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PHYLOGENESIS AND TAXONOMIC STRUCTURE OF THE ENTOMOPHTHORACEAE

[Filogeneza a struktury taksonomiczne Entomophthoraceae]

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Summary

Can a systematics of lower fungi be phylogenetic? Is a truthful reproduction of principal outlines of the history of a group of organisms which had left no fossil remains possible? Are mere neontological data a sufficient basis for a phylogenetic reconstruction or must a system of such organisms as lower fungi be of necessity a phenetic system based only on observed similarities between organisms and in detachment from supposed affinities?

Following an analysis of the taxonomic procedure which led to the construction of a new classification of entomopathogenic fungi belonging to the Entomophthoraceae, the author replies affirmatively to the first question. A phylogenetic reconstruction is possible as regards the groups of fungi discusssed, and may provide a basis for their rational classification. But the character of this reconstruction is different from the case of groups whose history has been inbestigated by means of paleontologic data. The reconstruction referred to is of limited historical character, it supplies the probable relationships of descendence between organisms but does not include information on chronological relations between taxa, neither does it deal with the sequence of individual, nonrepeatable events, but it does concern sequences of evolutionary processes. In the approach suggested here the set of contemporary forms did not originate from a common ancestral group but from an "initial phylogenetic state", which is but a compilation of features recognized as most ancestral but not ascribed to any ancestral taxon.

Despite the limitedly historical character of this phylogenetic reconstruction, the phylogenetic classification based on it is characterized by more significant cognitive and practical value – at least as regards lower fungi – than the phenetic classification. It is the author's opinion that the principles of the phenetic classification are hardly applicable to organisms with very simple morphoanatomy on account of the vagueness of the principal concept of "feature" in this case.

(based on original translation of summary by Jan Rudzki)

> *It is not extraordinary that young taxonomists are trained like performing monkeys, almost wholly by imitation, and that in only the rarest cases are given any instruction in taxonomic theory?* A. J. Cain

> *… entirely satisfactory and reliable work can be done in taxonomy … without philosophy. But there are times when we need to know what we are doing and why' and then we are faced with the philosophical problem … the need for the philosphy may come from the work itself …* D. P. Rogers

Cain's maxim quoted here as an epigram so aptly portrays the situation in biological systematics and is so close to the genesis of this paper that I decided to use it here, even at the risk of being reproached about the lack of originality (this sentence had earlier been used as a motto by Simpson in 1961). Indeed, most beginning taxonomists gain knowledge of a selected branch of biology by following some examples, and only after certain achievements in practical classification of the investigated groups of organisms do they begin to become conscious of the theoretical and methodological foundations of their work, Rogers' "need for the philosophy."

The present author became a taxonomist in a similar way. For this reason I shall present here an attempt at a critical analysis of the methodological aspects of my own classification comprising the group of lower fungi belonging to the family Entomophthoraceae developed in the 1950's and published in 1964-1966. The necessity of the present analysis originated from work on this classification, resulting from the difficult problems of grouping entomophthoraceous fungi into genera; therefore, I must preface the methodological considerations by a relatively extensive and detailed description of the many-sided diversity presented by the Entomophthoraceae.

1. Foes of our enemies

The specific biology of some representatives of the discussed fungi and their ability to cause mass deaths of noxious insects were and still are the main object of interest of numerous authors. Often observed and described violent epizootics caused by entomophthoraceous fungi in populations of various species of dipterous insects, aphids, orthopterous insects, lepidopterous larvae, etc., suggested the potential practical utility of these fungi. On these grounds entomophthoraceous fungi were for more than 100 years the object of interest of mycologists, entomologists and others, this resulting in many-sided insights into this group of fungi (MacLeod 1963, Madelin 1968, Weiser 1965).

The first formally named species of entomophthoraceous fungi, *Entomophthora muscae* (Cohn) Fresenius[1], which was described in 1855, displayed these sorts of properties. Namely, it caused and still causes destructive epizootics in populations of houseflies, *Musca domestica* L., an insect which has endangered human health in the past and in those of anthomyiid flies (Anthomyiidae) which include many pests of cultivated plants. Almost all species of entomophthoraceous fungi discovered and described in the 19th century are parasitic on common and economically important insect species: aphids, cabbage (white) butterfly caterpillars, caterpillars of Noctuidae, orthopterous insects, gnats, *etc.*

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[1] In this text I apply species and generic names of the Entomophthoraceae consistent with the nomenclature resulting from the author's taxonomic revision (Batko 1964a-d, 1966a-b; Batko and Weiser 1965).

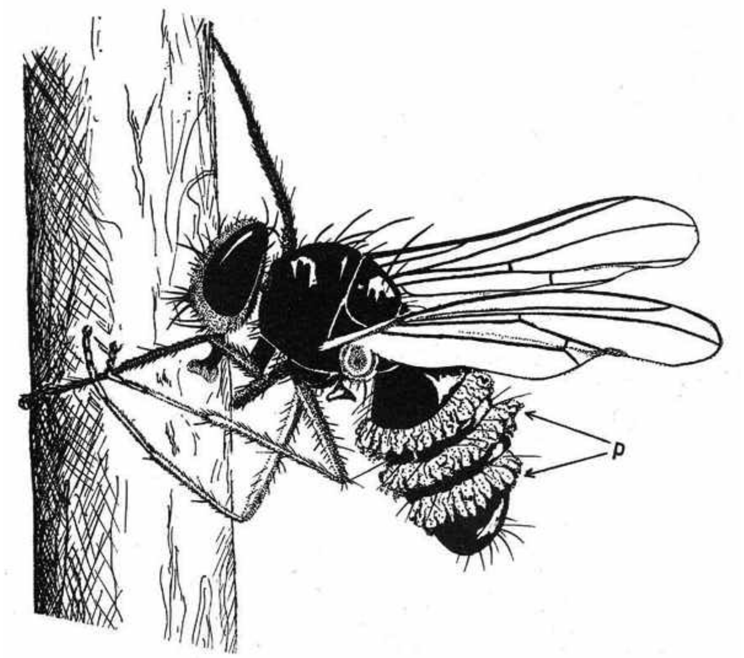

Figure 1. Anthomyiid fly killed by *Entomophthora muscae.* p = cushions of pseudohymenium. Drawn by E. Wisniewska from the author's material.

The discovery of a new species was often followed by attempts at its practical utilization but these attempts usually failed. However, a paradox soon arose: it is the entomophthoraceous species among all entomopathogenic fungi which most rapidly and effectively reduce the population densities of noxious insects, even though the so-called muscardine fungi with their lower effectiveness against host populations, were most often used because of practical considerations. This was due to the fact that muscardine fungi (Deuteromycetes including species of *Beauveria*, *Metarhizium*, *Paecilomyces*, *Sorosporella*, etc.) were more suitable for the operations involved in the mass production of the fungus, in the formulation of spore-containing insecticides, and in their introduction to the protected agrocoenosis. Thus, these fungi could be produced on a pilot-plant or industrial scale and applied for the protection of cultivated plants, forest, farm animals, and humans. The inappropriateness of entomophthoraceous fungi for these operations resulted from their distinct, more specific nutritional requirements, distinct biology, and the morphoanatomical properties of their spores, as well as from the more complex nature of their interrelationships with insect hosts.

The knowledge of the biology of different species of Entomophthoraceae accumulated over more than 100 years of studies of these fungi contained many valuable data resulting from close observation and experiments; however, these data often seemed contradictory and were not synthesized into one taxonomic system. Variation in data concerning different species exceeded the scope of the simple typological approach widespread in mycological systematics of the 19th century and first half of the 20th century; this testified to the great diversity of numerous aspects of the biology of entomophthoraceous fungi. Extrapolation of the results obtained in studies on certain species and strains of entomophthoraceous fungi to the whole group led to incorrect predictions and demonstrated the inability of the simplified taxonomic propositions being used to account for the real biological complexities (and diversities) of the Entomophthoraceae. This conflict discouraged the continuation of attempts to use these fungi for pest insect control.

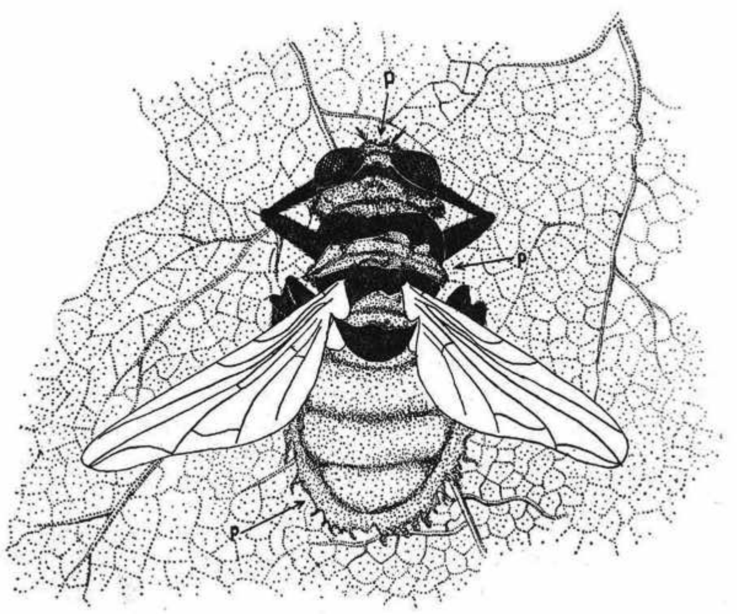

Figure 2. Bluebottle fly (*Calliphora erythrocephala Meig.*) killed by *Zoophthora vomitoriae* Roszypal on surface of a leaf. p = pseudohymenium. Drawn by E. Wisniewska from the author's material.

There was no taxonomic concept reflecting the whole range of complex relationships within the discussed group. No new or causal explanation was offered to account more accurately for the heterogeneity of entomophthoraceous fungi or which could permit predictions about the ranges of the characters and properties of the individual species within this entire fungal group. This role is usually played by the phylogenetic (or at least evolutionary[2]) classifications traditionally employed in mycological systematics[3]. However, the construction of a phylogenetic classification involves consideration of the total range of knowledge about the group, whereas the four basic monographs of Entomophthoraceae published in the 19th century and at the beginning of the 20th century were based mainly on morphological data (Fresenius 1858, Nowakowski 1883, Thaxter 1888, Lakon 1919). Most studies on the physiology and cytology of entomophthoraceous fungi, as well as on the pathology and epizootiology of insect diseases caused by them, appeared later (Boczkowska 1932, Dustan 1924, Goldstein 1927, 1929, Hall 1959, Schweizer 1947, Smith 1926, Weber 1939, *etc.),* so that the information contained in them has not been incorporated in these taxonomic syntheses.

After an initial period of interest in the epizootiology of insect diseases caused by entomophthoraceous fungi and in their prospective practical utilization (Batko 1957), I found it advisable to undertake studies on the basic problems of the systematics and classification of Entomophthoraceae. Results of these studies (Batko 1963, 1964a-d, 1965, 1966a-b, Batko and Weiser 1965) and the manner in which they were done are the object of the methodological analysis presented here. Therefore, it is something like an attempt of Cain's "performing monkey" to realize the sense of its own activities.

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[2] Phylogenetic classification is based on phylogenetic reconstruction, whereas the evolutionary classification is based on a set of assumptions concerning the presumed main processes and directions of the evolution of the classified group (however, it lacks full phylogenetic justification because of the scarcity of data).

[3] Luttrell (1958) calls attention to the importance of the informative function of biological classification which is not only a classification of organisms but also a classification of data about organisms.

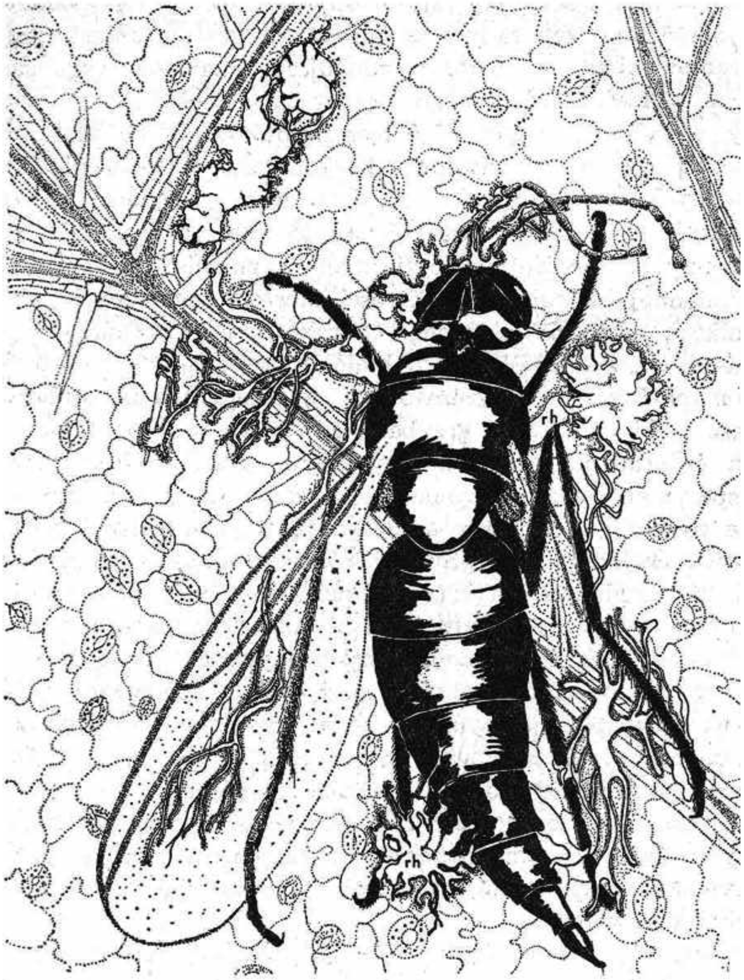

Figure 3. Fungivorid fly (Fungivoridae) killed by *Zoophthora dipterigena* (Thaxter) Batko. Fungus developed zygospores within host's body. Numberous rhizoids (rh) are visible attaching the insect cadaver to the surface of the leaf. Drawn by E. Wisniewska from the author's material.

The classification of this fungus group and its taxonomic justification has been the object of violent controversy among specialists for over 100 years. This controversy dealt with at least several problems concerning three fields of systematics in the broad sense:

1. What should be the nature of the generic concept in this group?
2. How many genera ought to be distinguished in the group?
3. What are the correct names of these genera?

The first problem deals with the field of taxonomy[4], the second with classification, and the third with nomenclature. As far as I know, the first problem has not been explicitly formulated by any participants in the discussion. The remaining two were usually considered jointly; it sometimes happened that the answer to the second question (which is of a primary nature) was subordinated to the answer to the third question (being clearly secondary with

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[4] I use the term "taxonomy" in the sense accepted by Simpson (1961) who defines it as follows: "Taxonomy is the theoretical study of classification, including its bases, principles, procedures and rules."

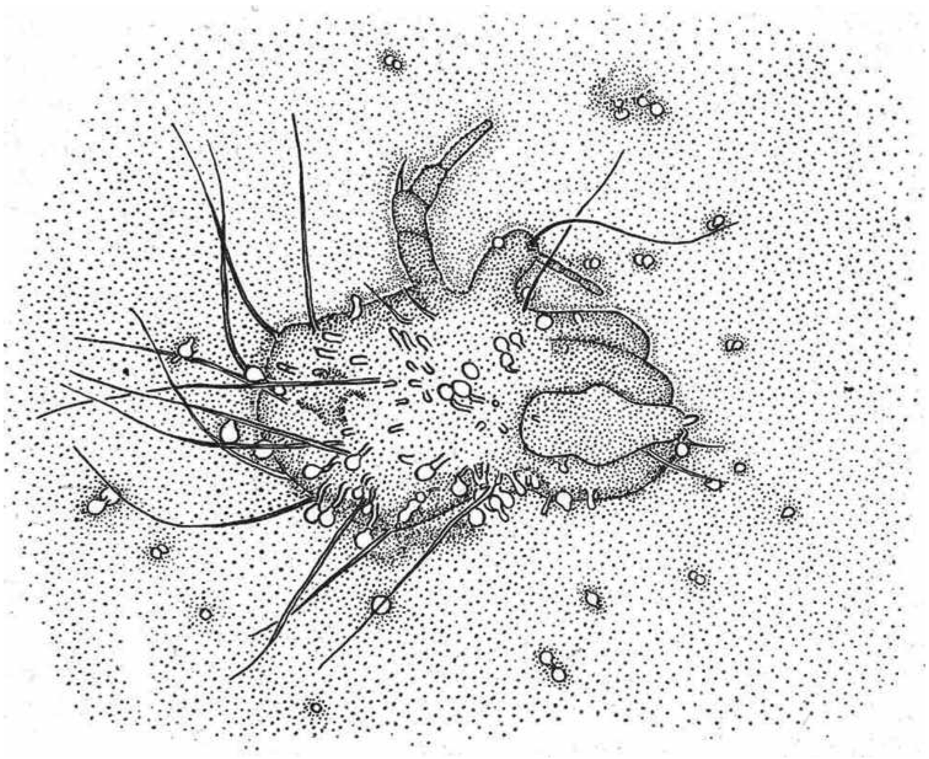

Figure 4. A mite, *Tyrophagus* sp., killed by *Conidiobolus* sp. on an agar medium. Numerous single conidiophores and discharged conidia are visible; the fungus does not form a pseudohymenium.

respect to the second question). The distinction between these problems and the resolution of the formal nomenclature aspects were treated in several recent publications as well as those of the present author (Batko 1963, 1964a-d). These problems will not be considered further in this paper.

Diverse aspects of the problems of taxonomy and classification being analyzed here were also considered during the second part of the 19th century and in the 20th century. Two or three schools of thought in this field arose following some of the earliest studies of this group, partly due to the conflict between two prominent mycologists, Nowakowski and Brefeld. During this early period a nomenclatural disagreement was superimposed with differences of scientific opinions and with many causes of a pragmatic nature. These implications led to the widespread simultaneous application of the same epithets in several different meanings. I analyzed these problems in an earlier study (Batko 1965) but I have to return to some of them here.

Generally, two divergent viewpoints were current when I undertook my taxonomic revision of the Entomophthoraceae. The first of them, as put forth by Nowakowski (1883), proposes that entomopathogenic entomophthoraceous species ought to be distributed among several different genera on account of their pronounced morphological diversity. The second one, as espoused by Thaxter (1888), merges almost all these species into one great genus that is nearly co-extensive with the range of the family.

It is stressed that both these standpoints were based mainly, if not exclusively, on morpho-anatomical data and on some very generally interpreted information about nutritional habits (parasitic vs. saprophytic). My analysis of data concerning other aspects of the biology of entomophthoraceous fungi pointed to many correlations between classes of characters and led to the construction of a phylogenetic hypothesis that testified to the soundness of Nowakowski's intuition in my opinion. The newly developed classification system, despite some formal terminological differences and improved accuracy resulting from the progress in studies of this group, is indeed a true continuation of Nowakowski's work.

2. Habits of entomophthoraceous fungi

Interest in the Entomophthoraceae has been directed primarily to those species that are our natural allies for their ability of rapidly decimating populations of noxious insect species during their destructive, mass occurrence, and being our natural allies in the struggle for life. However, this does not mean that all species of Entomophthoraceae parasitize insects, and (as concerns the insect-killing species) that they all cause mass deaths, *i.e.*, epizootics. What is more, only a certain small parts of the known species represent our natural allies acting effectively in natural biocoenoses and agrocoenoses. The remaining species of entomophthoraceous fungi have another mode of life, or (if they parasitize insects) they either cause no mass deaths or else attack insects deprived of any direct economic importance, which are included neither among pests nor among evidently useful species.

The great majority of the fungi included in the order Entomophthorales comprise nonaquatic fungi that are saprobes or parasites of various organisms. The diversity of their habits permits their classification with some simplification into the following categories:

1. ***Nonaquatic saprophytes occurring on substrates containing mainly cellulose, suberin, hemicellulose, or chitin***, substances which are difficult to degrade. These fungi belong to the genus *Conidiobolus* Brefeld. Some of them are able to develop within bodies of living insects or mites under experimental conditions (*e.g.*, Couch 1939) or even under natural conditions (*i.e.*, *Conidiobolus coronatus* (Costantin) Batko). They were also found in abscesses of the mucosal or subcutaneous tissues in horse (Emmons and Bridges 1961).
2. ***Specialized saprophytes***, coprophytes developing on feces on poikilothermic vertebrates (amphibians and reptiles), and being characterized by a complex system of adaptations to spreading in nature. These fungi belong to the genus *Basidiobolus* Eidam; some of them sporadically parasitize mammals, including man (Emmons *et al.* 1957).
3. ***Parasites of lower invertebrates***, *e.g.*, nematodes (*Meristacrum asterospermum* Drechsler) and tardigrades (*Ballocephala sphaerospora* Drechsler).
4. ***Parasites of arthropods, primarily of insects or (less commonly) mites and spiders***. This category comprises the majority of entomophthoraceous species, those in the genera *Entomophaga* Batko, *Entomophthora* Fresenius, *Triplosporium* (Thaxter) Batko, *Tarichium* Cohn, *Zoophthora* Batko, *Massospora* Peck and *Strongwellsea* Batko & Weiser.
5. ***Semiaquatic or aquatic parasites*** of fern prothalli (*Completoria complens* Lohde) or of Conjugatae (the genus *Ancylistes* Pfitzer).

The biology of entomopathogenic species will be described in detail in this paper whereas the remaining groups will be comment upon briefly.

More than 20 species of *Conidiobolus* (see Srinivasan and Thirumalachar 1967a) constitute a fairly uniform group of fungi occurring in the upper layer of forest litter, plant detritus decomposing in soil, dead fruit bodies of mushrooms, decaying wood, *etc.* These fungi are probably very common and geographically widespread. However, since their detection in a substrate requires special methods, they were only seldom noted during standard studies of the mycoflora of the above-mentioned substrates. A relatively full knowledge of their occurrence is known only for North America and India.

Studies on the physiology of nutrition of *Conidiobolus* species indicate that they are able to synthesize most vitamins and growth substances, and that they can utilize both amino and inorganic nitrogen sources, *i.e.*, they display a high degree of trophic plasticity. Moreover, these fungi produce a richly varied system of exoenzymes such as cellulase, chitinase, *etc.*, which allow them to utilize poor substrates little available to other saprophytes. On the other hand, *Conidiobolus* species are unable to compete for rich substrates containing readily degradable protein against the rapidly developing saprophytes of the order Mucorales, imperfect fungi producing antibiotics and toxins (Deuteromycetes), ascomycetous fungi or the order Plectascales (species of *Penicillium*, *Aspergillus*, or the like), and putrefactive bacteria. Rich enzymatic equipment and the ability to utilize poor substrates represent the main weapons in their struggle for life; however, the inability to compete with other saprophytes forces them to live in "marginal" ecological niches and assigns them a narrow biocoenotic role (definite links of destruction of plant skeletal substances).

The above-mentioned *C. coronatus* (or a group of nearly indistinguishable species grouped under this name) assumes a special position among these fungi. *Conidiobolus coronatus* was isolated from soil, rotten wood, keratin, grass leaves, living ferns, abscesses of the foot and nasal fossae of horses, aphids and other substrates. The author succeeded in experimentally infecting silverfish, *Thermobia domestica* (Thysanura: Lepismatidae), with a strain of this species; no entomophthoraceous species has been noted previously from this apterygote insect.

The relatively small genus *Basidiobolus* (five species) comprises the above mentioned specialized coprophytes and saprophytic fungi whose biology resembles that of *Conidiobolus* species isolated from soil where they decompose plant remains, etc. (see Srinivasan and Thirumalacahr 1967b).

Representatives of the genera *Meristacrum* (one species), *Ballocephala* (two species), *Completoria* (one species) and *Ancylistes* (three species) are not very well known. It can only be stated, on the one hand, that they belong to the family Entomophthoraceae and, on the other hand, that they are greatly distinct from the remaining species and genera. These fungi were not included in the discussed taxonomic revision and, therefore, will be omitted from the present considerations. It is only mentioned that *Ancylistes* species parasitize the algal genera *Closterium*, *Netrium* and other genera of the Conjugatophyta; they are, therefore, aquatic fungi. The way of their adaptation to spreading in host populations (by means of conidia forcibly discharged into air and dropping onto the water surface) seems to indicate that they are secondarily aquatic organisms.

3. Entomophthorous fungi vs. insects

As I have mentioned, about three fourths of entomophthoraceous fungi (*i.e.*, more than 100 species) parasitize insects.[5] They are mostly oligophagous fungi able to infect some or many related insect species (belonging to the same family or to a group of related families). There are only a few mono-phagous species occurring on only one host species but their

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[5] On these grounds Nowakowski (1883) named these fungi by the Latin name Entomophthoreae and Polish name "owadomorki" (corresponding to the English "entomophthorous fungi"). According to the requirement of present-day botanical nomenclature and in agreement with my own taxonomic concepts, I use the term "entomophthorous fungi" as a descriptive name without taxonomic rank and as a name for the whole order Entomophthorales. The family Entomophthoraceae is referred to by the term "entomophthoraceous fungi."

monophagy must be questions since these are uncommon and only poorly known species. The number of polyphagous species attacking insects belonging to different orders is also small; theses are the so-called "critical" species which are difficult to identify or are imprecisely defined, a fact which admits doubts as to their taxonomic uniformity.[6] Generally speaking the different species of entomopathogenic entomophthoraceous fungi are associated with a definite order or subordinal grouping of insects. The distribution of entomophthoraceous fungi hosts in the insect system as a whole is markedly irregular; namely, most of these fungi parasitize Diptera (about 40 species), Homoptera (about 25 fungal species), Lepidoptera (about 20 fungal species), and Coleoptera (more than 10 fungal species).[7] On insects belonging to the remaining nine orders entomophthoraceous fungi were noted only sporadically; they occur more or less regularly only on few species of Orthoptera, Hymenoptera, and Heteroptera. Thus, among the 27-30 orders of insects usually recognized, hosts of entomophthoraceous fungi are most usually members of only four orders, and ten orders of insects are not known to be affected by these fungi.

Orders of winged insects (Insecta: Pterygogenea) are divided into two groups of orders, Paleoptera and Neoptera (Martynov, quoted by Szwanwicz 1939). No entomophthoraceous fungi were found on mayflies (Ephemeroptera) and dragonflies (Odonata) belonging to the Paleoptera and regarded as being the phylogenetically oldest extant winged insects. Martynov divides Neoptera into three subgroups of orders: Polyneoptera, Paraneoptera, and Oligoneoptera. Polyneopterea are regarded as a group of phylogenetically older orders, and Para- and Oligoneoptera as treated as phylogenetically younger and, in a certain sense, parallel groups. The above-mentioned four orders of insects comprising the majority of hosts for the entomophthoraceous fungi do, indeed, belong to these two most recent subgroups of the Neoptera (Diptera and Homoptera to Oligoneoptera; Coleoptera and Lepidoptera to Paraneoptera). Moreover, these orders are regarded phylogenetically as the youngest within their subgroups. The flora of the Entomophthoraceae parasitizing insects from these four orders not only contain the majority of species, but also include the highest degree and the most complex nature of diversity.

In agreement with the so-called parasitogenic rule of Wardle and McLeod (Michajlow 1960, p. 294), this could permit concluding about the phylogenetic age of Entomophthoraceae on the grounds of the age of fossil records concerning their hosts. However, it seems that in relation to the considered parasite-host systems, the admission of the indispensable assumption of parallel evolution of entomophthoraceous fungi and insects is rather difficult. Therefore, I share the skeptical views of many parasitologists regarding the "parasitogenetic rules" (Michajlow 1960, p. 292-313) despite their undoubted value in many specific cases.

The above-discussed distribution of hosts of Entomophthoraceae in the insect classification clearly indicates that the phylogenetically youngest insect orders constitute the principle area for the evolutionary development of entomophthoraceous fungi. I cannot explain the causes of this phenomenon on the basis of the present state of knowledge.

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[6] The fungus known as *Entomophthora sphaerosperma* Fres. or *Zoophthora radicans* (Fref.) Batko is such a "polyphagous species." However, this name probably corresponds to a group of oligophagous species being mistaken because eof misdentification (see Batko 1964b, 1966b).

[7] These data refer to the state of knowledge as of 1965.

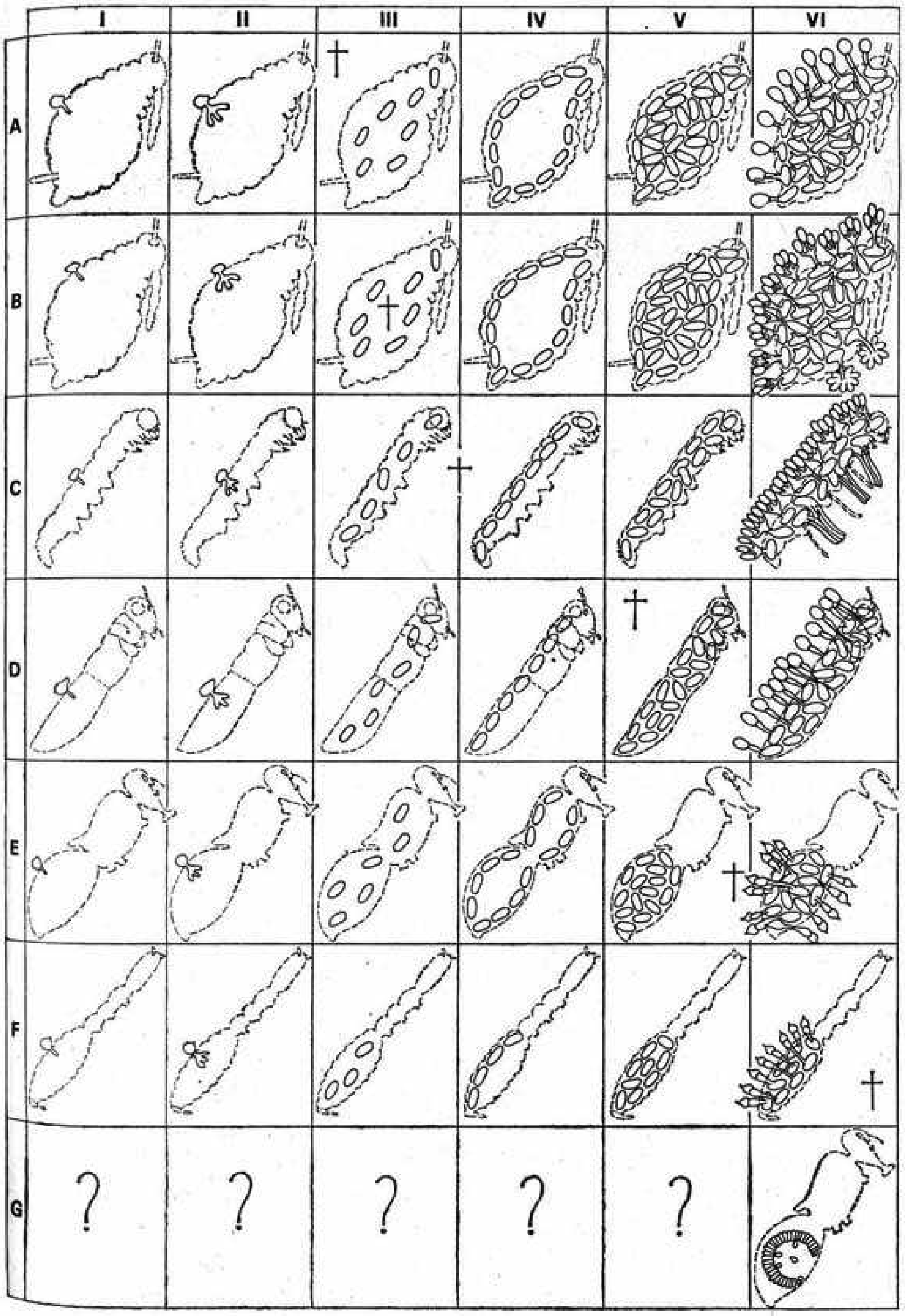

Figure 5. Scheme illustrating the diversity of host-parasite relationships in the course of development of insect mycoses caused by entomophthoraceous fungi. I-VI. Phases of development of disease. A. *Conidiobolus coronatus/Acyrthosiphon pisum* system. B. *Zoophthora aphidis*[Ed.: =*Pandora neoaphidis*]/ *Brevicoryne brassicae* system. C. *Zoophthora radicans/Pieris brassicae* system. D. *Entomophaga grylli/Calliptamus italicus* system. E. *Entomophthora muscae/ Musca domestica* system. F. *Entomophthoa weberi/Raphidia ophiopsis* system. G. *Strongwellsea castrans/Hylemyia cilicrura* system. Cross denotes the moment of the host's death. Additional explanations occur in the text.

4. Development in the host body

In the ontogenesis of entomopathogenic species of Entomophthoraceae as well as of the major part of entomopathogenic fungi, six main phases can be distinguished (Madelin 1968, Batko 1965):

1. ***Infection phase.*** Host infection takes place through integuments, *i.e.,* percutaneously. A fungal conidium sticks to the insect cuticle, germinates, and perforates the cuticle by enzymatic action (Fig. 6).

2. ***Lipolytic phase and localized development*** at the primary focus of infection in the fat body of the host. Histopathological and physiological examinations (Goldstein 1927, Boczkowska 1932, Schweizer 1947) showed that after penetration into the host organism the fungus at first grows slowly and does not spread within the insect body (Fig. 6). At this time the parasite secretes very active lipases which very actively digest fats.

In *Entomophthora muscae* (Schweizer 1947) this phase is also obligatory during in vitro development on an artificial medium. The fungus has to digest the available fat before it passes to the next phase as expressed by an increase in biomass. On fat-free media the fungus cannot pass to the growth phase, and "dies" in the form of a dwarf colony. For other entomophthoraceous fungi this phase is indispensable during development in vivo (Boczkowski 1929), but is facultative during development in vitro. Thus, this part of ontogenesis is regulated genetically in some species and by environmental factors in others.

3. ***Colonization of host body*** by generalization of infection. The fungus rapidly spread within the host body either as a result of growth of thread-like hyphae – *e.g.*, *Zoophthora radicans* developing in *Pieris brassicae* caterpillars (Boczkowska 1932) – or because of the rapid

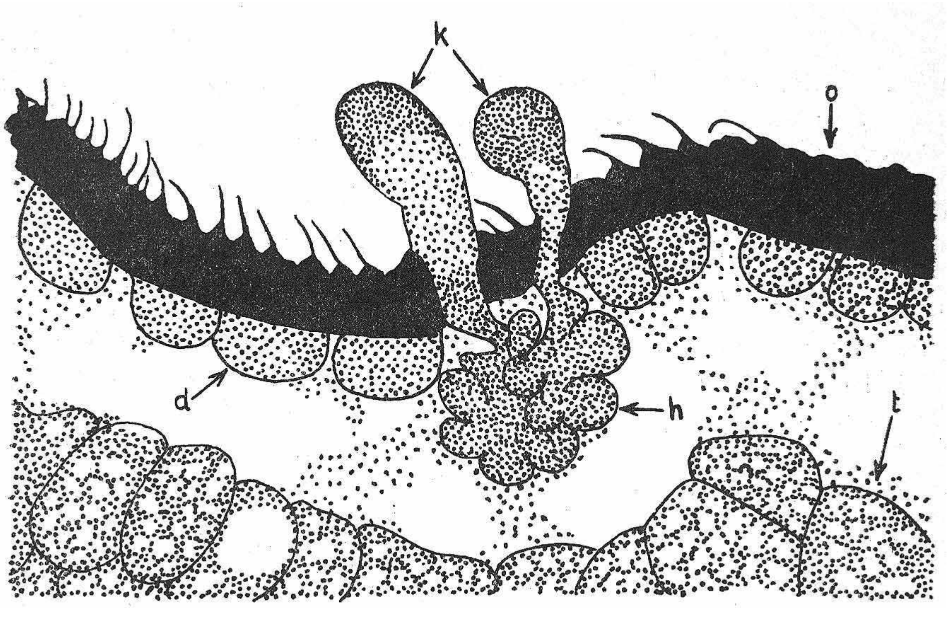

Figure 6. Two conidia of *Entomophthora muscae* on the cuticle of a house fly in the early stage of pathogenesis. k = conidium; o = cuticle; d= hypodermis; t = fat body; h= mycelium.

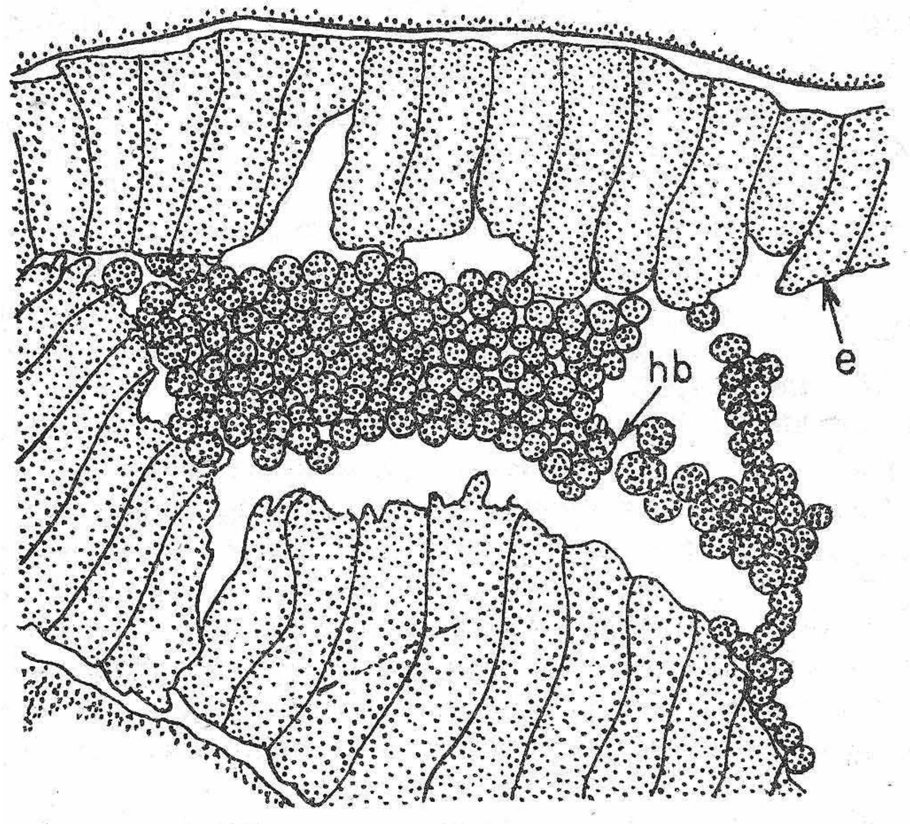

Figure 7. Hyphal bodies (hb) of *Entomophthora muscae*in an intestinal fold of a house fly in the third phase of infection. e = epithelial cells.

proliferation of numerous hyphal bodies (Fig. 7, *Entomophthora muscae* developing within the body of a fly) (see Schweizer 1947). As a result, the fungus penetrates into all tagmata of the host body (the abdomen, thorax, and head) irrespective of the infection site.

During this phase the fungus utilizes nutrients that were accumulated in part during the previous phase and from the host's hemolymph without actively digesting the host's tissues.

In some species – *e.g.*, *Entomophthora weberi* Lakon that parasitizes the larvae of *Raphidia ophiopsis* Weber – the fungus does not penetrate into the thorax or head, and infection takes place through the abdominal integument. At the division line between the abdomen and thorax of the host, a protective plug of proliferating tissue limits the spread of the parasite (Weber 1939). The course of development is also probably limited in a similar manner in some other entomophthoraceous fungi which develop only in the host abdomen (*e.g.*, *Massospora cicadina* Peck, *M. levispora* Soper, *Strongwellsea castrans* Batko & Weiser, and *Entomophthora erupta* Dustan). In *E. muscae*, however, this phase proceeds without restrictions (Batko 1965).

4. ***Proteolytic phase.*** After colonization of the host's whole body or at least of its abdomen, the fungus secretes very active proteolytic enzymes; it penetrates into the muscles and other tissues of the insect and very rapidly destroys the whole contents of its body (or only of the infected tagma). At the end of this phase, the contents of the host body are transformed into a milk-white fluid, a suspension of fat droplets and hyphal bodies of the fungus. At this time the body of the infected insect is like a thin-walled bag tilled with liquid, and the body is soft and flabby.

Only the chorion of mature eggs in bodies of females and (in Diptera) the cuticle of young larvae which often hatch from eggs within the cadavers of females, resist the destructive action of proteolytic enzymes. These eggs and larvae are often fully viable, a fact which indicates the impermeability of their integuments to fungal proteases (Batko 1965).

In *Entomophthora muscae* the development in this phase proceeds at first without restrictions so that the fungus penetrates the thoracic muscles. However, its subsequent development within the thorax (and head?) is inhibited, and only the abdominal tissues are fully destroyed (Batko 1965). This is important since it points to the attainment of the same final state (limitation of development to the abdomen) in closely related and morphologically almost indistinguishable species (*E. muscae*, *E. weberi* and *E. erupta*) by different ways, either via restrictions of spreading in the host's or because of limitation of the destructive effect on the host organism.

In *Massospora* species and *Strongwellsea castrans* the destructive action of fungus on the host's tissues seems even more limited; it concerns only some parts of the abdomen (at a given moment) or even only a part of tissues of a definite tagma (Goldstein 1929, Soper 1963, Strong, Wells and Apple 1960, Smith 1926).

5. Phase of host's body mummification. After completion of proteolysis, hyphal bodies of fungus suspended in fluid contents of the host's body rapidly absorb the surrounding liquid and grow quickly to form a spongy entanglement. The consistency of the body changes from flabby to rigid and cheese-like when fractured. At the end of this phase the infected tagmata of the host's body well strongly from the pressure of the mass of the parasite's mycelium; the individual skeletal plates of the insect part, and the connecting membrane extends and expands.

6. Sporulation. This phase can have a dual course: (A) Fungal hyphal pierce thin fragments of the host's integument, grow outside and are transformed into conidiophores with conidia or (B) hyphal bodies or cells of thread-like hyphae conjugate in pairs and the fungus forms thin-walled resting zygospores (Fig. 9). These zygospores usually form within the host's body. However, the sexual process is absent from many species, and the resting spores are formed as azygospores.

In *Massospora cicadina* the entire development proceeds somewhat differently. Phases 1 and 2 are unknown. The remaining phases proceed separately in each abdominal segment, beginning from the terminal; as a result the fungus colonizes and destroys the abdomen successively from the anal segment towards the thorax. At the time when the tip of the abdomen is destroyed and is dispersing fungal spores, basal segments contain undamaged organs and tissues (Goldstein 1929). The course of the final phase is also different; the fungus forms fine spherical capsules built of conidiophores which forcibly eject conidia into the interior spaces of these capsules.[8] The compact powdered mass of these capsules fills the abdomen and sprays off after the destruction of the integuments (Fig. 15D).

The course of development of *Strongwellsea castrans* within the body of *Hylemyia cilicrura* (Rond.) is unknown. However, according to the histopathological picture (Strong, Wells and Apple 1960, Batko and Weiser 1965), the whole organization of ontogenesis is different. The fungus forms a complex system of hyphae and conidiophores in the host's body, and this complex co-exists for a relatively long time with the functioning organs and tissues of the living host. A part of the fungal hyphae fulfill trophic functions by taking up food from the host's body whereas other hyphae transport food to sporulating hyphal bodies from which single conidiophores successively arise and discharge conidia. All conidiophores together

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[8] *Editor;s note:* The assumption that *Massospora* conidia are forcibly discharged into the interior chambers is incorrect. Conidial dispersal in *Massospora* is entirely passive (R.S. Soper, 1974. Mycotaxon 1: 13-40).

form a stable, long-functioning layer (pseudohymenium) rolled into a spherical capsule. This capsule communicates with the external environment through a large round opening in the ventral surface of the host's abdomen (Figs. 15G, 16A).

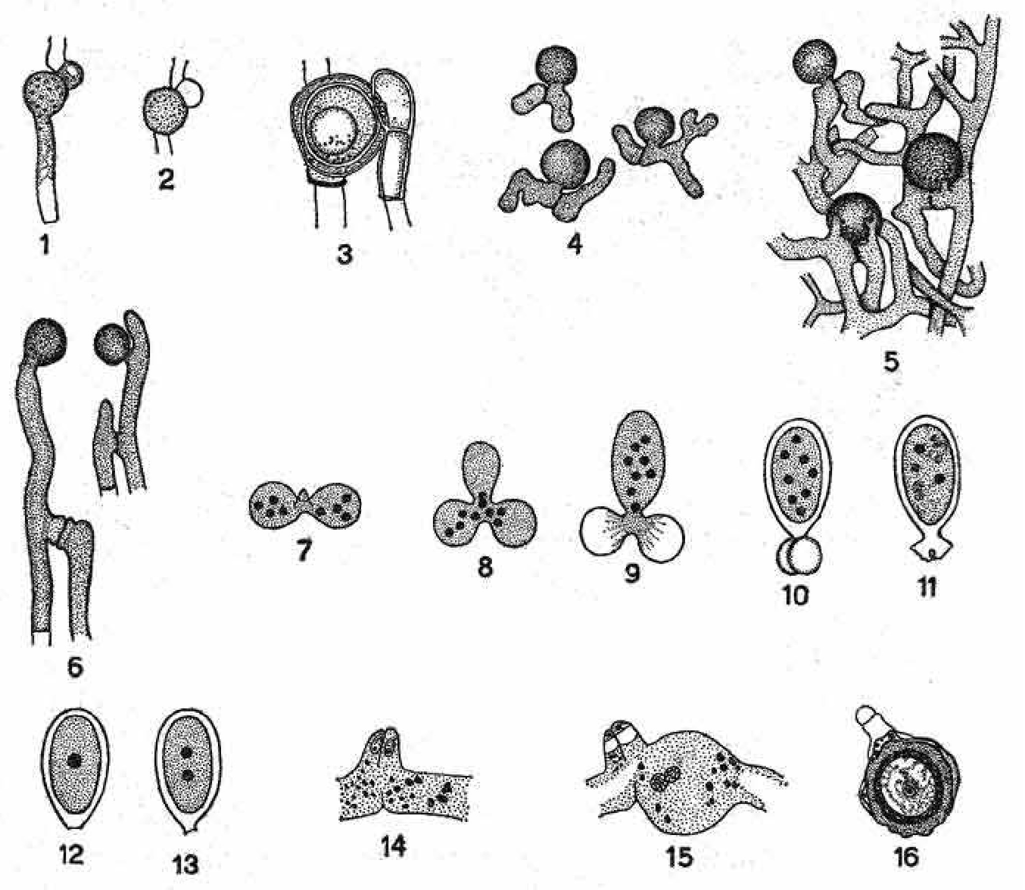

Figure 9. Zygosporogenesis of entomophthoraceous fungi. 1-3, *Conidiobolus brefeldianus*4-6, different species of *Zoophthora*. 7-13, course of zygosporogenesis and maturation of zygospore of *Triplosporium* [Ed.: = *Neozygites*] *fresenii*. 14-16, *Basidiobolus ranarum*. 1-3 after Couch, 1939; 4 after Nowakowski, 1882; 5-6 after Thaxter, 1888; 7-13, original; 14-16 after Fairchild.

There are great differences between insects in the resistance to Entomophthoraceae; this is expressed, among others, by the fact that various species of these fungi kill their hosts at different phases of their development. Figure 5 presents a scheme of the course of pathogenesis in some selected systems, the moment of the host's death being marked with a cross. This scheme based on data of many authors (Boczkowska 1932, Goldstein 1927, 1929, Schweizer 1947, Weber 1939, Batko 1965, and others) points to the pronounced diversity of the parasite-host relationships in these diverse systems despite a rather uniform course of pathogenesis. In each of the horizontal columns of the scheme the part situated to the left of the cross represents the period of true parasitism, *i.e.*, of life within the body of the living insect; the part to the right of the cross represents the period of development within the cadaver, *i.e.*, the period of saprophytic life. The relationship between these two periods is an objective index of the degree of specialization of a given fungal species as a parasite.

This scheme also illustrates the diversity of parasitic specialization of entomophthoraceous fungi. *Conidiobolus coronatus* kills its hosts as early as Phase 3 while *Entomophthora weberi* sporulates on a live though mortally sick host. A separate position is assumed by the last link of the chain, *i.e.*, *Strongwellsea castrans*, which is the only known nonlethal insect parasite within the family Entomophthoraceae. The fungus does not at all shorten the host's life; the only damage to the host is a parasitic castration involving gonad underdevelopment.

5. Effects on host behavior

The effect of the behavior of a host before its death, observed in many cases, is a characteristic property of entomophthoraceous fungi as insect parasites. This influence is of a distinctly adaptive nature, and leads to an increase in the probability for the conidia of infected insects to affect healthy members of the host population.

Insects are a substrate whose colonization is difficult' for fungi, since their populations usually represent "portions" of substrate well dispersed in space, mobile, and actively moving in dry air. In addition, this substrate is protected by the insect's own resistance systems. Lower fungi as a whole, and entomophthoraceous fungi in particular, are hygrophilic and immobile organisms. Conidia of entomophthoraceous fungi are, in most cases, very sensitive to drying, insolation, *etc.*, and can retain viability in the external environment for a short time (from several hours to several days). In fact, these conidia forcibly discharged from conidiophores are sticky, this facilitating their transport from insect to insect; however, the range of conidial discharge (from several millimeters to several centimeters) is incomparably smaller than the average distance between particular members of the host population. Thus, only under particularly favorable circumstances (*e.g.*, upon parasitizing aphids forming compact colonies) does the discharge of conidia from conidiophores create, in itself, a high probability of infection of a new host. In most cases, the probability is increased over the threshold level by coordination of the period of conidial discharge with a definite time and a definite ecological situation in the host population. In many cases this situation is additionally influenced by the parasite, due to its effect on the behavior of moribund insects.

The behavioristic adaptations of entomophthoraceous fungi to parasitism discussed in this part of the paper generally modify the behavior of the host before its death so that healthy members of the host population remain within the range of conidial discharge from the parasitized host. The extent of these adaptations, the degree of deformation of "normal" behavior in the presence of pathological changes, depends in the first place on host biology, ecological situation of the parasite-host system and closeness of association in this system (*i.e.*, upon the degree of parasitic specialization of fungus). In general, changes in the behavior of host occur if they are indispensable for increasing the probability of infection transmission in the host population, and if the fungus is able to cause such changes. Thus, these changes depend on diverse causes and are not necessarily correlated with the degree of parasitic specialization as considered separately from the remaining factors or with the biology of the host along.

I shall illustrate the above statements by some examples:

In the *Conidiobolus coronatus – Acyrthosiphon pisum* system (pea aphid based on the author's data), the death of the host occurs in Phase 3 (colonization of the host body). Before death, the infected aphid stops feeding and removes its proboscis from the tissues of the host plant. Dead insects remaining on the plant are only lightly attached by their legs; many hosts drop to earth. Much of the development of the fungus takes place saprophytically within the corpse of the aphid. The chances of successful spread of the infection are narrowed by the fact that the fungus often sporulates in ecologically unfavorable sites such as on the ground below and at a considerable distance from the host population.

Byford and Ward (1968) showed that the fungus reacts to the ecological situation of the host's corpse at the last phase of its development, since it develops different sporulation forms in dependence on this situation (*C. coronatus* displays polymorphism of its conidial apparatus). Thus, in this aspect, *C. coronatus* is a primitive parasite (corresponding with the primitive course of pathogenesis of diseases which it causes)> Since the fungus cannot affect the host's behavior or host nor, thereby, affect the nature of the ecological niche to be occupied by the parasite-host system, the fungus itself reacts adaptively during sporulation by responding to whatever random ecological situation it encounters. Thus, in *C. coronatus* a lack of behavioristic adaptation is compensated for by morphoanatomic and developmental adaptations.

In the *Zoophthora aphidis* (Hoffman ex Fresenius) Batko-*Brevicoryne brassicae* system (cabbage aphid, based on the author's data) the host does not change its behavior before death. Cabbage aphids live in dense colonies on the lower side of cabbage leaves. This host is an insect of low mobility, usually only some newborn winged virgins (*virgines alatae*) and winged individuals (*migrantes*) tend to move away from the parental colony. Most of the *virgines alatae* display a sedentary mode of life from birth until death with uninterrupted feeding; these forms contribute to colony growth throughout the summer.

Individuals killed by *Z. aphidis* remain in place, with the proboscis inserted in the tissues of cabbage leaves; the bodies also are attached by special fungal hyphae, the rhizoids. Consequently, the fungus sporulates in a very favorable ecological situation, since new potential hosts are situated within the range of discharge of its conidia and since the microclimate of the lower surface of cabbage leaves provides a very high relative humidity, protection from insolation, *etc.* As a result, the disease spreads very rapidly, attacking all individuals within the colony within several days, and is transferred to new colonies by migrating young aphids or by conidia falling from above (and also by the formation of secondary conidia, as is mentioned below).

Z. aphidis, in contrast to *C. coronatus*, exerts no effect on the behavior of the host before its death; however, this lack of effect is, by itself, a behavioristic adaptation. This is indicated by a small though essential difference in the behavior of dying aphids in both cases: In the first system the aphid infected by *C. coronatus* interrupts feeding and removes its proboscis from the plant tissues; this is doubtless the result of irritation of the insect by the parasite's toxins, but it cannot be regarded as an adaptive effect on the behavior of the host. In the second case the aphid infected by *Z. aphidis* does not interrupt feeding because the parasite does not "irritate" the host before its death; consequently, the corpse of the host remains attached to the cabbage leaf and the fungus sporulates in a favorable ecological situation. *Z. aphidis* displays no "compensatory" morphological adaptations characteristic of *Conidiobolus coronatus*; its conidial apparatus is monomorphic, comprising only ballospores (cf. below). In contrast to *C. coronatus* whose effect on the dynamics of host density is usually slight, *Z. aphidis* often causes mass deaths in populations of aphids (*Brevicoryne brassicae* L., *Aphis fabae* Scop., and others). This comparison demonstrates the greater effectiveness of behavioristic adaptations in relation to the compensatory morphological adaptations in entomophthoraceous fungi parasitizing aphids.

Behavioristic relationships in other entomophthorous fungus-aphid systems are similar; these systems comprise fungi which seem to be distantly related taxonomically and whose biology differs in many respects (*e.g.*, *Triplosporium fresenii* (Nowakowski) Batko, *Entomophaga thaxteriana* (Petch) Batko, *Culicicola chromaphidis* (Burger & Swain) Batko, *Zoophthora phalloides* Batko). It seems that in these systems, the biology of host (which in itself may provide a favorable ecological situation for the fungus), is the main factor regulating the behavioristic relationships. In some instances, the :lack of irritation" of host before death and possibly the additional attachment of the host after death to the substrate with rhizoids constitute adaptations by the fungus.

A lack of effect or an only slight effect on the behavior of the host also is encountered in other entomophthorous fungus-insect systems involving more mobile phytophagous or predacious hosts. In these cases, too, a "normal" behavior of host provides the most favorable ecological situation of the system for fungal dispersal. The possible small influence of a parasite consists of an enhancement of taxes or of instincts. As examples of such systems I shall describe the *Zoophthora radicans-Pieris brassicae*, *Entomophthora weberi-Raphidia ophiopsis* and *Strongwellsea castrans-Hylemyia cilicrura* systems.

Micropopulations of larval cabbage white butterflies (*Pieris brassicae* L.) on cabbage plants move progressively downward with time. The youngest caterpillars usually feed on fine top leaves, and then completely skeletonize the middle and bottom leaves by ingesting the parenchyma and leaving only the thickest veins. The caterpillars feed almost uninterruptedly, but occasionally change sites. In this micropopulation the disease caused by *Z. radicans* usually occurs by the middle of larval development and it infects third instar caterpillars, and less often second instars. During the hours immediately preceding death, infected caterpillars stop feeding and wander over the plant, as if searching for a new feeding site. However, they generally tend to move upwards (in a slightly expressed negative geotaxis) toward the open, partly devoured parts of the plant. Before death they bite strongly into the substrate with their mouthparts and attach with the legs in a position characteristic of normal feeding. As in all species of *Zoophthora*, the host is additionally attached by the formation of rhizoids immediately after its death. The fungus sporulates in an ecologically favorable situation since the host's cadaver is usually situated near and somewhat above the healthy caterpillars so that the fall of conidia to new hosts below facilitates their infection . As with *Z. aphidis*, *A. radicans* also often causes mass deaths in host populations.

Larvae of *Raphidia ophiopsis* are nocturnal predators living in crevices of tree bark. They avoid mutual contact although large larvae tend to cannibalize smaller ones. *Entomophthora weberi* sporulates on living larvae of this species. With the exception of the muscles in the last segment, musculature important for locomotion, the fungus destroys the abdominal contents of the host and the affected larvae are unable to feed effectively. However, they retain normal mobility because the fungus does not penetrate into the thorax and head (see above, p. 14). During the 6th phase of pathogenesis, the larval abdomen is covered with numerous cushions of fungal conidiophores from which conidia are continuously and forcibly discharged. Such larvae not only retain mobility but even attempt to prey on healthy larvae since their cannibalistic instincts are markedly enhanced (Weber 1939). In this case, the probability of infection of new hosts is enhanced further because the migrating sick larvae leave behind a trail of primary conidia attached to the substrate. Because secondary conidia formed on the primary ones (see below) can also infect new hosts, one mobile sick larva can form a whole network of trails of infective spores.

Male anthomyiid flies infected by *Strongwellsea castrans* do not lose their sexual instinct despite complete infertility. While the mode of transmission of this fungus to a new host is unknown, it seems that fly females act as infection transmitters, and the infection of a healthy male can result from copulation with a female previously covered by a sick male. Also in this case the lack of changes in the behavior of sick hosts, as compared with healthy ones, is of marked adaptive importance and promotes the dispersal of the parasite.

The comparison of those fungi discussed here that do not affect the behavior of the dying host indicates an evolutionary regularity. The lack of any effect on host behavior is found among fungi exhibiting very different levels of parasitic specialization (Fig. 5): The apparent absence of fungus-induced behavioral changes in immobile hosts such as aphids is wholly distinct from the habit of *Strongwellsea* in which the fungus draws nourishment from the host body without otherwise affecting the host's complete and normal locomotive, sensory, and even sexual activities. Whereas several levels of parasitic specialization are found among those fungal parasites showing an adaptive lack of behavioral alteration for their hosts, a very high degree of parasitic specialization is always found for those entomophthoraceous fungi (see lower rows of Fig. 5) attacking highly mobile insect hosts.

All the host-parasite relationships discussed here (except for those involving *C. coronatus*) reveal the effects of coevolution. In some instance, natural selection exerted a stabilizing effect and preserved the primary, primitive aspects for development of the pathogenesis; in other instances, selective pressures favored strains with decreased virulence but displaying increasingly specific adjustments to the host's biology.

A similar diversity of different courses of pathogenesis is observed in systems characterized by a distinct adaptive effect of parasite on host behavior. In the simplest cases this effect manifests itself by a change in taxis specific for a given insect species in a definite developmental phase such as geotaxis (as discussed above). In many entomophthorous fungus-insect systems, dying hosts tend to seek out the most elevated site; this tendency is weakly expressed by caterpillars of cabbage butterfly infected with *Zoophthora radicans* (see p. 18). Negative geotactic responses are characteristic for many hosts affected by diverse species of *Entomophthora*, *Entomophaga*, and *Zoophthora*; the affected insects differ greatly in their biologies, their habits (from phyllophagous to predaceous), the degrees of their mobility, their habitats, physiologies, *etc.*, and include caterpillars, larval hymenopterans (Symphyta), larval and adult beetles, flies, gnats, and the like.

In more complex cases, the effects of parasites on hosts' behavior do not concern an individual taxis but circadian rhythms or the whole behavior of the given insect species. *Entomophaga grylli* (Fresenius) Batko on the locust, *Calliptamus italicus* L., can serve as an example system: The population of *C. italicus* occurring in the Volga Steppes region in the vicinity of Saratov is periodically decimated by mass deaths caused by *E. grylli.* These deaths take place at the period of host density gradation, when the density of the *C. italicus* population is very high; the intensity of epizootics is usually greatest in July and August, when *Calliptamus* attains the imaginal phase. At this time the very mobile, alert, and large locust groups feed in the early morning and late afternoon hours on high steppe perennial plants (so-called "imaginal feeding" during which the gonads develop). After attainment sexual maturity, they copulate and lay clusters of egg masses in the soil along roads and on fallows. Locusts spend the hours of strongest insolation in sandy places devoid of plants and on roads during this period, and they warm themselves in loessial dust and copulate. Healthy individuals migrate onto high steppe perennial plants only in the late afternoon hours, feed there and remain for the height, often forming large assemblages called "locust bouquets."

Under these conditions the development of *E. grylli* in the body of *C. italicus* lasts about 5 days. The fungus enters the proteolytic phase on the last day of the host's life. During this phase the effect of the parasite on host behavior becomes manifest, and the host dies at the end of this phase. In the morning, both infected and healthy individuals fly to the above-mentioned sandy sites and roads. During the morning the infected individuals behave normally, but behavioral changes between 2:00 and 4:00 in the afternoon. The healthy individuals then still remain on the roads and at bare sites whereas the sick ones migrate prematurely to the tops of high perennial plants. During this same time, each insect found on high plants proved to be mortally ill due to infection either by *E. grylli* or the larvae of insect parasitoids of the Larvaevoridae (Diptera; = Tachinidae). After migrating to the high perennial plants, sick individuals remain motionless, although they temporarily retain their full sensory and locomotory activity since they are alert and fly away upon human approach. By 4:00 PM, however, many of them are so lethargic that they can be handled readily even though they still can fly a few meters to a new plant if they are thrown into the air. Thus, sensory activities are impaired first, while an hour or two later the insects also lose their flight ability, and their jumps become short and clumsy. At this time they cling very strongly to the plant with their legs and mouthparts, and it is difficult to remove them from there. The insect dies soon afterwards, usually between 5:00 and 7:00 PM. Upon its death, the whole insect body is filled with a milky liquid. The thoracic muscles are severely damaged, and the abdominal contents (except for mature eggs in females) are completely destroyed. In the head, the digestion of the central nervous system begins and proceeds very rapidly.

The proteolytic phase rapidly changes to the brief mummification phase. The abdomen of dying insects is flabby and filled with liquid, but after 1-2 hours it swells and becomes rigid and breakable. Sporulation usually takes place at night, between 9:00 PM and dawn. At this time the corpses of dead animals are surrounded everywhere by many healthy, intensely respiring insects resting for the night in dense clusters, often several layers of insect bodies deep. Conidia forcibly discharged from cadavers barrage the cuticle of healthy insects and immediately germinate, so that the infection of new hosts usually occurs during the same night. This fact is very important in semiarid climates characterized by extremely low air humidity, lack of dew, and high temperature during the day. Conidia which have no time to germinate and penetrate the host with their germ tubes before the dispersion of the host's nocturnal assemblage inevitably die; only within the dense mass of respiring and transpiring insects does the fungus encounter the high relative humidity necessary for its survival and perpetuation.

The above-described complex correlation of fungal development with normal host behavior derives from the rather primitive course of the pathology process (Batko 1957, 1965). The survival of *Entomophaga grylli* among pronouncedly xerothermic biotopes depends primarily if not exclusively upon adaptations which affect the host's behavior.

In the *Entomophthora muscae-Musca domestica* system, the situation is completely different. In this case, the parasite's effect on host behavior is equally complex, but is simultaneously correlated with the high degree of parasitic specialization by the pathogen (Goldstein 1927, Lakon 1919, Schweizer 1947, Batko 1965). The biology of houseflies is completely different from that of locusts. Populations of house flies or other hosts of *E. muscae* such as anthomyiid flies (Anthomyiidae) represent strongly dispersed sets of very mobile insects without pronounced daily rhythmicity (except for rest at darkness). Individual flies get in mutual contact for as long as a few seconds in two circumstances, during common feeding and upon copulation. Houseflies or anthomyiid flies (Fig. 1) killed by *E. muscae* die in an "unnatural" position with their wings characteristically lifted and turned out and with the abdomen held upward away from the substrates. Obviously, this position promotes release of conidia from conidiophores formed on the abdomen. This position bears no resemblance to the resting or feeding positions of healthy flies (in which the body is more or less parallel to the substrate with wings resting flat on the back). Nevertheless, healthy house flies frequently fly to such a cadaver, and either search intensely for food in its immediate vicinity or male flies may attempt to copulate with the corpse regardless of its sex.

Host behavioral modifications caused by *Entomophthora muscae* also include a negative geotaxis of sick flies before death; their corpses are usually situated at elevated, bare sites, and are visible from all sides. On account of the short duration of contacts between healthy flies and cadavers spreading *E. muscae* conidia, in this case it would not be purposeful to discharge a large mass of conidia in "volleys" as occurs with *Entomophaga grylli*. Therefore, changes in the behavior of sick house flies manifest themselves only in the last hour or two before death, possibly only because of the tagmatic restriction of *Entomophthora muscae* (see p. 14 and Fig. 5); the fly cadaver becomes a source of infection immediately after death or even during the final throes because of its assuming the "attractive" position described above. With favorable environmental conditions, the sporulation phase may extend for 2-3 days. More-over, numerous primary conidia stick on the surface around the corpse and usually form a wide ring and an additional, longer-lasting source of infection. These conidia are protected from drying out by a capsule formed by the conidiophore contents discharged together with the conidia; gradually, individual conidia develop and discharge a secondary conidium of the second type described below; the secondary conidia infect the approaching healthy houseflies.

The complex system of behavioristic developmental and morphoanatomic adaptations described above permits *Entomophthora muscae* to spread effectively in dipterous insect populations, and makes this fungus the causal agent for intense epizootics in populations of housefly and of many other dipterous insect species in families such as the Muscidae, Sarcophagidae, Anthomyiidae, and Drosophilidae.

In summary, these basic types of behavioristic relationships in entomophthorous fungi-host systems are listed:

1. Lack of adaptive influence on host behavior on the part of the most primitive parasites (*e.g., Conidiobolus coronatus*).

2. Adaptive lack of influence in systems in which the "normal" ecological situation of the host population promotes the maximal dispersal of the parasite.

3. Adaptive influence of fungus affects the behavior of the host insect in the period preceding its death.

Attainment of behavioristic adaptation by entomophthoraceous fungi was possible on different levels of their parasitic specialization. However, in systems involving mobile insects forming dispersed populations (larvae of *Raphidia ophiopsis*, dipterous insects, *etc.*), an adapative effect or an adaptive lack of effect on host behavior was attained only by highly specialized parasites (*e.g.*, *Entomophthora* species). Less specialized parasites (species of *Zoophthora* or *Entomophaga*) in most cases attained the state of effective behavioristic adaptation in systems with phytophagous insects of little mobility (aphids, caterpillars); these genera parasitizing mobile insects in "difficult" xerothermic biotopes have also attained effective behavioristic adaptations (*e.g.*, *Entomophaga grylli* on locust). Although most of these species belong to less common species occurring less frequently in biocoenoses, or have less impact on the densities of their host populations (*e.g.*, *Zoophthora vomitoriae* Rozsypal on *Calliphora* species, Fig. 2, or *Z. dipterigena* (Thaxter) Batko on small forest dipterous insects, Fig. 3). Thus, in the systems discussed here, the correlations between the mode of utilization of the host body, the parasite-host relationships at the population level, and behavioristic adaptations are very complex.

6. Conidia

Except for the resting forms, the conidia of entomophthoraceous fungi parasitizing insects are their only developmental form which are produced and function directly in the external environment. Also, in all cases known so far, conidia are the only infective agent spreading disease in host populations. It can be assumed that the conidia of entomophthoraceous fungi, as part of the fungal some, are the developmental phase subjected most intensively to the differentiating effects of natural selection. These selective pressures derive from the great

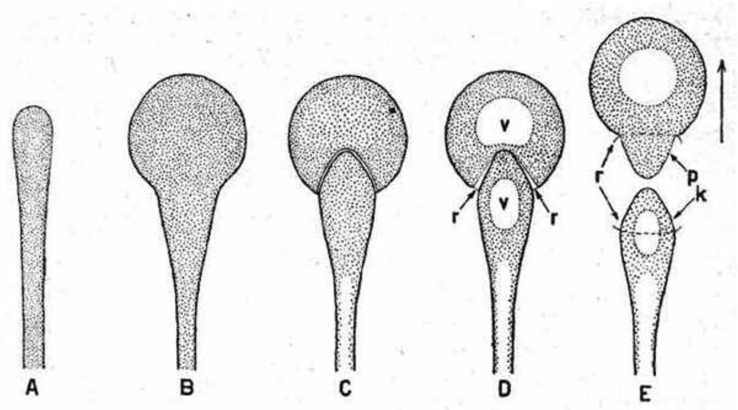

Figure 10. Development and discharge of a conidium in an entomophthoraceous fungus. A, immature conidiophore. B, conidiophore with distention that will form the conidium. C, conidium delimited from conidiophore by a papilla (upper septum) and columella (lower septum) system. D, vacuoles (v) in conidium and conidiophore form and exert pressure consequently causing the papilla to evert against the columella and causing the distention of the ring (r) which connects the conidium to the conidiophore. E, connecting ring (r) is ruptured, the papilla (p) is everted, and the conidium has been forcibly ejected; k = columella; p= papilla.

diversity of external environments in which fungus-insect systems occur, from the immensely diverse biologies of the hosts themselves, and from the substantial differentiation of the various host-parasite relationships discussed here at the levels both of individuals and of populations. It can be expected, therefore, that the conidia of entomophthoraceous fungi (1) are clearly adapted to fungal dispersal among insect populations, and (2) are themselves greatly differentiated structures. For these reasons, the development, function and structure of entomophthoraceous conidia will be discussed in some detail.

A. Ballospores

One of the most characteristic properties of entomophthorous fungal conidia consists of their being forcibly discharged from the conidiophores, sometimes to a distance of up to several centimeters. The mechanism of this discharge is relatively differentiated; however, in its typical and most widespread form it involves violent rounding off of turgid elements ("liberation due to rounding off of turgid cells" according to Ingold 1966). In entomophthoraceous fungi, as compared with other fungi, this mechanism is greatly perfected. The rounding off of elements comprises special parts of the conidial wall (papilla) and of the conidiophore wall (columella). This process is described in the explanation of Fig. 10. The forcibly discharged conidia of Entomophthorales species henceforward will be referred to as *ballospores*.[9]

Ballospores of entomophthoraceous fungi are thin-walled and sticky. This permits them to adhere to the surface on which they fall after discharge, and to react rapidly to the nature of this substrate by forming a germ hypha on the cuticle of an appropriate host or by forming a secondary conidium). On the other hand, these thin walls cause conidia to be very sensitive to drying, insolation, etc., and their stickiness combined with the relatively great mass renders their anemochorous dispersal by air currents difficult. Ballospores of entomophthoraceous fungi are thus typically autochorous (self-dispersing) spores.

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[9] The name reflects the essence of the mechanism of ejection of these spores, which bears a resemblance to the action of factors setting a kicked ball into motion.

I define primary ballospores as those formed on the host, on conidiophores growing from vegetative mycelium. When discharged onto an inappropriate substrate, these ballospores germinate to form one or more secondary conidiophores bearing an apical secondary conidium.

B. Secondary conidia

1. *Secondary conidia* are most often also ballospores. From any primary ballospore, usually only one secondary ballospore forms (Fig. 11), this spore is somewhat smaller than the primary, but generally resembles it in other respects. A secondary ballospore of the first order) can again from a secondary ballospore (this time of the second order); the latter can again form a secondary ballospore of the third order, etc., nearly until exhaustion of the substances and energy resources of the spore. The number of these generations of secondary ballospores depends on the environmental conditions, fungal species and dimensions of the starting primary ballospore.

In the case of the large-spored saprophyte *Conidiobolus brefeldianus*, Couch (1939) described more than ten-membered sequences of ballospores ejected, owing to phototropism of conidiophores, always in one direction and covering a distance of more than ten centimeters. Phototropism of conidiophores is fairly widespread in Entomophthorales, especially in saprophytic species (Callaghan 1969a). The described manner of spreading by way of multiple formation of autochoric conidia is one of their main weapons in the struggle for life (see 2, items 1 and 2). Primary ballospores of entomopathogenic species of entomophthoraceous fungi are usually smaller than the conidia of saprophytic species, and they are discharged to a shorter distance. The number of "generations" of secondary ballospores is also smaller.

However, the adaptive importance of this type of spreading of insect parasites in an ecological niche is very clear. The important factor is not the distance to which the ballospores are discharged (since it is usually smaller than the average distance between individuals of the host populations), but the fact of forcible discharge of a sticky spore and the possible prolongation of the process through secondary spore formation. These properties

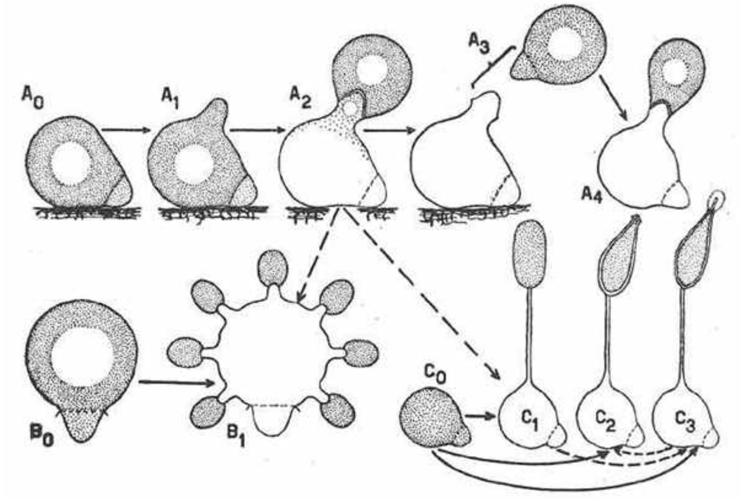

Figure 11. Secondary conidia of entomophthoraceous fungi. A, development and discharge of a secondary ballistospore. B, development of microconidia on a ballistospore. C, development of capillispores on a ballistospore (C_1, prohaptospore; C_2, ahaptospore, C_3, haptospore).

allow the dissemination in the environment of a certain reserve of infective material for many entomophthorous species; examples of this are the infective "trail" behind hosts infected by *Entomophthora weberi* or the round infective zone around the cadavers of house flies killed by *Entomophthora muscae*.

These properties allow for the evolutionary differentiation of the secondary sporulation systems of entomophthorous fungi leading to the development of morphofunctional differences between primary and secondary conidia, and to reduction of the number of "generations" of secondary conidia This phenomenon can be referred to as oligomerization of the conidial apparatus, according to the concept in evolutionary protozoology (Dogiel 1954).

Among saprophytic species of entomophthoraceous fungi encountering changing environmental conditions, the differentiation of the secondary conidia led to the development of microconidia and capillispores as well as secondary ballospores. These additional types of secondary conidia are also encountered as rudimentary structures in some entomopathogenic species.

2. *Microconidia* (Fig. 11b) consist of small ballospores simultaneously formed in great numbers on one primary ballospore. They occur in *Basidiobolus microsporus* Benjamin (Fig. 18a) and in some species of *Conidiobolus* such as *C. coronatus*.

3. *Capillispores* (Fig. 11c) are nonautochorous secondary conidia formed on thin, erect capillary conidiophores. Capillispores with a thin, elastic, and sticky wall – "prohaptospores"[10] – were observed only in *Entomophthora lampyridarum* Thaxter (Fig. $11c_1$) parasitizing beetles. The remaining categories of capillispores have a dry and thickened wall. The apex of some of them has a special outgrowth covered with a layer of adhesive substance (Fig. $11c_3$); these are the zoochorous spores spread by arthropods which I refer to as *haptospores*. In most cases, however, these capillispores have a reduced top adhesive outgrowth and are anemochoric spores (Fig. $11c_2$) to which I refer as *ahaptospores*.

Haptospores occur in many representatives of the genus *Basidiobolus*; these fungi, whose spores are transmitted by coprophilic flies, are coprophytic on the feces of insectivorous amphibians and reptiles. Ahaptospores are encountered in many species of *Conidiobolus* and in some entomopathogenic species of *Zoophthora* and *Triplosporium*.

This mosaic distribution of capillispores in entomophthorous fungi is one of the reasons for assuming the whole order Entomophthorales to be a monophyletic group. These are spores of a very specific structure, which is not encountered in other lower fungi. It is difficult to assume their evolutionary development by convergence.

C. Architectonics and development of the conidial apparatus

The morphological categories of conidia from entomophthorous fungi described above illustrate the diversity of their "external attire." Conidia of the Entomophthorales also differ in their internal organization since they contain a different number of nuclei. Nuclei are characterized by different sizes and different cytochemical properties (*e.g.*, staining with specific microscopical dyes) (see Batko 1964a-d). The conidial wall may have either one or two layers. The degree of dispersion and distribution of reserve substances in the conidia may also differ. In considering the above, certain selected relationships of the cytoanatomical

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[10] In previous publications I have named these spores and the two subsequent categories protoadhesispores, adhesispores, and anadhesispores, respectively. I am greatly indebted to Dr. Walter Gams (Baarn, Netherlands) for suggesting the etymologically more correct terms applied in this paper.

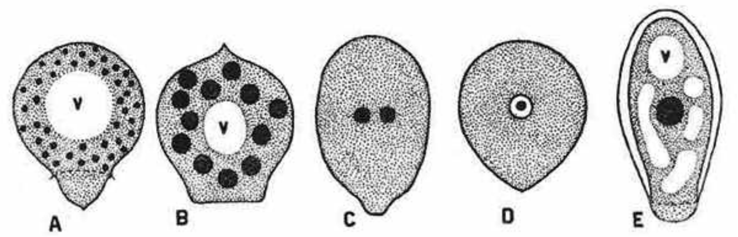

Figure 12. Architectonics of entomophthoraceous fungal conidia. A, polykaryotic conidium. B, oligokaryotic (duodecimkaryotic) conidium. C, oligokaryotic (dikaryotic) conidium. D, monokaryotic conidium of *Basidiobolus* (type 3). E, monokaryotic conidium of *Zoophthora* type (type 4). v = vacuole, nuclei are marked in black; in D, nucleolus is marked in black.

organization of the conidia constitute what is referred to here as spore *architectonics.*[11] By using the nuclear apparatus of the conidium and its coat (whether it includes one or two walls), I distinguish the following architectonic categories:

Type I. Polykaryotic conidia with a single wall, containing a great and varying number of small nuclei (Fig. 12a).

Type II. Oligokaryotic conidia with a single wall, containing large nuclei in a number constant for a given species and varying between 2 and 24 per conidium (Fig. 12b-c). A series of species can also be distinguished based upon conidia containing 2, 4, 6, 8, *etc.* nuclei.

Type III. Monokaryotic conidia with a double wall (Fig. 12d), containing one large nucleus with a distinct nucleolus.

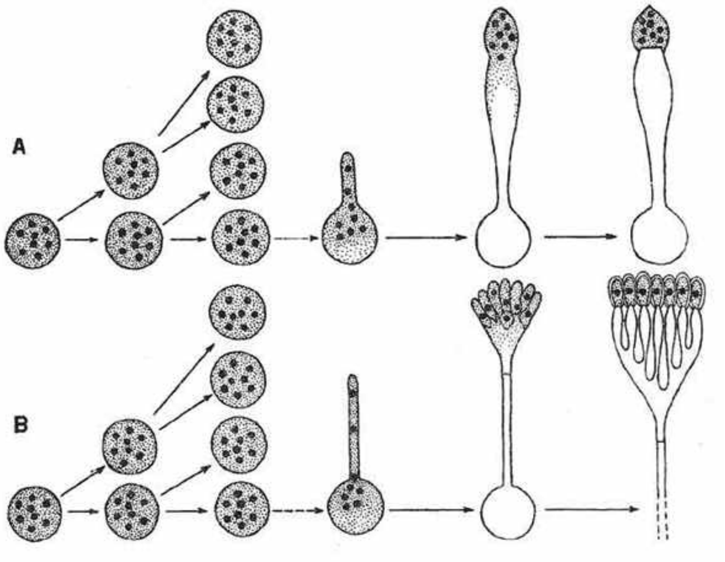

Figure 13. Sporogenesis in entomophthoroaceous fungi. A, sporogenesis in species whose development involves only archetomic division. B, sporogenesis in species developing with conribution of archetomy and syntomy (*Zoophthora* type).

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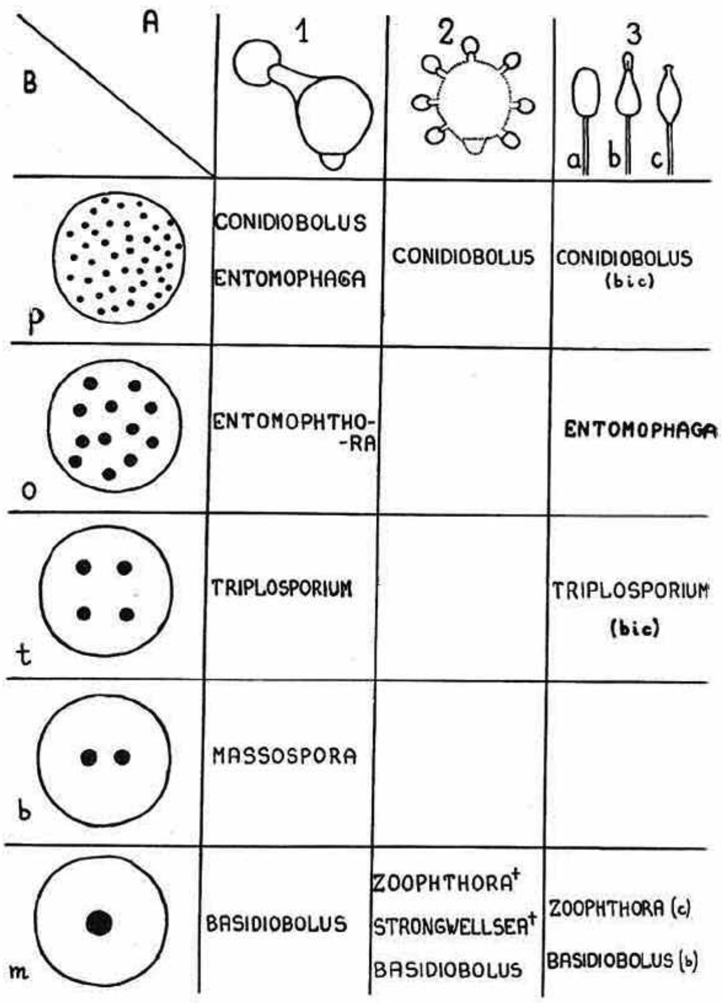
[11] I employ the term "architectonics" of the fungal body in the sense attributed to it by Beklemishev (1964) with respect to invertebrates.



B \ A	1	2	3 a b c
p	CONIDIOBOLUS ENTOMOPHAGA	CONIDIOBOLUS	CONIDIOBOLUS (b,c)
o	ENTOMOPHTHO-RA		ENTOMOPHAGA
t	TRIPLOSPORIUM		TRIPLOSPORIUM (b,c)
b	MASSOSPORA		
m	BASIDIOBOLUS	ZOOPHTHORA^{+} STRONGWELLSEA^{+} BASIDIOBOLUS	ZOOPHTHORA (c) BASIDIOBOLUS (b)

Figure 14. Morphoanatomical correlations in conidial apparatus of entomophthorous fungi. A. Morphological form: 1, ballistospores; 2, microconidia; 3, capillispores, 3a, prohaptospores, 3b, haptospores, 3c, ahaptospores. B. Architectonics: p, polykaryotic conidia; o, oligokaryotic conidia; t, tetrakaryotic conidia; b, dikaryotic conidia; m, monokaryotic conidia. "+" indicates monokaryotic state for primary conidia.

Type IV. Monokaryotic conidia with a double wall (Fig. 12e), containing one large nucleus similar to those of oligokaryotic conidia.

A common feature of conidia of types I through III consists in their architectonic identity with the cell from which the unbranched conidiophore holding the conidium has grown. During the formation of these conidia the cell contents flow through the conidiophore into the rudiment of the spore, and they separate themselves by a septum (Fig. 13a).

The formation of Type IV conidia is more complex. They are formed only in fungi with oligokaryotic vegetative cells. From such a cell there grows a conidiophore which, after penetration of the host integuments (these species parasitize only invertebrates), becomes irregularly and richly branched. The contents of the parental cell move to the top of the conidiophore and, during the course of this translocation, are divided into uninucleate fragments. Each of these fragments passes to the top of one of the conidiophore branches, becomes surrounded with its own wall and is transformed into a conidium (Fig. 13b). These conidia differ from other types not only in their architectonics, but their development also includes an event not encountered in other entomophthoraceous fungi, *i.e.*, cytokinesis leading to the division of multinucleate protoplasts into many uninucleate ones. This type of division is referred to by Zakhvatkin (1949) as *syntomy*, and the division of multinucleate protoplasts into multinucleate ones as *archetomy*. Thus, whereas in the ontogenesis of all remaining Entomophthoraceae only archetomic divisions are encountered, in the ontogenesis of fungi forming Type IV conidia we deal with a sequence of many archetomic divisions in the course of the vegetative development of the thallus, ending with a series of syntomic divisions at sporogenesis. Conidia of Type IV occur in all species of *Zoophthora* and, with certain modification, S*trongwellsea castrans*. In the further text they will be referred to as conidia of the *Zoophthora* type.

Monokayotic conidia of Type III are found in species of *Basidiobolus*. These spores differ from all remaining conidia of the Entomophthorales not only in the internal structure of the nucleus, but also in the course of further development after their discharge from the conidiophore. Under certain environmental conditions the conidial nucleus undergoes division, followed by the division of the conidial contents into two protoplasts; this process can be repeated 2-4 times more with the formation of 4, 6, 16 or even 32 uninucleate protoplasts within the spore (see Benjamin 1965; Callaghan 1969c). This division is referred to by Zakhvatkin as *palintomy*; it leads to the same result as syntomy but in this case a uninucleate protoplast is the starting point. Vegetative cells of *Basidiobolus* are uninucleate and their divisions during the vegetative growth of the thallus are the most widespread monotomic division in nature (uninucleate cell divided into two uninucleate ones). Thus, the ontogenesis of *Basidiobolus* comprises a sequence of monotomic divisions ended by a series of palintomic ones; this means that its developmental sequence differs wholly from the ontogenetic patterns discussed earlier for the remaining entomophthoraceous fungi.

The various combinations between the morphological types of conidia discussed in the previous section, and the architectonic types discussed here are characteristic for entomophthoraceous fungi as a whole. Each “morphological attire” of these conidia can have several “architectonic contents” (Fig. 14). In sum, there arises an immense morphoanatomic and morphogenetic diversity whose analysis can be a basis for the construction of a phylogenetic concept.

However, before passing to the central part of these considerations, I shall briefly describe the individual developments of entomophthorous fungi. Up to here only the development of their sporulation was discussed.

7. Organization of ontogenesis in entomophthoraceous fungi

From the conidium that initiates the development of the vegetative thallus of the discussed fungi in the host body or on inert substrates, there arises a germ hypha penetrating into the substrate. Conidial contents pass to the apex of this hypha and begin growth (in the case of the *Zoophthora*-type conidia, after reconstituting the number of nuclei specific for the given species via karyokinesis). In fungi with polykaryotic cells (*Conidiobolus* and *Entomophaga* species), the number of nuclei increases with the growth of the cell and after a certain time archetomic division of the cell takes place. Multinuclear cells of these fungi, dividing archetomically can become separated as so-called hyphal bodies or make up elongated hyphae divided into cells by septa. Nevertheless, the whole system remains integrated, and interacts as a whole with the host organism or dead substrate. Thus, cell divisions are in this case associated with the vegetative growth of a spatially continuous or diffusive, dispersed thallus;

they do not represent multiplication of unicellular organisms as in insect infections caused by yeast-like fungi (see Weiser 1965).

In fungi with oligokaryotic cells, archetomy proceeds in a more ordered fashion, and nuclear divisions occur more or less synchronously. Thus, in these fungi the number of nuclei in vegetative cells is more or less constant and is characteristic of the given species or even of a genus (*e.g.*, in *Triplosporium* species it is four; two in *Massospora*, four in *Entomophthora erupta*, but six in *E. weberi* and twelve in *E. muscae*). This course of ontogenesis is found in all entomopathogenic species of the Entomophthoraceae whose nuclear histories are known, except for *Conidiobolus coronatus* and species of the genus *Entomophaga*; however, as far as is known, this pattern is absent from saprophytic species.

The ontogenesis of *Basidiobolus* was described above.

After completion of vegetative development, *i.e.*, in entomopathogenic species after the attainment of the mummification phase and in saprophytes after the exhaustion of food reserves, each vegetative cell produces a hypha which penetrates the surface of the substrate and grows aerially. In saprophytes and many parasites, such hyphae are transformed into conidiophores and form conidia apically. However, in some entomopathogenic species – all species of *Zoophthora* and *Culicicola* Nieuwland and some of those in *Entomophaga* – some of these hyphae are transformed into barren structures, *rhizoids* (Fig. 3, *rh*) which attach the host body to the substrate or into frequently large hyphae protruding among the conidiophores, the so-called *pseudocystidia.*

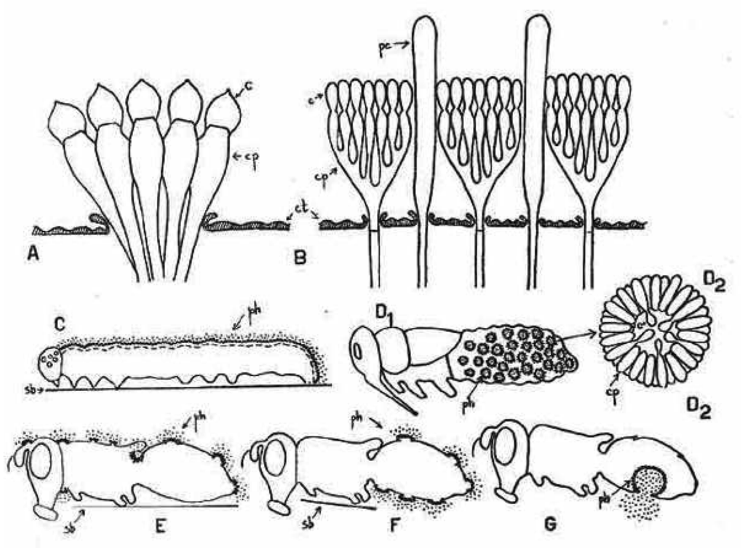


Figure 15. Pseudohymenium of entomophthoraceous fungi. A. *Entomophthora* type, composed only of conidiophores. B. *Erynia* type, composed of conidiophores and large pseudocystidia. C. Localization of continuous pseudohymenium on host body. D. Internal pseudohymenium of *Massospora* type. E. Pseudohymenium localized by the structure of host integuments. F. Pseudohymenium localized by nature of host-parasite relationships. G. Internal pseudohymenium of *Strongwellsea* type. c= conidia; cp = conidiophores; ct = host cuticle; ps = pseudocystidia; ph pseudohymenium; sb = substrate.

The function of pseudocystidia is unclear. However, it seems that they are rudimentary structures, inactive rhizoids that grew from the host mummy opposite to the substrate or aside of it. I discussed in greater detail this hypothesis and arguments in its favor in another study (Batko 1966b).

Conidiophores of saprophytes and of some nonspecialized parasites of arthropods grow asynchronously from the substrate or from different sites on the host body so that the aggregation of conidiophores shows no definite organization (Fig. 4). In insect parasites, the conidiophores grow simultaneously during the last phase of pathogenesis and together form a compact layer (*pseudohymenium*). In some *Zoophthora* species, the pseudohymenium may also include pseudocystidia as well as conidiophores (Fig. 15b), while in other species the pseudohymenium is composed solely of bundles of conidiophores (Fig. 15a).

Localization of the pseudohymenium on the host body (or inside it) depends on the properties of host integuments, as well as on the degree of parasitic specialization of the fungus and its pattern of development. In insects with thin elastic cuticles (*e.g.*, aphids or caterpillars) the pseudohymenium covers the whole body surface wherever it does not adhere to the ground and is a continuous pseudohymenium (Fig. 15c). In insects with integuments made up of hard sclerites connected by thin membranes (*e.g.*, dipterans or beetles), even those parasites showing no tagmatic specialization and developing within the whole host body form pseudohymenia only on the surface of thin-walled fragments of insect integuments between the sclerites (Figs. 2 and 15e). This pseudohymenium is localized by the structure of host integuments. Parasites with development restricted only to the host abdomen form pseudohymenia only on the thin-walled fragments of abdominal integuments (*i.e.*, pseudohymenia localized by the nature of the parasite's development, Figs. 1 and 15f). Finally, pseudohymenia of *Massospora* and *Strongwellsea* represent still another type of organization formed within the host body and :curled up" into many spherical capsules (*Massospora*, Fig. 15d) or into one stable, long functioning, and open capsule (*Strongwellsea*, Fig. 15g).

8. Sexual process and cycles of nuclear phase transformations

In all known cases, the sexual process of the Entomophthorales is of the type called zygogamy, and involves the conjugation of two gametangia. Variations in the course of conjugation among diverse species reflect differing degrees of differentaitions of gametangia,

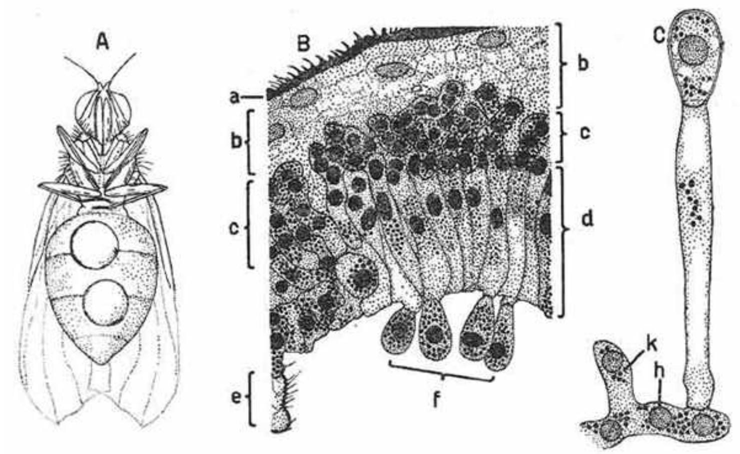


Figure 16. *Strongwellsea castrans*. A. Round openings in abdominal cuticle of male anthomyiid fly caused by parasite (after Smith, 1926). B. Cross section through capsule of fungal pseudohymenium and insect abdomen. C. Hypha, conidiophore and conidium of fungus. a = cuticle; b - host tissues; c - trophic hyphae; d = conidiophore layer; e = edge of opening; f = conidia; k = characteristic granulation in fungal plasm; n = nucleus. Original drawing (B, C).

sites of formation of zygospores, architectonics of the nuclear apparatus of both gametangia and zygotes, *etc.* This diversity is illustrated in Fig. 9.

The exact course of nuclear ploidal changes is known so far only in *Basidiobolus* in which meiosis in gametangia before conjugation was frequently observed. In all known species of this genus on gametangia characteristic processes are formed, and in *B. ranarum* from these processes there depart supernumerary haploid nuclei not participating in karyogamy; thus, all species of this genus are considered to exhibit pregamic meiosis, and they are regarded as diplobionts.

No similar exact data exist for the remaining species of the Entomophthoraceae. However, observations of the nuclear apparatus in different phases of conjugation and maturation of the zygospores of *Triplosporium fresenii*(Fig. 9) and in some species of *Zoophthora* seem to indicate that these fungi are haplobionts. Processes attesting to pregamic meiosis such as those on the gametangia of *Basidiobolus* species are found in no other representatives of the entomophthorous fungi.

Many representatives of the genus *Conidiobolus*, with their saprophytic mode of life, and many parasitic species (all species of *Entomophthora* and many of *Zoophthora* and *Entomophaga* exhibit no sexual process, and these fungi do not undergo nuclear ploidal changes.

9. Diversity within the group as a whole

The picture of the group traced to this point, comprises many planes reflecting different aspects of life of the discussed fungi. It is a mosaic made up of partial classifications based on different types of relationships: entomophthorous fungi with individual insects, entomophthorous fungi with the host population, entomophthorous fungi with insects in the taxonomic sense, developmental relationships within the entomophthorous fungi themselves, morphological as well as cytoanatomical and morphogenetic relationships within the range of spore forms of entomophthorous fungi, etc. This analytical picture of the group reveals a certain objective naturalnes ("order in nature" fide Simpson, 1961) more effectively than a list of all descriptions of known Entomophthorales. This picture even contains certain explanatory elements or statements of causality for given structures – *e.g.*, for conidia by associating them with a given morphogenetic pattern, or for elucidating the behavioral aspects of development in entomophthorous fungus-insect systems by stressing their adaptive importance and the most probable paths of their evolutionary derivation. In this respect, this picture is a certain step forward in gaining knowledge of the Entomophthorales in relation to the initial set of descriptions.

On the other hand, however, the descriptions constituting the starting point for comparative analysis dealt with certain groups as a whole, organisms, as well as their populations, strains, etc. The splitting of these descriptions into parts for different plans of comparative analysis blurred the picture of these whole groups, and, therefore, it requires their reconstruction in light of the results of their analyses. The reconstructed picture of the entire group discussed here will be a certain preliminary classification, very heterogeneous in its nature: some of its fragments will reflect only the observed resemblances and differences, and correlations between them. Other fragments will partly explain the nature of these resemblances, and still other fragments will be adopted without reservations from earlier taxonomic classifications. Reconstruction of this picture ought to prepare the ground for construction of a natural classification in Simpson's sense (1961), based on the overall relationships making up the entire structure of the classified group. This reconstruction ought to disclose these fragments of the first picture of the whole group (*i.e.*, of the preliminary classification), which in the first place require additional explanation. Moreover, this reconstruction should form the background for the discussion of the so-called "critical" groups in a taxonomic sense. Thus, I shall synthetically discuss the various genera of entomophthoraceous fungi, beginning with those admitted without any essential reservations during the revision of the group and incorporated into the new classification.

The often-mentioned genus *Basidiobolus*, including coprophytes and soil saprophytes, differs greatly from the remaining fungi in the Entomophthorales. *Basidiobolus* species are diplobionts with a somatic mycelium composed of monokaryotic cells, and an ontogeny comprising monotomic and, possibly, palintomic divisions. They may form endogenous sporangiospores within the conidia, and exhibit a greatly different mechanism of conidial discharge (in which the top of the conidiophore breaks off with the conidium). In the existing classifications, this genus has been singled out in the separate family Basidiobolaceae. This family together with the monotypic Ancylistaceae (not discussed here) and entomophthoraceous fungi proper, Entomophthoraceae, form the order Entomophthorales. In the revision discussed here, I accept this taxonomic arrangement for the order.

Despite the extent and importance of the differences between *Basidiobolus* and representatives of entomophthoraceous fungi in their strict sense, it is necessary to stress the resemblances between these two groups in order to regard the order Entomophthorales as monophyletic. These resemblances include the formation of microconidia and capillispores by many species in both groups, and the affinity for the tissues of homeothermic vertebrates, etc.

It is of interest that the major differences between *Basidiobolus* and *Conidiobolus* concern the structure of development and architectonics of the thallus (characters which are intuitively regarded by biologists as “essential”). However, these similarities depend upon the external morphological “attire” and relationships with the habitat (characters developing from the pressure of natural selection which are, in a sense, “directly” adaptive). The attribution of higher taxonomic value to the former set of characters (through familial standing for *Basidiobolus*) reflects the taxonomist’s deep-rooted or subconscious conviction about the unequal taxonomic importance of the different elements of a description as well as the possibility and the need to evaluate their taxonomic importance.

As with *Basidiobolus*, the genus *Conidiobolus* was not included in the discussed taxonomic revision. However, information on the body structure, individual development, and the biology of its members played an important role as a reference system during the construction of the phylogenetic hypothesis. This genus comprises about 20 primarily saprophytic species of fungi with multinucleate mycelium, a strongly differentiated multinucleate conidial apparatus (producing ballospores, microconidia, ahaptospores), and great ecological plasticity related to its rich enzymatic equipment. Zygo- or azygospores of these fungi are formed endogenous in recipient (female) gametangia or in azygosporangia.

Massospora and *Strongwellsea* differ from the remaining entomophthoraceous genera in their course of pathogenesis and in the organization of their pseudohymenia. Moreover, the only known representative of *Strongwellsea*, *S. castrans*, differs from all remaining entomophthoraceous fungi in its nonlethal parasitism although it exhibits a marked ontogenetic and structural resemblance to the genus *Zoophthora* (Batko and Weiser 1965).

The genus *Tarichium* comprises poorly known species, described from their resting spores and without a known conidial apparatus. This genus was omitted from the revision, although information about all species included in *Tarichium* was published by MacLeod and Müller-Kögler (1970).

After subtracting the species of these little known genera listed on p. 309, but not otherwise discussed here, there remain about 100 species of entomopathogenic entomophthoraceous fungi which are the object of the discussed taxonomic analysis. All of these fungi are characterized by a set of common characters diagnostic for the Entomophthoraceae (*e.g.*, formation of ballospores, bi- or multinuclearity of vegetative mycelial cells, zygogamic sexual process or lack of a sexual process, ability to form secondary conidia. The ability to parasitize insects is the only common denominator of the group. These fungi do not form within entomophthorous fungi a distinct group that could be distinguished nonarbitrarily; they do not satisfy Simpson's criterion for genera since they are not "nonarbitrary as to exclusion"). Aspects of some species closely resemble representatives of *Conidiobolus* while other characters of the same species differ from *Conidiobolus*. This group is in every respect greatly differentiated among itself, and it represents the core of the family Entomophthoraceae. It is this part of the family that has achieved the greatest success in the struggle for life and has already undergone such evolutionary proliferation.

Section II

10. Lower plant taxonomy: phenetic or phylogenetic?

Most present-day taxonomists, both botanical and zoological, believe that the diversity of organisms and of their groups now observed developed after this prolonged action of natural selection on populations of organisms exhibiting variability. This means that the differences and resemblances between present-day organisms are, in some measure, a reflection but not a direct copy of their genealogical relationships, *i.e.*, their descendency relationships. The goal of the classification aspires to represent the whole of the relationships between organisms, *i.e.*, of the structure ("order" according to Simpson, 1961) of the living world diversity.[12] This consistency of views embraces, however, general theoretical assumptions rather than detailed methodological rules. Admission of the historical background of the present day diversity of the living world does not yet mean that the history of its development and differentiation is considered an adequate basis for its classification.

Despite the differences in views on this matter, taxonomists can be resolved currently into two basic groups – partisans of phenetic taxonomy and the advocates of phylogenetic taxonomy. Differences between these two schools can be characterized briefly as follows:
1. For partisans of the phenetic approach, the past events comprising the phylogeny of animals and plants are in effect knowable only if sufficiently abundant and complete paleontological records are available. In other words, the relationships of descendency are indicated only by the material remnants of the consecutive stages of phylogeny, as found for a given group of organisms. If there are no such data, or if they are incomplete – as Davis and Heywood (1963) consider the paleontological records of the Angiospermae to be – then the knowledge of phylogeny becomes very inexact and uncertain, and the phylogenetic approach can be neither a basis for classification nor an auxiliary source of information for the construction of one. Therefore, the classification ought to be constructed with regard for the similarities and differences ascertained directly or from experimental observations. Relationships or descendencies among organisms can be known only indirectly if they are based upon observable morphological similarities. Insights into phylogeny may be gained by arranging the differences that link or separate organisms, and by understanding the correlations between many aspects of the organisms' biologies. Thus, phylogeny is not a basis of the classification; to the contrary, the classification becomes the main source of knowledge of phylogeny.[13]

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[12] "… classification is the ordering of (animals) into groups on the basis of their relationships" (Simpson, 1961).

[13] Davis and Heywood (1963, p. xviii-xix) write: "Classificaiton, many taxonomists claim, should be based on, or reflect phylogeny. This aim, we believe, is unrealistic in a group with extremely inadequate fossil records. As an initial procedural step, classification must be based on overall resemblance, and though it may then be interpreted in phylogenetic terms…" And further on p. 2, "A classification based on overall resemblances is … more likely to be serviceable for more purposes than one based on known or assumed "phylogenetic"

2. The phylogenetic approach assumes at least some understandability of the past, of the history of the phylogeny of organisms' groupings. Obviously, though, the degree to which this past history can be known varies among different groups. Phylogenetic reconstructions form appropriate theoretical bases and serve as important sources of information for the taxonomist constructing the classification. This reconstruction, therefore, must precede the classification. Multifaceted resemblances and differences or sets of common characters fail to be an appropriate basis for the classification; in a broad sense, they are only manifestations of the phylogenetic relationships. The past of the group as reconstructed with available characters and with the principles of evolutionary theory – a phylogenetic reconstruction – is the basis for the classification although the classification is not a direct copy of this reconstruction.[14]

The succession of the taxonomist's activities in the case of the phenetic approach is thus as follows: from observation of the resemblances and of their correlations to the construction of the classification and then to the phylogenetic interpretation. In the case of the phylogenetic approach, the succession is as follows: from observation of the resemblances and differences as well as of their correlations to the reconstruction of the past of the group and only then to the construction of the classification.

It is characteristic that both Simpson (1961) as a prominent representative of phylogenetic taxonomy, and Davis and Heywood (1963) as partisans of phenetic taxonomy believe that their separate classifications constructed for groups which interest them as taxonomists (*i.e.*, vertebrate animals and angiosperm plants, respectively) are often comparable to those derived from the other viewpoint despite the diametrically opposed methodological assumptions used by their authors. The situation in mycological systematics, particularly for the lower fungi, is quite different. In this instance, the methodological principles adopted by all taxonomists are

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evidence. The two may frequently coincide in practice. … The thesis that the only reputable scientific classification is that based on phylogenetic or evolutionary principles is one that cannot be accepted for the Angiosperms on either theoretical or practical grounds." However, it is important that in the subsequent paragraph of this text Davis and Heywood (1962, p. 2) make it clear that "the reader should not be misled into thinking that we suggest ignoring evolution or evolutionary principles. … We are so impressed by such evolutionary phenomena as convergence and parallelism that we advocate the production of general classifications based on maximum numbers of attributes and that they be accepted as such, in their own right, and not necessarily as relctions of phylogeny." Consequently, the concept of "phylogeny" is conceived by these authors only as the relationships of descendence, *i.e.*, as genealogical closeness or distance of kinship. This means that the difference in views between these authors nnd Simpson is mainly due to a lack of semantic precision. Davis and Heywood specify their standpoint as an "empirical approach", and contrast it with the "interpretive approach" in which the classification is improved and interpreted in evolutionary or phylogenetic terms. They are of the opinion that "already existing classification must precede its evolutionary interpretation."

[14] Simpson (1963, p. 50) writes: "phylogeny is the appropriate theoretical background for taxonomy. … It is essential for understanding and explaining all the associations involved in classification." And further, on p. 67-68, "Modern taxonomy is evolutionary and its basis involved phylogeny, which cannot be directly observed and often must be inferred from nonpaleontological ddata lacking the essential time dimension. … To form evolutionary taxa, their propinquity of descent is crucial and this is to be judged largely on similarities among them. Similarities … arise by homology, parallelism, convergence, mimicry and chance. These processes must be defined, and then their results must be interpreted in evolutionary taxonomic ways." However, it is emphasized that Simpson as well as Davis and Heywood consider both approaches, phenetic and phylogenetic, to be evolutionary in their essence. Simpson stresses that Darwin, himself, as a taxonomist was not a phylogeneticist because his main studies of systematics were preceded by the publication of " Origin of Species" (see the chronology of Darwin's papers in Kuznicki and Urbanek, 1967, p. 74-77). The contribution of Darwin to systematics in the first place consists in his pointing out the evolutionary origin of taxa and the possibility of evolutionary explanations, by means of phylogeny, of the order in nature that has been already discovered by other means. "His own major classificatory work (that on barnacles) was completed not before he had formed, but therefore he had published his own views on evolution, and it is not overtly evolutionary." (Simpson, 1963, p. 52).

identical in their assumptions, whereas the individual treatments using the same information pool (or classification) are, as a rule, different. The causes of this situation will be discussed later on, but first I shall evaluate the possibility of using methodological approaches to the material analyzed in this paper.

Systematics of higher organisms characterized by great morphoanatomical complexity has advanced and will continue to advance with the accumulation of more data from this particular field. The morphoanatomical complexity of higher vertebrates and vascular plants is, of course, inseparably related to the complexity of the ontogenies of these organisms, even though the former is easier to observe. It can be stated that divergent courses of ontogeny in these cases always lead to markedly different morphoanatomical results. For these organisms the possible structural convergences never affect most of the observable characters. In the ontogeny of higher organisms we deal with a distinct "adult" or "mature" phase or form whose body structure more or less legibly reflects its development. Whereas data on the embryonic or postembryonic development are of course necessary for the elucidation of this structure, they are not indispensable for the delimitation and identification of taxa or for the evaluation of their similarity or dissimilarity. In case of the phylogenetic approach with its "a priori" evaluation, data evaluated by some theory of the taxonomic importance of characters can be of great significance for any theoretical explanation of the classification. An example of this is the taxonomic evaluation of the nature of individual development in dividing the mammals into the Marsupialia and the Placentalia.

In the systematics of lower organisms we deal with the opposite situation since in many of these organisms it is impossible to distinguish the developmental form whose description could be admitted in the diagnosis. With respect to many lower fungi (such as those in the Chytridiomycetes, Lagenidiales, etc.), the opinion of de Beer (1951, as cited by Davis and Heywood, 1963) that phylogeny is a sequence of modified ontogenies is particularly pertinent. In these fungi the description of a taxon (especially of a genus) is equivalent to the description of the basic ontogenetic scheme of the organisms belonging to this taxon. Compare, for example, the descriptions and keys for genera in Sparrow (1960) or Batko (1975). Therefore, attempts to classify these organisms were at first based on morphoanatomical data, but the diagnoses of taxa were soon enriched by information about the course of individual development of the organisms being classified. Similarly, it was often found that many taxa (especially genera and higher ranks) distinguished on the grounds of somatic or morphological resemblances (usually of the largest or most easily observed developmental forms) are artificial groups, and the resemblances uniting them are in the nature of a so-called "convergence of poverty." In lower organisms, especially in lower holocarpic zoosporic fungi,[15] the descriptions of organisms and of their populations were used to construct classifications but contained less information than the analogous descriptions of higher organisms such as those of angiosperm plants, insects, or mammals. Descriptions of fungal populations and species usually include information on the structure of some (but rarely all) particular developmental forms, include certain ecological or habit relationships between the investigated organisms and their living environment (*e.g.*, saprophyte or parasite, living inside or on the substrate surface, etc.), and, in most instances, only fragmentary data on the course of ontogeny. This description or set of descriptions of different characters often

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[15] The term "holocarpic thallus" refers to a thallus which is completely transformed into a sporangium or gametangium in the final phase of ontogeny. Because the thallus of thuni is not differentiated into a generative and vegetative part, only the vegetative and generative developmental phases can be distinguished in these fungi. Holocarpic thalli are usually very small and of simple structure; they occur in the form of vesicles or tubules, so that the vegetative phases of fungi belonging to different orders or even classes (*e.g.*, Olpidiaceae and Olpidiopsidaceae) are indistinguishable. Such similarities are referred to as "poverty convergence."

contains information about a relatively small number of potential characters. Therefore, in these cases the correlations between the different characters and the taxa in which they occur are more difficult to detect and are less pronounced. Consequently, *post facto* taxonomic evaluation or the "*a posteriori* weighting of characters" (Davis and Heywood, 1963) based on character correlations becomes difficult or even impossible according to pheneticists.

Ranking of different characters and their groups is a logically indispensable step in the classification of organisms. Understandably, two tendencies are now manifest in the systematics of lower organisms: 1) To enrich descriptions with new data concerning the ultrastructure, biochemical and immunological characters, etc., and (2) to precede the classification by the construction of an appropriate phylogenetic hypothesis permitting "aprioristic" evaluation of characters. The most recent history of mycological systematics demonstrates that the general regard with which a taxonomist's work (classification) is held depends not so much on the accepted methodological assumptions as on the wealth and diversity of information about the classified organisms included in the descriptions which formed the starting point of the taxonomist's work.

Thus, the practical applicability of either approach discussed above seems to depend neither on the degree of complexity of the classified organisms nor on the degree of knowledge of the given group. If the information contained in the descriptions is sufficiently rich and diversified, then the construction of a natural classification (in the sense of the accepted principle) is possible with the use of either phenetic or phylogenetic methodologies; moreover, such classifications are often partially or completely congruous. Conversely, if the information is too scanty, then the classification will fail to be natural in any sense regardless of the methodological assumptions used.

The question arises, then, as to what the difference between the phenetic and phylogenetic approaches to the classification is, because this difference is important to the taxonomist classifying a given group of organisms.

There seem to be several differences concerning, for example, the views on the cognition of phylogeny, and recommended procedures for evaluation of characters, the means of preliminary selection of data introduced into the description, etc.[16] However, the most important difference lies in the essence of the constructed classification and of the notions of concepts or names for taxa included in the classification. The phenetic approach produces a classification of a descriptive nature, whereas a phylogenetic classification is simultaneously descriptive and explicative. The phylogenetic hypothesis formulated explicitly or assumed implicitly is not only the theoretical basis for the classification, but also enters into its composition through its integral role in forming hypotheses about which characters are "primary" or "primitive", "derived", "secondary" or "advanced", etc.

In the case of the phenetic approach, the "interpretation of the classification in terms of phylogenetics" is something distinct from the classification and exerts no effect on its final form. In fact, the classification prepared by pheneticists was discussed in Section 9 (Diversity within the group as a whole, p. 30), and corresponds to a certain preliminarily ordered set of information about the diversity of the group which serves the taxonomist-phylogenetics as a starting point from which to construct a phylogenetic hypothesis although during the subsequent stages of his work, the classification often may be transformed into a rather different form altogether.

Whereas the practical value of both classifications – their suitability for identification of organisms – may be similar, their cognitive meanings in the explication of the relationships between taxa is different. Moreover, phylogenetic classifications permit drawing "test

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[16] Sokal and Camin (1965), the founders of neo-Adansonian numerical taxonomy, have recently compared the two discussed approaches.

implications" (Hempel 1966) so that the testing of these assumptions may tend to verify the classification.

The above differences in the contents of these classifications indicate yet another difference in the nature of the possible classification-based predictions. Because of its underlying correlation analysis, phenetic classifications permit the extrapolation of the range of the different characters in the set of the classified taxa; they enable predictions regarding characters not yet detected in representatives of a given taxon because of the constant correlation of sets of these characters. The phylogenetic classification, moreover, allows prediction of an entirely different sort, related to the historical basis of this classification.

In its essence, the phylogenetic classification does not represent merely an ordered set of forms, rather it is a reflection of a certain time section through a set of developmental linkages taking a parallel course with time and leading to related groups of organisms. This classification evaluates the directions of the activity of natural selection within particular taxa and the state of their developmental advancement, and it also assesses the phylogenetic stage through which each given taxon is now passing. For these reasons, the prediction of the further development of some particular taxon cannot be considered impossible.

The phylogenetic classification permits one more kind of prediction. Because the phylogenetic reconstruction does not have to concern a sequence of discrete past events, it can, however, comprise descriptions of processes or sets of sequential events occurring under given reproducible conditions (as described in the subsequent chapter). Thus, in some cases, verifiable auxiliary hypotheses concerning the origin of particular taxa can be derived from the phylogenetic classification. These hypotheses permit experimental reconstruction of certain phases of phylogeny of the investigated groups, a task which is the entire object of experimental taxonomy. Despite the contrary opinions of many taxonomists, experimental taxonomy is one of the developmental branches of phylogenetic taxonomy and is inseparably linked to it through its theoretical basis. Experimental taxonomy differs fundamentally, however, from phenetic taxonomy because of their divergent methodologies.

The above arguments although neither fully nor consciously realized, led me intuitively to adopt the phylogenetic approach during my work on the classification of the entomophthoraceous fungi. In this particular instance, my choice also resulted from the fact that the application of the phenetic approach to lower fungi creates many pronounced technical difficulties. one of the shortcomings of the phenetic method is the vagueness of the 'character' concept which is of essential importance of this method. The fragmentation of the description into its individual characters is one of the main stages of a pheneticist's work; so that the distributions of character states may be compared later to detect any correlations, then, on this basis the characters are weighted *a posteriori*, etc. In this case, it must be assumed that characters are regarded initially as unweighted and mutually independent, irrespective of their biological importance and probable evolutionary significance. Such processing of information about characters during the course of taxonomic analysis requires the putting aside of their importance for the life and development of organisms. However, the recognition of characters is, in itself, a highly subjective and selective activity When the analysis is limited to a set of morphoanatomical characters (as is usually sufficient for the systematics of higher organisms), this recognition is, in effect, possible. In this case, certain habits prevailing in a given field of taxonomy play an important role (e.g., taxonomists of angiosperm plants usually agree as to what constitutes a character in these organisms). matters are complicated, however, by the introduction of data about the functioning of organisms into the pool of analyzable information. No convention currently exists for inserting physiological processes or the course or mechanisms of development into the character concept.

I shall illustrate the above considerations by an example: If, according to current conventions, I should regard some descriptive elements such as ‘uninucleate conidia’, ‘double conidial wall’, ‘branched conidiophores’ and ‘in ontogeny syntomic division occurs’ as characters for a certain entomophthoraceous species, and if I should search subsequently for the correlations between these characters, then I would perform a paradoxical activity, as if playing blindman’s bluff; namely, I know that these ‘characters’ are causally related and not only simply correlated, that they represent one complex and are manifestations of a certain way of development. However, if, because of the complex nature of correlations with other characters, I should regard them together as one ‘character’ (‘ontogeny of, *e.g.*, type *A* together with all manifestation’), I would be lowering their taxonomic rank despite their obvious phylogenetic importance. Accordingly, I should refer species displaying the discussed ‘character’ to different genera because of the stronger correlations between other discrete and ‘clear’ characters such as spore size, spore shape, sculpture of the surface of zygospores, etc., even though these characters may be evolutionarily secondary. Thus, the same means of distinguishing the different characters, despite its objective assumption, is clearly a selective and subjective process in this case. The proper selection of characters would here require their subordination to the final product of taxonomists’ work, the finished classification. The improper selection of characters would render the classification random and artificial in every sense.

In entomophthoraceous fungi, on account of the most readily perceptible correlations between the degree of parasitic specialization and structure of pseudohymenium, course of pathogenesis, etc., this procedure would lead to the recognition of genera according to their differing degrees of parasitic specialization. It is clear that this classification is constructed with reference to one class of characters but not with consideration for the ‘overall resemblance’ as used by pheneticists. Because of the developmental nature of the descriptions, the adoption of the phenetic approach with respect to the lower (entomophthoraceous or zoosporic) fungi could lead to the distinction of characters depending upon the perceived correlations rather than the finding of correlations among ‘objectively’ distinguished characters. Irrespective of this, the misinterpretation of causally related characters as being merely ‘correlated’ is a backward step away from understanding the nature of the observed and classified biological diversity.

However, the phenetic approach to the classification includes aspects which are very attractive to modern biologists, and which are responsible for a certain renaissance of this approach in the last decade. Phenetics tends to objectify systematics and to foster a healthy criticism of numerous earlier, poorly founded or unjustified ‘phylogenetic trees’ devised to elucidate the arbitrarily constructed taxonomic structures. The grain of this criticism finds an especially fertile breeding ground among mycological taxonomists because the invasion of their discipline by such pseudonatural systems based on ‘phylogenetic’ speculations is a particular nuisance. A common feature of these classifications and attendant considerations of phylogeny consists in the disregard of their authors for the present-day knowledge of evolution, and for the basic assumptions and empirical regularities of that doctrine; Savile (1968) regarded this situation as due to a “lack of attention to guiding principles.”[17] The phenetic approach is, in great measure, a reaction to the unscientific approach of these “naively phylogenetic” classifications.

Repudiation of the arbitrary “naively phylogenetic” approach to the classification does not imply the abandonment of phylogenetic taxonomy for groups of organisms deprived of sufficient paleontological records. A lack of paleontological records essentially limits the

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[17] “The naïve, insupportable schemes often proposed for the fungi do not advance our understanding, but serve only to lower the prestige of mycology,” (Savile 1968).

cognition of phylogeny without, however, making it unknowable. Phylogenetic reconstruction of groups of extant organisms are always based on neontological data. Paleontological data–if available–introduce many important elements (such as the time dimension) and render the reconstructions more exact and more reliable, but these data are not indispensable.

11. Cognition of Phylogeny

The concept of phylogeny or of phylogenetic relationships cha be differently interpreted. In a narrow sense of the term, it comprises only the relationships of descendence. In a broader sense, it includes the time relationships, the effect of natural selection expressed by a different rate of divergence in various lines, and the effect of convergence and even of probability. A lack of paleontological records limits the cognizance of phylogeny in so far as it deprives it of a time dimension, and hinders the postulation of a sequence of reconstructed intermediate forms between the common ancestor of a monophyletic taxon and its present-day members. By themselves, paleontological records are neither decisive nor direct evidences of evolution, and do not testify to the origin of organisms from other ones. Even long and complete sequences of fossil forms are only implicitly phylogenetic. These sequences testify directly only to a definite chronology in the occurrence and succession of organisms. The cognizability of phylogeny allows for the possible establishment of the descendence relationships by means of the assumptions resulting from the theory of natural selection and through the interpretation of the chronological succession of fossil forms as indications of descendence relationships (Simpson, 1961, p. 54). The relationships of descendence and generally the genealogical relationships (*e.g.*, co-descendence) are hardly observable from extant organisms only. In these cases, the establishment of exact genealogical relationships can be difficult, and particularly so for organisms reproducing sexually and forming panmictic populations.[18]

Phylogenetic relationships are thus always inferred from the overall paleo- and neontological relationships available for direct observation, and are reconstructed hypothetically by the application of those laws of the evolution theory which elucidate the currently observed similarities and differences resulting from specific past events.

In their essence, phylogenetic reconstructions are synthetic sequences of past events incorporating chains or linkages of chronologically successive and more or less modified populations. This reconstruction is usually presented as branched sequences of forms (reconstructed organisms) comprising genealogical trees in which the sequences of events are either concealed in its graphic picture, implied, or noted by descriptive comments of the ‘tree.’ However, the phylogenetic reconstructions can equally well be presented in the form of *sequences of events* leading from a certain *initial state* (common ancestor) to a whole set of the considered present-day forms.[19] If the reconstruction is based largely or even principally upon

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[18] Simpson (1963, p. 69) writes about identical twins and their genetic relationships: “We define such twins as two individuals developed from one zygote. No one has ever seen this occur in humans, but we recognize when the definition is met by evidence of similarities sufficient to sustain the inference.” About the descendence relationship, in general, he writes (P. 68), “the actual process of reproduction and descent are not observed (Even in the best … examples … it is highly unlikely that specimens in an earlier sample include all or many of the individual ancestors of those in a later sample.”). Nowinski and Kuznicki (1965, p. 223-230) also stress several times that Darwin answers the questions about the genealogical relationships between species by applying the hypotheses of natural selection to the interpretation of the observable similarities and differences.

[19] This approach to phylogeny is representaed also by Raper (1968), and recently even by Camin and Sokal who are the founders and partisans of neo-Adansonian numerical taxonomy (1969).

paleontological data, then its presentation as sequences of forms follows quite naturally since the intermediate forms can, indeed, be reconstructed. In fact, in these cases, the events are often explicitly incorporated into the graphic picture as in the schemes of adaptive radiations for the different orders of vertebrates. If, however, the reconstruction is based only on neontological data, its presentation as sequences of forms is very difficult or even impossible because of the immense margin of arbitrariness. In these cases it seems much more natural to reconstruct phylogeny as a sequence of the main evolutionary events making up the history of development of a given group.

The concept of 'evolutionary event' is in this context applied in different meanings. The change regarded as an evolutionary event depends on the scale of the evolutionary processes analyzed in a particular situation In the reconstruction of microevolutionary processes, this change involves an elementary evolutionary event (a certain irreversible change in the genetic structure of the population) brought about by natural selection. on consideration of the phylogenetic relationships between groups of the rank of classes and divisions (phyla), the evolutionary event, of course, consists of a transformation of an entirely distinct rank. In the phylogeny of fungi as a whole, it can involve, for example, a change in the mode of life from parasitism to saprophytism, the development of a sexual incompatibility system, the transition to heterokaryotic organization of the genome, etc. (Raper, 1968).

The meaning of the concept 'evolutionary event' may be quite different, however. Very seldom, although this possibility cannot be ruled out, a single unrepeatable event is regarded as an evolutionary event. Examples are a single change in the genetic structure of a population, or the appearance of one polyploidal plant, or the occurrence of one hybrid, etc. More often an evolutionary event is considered to be a set of identical or similar events taking place in some time interval as a result of the same causes and acting under fairly similar conditions on conspecific populations, congeneric species, or the like. This interpretation seems to be the most common.

A third interpretation deprived of the time dimension is also possible. In this case an evolutionary event is considered to be a *certain class of events* which have taken place, continue to take place and will take place whenever a prescribed set of conditions is encountered by a taxon-ancestor exhibiting certain variability and so long as this variability will be controlled by natural selection of a given direction and intensity of action. It seems from the example quoted above that Raper regards the "critical events in the evolution of fungi" in this manner. A sequence of events interpreted in this manner is, however, a *process*; consequently, the phylogenetic reconstruction proposed as a system of processes is, at best, of a slightly more historical nature.

I shall illustrate the above considerations by an example. one of the populations of species *A* is transformed into a population of species *B* through a certain sequence of microevolutionary events. Within this individual sequence, event *a* precedes event *b*, the latter precedes event, etc. However, Species *A* coexists for a long period with species *B*. During all this time the causes responsible for the transformation of one of the populations of *A* into the population of species *B* are operative. As a result, further populations of species *A* pass asynchronously at a certain frequency through the sequence of transformation *a•b•c*, and are transformed into new populations of species *B*. In this situation it can no more be assumed that every event *a* precedes every event *b*, etc. When evaluating the results of this phylogeny i.e., the populations of species *A* and *B* in a certain late time frame), we can reveal the logical sequence of events causing the above discussed transformation and establish the structure of the process. However, in view of a lack of paleontological data we cannot attribute to this reconstruction a time dimension or a fully historical nature. This reconstruction is, however, historical in a limited sense since it enables the establishment of the most probable descendence relationships, i.e., the reconstruction of a genealogy.

It seems that such limited historical, categorical interpretation of the "evolutionary event" concept is most relevant to the real degree of the ability to know a phylogeny in the case of a complete lack of paleontological records. its acceptance permits the avoidance of Savile's "naïve, insupportable schemes" and remains on the ground of the real available information. Moreover, it has the advantage of being the most extensive interpretation since the remaining interpretations can be regarded as its particular cases. If indeed only one population of species *A* only once underwent the transformations leading to species *B*, then this fact can be described, though not very precisely, by means of the above scheme. However, since we do not know whether this transformation affected only one population or many of them, as well as whether these transformations were related to some past time interval or still proceed, we must limit ourselves to the interpretation of an evolutionary event as a class of events having a set of resultant consequences.

Reconstruction of sequences of events linking the present-day organisms with their common ancestor and which causally explain their present diversity depends first upon the 'reconstruction' of this common ancestor. However, because of a lack of paleontological data, the reconstruction of a common ancestor seems to be unfeasible in view of the assumption that this reconstruction ought to take the form of a description of a certain unit or taxon (*e.g.*, of an organism, population, species, etc.).[20] Comparative analysis of the present-day morphoanatomical, ecological, physiological, and other sorts of diversity of the investigated group permits the establishment of a certain set of characters considered to be 'primary', 'original', or 'primitive.' This set of characters can be attributed to the *initial state* of the reconstructed phylogenetic sequences to that this initial state can play the role of common ancestor in the new proposed "limitedly historical" phylogenetic reconstruction.

However, the "initial state" greatly differs from the "common ancestor" since it is neither the diagnosis of a taxon nor the description of an organism or population. It is only a list of those characters considered to be most primary during some given earlier period of time for the organisms and populations comprising some given group. These characters compose an incomplete picture of the initial diversity of the group to which the real common ancestor of the classified organisms has belonged. However, it cannot be established which combination of these characters would correspond to the common ancestor's description. What is more, owing to the irregular rate of evolution of the different phylogenetic lines and of transformations of the various classes of characters in different lines, it cannot be assumed *a priori* that the set of characters considered to be the most primary was ever exhibited by any group of organisms which actually existed in the past. on account of the possible–and highly probable–asynchrony of the appearances of different characters in the discussed set, the initial state becomes blurred in time and should be regarded only as an auxiliary abstract concept.

In one respect, however, the initial state can play the role of the "common ancestor": It permits the definition of a monophyletic group as arising from the action of a common sequence of evolutionary events on a common initial state. The description of the ancestral group is, therefore, contained implicitly in the concept of the initial state but cannot be postulated more precisely because of the lack of sufficient factual information. Accordingly, the description of the initial state is a *set of all possible descriptions of the common ancestor.*

It seems that this approach to the discovery of phylogeny using only neontological data allows a classification of organisms which is phylogenetic in its essence although in an only limitedly historical sense. However, the approach presented here draws upon the

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[20] "Monophyly is the derivation of a taxon through one or more lineages … from one immediately ancestral taxon of the same or lower rank" (Simpson 1963, p. 124). In the approach presented in this paper the monophyletic taxon is a group formed from a common initial state (which is not the same as the description of a taxon) as a result of passing the same sequence of phylogenetic events. This definition is broader than that of Simpson but it is not contradictory to it.

contemporary phenetic approach for its important elements of criticism and the resulting postulate of a limited ability to know the phylogenies of groups whose past history is not recorded by fossil data. In this case, also, the understanding of the phylogenetic reconstruction itself is different. Despite these reservations it seems that the proposed approach retains the main qualities of phylogenetic systematics as a means of explaining and, in a broader sense, for its historical nature.

It is possible to pass from the observable relationships of resemblances and differences to the presumed phylogenetic relationships by applying the laws and rules of evolutionary biology to the interpretation of the present diversity of the investigated group. However, these laws and rules are of a dual nature: They concern the mechanisms of the evolutionary processes (they follow deductively from the principle of natural selection), but evolutionary biology also comprises phylogenies whose rules describe the main regularities of the course of phylogeny and are empirical generalizations. Laws following by deduction from the theory of natural selection are highly abstract and require considerable reduction and solidification of particular facts when applied to the interpretation of resemblances. These laws are universal, and no links in the reconstructed phylogeny can be contradictory to them in any way. The empirical rules describing the main directions of the course of evolutionary processes are usually less abstract, and are not universal so that the processes described by them do not occur in every phylogeny. Some of these evolutionary processes or tendencies often manifest themselves as complementary pairs in the phylogeny–e.g., the tendency to polymerization of homologous structures and tendency to their oligomerization (Dogiel, 1929, 1954). It is possible to establish which one of these tendencies could be responsible for the formation of the present diversity of classified organisms, because these tendencies are an empirical generalization not only of the course of many phylogenies, but also of the conditions under which these phylogenies proceeded. Dogiel (1929, 1954) stresses that the tendency to polymerization manifests itself in the early phases of phylogenies; it concerns rather the phylogeny of relatively simple organisms with small bodies, and leads to an enlargement of body size and to an increase in the complexity of its structure. on the other hand, the tendency to oligomerization manifests itself primarily in the later phases of phylogeny. It causes reorganization of the structure of organisms, intensification of the functions of the different systems, and an increase in the degree of integration of the organism.

Selection of an appropriate evolutionary tendency for the interpretation of the diversity of classified organisms mainly depends on the heuristic inventiveness of the investigator. In this sense, phylogenetic systematics are not only a science but also an art.[21]

12. Construction of Phylogenetic Hypotheses

The discussed "critical" set of entomopathogenic species of entomophthoraceous fungi (p. 31f) is characterized by a wide range of diversity. This diversity can be split into different planes and presented in the form of the following series:

1. Architectonic diversity and ontogenetic diversity related to the former (p. 24ff): There belong fungi with 2, 4, 6, 8, and so on up to 24 nuclei per cell and fungi with polykaryotic cells; conidia of some forms (type *Zoophthora*) are uninucleate. In the ontogeny there occur either archetomic divisions alone or both archetomic and syntomic divisions.

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[21] "Like many other sciences, taxonomy is really a combination of a science … and of an art … Taxonomy becomes largely artistic … when applied to construction of classification … even if there were complete agreement about the scientific principles to be applied, innumerable difference classifications should be made. … Selection among those alternatives is decidedly an art" (Simpson 1963, p. 110).

2. Morphological diversity of conidia is also considerable. These fungi form ballospores, ahaptospores, prohaptospores, and haptospores (Section 6.B, p. 22). The vegetative mycelium can comprise thread-like, branched, and septate hyphae with septa or discrete hyphal bodies of various shapes. Conidiophores may be simple or branched; they can grow singly from the host body, but occasionally together with pseudocystidia they usually form a pseudohymenium of different structures (Section 6.C, p. 24). After its death, the host may become additionally attached to the substrate with rhizoids; however, many species do not form rhizoids. All elements of the thallus of the fungi discussed here can, of course, display different shapes, dimensions, color, etc..

3. Diversity of the course of sexual processes (Section 8, p. 29; Fig. 9).

4. Diversity of the course of development for insect diseases caused by the discussed fungi (Section 4, p. 12; Fig. 5).

5. Diversity of the effect on the behavior of host and, consequently, on the ecological situation of the whole fungus-insect system (Section 5, p. 16).

6. Taxonomic and biological diversity of hosts (Section 3, p. 9).

Many such series could be distinguished, as is customary in the case of arbitrary divisions of the spectrum of living organisms into "categories", "plans", and the like. Despite the scarcity of data, attention could also be given to the physiological diversity of the discussed fungi, expressed by various nutritional requirements in artificial culture, as well as to the diversity concerning the numerous modifications of the mechanism of conidial discharge (which are not discussed here), and to some associated morphological diversity of conidia as characterized by Lakon (1919).

The above series of diversities exhibit no definite polarization. They are not sequences leading from "lower" to "higher", from "more primitive" to "more specialized" relationships. This polarization with respect to the characters can be ascertained, however, even within the phenetic approach[22] by applying the set of rules (established for a given group of organisms) to interpret the diversity by defining what is to be considered evolutionarily lower or higher. Davis and Heywood (1963) quote such a list of rules for angiosperm plants, whereas Savile (1968) adapts these rules from phylogenies of vertebrates (sic!) and elevates them to the rank of "guiding principles of the evolutionary theory" on a par with the basic laws of the theory of evolution. Irrespective of the fact that this approach is generally very deceptive, it could not be used here because there is no such set of rules established for lower fungi.

Another possibility of an evolutionary evaluation of the presented series involved the application of rules which –though also evolutionary—are more general and far-ranging, such as those concerning evolutionary tendencies (Kuznicki and Urbanek, 1967l p. 215-225). However, an application of these rules requires choosing between the alternative regularities, such as between the tendency of homologous systems to polymerization and their tendency to oligomerization. Other regularities can be taken into consideration because their manifestations are universal. These regularities comprise, for example, the assertion on the secondariness of parasitic mode of life as compared with "free" life in the external environment (Michajlow, 1960), though this statement also has its converse in the assertion

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[22] Owing to this circumstance, the phenetic approach of Davis and Heywood is indeed an evolutionary approach, and in this respect it differs from the neo-Adansonian numerical taxonomy of Sokal and others.

that, for fungi, saprophytism is secondary in comparison to parasitism (Savile, 1968; Raper, 1968).[23]

The reasoning of Savile and Raper is based on admittedly true premises: 1. All fungi which are most primitive from the morphoanatomical and developmental standpoint are parasites. 2. The oldest (Paleozoic and Pre-Cambrian) fossils attributable to fungi were always found together with fossils of autotrophic plants (blue-green algae, psilophytes, etc., cf. Martin, 1968). 3. Fungal geneticists have described many mutations of the nutritional deficiency type which cause fungi to lose the ability to synthesize certain compounds indispensable for normal development such as biotin, thiamin, different amino acids, and others. These mutations are reversible.

On these grounds the above authors draw the following conclusions: Fungi originated and developed as a group of parasites; their evolution proceeded mainly under conditions of parasitism; saprophytic groups frequently originated from parasitic groups and, sometimes, they passed over secondarily to the parasitic mode of life. This assertion is supposed to be obligatory for the whole of fungal phylogeny, but it does not have to concern any individual fungal group, and it fails to be categorical. It is, therefore, unverifiable. It can neither be refuted nor confirmed, even if it were possible to demonstrate its inconsistency or consistency with the finite set of assertions of real states. However, it is essential to note that Savile's conclusion does not in fact follow from the above premises. The fact that the most primitive extant fungi are parasites could be due to their expulsion from the ecological niches of saprophytes (in which the struggle for life is much more violent) by more evolutionarily advanced fungi. Among the numerous and biologically diversified groups of the most primitive fungi, only those having avoided competition with the more perfect forms by becoming parasitic would have survived up to now. The fact that the oldest fungal fossils seem to be those of parasites testifies, in view of their scarcity, only to the circumstance that delicate fungal hyphae have better chances for preservation as fossils when protected in tissues of psilophytes or bundles of blue-green algae. Also, the fact that mutations of the nutritional deficiency type are reversible does not mean that the evolutionary transition from the state of multifunctionality and plasticity of the enzymatic system to parasitic specialization along with an immense intensification of some fungal enzymatic functions, transformation of many ectoenzymes from adaptive into constitutive ones and the acquisition of many deficiencies, could not assume the opposite course with an equal (or even greater!) probability. The direction of evolution is not determined by the mutations but by the vector of natural selection which in all known cases acts rather to proceed from a multifunctional state (*i.e.*, from a state of adaptive plasticity) to the intensification of some functions, together with

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[23] Savile (1968, p. 651) writes: "Obligate parasitism in the fungi is not a belated evolutionary bypath, but a fundamental attribute of primitive groups; and saprophytism arose repeatedly from it. The first typical fungi were probably parasites; and it was as parasites that the fungi left the water protected by the tissues of their hosts. Destructive parasites, which are facultative saprophytes, may in some cases be derived from saprophytes. The common view that parasitic animals are generally derived from free-living species has no bearing on the fungi, which always had quite different physical and nutritional problems." Raper (1968, p. 681-682) refers to this text: "Obligatory heterotrophy as a universal characteristic of the fungi would seem to justify Savile's theses … that all fungi have been derived from parasitic ancestors and that the major lines of fungal evolution have occurred in parasitic forms or in forms that had recently "escaped" from the parasitic habit. Primeval fungi are accordingly visualized as generalized obligate parasites, their growth and survival dependent upon a number of protoplasmic constituents common to all hosts … a gradual acquisition of synthetic competence, through which the fungus would be able to utilize progressively simpler protoplasmic constituents or products, would finally lead to the saprophytic habit. … The competence to synthesize each specific nutrient formerly required from the host would decrease the dependence of the fungus upon the living host and thereby would increase the range of acceptable substrates. The gradual escape from the parasitic habit must have occurred repeatedly to establish numerous types of primitive, plastic forms leading to the several great assemblages of saprophytic fungi."

general complications of the relationships with the immediate environment or host organism (i.e., to a state of parasitic specialization). At least with respect to lower fungi, it thus appears that Savile's assertion finds much more limited application than the above-mentioned rules of evolutionary parasitology (Michajlow, 1960).

We shall now try to apply the above rules to our material. Thalli of the considered entomophthoraceous fungi—except for *Meristacrum* and *Ballocephala*—are highly polymerized systems in two senses: They comprise many cells, and these cells are multinuclear. According to Dogiel (1954), polymerized systems of this kind usually become the substrate for transformations (oligomerizations) which reduce the number of the constituent elements and fix this number as well as to differentiate and to intensify the function of the particular elements. These events are associated with an increase in their size and the reorganization of their structure.

In entomophthoraceous fungi, the symptoms of oligomerization can be found in a series of architectonic diversity whose polarization is evident in an increase of the degree of ordering from polykaryotic cells through oligokaryotic cells with 24 or 16 nuclei to quadri- and binucleate cells. In such a sequence the reduction of the number of nuclei is associated with an increase in their size and synchronization of divisions. Attribution to this sequence of the reverse polarization—from dikaryotic toward polykaryotic cells—would render unexplainable the general disorganization of the system (through an increase in the number of nuclei). By applying the thesis that parasitism is secondary, the series of diversity of modes of life can also be transformed into a polarized sequence by assuming saprophytism as the primary habit for entomophthorous fungi with parasitism as the secondary habit. Among the different forms of parasitism, the most primary form is considered to consist of occasional parasitism (associated with preservation of the saprophytism ability under natural conditions), followed by facultative parasitism (lack of tagmatic or tissue specialization, and capable of saprobic life under experimental conditions *in vitro*), leading to obligatory lethal parasitism (with segmental and physiological specialization, and a greatly limited ability to develop on dead substrates), and finally achieving the highest form, the obligatory nonlethal parasitism of *Strongwellsea castrans*. Both polarized sequences of diversity discussed so far exhibit a high degree of correlation with the entomophthoraceous fungi, and this correlation is convincing evidence for the validity of their interpretations. Extrapolation of these series affords the first two components of the sought-after phylogenetic "initial state": polymerization of the nuclear apparatus and its slight structural and developmental ordering, as well as a free, saprophytic mode of life and the low nutritional selectivity associated with it.

Confining ourselves to only these criteria does not enable a complete phylogenetic reconstruction; therefore. It is necessary to attempt to determine the polarization for the remaining series in which no ready evolutionary regularities (tendencies) are discernible. This seems possible if the approach is changed so that we move from considerations of characters to the analysis of the whole discussed set of organisms.

I have earlier stated that the characters included on different "planes" of diversity are not only correlated but, moreover, evidently are interrelated causally by the processes of individual development. Some of these causal links are obvious (p. 36) others are still unclear (e.g., the link between cell architectonics and the course of sporogenesis), and, in other instances, it is possible that no essential causal links may be discerned from these correlations. Within the discussed set we distinguished two groups of species: entomophthorous fungi with polykaryotic cells and oligokaryotic fungi. Distinguishing between theses categories in the first context discussed above was not accidental since the characters associated with them treat the most fundamental properties of organisms—the structure of their cells. The remaining groups of characters involve hierarchically higher systems, the whole organism or organism-environment interactions. The tendency to attribute a higher taxonomic rank to the characters concerning the hierarchically lowest systems distinguishable tat the molecular, subcellular, or cellular levels of biological organization is fairly universal among taxonomists of lower organisms.[24] This tendency can be assumed to reflect a certain very general, wide-ranging regularity of the evolutionary course which is sensed intuitively by the taxonomist although not formulated explicitly. The causal link between the structure of the nuclear apparatus of entomophthoraceous fungi and the remaining groups of characters doubtless exists, but its nature is unknown. Correlations between the two distinguished structural types of nuclear apparatus (poly- and oligokaryotic) will not be presented.

Among the entomopathogenic Entomophthoraceae, relatively few fungi have polykaryotic cells. These species always form conidia of architectonic type 1 (p. 24), and their secondary conidia are always ballospores (there are neither microconidia nor capillispores). As insect parasites, these fungi exhibit no segmental or tissue specialization, and destroy the whole contents of the host body. on the other hand, they display great diversity with respect to the effect on host behavior from adaptive lack of effect to complex adaptive effects modifying the circadian rhythms of the host (*c.f.*, p. 19ff). some of these fungi attach the dead host with rhizoids, and other cause its autofixation before death. In so far as is known, these fungi easily develop on dead substrates (e.g., Sabouraud agar). In many respects these fungi resemble species of *Conidiobolus* (p. 31) from which they differ in an almost exclusively parasitic mode of life, scantiness of forms of secondary conidia and exogenous origins of zygo- and azygospores (Fig. 9).

Insect pathogenic species of Entomophthoraceae with oligokaryotic cells differ from the members of the previous group in their greater number and diversity. They form conidia of architectonic types 2 or 4 (p. 25f); their secondary conidia include ballospores, ahaptospores, and haptospores. These fungi present a full spectrum of individual parasite-host relationships from parasites without segmental specializations (e.g., *Zoophthora aphidis*) through lethal parasites developing only in the abdomen (e.g., *Entomophthora muscae*) to *Strongwellsea castrans* which exhibits tissue specialization and is nonlethally parasitic. the pseudohymenium of these fungi also exhibits the greatest diversity; it can include pseudocystidia, and can be superficially or internally continuous or discrete (see p. 29). These fungi attach the host body to the substrate with rhizoids or cause its autofixation onto the substrate; they affect the host behavior before death or exhibit an adaptive lack of this effect (e.g., *Zoophthora aphidis*, p. 17; *Z. radicans*, p. 18; *Entomophthora muscae*, p. 20f).

The above comparison indicates that the correlations between the polykaryotic-oligokaryotic relationship and other relationships making up the diversity of entomopathogenic entomophthoraceous fungi are weakly expressed (e.g., reduction of secondary sporulation in oligokaryota, enrichment of the diversity of parasite host relationships). On the other hand, the correlation between the polykaryotic-oligokaryotic relationship and the overall remaining characters is clearly perceptible. when considering this relationship among all entomophthoraceous fungi (including sporophytes) it can be stated that polykaryota are saprophytes or nonspecialized parasites, whereas oligokaryota are parasites exhibiting differing degrees of parasitic specialization. Thus, the ranges of both groups (polykaryota and oligokaryota), as considered from this standpoint, partially overlap to form a set of nonspecialized parasites. Moreover, in the first group the greater diversity is displayed by saprophytes, and, in the second group, by parasites. Consequently, the

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[24] For example, phycological taxa of the highest rank (divisions or phyla) are distinguished on the basis of criteria concerning the type of metabolism (pigment composition of chromatophores, chemistry of reserve substances), and classes are distinguished by means of a general schema of cell organization (Bacillariophyta, Dinophyta, Conjugatophyta, etc.). Morphoanatomical criteria (thallic structure) developmental criteria, and those related to the sexual process are usually attributed to taxa of ordinal or lower rank (*e.g.*, Volvocales, Pennales, Laminariales).

prerequisite for adaptive radiation by entomophthoraceous fungi to the niche of saprophytes consisted of the polykaryotic type of organization of their nuclear apparatus, and that the insect parasitic niche required the oligokaryotic type.

Thus, intuitive acceptance of the taxonomic priority of the character concerning cell organization in entomophthoraceous fungi permits an interpretation of the overall remaining characters of these organisms, and, thereby, the polarization of several "diversity series" found within this group. Thus, the polarization of the individual series is in this case carried out neither by application of an empirical evolutionary rule, nor as a result of an analysis of the correlation between the individual sequences. Instead, it results from an overall evaluation which subordinates the remaining relationships to a certain relationship (e.g., the architectonic relationship) which is regarded *a priori* as basic. This evaluation analyzes these relationships and leads to the construction of a certain partial auxiliary phylogenetic hypothesis concerning the adaptive radiation of entomophthoraceous fungi to the two main classes of ecological niches. Thus, the third way to order a diversity series involves a devaluation of taxonomic characters by using some theoretical model of the evolutionary process rather than a set of empirical rules. In this case the model is derived from Severtsov's (1956) view concerning the course of evolution and which distinguishes progressive events (aromorphoses) and idioadaptations (adaptations to the particular environment) among those events affecting the course of evolution.

Oligomerization of the nuclear apparatus of entomophthoraceous fungi can be interpreted according to Severtsov's propositions as an aromophotic transformation. Namely, the complex correlations between the thallic architectonics of these fungi and their mode of life, structure of their conidial apparatus, etc., indicate that the organization of the nuclear apparatus (and its associated genetic structure) determines the limits of the possible idioadaptations and, thereby, the range of adaptive radiation. The organization of the nuclear apparatus of the oligokaryota (as compared with polykaryota) exhibits greater ordering (fixing of the number of nuclei, coordination of karyokinesis of individual nuclei), and a more complex structure and thus creased the basis for the development of a more complex system of relationships between the organism and environment.

Figure 17 presents a scheme illustrating this aspect of the phylogenetic reconstruction for entomophthoraceous fungi. This scheme visualized the differences in the adaptive possibilities of poly- and oligokaryota. Adaptive radiation on the lower polykaryotic level of cytoanatomical organization of entomophthoraceous fungi brought about their differentiation and development of morphological adaptations (morphological differentiation of conidial apparatus), primarily in saprophytic niches (in the genus *Conidiobolus*). Certain characters of saprophytic entomophthoraceous fungi—their enzymatic equipment, stickiness and self-propagation of conidia—permitted the transition of these fungi to the parasitic mode of life; these characters proved to be preadaptive for parasitism. This transition, without prior changes in architectonic organization, enabled entomophthoraceous fungi to occupy the niche of facultative parasites, rather poorly specialized from the physiological standpoint. This transition was associated with a certain morphological simplification of the fungal body (such as the disappearance of microconidia and capillispores), and is consistent with the phenomena already known to evolutionary parasitology (Michajlow, 1960). The group of entomopathogenic species of polykaryotic entomophthoraceous fungi underwent no further developmental and morphoanatomical transformations concerning the improvement of these fungi as parasites, except for the development in some of its representatives of behavioristic adaptations (*e.g.*, in *Entomophaga grylli*, p. 19ff). After a change in the mode of life, these fungi achieved a relatively small success in the struggle for life (as compared with

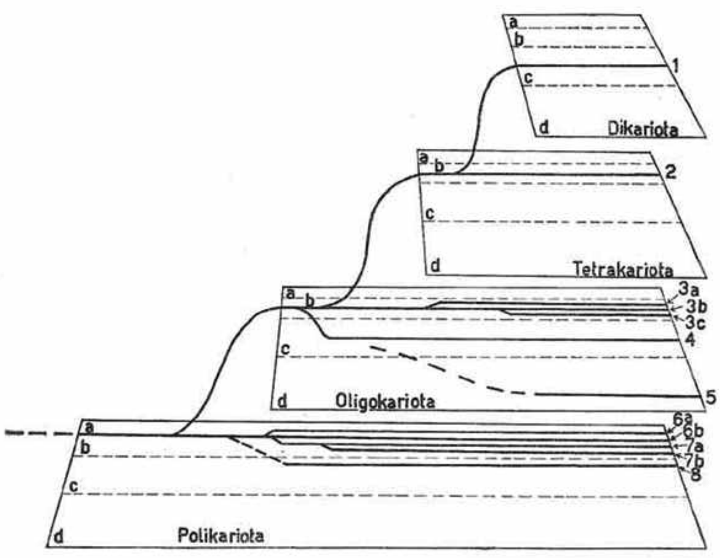

Figure 17. Scheme illustrating aromorphoses and adaptive radiations in phylogeny of entomophthoraceous fungi. Planes symbolize the architectonic organization levels of the nuclear apparatus (within oligokaryota, the tetra- and dikaryotic levels are also distinguished). Each plane is divided into four ecological niches: a = saprophytes, b = parasites deprived of tagmatic or tissue speciali-zation ("facultative"), c = obligatory, lethal parasites developing in host's abdomen; d = highly specialized nonlethal parasites. The individual lines symbolize groups of closely related species (genera and subgenera): 1 = *Massospora*; 2 = *Triplosporium* [Editor: *Neozygites*]; 3 = *Zoophthora*; 4 = *Entomophthora*; 5 = *Strongwellsea*; 6 = *Conidiobolus*; 7,8 = *Entomophaga*.

oligokaryotic species); namely, they comprise a very small number of common species showing high virulence and regularly causing mass deaths of insects.

The picture of adaptive radiation of entomophthoraceous fungi on the oligokaryotic level of cytoanatomical organization is completely different. In the scheme shown in Fig. 17, the saprophytic niche is empty. However, it remains unclear whether this is due to a lack of saprophytic species of oligokaryota or to the fact that they have not so far been discovered. In any event, it seems that the transition of entomophthoraceous fungi to a higher level of thallic architectonics caused a total or partial loss of fitness in the saprophytic niche. The fungi of this group retain the ability to develop on lifeless substrates in vitro, and thus their absence on nonliving substrates in nature is due to ecological rather than to physiological factors.

Ecological niches of lethal parasites with segmental specialization and nonlethal parasites are unequally occupied on the oligokaryotic level of thallic organization in entomophthoraceous fungi. These fungi attained their greatest prosperity as expressed by their greatest speciation—more than 40 species—in the niche as parasites without segmental specialization; this is about twice the number of species in the same niche on the previous level. These fungi exhibit the highest degree of morphoanatomical and developmental complexity when compared to the whole family. The occurrence in some species of ahaptospores as rudimentary structures testifies to their genealogical relationship with fungi of the genus *Conidiobolus*, and it seems to indicate that in their phylogeny they first underwent aromorphotic transformation (oligomerization of the nuclear apparatus), and only then passed over to parasitism. In fact, it is possible that these events took place simultaneously or nearly so (considering the lack of saprophytic oligokaryota!), but in this instance the former event also predetermined the latter.

In contrast to the transition of polykaryota to parasitism, entomopathogenic oligokaryota did not undergo "morphological reduction" specific for parasitic organisms. Thus, the manifestation here of one strictly empirical phylogenetic regularity (morphoanatomical regression of parasites) is limited by the action of another regularity having a wider range and resulting from evolutionary theory (aromorphotic transformation leads to morphophysiological progress). Oligokaryotic entomopathogenic entomophthoraceous species attained evolutionary prosperity in a niche of facultative insect parasites because during their phylogeny various developmental and morphoanatomical changes of a post-adaptive nature added to their preadaptation.

The main developmental property of entomophthoraceous fungi occupying the niche of parasites without segmental specialization on the level of the oligokaryota consists of the occurrence during their individual development of syntomic divisions which culminate in the formation of branched conidiophores and conidia or architectonic type 4 (p. 26). As far as it is known, ontogeny of this type, and the sporogenesis and morphoanatomical form of conidia inherent to it, occur only in the set of species occupying this particular ecological niche on just this level. Thus, the achievement of this ontogeny can be regarded as the third "main event" after oligomerization of the nuclear apparatus and the transition to parasitism which led to the origin of these fungi.

The origin of this ontogeny can be additionally explained by means of an auxiliary hypothesis. The different kinds of cell division mentioned above, as distinguished by Zakhvatikin (1949) often form pairs in the ontogenies of various lower organisms (in the Protista). In such a pair the first kind of division involves cell division into two, and the second one into many daughter cells. If the first member of the pair consists of monotomic division (the division of uninucleate cells into two uninucleate ones), then the second member usually comprises palintomic divisions, a series of monotomies uninterrupted by cell growth. It is clear that palintomy is a division pattern derived from monotomy since both these patterns involve a close karyokinetic-cytokinetic linkage while the cells exhibiting them are uninucleate. The division of a multinucleate cell into two (or more) multinucleate ones (archetomy) is usually coupled with the division of a multinucleate cell into many uninucleate ones (syntomy).

As previously mentioned, the Entomophthorales exhibit both cell division systems; the monotomic-palintomic system occurs in representatives of the family Basidiobolaceae, whereas the one member archetomic system or archetomic-syntomic system occurs in the Entomophthoraceae. The different course of the basic ontogenetic process in representatives of the two mentioned families of entomophthorous fungi points to their early divergence in phylogeny. At the same time, the pronounced morphological and morphoadaptive resemblances between *Basidiobolus* and *Conidiobolus* testify to their common origin, and can be interpreted, therefore, as the result of evolutionary parallelism caused by a certain community of the genetic structure (cf. Simpson, 1961, p. 103-106). Thus, it seems probable that entomophthorous fungi diverged into two branches with different ontogenetic and cellular organizations. In one branch, the Basidiobolaceae, the "ordering" of the organization and development of cells by the close coupling of karyokinesis and cytokinesis led to the transformation of the primary archetomic-syntomic ontogenetic system into the monotomic-palintomic system. The second branch led to *Conidiobolus*, and initially exhibited only a simplification of the structure of ontogeny by way of reduction of the archetomic-syntomic system to a one-member archetomic system.

Let us assume that the loss of syntomy was not irreversible and that is reoccurrence in oligokaryotic entomophthoraceous fungi results from unblocking of genetic information regulating this process. This unblocking might result from the radical karyological reorganization associated with oligomerization of the nuclear apparatus. A new ontogenetic scheme generated with this assumption facilitates a fuller appreciation of the ontogenetic and phylogenetic parallelisms between the Basidiobolaceae and Entomophthoraceae.

In Figure 18A, the course of sporogenesis in *Basidiobolus microsporus* Benjamin (1962) is presented. This fungus forms uninucleate conidia of type 3 (p. 25). After forcible discharge, these conidia undergo transformations associated with palintomic division of the conidial contents into numerous sporangiospores. In this species the sporangiospores are translocated to the conidial wall processes and transformed into microconidia. Each microconidium is, in fact, a monosporic sporangiole with two walls—an internal sporangiospore wall and an external sporangial wall.

Let us assume the existence of a hypothetical representative of oligokaryotic Entomophthoraceae (Fig. 18B) with sporogenesis analogous to that of *Basidiobolus ranarum*. This fungus ought to produce multinucleate conidia, whose contents would be syntomically divided among numerous sporangiospores after forcible discharge from the conidiophores, and which would become transformed into microconidia of a structure identical with that of *B. microsporus* microconidia. Such a fungus has not been detected, and probably never existed

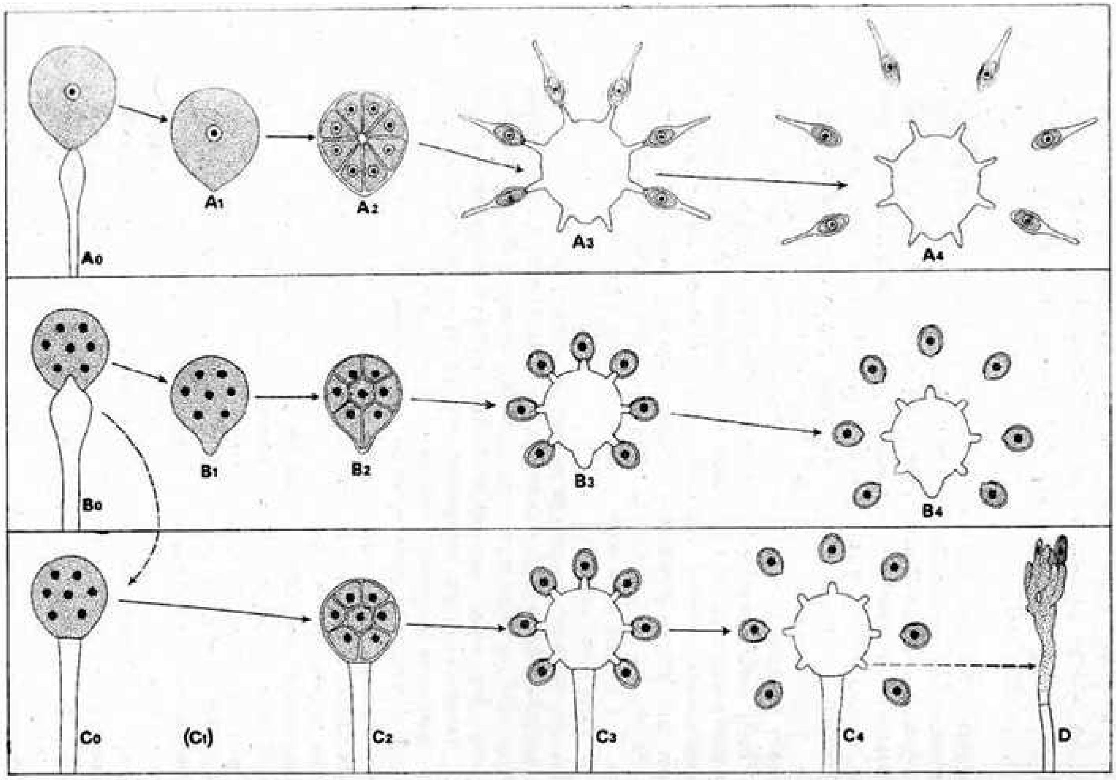

Figure 18. Scheme illustrating the hypothesis which explains the origin of the conidial apparatus of the *Zoophthora* type. A. Sporogenesis of microconidia in *Basidiobolus microsporus* [after Benjamin, 1962]. B. Hypothetical "intermediate" form of sporogenesis analogous to sporogenesis in *Basidiobolus* but proceeding in oligokaryota. C. Sporogenesis derived from B as a result of inactivation of the papilla-columella system of primary ballistospores which became transformed into a part of the conidiophore, whereas secondary spores – microconidia – were transformed into primary conidia. D. Conidiophore of *Zoophthora* subgenus *Erynia* with a visible septum (the homologue of a reduced papilla-columella system) and distention at the base of the branch, a rudimentary structure representing the remainder of the wall of the primary ballospore. Continuous arrows denote ontogenetic links; broken arrows are phylogenetic transformations.

in the described form. The scheme presented in Fig. 18B illustrates a certain hypothetical course of ontogeny resembling the ontogeny of *B. microsporus*, and which—although parallel to it—is based on the ontogenetic structure specific for Entomophthoraceae.

From this "transient" ontogeny, we can easily derive the actually existent *Zoophthora* type of ontogeny (Fig. 18C) by assuming that the primary conidium became transformed into a part of the conidiophore after the reduction of the papilla-columella mechanism. The secondary conidial apparatus (microconidia), as the homologue of the monosporic sporangiole, then became transformed into the *Zoophthora*-type conidia. A proof for the validity of this hypothesis is that, in many species of entomophthoraceous fungi with branched conidiophores, a septum (the rudiment of the papilla-columella system of the primary ballospore) occurs at the base of the branched part of the conidiophore while the often noted distension of the conidiophore above this septum represents the rudiment of the ballospore itself (Fig. 18D).

This hypothesis explains the correlation between branched conidiophores and the specific structure of *Zoophthora*-type conidia. Because the hypothesis is not inconsistent with the known facts, it is justified. Its assertion better permits us to understand the evolutionary directions of the oligokaryotic species of entomophthoraceous fungi. Those species following the pathway of progressive morphoanatomical development were successful in the struggle for life in the niche of segmentally nonspecialized insect parasites. These represent the largest group—with more than 40 species—among the entomopathogenic Entomophthoraceae. This fairly uniform group is set off by its common ontogenetic structure and greatly differentiated morphoanatomy. The primary and secondary conidia, pseudocystidia, rhizoids, zygo- and azygospores, etc. of these fungi are the objects of additional sets of diversity. The remaining species of oligokaryotic entomophthoraceous fungi followed the pathway of parasitic specialization, occupying the niches of lethal insect parasites with tagmatic specializations and the niche of nonlethal parasites. These fungi were also successful in the struggle for life, despite the small number of their known species (about 10 species). They often cause mass deaths of insects and substantially regulate the density of their host populations. However, they owe this success to intense speciation rather than to progressive evolution. In this group of fungi, the primary aromorphosis (oligomerization of the nuclear apparatus) was supplemented with many post-adaptations for parasitism which involve primarily physiological characters. These fungi underwent "morphological reduction" similar to those in the polykaryotic entomopathogenic species. The genealogical unity of this group with the remainder of the family, and its probable phylogenetic link with the genus *Conidiobolus* further supported by the capillispores formed by some members of the group. In fact, these fungi constitute a fairly well differentiated, though not very numerous group. Among them several subgroups (genera?) can be distinguished whose representatives form ballospores characteristic of each subgroup (bell-shaped, lageniform, etc.); these subgroups differ in the course of pathogenesis, etc. In addition to *Massospora* (2 species) and *Strongwellsea* (1 species), some species of *Entomophthora* sensu stricto also belong to this group.

Indeed, *Strongwellsea castrans* occupies a fairly specific position in the discussed system. This fungus attained the highest level of parasitic specialization (to certain tissues), a phenomenon undoubtedly related to its high physiological specialization. However, its ontogeny proceeds with certain deviations according to the pattern described above for species of *Zoophthora*. Thus, while the remaining species of specialized insect pathogenic entomophthoraceous fungi seem to be phylogenetically related to the polykaryotic representatives of the family (because of the similarity of their ontogeny), *Strongwellsea* exhibits a marked resemblance, resulting from genealogical relationships, to the unspecialized oligokaryotic insect parasites. It seems that the existence of this unique species testifies to the evolutionary potency of the mentioned large group of parasitic oligokaryota, and that this species might be their first affiliation to a new ecological niche.

Thus, while analyzing the polarization of the diversity series of entomophthoraceous fungi, we passed from establishing what is "lower" or "higher" in the different sequences to an overall evaluation of the probable evolutionary directions of the particular fungal groups. Therefore, in the analyzed cases the polarizations of the different diversity sequences was established only partly on the basis of empirical phylogenetic regularities. With respect to many diversity series, establishing what is "lower" and what is "higher" by analogy and assessment of correlations was difficult, and proved possible only within the above-mentioned overall analysis of the evolutionary tendencies. Nevertheless, this establishment creates bases for determining the initial states of the phylogeny of entomophthoraceous fungi and for specifying the sequences of the main evolutionary events leading to the separation of their different groups.

The initial state of the phylogeny of the Entomophthoraceae includes the following set of characters: saprophytic mode of life; multinucleate hyphae and spores; the ability to form ballospores, microconidia, and capillispores; and physiological pre-adaptations to parasitism (the ability to secrete chitinase curing conidial germination, etc.).

This characterization of the "initial state" coincides with the diagnosis of the contemporary genus *Conidiobolus* (p. 31), and permits the assumption that evolutionary sequence leading from the "initial state" to at least some contemporary groups of the insect pathogenic Entomophthoraceae describe present-day events.

The main radiative events for entomophthoraceous fungi can include :

a) oligomerization of the nuclear apparatus;
b) transition to the parasitic mode of life;
c) morphological reduction of the apparatus of secondary conidial sporulation;

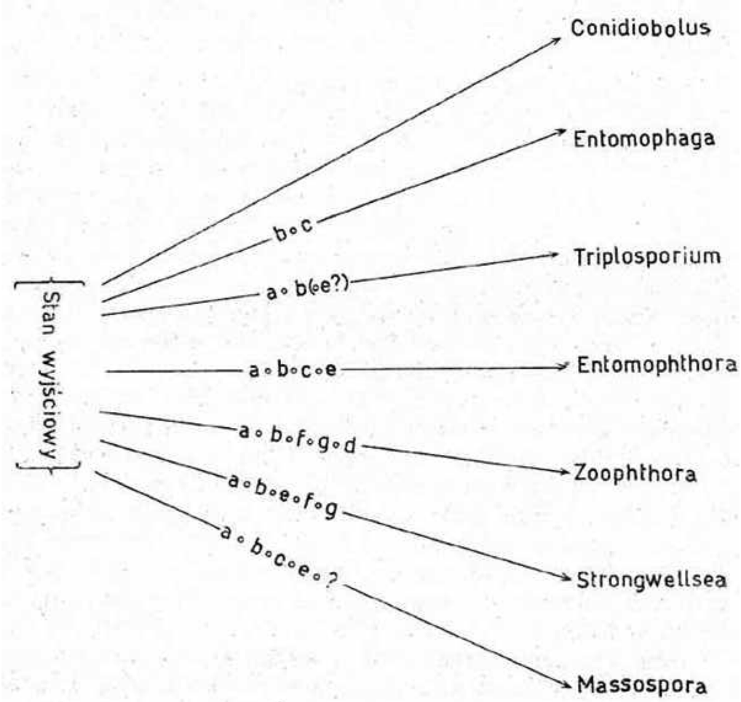

Figure 19. Scheme of phylogenetic reconstruction of entomophthoraceous fungi from their initial state. See explanations of letters in text on p. 51f.

d) development of morphological post-adaptations to parasitism (rhizoids, pseudocystidia);
e) development of physiological post-adaptations to parasitism (affinity to all or only some abdominal tissues or the limitation of the destructive action of the fungus on its host organism);
f) reduction of primary ballospores and taking over of their functions by microconidia.

Phylogeny of the different groups of the entomopathogenic entomophthoraceous fungi comprises various sequences made up of the events mentioned (Fig. 19). The shortest sequence, b•c, leads to nonspecialized polykaryotic parasites, and the longest sequence, a•b•f•g•d, leads to similar oligokaryotic parasites. As presented, the reconstructed derivation

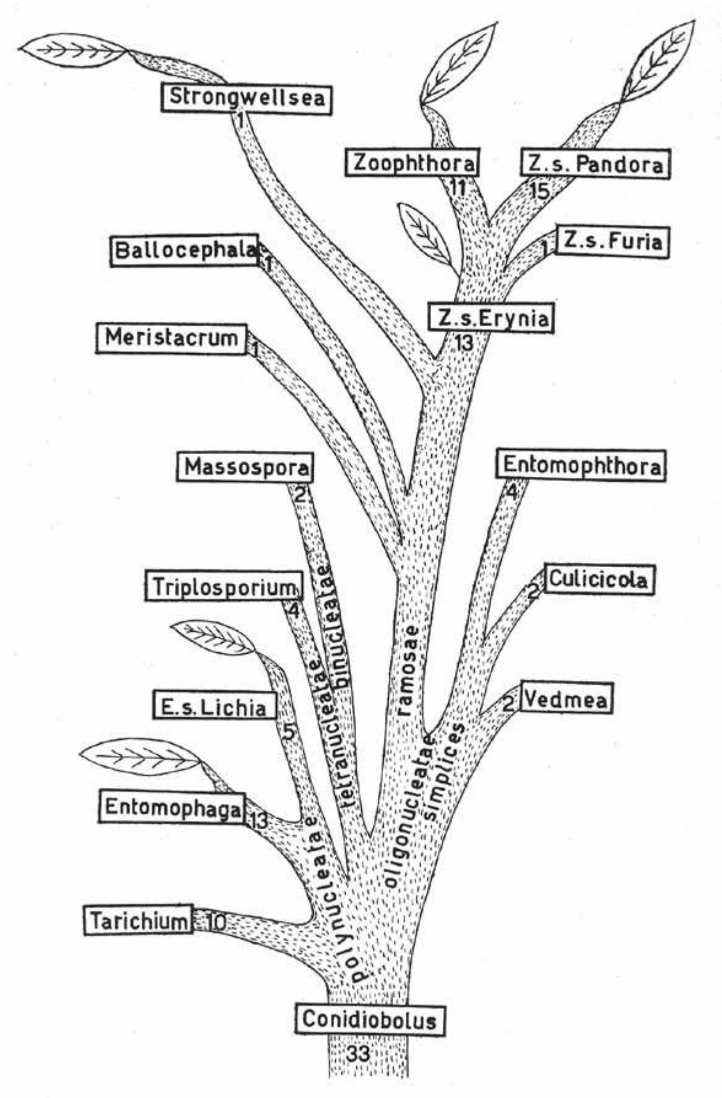

Figure 20. Traditional genealogical tree of entomophthoraceous fungi prepared by A. Batko (1964, unpublished). Numbers next to generic names denote the number of species in that genus.

for entomophthoraceous fungi clearly points to the phylogenetic heterogeneity of the entomopathogenic species of the Entomophthoraceae comprising the “critical group” analyzed here (p. 31f).

The scheme of this phylogeny (Fig. 19) differs from the classical genealogical tree not only its graphic form. The most essential property of such a scheme is the fact that it contains information on events either observed or somehow observable (whether directly, indirectly, or deduced through appropriate auxiliary hypotheses). Nevertheless, the phylogenetic information contained in the scheme is given in a completely distinct form. The general concept of “phylogenetic closeness” or “phylogenetic distance” is translated into sequences of defined evolutionary events. It seems that this scheme bears more information than the classical genealogical tree.

In 1966, on the basis of the whole pool of available information on entomophthoraceous fungi, I prepared such a “classical” genealogical tree for the Entomophthoraceae and tried to be maximally objective. The genealogical relationships shown in the unpublished tree (Fig. 20) were derived intuitively. Nevertheless, these relationships closely parallel those established in the present analysis and shown in Fig. 19. However, the comparison of the two schemes indicates that the “classical” tree contains some “misinformation” in the structure of its branches. Phylogenetic relationships in the earlier scheme are presented in a very general manner (“closer” and “more distant”) and in an excessively detailed way. For example, the common trunk of *Massospora* and *Triplosporium* symbolized only one resemblance (the highest degree of oligomerization of the nuclear apparatus) whereas it suggests a close genealogical relationship. On the other hand, the same common trunk for *Zoophthora* (and its four subgenera) and *Strongwellsea* symbolizes the much close phylogenetic relationships resulting from the commonality of the ontogenetic structure. The comparison of the schemes in Figs. 19 and 20 indicates the preferability of the phylogenetic analysis and presentation given here when considering groups deprived of fossil records.

13. From Phylogeny to Taxonomy

The completed phylogenetic reconstruction in Fig. 19 resolves distinct radiative pathways for the different groups of species within the “critical” group of species comprising the genus *Entomophthora* in its broadest sense.

The nomenclatural type of *Entomophthora*, *E. muscae*, holds a phylogenetic position different from that of most species. This fungus differs from the majority of entomopathogenic entomophthoraceous fungi not only in the unique sequence of evolutionary events assumed to lead to its derivation, but also in its distinctive bell-shaped conidial morphology, particular conidial discharge mechanism, complex nutritional requirements for in vitro culture, et. The phenetic distinctness of *E. muscae* is, therefore, an important factor to consider when passing from phylogenetic to taxonomic relationships. This distinctness additionally suggests restricting the circumscription of *Entomophthora* to a few species differing only in hosts and with only slight adaptations related to these different hosts; *Entomophthora weberi* and *E. erupta*, fungi parasitizing phytophagous bugs and sporulating on mobile, living hosts have to be referred to the strictly redefined genus *Entomophthora.*

I singled out the remaining few species of little known oligokaryotic entomophthoraceous fungi with quadrinucleate primary ballospores and forming ahaptosporic and haptosporic secondary spores into the separate genus *Triplosporium* mainly with phenetic criteria. A lack of data on the course of pathogenesis prevented the reconstruction of the phylogeny for these fungi. The species of *Triplosporium* exhibit many similarities to *Entomophthora* s. str., but differ from them in their unique course of conjugation and development of zygospores (Fig. 9).

The phylogenetically compact group of oligokaryotic entomopthhoraceous fungi forming type 4 conidia (p. 26) on branched conidiophores, and occupying the ecological niche of relatively slightly specialized insect parasites, was separated into the genus *Zoophthora* on account of their phylogenetic and phenetic distinctiveness Because of the great differentiation within this group, I later distinguished four subgenera (Batko, 1966b). The simultaneous inclusion by some authors of these fungi in *Entomophthora* (in its broadest sense) along with species of *Conidiobolus* seems completely unjustified in view of the clear phenetic distinctness of these fungi.

The inclusion of multinucleate entomopathogenic species in *Entomophthora* seems equally unjustified for both phylogenetic and phenetic reasons. These species are much closer to fungi n the genus *Conidiobolus* than to the specialized oligokaryotic insect parasites such as species of *Entomophthora* sensu stricto.

Singling out of one of the evolutionary transformations in the phylogeny of the Entomophthoraceae, that of oligomerization of the nuclear apparatus, as an aromorphotic transformation should be reflected in the taxonomic structure of this group. It would appear to be correct to attribute separate familial status to the polykaryotic and oligokaryotic groups of entomophthoraceous fungi. However, such a designation is impeded by the lack of data on the structure of the nuclear apparatus for many species and for the genera *Ballocephala*, *Meristacrum*, *Completoria*, and *Tarichium*. A familial separation would necessitate a separate listing for genera of uncertain affinity; such a list would be undesirable as regards the functionality of the classification.

14. Conclusions

1. Phylogenetic reconstructions based only on neontological data are possible, but are of a different nature than those based also on paleontological data. Information included in neontologically derived reconstructions concerns only the descendence relationships (closeness of genealogical relationships), but does not indicate any chronological sequence of relationships (lacks a "time dimension"). This reconstruction, however, does indicate the third component of the concept of "phylogenetic relationships", the degree of group divergence.
2. In a phylogenetic reconstruction conceived as above, the role of the "common ancestor" is played by the "initial state of phylogeny." This broader concept comprises the descriptions of all logically possible common ancestors (i.e., possible from the present-day standpoint). The "initial state of phylogeny" is not the description of a hypothetical taxon but is merely the set of characters regarded as the most primary.
3. In such a phylogenetic reconstruction, the phylogeny of the different groups is described as a sequence of the main evolutionary events.
4. The determination of the main phylogenetic events depends on the hierarchical level of the group (taxon) being treated in the reconstruction.
5. In these reconstructions, and "evolutionary event" is conceived of neither as a unitary event nor as a set of unitary events, but as a class of events. Consequently, the "sequences of events" are processes and the whole reconstruction is not of an idiographic nature since nomothetic elements predominate therein. A phylogenetic reconstruction conceived in this manner is of a limitedly historical nature.
6. A phylogenetic reconstruction can form the theoretical basis for a classification, and it permits the phylogenetic classification of groups deprived of paleontological records.

7. Within such a phylogenetic reconstruction, a "monophyletic group" is conceived of as a set of groups (taxa) which can be assumed to originate from a common initial state and to have undergone the same sequence of evolutionary events.

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