MARINE MYCOLOGY

THE HIGHER FUNGI

Jan Kohlmeyer/Erika Kohlmeyer

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Preface

Growing general interest in marine and estuarine habitats in recent years has also led to an increase in studies on marine fungi which were often overlooked as participants in ecological processes. Because of this rapid growth of knowledge in marine mycology, the first comprehensive treatise on marine fungi by Johnson and Sparrow (1961) is partly out-of-date. G. C. Hughes (1975), in a very informative review, has summarized papers published since 1961. However, extensive descriptions and complete keys are not available for all marine fungi. The "Icones Fungorum Maris" and "Synoptic Plates of Higher Marine Fungi" (Kohlmeyer and Kohlmeyer, 1964–1969, 1971b) include diagnoses for only 90 species and keys for the identification of all taxa described up to January 1971, respectively. An updated treatise was clearly needed.

This book deals with the higher marine fungi, i.e., Ascomycotina, Basidiomycotina, and Deuteromycotina. This book combines features of a monograph with those of a text. It includes sections on ecological groups of fungi and other topics, such as phylogeny, ontogeny, physiology, and vertical and geographical distribution, providing information on known facts and open questions. The taxonomic–descriptive part contains complete descriptions of each genus and species, together with substrates, range, etymology of generic and specific names, and literature. There are keys for all species within a given genus, and a general illustrated key leads to the individual species. The taxonomic section is based on our examinations of almost all of the filamentous marine fungi, and unpublished data on new hosts and geographical distributions are included for many species. The filamentous higher marine fungi are represented by 149 Ascomycetes, 4 Basidiomycetes, and 56 Deuteromycetes. The majority, namely 191(91%) of the filamentous fungi, are obligately marine species, whereas the remainder are facultatively marine. One new species and seven new combinations are proposed (see Table I). Excluded

TABLE I
New Species and Combinations Proposed

Ascomycotina

1. *Didymella gloiopeltidis* (Miyabe et Tokida) Kohlm. et Kohlm. (=*Guignardia gloiopeltidis*)
2. *Haligena amicta* (Kohlmeyer) Kohlm. et Kohlm. (=*Sphaerulina amicta*)
3. *Halosphaeria galerita* (Tubaki) Schmidt ex Kohlm. et Kohlm. (=*Remispora galerita*)
4. *Leiophloea pelvetiae* (Sutherland) Kohlm. et Kohlm. (=*Dothidella pelvetiae*)
5. *Massarina cystophorae* (Cribb et Cribb) Kohlm. et Kohlm. (=*Otthiella cystophorae*)
6. *Pontogeneia codiicola* (Dawson) Kohlm. et Kohlm. (=*Sphaerulina codiicola*)
7. *Turgidosculum complicatulum* (Nylander) Kohlm. et Kohlm. (=*Leptogiopsis complicatula*)

Deuteromycotina

1. *Camarosporium palliatum* Kohlm. et Kohlm. sp. nov.

are 49 *nomina confusa, dubia,* or *nuda*. The yeasts are treated in a separate chapter and comprise 177 species or varieties. Authorities on fungal names and hosts are given in the Organism Index. We have considered all literature except for unpublished reports or theses.

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* Abbreviations follow Holmgren and Keuken (1974).

ing colleagues for permission to reproduce illustrations: G. E. Cole (Fig. 34), J. W. Fell (Fig. 129), R. V. Gessner (Fig. 22), and L. Vitellaro Zuccarello (Fig. 31). Stearn's (1966) "Botanical Latin" was invaluable in clarifying the etymologies of many generic and specific names. T. L. Herbert and B. J. Lamore ably assisted us in the laboratory, B. B. Bright and J. W. Lewis provided us with quick library service and administrative assistance, respectively, and J. B. Garner carefully typed the manuscript. We are greatly indebted especially to L. S. Olive, R. V. Gessner, and J. W. Fell for reading parts of the manuscript and making helpful suggestions. Many thanks go also to T. L. Herbert for collecting in Trinidad, for proof-reading and indexing; to B. J. Lamore for help in the preparation of indexes; to P. E. Boyd for typing; and to V. A. Zullo for giving advice on authorities of host species.

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1. Introduction

One single publication has probably influenced the development of marine mycology more than any other paper, namely, "Marine Fungi: Their Taxonomy and Biology" by Barghoorn and Linder (1944). These authors demonstrated that there was an indigenous marine mycota, showing growth and reproduction on submerged wood after defined periods of time. The existence of true marine saprobic fungi was often questioned, for instance, by Bauch (1936), who wrote: "Saprobic Ascomycetes which play an important role in forest and soil in the deterioration of organic material, especially of wood, appear to be completely absent in seawater" (translation from the German). Investigations by Barghoorn and Linder and later authors have proven without a doubt that fungi, including Ascomycetes, do contribute to the decomposition of organic substrates in the oceans, although the extent of biodeterioration caused by fungi in the sea is still not fully understood.

The first facultative marine fungus, *Phaeosphaeria typharum*, was described by Desmazières (1849) as *Sphaeria scirpicola* var. *typharum* from *Typha* in freshwater. Durieu and Montagne (1869) discovered the first obligate marine fungi on the rhizomes of the sea grass, *Posidonia oceanica*, and marveled at the most remarkable life-style of *Sphaeria posidoniae* (=*Halotthia posidoniae*), which spends all parts of its cycle at the bottom of the sea. Figure 1 summarizes the numbers of species of higher marine fungi described per decade since 1840. If numbers of new descriptions can be used to indicate the activity dealing with a particular group of organisms at a certain time, this figure shows that up to the period of 1930–1939 there was only sporadic interest in marine fungi. Descriptions of marine species during these first hundred years were supplied mostly by authors working on a wide variety of fungi with no particular interest in the marine habitat. Exceptions may be the Crouan brothers (Kohlmeyer, 1974a), who described five marine fungi in 1867 in

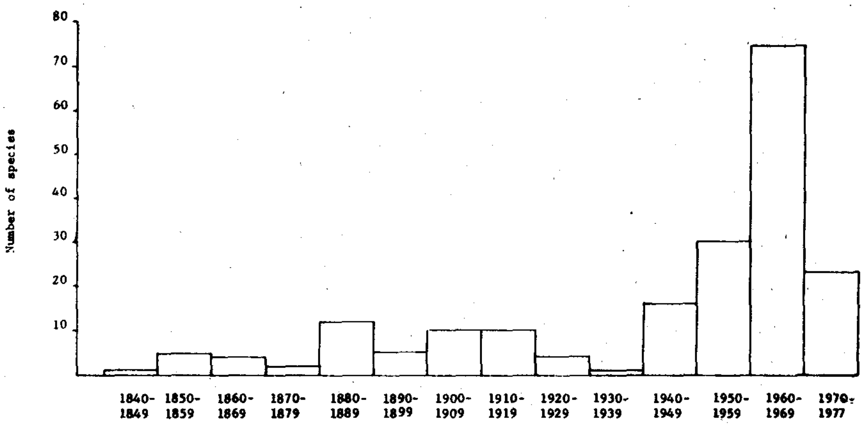

Fig. 1. Numbers of accepted filamentous higher marine fungi described per decade since 1840. Research in marine mycology was stimulated by a paper of Barghoorn and Linder in 1944. The numbers of newly described species show a decreasing trend since 1970.

their *Florule du Finistère* and prepared eleven others for publication (remaining unpublished), and particularly Sutherland (1915a–c, 1916a,b), who published a series of papers dealing exclusively with marine fungi. Almost three-quarters of all recognized higher marine fungi have been described in the last four decades (Fig. 1). This sudden increase in new descriptions after 1940 can be attributed mostly to the publication of Barghoorn and Linder (1944), which stimulated worldwide research in marine mycology. A proliferation of literature on the higher marine fungi occurred, as I. M. Wilson (Great Britain) in 1951, W. Höhnk (Germany) in 1952, S. P. Meyers (United States) in 1953, A. B. Cribb and J. W. Herbert (Australia) in 1954, T. W. Johnson (United States) in 1956, G. Feldmann (France) in 1957, J. Kohlmeyer (Germany) in 1958, and G. Doguet (France) in 1962 and E. B. G. Jones (Great Britain) also in 1962 published their first papers in this field. The first monograph on marine mycology by Johnson and Sparrow appeared in 1961.

I. DEFINITION OF MARINE FUNGI

Past definitions of marine fungi have often been based on their ability to grow at certain seawater concentrations (Johnson and Sparrow, 1961;

Tubaki, 1969). It has been shown that marine fungi cannot be defined on a strictly physiological basis (see discussions in Kohlmeyer, 1974a; G. C. Hughes, 1975), and we use a broad, ecological definition, namely: *Obligate marine fungi* are those that grow and sporulate exclusively in a marine or estuarine habitat; *facultative marine fungi* are those from freshwater or terrestrial milieus able to grow (and possibly also to sporulate) in the marine environment (Kohlmeyer, 1974a).

Marine or estuarine habitats are the oceans and ocean-associated smaller bodies of water that contain salt or brackish water, including river mouths, sounds, lagoons, tidal creeks, salinas, étangs, and the like. Fungi from inland salt lakes are not well known, but the mycota of these habitats appears to be identical with that of the oceans (Anastasiou, 1961, 1963b; Davidson, 1974b).

Some authors feel that attempts to define marine fungi are premature (Schaumann, 1975b), but, in our opinion, such efforts are necessary to understand the role of fungi in a particular environment such as the oceans. Fungi are often obtained by culture methods, for example, plating techniques or incubation, from marine substrates. Most investigators using such methods have failed to demonstrate conclusively that the species isolated in the laboratory can actually grow (and, possibly, reproduce) in the marine habitat. The mere isolation of a species from marine samples does not prove that this fungus is active in the marine environment. Such species are possibly dormant in the form of spores or hyphal fractions until the surrounding conditions become favorable for germination and growth. Research by Tyndall and Kirk (1973) and preliminary experiments carried out by Dr. R. V. Gessner and ourselves indicate that a mycostatic factor in fresh seawater inhibits germination of spores of terrestrial fungi but does not affect certain marine fungi. Mycostasis is a well-known phenomenon in terrestrial soils and on leaf surfaces (Lockwood, 1977). The unidentified mycostatic principle in raw seawater is destroyed by heat sterilization. Conidia of terrestrial fungi, for example, *Penicillium* sp., germinate in sterilized or aged seawater or in distilled water, but they do not germinate in the natural habitat. Therefore, fungi isolated from seawater by means of culture methods cannot be considered to be marine species unless their growth in the marine environment is demonstrated. A valid criterion for the definition of a marine fungus might be its ability to germinate and to form a mycelium under natural marine conditions. These conditions may vary, depending on the species. Some fungi might require permanent submergence, whereas others, such as species occurring in beach sands, may need a greater supply of oxygen for germination.

II. NUMBERS OF MARINE FUNGI

About 50,000 fungal species are known from terrestrial habitats (Ainsworth, 1968), but, in contrast, less than 500 species have been described from oceans and estuaries, which cover a much larger area, namely, three-quarters of the world. The higher filamentous marine fungi include 209 species, the marine-occurring yeasts comprise 177 species, and the lower marine fungi comprise probably less than 100 species. The decrease of new descriptions of marine fungi during the period 1970–1977 (Fig. 1) indicates that the most common species have been named and that considerable additions of new species in the future are unlikely. Undescribed fungi can be expected in some less explored habitats, for example, in temperate salt marshes, in mangrove forests, particularly of the Pacific and Indian oceans, and in the deep sea.

The oceans, compared to the land masses, provide stable environments with small changes in temperatures and salinities. Organic substrates, such as algae, marsh plants, and plant litter, are concentrated mostly along the shores, where they provide nutrients for fungi. The open ocean is a fungal desert where only yeasts or lower fungi may be found attached to planktonic organisms or pelagic animals. The existence of such organisms in a free-living state has not been demonstrated convincingly, in our opinion. In contrast to terrestrial habitats, the incubatorlike stable environment of the oceans and the comparable small number of hosts and substrates in the marine environment have probably not exerted enough selective pressure during the course of evolution to induce the formation of a high number of different types of fungi. Ainsworth (1968) estimates the number of named and undescribed terrestrial fungi to be 250,000 or more. We expect the number of marine fungi to be about 1% of the terrestrial species, namely, the same ratio as is found between the presently known marine and terrestrial fungi.

III. SIZES OF MARINE FUNGI

Most of the fungi found in marine habitats are microscopic. The largest ascocarps occur in *Amylocarpus encephaloides,* which do not exceed 3 mm, and the Basidiomycetes *Digitatispora marina* and *Nia vibrissa* have fruiting bodies 4 mm in length and 3 mm in diameter, respectively. Obviously, the marine environment does not permit the development of large, fleshy fruiting bodies, because abrasion by waves and grains of sand impedes formation of such structures. Macromycetes growing in the leaf litter of forests need an extended nutrient-supplying mycelium and an undisturbed habitat. Similarly, soft fruiting bodies of large marine species (*A. encephaloides, Eiona tunicata, D. marina, N. vibrissa,* and *Halocyphina villosa*) develop mostly in sheltered habitats, namely, on firmly anchored wood at or above the high-tide line or protected in cracks of the wood or under bark. The deep sea appears to be another environment where large fruiting bodies could develop because water currents are weak, and, indeed, the Ascomycete *Oceanitis scuticella*, occurring at a depth of about 4000 m, has fleshy ascocarps up to 2 mm in height.

IV. THE MODE OF LIFE AND DISTRIBUTION OF MARINE FUNGI

The higher marine fungi occur as parasites on plants and animals, as symbionts in lichenoid associations with algae and as saprobes on dead organic material of plant or animal origin. Examples of the occurrence of marine fungi in different substrates and habitats are given in the following chapters. These organisms are found in all marine environments from the high-water line down to the deep sea. Their distribution is mainly limited by dissolved oxygen and temperature of the water, less so by salinities. Besides ubiquitous species, there are fungi restricted to temperate waters and others restricted to tropical or subtropical waters.

V. UNSOLVED MAJOR PROBLEMS

Among the topics to be solved in marine mycology, we consider the following three to be of foremost importance.

A. Quantification

So far we have no means to measure the biomass, numbers or activity of marine fungi in a particular habitat. Microscopic observation of decaying marsh plants or marine wood indicates that fungi play a major role in the decomposition of these plants and wood, but fungal hyphae and substrate cannot be separated.

B. Definition of Marine Fungi

To obtain a better understanding of the role of fungi in the marine environment, we need to separate the indigenous marine species (obligate and facultative) from the "contaminants." The latter are terrestrial or freshwater species [sometimes called "transients" (Park, 1972b)] that are dormant in marine habitats. A way of separating indigenous from nonindigenous species appears to be a test of their germination ability in the natural environment, as discussed above.

C. Fossil Records

In the absence of fossil higher marine fungi, discussions on the phylogeny of this group are more or less speculative. A search for parasitic fungi on fossil marine algae, for instance, on calcified Rhodophyta, might supply data on the origin of marine fungi.