modern Trepostomata (where the family Heteroporina has been classified by Borg, 1944, p. 19; previously referred to Cyclostomata, Borg, 1933, p. 373).

The same or closely related fungi have been, however, repeatedly briefly mentioned and crudely illustrated as the bryozoan's own mural " spines," " hair-like teeth," etc., in various Stenolaemata (Cyclostomata and Trepostomata) in the Recent, Cenozoic, Cretaceous, and Paleozoic seas.

Family MONOBLEPHARIACEAE

(Order Monoblepharidales of authors)

The family contains very few genera, only two of which, " *Monoblepharis* and *Monoblepharella*, have been studied extensively " (GÄUMANN & WYND, 1952, p. 51). The genus *Gonapodya*, with periodic constrictions of the hyphae similar to those in many Monoblephariaceae, was placed among them by Smith (1938, p. 386), but is removed by Gäumann & Wynd (1952, p. 72) to Leptomitaceae, a family classified by Smith (1938) with Saprolegniales.

Fitzpatrick aptly describes the mycelium of *Monoblepharis* (his description fitting also all species of Monoblephariaceae) as " coenocytic . . . [whose] cytoplasm forms a network of meshes which are regular in size and form, a strikingly uniform vacuolation resulting. The strands of protoplasm tend to cross the hyphae at right angles rather than to run longitudinally as in Saprolegniales " (FITZPATRICK, 1930, p. 139; see PL. 2, FIGS. 27, 28). This tendency is observable also in the hyphae of *Sapromyces*, family Leptomitaceae (see SMITH, 1938, TEXT-FIG. 219-A, C).

All Monoblephariaceae are " aquatic saprophytes that grow in permanent pools of clear fresh water. They are usually found on dead twigs of various trees, but they have also been found on other substrata " (SMITH, 1938, p. 386), " such as animal cadavers (insects?) " (SPARROW, 1933, p. 518).

Because the endozoic marine *Monoblepharis* (?) *thalassinosus* described below is established on a single, although well developed fertile hypha, it is classified with *Monoblepharis* provisionally. It is the first occurrence of the genus in a typically marine bryozoan, to the zooecial wall of which it is firmly attached by a deeply immersed hyphal base, with no evidence of rhizoidal system (so typical for Monoblephariaceae and Blastocladiaceae). Finding of additional hyphae of *M. thalassinosus* is desirable for its differentiation into a new, strictly marine genus of the family Monoblephariaceae.

Phylogeny — When discussing phylogeny of Monoblepharidales and the related Blastocladiales, Gäumann & Wynd (1952, p. 45 and 53) state that "it is not reasonable to seek for their phylogenetic precursors among the autotrophic green algae because there are no analogous algal forms possessing one trailing flagellum" (*ibid.*, p. 45). They propose, instead, that these two "orders" have originated from Flagellatae through Chytridiales (*ibid.*, FIG. 1). On the other hand, they indicate Siphonales as an ancestral stock for Oomycetes (in which Monoblephariaceae are not included).

It may be pointed out, however, that some Green algae, particularly *Sphaeroplea* of Ulotrichales, are morphologically close to Monoblephariaceae. The somewhat isolated genus *Sphaeroplea* has unbranched coenocytic filament in which subequal, wider than high, vacuoles are developed, divided by thin transverse concave discs built by parietal chloroplasts; and the thin wall of the filaments, where vacuolation is developed, has its thickness increased by an internal layer of cytoplasm. Indeed, the spermatozoids in this genus are biflagellate, and so are the swarmers. However, in *Sphaerocladia* and *Allomyces* of Blastocladiales, wherever the uniflagellate female and male planogamets are united, they make a biflagellate zygote.

Monoblepharis (?) *thalassinosus* sp. nov.

Pl. 2, Fig. 26

Description — Only one hypha known. It is a slender upright tube, with a slight offsetting deformity, apparently indicating a degree of laxity prior to maturity. Hypha has an attractive blue-green (wall) color; it is 70 μ long above substratum (which is the zooecial wall), where its base is deeply immersed. Primary (vegetative) tube 55-60 μ long above substratum, slightly tapering in lower non-vacuolated half, from 7 to 5μ in diameter; upper part regularly divided by twelve transverse cytoplasmic strands into thirteen 2·5-3 μ high vacuoles. Terminal vacuole bulges the hypha to 6 μ in diameter.

Secondary tube is extruded, as it were, from the bulging terminus of the primary one, with initial diameter of 3·5 μ, and expands into a clavate structure with 4·5 μ maximal bulge. It may be considered an immature oogonium, crowned by an immature palmate antheridium.

Hyphal wall invariably 1 μ thin, but has an additional internal cytoplasmic layer within the vacuolated part.

Discussion — Differs from freshwater species of Monoblephariaceae by endozoic marine habitat, blue-green color, terminal flange-like (bulging) expansion of primary tube, and extrusion-like iniciation of secondary, oogonium like tube.

Occurrence — Occurs in same zoarium of *Heteropora neozelanica* where *Heteroporimyces spinosa* Elias is abundant, but does not grow in the same zooecia with the latter fungus.

Family PYTHIACEAE

The following characteristics of Pythiaceae are modified from those formulated by Gäumann & Wynd (1952, p. 61) for the Peronosporaceae *sensu lato*, inclusive "subfamily" Pythiaceae.

"The zoosporangium . . . is significantly different from the mother hypha," and "the supression of fertility has led to the maturation of only one oospore in the female gametangium or oogonium. The oospore always is surrounded by a peripheral layer of vegetative cytoplasm called the periplasm."

The Peronosporaceae, which are separated from Pythiaceae by Smith, differ from the latter family "by the development of the conidia" in which the zoosporangia become detached from the mother hypha and are scattered by wind; and they all "have a branching sporangiophore projecting beyond the host" (SMITH, 1938, p. 400).

Many previously described fossil "Saprolegniales", whose names imply affiliation with *Peronospora*, should be placed rather in Pythiaceae. Such are the Carboniferous *Peronospora* Smith (1877) and *Peronosporites antiquarius* Smith (1877, p. 499), which are encountered in the cells of the apparently submerged dead stems and barks of *Lepidodendron* (see SEWARD, 1898, p. 215-219). To Pythiaceae belong also the fossil *Palaeomyces gracilis* Renault (1896), *Protomycites protogenes* (W. SM.) Meschinelli (1902) and the numerous species of the "form-genus" *Palaeomyces* established by Kidston & Lang (1921, p. 857-870).

Genus *Propythium* gen. nov.

Diagnosis — Hyphae fully endobryozoan, straight, usually non-septate, except when old, and in no connection with zoosporangia (FIG. 14). Periplasm mostly not developed; or, on the contrary, becomes very thick and may extend over the adjacent hypha (FIGS. 17, 18). Rhythmic transverse vacuolation occasionally develops in distal part of the narrower than usual, apparently vegetative hyphae (FIG. 13). Apical papillae of varied length are frequently developed. Antheridia, if correctly so interpreted (FIG. 12-a), are developed far from oogonia.

Comparison — Differs from the above named fossil Pythiaceae by the prominently developed apical papillae, and long and straight tubular hyphae. Differs from *Peronospora* and other Peronosporaceae *sensu stricto* by these same characters, by the absence of branching of hyphae, and the absence of independent conidia. Differs from the nearest to it *Pythium*, *Pythiopsis*, and *Pytophtora* by much straighter hyphae, longer hyphae-like apical papillae, and development of antheridia — if any — far from oogonia.

Propythium carbonarium sp. nov.

Pl. 1, Figs. 12-20

Description — Hyphae 10 to 20 μ long, straight to slightly bent or curved, unbranching, with uniformly thin wall, thicker at maturity. Occasional rhythmic vacuolation in vegetative hyphae (FIG. 13).

Typical apical papillae (FIG. 12 below, and FIG. 14) are comparable to " normal papilla" in *Pythium helicoides*, which are 2½ times as long as wide (MIDDLETON, 1943, p. 78, FIG. 6-C), Fig. 23.

Oogonia-like reproductive bodies are intercalating to subapical in hyphae (FIGS. 17, 18), somewhat angular when young (FIG. 13), becoming spherical when reaching maturity (FIG. 12c, 16-18). A possible antheridium (FIG. 12a) is developed in a hypha which bears no oogonium.

Only one cytoplasm-filled oospore was observed (FIG. 12c). The spherical bodies in the cytoplasm are of varied diameter and are apparently homologous to " reserve globules " and " refringent bodies," so described in four " exceptional " species of *Pythium* by Middleton (in TOMPKINS *et al.*, 1939, p. 6; also 1943, FIGS. 6, 7), Fig. 25, 79.

Comparison — Differs from the *Peronosporites antiquarius*, the nearest to it among the fossil Pythiaceae, by the absence of branching, the absence of transverse septa under oogonia-like bodies, and by intercalated development of some of them. *P. carbonarium* is decidedly more primitive than the latter, and it differs from the only known marine species of *Pythium*, *P. marinum* Sparrow (1934), by straighter and unbranching hyphae, and the absence of the transverse septa under oogonia-like bodies and of appressoria.

Occurrence — Common in mature (cortical) region of " *Batostomella* " *polyspinosa* (Condra) Girty, together with rarely occurring *Prochamaesiphon geitleri* Elias; in Southbend limestone, upper part of Missouri series, upper Pennsylvanian, near South Bend, eastern Nebraska.

Family HETEROPORIMYCEAE fam. nov.

The new family is proposed for the single new genus *Heteroporimyces* because it differs strikingly from all other extant Saprolegniales by being the only extant genus occurring in a marine bryozoan, and there is an indication in it of a peculiar sexual process within zoosporangia, as described below. Further investigation may result even in removal of the family from Saprolegniales.

Genus *Heteroporimyces* gen. nov.

Characteristics — Hyphae mostly stout, coenocytic, unbranching, growing upright from zooecial walls of bryozoan colonies, with blunt bases immersed in the walls without development of rhizoids. Zoosporangia terminal on hyphae, differentiated from them by slight expansion and development of spines. Zoosporangia not separated by transverse septa. Encysted spherical zoospores (aplanospores) germinate inside zoosporangia.

Heteroporimyces spinosa sp. nov.

Pl. 2, Figs. 29-43

? 1880. " Septal spines " in *Heteropora neozelanica*, Nicholson: *Ann. Mag. nat. Hist.*, ser. 5, v. 6, p. 336.

1933. " Spine-like processes " in *Heteropora neozelanica*, Borg: *Zool. Bidr. Uppsala*, Bd. 4, p. 313; Text-fig. 3; Pl. 7, Fig. 2-sp.

Description and interpretation — Mycelium in form of unbranched, usually stout, more or less straight hyphae, with no specialized haustoria, but with immersed blunt base, probably gradually sinking in the zooecial wall by mere accreation of the latter. Hypha seemingly germinates from a " resting spore" (FIG. 29) by protrusion from its heavy (2 μ thick) enclosing wall, similar to the germination of the chlamidospore in *Protomyces* (GÄUMANN & WYND, 1953, FIG. 100).

Slight terminal expanse of hypha develops into a larger subspherical spinose zoosporangium, which is not separated, however, by a constriction or septum. Diameter of hyphae varies from 4 to 7 μ, with almost imperceptible distal tapering, if any. Height of adult hyphae mostly 15-20 μ, a few growing to 30 or even up to 90 μ (FIG. 38). Walls maintain uniform thickness of about 1 μ.

Young sporangia are bluntly spinose or papillose (FIGS. 31, 32), becoming sharply spinose at maturity (FIGS. 33-34). Cytoplasm ascends toward zoosporangium where it becomes transformed into about 1 μ wide, rounded, apparently encysted zoospores (aplanospores) (FIGS. 31-35), which fill the periphery of the sporangium. The spores which enter spines, usually one in each, germinate there, at least occasionally, sending their germinal tubes toward central vacuole of the sporangium (FIG. 37). The exceedingly small, about 0·3-0·4 μ dark spheres at the sharp tips of spines (FIG. 36) resemble in their size and location the " non-functional nuclei" which are formed in the course of sexual process in *Basidiobolus ranarum* Eid., one of the most advanced species of the order Zygomycetes (as per GÄUMANN & WYND, 1952, p. 73). In the light of the observation on this process by Fairchild (1897, reviewed by GÄUMANN & WYND, 1952, p. 91, FIG. 81), Figs. 44, 45, and the presence of the larger spherical bodies (aplanospores) in the described spiny zoosporangia, I postulate the following hypothetical sexual process in them: cytoplasm in zoosporangia differentiates into smaller male and larger female bodies, the male tending to drift into the spines. Functional female bodies approach them, are fertilized by them, and then germinate inside zoosporangium. Non-functional male bodies reach the tips of spines and eventually disintegrate (FIGS. 36, 37).

T-shaped termini in some short hyphae may be interpreted as remnants of emptied zoosporangia (FIGS. 38, 39). Irregularly shaped bodies adhered to the upper part of the broken, unusually long hypha (FIG. 38, left) perhaps are mere abortive spores breaking through the lateral wall of this abnormal hypha.

Occurrence — Growing immersed in and perpendicular to zooecial walls in mature zone of *Heterospora neozelanica*, dredged off Stewart Island near the southern coast of New Zealand. The colonies of this same species with similar hyphae of *Heterosporimyces spinosa* studied by Borg (1933, p. 306-317, TEXT-FIG. 13) were dredged from " a depth of 40 m. . . . at Stewart Island or at the Campbell Islands (Perseverance Harbor . . .)" (*ibid.*, p. 307).

Family ORDOVICIMYCEAE fam. nov.

The new family is proposed for the single genus *Ordovicimyces* Elias, whose origin appears to be different from that of the other Saprolegniales. The modern Saprolegniales are considered to be evolved from the Siphonales algae, or from some unicellular coccoid member of the Xantophyceae (GÄUMANN & WYND, 1952, p. 55); whereas the described *Ordovicimyces* appears to have evolved from an ancient stock of septate filamentous Chlorophyta. The recent discovery of the numerous and highly advanced genera of Siphonales (KORDE, 1961, p. 60-71)[1] in the early Cambrian of the south central Siberia shows that this order has differentiated from the rest of Chlorophyta already at Cambrian and probably even pre-Cambrian time; and now the presence in an Ordovician bryozoan of an apparent evolutionary development of a fungus from a septate filamentous Green alga indicates the existence at this same and even earlier time of similar septate filamentous chlorophytes.

Because the numerous individuals of *Ordovicimyces* display assorted combinations of algal and fungal morphology, a combination of both algal and fungal terminologies are appropriately used in their description.

Genus *Ordovicimyces* gen. nov.

The genus is based on a single marine endobryozoan species. It unites the individuals

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[1] I take this opportunity to state that the latest, more detailed evidence favoring the algal nature of the siphonal *Cambroporella* Korde (1950) and of *Chabakovia* Vologdin (1939), now published by Korde (1961, p. 66-68, Text-fig. 24; pl. 5, Fig. 3, 4; p. 127-128; pl. 24, Fig. 3-6), and the illustrated thin sections cordially demonstrated to me by Korde in 1963, fully convinced me in the correctness of her and Vologdin's algal interpretations. Therefore, I no longer consider either *Cambroporella* a bryozoan, or *Chabakovia* as belonging to the American Carboniferous foraminifer (Elias, 1950).

in which the following characters are encountered in various combinations with each other:

1. Growth forms, which in shape, size, and septation, resemble that of germlings of various extant filamentous algae;
2. Unseptate, coenocytic, hyphae-like growth forms, with complete or partial development of a subcentral, apparently cytoplasmic strand, a character known to occur only in some extant Saprolegniales.
3. Individually developed transverse septa, whose complex structure is very similar to that known only in certain extant representatives of the orders Ulotrichales (particularly the suborders Spheropleineae), Cladophorales, and Chaetophorales;
4. Rare, individually developed double-septa with remains of cytoplasm sandwiched in between.

Ordovicimyces gallowayi sp. nov.

Pl. 2, Figs. 46-67

1915. "Excessively minute, apparently hollow, spines, projecting into zooecial cavity" of *Nicholsonella cornula*. Cumings & Galloway: *Bull. geol. Soc. Amer.*, vol. 26, p. 358; Pl. 13, Fig. 32-39.

Description — Unbranching hypha-like filaments, mostly slightly tapering distad; some (Fig. 46) resembling "phialides" of *Aspergillus* and *Bombardia* (Gäumann & Wynd, 1952, Fig. 106, 184, 185); very few with slight medial bulge (Fig. 47, left, Fig. 53); some with slight to substantial, usually lopsided basal bulge (Figs. 49-51); terminated by smooth, subsphaerical to elliptical zoosporangium; it is differentiated by a slight, abrupt expansion (Fig. 46), and is occasionally accompanied by slight constriction (Figs. 50-53); few hyphae have a shape of an inverted funnel (Fig. 52). Hyphae have few transverse septa or none; septa are simple or complex, greatly varying in structure and location; where two or three are developed they are mostly simple and as thick as the walls (Figs. 48, 49); complex septa are extremely variable; some consist of two to three layers (Figs. 54, 55), and may have a very narrow or moderately wide central hole (Fig. 55), similar to the septa originating by growth of an "annular bar" so characteristic for *Cladophora* (Fritsch, p. 234, Figs. 69-D, E, I); other complex septa have asymmetrical development of one or two layers (Figs. 54, 63), similar to the septa in *Sphaeroplea* (Fritsch, 1929, p. 22; Fig. 66-H, J)—Fig. 73, 75. Wherever two ordinary septa develop close together, the dense cytoplasm caught between them (Fig. 56) makes the whole structure look much like the doubled septa at the base of the sporangium in *Sphaeroplea africana* (Fritsch,. 1929, Fig. 2-E),—Fig. 76.

Septa which occur at the base of zoosporangium, or at the top of basal hyphal bulge are usually simple.

Septate hyphae are almost always empty (and so are many coenocytic hyphae), as if no cytoplasm capable of producing spores has developed in them. One of the hyphae has its cytoplasmic strand in central (axial) position below a complex septum (Fig. 54); in another hypha there is a central strand only above a narrowly perforated septum (Fig. 55), as if the solidification of the upwardly flowing cytoplasm in a strand occurred after all of it has flown through the septum.

A few coenocytic hyphae are traversed throughout their length by a subcentral strand (Fig. 51; 52 left; 53), much like in *Saprolegnia* (Bessey, 1950, Fig. 35-A), *Conidiobolus* (*Ibid.*, Fig. 60-A), and other Phycomycetes. Most demonstrative is the concentration of dense cytoplasm in the upper part of a secondary coenocytic hypha, and a central strand trailing down the hypha below (Fig. 57); this secondary hypha is inside a transluscent, apparently non-functional primary hypha.

Zoosporangia vary greatly in size, shape, and orientation. A typical blunt or somewhat acuminate columella is developed in many zoosporangia (Fig. 46, 51, 54,), usually directly above the upper end of strand. Columella remains intact after discharge of zoospores (aplanospores), and apparently seals effectively the emptied hypha; whereas zoosporangial walls apparently disintegrate after discharge of the spores (Fig. 47, 60).

Apparently encysted zoospores (aplanospores) develop from cystoplasm in functional hyphae, in some cases apparently only within their zoosporangia. Aplanospores are subspherical, about 1 μ in diameter, with no recognizable flagella.

They apparently creep out of zoosporangia in loosely bound multitude, as indicated by the habitual adherence of their clusters to the outer surface of functional hyphae, close below zoosporangia in which they have originated (Fig. 58, 60).

Some sporangia undoubtedly have had terminal opening (FIGS. 53-55).

Some hyphae have adhered to substratum by variously expanded (FIGS. 51-53) and festooned (FIG. 55) base; others have subhemispherical basal expansion (FIG. 48), resembling " flattened zoospores " in *Oedogonium rutescens* alga (FRITSCH, 1935/1945, FIG. 93-C); some have lopsided basal bulge (FIGS. 50, 51), resembling that in stalked sporangia of *Trentepohlia* and other Chaetophorales (FRITSCH, 1935/1945, FIG. 85-J, K), — Figs. 69-71.

However, most hyphae have a more or less blunt basal extension, immersed in zooecial wall, and apparently serving as a rudimentary haustorium. By this means the hyphae could have obtained nourishment from organic strands, which intermingle with the calcite of walls in the stenolaematous bryozoans.

Length of mature hyphae above substratum 15 to 30 μ, the average closer to the higher figure; diameter from 3-4 μ below zoosporangium to 4-6 μ in middle part, and from 6 to 20 μ at base of hyphae. Thickness of wall 0·5 to 1·5 μ, rarely locally to 2 μ.

Hyphae very rarely bifurcate (FIG. 61) and trifurcate (FIG. 62). Zoosporangia occasionally display incipient proliferation (FIG. 65); and normally developed secondary hyphae develope inside the abnormally swollen, transluscent primary hyphae, somewhat like the " secondary sporangia " in *Pythium* (MIDDLETON, 1943, FIG. 7-B; see also BESSEY, 1950, FIG. 40-g),— Fig. 79.

Discussion — The described Ordovician microfossil could hardly be expected to fit into this or that of the extant orders of algae or fungi, and its postulated relationship to a hypothetical ancient stock of filamentous Green alga is meant as a broad approximation. Indeed, the described characters, when considered separately, can be found in this or that taxon among the extant representatives of more than one major order of algae. The suggested ancestral stock for the microfossil, as can be noticed in the description, is influenced by the evidence of the structure of the complex septa, and ,to less extent, of the shape of the hyphal bases, that appear so strikingly similar to the corresponding structures in the orders of Sphaeropleineae, Cladophorales, and Chaetophorales; their broad relationship to each other calls for a logical assumption of an original common stock, and from which *Ordovicimyces* could have evolved. The surprising evidence of the existence in early Cambrian of the highly evolved representatives of Siphonalee, which order is elevated by Korde to the status of Siphonocladineae (KORDE, 1961, p. 60), implies its early differentiation from the rest of the marine benthonic Chlorophyta, and it is the septate group among them, from which *Ordovicimyces* appears to have been evolved.

Ordovicimyces (?) *recensis* sp. nov.

Pl. 2, Fig. 68

Only two hyphae recorded; the better preserved illustrated (FIG. 68).

Simple tubular uprights, deeply rooted in zooecial wall of *Heteropora neozelanica.* Non-septate, except apparently an inverted cone-like septum separating subspherical zoosporangium, which is only slightly expanded above very narrow and shallow hyphal constriction. Small columella (?) is an apparent prolongation of the septum.

Discussion = Resembles some non-septate hyphae of *Ordovicimyces spinosa* Elias but differs by shape of columella (?), and thinner hyphal wall. It may be considered a " living fossil " closely related to the Ordovician *O. spinosa.*

Occurrence — Solitary hyphae in zooecia of *Heteropora neozelanica*, where *Heteroporimyces spinosa* is abundant.

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EXPLANATION OF PLATES

Algae

1. *Porphyra* (?) cf. *pelliculata* Elias. " Denticles circavité " of Pergens, 1889, fig. 1; in *Mecyconoecia* (*Entalophora*) *proboscidea* (Milne-Edw.) Canu and Bassler, 1920. Cretaceous. × 800.

2, 3. Conchocelis phase of *Porphyra drewae* Elias, new species; in walls of *Heteropora pelliculata* Waters. Tatarskii Zaliv (Gulf), near Sakhalin and Yezo Islands.

2. Primary and secondary boring filaments. × 480.

3. Fertile cell-row and sub-transverse plant-initial (?). × 960.

4-6. " *Conchocelis rosea* " phase of *Porphyra umbilicalis* (L.) var. *laciniata* (Lightf.) J. Ag. Cultivated in " shell " by Drew. After Drew, 1954.

7. *Prochamaesiphon cumingsi* Elias, gen. et sp. nov. with apparently mucilaginous inner pseudovagina. Middle Ordovician, Illinois. Univ. Indiana slide 150-5. × 660.

8. *Prochamaesiphon geitleri* Elias, sp. nov. with empty basal pseudovagina. Upper Pennsylvanian. Nebr. Geol. Survey slide 14-3-52-29. × 660.

9, 10. *Chamaesiphon polymorphus* and *C. fuscus*. After Geitler, 1931, fig. 253; — see Fritsch, 1945/52, fig. 315, A, E.

9. A single cell with pseudovagina. × 660.

10. Empty pseudovagina, in which the inner layers have become mucilaginous. × 660.

11. *Chamaesiphon sideriphilus* Starmach. From Geitler, 1929, Text-fig. 251 (after Starmach). × abt. 600.

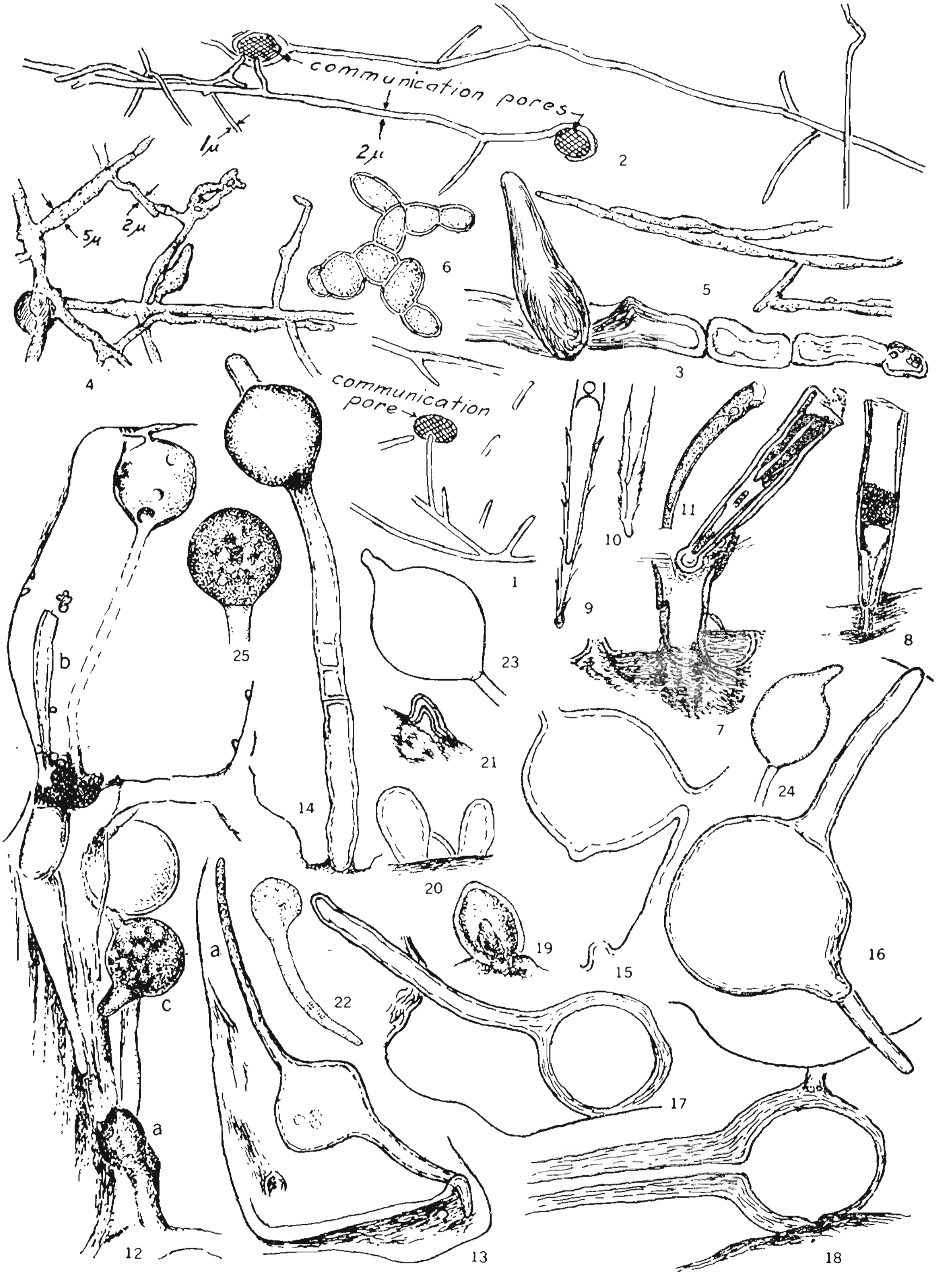
Figs. 2-6, 9-11 Extant, Figs. 1, 7, 8 Fossil.

Fungi

12-21. *Propythium carbonarium* gen. et sp. nov. In " *Batostomella* " *polyspinosa* (Condra) Girty. Upper Pennsylvanian, Nebraska.

Fig. 12, 13. Slide SB-X-14-3-52.
Fig. 14. Slide SB-39-14-3-52.
Fig. 15. Slide SB-29-14-3-52.
Fig. 16, 17, 19. Slide SB-40-14-3-52.
Fig. 18. Slide SB-42-14-3-52.
Fig. 12, 13 × 200; Fig. 14-18, × 340; Fig. 19 × 660.
Fig. 20. Bag-like hyphae (?), × 660. Slide SB-29-14-3-52.

21. Very young primary and secondary hyphae (?), × 660.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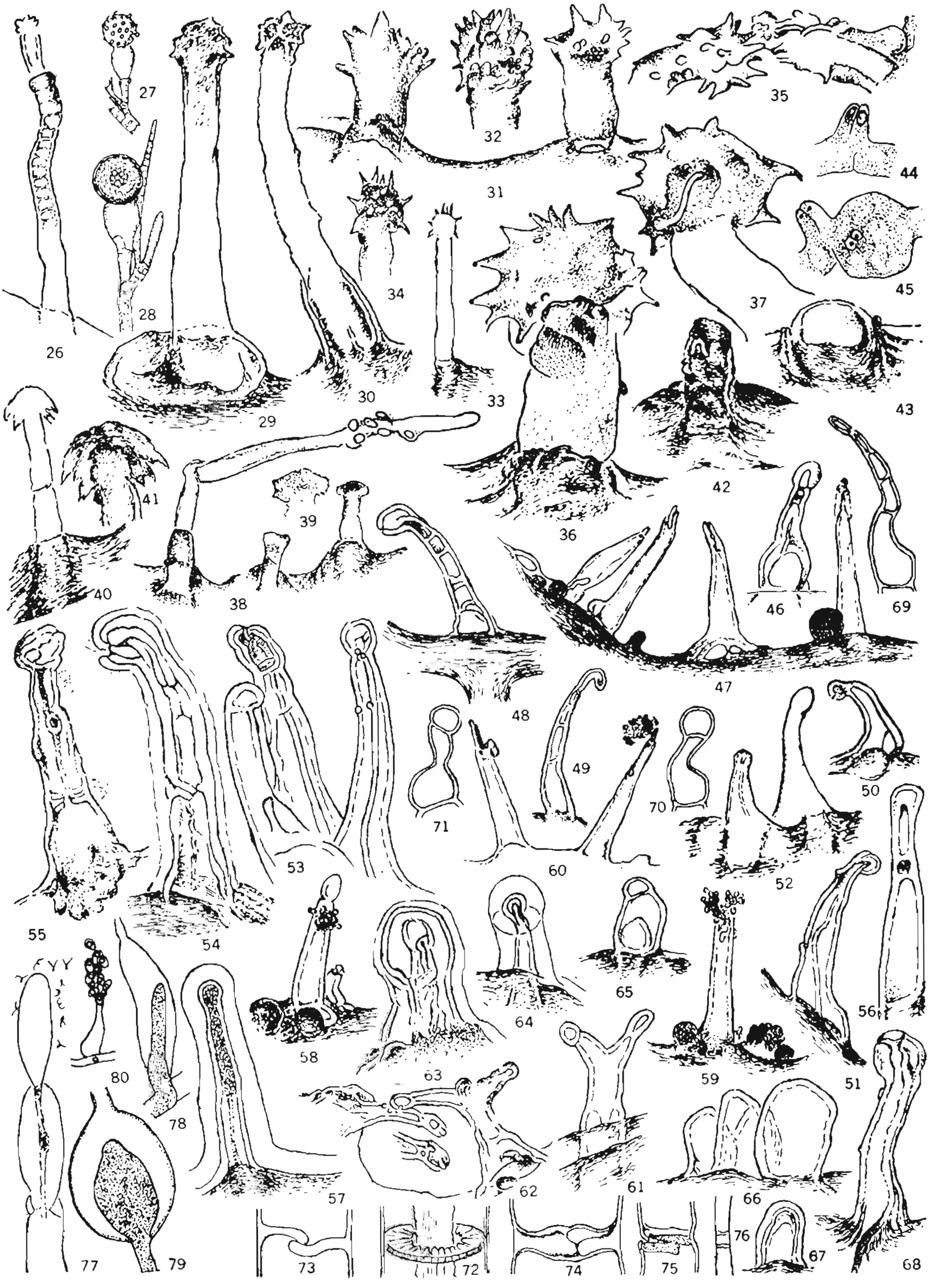
FIGS. 1-25.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Figs. 26-80.

22. *Monoblepharis polymorpha* Cornu. Germinating zoospore, × 800. After Sparrow, 1933, Text-fig. 1-h.

23. *Pythium helicoides* Drechsler. Sporangium with "normal papilla." Fresh water and soil. Produced in cultivation. From Middleton, 1943, Text-fig. 6-C. × *ca*. 750.

24. *Pythium anandrum* Drechsler (Middleton). "Skewly beaked" sporangium. Fresh water and soil. From Middleton, 1943, Text-fig. 16-B. × *ca* 750.

25. *Pythium* sp. vesicle with contents not fully differentiated. Composite mostly from Middleton, 1943. × *ca* 750.

26. *Monoblepharis* (?) *thalassinosus* sp. nov. × 660. Slide HNZ-1.

27, 28. *Monoblepharis macrandra* (Lagerheim) Woronin. × 250. From Sparrow, 1933, Pl. 20, Fig. 29 and 14.

29-43. *Heteroporimyces spinosa* gen. et sp. nov. Slide HNZ-1.

Fig. 29. Development of hypha from resting (?) spore. × 1330.

Fig. 30. Young hypha. × 1330.

Fig. 31, 32. Adolescent hyphae. × 1330.

Fig. 33. Mature hypha. × 660.

Fig. 34. Zoosporangium of same (Fig. 33). × 1330.

Fig. 35. Mature hyphae, with scattered aplanospores in zoosporangia and in adjacent parts of hyphae; some spores in various stages of germination. × 1330.

Fig. 36. Mature hypha with non-functional male (?) nuclei in tips of spines. × 2000.

Fig. 38. Broken long hypha and remnants of emptied hyphae. × 660.

Fig. 39. Detail of Fig. 38. × 1330.

Fig. 40. Hypha with wilted emptied zoosporangium, × 660.

Fig. 41. Detail of Fig. 40. × 1330.

Fig. 42. Non-functional hypha. × 1330.

Fig. 43. Initiation of secondary hypha inside stump of primary hypha. × 2000.

44, 45. *Basidiobolus ranarum* Eidam. Copulation and development of zygospore. Small circles (Fig. 45) are non-functional nuclei. After Gäumann and Wynd, 1952, Text-fig. 81-1, 2. × 500.

46-67. *Ordovicimyces gallowayi* gen. et sp. nov.

Fig. 46, 47. Hyphae with typical columellae. × 660. Slide 150-5.

Fig. 48, 49. Hyphae nearest to algal germlings. × 660. Slides 172-22-2 & 210-7.

Fig. 50, 51. Hyphae with lopsided bases. × 660. Slides 175-66 and 150-5.

Fig. 52-55. Hyphae with expanded and crenulated bases. 52-× 660; 53-55-× 1330. Slide 175-23.

Fig. 56. Hypha with double septum. × 1330. Slide 175-23.

Fig. 57. Cytoplasm-filled secondary hypha inside non-functional primary one. × 660. Slide 175-23.

Fig. 58-60. Hyphae with clusters of discharged spores. × 660. Slide 150-5.

Fig. 61. Bifurcated hypha. × 660. Slide 150-5.

Fig. 62. Trifurcated hypha. × 660. Slide 150-5.

Fig. 63-65, 67. Secondary hyphae inside primary ones. × 660. Slide 175-23.

Fig. 66. Bag-like hyphae (?). × 660. Slide 175-23.

68. *Ordovicimyces* (?) *recensis*, sp. nov. In *Heteropora neozelanica*. × 660. Slide HNZ-2.

Figs. 22-45, 68 Extant, Figs. 12-21, 46-67 Fossil.

ALGAE

69. *Trentepohlia annulata* Brand. × 230. (after Brand, 1910, Pl.4)

70, 71. *Trentepohlia iolithus* (L.) Wittrock. × 230. (after Brand, 1910, Pl. 4)

72-74. *Sphaeroplea africana* Fritsch, transverse septa. After Fritsch, 1929, Text-fig. 1-K. × 130; (Text-fig. 1-E, H) × 330.

75. *Sphaeroplea wilmani* Fritsch & Rich, septum. After Fritsch 19,29, Text-fig. 2-L. × 430.

76. *Sphaeroplea africana* Fritsch, "short segment." After Fritsch, 1992, Text-fig. 2-E. × 100.

Figs. 69-76 Extant.

FUNGI

77. Cytoplasmic strand in proliferated hypha.

78. *Saprolegnia monoica* var. *glomerata* Tiesenhausen. Sporangium growing from beneath an old one. × 250. After Coker, 1923, Pl. 13, Fig. 7.

79. *Pythium oedochilum* Drechsler. Middleton, 1943, Fig. 7-B. × 660.

80. *Bombardia lunata* Zickler. (from Gäumann & Wynd, 1952, Fig. 185).

Figs. 77-80 Extant.