

MYCOTAXON

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OF RESEARCH ON TAXONOMY & NOMENCLATURE OF FUNGI & LICHENS

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FEATURES-CRITERIA OF TAXONOMIC VALUE IN THE ENTOMOPHTHORALES: I. A REVISION OF THE BATKOAN CLASSIFICATION

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"The underlying assumption of scientific classification is that there is a natural order, a system of similarities, which can be discovered by investigation. In its simplest form it says that A is very similar to B but is less similar to C. The distinctive concept of scientific classification is that it attempts to measure overall similarity; its distinctive value is in prediction."

P.H.A. SNEATH, 1957.

ABSTRACT

Various morphological, cytological and other features used as taxonomic criteria (features-criteria) in the different ENTOMOPHTHORALES classifications are reviewed and reconsidered from an evolutionary standpoint. Levels of taxonomic importance are judged here to be inversely proportional to the relative length of time during which features used as taxonomic criteria evolved at their present state. An arrangement of features-criteria according to

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this pattern of judgement reveals a four level hierarchical system.

The structure of vegetative nuclei is considered as a feature-criterion of the highest level; species grouped in categories traced by this criterion are considered co-familial within each category. The conidial nuclear number and conidial wall structure, together with the structure and function of primary conidiophores are considered important at the generic level. Species grouped in frames traced by these criteria are considered congeneric within each frame. Production patterns of secondary conidia, structural-morphological features of rhizoids and pseudocystidia and possibly the morphology of primary conidia are considered important at the subgeneric level. Differences in the shapes and dimensions of all comparable structures, together with physiological and pathological features are considered important at the specific level. Every feature can be considered as a secondary characteristic, but not as a criterion at the next upper taxonomic level.

Batko's classification, as well as recent ones derived from it (neobatkoan classifications) are discussed in the light of these taxonomic views. Three families and sixteen (or possibly more) generic frames are recognized in the ENTOMOPHTHORALES: ANCYLISTACEAE comprising the genera *Ancylistes*, *Conidiobolus* and *Meristacrum*, and probably but not yet established, *Ballocephala*, *Zygnemomyces* and possibly one or more, still undefined, generic frames; BASIDIIOBOIACEAE comprising for the present one genus - *Basidiobolus*; ENTOMOPHTHORACEAE comprising the genera *Entomophthora*, *Massospora*, *Triplosporium*, *Completozia*, *Macrobiotophthora*, *Strongwellsea*, *Erynia* and *Entomophaga*; the last mentioned undefined with regard to its conidial nuclear number, but fitting one of three (or possibly more) unnamed generic frames affiliated to this family. The synonymies of the other generic names are discussed. Two groups devoid of formal generic status are adopted: *Tarichium* sensu Lakon, for species known from their resting spores only; *Entomophthora* (nomina provisoria) for conidial species with crucial features-criteria unknown. Two new subgenera are described in *Conidiobolus* in addition to *C. (Delacroixia)*: *C. (Conidiobolus)* subgen. nov. and *C. (Capillidium)* subgen. nov. The description of *Triplosporium* is emended and *T. lecanii* is transferred there from *Entomophthora*.

TAXONOMIC CRITERIA AND CLASSIFICATIONS OF ENTOMOPHTHORALES:
HISTORICAL

The class ZYGOMYCETES of the subdivision ZYGOMYCOTINA is comprised of three, or possibly four orders. One of them, the ENTOMOPHTHORALES, is characterized by asexual spores believed to be sporangia that have been reduced to function as single conidia and are forcibly discharged at maturity (Benjamin, 1979; Hesselstine and Ellis, 1973). Three families have been described in this order (cited in Waterhouse, 1973): ENTOMOPHTHORACEAE Warming 1884; BASIDIOLACEAE Engler & Gilg 1924, and ANCYLISTACEAE Ubrizsy & Vörös 1966. Some authorities accept only the ENTOMOPHTHORACEAE (e.g. Waterhouse, 1973) others accept the BASIDIOLACEAE as well (e.g. Benjamin, 1979) while still others accept all three families (Batko, 1974, Humber, 1982 b; Tucker, 1981; Ubrizsy and Vörös, 1966). Taxonomic criteria based on new findings, for the division of the ENTOMOPHTHORALES at the family level are being currently revised by R. Humber (1982 b; and pers. comm.).

The family ENTOMOPHTHORACEAE has been subject to many different classifications, most of them belonging conceptually to two basic groups: distinctive vs. collective classifications. The distinctive classifications employed morphological and structural features as criteria (called hereinafter features-criteria) for grouping species together and for distinction between the different groups. In the distinctive group belong the classifications of Brefeld (1877), who placed the entomophthoraceous fungi in the vicinity of the OOMYCETES and near the USTILAGINACEAE [BASIDIOMYCETES]; that of Nowakowski (1883), who correctly placed these fungi in the ZYGOMYCETES and proposed (without description) the family ENTOMOPHTHOREAE, and those of Thaxter (1888) and Lakon (1915, 1919).

The features-criteria employed by Nowakowski (1883) were conidiophore structure, occurrence of rhizoids, cystidia, zygospores or azygospores, conidia, and parasitism in insects or in plants. His genus *Empusa* (see Fig. 1 for the citation of generic names) was characterized by unbranched conidiophores (rarely slightly branched), production of azygospores and lack of rhizoids and cystidia. Nowakowski's genus *Entomophthora* was characterized by branched conidiophores, production of both zygospores and azygospores and possession of rhizoids and cystidia. His genus *Lamia* was similar to *Empusa* with regard to conidiophores and resting spores, but possessed rhizoids like *Entomophthora*. Nowa-

kowski accepted Cohn's (1875) genus *Tarichium*, characterized by smooth-walled or warted azygospores and inability to produce conidia. Nowakowski (1883) included *Completozia* Lohde 1881 (parasitic on fern prothallia) in his proposed family ENTOMOPHTHOREAE (Fig. 1).

Thaxter (1888) regarded the features of *Lamia* (intermediate between *Empusa* and *Entomophthora*) as proof that Nowakowski's (1883) features-criteria did not provide a clear-cut distinction, at the generic level, between these taxa. In his treatment Thaxter (1888) employed one genus, *Empusa* for all the insect attacking species. This genus comprised three subgenera: *Empusa* (*Empusa*), including Nowakowski's species of *Empusa* and *Lamia*, *E.* (*Entomophthora*) including Nowakowski's species of *Entomophthora*, and *E.* (*Triplosporium*). The last subgenus was characterized by smoky conidia, black, oval zygospores produced by isogamous conjugation of spherical hyphal bodies and was similar to *E.* (*Empusa*) in the other characters. Thaxter accepted the genera *Basidiobolus*, *Conidiobolus* and *Completozia* as belonging to the ENTOMOPHTHORACEAE and pointed out [simultaneously with Forbes (1888) - cited in Thaxter (1888) p. 191] that *Massospora* belongs to the same family as well. He did not regard *Tarichium* as a genus but merely as a group of *Empusa* species with unknown conidial stage.

Lakon's classification (1915, 1919) was limited to the insect-attacking species of the family and was basically an emended version of Nowakowski's system, based on descriptions of a substantially larger number of species. Lakon's other contributions to the classification were his proposal to use the name *Tarichium* as a "temporary-auxiliary genus" for all entomophthoraceous species known from their resting spores only, and his glossary of conidial morphology. Unfortunately, this glossary, meant by Lakon to facilitate and standardize conidial description, seems to have become one of the bases for the later collective classifications.

Cytological studies (Cavara, 1899a, b; Riddle, 1906) provided evidence that the uninucleate condition in the primary conidia of all investigated *Entomophthora* species was correlated with the branched, multicellular structure of the primary conidiophores producing those conidia. The multinucleate condition of the *Empusa* conidia was correlated with the simple (unicellular, rarely slightly ramified) structure of their conidiophores. Riddle (1906) and Cavara (1899 a, b) were among the earliest to discuss phylogenetic aspects of the ENTOMOPHTHORACEAE, relating the dif-

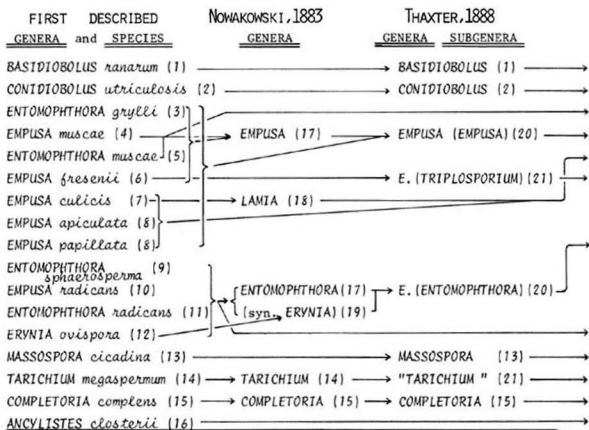
ferences between *Empusa* and *Entomophthora* to evolutionary trends observed in the related order MUCORALES. Cavara's and Riddle's findings were correctly regarded by Lakon (1919) as important but still impractical in classification due to the small number of species in which the cytological /karyological studies were carried out.

It is now agreed by an ever increasing number of authorities that the most comprehensive, distinctive classification was that developed in several steps by Batko (1964a, b, c, d, e; 1966a, b; 1974; Batko and Weiser, 1965). His first step toward the new classification was to transfer *Entomophthora coronata* (Cost.) Kevorkian (1937) to the genus *Conidiobolus* (Batko, 1964a). Accepting the recommendations of previous authorities (Fresenius, 1856; Kevorkian, 1937; Hall and Bell, 1962) that *Entomophthora* Fresenius 1856 is the later but valid synonym of the invalid generic name *Empusa* Cohn 1855 (preoccupied by the orchid *Empusa* Lindley 1824), Batko (1964b) proceeded to the next step - he restricted *Entomophthora* to a few obviously related species possessing: "...simple, clublike [conidiophores] distended abruptly toward the tips frequently with perishable columella which breaks when the conidium is ejected. Conidia homologous with asexual sporangium, bell-shaped, coated with a single-layer elastic adhesive thin membrane, pointed at the apex, the base somewhat narrowed and widely truncated (type *truncata-campaniformis* according to Lakon's classification...); nuclei spherical, relatively few, generally at most 10-12 per 1 spore, ...Resting spores...azygospores. Pseudocystides and rhizoids absent. ...Type of the genus: *Entomophthora muscae* (Cohn) Fres. 1856."

The next step in Batko's system was to classify all the remaining species, formerly placed in *Entomophthora* Nowakowski and in *Empusa* Cohn *sensu* Nowakowski. This was accomplished (Batko, 1964c) by proposing three new genera:

1) *Zoophthora* Batko 1964, characterized by: "...Conidiophores dichotomically or irregularly ramified. Conidia homologous with monosporic sporangiola, mononuclear, with double membrane (single membrane only on the basal papilla). Pseudocystides either occur or not, whereas rhizoids occur invariably... Type of genus: *Empusa radicans* Brefeld, 1870. New combination: *Zoophthora radicans*..."

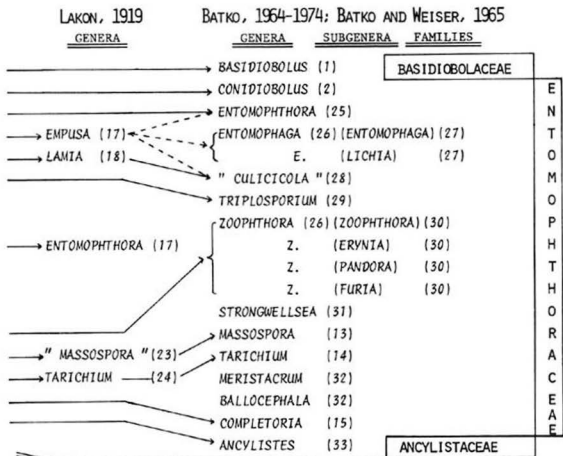
2) *Triplosporium* (Thaxter) Batko 1964, characterized by: "...Mycelium coenocytic generally composed of 4-nuclear spherical or irregularly shaped hyphal bodies. Conidiophores simple. Primary conidia homologous to asexual



AUTHOR QUOTATIONS: When in parentheses -- are listed in the REFERENCES, others are cited from MacLeod (1963).

- | | |
|---|---|
| (1) Eidam 1886 | (14) Cohn 1875 |
| (2) Brefeld 1884 | (15) Lhode 1874 (Nowakowski, 1883) |
| (3) Fresenius 1858 (Thaxter, 1888) | (16) Pfitzer 1872 (Berdan, 1938) |
| (4) Cohn 1855 | (17) Sensus stricto Nowakowski 1883 |
| (5) Fresenius 1856 (=Empusa Cohn, nomen preoccupatum by Empusa Lindley 1824) | (Empusa s.str. Nowakowski - invalid, see (5), Entomophthora s.str. Nowakowski 1883 - invalid, since E.muscae, the type species was excluded. According to Batko, 1964b) |
| (6) Nowakowski 1883 | (18) Nowakowski 1883 |
| (7) A. Braun 1855 (Nowakowski, 1883) | (19) Erinia Nowakowski 1881 reduced to synonymy with Entomophthora sensu Nowakowski (1883) |
| (8) Thaxter 1888 | (20) Nowakowski's (1883) genera, reduced by Thaxter (1888) to subgeneric rank. |
| (9) Fresenius (1856 =nomen nudum, 1858 =nomen confusum according to Batko, 1964c) | |
| (10) Brefeld 1870 (Batko, 1964c) | |
| (11) Brefeld 1877 | |
| (12) Nowak. 1881 (Nowakowski, 1883) | |
| (13) Peck 1879 (Thaxter, 1888) | |

FIG. 1 Distinctive classifications as landmarks in the evolution of the Batkoan classification (adopted with some changes from Ben-Ze'ev, 1980).



(21) Thaxter 1888, new subgenera

(22) Mentioned but not accepted by Thaxter (1888)

(23) Suspected by Lakon (1919) as not belonging in the ENTOMOPHTHORACEAE

(24) Proposed by Lakon (1919) as a "temporary - auxiliary genus"

(25) Sensus stricto Batko 1964(b)

(26) Batko 1964(c) new genera

(27) Batko & Weiser 1965 (new subgenera - invalid; lacking Latin descriptions, according to Remaudiere and Keller, 1980)

(28) Nieuwland 1916 (Batko, 1964d), apparently abandoned by Batko (1974)

(29) (Thaxter) Batko 1964(c) = *Empusa* (*Triplosporium*) Thaxter 1888, erected to generic rank

(30) Batko 1966(b) new subgenera

(31) Batko & Weiser 1965

(32) Drechsler 1940, 1951 respectively

(33) Pfitzer 1872 (cited as family by Batko, 1974).

sporangium (prosporangium) with single layer membranes, 4-nuclear with a handlelike widely truncate basal papilla (type truncata-lageniformis according to Lakon's classification...)...Zygosporoes binuclear at the mature phase, extrasporangially formed by...isozygogamy... Type of the genus: *Empusa fresenii* Nowakowski 1883. New combination: *Triplosporium fresenii* (Nowak.)..."

3) *Entomophaga* Batko 1964, characterized by: "...Conidiophores simple. Conidia spherical to oval or pear-shaped, homologous to aposporic sporangium (prosporangium) with a single-layer thin elastic adhesive membrane, with a rather pronounced nipple-like rounded basal papilla (type subpapillata or papillata according to Lakon's classification...), multinuclear; nuclei minute, very numerous (up to several score in one spore)...Zygosporoes or azygosporoes form extrasporangially... Type of the genus: *Entomophthora grylli* Fresenius, 1858. New combination: *Entomophaga grylli* (Fres.)..."

Batko's (1964d) next step was to add to his classification the genus *Culicicola* Nieuwland 1916 (syn.: *Lamia* Nowakowski 1883 - nomen preoccupatum by *Lamia* Endlicher, 1841) characterized by: "...Conidiophores generally simple, rarely-poorly ramified at the base. Conidia homologous to aposporic sporangium. Resting spores-zygosporoes or azygosporoes. Pseudocystidia absent, rhizoids present. Type of the genus: *Culicicola culicis* (A. Braun) Nieuwland, 1916."

Batko (1964d) admitted that he purposely omitted the nuclear number from *Culicicola*'s description, since in this genus the non-ramified conidiophores and the presence of rhizoids were the leading features-criteria. Another admitted reason for this omission was the fact that in nuclear numbers and in conidial morphology as well, some species resembled *Entomophthora* while others resembled *Entomophaga*.

Analysing the findings and some of the material of Strong, Wells and Apple (1960), Batko and Weiser (1965) proposed a new genus of ENTOMOPHTHORACEAE: *Strongwellsea* Batko & Weiser, characterized by: "...Conidiophores...unbranched, separated by septa from hyphal bodies, and contain 1 or 2 nuclei. Only one of them takes part in conidia formation... Conidia homologous to monosporal sporangiolae, uninuclear, with two covering membranes except the papilla, ovoid, obovoid or obtuse cone-shaped, of the papillata type ... Pseudocystids and rhizoids absent. Resting spores not known. A nonlethal parasite of adult Diptera."

In the discussion of this paper, Batko and Weiser (1965) apparently tried to purify *Culicicola* from the rhizoidal, *Entomophaga*-like species, by proposing a new subgenus, *Entomophaga (Lichia)* (*nomen nudum* - as noted by Remaudière and Keller, 1980).

The last step in Batko's classification (Batko, 1966b) was to rearrange the species classified in *Zoophtora* (Batko, 1964c; e; 1966a) into four groups of subgeneric level: *Z. (Zoophtora)*, *Z. (Erynia)*, *Z. (Pandora)* and *Z. (Furia)*. The features-criteria used by Batko at the subgeneric level are discussed in the next chapter.

Batko's (1974) work is an evolutionary-phylogenetic approach to the taxonomy of the ENTOMOPHTHORACEAE. In this study he tried to work out the possible evolutionary trends in the invertebrate-attacking genera of this family and to justify his classification. The controversial genus *Culicicola* was completely omitted from this work, a fact seemingly overlooked by some of his critics, but the species remaining in it were not transferred to other genera until Remaudière and Keller's (1980) study.

Parallelisms and differences between the distinctive classifications and the emergence of the Batkoan classification are shown in Fig. 1. New classifications derived from Batko's (hereinafter referred to as Batkoan or neobatkoan classifications) are discussed in the last chapter of this paper.

Collective classifications of the ENTOMOPHTHORALES are defined here as those classifications in which all or most of the entomophthoralean species were catalogued in one collective genus, *Entomophthora* Fres. *sensu lato*. More collectiveness is added in classifications in which only the family ENTOMOPHTHORACEAE is recognized. Thaxter's (1888) classification, although being a distinctive one, was probably the basis for the collective ones. He de-emphasized Nowakowski's (1883) features-criteria by lowering their importance to the sub-generic rank, and returned to the use of the collective genus *Empusa*. As pointed out by Batko (1964d), Thaxter's authority influenced many authors who, apparently puzzled by the ever-increasing diversity found in this group of fungi, employed collective classifications in which most invertebrate-attacking species of the order were kept in *Entomophthora s.l.*, usually catalogued into "groups" without any legitimate status (e.g., Hutchison, 1963; Gustafsson, 1965; MacLeod and Müller-Kögler, 1973; MacLeod et al, 1976; Waterhouse, 1973; 1975).

A PHYLOGENETIC EVALUATION OF TAXONOMICALLY SIGNIFICANT FEATURES-CRITERIA

1. Definitions and Evolutionary Trends in the Entomophthorales.

A good distinctive classification is a predictive one; its taxa are so defined that all isolates, whether known or to be found, fit in their specific, subgeneric and generic place, guided by features-criteria that frame each taxon. Flexibility in the system, allowing for new taxa to be incorporated, is achieved by defining the new taxa according to the correlations observed among their features-criteria. Taxonomic rank should be decided according to the relative values attributed to individual features-criteria; this value is difficult to establish (Sneath, 1957); its best indicator seems to be the degree of correlation between an individual feature and the other features: "...The reason for regarding a feature as 'essential' is simply that it always goes with some other feature" (Sneath, 1957).

Three rules apply to the distinctive classification. Firstly, features-criteria given a certain taxonomic rank (e.g. generic) have to be applied in an even-handed manner to all taxa at that level, within the initial pool of species for which the classification is built. Secondly, a feature-criterion characterizing a taxon of a given rank (e.g. a subgenus) is fully characteristic for the lower taxa belonging to it (the species of that subgenus) but may be only partially characteristic for the higher rank (e.g. the genus to which the subgenus belongs - the subgeneric feature-criterion is a feature, but not a criterion, at the generic level). Thirdly, species belonging to the initial pool cannot be left outside the classification because they do not fit into any of the higher taxa delimited by the features-criteria employed; such species are either indications that the features-criteria were badly chosen or incorrectly weighed, or are incompletely known species for which temporary groups have to be devised. None of the descriptive classifications of ENTOMOPHTHORALES reviewed here met the abovementioned requirements, therefore the appeal of collective classifications is easily understood. When a broadly defined genus is employed, any species, known or when discovered, fits in it.

Features-criteria used in the taxonomy of ENTOMOPHTHORALES are mostly morphological. Different terms used by various authorities for the same organ may mislead; we

therefore attempt to clarify some of the most frequently used ones.

CONIDIA - as stated before, are the asexual spores of ENTOMOPHTHORALES and in most of them are considered to be modified sporangia (monosporic sporangiola - Batko, 1964c; unisporic sporangiola - Benjamin, 1979).* In some species the outer layer of the conidial wall (assumed to be the sporangial wall) separates from the inner layers (assumed to be the sporangiolar wall), and it is easily seen with the light microscope that the outer wall does not cover the papilla. In other species there is no separation of the conidial wall layers (as seen with the light microscope); conidia of this kind were wrongly considered by Batko (1964b, c) as "...homologous to aposporic sporangia (prosporangia)". However, an ultrastructural study in a species with no visible separation of conidial wall layers, *Conidiobolus coronatus* (Garrison et al., 1975), showed that its conidia possess a thin external wall layer, not continuous over the papilla, apparently homologous with the separating wall layer of those conidia considered "monosporic sporangiolae". In view of the confusing evidence about the sporangial or true conidial nature of these propagules, some authorities advocate the use of the general term SPORES (see Humber, 1981a). We hold that the asexual propagules of most ENTOMOPHTHORALES fit the definition of CONIDIUM reached at the Kananaskis Mycological Conference, 1969 (see Kendrick, 1971; Hughes, 1971). We advocate the use of CONIDIA instead of SPORES in order to minimize the possible confusion arising from the existence of several different kinds of asexual and sexual spores in this order. The apparent two types of conidia, regarding the visible separation vs. unseparation of the (assumedly sporangial) wall were descriptively termed by Remaudière and Keller (1980) unitunicate and bitunicate. Humber (1981a) elaborated on the justification of these two terms and we concur in this opinion.

SECONDARY CONIDIA - are of four or more types: Type I (after Thaxter, 1888) are those produced singly and forcibly ejected from short outgrowths arising on primary conidia, the mother conidium and its outgrowth acting together both as a one-celled conidiophore and a conidiogenous cell.

* In the present paper the prefixes "uni-" and "mono-" have the same meaning and are used interchangeably due to their common usage in literature.

There are two kinds of Type I secondary conidia: those resembling in shape the primary ones (termed here Type Ia) and those morphologically different from primary conidia (Type Ib). Most species of ENTOMOPHTHORALES, differing at the generic level, tend to produce Type Ia secondary conidia, however, many species produce both Types I, a and b, while some species are known to produce only Type Ib.

Type II (after Thaxter, 1888) are secondary conidia morphologically distinct from the primary ones, arising on slender "capillary tubes" ("*capillary conidiophores*") growing from primary or secondary conidia. At maturity a septum is formed near the tip of the capillary tube and a circumscissile ring develops immediately below the septum, allowing the conidium to be torn off by water splashes or by moving invertebrates. They were called different lengthy or inadequate names [e.g.: "*almond-shaped conidia*" Thaxter (1888), "*anadhesis spores*" (Batko, 1964c), etc.] until Batko (1974) coined the short, precise and descriptive term CAPILLISPORES, modified to the still better term CAPILLICONIDIA (Remaudière and Hennebert, 1980)*. This type of secondary conidia is produced by different species of ENTOMOPHTHORALES, belonging to different genera and families, and contrary to a former statement of the present authors (Ben-Ze'ev and Kenneth, 1981a) it appears that similar (probably homologous) conidia are produced in *Stylopage rhyncospora* Drechsler [ZYGOMYCETES: ZOOPAGALES] on capillary conidiophores arising from hyphae. This, and the ability to produce secondary conidia by resporulation, reinforce the assumed phylogenetic relationship between the ENTOMOPHTHORALES and ZOOPAGALES (Hughes, 1971 - see Fig. 2.1A; Webster, 1970; Hesselstine and Ellis, 1973). It should be mentioned here that in Thaxter's (1888) monograph the term "*secondary conidium of the second type*" was used for both capilliconidia and for Type Ib (forcibly ejected secondary conidia differing in shape from the primary ones).

The production of secondary conidiophores and conidia appears to be under two different classes of genetic controls: a) Responsible for the structure and function of the secondary conidiophore - producing either short, broad ones upon which Type I secondary conidia are produced and forcibly discharged, or producing capillary conidiophores upon which passively dehisced Type II secondary conidia

* Published with orthographic error as '*capilloconidia*'

(capilliconidia) are produced. b) Responsible for the number and size of the latter, expressed either as *singular resporulation* - the production of one, relatively large secondary conidiophore and conidium/primary conidium, or *multiplicative resporulation* * - the multiple production of secondary conidiophores and conidia upon one primary conidium. The next two types of secondary conidia, Type III and IV, are best explained as combinations of Types I and II, respectively, with the multiplicative pattern.

Type III are forcibly ejected secondary conidia, each produced on one of many tubular outgrowths arising from a primary conidium, resembling the primary ones in shape and termed MICROCONIDIA by Kevorkian (1937).

Type IV are passively detached secondary conidia (with a similar or identical detaching mechanism as Type II sec. conidia) each produced on one of many capillary outgrowths, each of which issues from a uninucleate cell produced by a successive internal cleavage of the cytoplasm in the primary conidia of *Basidiobolus microsporus* Benjamin 1962. These conidia differ in shape from the primary conidia producing them and resemble the Type II secondary conidia of *Basidiobolus*. Benjamin (1962), being aware of their analogy to the microconidia of *Conidiobolus*, termed them MICROSPORES. We advocate the use of Benjamin's term for this particular type of secondary conidia, in order to distinguish between them and the non-homologous *microconidia*. It is our view that the difference between *microconidia* and *microspores* might be as important as the difference between Type I secondary conidia and capilliconidia.

Type V - AQUATIC SECONDARY CONIDIA or "*tetroradiate propagules*" (Webster et al., 1978; Descals et al., 1981) are secondary or tertiary, usually tetroradiate conidia produced under water by primary or secondary conidia of *Erynia* species attacking aquatic insects. These conidia are produced by species (*E. rhizospora*, *E. conica* and two other unidentified species) which, when submerged, produce also aquatic, usually tetroradiate, primary conidia. Upon germination, the aquatic secondary conidia produce either a germ tube or, depending on whether they germinate in air or under water, they resporulate to produce tertiary aerial or aquatic conidia. Primary and secondary aquatic conidia are similar in being unitunicate, usually tetroradiate, and

* Derived here from Drechsler's (1955) term *multiplicative conidia*.

being probably passively discharged. They differ from each other by the direction of their branches: in primary aquatic conidia these branches give the conidium an Y outline and are called "*coronate primary conidia*"; in secondary aquatic conidia the branches point backwards and inspired the name "*stellate secondary conidia*" (Descals et al., 1981). Thaxter (1888, Figs. 366-369) found hyphal bodies producing such conidia "...in the form of an irregular kind of cross ..." in *E. rhizospora* and termed them "*pseudoconidia*". The aquatic (primary and secondary) conidia of these *Erynia* species are similar to the aerial (primary and secondary) conidia in being uninucleate and capable of resporulation. Their taxonomic importance, if any, is not apparent. Descals et al. (1981) concluded that since the occurrence of aquatic conidia was not mentioned in Remaudière and Keller's (1980) definition of *Erynia*, *E. conica* should be retained in *Entomophthora* "...until the occurrence of such conidia in other species assigned to this genus [*Erynia*] has been tested...". This obviously contradicts their own report on four species producing such conidia, two of them transferred to *Erynia* by Remaudière and Keller (1980).

CONIDIOPHORES - this term is used here instead of other alternative terms to match the use of the term conidia.

PSEUDOCYSTIDIA - named "*cystidia*" and "*paraphyses*" by different authors are not homologous with the cystidia of BASIDIOMYCETES. Therefore, as pointed out by Waterhouse (1973), Batko's (1964b) term is recommended.

MONOHYPHAL RHIZOIDS (Ben-Ze'ev and Kenneth, 1979) - named "*simple rhizoids*" or "*hypha-like rhizoids*" by different authors are composed at maturity of a rhizoidal hyphal body empty of cytoplasm and appearing to anchor the rhizoid inside the host's body; a simple or sometimes ramified rhizoidal thread, and a "*holdfast*" or "*foot*" at the contact point with a solid substrate. The holdfast develops by more or less profuse branching of the rhizoidal thread tip (Ben-Ze'ev and Uziel, 1979-Fig. 6; Ben-Ze'ev and Kenneth, 1981b-Fig. 5). The holdfast is not present in all species possessing monohyphal rhizoids. Some authors use the term "*holdfast*" misleadingly, meaning "*rhizoid*".

PSEUDORHIZOMORPHS (Batko, 1966a) - are multihyphal rhizoids in which rhizoidal threads from independent hyphal bodies grow parallel to each other to form sheets or tubes. On touching a solid substrate the tips of the individual threads branch profusely and interlace to produce a flat holdfast. The developmental stages appear to be synchron-

ized in most hyphae comprising a pseudorhizomorph.

PSEUDORHIZOMORPH-LIKE STRUCTURES (PLS) - are groups of unorganized, interlacing individual monohyphal rhizoids functioning as, and superficially resembling pseudorhizomorphs. True pseudorhizomorphs have been described so far only from species belonging to the "*sphaerosperma* group". PLS is known from one species only: *Entomophthora planchoniana*.

Batko (1966a) introduced the term pseudorhizomorph and gave a very brief definition: "...Rhizoids thin, thread-like, unramified, very numerous, tightly interlaced forming 2-4 pseudorhizomorphs." According to this definition the rhizoids of *E. planchoniana* could and have been considered pseudorhizomorphs (e.g. Ben-Ze'ev and Uziel, 1979; Milner et al., 1980). However, studying in vivo formation of rhizoids growing from moribund insects placed in humid environment on glass slides, a significant difference became apparent between the rhizoids of *E. planchoniana* and the pseudorhizomorphs of "*sphaerosperma* group" species. The first hyphal structures appearing shortly after the death of plant-hoppers (moribund when collected) were independent hyphae growing out from the host's leg joints and becoming ramified upon contact with the glass slide. As more hyphae grew out from the host's legs and ventral part of the abdomen, they became interlaced and formed a PLS. This is the invariable rhizoidal structure accompanying the conidial stage of *E. planchoniana*, and the cases described above ended with *E. planchoniana* conidiation (Ben-Ze'ev, unpublished), until then unknown in insects other than aphids (Ben-Ze'ev et al., 1981). Similar observations on rhizoid formation were carried out on houseflies artificially inoculated with *Erynia radicans* (A. Uziel, unpublished; partially described by Ben-Ze'ev and Uziel, 1979) and on alfalfa weevil larvae dying with *E. phytonomi* (partially described by Ben-Ze'ev and Kenneth, 1980). The following behavior was observed in all cases: groups of hyphae grew out from the ventral part of the thorax and leg joints of adult houseflies. Most hyphae in a group grew synchronously, tightly appressed and parallel to each other, the group as a whole having a tubular shape. The pseudorhizomorph of *E. phytonomi* observed in formation was sheet-like (Ben-Ze'ev and Kenneth, 1980, Fig. 4), but tubular ones were observed and photographed by Wallis (1972). Upon contacting the substrate, most hyphae in a group started a profuse, synchronous branching and interlacing, the growth ending with the formation of the characteristic holdfast. The main differ-

ence between pseudorhizomorphs and PLS appears to be, apart from the morphological one, the synchronous control of development in the pseudorhizomorph, in contrast to the independent behavior of each hypha in the PLS.

Evolutionary trends in the ENTOMOPHTHORALES, as well as in any other group of organisms, should be the base for any attempt of a phylogenetically based classification. Since a fossil record for this order is not available, the next reasonable approach would be to infer from what is known as the generally accepted evolutionary trends in the ZYGOMYCETES: "...Asexual evolution appears to have gone from multispored sporangia, to reduced number of sporangiospores, to one-spored sporangiola where the sporangial wall is distinct from the sporangiospore wall, to forms on which it is difficult to demonstrate the two walls except with special techniques" (Hesseltine and Ellis, 1973). Other evolutionary trends in the ENTOMOPHTHORALES, believed to have taxonomic importance, are the reduction in the number of nuclei in the hyphal bodies and in the conidia, from multinucleate to paucinucleate, to tetranucleate and uninucleate - the last nuclear condition being related to the development of branched conidiophores in some genera (Riddle, 1906; Batko, 1974). In the light of these evolutionary trends, we attempt below first a classification of features-criteria, followed (in the next chapter) by a classification of taxa.

2. Features-Criteria for the Generic Level.

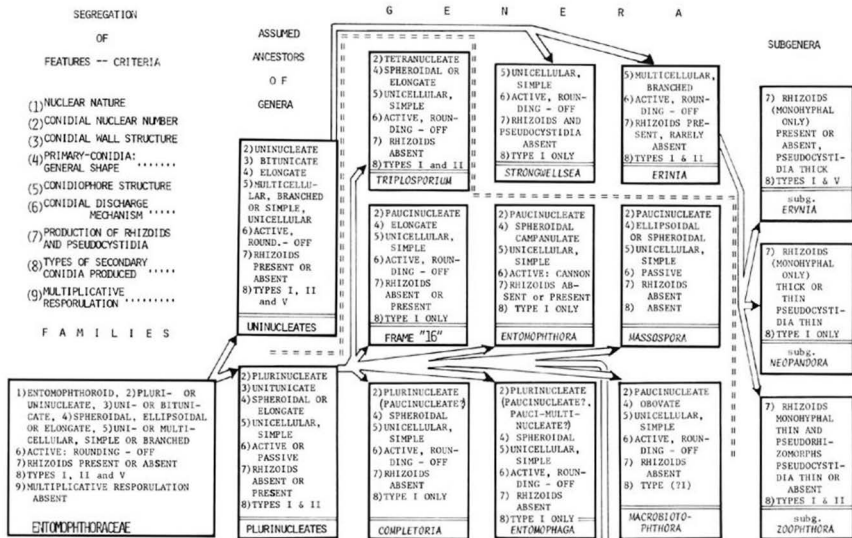
THE NUCLEAR NUMBER AND WALL STRUCTURE OF PRIMARY CONIDIA. - The early students of ENTOMOPHTHORACEAE were impressed by the apparent correlation found in some species between branched conidiophores and the presence of rhizoids in contrast to simple conidiophores and lack of rhizoids. It was this correlation between two features-criteria, which taken together were used to segregate *Entomophthora* Fres. 1856 into two genera (Brefeld, 1877; Nowakowski, 1883) or two subgenera (Thaxter, 1888). The subsequent finding of species with simple conidiophores, but possessing rhizoids, and the observation that some species with simple conidiophores have also some slightly ramified ones caused Thaxter (1888) to de-emphasize both features-criteria from generic to subgeneric rank. Nowakowski (1883) and Lakon (1919) interpreted these findings differently and employed the new genus *Lamia* Nowak. for species with simple conidiophores and rhizoids. Cavara (1899a, b), Riddle (1906) and Batko (1964b, c, d) found that branched conidiophores were

associated with uninucleate, bitunicate conidia and with the invariable presence of rhizoids, while simple conidiophores were always associated with multinucleate, unitunicate conidia, but not always with the absence of rhizoids*. This correlation between the structure and function of the primary conidiophore and the nuclear number and wall structure of the primary conidia is the most obvious in the ENTOMOPHTHORALES. The nuclear number divides the order into groups larger than the genera accepted even by the most collective classification: uninucleate vs. plurinucleate**. The addition of conidial wall structure and conidiophore structure and function enhances a further division, into the generic groups emerging from the Batkoo classifications (Batkoo, all references; Remaudière and Hennebert, 1980; Remaudière and Keller, 1980; Ben-Ze'ev, 1980; Ben-Ze'ev and Kenneth, 1981a; Humber, 1981a, b; Humber and Ben-Ze'ev, 1981; Tucker, 1981). Because of this "division in steps" it seems likely that segregation of the nuclear number in the cells (or hyphal bodies) and in the conidia was one of the early steps in the evolution of this order, probably accompanied and certainly followed by the segregation of conidial wall structure and conidiophore structure (Fig. 2).

THE STRUCTURE OF THE PRIMARY CONIDIOPHORES is complex, the usual characterizations "*conidiophores simple*" and "*conidiophores branched*" being an oversimplification (see also Humber, 1981a). The "simple" conidiophores, even when ramified to possess 2-3 branches, remain unicellular, coenocytic structures. The "ramified" conidiophores, even when poorly branched, are pluricellular structures divided by septa, so that terminal, conidiogenous cells are usually uninucleate, the other, non-conidiogenous cells having one to several nuclei. The complexity is increased when considering the usually unramified, but pluricellular conidiophores of *Meristacrum* Drechsler (1940) and *Tabanomyces* Couch *et al.* (1979), or the coenocytic, indeterminate conidiophores of *Ballocephala* Drechsler (1951) and *Zygnemomy-*

* These authors obviously did not consider the saprobic genus *Basidiobolus* and the (unknown then) entomogenic *Strongwellsea*, neither were they aware of species with ramified conidiophores, and bitunicate, uninucleate conidia, that lacked rhizoids.

** Meaning: more than one nucleus/conidium and including all the other 'multinucleate', 'paucinucleate' and 'tetranucleate' categories as defined on p. 426.



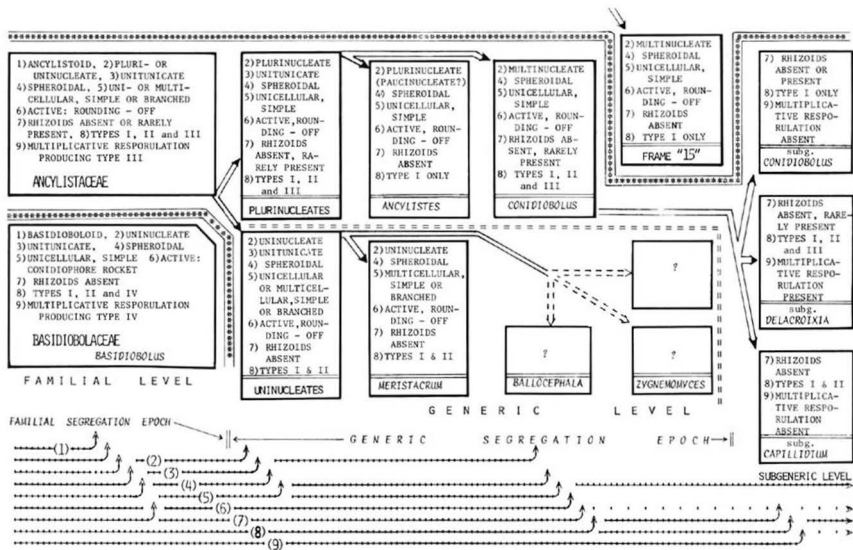


FIG. 2 A tentative scheme of evolution and phylogeny in the ENTOMOPHTHORALES.

ces Miura (1973), which produce uninuclear conidiogenous side branchlets. The sometimes ramified conidiophores of *Meristacrum* are not homologous to these of the uninucleate, bitunicate genera of ENTOMOPHTHORACEAE; they are better interpreted as a septate (multicellular, uninucleate) version of the sometimes ramified, unicellular conidiophores of the multinucleate genus *Conidiobolus*.

Fig. 2 shows a tentative scheme of evolution in ENTOMOPHTHORALES, based on the concept that certain ancestral features found in some taxa were partially lost along the way in other taxa and totally lost in still others, while new features were acquired by some taxa during different periods of their evolution. Definitions of the genera in this scheme are derived from proposals (Ben-Ze'ev, 1980; Ben-Ze'ev and Kenneth, 1979; 1981a) to consolidate Batko's (1964b, c, d, e; 1966a, b; 1974) classification. First, genera were defined solely by the four features-criteria that appeared to be most obviously correlated: the nuclear number and wall structure of the primary conidia and the structure and function of the primary conidiophores. According to these definitions, *Entomophthora*, in the collective sense, appeared as unacceptably heterogeneous, while most genera included in Batko's classification (see list in Fig. 1) appeared as well defined natural groups. By stripping Batko's generic definitions from all, but the four abovementioned criteria, the way was cleared for species devoid of rhizoids to be included into *Zoophthora* (e.g. *Z. erinacea*: Ben-Ze'ev and Kenneth, 1979), for the remaining species of the abandoned *Culicicola* to be transferred to *Entomophthora sensu stricto*, and for all species of *Entomophaga* to be transferred in bulk to *Conidiobolus* (Remaudière and Keller, 1980). However, it soon became apparent* (R. Humber pers. commun. dating 1980, followed by: Humber 1981a, b; 1982b) that according to structural features of their nuclei, the ENTOMOPHTHORALES form three major groups, coinciding surprisingly well with some (generally unaccepted in the past) divisions of this order into three families.

* According to Humber (as referred above; in Humber and Ben-Ze'ev 1981; and cited in Tucker, 1981), the nuclei of *Entomophthora sensu stricto* show heterochromatin, but no visible central nucleolus. Other genera having similar nuclei are therefore included in the family ENTOMOPHTHORACEAE. The nuclei of *Ancylistes*, the type genus of the ANCYLISTACEAE, have a visible central nucleolus, but little or no hetero-

Humber's new criterion did not cut across any of the newly defined genera, except *Conidiobolus* and seemed to be consistent with another group of nuclear characters related to the different mitotic mechanisms found in ENTOMOPHTHORALES (Heath, 1980). Some of the species transferred there from *Entomophaga* by Remaudière and Keller (1980), including the type species, *E. grylli*, were found to possess entomophthoroid* nuclei, in contrast to the ancylistoid* nuclei of *Conidiobolus*. This led Humber (1981a) to confirm the validity of *Entomophaga* and led us to rearrange our scheme (Fig. 2) into familial groups, *Entomophaga*, as redefined (in Humber, 1981a) added to the scheme. This scheme is used here as a model from which we try to infer the probable sequence of evolutionary events that affect those features of ENTOMOPHTHORALES used as taxonomic criteria.

The nuclear number in conidia is related to the nuclear number of the conidiogenous cells. Where the conidiophores are unicellular, their nuclear number is related to that in the hyphal bodies, whereas in multicellular conidiophores the nuclear number in the individual cells seems to depend on the nuclear number in the hyphal bodies and on some kind of control related to the septation and restriction of nuclear number in each cell. According to the scheme in Fig. 2, these related features have possibly started to segregate during the epoch of family segregation, their most obvious segregation taking place during the epoch of generic segregation--being at the base of the two major groups found in both ENTOMOPHTHORACEAE and ANCYLISTACEAE: the 'uninucleates' and the 'plurinucleates'. This segregation seems to have continued within the plurinucleate ENTOMOPHTHORACEAE, producing the 'multinucleates', 'paucinucleates' and 'tetranucleates'. Another possible evolutionary sequence that cannot be excluded is a gradual reduction in nuclear numbers in the ENTOMOPHTHORACEAE, with the 'uninucleates' being the last segregated ones, from plurinucleate ancestors similar to *Triplosporium* or to the paucinucleate species with elongate conidia, like *E. caroliniana*. The association

* (cont'd) chromatin and are usually smaller than entomophthoroid ones. The nuclei of *Basidiobolus* (BASIDILOBOLACEAE) are the largest in ENTOMOPHTHORALES, with a visible central nucleolus and clear nucleoplasm (basidioboloid nuclei). All further mentions of nuclear nature in the genera of ENTOMOPHTHORALES are related to the abovementioned references. The nucleoli of entomophthoroid nuclei are visible with fluorescence microscopy (Dr. D. Tyrell - pers. comm.).

of simple, unicellular conidiophores with spheroidal, plurinucleate conidia shows the strongest correlation throughout this order and therefore appears to involve two ancestral features. The association of multicellular conidiophores (ramified in some genera in both ENTOMOPHTHORACEAE and ANCYLISTACEAE) with uninucleate conidia (bitunicate, in one genus of ENTOMOPHTHORACEAE) shows a similarly strong correlation, but being found in fewer generic groups, is regarded as new, both features being considered as derived from the ancestral ones.

In the ANCYLISTACEAE the evolution of these two associated features seems to have gone from the simple, unicellular conidiophores and plurinucleate conidia of *Ancylistes* and *Conidiobolus* toward the simple, unicellular conidiophores of *Zygnemomyces* Miura emend. Tucker (Miura, 1973; Tucker, 1981) which produce several conidia (? uninucleate) each on a conidiogenous pedicel unseparated by septum from the conidiophore - to the multicellular conidiophores of *Ballocephala*, composed of a multinucleate stem and uninucleate side branchlets (conidiogenous cells), each producing one uninucleate conidium - to the multicellular, sometimes ramified conidiophores of *Meristacrum*, in which each uninucleate conidiogenous cell produces a uninucleate conidium.

In the ENTOMOPHTHORACEAE six genera and two generic frames ("15" and "16"), assumedly derived from the entomophthoraceous 'Plurinucleates' (Fig. 2) have unicellular simple conidiophores associated with plurinucleate conidia, while the largest genus, *Erynia* Nowakowski emend. Humber & Ben-Ze'ev (Nowakowski, 1881; Humber and Ben-Ze'ev, 1981) has multicellular, ramified conidiophores associated with uninucleate, bitunicate conidia. The exception in this family is the genus *Strongwellsea*, which produces uninucleate, bitunicate, *Erynia*-like conidia, on unicellular, simple, mostly uninucleate conidiophores. It appears most likely that *Strongwellsea* evolved from an erinaceous ancestor and that its simple conidiophores are the product of a further nuclear reduction in its hyphal bodies (see Humber, 1982a).

In the BASIDIOLACEAE (monogenic at present)* the co-

* A possibly new genus with basidioboloid nuclei being studied by R. Humber (pers. comm.).

nidiophores are unicellular, simple, uninucleate, each producing one uninucleate conidium.

The structure and function of the conidiophores (in conidiogenesis and control of the nuclear number in conidia) appear to have completed their evolution during the epoch of generic segregation; there are no different types of conidiophores within any of the genera accepted here, therefore this feature is considered as a valid and useful one at the generic level.

THE MECHANISM OF CONIDIAL DISCHARGE is another feature of the conidiophore function. There appear to exist two categories of conidial discharge in ENTOMOPHTHORALES: a) passive secession--as in the capilliconidia of those species that produce them and in the microspores of *Basidiobolus microsporus*. Seemingly different evolutionary paths are responsible for the passive secession of primary conidia in *Massospora* (Humber, 1982a; and pers. comm.) and in *Zygnemomyces* (Tucker, 1981); b) forcible discharge--as in the majority of primary and secondary conidia of this order. However, the mechanism of forcible discharge, driven by hydrostatic pressure built up in the conidiophore and conidium, appears to be one of the ancestral features of ENTOMOPHTHORALES and to have evolved in three or four different ways: 1) "Rounding off or papilla eversion"* in which both the conidiophore and the conidium have a high turgor pressure and play an active role in discharge. This way of conidial discharge is characteristic for most genera of ENTOMOPHTHORACEAE and ANCYLISTACEAE and is still present in a certain degree in *Basidiobolus* (BASIDILOBOLACEAE). 2) "Sporophore cannon"* in which the conidium, apparently less turgid than the conidiophore, is discharged and carried away by a stream of water and cytoplasm erupting through a rupture at the conidiophore tip. This kind of conidial discharge is characteristic for a small group of related species belonging to *Entomophthora* Fres. *sensu stricto* (*sensu* Batko, 1964b; *sensu* Remaudière and Keller, 1980). 3) "Sporophore rocket"* in which the conidiophore is ruptured as well, though not at its tip as in *Entomophthora*, but along a circumcissile ring located below the "subconidial bulb"* (which is the inflated, upper part of the conidiophore). Following rupture, the pressurized sap erupts downward, sending the subconidial bulb "...flying off on the recoil rocketwise with spore. In flight the contracted subconidial bulb usu-

Terms coined by Ingold (in different publications) and cited by Ingold (1966), Humber (1981a) and Tucker (1981).

ally separates from the conidium" (Ingold, 1966). In fact, it is the conidium that separates from the subconidial bulb, by everting its papilla against the bulb. This kind of conidial discharge is known only from the genus *Basidiobolus*, and as described above, papilla-eversion is part of it. Another discharge mechanism, practically similar to the sporophore rocket, occurs in *Ballocephala* (ANCYLISTACEAE). In this genus each conidium is produced upon a conidiogenous cell, which is practically a short, one-celled side branch, divided by a septum from the otherwise straight, unseptated conidiophore. At maturity, each conidiogenous cell ruptures near its base, its pressurized sap sending it, together with the attached conidium, flying away from the conidiophore. This mechanism differs from the *Basidiobolus* "rocket" mainly by the lack of papilla eversion during flight, since there is no columella in *Ballocephala*, the conidium being divided by a septum from its conidiogenous cell and remaining attached to its remnants after discharge. Tucker (1981), aware of the similarity between the last two discharge mechanisms, sustains Drechsler's (1951) hypothesis that in *Ballocephala* the primary conidium was reduced to a conidiogenous cell firmly attached to the conidiophore, the actual conidium being a secondary one. Based on this hypothesis, Tucker (1981) proposes the *Ballocephala* discharge mechanism as the fourth way in which the basic forcible discharge mechanism of ENTOMOPHTHORALES has evolved. However, if Drechsler's hypothesis reflects reality, the discharge mechanism of *Ballocephala* is not a version of forcible discharge, but is totally different: a secondary-conidial-discharge mechanism, superimposed upon a degeneration of the primary conidium resulting from the degeneration of its own discharge mechanism.

Passive vs. active discharge mechanisms of primary conidia were considered features-criteria of generic importance, conferring on *Massospora* its independent generic status even in the collective classifications (e.g. Waterhouse, 1973). The difference between the two ways of active discharge in the ENTOMOPHTHORACEAE (rounding-off vs. sporophore cannon) was considered as a generic feature-criterion by most authors of Batkoan classifications (Batko, 1964b; Remaudière and Keller, 1980; Humber, 1981a). Ben-Ze'ev (1980) considered only the passive vs. active discharge of primary conidia to be of generic importance - on the grounds that the different active discharge mechanisms are basically turgor pressure and enzymatic secession of the conidiophore wall. According to our views on weighing criteria, conidial dis-

charge seems to have completed its evolution during the generic epoch, except in *Entomophthora*, the genus for which discharge by 'conidiophore cannon' is considered by above-mentioned authors as a generic criterion. Four of the six species classified here in this genus were found to discharge their secondary conidia by rounding-off: *E. muscae* (Ingold and Plunkett, 1979), *E. thripidium* (Samson et al., 1979), *E. culicis* and *E. planchoniana* (Ben-Ze'ev and Kenneth, unpublished). Moreover, *Entomophthora dysderci* (Viegas) MacLeod & Müller-Kögler 1973, a species with a nuclear number of 17-20/conidium, obviously not an *Entomophthora* s. str., discharges its primary conidia by 'conidiophore cannon', while all the other known species with the same nuclear number and simple, unicellular conidiophores employ rounding-off for the discharge of their primary conidia. For the time being, all arguments for and against considered, we remain undecided about the absolute value of variations in forcible discharge (i.e. rounding-off vs. conidiophore cannon) as a generic feature-criterion, with an inclination to accept it when more is known about it. Active vs. passive discharge is considered as a fully important generic criterion.

PRODUCTION OF RHIZOIDS AND PSEUDOCYSTIDIA is quite closely correlated to multicellular, branched conidiophores and to bitunicate, uninucleate conidia, and was therefore used as a feature-criterion characterizing the genus *Entomophthora* Nowak. However, its correlation with some species possessing unicellular, simple conidiophores and plurinucleate, unitunicate conidia currently classified in *Entomophthora* Fres. sensu stricto and in *Conidiobolus* (Remaudière and Keller, 1980), as well as its absence from some species with multicellular, branched conidiophores and uninucleate, bitunicate conidia, shows that the production vs. non-production of rhizoids and/or pseudocystidia are characters which have not been segregated completely when the other features-criteria of generic importance did. On the other hand they continued to segregate afterwards, within the already formed generic groups. Such a segregation pattern excludes rhizoidal and pseudocystidial production from the generic level features-criteria (see Fig. 2 and also Humber, 1981a).

Differentiated pseudocystidia exist only in some species of one frame of the ENTOMOPHTHORACEAE, this feature seemingly being a rather new one, possibly evolved by modification of rhizoidal initials. This assumption is based on the presence of true pseudocystidia in the genus endowed

with the most frequent occurrence of rhizoids, *Erynia*, and on the similarity found in this genus, between rhizoidal and pseudocystidial initials (hyphal bodies) (see Ben-Ze'ev and Uziel, 1979; Ben-Ze'ev and Kenneth, 1981b). Moreover, we assume that both rhizoids and pseudocystidia are modifications of conidiophores. In entomophthoralean species devoid of rhizoids and pseudocystidia, the conidiophores have to penetrate the host's cuticle before producing and discharging conidia. Both rhizoids and pseudocystidia fulfill this function in species possessing them. It appears 'biologically reasonable' that the evolution from unicellular, simple conidiophores to multicellular, ramified ones, went through a stage of producing both kinds in one species. The multicellular, ramified ones, being more efficient in conidial production (many conidia/conidiophore), enabled the simple ones to evolve into pseudocystidia by gaining more enzymatic activity on the expense of conidial productivity. A similar evolutionary scenario could apply to pseudocystidia being derived from monohyphal rhizoids in species with large numbers of the latter, in which pseudocystidia are indeed frequent.

THE SHAPES OF PRIMARY CONIDIA served as distinguishing features in the catalogues of ENTOMOPHTHORACEAE, in identifying species (Hutchison, 1963; MacLeod and Müller-Kögler, 1973; MacLeod *et al.*, 1976) and recently served as a generic criterion in the classification of Remaudière and Keller (1980). In the ENTOMOPHTHORACEAE conidial shape was apparently segregated between its two main groups of genera (Fig. 2), the elongate form going with the uninucleate bitunicate conidia and the generally spheroidal* form going with the multinuclear, unitunicate conidia. However, this segregation was obviously not completed then -- at least one species, *Entomophthora carpentieri* Giard (Turian, 1957) was reported to possess branched conidiophores, rhizoids characteristic to *Erynia* subgen. *Zoophthora* (Ben-Ze'ev and Kenneth, 1982) (*Zoophthora* subgen. *Zoophthora* Batko, *sensu* Ben-Ze'ev and Kenneth, 1981a) and spherical, uninucleate conidia. At least five species of the plurinucleate group produce elongate conidia: *Triplosporium fumosum* (Speare) Batko (Speare, 1922; Batko 1964e), *Entomophthora lecanii* Zimmermann (1901), *E. turbinata* Kenneth (1977), *E. carolin-*

* Meant here to include globose and nearly globose conidia like those described as broad-pyriform or those of Lakon's (1919) *truncata-campaniformis* and *truncata-lageniformis* types.

iana (Thaxter) Keller (1978) and a yet unnamed species discovered recently by Bałazy (1978b; see also Humber, 1981a). Another plurinucleate genus is *Massospora*, comprising species with different conidial shapes (Soper, 1981). The continued segregation of conidial shape, inside the generic frames based on conidiophore structure and function and on conidial karyology and wall structure, strongly argues against the use of this feature-criterion at the generic level. Undoubtedly, conidial shape is correlated with the other generic-level features-criteria, but the correlation is not strong enough and is therefore of lower taxonomic (and predictive) value. In all genera of ENTOMOPHTHORACEAE discussed in the next chapter, a certain conidial shape appears to be characteristic for each genus. However, any genus with more than six recognized species has its exceptions from the 'conidial shape rule', one or more species having conidia with 'uncharacteristic' shape. For these reasons conidial shape is a feature, but not a generic criterion.

PRODUCTION OF SECONDARY CONIDIA other than Type I was used in the ENTOMOPHTHORALES in the past to characterize the genus *Delacroixia* Saccardo & Sydow (1899, quoted by Tyrrell and MacLeod, 1972). Recently Remaudière and Hennebert (1980) used this as the principal feature-criterion for separating *Zoophthora* Batko into *Zoophthora* Batko sensu stricto (species producing capilliconidia) and *Erynia* Nowak (species without capilliconidia). The production of different kinds of secondary conidia and the singular vs. multiplicative patterns of resporulation are undoubtedly ancestral features in the ZYGOMYCETES, possibly dating before the segregation of ENTOMOPHTHORALES and ZOOPAGALES, as shown by the resporulation ability and the striking resemblance of capilliconidia found in both orders. The segregation of these features-criteria in the ENTOMOPHTHORALES probably began when the family ancestors segregated, since Types I, II and III of secondary conidia were so far found in *Conidiobolus*; Types I, II and IV in *Basidiobolus*, but only Types I and II in the ENTOMOPHTHORACEAE, the multiplicative feature being apparently absent in this family. However, these features-criteria seem to have continued their segregation along most of the evolutionary stages, various patterns of production being present in otherwise congeneric species. Certain species of *Conidiobolus* produce Types I and II secondary conidia, others produce Type I and III, most of them produce Type I only. A similar segregation is apparent in *Basidiobolus* and in *zoophthora* sensu Batko, whereas other

genera are homogeneous for types and patterns of secondary conidia production. Again, the continued segregation of these features, producing sub-groups in otherwise homogeneous genera, excludes them from the generic-level group of features-criteria.

THE OCCURRENCE AND TYPE OF RESTING SPORES (zygospores vs. azygospores) were used as features-criteria at the generic level, as characterizing the genera *Tarichium* Cohn (lack of conidia, production of azygospores), *Erynia* Nowakowski (1881) (zygospores), *Entomophthora* Nowak. (1883) (azygospores), *Entomophaga* Batko (differentiated from *Conidiobolus* by the relationship between the resting spores and gametangia: Batko and Weiser, 1965), *Triplosporium* (Thaxter) Batko (isogamous production of elliptical zygospores). Remaudière and Keller (1980) and Humber (1981a) have explicitly de-emphasized the importance conferred to the resting-spore-linked features. Humber (1981a) notes that unless more is known about karyologic events during the initiation, formation and germination of resting spores, the term "zygospore" and "azygospore" may mislead, and classification according to these features is impossible in species with unknown resting spores. Moreover, species in which apparent conjugation of hyphal bodies produce zygospores and species apparently producing azygospores are sometimes congeneric, if to judge by the other generic-level features criteria, making this criterion to appear as continuing its segregation inside generic groups and therefore unacceptable at the generic level.

PARASITISM VS. SAPROPHYTISM was considered until recently a generic-level criterion for segregating *Entomophthora* sensu lato from *Conidiobolus* (MacLeod, 1963; cited by King, 1976a) and from *Basidiobolus*. Some insect parasitic species were recently transferred from *Entomophthora* s. l. to *Conidiobolus*: *C. coronatus* by Batko (1964a) and by Srinivasan and Thirumalachar (1964), *C. pseudococci* by Tyrrell and MacLeod (1972) and a series of 11 species by Remaudière and Keller (1980), while a few *Conidiobolus* species originally described as saprobes were found to be pathogens of insects: *C. osmodes* Drechsler (1954) pathogenic to aphids (Remaudière et al., 1976b; Papierok and Coremans-Pelseneer, 1980) and to COLEOPTERA larvae (Ben-Ze'ev and Kenneth, 1980) while *C. thomboides* Drechsler proved to be the earlier and valid name of the pathogen *Entomophthora virulenta* Hall & Dunn (Latgé et al., 1980). These findings exclude parasitism vs. saprophytism, as a feature-criterion, at the generic level (see also King and Humber, 1981; Humber,

1982a-b). The genera *Ancylistes* Pfitzer 1872 emend. Berdan (1938) and *Completozia* Lohde 1874 (quoted by Berdan, 1938) are segregated from the other ENTOMOPHTHORALES by their specialized parasitism in plants (algae and ferns, respectively) and by the familial and generic features-criteria discussed and accepted here at these levels (Tucker, 1981).

To summarize, the only features-criteria we find as important at the generic level are the structure and function of the primary conidiophores (with some reservations about the mechanisms of forcible conidial discharge) and the nuclear number and wall structure of the primary conidia. Since these features appear to be correlated with the hyphal bodies which produce conidiophores, it seems logical to look for more generic features connected with the cytology and structure of the latter, such as the relative number and spatial distribution of nuclei in hyphal bodies, as noted by Riddle (1906), in order to establish additional generic criteria.

3. Features-Criteria for the Subgeneric Level.

Genera, well defined by carefully weighed features-criteria, appear sometimes to be comprised of clusters of species, each cluster being characterized by features shared only by its members but not by the other congeneric species. Subgenera are justified when characterized by features as mentioned above, these features being by definition of a lower than generic status. Such features are usually too general to allow distinction between species and are therefore of an intermediate status, between the generic and the specific ones -- they are subgeneric features-criteria.

Thaxter (1888) was apparently the first to use subgenera in his classification of ENTOMOPHTHORALES, although he used the same features-criteria as Nowakowski (1883) had previously employed at the generic level (Fig. 1).

Batko and Weiser (1965) proposed the subgenus *Lichia* for the rhizoid producing species of *Entomophaga*. This subgenus has neither been validated by Latin description, nor has it been validly used for any named species. However, this subgenus was obviously proposed in order to eliminate the heterogeneous genus *Culicicola* (Batko, 1964d), originally based mainly on rhizoid production, from the Batkoan classification. According to the description of *Entomophaga* (Batko, 1964c) and the characters attributed to its subgenus *Lichia* (Batko and Weiser, 1965 - Table 1) only four species fitted this taxon: (1) '*Entomophaga (Lichia)*

destruens Weiser & Batko * originally intended as the subgeneric type, two species formerly placed by Batko (1964e) in *Culicicola*: (2) *Empusa papillata* Thaxter, (3) *E. apiculata* Thaxter, and (4) *E. apiculata* var. *major* Thaxter, apparently overlooked by Batko (1964e). *E. destruens* appears from its description (cited in MacLeod and Müller-Kögler, 1973) and from its multinucleate (70-140 nuclei/conidium) conidia with very small nuclei (figured in an unquotable information document issued in April 1981 by the World Health Organization) to be a species of *Conidiobolus*. This opinion is also shared by other authorities (R. Humber and R. Soper, pers. comm.). The last three species were transferred to *Conidiobolus* by Remaudière and Keller (1980). According to Humber (1981a) their nuclei are ancylistoid as these of *Conidiobolus*, but their production of rhizoids and neck-like constriction of their conidiophore tips might entitle them to a subgeneric status within *Conidiobolus* or even to an independent, closely related genus.

Batko (1966b) employed the external and cytological structure of conidia, rhizoids and pseudocystidia as subgeneric features-criteria in his genus *Zoophthora*, employing the ability to produce capillispores as a less important, descriptive feature. According to these criteria he divided *Zoophthora* in four subgenera (Figs. 1 and 3; see also Ben-Ze'ev and Kenneth, 1982).

Tyrrell and MacLeod (1972) proposed the subgenus *Delacroixia* based on the ability for multiplicative resporulation (occurrence of Type III secondary conidia [microconidia]) as found in 10 *Conidiobolus* species. They also noticed a certain pattern of fatty acids production, characteristic for these microconidial species. King (1976b) found similar correlations between the ability to produce microconidia and certain biochemical/nutritional abilities and requirements, and his results show that in another group of *Conidiobolus* species, the production of capilliconidia was correlated to a different set of biochemical abilities and requirements. Although King's (1976a) results provided further evidence for the justification of subgen. *Delacroixia*, he (King, 1976b) was undecided, criticizing Tyrrell and MacLeod's (1972) proposal, but admitting that such correlations "...appear to indicate the validity of such a [sub-

* Mentioned under this name in the REFERENCES of Batko and Weiser (1965) and subsequently published under the name *Entomophthora destruens* Weiser and Batko (1966).

generic] *subgrouping...*".

Our analysis of features-criteria evolution and segregation (Fig. 2) shows that the following continued to segregate during and after the formation of the contemporary genera:

- 1) Production and structure of rhizoids and pseudocystidia.
- 2) Morphology of primary conidia.
- 3) Production of different types of secondary conidia, including the ability for multiplicative resporulation.

These features-criteria had to be excluded from use at the generic level because of their continued segregation, but are too general to allow species identification. They do delimit smaller, distinct groups of species within different generic groups. Accordingly they qualify for subgeneric rank. Patterns of biochemical abilities and requirements seem to have an equal importance as subgeneric features in *Conidiobolus*. However, such features are still unknown in the other genera. We believe that existing, validly published subgenera characterized by these subgeneric criteria have to be accepted, and additional subgenera should be delimited whenever genera of ENTOMOPHTHORALES are intersected by these features-criteria. However, subgeneric features-criteria remain descriptive features (but not criteria) for their genera. There seems to be very little taxonomic reason to divide genera comprised of a few species only, even when subgeneric features-criteria intersect them.

4. Features-Criteria for the Species Level.

Species sharing subgeneric and generic features still differ from one another in many other distinct features.

THE DIMENSIONS OF PRIMARY CONIDIA AND CAPILLICONIDIA were shown by Remaudière *et al.* (1976a) to be precise quantitative and qualitative features-criteria at the species level in some species of the "*sphaerosperma* group" (= *Zoophthora* sensu Remaudière and Hennebert, 1980; = *Erynia* subgen. *Zoophthora* sensu Ben-Ze'ev and Kenneth, 1982). Genera producing elongate primary or secondary conidia are advantageous for the taxonomist in this respect, since they display three quantitative features-criteria of the species level:

- 1) Conidial length
- 2) Conidial diameter

3) Conidial length/diameter (l/d) ratio.

However, much confusion existed in the so called "*sphaerosperma* group" (named by Thaxter, 1888) because of the close resemblance between primary and secondary (similar, but smaller Type Ia) conidia. Statistical analyses of conidial measurements performed on pure populations of primary conidia, secondary (Type Ia) ones, and mixtures of both have shown that in many species of this group the conidial length and diameter behave as normal variables, forming symmetrical normal distribution curves. These curves are characteristic for, and facilitate distinction between primary and secondary (Type Ia) conidia, even in mixed populations (Ben-Ze'ev, 1980). Having thus solved the problem of distinction between the two kinds of conidia (previously mentioned by many authorities as similar in shape, differing only in dimensions), precise measurements can be made separately of primary and secondary (Type I) conidia and the dimensions of the latter can be added as features-criteria for the specific level (Ben-Ze'ev, 1980; Ben-Ze'ev and Kenneth, 1979, 1980, 1981b; Ben-Ze'ev and Uziel, 1979). Being aware that old descriptions of species might have been biased by including secondary (Type Ia) conidial dimensions in those given for the primary conidia, new descriptions should include precise dimensions of all kinds of conidia produced by a certain species. Humber (1976) warns that the conditions of microscopic preparation and mounting (e. g. in water vs. lactophenol; applying heat to the preparation, etc.) may cause significant changes in the conidial dimensions measured, therefore preparation conditions should be described as well.

In some genera with spheroidal conidia different species have morphologically similar conidia, displaying large overlappings of conidial dimensions, with the range being very wide.

BIOCHEMICAL FEATURES. Finding that conidial dimensions were unuseful in species with spheroidal conidia, Remaudière *et al.* (1979) employed fatty-acids analysis, resting spore dimensions, relative virulence and cultural characters. Their conclusions were that fatty-acids content is a reliable specific-level feature-criterion, whereas resting spore dimensions may be similar in different species; cultural characters and relative virulence had to be excluded as well, since they differed in otherwise conspecific isolates. The study of Remaudière *et al.* (1979) dealt with species now recognized as belonging in *Conidiobolus* (Remau-

dière and Keller, 1980; Humber, 1981a). Similar conclusions, however, were drawn about cultural characters (*i.e.*: growth rate in culture, optimal temperatures for growth and sporulation, and production or non-production of resting spores) in species belonging to a different genus and family, *Erynia* (ENTOMOPHTHORACEAE) by Ben-Ze'ev (1980 and unpublished data). Moreover, production vs. non-production of resting spores had to be de-emphasized at this level since species previously thought to be devoid of resting spores, such as *Erynia phalloides* (Batko) Humber & Ben-Ze'ev (Batko, 1966; Remaudière *et al.*, 1976a) were shown to produce them in culture (Ben-Ze'ev, 1980), while Israeli isolates of *E. occidentalis* (Thaxter) Humber & Ben-Ze'ev did not produce resting spores in culture and apparently neither in nature, despite findings of resting spores of this species elsewhere (Thaxter, 1888; Mietkiewski *et al.*, 1981).

PRODUCTION VS. NON PRODUCTION OF RHIZOIDS, although considered as part of the subgeneric features-criteria, appears to have continued its segregation within subgenera comprised of otherwise very closely related species. The structure of rhizoids is a feature permitting distinction between the subgenera of *Erynia* (Ben-Ze'ev and Kenneth, 1982), however, *Erynia delphacis* (Hori) Humber 1981 is distinguished from *E. neoaphidis* Remaudière & Hennebert 1980, both belonging to subgen. *Neopandora*, by the lack of rhizoids in *E. delphacis*, combined with other species-level features. The apparent continued segregation of rhizoidal production is therefore more helpful as a feature-criterion at the specific level than at the subgeneric one.

HOST RANGE AND HOST-PATHOGEN RELATIONS such as virulence toward different (invertebrate) hosts or non-hosts have to be very carefully considered, since some species show narrow host-specificity while other show wide host-ranges. These features can be useful at the species level for distinguishing between species for which a large amount of information was accumulated (*e.g.*: *E. neoaphidis* vs. *E. delphacis*), but not for newly discovered or rare species.

To summarize, the features-criteria found by us as useful for the classification at the specific level are:

- 1) qualitative (shape) and quantitative (statistical distribution of dimensions) morphological features of all kinds of conidia, resting spores and other propagules,
- 2) qualitative and quantitative morphological features of hyphal bodies, conidiophores, rhizoids and pseudocystidia

- as well as the very production of the last two structures,
- 3) qualitative and quantitative biochemical characters (although some differences exist between conspecific isolates -- see May *et al.*, 1979), and in a more restricted way:
 - 4) host range and host-pathogen relations.

PROPOSED FRAMES OF GENERA AND SUBGENERA IN THE ENTOMOPHTHORALES: NOMENCLATURE AND CLASSIFICATION

This work was originally intended to detail the taxonomic reasons supporting a classification of ENTOMOPHTHORALES (Ben-Ze'ev, 1980; Ben-Ze'ev and Kenneth, 1981a) published with brief explanations only and placing all genera in one family. However, we realize that in the light of recently found familial-level criteria (Humber, 1981a; 1982b and pers. commun.; see also Tucker, 1981) the genera of ENTOMOPHTHORALES are better classified in three families (see footnote on page 412).

The following description of generic frames attempts to demonstrate that any known or new species can be classified, according to the generic features-criteria discussed in the previous chapter, into one of the genera accepted here, or placed into a new generic frame, by using the same criteria and possible new ones in a modular way. The four features-criteria considered by us as important at the generic level are symbolized by initials: Conidial-wall structure = CW; Conidial nuclear number = CNN; Conidiophore structure = CS; Conidiophore function in conidial discharge = CD. Each of these features has two general states: CW can be unitunicate or bitunicate; CNN can be plurinucleate or uninucleate; CS can be unicellular or multicellular; CD can be active or passive. We listed the state considered as ancestral first, the one considered as derived - second. They are represented respectively by the Roman numerals I or II. The last three criteria have a second degree of complexity: CNN-I can be multinucleate (>20 , usually ~ 50 or more nuclei/conidium) symbolized by 'm'; paucinucleate (after Remaudière and Keller, 1980; = a varying number of nuclei/conidium, sometimes falling to 1, frequently 2-8, usually not exceeding 12) symbolized by 'p'; some species show a conidial nuclear number of 10-20, sometimes slightly exceeding 20 nuclei/conidium - this condition being best symbolized by 'p-m' (pauci-multinucleate); tetra-

nucleate (conidia regularly having four nuclei each) = 't'. Conidiophore structure, besides being uni- or multicellular, can be simple - 's', or branched - 'b'. Conidial discharge I (active) has also a second degree of complexity (less emphasized by us as a generic criterion): rounding-off - symbolized by 'a'; conidiophore cannon - 'b'; conidiophore rocket - 'c'. Last but not least, the nuclear nature, showing the familial affiliation is symbolized by a colon followed by the familial initial: A for ANCYLISTACEAE -: B for BASIDIOLACEAE -: E for ENTOMOPHTHORACEAE.

Subgeneric GROUPS are delimited within the generic FRAMES, by the features-criteria considered to be of subgeneric importance. The groups are symbolized by Arabic numerals, not necessarily analogous to their equivalent in other frames. Production of secondary conidia of Types I and II, and multiplicative resporulation are considered here as ancient features, since they are found in species belonging to all three families. So apparently is rhizoid production, found in two families: ANCYLISTACEAE and ENTOMOPHTHORACEAE. The evolutionary trend emerging from the above is a gradual loss of ability to produce some types of secondary conidia (or rhizoids) and a partial or total loss of multiplicative resporulation.

ANCYLISTACEAE

FRAME (1): (CW)I-(CNN)Im-(CS)Is-(CD)Ia: A

CONIDIOBOLUS Brefeld 1884 (see Table 1, p. 445)

Nuclei ancylistoid; conidia unitunicate, multinucleate; conidiophores unicellular, simple, rarely unicellular slightly branched; conidial discharge active, by rounding-off.

GROUP:

- 1) Type Ia secondary conidia only; multiplicative resporulation absent; rhizoids absent.
- 2) Types Ia + b secondary conidia; multiplicative resporulation absent; rhizoids absent.
- 3) Type Ia secondary conidia only; multiplicative resporulation absent; rhizoids present.
- 4) Types Ia and II secondary conidia (capilliconidia); multiplicative resporulation absent; rhizoids absent.
- 5) Types Ia and III secondary conidia (microconidia) by multiplicative resporulation; rhizoids absent, rarely present.

King's (1976a, b; 1977) study of *Conidiobolus* systematics yielded a better knowledge of this group than available for most other genera of ENTOMOPHTHORALES. Using numerical taxonomy, based on morphological, physiological and behavioral features, he organized the rather complicated list of species, placing some in synonymy, and produced a list of 27 well described and distinct species and four "Possible Additional Species" insufficiently described and unnamed by their authors.

Remaudière and Keller (1980) have transferred eleven species with spheroidal, subspheroidal or pyriform conidia (characteristic to *Conidiobolus*, but not exclusively so) to *Conidiobolus*. Humber (1981a) believes that only four: *C. apiculatus* (Thaxter) Remaudière & Keller, *C. major* (Thaxter) Rem. & Kell., *C. obscurus* (Hall & Dunn) Rem. & Kell. and *C. papillatus* (Thaxter) Rem. & Kell. possess conidioboloid nuclei. Other three (under their previous names): *Entomophaga grylli* (Fres.) Batko, *Entomophthora batkoi* Bałazy (1978a) and *E. gigantea* Keller (1978) possess entomophthorid-like nuclei (Humber, 1981a) and according to the features-criteria advocated here belong in different frames of ENTOMOPHTHORACEAE, while *E. carpentieri* Giard, as described by Turian (1957) is clearly belonging to a totally different frame (and genus), because of its branched conidiophores and pseudorhizomorphs (Ben-Ze'ev, 1980; Humber, 1981a). The remaining three species: *E. conglomerata* Sorokin, *E. tenthredinis* Fres. and *E. tipulae* Fres. were not mentioned in Humber's (1981a) study, probably because their nuclear sizes and structures are unknown (see the section on *Entomophthora nomina provisoria*, p.442).

Following the example set by Tyrrell and MacLeod (1972) we continue to organize the genus *Conidiobolus* into subgeneric groups. Subgenus *Delacroixia* (Sacc. & Syd.) Tyrrell & MacLeod is our Group 5. The original list of 10 species placed by Tyrrell and MacLeod (1972) in this subgenus is modified here by one addition and two name changes due to synonymy, according to King's (1977) study:

<i>Conidiobolus</i> subgen.	Microconidial <i>Conidiobolus</i>
<i>Delacroixia</i>	spp.

<u>Tyrrell and MacLeod (1972)</u>	<u>King (1977)</u>
-----------------------------------	--------------------

- | | | | |
|-----------------------------------|------|-----------|----|
| 1) <i>C. coronatus</i> (Cost.) | | unchanged | 1) |
| Batko 1964 | | | |
| 2) <i>C. pseudococci</i> (Speare) | .. | unchanged | 2) |
| Tyrrell & MacLeod 1972 | | | |

- | | | | |
|--|--------|--|-----|
| 3) <i>C. brefeldianus</i> Couch
1939 | ... | unchanged | 3) |
| 4) <i>C. chlamidosporus</i>
Drechsler 1955 | | = <i>C. firmipilleus</i>
Drechsler 1953 | 4) |
| 5) <i>C. gonimodes</i>
Drechsler 1961 | | = <i>C. incongruus</i>
Drechsler 1960 | 5) |
| 6) <i>C. macrosporus</i> Srin. &
Thirum. 1965 | ... | unchanged | 6) |
| 7) <i>C. megalotocus</i>
Drechsler 1956 | | unchanged | 7) |
| 8) <i>C. mycophagus</i> Srin. &
Thirum. 1965 | }..... | conspecific
= <i>C. mycophilus</i> | 8) |
| 9) <i>C. mycophilus</i> Srin. &
Thirum. 1965 | | | |
| 10) <i>C. polytocus</i>
Drechsler 1956 | | unchanged | 9) |
| | | <i>C. humicolus</i> Srin &
Thirum. 1961 | 10) |

The last species in King's (1977) list was not listed by Tyrrell and MacLeod (1972) in subgenus *Delacroixia* since its ability to produce microconidia was discovered by King several years later. *C. humicolus* is added to *Delacroixia* in this paper. The production of rhizoids by *C. pseudococci* (King, 1977) appears to further diminish the importance of their production, as a feature-criterion for the subgeneric level.

For the species producing secondary conidia of Type Ia + b only, lacking multiplicative resporulation and lacking or possessing rhizoids (Groups 1, 2 and 3) we propose a new subgenus:

Conidiobolus subgen. *Conidiobolus* subgen. nov.
Conidia secundaria primariis similia vel cylindrica, vehementer ejecta. Capilliconidia, microconidia et microsporas desunt. Rhizoidea desunt vel adsunt.

Typus subgeneris: *Conidiobolus utriculosus* Brefeld,
Unters. Ges. Mykol. 6: 37. 1884.

The other species allocated to this subgenus are:

- | | |
|---|--|
| 2) <i>C. adiaeretus</i>
Drechsler 1953; | 5) <i>C. couchii</i> Srin. &
Thirum. 1968; |
| 3) <i>C. apiculatus</i> (Thaxter)
Rem. & Kell. 1980; | 6) <i>C. eurymitus</i>
Drechsler 1965; |
| 4) <i>C. bangalorensis</i> Srin. &
Thirum. 1967; | 7) <i>C. khandalensis</i> Srin.
& Thirum. 1962; |

- | | |
|---|--|
| 8) <i>C. lachnodes</i>
Drechsler 1955; | 13) <i>C. osmodes</i>
Drechsler 1957; |
| 9) <i>C. lamprauges</i>
Drechsler 1953; | 14) <i>C. papillatus</i> (Thaxter)
Rem. & Kell. 1980; |
| 10) <i>C. major</i> (Thaxter)
Rem. & Kell. 1980; | 15) <i>C. paulus</i>
Drechsler 1957; |
| 11) <i>C. multivagus</i>
Drechsler 1960; | 16) <i>C. stromoideus</i> Srin.
& Thirum. 1962; |
| 12) <i>C. obscurus</i> (Hall & Dunn)
Rem & Kell. 1980; | 17) <i>C. thromboides</i>
Drechsler 1953. |

Of the seventeen species placed here, thirteen were listed by King (1977) as producers of Type I secondary conidia only. Two of them: *C. couchii* and *C. eurymitus* produce elongate secondary conidia (differing in this from the globose primary and Type Ia secondary ones) of Type Ib. We see no reason to separate them from this subgenus at present. All four species transferred to *Conidiobolus* by Remaudière and Keller (1980) produce Type I secondary conidia only, and are pathogenic to invertebrates, a feature shared with two other members of this group: *C. osmodes* and *C. thromboides*. *C. apiculatus*, *C. major* and *C. papillatus* are rhizoid producing species, considered by Humber (1981a), because of their rhizoids and cylindrical constrictions at their conidiophores apices, as possibly deserving a separate, subgeneric status within *Conidiobolus*, or even a generic status closely allied to *Conidiobolus*. As already stated elsewhere in this paper, rhizoidal presence or absence seems to have little subgeneric importance, as compared with the other subgeneric criteria, rhizoidal production being presumably lost during subgeneric evolution, except in species in which their presence could be of selective advantage - e.g. in entomopathogenic species. The peculiarity of their conidiophores seems to be only superficially related to a generic criterion: conidiophore structure and function. In retaining these three species in *Conidiobolus* and placing them in this particular subgenus, we have considered the following: *C. osmodes*, a non-rhizoidal species of this group shares with the three rhizoidal species two of their characters - pathogenicity to insects and the cylindrical constriction at the conidiophore apex (see Fig. 9 in Ben-Ze'ev and Kenneth, 1980). Moreover, two other species in this group: *C. adiaeretus* and *C. bangalorensis* possess another peculiar modification of their conidiophore tips, resembling "...in a general way the propulsive swellings or vesicles present in *Basidiobolus*" (Srinivasan and Thirumalachar, 1967). We conclude

that since conidiogenesis and conidial discharge in the species with modified conidiophore tips proceeds as in those with unmodified tips (in this group), these modifications should not be connected with the generic feature-criterion, conidiophore structure and function. Therefore we feel as more appropriate to characterize this subgenus as possessing conidiophores with unmodified or with variously modified apices. *Entomophthora destruens*, when formally transferred to *Conidiobolus*, is another candidate for this subgenus.

For the species producing secondary conidia of Types I and II (capilliconidia), and lacking multiplicative resporulation and rhizoids (Group 4) we propose the new subgenus:

Conidiobolus subgen. *Capillidium* subgen. nov.
Conidia secundaria primariis similia vel capilliconidia sunt. Microsporas, microconidia et rhizoidea desunt.

Typus subgeneris: *Conidiobolus heterosporus*
 Drechsler, *Am. J. Bot.* 40: 107. 1953.

We place in this subgenus three more species listed in King (1977):

- | | |
|--|---|
| 2) <i>C. lobatus</i>
Srin. & Thirum.
1968; | 3) <i>C. rhyzosporus</i>
Drechsler 1954; |
| | 4) <i>C. pumilus</i> Drechsler 1955. |

A correlation is apparent throughout the genus *Conidiobolus*, among the following features-criteria: pathogenicity to invertebrates, possession of rhizoids, production of microconidia and a cylindrical constriction at the conidiophore tip. However, this correlation doesn't appear to be strong enough even at the subgeneric level, the pathogenic species being divided between two of the proposed subgenera.

FRAME(2): (CW)I-(CNN)I[?p]-(CS)Is-(CD)Ia:A
 ANCYLISTES Pfitzer 1872

Nuclei ancylistoid; conidia unitunicate, plurinucleate - the average conidial nuclear number (CNN) unknown, mentioned as "several" in Couch (1949), suggesting a paucinucleate condition; conidiophores unicellular, simple; conidial discharge active, by rounding-off; intracellular parasites of desmide algae.

Only three species have so far been described and recognized in this genus:

- | | |
|--|--|
| 1) <i>A. closterii</i> Pfitzer
1872 - generic type; | 3) <i>A. netrii</i> Couch ex Tucker
1981 [described by Couch
(1949) without Latin description, validated with Latin Description by Tucker (1981)]. |
| 2) <i>A. pfeifferi</i>
Beck 1896; | |

The genus, containing then two species, was transferred to the ENTOMOPHTHORALES by Berdan (1938). Conidia are spheroidal, secondary conidia unknown. For a more complete treatment of this and the following genera of ANCYLISTACEAE the reader is directed to Tucker's (1981) study.

FRAME (3): (CW)I-(CNN)II-(CS)IIb-(CD)Ic: [?A]
BALLOCEPHALA Drechsler 1951

Nuclei (?) ancylistoid (Tucker, 1981); conidia unitunicate, uninucleate; conidiophores composed of a unicellular main stem which produces at the apex conidiogenous cells, one at a time. As the main stem continues its growth the apical conidiogenous cell is pushed aside and becomes septate at its base, becoming a unicellular side branchlet. A mature conidiophore may have 2-80 side branchlets, more or less sympodially distributed. Each conidiogenous cell produces one globose conidium. Conidial discharge is active, by a mechanism apparently similar to the conidiophore rocket.

This genus contains three species:

- | | |
|--|--|
| 1) <i>B. sphaerospora</i>
Drechsler 1951 -
generic type; | 2) <i>B. verrucospora</i>
Richardson 1970; |
| | 3) <i>B. pedicellata</i>
Pohlad & Bernard 1978. |

FRAME (4): (CW)I-(CNN)II-(CS)IIb-(CD)Ia:A
MERISTACRUM Drechsler 1940, emend. Tucker &
Humber (in Tucker, 1981)

Nuclei ancylistoid; conidia unitunicate, uninucleate; conidiophores multicellular usually simple, sometimes branched, each cell usually uninucleate and potentially conidiogenous, producing one globose conidium/conidiogenous cell; conidial discharge active, by rounding-off.

This genus contains two species:

- | | |
|---|--|
| 1) <i>M. asterospermum</i>
Drechsler 1940 -
generic type; | 2) <i>M. milkoi</i>
(Dudka & Koval)
Humber 1981. |
|---|--|

Secondary conidia are passively dehisced capilliconidia in *M. asterospermum* (see Fig. 4 in Davidson and Barron, 1973),

and Type Ia in *M. milkoii* (Couch et al., 1979). However, we see no advantage in subdividing such a small genus.

FRAME (5): (CW)I-(CNN)[?II]-(CS)Ib-(CD)II: [?A]
ZYGNEOMYCES Miura 1973, emend. Tucker 1981

Nuclei unknown; conidia probably unitunicate, CNN unknown; conidiophores unicellular, acropetally producing branchlets undivided by septa from the main stem, one globose conidium being produced on each branchlet and passively detached by moving animals.

This genus contains two species:

- | | |
|---|--|
| 1) <i>Z. echinulatus</i>
Miura 1973 -
generic type; | 2) <i>Z. pendulatus</i>
(McCulloch)
Tucker 1981. |
|---|--|

Tucker (1981) tentatively placed this genus in the vicinity of the other nematode and tardigrade-attacking genera of ANCYLISTACEAE, although its nuclei had not been observed. Obviously this choice appears to be the most logical one, to judge by the hosts of this genus, its ecology and morphological resemblances to *Ballocephala*. No secondary conidia were reported in this genus.

BASIDIOBOLACEAE

FRAME (6): (CW)I-(CNN)II-(CS)Is-(CD)Ic: B
BASIDIOBOLUS Eidam 1886.

Nuclei basidioboloid; conidia unitunicate, uninucleate; conidiophores unicellular, simple, with a distended subconidial vesicle at the tip; conidial discharge active, by conidiophore rocket with vestigial rounding-off.

Five species are recognized in this genus:

- | | |
|--|--|
| 1) <i>B. ranarum</i>
Eidam 1886 - generic type; | 4) <i>B. microsporus</i>
Benjamin 1962; |
| 2) <i>B. haptosporus</i>
Drechsler 1947; | 5) <i>B. magnum</i>
Drechsler 1964. |
| 3) <i>B. meristosporus</i>
Drechsler 1955; | |

Synonymies and specific-level criteria are discussed in Benjamin (1962) and in Drechsler (1964). The genus is small and we do not propose any subgenera; however, two groups are easily distinguished:

GROUP:

- 1) Type Ia and II secondary conidia (capilliconidia); multiplicative resporulation absent; rhizoids absent.

- 2) Type Ia and IV secondary conidia (microspores) produced by multiplicative resporulation; rhizoids absent.

The first three species and the last one listed belong to GROUP 1, while *B. microsporus* belongs to GROUP 2. We employ Benjamin's (1962) term 'microspores' because of its relative brevity; a more descriptive term should be 'microcapilli-conidia', emphasizing the difference between Type IV secondary conidia and the microconidia of *Conidiobolus*. Primary conidia are spheroidal in all species.

ENTOMOPHTHORACEAE

FRAME (7): (CW)I-(CNN)Ip-(CS)Is-(CD)Ib: E

ENTOMOPHTHORA Fresenius 1856, *sensu stricto*
Batko (1964b), *sensu stricto* emend. Remaudière
& Keller (1980).

Nuclei entomophthoroid; conidia unitunicate, paucinucleate; conidiophores unicellular, simple, usually clavate; conidial discharge active, by conidiophore-cannon (secondary conidia discharged by rounding-off).

There are six species in this genus:

- | | |
|---|---|
| 1) <i>E. muscae</i> Fres. 1856
- generic type; | 4) <i>E. culicis</i> (A. Braun)
Fres. 1858; |
| 2) <i>E. erupta</i> (Dustan)
Hall 1959; | 5) <i>E. planchoniana</i>
Cornu 1873; |
| 3) <i>E. weberi</i> Lakon
ex Samson 1979; | 6) <i>E. thripidium</i>
Samson <i>et al.</i> 1979. |

The first three species were originally retained by Batko (1964b) when he restricted this genus, along with *E. scatophagae* Giard 1888, regarded here as a synonym of *E. muscae*, according to Petch (1934) and MacLeod *et al.* (1976). Remaudière and Keller (1980) removed Batko's restriction of this genus as regarding rhizoids, and placed in it the next three species (listed here 4, 5 and 6), the first two possessing rhizoids, the last one being newly discovered. Our generic frame coincides with Remaudière and Keller's (1980) less restrictive circumscription of *Entomophthora*. The possession of rhizoids in *E. culicis* and *E. planchoniana* and their absence in the other species seems to divide *Entomophthora* into two groups. However, in the light of our treatment of *Conidiobolus*, and the role played there by the presence or absence of rhizoids, we conclude that this feature, when not reinforced by other correlated ones, does not deserve an independent subgeneric rank.

FRAME (8): (CW)I-(CNN)Ip-(CS)Is-(CD)II: E
MASSOSPORA Peck 1879, emend. Soper 1974.

Nuclei entomophthoroid; conidia unitunicate, paucinuclate (1-6, usually 2-3 nuclei/conidium); conidiophores unicellular, simple; conidial discharge passive.

This genus contains thirteen species, all listed in Soper (1981):

- | | |
|--|---|
| 1) <i>M. cicadina</i> Peck
1878 - generic type; | 7) <i>M. carinetae</i> Soper 1974; |
| 2) <i>M. spinosa</i>
Ciferri et al. 1957; | 8) <i>M. diminuta</i> Soper 1974; |
| 3) <i>M. levispora</i> Soper 1963; | 9) <i>M. platipediae</i> Soper 1974; |
| 4) <i>M. dorisiana</i> Soper 1974; | 10) <i>M. diceroproctae</i> Soper 1974; |
| 5) <i>M. ocypetes</i> Soper 1974; | 11) <i>M. fidicinae</i> Soper 1974; |
| 6) <i>M. tettigatis</i> Soper 1974; | 12) <i>M. cicadettae</i> Soper 1981; |
| | 13) <i>M. pahariae</i> Soper 1981. |

The predominant conidial shapes appear to be the ellipsoidal and ovoid ones, some species having part of their conidia departing from the characteristic shape (e.g. from ovoid to obovate or from ellipsoidal to fusiform or navicular) and one species having globose and subglobose conidia. This is the only known genus with conidial wall ornamentation in the ENTOMOPHTHORACEAE, three species having verrucose conidial walls, four having them verruculose, four species lacking wall ornamentation, conidia remaining unknown in two species (Soper, 1981). *Massospora* is so distinctive that it was never placed into synonymy with another genus. For taxonomic studies see Soper (1963, 1974, 1981).

FRAME (9): (CW)I-(CNN)It-(CS)Is-(CD)Ia: E
TRIPLOSPORIUM (Thaxter) Batko 1964, *nom. gen.*
conserv. prop. (Humber et al., 1981), *syn:*
NEOZYGITES Wiltaczil 1885.

Nuclei entomophthoroid; conidia unitunicate, regularly tetranucleate; conidiophores unicellular, simple; conidial discharge active, by rounding-off.

Batko's (1964c) generic name, based on Thaxter's (1888) subgeneric one is antedated by Wiltaczil's (1885) *Neozygites*, as pointed out by Gustafsson (1965). Remaudière and Keller (1980), based on nomenclatural priority, placed *Triplosporium* in synonymy under *Neozygites*, adding to this genus three species found after Batko's (1964c, e) treatment. Humber et al. (1981) proposed to conserve the name *Triplosporium* against *Neozygites*. We prefer the generic name *Triplosporium* for the reasons listed in Humber et al. (1981) and use

it for listing species belonging in this generic frame, except for two listed here under their original designation as *Neozygites* (Remaudière and Keller, 1980), pending a decision on the name of this genus at the 13th International Botanical Congress, 1981 (unpublished yet):

- 1) *T. fresenii* (Nowak.) Batko 1964 (c) - generic type;
- 2) *T. lageniformis* (Thaxter) Batko 1964 (e);
- 3) *T. fumosum* (Speare) Batko 1964 (e);
- 4) *T. floridanum* (Weiser & Muma) Weiser 1968;
- 5) *T. tetranynchi* Weiser 1968;
- 6) *N. adjarica* (Tsintsadze & Vartapetov) Rem. & Kell. 1980;
- 7) *N. parvispora* (MacLeod & Carl) Rem. & Kell. 1980;
- 8) *Triplosporium lecanii* (Zimmermann) Ben-Ze'ev & Kenneth comb. nov., Basionym: *Empusa lecanii* Zimmermann, *Meded. Lands Plantent.* 44: 25-27. 1901.

Synonyms: 1) *Derexia lecani* Narasiman, *Indian Phytopathol.* 23: 16-16. 1970 (*nomen nudum*, published without Latin description and type). 2) *Derexiomyces lecanii* Narasimhan & Thirumalachar, *2nd Int. Mycol. Congress, Tampa, Abstracts*: 466. 1977 (*nomen nudum*, published without Latin description and type).

Zimmermann (1901) described *E. lecanii* as possessing dark-colored, spherical resting spores and dark conidia, measuring approximately 18 X 9-10 μm , produced by simple conidiophores arising from spherical tetranucleate hyphal bodies. He did not observe secondary conidia. Petch (1926, Figs. 1-6), while looking for entomogenous fungi on the host of Zimmermann's fungus, observed and figured what he then thought to be sporangia of a *Pythium* or *Phytophthora*. They were hyaline becoming fuscous or pale brown, narrow-oval or pyriform, 12-20 X 5-10 μm , few being broader and more globose, 12 X 9 μm , producing a spherical haptor ("vesicle") and borne on a simple conidiophore, 0.5-0.75 μm wide and up to 60 μm long. Petch (1926) also estimated, from Zimmermann's (1901) figures, that the primary conidiophores of *E. lecanii* measured approximately 55 μm in length and 7-9 μm in diameter. A few years later, Petch (1931) recognized his 'sporangia' as capilliconidia comparable to those of *T. fresenii*. Narasimhan (1970), criticizing Petch's (1926) misinterpretation and being obviously unaware of Petch's (1931) correction, described his own studies aimed at the rediscovery of Zimmermann's fungus. He found a species attacking the same host, *Lecanium viride* and resembling *E. lecanii* in possessing spherical hyphal bodies instead of mycelium, simple conidiophores which forcibly discharged

oval conidia, and dark-colored, smooth-walled *Tiletia*-like resting spores. Unfortunately, Narasimhan gave no dimensions of any of the fungal structures described. In his figures (2, 5 and 7), the resting spores appear as broad-ovoid rather than spherical. His Fig. 5 is a photomicrograph of a resting spore which produced, upon germination, a capillary conidiophore bearing an amygdaliform capilliconidium. This pattern of resting spore germination has been described and figured in the ENTOMOPHTHORACEAE only for *T. fresenii* (Wilding, 1971; Bitton *et al.*, 1979, Fig. 5). However, Narasimhan (1970) based on his success on isolating and culturing an apparently sporobolomycetaceous yeast, concluded that Zimmerman's fungus was a member of SPOROBOLOMYCETACEAE (HETEROBASIDIOMYCETES) and proposed (without a Latin description) a new genus, *Derexia*. Narasimhan and Thirumalachar (1977), following the same idea, changed the generic name to *Derexiomyces*, still without Latin description, and provided a photomicrograph (their Fig. 1) of an ellipsoid conidium, resembling those of *E. lecanii* figured by Zimmermann (1901), but bearing a capilliconidium atop a capillary conidiophore. The capilliconidia figured by Narasimhan (1970) and by Narasimhan and Thirumalachar (1977) are similar to those figured by Petch (1926, Figs. 3-5). It should be mentioned that many of our attempts to isolate ENTOMOPHTHORALES from dead insects ended with isolates of SPOROBOLOMYCETACEAE. *Triplosporium lecanii*, being described here by combining the descriptions of four different authors, still requires accurate dimensions of its resting spores.

Batko's (1964c) definition of *Triplosporium*, based on three species is emended here according to new information available from the eight presently recognized species:

Triplosporium (Thaxter) Batko 1964, nom. gen.
conserv. prop. (Humber *et al.*, 1981), emend.
Ben-Ze'ev & Kenneth

- = *Empusa* (*Triplosporium*) Thaxter, *Mem. Boston Soc. Nat. Hist.* 4: 169. 1888.
- = *Neozygites* Wlaczil, *Arch. F. Mikr. Anat.* 24: 299-603. 1885.

Mycelium coenocytic, generally composed of tetranucleate hyphal bodies (spherical, oval, cylindrical or irregularly shaped); nuclei entomophthoroid; conidiophores unicellular, simple, each arising from one hyphal body. Primary conidia unitunicate, tetranucleate, spherical-truncate or oval-truncate (truncata-lageniformis acc. to Lakon's 1919 classification) or elongate: ellipsoid with or without a slight

constriction above the papilla. Secondary conidia of Types Ia and II (capilliconidia) tetranucleate, passively detached from a capillary conidiophore. Primary and secondary Type I conidia forcibly ejected by rounding-off. All conidial types usually smoky colored. Resting spores usually dark colored, arising either by isogamous conjugation of two hyphal bodies, or by budding from one hyphal body, without apparent conjugation (zygospores and azygospores respectively). Resting spore germination, where observed, by a capillary germ-conidiophore upon which a germ-capilliconidium is produced. Rhizoids and pseudocystidia absent in all eight known species. Obligate parasites of arthropods.

The first three species listed here were placed in *Triplosporium* by Batko (1964c, e) according to Thaxter (1888). Weiser (1968) added the next two species (no. 4 and 5). *Entomophthora turbinata* Kenneth 1977, added to this genus by Remaudière and Keller (1980) under the generic name *Neozygites* is excluded. This species resembles *Triplosporium* in possessing dark, ovoid resting spores and simple conidiophores, but differs in having paucinucleate conidia (with 5-7 nuclei) and does not produce secondary conidia of any type. Its author (Kenneth, 1977) who recognized *Triplosporium* as a separate genus previous to the discovery of this species (Kenneth *et al.*, 1972) would have placed it there, if the conidia were found to be regularly tetranucleate, which is not the case.

FRAME (10): (CW)I?-(CNN)Ip-(CS)Is-(CD)Ia: E
MACROBIOTOPHTHORA Reukauf 1912, emend Tucker
 1981 (frame formula acc. to B. E. Tucker, pers.
 commun.)

Nuclei entomophthoroid; conidia unitunicate, paucinucleate (4-9 nuclei/conidium); conidiophores unicellular, simple; conidial discharge active, by rounding off (Tucker, 1981).

This genus contains two species:

- 1) *M. vimariensis* Reukauf 1912 - generic type;
- 2) *M. vermicola* (McCulloch) Tucker 1981.

Primary conidia are obovoid in *M. vimariensis* and secondary conidia are unknown. Some of its primary conidiophores, as well as secondary ones arising from primary conidia were illustrated by Reukauf (1912, Figs. 7 and 9) as producing thick-walled resting spore-like spherical structures at their tips. In *M. vermicola* primary conidia are elongate-pyriform, secondary conidia appear to be of Type Ia according to McCulloch (1977). Tucker (1981) interpreted the

epapillate appearance of these secondary conidia as proof that they are passively detached. Since epapillate shape of conidia provides no proof of passive detachment, we are inclined to believe McCulloch's (1977) report from living material, rather than Tucker's (1981) impression from examining one of McCulloch's slides. Tucker (1981) mentioned the conidia of *M. vimariensis* as uninucleate, despite the fact that the CNN of this fungus was never mentioned in the literature. We believe that this confusion arose due to the erroneous description of *M. vermicola* (by McCulloch, 1977) as uninucleate.

A *Conidiobolus*-like fungus (Castaner, 1968) listed by King (1976b) in his *Possible Additional Species [of Conidiobolus]* resembles in a certain degree the genus *Macrobiotophthora*. Castaner (1968) did not describe the nature or the conidial number of nuclei, however, since this fungus produces microconidia it can be inferred that, like *Macrobiotophthora*, its conidia are plurinucleate. From the small conidial size, 7.5 X 8.5 μm , and from the low number of microconidia produced (up to six) it seems very likely that this fungus is not multinucleate like *Conidiobolus*, but merely paucinucleate. Further information is needed about this still unnamed species, but it appears as quite close to *Macrobiotophthora*, although it may prove to be affiliated to the ANCYLISTACEAE if it turns out to have ancylistoid nuclei.

FRAME (11): (CW)I-(CNN)I[?p]-(CS)Is-(CD)Ia: E
COMPLETORIA Lohde 1874

Nuclei entomophthoroid (R. Humber, pers. comm.; Tucker, 1981); conidia unitunicate, plurinucleate, but exact conidial nuclear number (CNN) unknown; conidiophores unicellular, simple; conidial discharge active, by rounding-off. This genus is monotypic for *C. complens* Lohde 1874, an intracellular parasite of fern prothalli.

FRAME (12): (CW)II-(CNN)II-(CS)Is-(CD)Ia: E
STRONGWELLSEA Batko & Weiser 1965, emend.
 Humber 1976

Nuclei entomophthoroid; conidia bitunicate, uninucleate; conidiophores unicellular, simple; conidial discharge active, by rounding-off. Primary conidia are ellipsoidal to obovoidal, papillate, and produce Type Ib (spheroidal) secondary conidia.

There are two species in this genus:

- 1) *S. castrans* Batko & Weiser 1965, emend. Humber 1976 - generic type;
- 2) *S. magna* Humber 1976.

FRAME (13): (CW)II-(CNN)II-(CS)IIb-(CD)Ia: E
Erynia Nowakowski 1881, emend. Humber & Ben-
 Ze'ev 1981.

Nuclei entomophthoroid; conidia bitunicate, uninucleate; conidiophores multicellular, usually branched; conidial discharge active, by rounding-off. Primary conidia are of many elongate shapes (in all presently known species), while secondary conidia are of Types Ia, Ib, II and V.

The species belonging to this generic frame are as numerous or more than all species of the other genera of ENTOMOPHTHORACEAE together. *Erynia* with its subgeneric groups is therefore treated separately in part II of this paper (Ben-Ze'ev and Kenneth, 1982).

The remaining species possessing nuclei of entomophthoroid nature have to be divided between the following three FRAMES:

14): (CW)I-(CNN)Ip-m-(CS)Is-(CD)Ia: E

15): (CW)I-(CNN)Im-(CS)Is-(CD)Ia: E

16): (CW)I-(CNN)Ip-(CS)Is-(CD)Ia: E

According to Batko's (1964c) definition of *Entomophaga* Batko 1964, this genus fits the second of these two frames. However, the generic type, *Entomophaga grylli* (Fres.) Batko 1964 is known as having plurinucleate conidia, but its exact CNN was apparently never mentioned in the literature. A closely allied species, *Entomophthora aulicae* (Reich) Sorokin 1876, considered by many authors as a synonym of *E. grylli* (see review in MacLeod and Müller-Kögler, 1973) was reported to average 12-15 nuclei/conidium (Riddle, 1906, as '*E. grylli*'). This average is closely matched by recent observations of 13-21 nuclei/conidium (D. Tyrrell, pers. comm. of unpublished results). It seems very possible that Batko (1964c) defined *Entomophaga* having in mind the CNN of three other species he placed in that genus: *E. thaxteriana* (now: *Conidiobolus thromboides*), *E. obscura* (now: *C. obscurus*) and *E. kansana* Hutchison 1962, all known to possess multinucleate conidia. The generic features-criteria advocated here, superimposed on Humber's (1981a) confirmation of the validity of *Entomophaga*, restrict for the present this genus to its type species, *E. grylli* only. As soon as the CNN of *E. grylli* is established, other species will find their place in this genus. However, if the CNN of *E. grylli* is found to be in the same range as that of *E. aulicae* (pauci-multinucleate) *Entomophaga* will fit the first

of the three frames outlined above, while new genera will have to be proposed for the other two. The following species are listed under FRAME (14) (pauci-multinucleate) and provisionally under their former generic designation, *Entomophthora* (in its collective sense):

- 1) *E. aulicae* (Reich) Sorokin 1876;
- 2) *E. tabanivora* Anderson & Magnarelli 1979.

E. aulicae and *E. tabanivora* have pyriform and pyriform to spheroidal conidia respectively (Anderson and Magnarelli, 1979; MacLeod and Müller-Kögler, 1973). Another species with spheroidal conidia and large papillae and in the same range of CNN (17-20 nuclei/conidium) is *E. dysderci* (Viegas) MacLeod & Müller-Kögler 1973. However, the conidial discharge mechanism in this species is by 'conidiophore-cannon' as in *Entomophthora* s. str., in which it could fit except for its CNN. It appears from the available data that *E. dysderci* will fit another new frame, unless the differences between the three active discharge mechanisms are de-emphasized at the generic level.

The following species are listed under FRAME (15) (multinucleate):

- 1) *E. batkoi* Baĭazy 1978;
- 2) *E. gigantea* Keller 1978;
- 3) *E. kansana* Hutchison 1962.

All three species have been described as multinucleate, with conidial nuclear numbers of 40-50 in *E. batkoi* (counted from Baĭazy, 1978a, Figs. 2-3), ~ 50 in *E. gigantea* (Keller, 1978) and 24-78 in *E. kansana* (Hutchison, 1962). *E. batkoi* and *E. kansana* have pyriform conidia of the *E. grylli* shape, *E. gigantea* has spheroidal, papillate conidia.

The last (paucinuclate) of these three, FRAME (16) also contains three species:

- 1) *E. turbinata* Kenneth 1977;
- 2) *E. caroliniana* (Thaxter) Keller 1978;
- 3) ? *Culicicola* sp. (Baĭazy, 1978).

These three species are similar in having paucinuclate conidia (5-7 nuclei/conidium; 6-10 and 4-10 nuclei, respectively), all three have unicellular, simple conidiophores and the last two have been reported to be unitunicate, while *E. turbinata* was reported as sometimes showing a partially separating outer conidial wall (Kenneth, 1977). These three species differ from *Entomophthora* s. str. by their active (rounding-off) conidial discharge and by having elongate conidia, and appear to be similar in all the im-

portant generic features-criteria (*E. turbinata*, only if its 'bitunicate' condition turns out to be an artifact, as we now suspect). This frame is clearly a case in which a feature-criterion unaccepted by us in the past (variations in the mechanisms of active conidial discharge - Ben-Ze'ev, 1980) is strengthened by a generic feature (conidial shape) which is not considered a generic criterion.

This last frame seems to be close to *Macrobotophthora*, since it has the same frame formula. However, since there are still some uncertainties about *Macrobotophthora*'s conidial wall, and its description is based on *M. vermicola* rather than on the generic type, *M. vimariensis*, we prefer to keep these generic frames as separate until more data is gathered.

The following Table (1) shows all the frames discussed in this chapter and allows a comparison based on the generic features-criteria advocated here.

Species incompletely studied, with important generic features missing from their descriptions were classified by us in the past in a provisional group referred to as *Entomophthora sensu lato* (Ben-Ze'ev, 1980; Ben-Ze'ev and Kenneth, 1979; 1981a). However, as pointed out by the reviewers of this paper, that name may lead to confusion and implies a generic status. In order to clarify that such a group is only a provisory refuge for insufficiently described species, and does not have a generic status under the International Code of Botanical Nomenclature (Art. 34.1-provisional names) we propose to classify such species under the name (suggested by R. S. Soper):

Entomophthora nomina provisoriorum or (*n.p.*)

Species presently belonging here (cited from MacLeod and Muller-Kogler, 1973, and other sources) are:

- 1) *E. acaricida* (Petch 1940) - its description lacks details about the conidial wall structure and conidial nuclear number, the conidiophores being described as unbranched and rhizoids as absent.
- 2) *E. acaridis* (Petch 1943) - its description lacks details about the conidial wall structure, conidial nuclear number and conidiophore structure. Nuclear nature is unknown in both of the above species. We do not propose new combinations for these species, described by Petch (1940; 1943 respectively) under the generic name *Empusa*, due to the provisory nature of *Entomophthora n.p.*

- 3) *E. anglica* Petch 1943 - its description lacks details about the conidial wall structure, conidial nuclear number and conidiophore structure. The elongate shape of its conidia and the possession of (undescribed) rhizoids suggest a possible affiliation to either *Erynia* or Frame "16".
- 4) *E. aphrophorae* Rostrup 1896 was described without any mention of its conidial wall structure, conidial nuclear number or conidiophore structure. A different fungus (*Erynia petchii*) was described by Petch (1934) under this name, because both species have elongate conidia, produce rhizoids and attack the same host (Ben-Ze'ev and Kenneth, 1981b).
- 5) *E. blissi* (Lakon) MacLeod & Muller-Kogler 1973 - the conidiophore structure (branched) and conidial shape (elongate) point toward *Erynia*, but other generic features are unknown.
- 6) *E. carpentieri* Giard 1888 (sensu Turian, 1957) - the branched conidiophores, uninucleate conidia and pseudorhizomorphs point toward *Erynia* subgen. *Zoophthora* (see Ben-Ze'ev and Kenneth, 1982), but the conidia were described as spheroidal and the conidial wall structure is unknown.
- 7) *E. conglomerata* Sorokin 1876 - the nature and average number of nuclei in conidia is unknown, therefore its transfer to *Conidiobolus* by Remaudiere and Keller (1980) might have been premature. MacLeod and Muller-Kogler (1973) described its conidia as "multinucleate", using this term in the sense we use "plurinucleate" (any number > 1).
- 8) *E. jassi* (Cohn) MacLeod & Muller-Kogler 1973 - none of the generic features-criteria is known.
- 9) *E. lampyridarum* (Thaxter) MacLeod & Muller-Kogler 1973 - in spite of a recent encounter (Carner, 1980) none of the generic features-criteria is known.
- 10) *E. pyralidarum* Petch 1937 - the conidial wall structure and the conidial nuclear number are unknown.
- 11) *E. saccharina* Giard 1888 - was placed by Batko (1964e) in *Entomophaga*, but the nature and average number of nuclei in its conidia are unknown, and therefore it may belong to *Conidiobolus* or to one of Frames (14), (15) or (16).
- 12) *E. schroeteri* Brumpt 1940 - conidial wall structure and nuclear nature and number in conidia are unknown, the other features-criteria point toward *Erynia*.
- 13) *E. tenthredinis* Fres. 1858 - nuclear nature and number in conidia are unknown and its transfer to *Conidiobolus*

- (Remaudière and Keller, 1980) might be unjustified.
- 14) *E. thaxteri* (Brumpt) MacLeod & Müller-Kögler 1973 - conidial wall structure, nuclear nature and number in conidia are unknown.
- 15) *E. tipulae* Fres. 1858 (cited from Taxter, 1888; Lakon, 1919) - the nature and number of nuclei in conidia are unknown, the conidiophore structure was unclearly described. Its transfer to *Conidiobolus* (Remaudière and Keller, 1980) seems unjustified, in the light of unknown generic characters.

All the species mentioned under Frames nos. (14), (15) and (16), except *E. grylli* may be considered, for the present, as belonging to this group, until the CNN of *Entomophaga* is precisely established and the other two Frames are given generic descriptions and names.

No species were purposefully omitted from this list, although some species might have been overlooked. The synonymies are those proposed or adopted by MacLeod and Müller-Kögler (1973). Other species formerly classified in *Zoophthora* Batko 1964, or having features-criteria suggesting Frame (13) are discussed elsewhere (Humber and Ben-Ze'ev, 1981; Ben-Ze'ev and Kenneth, 1982).

Tarichium Cohn 1875 *sensu* Lakon 1919

Thaxter's (1888) attitude that this genus is "...merely the resting stage of some *Empusa*, the conidia of which are as yet unknown" and that of Remaudière and Keller (1980): "genus *incertae sedis*" are correct, but do not solve the question: where to keep those species in the classification? Consistent with our view that no species should be ignored or kept outside the classification because of its incompatibility with accepted criteria, we adopt the practice pro-

TABLE 1. A comparative list of the sixteen generic frames of *Entomophthorales* described above. Under CW: I = unitunicate, II = bitunicate. Under CNN: I = plurinucleate, with the following secondary groups: m = multinucleate (>20, usually around 50 nuclei/conidium); p-m = pauci-multinucleate (10-20 nuclei/conidium, rarely exceeding 20); p = paucinucleate (2-8 nuclei/conidium, rarely 1 or up to 12); t = tetranucleate (regularly 4 nuclei/conidium); II = uninucleate (regularly 1 nucleus/conidium). Under CS: I = unicellular; II = multicellular, with the following secondary groups: s = simple; b = branched; s-b = simple or branched. Under CD: I = active discharge, with the following secondary groups (discharge mechanisms): a = rounding-off; b = conid-

iophore-cannon; c = conidiophore-rocket. Under Familial Affiliation: A = Ancylistaceae; B = Basidiobolaceae; E = Entomophthoraceae. Any symbol placed together with a question mark in square parentheses means that the certain feature-criterion is unknown and inferred from the conjecture of the other, known features.

Frame no.	Nuclear structure	Conidial wall structure (CW)	Conidial nuclear number (CNN)	Conidiophore structure (CS)	Conidial discharge (CD)	Familial affiliation	Genus
1.	ancylistoid	I - Im - Is	-Ia: A				<i>Conidiobolus</i>
2.	"	I - I[?p] - Is	-Ia: A				<i>Ancylistes</i>
3.	?	I - II - IIb	-Ic: [?A]				<i>Ballocephala</i>
4.	ancylistoid	I - II - IIs-b	-Ia: A				<i>Meristacrum</i>
5.	?	I - [?II] - Ib	-II: [?A]				<i>Zygnemomyces</i>
6.	basidioboloid	I - II - Is	-Ic: B				<i>Basidiobolus</i>
7.	entomophthoroid	I - Ip - Is	-Ib: E				<i>Entomophthora</i>
8.	"	I - Ip - Is	-II: E				<i>Massospora</i>
9.	"	I - It - Is	-Ia: E				<i>Triplosporium</i>
10.	"	I? - Ip - Is	-Ia: E				<i>Macrobotophthora</i>
11.	"	I - I[?p] - Is	-Ia: E				<i>Completozia</i>
12.	"	II - II - Is	-Ia: E				<i>Strongwellsea</i>
13.	"	II - II - IIb	-Ia: E				<i>Erynia</i>
14.	"	I - Ip-m - Is	-Ia: E				? <i>Entomophaga</i> or unnamed
15.	"	I - Im - Is	-Ia: E				? <i>Entomophaga</i> or unnamed
16.	"	I - Ip - Is	-Ia: E				unnamed

posed by Lakon (1919) and by MacLeod and Müller-Kögler (1970) to place these species in a provisional group without nomenclatural validity under the ICBN but which is, nonetheless, part of the classification. We adopt the name used by Lakon (1919) and not *Entomophthora* (*Tarichium*) as proposed by MacLeod and Müller-Kögler (1970), since the last name has both a subgeneric meaning and appears to tie those species exclusively with the genus *Entomophthora*, which may not be true in most cases. For species classification the reader is directed to MacLeod and Müller-Kögler's (1970) study.

Goniomochaete Drechsler 1946

Typified by *G. horridula* Drechsler 1946, this nematode parasitic genus is completely different from all the other genera of ENTOMOPHTHORALES by producing sporangiospores inside a tubular sporangium which morphologically resembles the unicellular, simple conidiophores of ENTOMOPHTHORALES. Another similarity is the septation of its thallus and its disjunction into hyphal bodies, as in *Meristacrum*. The wall structure and nuclear condition of the sporangiospores remains unknown. Drechsler (1946) considered this genus as the most primitive one in the ENTOMOPHTHORACEAE. Other authorities consider it to be an OOMYCETE (Barron, 1977; Benjamin, 1979). A cell-wall composition test is needed to resolve at least part of this uncertainty.

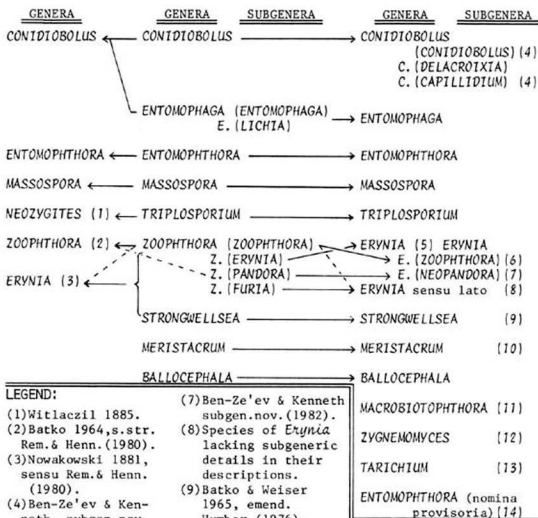
NEOBATKOAN CLASSIFICATIONS - DISCUSSION

We know not why Batko's classification was accepted by so few during its 15 years of published existence. One reason, however, may be the apparent inconsistency with which Batko treated his criteria: the conidial nuclear number is undoubtedly very important - inexplicably disregarded by Batko in the genus *Culicicola*. In his discussion of this genus, Batko (1964d) expressed some doubts about the phylogenetic homogeneity of this genus, later he tried to purify it by transferring multinucleate species to the invalidly published subgenus *Lichia* of *Entomophaga* (Batko and Weiser, 1965) and finally *Culicicola* was rather quietly abandoned (in Batko, 1974) instead of being publicly rejected. Batko (1974) studied in depth the evolutionary trends of conidial ontogeny and parasitism vs. saprobism, but had not, apparently, considered enough the evolutionary path of rhizoids production. As a result he overestimated

the taxonomic level of this feature-criterion - as pointed out by Remaudière and Hennebert (1980). Another disadvantage in Batko's classification, pointed out by Remaudière and Keller (1980), is the lack of competent criteria for distinction between *Entomophaga* and *Conidiobolus*.

Remaudière and Hennebert (1980) and Remaudière and Keller (1980) tried to improve Batko's classification and succeeded in some places while failing in others. Their successes are: (1) the categorical rejection of *Culicicola* and the transfer of some of its former species to *Entomophthora* s. str. and transfer of others to *Conidiobolus* (Fig. 3); (2) the rejection of Batko's resting-spore criteria; and (3) the transfer of two more species to *Neozygites* (= *Triplosporium*). However, four major misconceptions are apparent in their own classification: First, each of their generic criteria is employed selectively in one or some genera but not in others. Secondly, Batko's generic criterion of conidial nuclear number is applied as a secondary one, conidial morphology being applied instead as the primary generic criterion. Thirdly, they employ production of capilliconidia as a criterion of generic value, but do so very selectively, dividing only one of the genera possessing capilliconidia into two separate genera, despite similarity of these "two genera" in conidial nuclear number, conidial morphology and conidiophore structure - all being criteria accepted by them. Fourth, despite their own de-emphasis of resting-spore criteria at the generic level, and despite other incompatible features-criteria, they included *E. turbinata* in *Neozygites* because of morphological similarity between its resting spores and those of other species of *Neozygites*. The consequences are that the genera *Conidiobolus*, *Neozygites* and *Erynia* in their classification are heterogeneous with regard to the conidial nuclear number; *Entomophaga* is absorbed into *Conidiobolus*; *Strongwellsea* with unicellular, simple conidiophores is absorbed into *Erynia*, which is already heterogeneous in a formerly mentioned aspect, while *Zoophthora* is retained as a genus on the account of its capilloconidia only. Another consequence of these misconceptions is that species not meeting their "rules" were left outside the classification - a procedure formerly employed by Batko as well.

Ben-Ze'ev (1980), Ben-Ze'ev and Kenneth (1981a), Humber (1981a, b) and Humber and Ben-Ze'ev (1981) outlined another Batkoan classification, also trying to improve Batko's original one. Tucker (1981) presented a classification of non-entomogenous ENTOMOPHTHORALES, consistent with the cri-

REMAUDIÈRE &
HENNEBERT 1980BATKO 1964-1974
BATKO & WEISER 1965BEN-ZE'EV & KENNETH
(THIS PAPER)*REMAUDIÈRE &
KELLER 1980

LEGEND:

- | | | |
|--|--|--|
| (1) Witlaczil 1885. | (7) Ben-Ze'ev & Kenneth subgen. nov. (1982). | (12) Miura 1977, emend. Tucker (1981). |
| (2) Batko 1964, s. str. Rem. & Henn. (1980). | (8) Species of <i>Erynia</i> lacking subgeneric details in their descriptions. | (13) Sensu Lakon (1919). |
| (3) Nowakowski 1881, sensu Rem. & Henn. (1980). | (9) Batko & Weiser 1965, emend. Humber (1976). | (14) ENTOMOPHTHORALES lacking generic details in their descriptions. |
| (4) Ben-Ze'ev & Kenneth, subgen. nov. | (10) Drechsler 1940, emend. Tucker & Humber in Tucker (1981). | |
| (5) Nowakowski 1881, emend. Humber & Ben-Ze'ev (1981). | (11) Reukauf 1912, emend. Tucker (1981). | |
| (6) Batko 1966, sensu Ben-Ze'ev (1980), emend. Ben-Ze'ev & Kenneth (1982). | | |

* A synthesis of classifications outlined by Ben-Ze'ev (1980), Ben-Ze'ev and Kenneth (1981a), Humber (1981a,b), Humber and Ben-Ze'ev (1981), Remaudière and Keller (1980), and Tucker (1981).

FIG. 3 A comparison of three Batkoan classifications of ENTOMOPHTHORALES (adopted with changes from Ben-Ze'ev, 1980, including only the invertebrate-attacking genera). Authors quotations of taxa are like in Fig. 1, or if different are given in the legend above.

teria used by us. This paper, originally meant to detail the classification outlined by Ben-Ze'ev (1980) and Ben-Ze'ev and Kenneth (1981a), had to be changed according to the findings of Humber (1981a, b; 1982a, b) and Tucker (1981). In its present form, the classification of Entomophthorales detailed here (Fig. 3) is seen by us as a synthesis of elements taken from the descriptive prebatkoan- and from the neobatkoan classifications- the common denominators being the features-criteria advocated here and the rules applying to their correct usage.

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REFERENCES

- Anderson, J. F. and Magnarelli, L. A. (1979). *Entomophthora tabanivora*, a new pathogen in horseflies (Diptera: Tabanidae). *J. Invertebr. Pathol.* 34: 263-266.
- Bałazy, S. (1978a). A new species of Entomophthoraceae (Mycophyta: Entomophthorales) from Poland. *J. Invertebr. Pathol.* 31: 274-279.
- Bałazy, S. (1978b). A peculiar type of the conidia in Entomophthoraceae. *Abstr. Intl. Colloq. Invertebr. Pathol., Prague (1978):* 5.
- Barron, G. L. (1977). THE NEMATODE-DESTROYING FUNGI. *Canadian Biol. Publ., Guelph.*
- Batko, A. (1964a). Notes on entomophthoraceous fungi in Poland. (*Coll. Int. Pathol. Insectes, Paris. 1962*). *Entomophaga, Mém. Hors. Sér.* 2: 129-131.
- Batko, A. (1964b). Remarks on the genus *Entomophthora* Fresenius 1856 non Nowakowski 1883 (Phycomycetes: Entomophthoraceae). *Bull. Acad. Polon. Sci., Sér. Sci. Biol.* 12: 319-321.

- Batko, A. (1964c). On the new genera: *Zoophthora* gen. nov., *Triplosporium* (Thaxter) gen. nov. and *Entomophaga* gen. nov. (Phycomycetes: Entomophthoraceae). *Bull. Acad. Polon. Sci., Sér. Sci. Biol.* 12: 323-326.
- Batko, A. (1964d). Remarks on the genus *Lamia* Nowakowski 1883 vs. *Culicicola* Nieuwland 1916 (Phycomycetes: Entomophthoraceae). *Bull. Acad. Polon. Sci., Sér. Sci. Biol.* 12: 399-402.
- Batko, A. (1964e). Some new combinations in the fungus family Entomophthoraceae (Phycomycetes). *Bull. Acad. Polon. Sci., Sér. Sci. Biol.* 12: 403-406.
- Batko, A. (1966a). A new aphidicolous fungus from Poland, *Zoophthora phalloides* sp. nov. (Entomophthoraceae). *Acta Mycol.* 2: 7-13.
- Batko, A. (1966b). On the subgenera of the fungus genus *Zoophthora* Batko 1964 (Entomophthoraceae). *Acta Mycol.* 2: 15-21.
- Batko, A. (1974). Filogeneza a struktura taksonomiczne Entomophthoraceae [Phylogenesis and taxonomic structures of Entomophthoraceae]. In: EWOLUCJA BIOLOGICZNA, SZKICE TEORETYCZNE I METODOLOGICZNE. (ed. C. Nowinski) *Polska Akad. Nauk., Inst. Filozof. Sociol. Wrocław.*
- Batko, A. and Weiser, J. (1965). On the taxonomic position of the fungus discovered by Strong, Wells, and Apple: *Strongwellisea castrans* gen. et sp. nov. (Phycomycetes: Entomophthoraceae). *J. Invertebr. Pathol.* 7: 455-463.
- Benjamin, R. K. (1962). A new *Basidiobolus* that forms microspores. *Aliso* 5: 223-233.
- Benjamin, R. K. (1979). Zygomycetes and their spores. In: THE WHOLE FUNGUS (ed. B. Kendrick) Vol. 2. *National Museum of Natural Sciences, Ottawa, Canada.*
- Ben-Ze'ev, I. (1980). Systematics of entomopathogenic fungi of the "*sphaerosperma* group" (Zygomycetes: Entomophthoraceae) and their prospects for use in biological pest control. *Ph.D. dissertation, Hebrew University of Jerusalem* (in Hebrew, with English Abstract).
- Ben-Ze'ev, I. and Kenneth, R. G. (1979). *Zoophthora erinacea* sp. n. (Zygomycetes: Entomophthoraceae), a fungal parasite of aphids. *Mycotaxon* 10: 219-232.
- Ben-Ze'ev, I. and Kenneth, R. G. (1980). *Zoophthora phytonomi* and *Cnidobolus osmodes* (Zygomycetes: Entomophthoraceae), two pathogens of *Hypera* species (Col.: Curculionidae) coincidental in time and place. *Entomophaga* 25: 171-186.
- Ben-Ze'ev, I. and Kenneth, R. G. (1981a). *Zoophthora orientalis* sp. nov., a fungal pathogen of *Aphis citricola* (Homoptera: Aphididae), and two new combinations of other species of Entomophthoraceae. *Phytoparasitica* 9: 33-42.
- Ben-Ze'ev, I. and Kenneth, R. G. (1981b). *Zoophthora radicans* and *Zoophthora petchi* sp. nov. (Zygomycetes: Entomophthorales), two species of the "*sphaerosperma* group" attacking leaf-hoppers and frog-hoppers (Hom.). *Entomophaga* 26: 131-142.
- Ben-Ze'ev, I. and Kenneth, R. G. (1982). Features-Criteria of taxonomic value in the Entomophthorales: II. A revision of the genus *Erynia* Nowakowski 1881 (= *Zoophthora* Batko 1964). *Mycotaxon* 14: 456-475.
- Ben-Ze'ev, I., Kenneth, R. G. and Bitton, S. (1981). The Entomophthorales of Israel and their arthropod hosts. *Phytoparasitica* 9: 43-50.
- Ben-Ze'ev, I. and Uziel, A. (1979). *Monellia costalis* (Fitch), a new host for *Zoophthora radicans* (Brefeld) Batko and *Entomophthora planchoniana* Comu (Zygomycetes: Entomophthoraceae) in Israel. *Phytoparasitica* 7: 159-167.

- Berdan, H. (1938). Revision of the genus *Ancylistes*. *Mycologia* 30: 396-415.
- Bitton, S., Kenneth, R. G. and Ben-Ze'ev, I. (1979) Zygosporic overwintering and sporulative germination in *Triplosporium fresenii* (Entomophthoraceae) attacking *Aphis spiraeicola* on citrus in Israel. *J. Invertebr. Pathol.* 34: 295-302.
- Brefeld, O. (1877). Über die Entomophthoreen und ihre Verwandten. *Bot. Ztg.* 35: 345-355; 368-372.
- Carner, G. R. (1980). *Entomophthora lampyridarum*, a fungal pathogen of the soldier beetle, *Chauliognathus pennsylvanicus*. *J. Invertebr. Pathol.* 36: 394-398.
- Castaner, D. (1968). A *Conidiobolus*-like fungus destroying nematodes in Iowa. *Mycologia* 60: 440-443.
- Cavara, D. F. (1899a). I nuclei delle Entomophthoreae in ordine alla filogenesi di queste piante. *Boll. Soc. Bot. Ital.* 29: 55-60.
- Cavara, D. F. (1899b). Osservazioni citologiche sulle Entomophthoreae. *Nov. G. Bot. Ital., (N.S.)* 6: 411-466.
- Cohn, F. (1875). Über eine neue Pilzkrankheit der Erdräupen. *Beitr. Z. Biol. D. Pflanz.* 1: 58-86.
- Couch, J. N. (1949). A new species of *Ancylistes* on a saccoderm desmid. *J. Elisha Mitchell Sci. Soc.* 65: 131-136.
- Couch, J. N., Andreeva, R. V., Laird, M. and Nolan, R. A. (1979). *Tabanomyces milkoi* (Dudka and Koval) emended, genus novum a fungal pathogen of horseflies. *Proc. Natl. Acad. Sci. USA* 76: 2299-2302.
- Davidson, J. G. N. and Barron, G. L. (1973). Nematophagous fungi: *Meristacrum*. *Can. J. Bot.* 51: 231-233.
- Drechsler, C. (1940). Three fungi destructive to free-living terricolous nematodes. *J. Washington Acad. Sci.* 30: 240-254.
- Drechsler, C. (1946). A nematode-destroying Phycomycete forming immobile spores in aerial evacuation tubes. *Bull. Torrey Bot. Club* 73: 1-17.
- Drechsler, C. (1951). An entomophthoraceous tardigrade parasite producing small conidia on propulsive cells in spicate heads. *Bull. Torrey Bot. Club* 78: 183-200.
- Drechsler, C. (1954). Two species of *Conidiobolus* with minutely ridged zygosporic. *Am. J. Bot.* 41: 567-575.
- Drechsler, C. (1955). Two new species of *Conidiobolus* that produce microconidia. *Am. J. Bot.* 42: 793-802.
- Drechsler, C. (1964). An odorous *Basidiobolus* often producing conidia plurally and forming some declivous sexual apparatus. *Am. J. Bot.* 51: 770-777.
- Forbes, S. A. (1888). On the present state of our knowledge concerning contagious insect diseases. *Psyche* 5: 3-12.
- Fresenius, G. (1856). Notiz, Insecten-Pilze betreffend. *Bot. Ztg.* 14: 882-883.
- Garrison, R. G., Mariat, F., Boyd, K. S. and Tally, J. F. (1975). Ultrastructural and electron cytochemical studies of *Entomophthora coronata*. *Ann. Microbiol. (Inst. Pasteur)* 126B: 149-173.
- Gustafsson, M. (1965). On species of the genus *Entomophthora* in Sweden. I. Classification and distribution. *Lantbrukshögsk. Ann.* 31: 103-212.
- Hall, I. M. and Bell, J. V. (1962). Nomenclature of *Empusa* Cohn 1855 vs. *Entomophthora* Fresenius 1856. *J. Insect. Pathol.* 4: 224-228.
- Heath, I. B. (1980). Fungal mitoses, the significance of variations on a theme. *Mycologia* 72: 229-250.

- Hesseltine, C.W. and Ellis, J. J. (1973). Mucorales. I. General discussion of the class Zygomycetes. In: THE FUNGI, AN ADVANCED TREATISE. (ed. G. C. Ainsworth, F. K. Sparrow and A. S. Sussman) Vol. IVb. Academic Press.
- Hughes, S. J. (1971). Phycomycetes, Basidiomycetes and Ascomycetes as Fungi Imperfecti. In: TAXONOMY OF FUNGI IMPERFECTI. (ed. B. Kendrick) University of Toronto Press.
- Humber, R. A. (1976). The systematics of the genus *Strongwellsea* (Zygomycetes: Entomophthorales). *Mycologia* 68: 1042-1060.
- Humber, R. A. (1981a). An alternative view of certain taxonomic criteria used in the Entomophthorales (Zygomycetes). *Mycotaxon* 13: 191-240.
- Humber, R. A. (1981b). *Erynia* (Zygomycetes: Entomophthorales): Validations and new species. *Mycotaxon* 13: 471-480.
- Humber, R. A. (1982a). *Strongwellsea* vs. *Erynia*: the case for a phylogenetic classification in the Entomophthorales (Zygomycetes). *Mycotaxon*: (in press)
- Humber, R. A. (1982b). Nuclear cytology, a criterion separating *Conidiobolus* from *Entomophthora* and delimiting three families in the Entomophthorales (Zygomycetes). (in preparation for *Mycotaxon*).
- Humber, R. A. and Ben-Ze'ev, I. (1981). *Erynia* (Zygomycetes: Entomophthorales): Emendation, synonymy, and transfers. *Mycotaxon* 13: 506-516.
- Humber, R. A., Soper, R. S., MacLeod, D. M. Tyrrell, D., Kenneth, R. G. and Ben-Ze'ev, I. (1981) Proposal to conserve the entomopathogenic fungal genus *Triplosporium* (Thaxter) Batko against *Neozygites* Wiltaczil (Entomophthorales). *Taxon* 30: 353-357.
- Hutchison, J. A. (1962). Studies on a new *Entomophthora* attacking callypstrate flies. *Mycologia* 54: 258-271.
- Hutchison, J. A. (1963). The genus *Entomophthora* in the Western Hemisphere. *Trans. Kansas Acad. Sci.* 66: 237-254.
- Ingold, C. T. (1966). Spore release. In: THE FUNGI, AN ADVANCED TREATISE. (ed. G. C. Ainsworth, F. K. Sparrow and A. S. Sussman) Vol. II. Academic Press.
- Ingold, C. T. and Plunkett, B. E. (1979). An epidemic of *Entomophthora* on flies and its relationship with the *Sphacelia* stage of *Claviceps*. *Bull. Br. Mycol. Soc.* 13: 35-37.
- Keller, S. (1978). *Entomophthora gigantea* sp. nov. and *E. caroliniana* (Thaxter) comb. nov., two pathogens of *Tipula paludosa* Meig. *Sydowia*, *Ann. Mycol.*, Ser. II - 31: 87-93.
- Kendrick, B. (1971). Conclusions and Recommendations. In: TAXONOMY OF FUNGI IMPERFECTI. (ed. B. Kendrick) University of Toronto Press.
- Kenneth, R. G. (1977). *Entomophthora turbinata* sp. n., a fungal parasite of the peach trunk aphid, *Pterochloroides persicae* (Lachnidae). *Mycotaxon* 6: 381-390.
- Kenneth, R., Wallis, G., Gerson, U. and Plaut, H. N. (1972). Observations and experiments on *Triplosporium floridanum* (Entomophthorales) attacking spider mites in Israel. *J. Invertebr. Pathol.* 19: 366-369.
- Kevorkian, A. G. (1937). Studies in the Entomophthoraceae: I. Observations on the genus *Conidiobolus*. *J. Agric. Univ. Puerto Rico* 21: 191-200.
- King, D. S. (1976a). Systematics of *Conidiobolus* (Entomophthorales) using numerical taxonomy. I. Biology and cluster analysis. *Can. J. Bot.* 54: 45-65.

- King, D. S. (1976b) Systematics of *Conidiobolus* (Entomophthorales) using numerical taxonomy. II. Taxonomic considerations. *Can. J. Bot.* 54: 1285-1296.
- King, D. S. (1977). Systematics of *Conidiobolus* (Entomophthorales) using numerical taxonomy. III. Descriptions of recognized species. *Can. J. Bot.* 55: 718-729.
- King, D. S. and Humber, R. A. (1981). Identification of the Entomophthorales. In: MICROBIAL CONTROL OF PESTS AND PLANT DISEASES 1970-1980. (ed. H. D. Burges) *Academic Press*.
- Lakon, G. (1915). Zur Systematik der Entomophthoreen Gattung *Tarichium*. *Z. Pflanzenkrankh.* 25: 257-272.
- Lakon, G. (1919). Die Insektenfeinde aus der Familie Entomophthoraceen. *Z. Angew. Entomol.* 5: 161-216.
- Latgé, J. P., King, D. S. and Papierok, B. (1980). Synonymie de *Entomophthora virulenta* Hall et Dunn et de *Conidiobolus thromboides* Drechsler. *Mycotaxon* 11: 255-268.
- MacLeod, D. M. (1963). Entomophthorales infections. In: INSECT PATHOLOGY. (ed. E. A. Steinhaus) Vol. 2. *Academic Press*.
- MacLeod, D. M. and Müller-Kögler, E. (1970). Insect pathogens: species originally described from their resting spores mostly as *Tarichium* species (Entomophthorales: Entomophthoraceae). *Mycologia* 62: 33-66.
- MacLeod, D. M. and Müller-Kögler, E. (1973). Entomogenous fungi: *Entomophthora* species with pear-shaped to almost spherical conidia (Entomophthorales: Entomophthoraceae). *Mycologia* 65: 823-893.
- MacLeod, D. M., Müller-Kögler, E. and Wilding, N. (1976). *Entomophthora* species with *E. muscae*-like conidia. *Mycologia* 68: 1-29.
- May, B., Roberts, D. W. and Soper, R. S. (1979). Intraspecific genetic variability in laboratory strains of *Entomophthora* as determined by enzyme electrophoresis. *Experimental Mycology* 3: 28-29.
- McCulloch, J. S. (1977). New species of nematophagous fungi from Queensland. *Trans. Br. Mycol. Soc.* 68: 173-179.
- Mietkiewski, R., Soper, R. S. and Bałazy, S. (1981). Notes on *Zoophthora occidentalis* (Thaxter) Batko (Entomophthorales: Entomophthoraceae). *Mycotaxon* 13: 41-49.
- Milner, R. J., Teakle, R. E., Lutton, G. G. and Dare, F. M. (1980). Pathogens (Phycomycetes: Entomophthoraceae) of the blue-green aphid *Acyrtosiphon kondoi* Shinji and other aphids in Australia. *Aust. J. Bot.* 28: 601-619.
- Miura, K. (1973). Three entomophthoralean parasites of nematodes collected from Japan. *Rept. Tottori Mycol. Inst. (Japan)* 10: 517-522.
- Narasimhan, M. J. (1970). Entomogenous fungi and possibility of their use for biological control of insect pests in India. *Indian Phytopath.* 23: 16-26.
- Narasimhan, M. J. and Thirumalachar, M. J. (1977). Entomogenous fungus attacking scale insects on coffee leaves in India. *Abs. 2nd Int. Mycol. Congr. Tampa, Florida, Vol. 2: 466*.
- Nowakowski, L. (1881). O grupie owadomorków (Empusaceae). *Dzienn. III Zjazdu Lek. Przym. Polak. Kraków, Sekc. Bot.* 6: 67.
- Nowakowski, L. (1883). Entomophthorae. Przyczynek do znajomości pasorzytnych grzybków sprawiających pomór owadów. *Pamiętn. Wydz. Akad. Umiej. Kraków* 8: 153-183.
- Papierok, B. and Coremans-Pelseneer, J. (1980). Contribution à l'étude de *Conidiobolus osmodes* Drechsler (Zygomycetes Entomophthoraceae) agent occasionnel d'épizooties chez les pucerons (Homoptères, Aphididae). *Cryptog. Mycol.* 1: 111-117.

- Petch, T. (1926). Studies on entomogenous fungi. IX. *Empusa lecanii* Zimm. *Trans. Br. Mycol. Soc.* 11: 254-258.
- Petch, T. (1931). Notes on entomogenous fungi. 38. *Empusa lecanii* Zimm. (p. 229). *Trans. Br. Mycol. Soc.* 16: 209-245.
- Petch, T. (1934). Notes on entomogenous fungi. 86. *Entomophthora aphrophorae* Rostrup. 87. *Empusa muscae* Cohn (pp. 179-181). *Trans. Br. Mycol. Soc.* 19: 161-193.
- Petch, T. (1940). An *Empusa* on a mite. *Proc. Linnæan Soc. New South Wales* 65: 259-260.
- Petch, T. (1943). Notes on entomogenous fungi. 189. *Empusa acaridis* Petch, n. sp. (p. 87). 193. *Entomophthora anglica* Petch n. sp. (p. 89). *Trans. Br. Mycol. Soc.* 26: 81-93
- Remaudière, G. and Hennebert, G. L. (1980). Révision systématique de *Entomophthora aphidis* Hoffm. in Fres. Description de deux nouveaux pathogènes d'aphides. *Mycotaxon* 11: 269-321.
- Remaudière, G. and Keller, S. (1980). Révision systématique des genres d'Entomophthoraceae à potentialité entomopathogène. *Mycotaxon* 11: 323-338.
- Remaudière, G., Keller, S., Papierok, B. and Latgé, J. P. (1976a). Considérations systématiques et biologiques sur quelques espèces d'*Entomophthora* du groupe *sphaerosperma* pathogènes d'insectes (Phycomycètes: Entomophthoraceae). *Entomophaga* 21: 163-177.
- Remaudière, G., Latgé, J. P., Papierok, B. and Coremans-Pelseneer, J. (1976b). Sur le pouvoir pathogène de quatre espèces d'Entomophthorales occasionnellement isolées d'aphides en France. *C. R. Acad. Sci. Paris, D.*, 283: 1065-1068.
- Remaudière, G., Latgé, J. P. and Papierok, B. (1979). Reconsidération taxonomique de *Entomophthora obscura* Hall et Dunn. *Ann. Microbiol. (Inst. Pasteur)*, 130A: 151-162.
- Reukauf, E. (1912). Ein Verderber des Wasserbaren *Macrobiotus lacustris* Duj., *Macrobiotophthora vimariensis* (Reukauf). *Centralbl. f. Bact., Parasitenk. Infektkrankh.* 63: 390-393.
- Riddle, L. W. (1906). On the cytology of the Entomophthoraceae. *Proc. Am. Acad. Arts, Sci.* 63: 177-197.
- Samson, R. A., Ramakers, P. M. J. and Oswald, T. (1979). *Entomophthora thripidum*, a new fungal pathogen of *Thrips tabaci*. *Can. J. Bot.* 57: 1317-1323.
- Sneath, P. H. A. (1957). Some thoughts on bacterial classification. *J. Gen. Microbiol.* 17: 184-200.
- Soper, R. S. (1963). *Massospora levispora*, a new species of fungus pathogenic to the cicada, *Okanagana rimosa*. *Can. J. Bot.* 41: 875-878.
- Soper, R. S. (1974). The genus *Massospora* entomopathogenic for cicadas, Part I. Taxonomy of the genus. *Mycotaxon* 1: 13-40.
- Soper, R. S. (1981). New cicada pathogens: *Massospora cicadettæ* from Australia and *Massospora pahariae* from Afghanistan. *Mycotaxon* 13: 50-58.
- Speare, A. T. (1922). Natural control of the citrus mealy-bug in Florida. *U.S.D.A. Bull.* 1117: 1-19.
- Srinivasan, M. C. and Thirumalachar, M. J. (1964). On the identity of *Entomophthora coronata*. *Mycopathol. Mycol. Appl.* 24: 294-296.
- Srinivasan, M. C. and Thirumalachar, M. J. (1967). Evaluation of taxonomic characters in the genus *Conidiobolus*, with key to known species. *Mycologia* 59: 698-713.

- Strong, F. E., Wells, K. and Apple, J. W. (1960). An unidentified fungus parasitic on the seed-corn maggot. *J. Econ. Entomol.* 53: 478-479.
- Thaxter, R. (1888). The Entomophthorae of the United States. *Mem. Boston Soc. Nat. Hist.* 4: 133-201.
- Tucker, B. E. (1981). A review of the nonentomogenous Entomophthorales. *Mycotaxon* 13: 481-505.
- Turian, G. (1957). Entomo-mycoses dans la région de Genève. *Mitt. Schweiz. Ent. Ges.* 30: 93-98.
- Tyrrell, D. and MacLeod, D. M. (1972). A taxonomic proposal regarding *Delacroixia coronata* (Entomophthoraceae). *J. Invertebr. Pathol.* 20: 11-13.
- Ubrizsy, G. and Vörös, J. (1966). A new conception in the review on the phylogeny and system of fungi. *Acta Botan. Acad. Sci. Hung.* 12: 199-220.
- Wallis, G. (1972). [Survey of entomogenous fungi in Israel] *M. Sc. dissertation, Hebrew University of Jerusalem* (in Hebrew).
- Waterhouse, G. M. (1973). Entomophthorales. In: THE FUNGI, AN ADVANCED TREATISE. (ed. G. C. Ainsworth, F. K. Sparrow and A. S. Sussman) Vol. IVb. Academic Press.
- Waterhouse, G. M. (1975). Key to the species *Entomophthora* Fres. *Bull. Br. Mycol. Soc.* 9: 15-41.
- Webster, J. (1970). INTRODUCTION TO FUNGI. Cambridge University Press, Cambridge.
- Webster, J., Sanders, P. F. and Descals, E. (1978). Tetraradiate aquatic propagules in two species of *Entomophthora*. *Trans. Br. Mycol. Soc.*, 70: 472-479.
- Weiser, J. (1968). *Triplosporium tetranychii* sp. n. (Phycomycetes, Entomophthoraceae), a fungus infecting the red mite *Tetranychus altheae* Hanst. *Folia Parasitol. (Praha)* 15: 115-122.
- Weiser, J. and Batko, A. (1966). A new parasite of *Culex pipiens* L., *Entomophthora destruens* sp. nov. (Phycomycetes, Entomophthoraceae). *Folia Parasitol. (Praha)* 13: 144-149.
- Wilding, N. (1971). Resting spore formation and germination in *E. fresenii*. *Rept. Rothamsted Exp. Stn. for 1970*, pt. I: 206.
- Witlaczil, E. (1885). *Neozygites aphidis*, eine neue Gregarine. *Arch. F. Mikr. Anat.* 24: 299-603.
- Zimmermann, A. (1901). De dierlijke Vijanden der Koffiecultuur op Java Deel II. *Meded. Lands Plantent.* 44: 25-27.

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FEATURES-CRITERIA OF TAXONOMIC VALUE IN THE ENTOMOPHTHORALES: II. A REVISION OF THE GENUS ERYNIA NOWAKOWSKI 1881 (=ZOOPHTHORA BATKO 1964)

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ABSTRACT

The subgenera *Zoophthora* subgen. *Erynia* Batko 1966 and *Z.* subgen. *Zoophthora* are emended and transferred to the genus *Erynia* Nowakowski 1881, emend. Humber & Ben-Ze'ev. The subgenus *Z.* subgen. *Pandora* Batko 1966 is redescribed as *Erynia* subgen. *Neopandora*, subgen. nov., while *Z.* subgen. *Furia* Batko 1966 is rejected. All recognized species of *Erynia sensu* Humber & Ben-Ze'ev are reclassified in the three aforementioned subgenera and in the temporary, auxiliary group, *Erynia sensu lato*, proposed for *Erynia* species with incompletely described subgeneric characters. *Entomophthora zabrii* Rozsypal 1951 (*nomen nudum*) is validated and reclassified as *Erynia zabrii* sp. nov.; its previous synonymy with *Tarichium jaczewskii* Zaprometov in Jaczewski & Jaczewski 1931 is rejected as unjustified. *Empusa sciarae* Olive 1906 is transferred to *Erynia* as *E. sciarae* comb. nov., its previous synonymies with *Entomophthora montana* (Thaxter) Lakon 1919 being rejected as unjustified.

INTRODUCTION

A revised Batkooan classification of Entomophthorales, based on a preliminary classification of features-criteria**, was proposed in part I of this study (Ben-Ze'ev and Kenneth, 1982). According to this classification, species characterized by entomophthoroid nuclei; bitunicate, uninucleate conidia; multicellular, usually ramified conidiophores, and

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** For definitions see part I.

active (rounding-off) discharge of conidia, comprise the generic frame (13) [(CW)II-(CNN)II-(CS)IIb-(CD)Ia: E] which corresponds perfectly with the genus *Erynia* Nowakowski 1881, emend. Humber and Ben-Ze'ev 1981. This frame corresponds as well with the genus *Zoophthora* Batko 1964(a). However, as stressed by recent studies (Remaudière and Hennebert, 1980; Humber, 1981 a; Humber and Ben-Ze'ev, 1981), the generic name *Erynia* Nowakowski 1881, despite rejection by its own author (Nowakowski, 1883), has priority over *Zoophthora*, since its type, *Erynia ovispora* Nowakowski 1881, was included by Batko (1964b) in *Zoophthora*. Batko (1966b) used the name *Erynia* for one of the four subgenera proposed by him in *Zoophthora*. This subgenus comprised Nowakowski's (1881) three original species of *Erynia* and seven additional ones. The description of this subgenus (Batko, 1966b) and most of the species allocated in it correspond to group (1) of *Erynia* as defined in the next chapter.

Remaudière and Keller (1980) redefined *Erynia* Nowakowski, altering both Nowakowski's (1881) generic description and Batko's (1966b) subgeneric one. According to their definition and implied by the species classified in it, *Erynia* comprised species with bitunicate, uninuclear conidia and multicellular, ramified conidiophores, along with species possessing unitunicate, plurinucleate conidia and simple, unicellular conidiophores. The most important characters of *Erynia sensu* Remaudière and Keller (1980) appear to be the elongate shape of the primary conidia and lack of capilliconidia. These criteria were explicitly rejected by us from use at the generic level in part I of this study as well as in previous ones (e.g., Ben-Ze'ev, 1980; Ben-Ze'ev and Kenneth, 1981a; Humber, 1981a; Humber and Ben-Ze'ev, 1981). Consequently, the description of *Erynia* Nowakowski was emended (Humber and Ben-Ze'ev, 1981) to match the features-criteria classified in part I, in frame (13), and the generic name *Zoophthora* Batko has been placed in synonymy under *Erynia*.

Certain similarities and dissimilarities among the species classified in *Erynia* by Humber and Ben-Ze'ev (1981) or in its synonym, *Zoophthora* (Batko, 1964a, b; 1966a, b), suggested the existence of natural subgroups, called by Thaxter (1888) "*sphaerosperma* group", "close to, or allied to *E. aphidis*" and "*ovispora* type". Batko (1966a, b) used these similarities and dissimilarities to divide *Zoophthora* into four subgenera: subgen. *Zoophthora*, centered around Thaxter's "*sphaerosperma* group"; subgen. *Pandora* centered around the "*aphidis* group", subgen. *Erynia* centered

around the "ovispora group", and subgen. *Furia*, which was monotypic for *Z. virescens* (Thaxter) Batko 1964(e).

According to our analysis of the importance of certain features-criteria at the subgeneric level (in part I), we attempt in the next chapter a classification of features-criteria which appear to delimit subgeneric groups within *Erynia*. Batko's (1966b) subgenera of *Zoophthora* are discussed; subgen. *Erynia* and *Zoophthora* are emended, a new subgenus, *Neopandora*, is proposed as replacement for subgen. *Pandora* Batko, and the subgenus *Furia* is rejected. All species belonging to *Erynia* are reclassified in subgenera, except for those in which characters used to define subgenera are incompletely known. For such species an extra group, here termed *Erynia sensu lato*, is proposed.

THE SUBGENERA OF THE GENUS *ERYNIA* NOWAKOWSKI

The features-criteria considered by us important at the subgeneric level suggest the following subgeneric groups within frame (13), *Erynia* Nowakowski, emend. Humber and Ben-Ze'ev 1981:

GROUP:

- 1) Types Ia and/or Ib, and V secondary conidia; rhizoids monohyphal, as thick or thicker than conidiophores, usually without a differentiated holdfast, rarely absent; pseudocystidia twice to several times thicker than conidiophores.
- 2) Type Ia and/or Ib secondary conidia only; rhizoids monohyphal, as thick or several times thicker than conidiophores, possessing well differentiated holdfasts, rarely absent; pseudocystidia usually present, as thick as conidiophores, sometimes with much thicker, bulbous bases.
- 3) Types Ia and II secondary conidia (capilliconidia); rhizoids monohyphal, as thick as conidiophores, or pseudorhizomorphs, both types usually present together and possessing differentiated holdfasts; pseudocystidia as thick as conidiophores, present or absent.

Multiplicative resporulation, a subgeneric feature-criterion in ANCYLISTACEAE and BASIDILOBOLACEAE, is not mentioned since it appears to be absent throughout the family ENTOMOPHTHORACEAE.

1. The Subgenus *Erynia*

Group (1) has the same characteristics as described by Batko (1966b) for *Zoophthora* subgen. *Erynia*. This subgenus is therefore transferred here to the genus *Erynia* and its description is emended to include details found after Batko's original description:

ERYNIA Nowakowski subgen. *ERYNIA*, emend.

SYNONOYM: *Zoophthora* Batko subgen. *Erynia* (Nowak.)

Batko, *Acta Mycol.* 2: 15-21, Figs. 4 and 5, 1966.

Primary conidia are elongate and belong to the papillata-sporangiata or turbinata type (according to Lakon's (1919) classification), and have a highly vacuolized cytoplasm. Secondary conidia are of Type Ia, or more frequently Ib, some species produce aquatic secondary conidia (Type V). Pseudocystidia, present in all known species, are twice to several times thicker than the conidiophores, frequently being branched or expanded at their distal ends, and stand out high above the conidiophorous layer. Rhizoids are as thick as the pseudocystidia or thinner, generally devoid of a distinct holdfast, or absent. Resting spores are usually produced by distinct conjugations between two hyphal bodies or hyphal segments. Most species attack DIPTERA, one species attacking TRICHOPTERA and another one HOMOPTERA.

The species allocated to this subgenus are:

- 1) *Erynia ovispora* Nowakowski 1881 - subgeneric type;
- 2) *E. curvispora* Nowak. 1881;
- 3) *E. conica* (Nowak. 1883) Remaudière & Hennebert 1980;
- 4) *E. delpiniana* (Cavara 1899) Humber 1981(a);
- 5) *E. erinacea* (Ben-Ze'ev & Kenneth 1979) Rem. & Henn. 1980;
- 6) *E. gracilis* (Thaxter 1888) Rem. & Henn. 1980;
- 7) *E. montana* (Thaxter 1888) Rem. & Henn. 1980;
- 8) *E. rhizospora* (Thaxter 1888) Rem. & Henn. 1980;
- 9) *E. sepulchralis* (Thaxter 1888) Rem. & Henn. 1980;
- 10) *E. variabilis* (Thaxter 1888) Rem. & Henn. 1980.

Eight species (Nos. 1-3 and 6-10) of the above-listed ten were allocated to this subgenus by Batko (1966a,b) along with the following two: *Zoophthora jaczewskii* (Zaprometov) Batko and *Z. blunckii* (Lakon) Batko. New findings and a careful interpretation of their descriptions led us to transfer these two species to the next subgenus. *E. erinacea* was added to this subgenus by Ben-Ze'ev and Kenneth (1979), and *E. delpiniana* is added in the present paper.

2. The Subgenus *Neopandora*

Group (2) corresponds with Batko's (1966b) *Zoophthora* subgen. *Pandora*, typified with "*Zoophthora (Pandora) aphidis*" (Hoffm. in Fres.) Batko 1964(b). However, Remaudière and Hennebert (1980) revealed that the fungus originally described by Hoffman as *Entomophthora aphidis* is different from the species considered by later authors, including Batko, as "*Entomophthora (or Zoophthora) aphidis*". The two different species were redescribed by Remaudière and Hennebert (1980): the misapplied species under the new name, *Erynia neoaphidis*, and *Zoophthora aphidis* for Hoffman's rediscovered species. As a consequence of their taxonomic and nomenclatural clarification, they placed Batko's subgenus *Pandora* in synonymy with the genus *Zoophthora* Batko (*sensu* Remaudière and Hennebert, 1980).

According to our subgeneric criteria, however, group (2) of *Erynia* is distinct from the other two groups and is entitled to a subgeneric status and name. Furthermore, group (2) is characterized by the same features-criteria and is comprised of the same species as Batko's subgenus *Pandora*. Its type-species was renamed by Remaudière and Hennebert (1980) as *E. neoaphidis*, apparently in order to retain its meaning (this species being the first discovered of the few aphid-attacking ones in this group). We prefer to propose formally a new subgenus, with a new name, since the subgeneric epithet *Pandora* is tied to a species name which has been misapplied. In order to retain Batko's original meaning of *Pandora*, the new subgenus is named *Neopandora*, and Batko's original Latin description is used without any emendations. The subgeneric type is the one which Batko (1966b) originally intended to designate, but under its new name. The English description is, however, emended by addition of characters concerning the secondary conidia and other structures:

ERYNIA Nowakowski subgen. *Neopandora*
Ben-Ze'ev and Kenneth, subgen. nov.

"*Conidia cylindrica, ovulata, adverse ovulata, pyriformia, rarius - fusiformia, in classificatione Lakonii (1919) ad typos subpapillata, rarius papillata vel sporangiata pertinentia, saepe symmetria laterali vix respecta distincta. Una ex parte (ventrali) leviter complanata, altera ex parte (dorsali) magis ventriosa, tertia ex parte (lateralis) leviter ad partem ventralem*

curvata, et paulum asymetrica. Papilla parti ventrali proximier. Plasma multis cum vacuolis, squamosa et granulosa, saepe cum cristallico corpore lucem fortiter fractantem, non longe a basi posite. Nucleus sphaericus vel lensiformis saepe ventrali superficiei conidii proximier, aliquando irregularis. Pseudocystidia tenua, conidiophoris non maceriora, vel omnine desunt. Rhizoidea singularia, macria, terminata lato scutalique pede, aliquando irregulariter ramosa; termini ramorum in brevium processorum faciculos congregati."

Typus subgeneris: Erynia neoaphidis Remaudière & Hennebert, Mycotaxon 11: 269-321, 1980. ("Entomophthora aphidis" sensu Nowakowski 1883, sensu Thaxter 1888; non sensu Petch 1939; = "Zoophthora (Pandora) aphidis" sensu Batko 1966b; non Zoophthora aphidis sensu Remaudière and Hennebert 1980).

[Primary]* conidia [are] oval, ovoid, obovoid, pyriform, less frequently fusiform, according to Lakon's classification (1919) of subpapillata type, less frequently papillata or sporangiata, often with weakly outlined bilateral symmetry: on one side (abdominal) slightly flattened, on [the] opposite (dorsal) side more convex, on the third (lateral) side somewhat curved towards the abdominal side and slightly asymmetrical, papilla nearer [the] abdominal side: plasma highly vacuolated, foamy or granulated, sometimes contains large, highly refractive crystals near [the] base of [the] conidium; [the] nucleus [is] spherical or slightly depressed, frequently closer to [the] abdominal surface of [the] conidium, sometimes slightly irregular, [it] stains only a little more intensively with cotton blue than the plasma. [Secondary conidia are of Type Ia, with a lower length/diameter ratio than the primary ones, or are of Type Ib - resembling the primary (or sometimes the secondary) conidia of *Entomophthora planchoniana*. No capillconidia are produced]. Pseudocystidia [are] thin, not thicker than the conidiophores [sometimes issuing from much thicker, bulbous cells found at their bases] or absent. Rhizoids [are monohyphal] single, thick[er than conidiophores] or [as] thin [as them], ending in [a] broad scutellar or irregular foot, sometimes irregularly branched. The ends of the ramifications have the form of bunches of short

* Additions [in square parentheses] are ours, inserted in Batko's (1966b) original description.

processes.

The species allocated to this subgenus are:

- 1) *Erynia neoaphidis* Remaudière & Hennebert 1980 - subgeneric type;
- 2) *E. blunckii* (Lakon ex Zimmermann 1978) Rem. & Henn. 1980;
- 3) *E. brahminae* (Bose & Mehta 1953) Rem. & Henn. 1980;
- 4) *E. calliphorae* (Giard 1879) Rem. & Henn. 1980;
- 5) *E. delphacis* (Hori 1906) Humber 1981(a);
- 6) *E. dipterigena* (Thaxter 1888) Rem. & Henn. 1980;
- 7) *E. echinospora* (Thaxter 1888) Rem. & Henn. 1980;
- 8) *E. formicae* Humber & Bałazy, in Humber 1981(b);
- 9) *E. gloeospora* (Vuillemin 1883) Rem. & Henn. 1980;
- 10) *E. ithacensis* Kramer 1981;
- 11) *E. nouryi* Rem. & Henn. 1980 (= *Entomophthora exitialis* Hall & Dunn 1957, *sensu* Gustafsson, 1965);
- 12) *E. phalangicida* (Lagerh. 1898) Rem. & Henn. 1980;
- 13) *E. vomitoriae* (Rozsypal 1966) Rem. & Henn. 1980;
- 14) *E. zabrii* Rozsypal ex Ben-Ze'ev and Kenneth, sp. nov. (Latin description at the end of this section).

Nine species (Nos. 1, 3, 4, 6-9 and 11-13; Nos. 1 and 6 under different specific epithets - *aphidis* and *exitialis* respectively) were allocated in what corresponded to this subgenus by Batko (1966b), along with *Zoophtora (Pandora) ferruginea* (Philips 1886) Batko 1966(b). This last species is considered *nomen confusum*, as explained in detail by Remaudière and Hennebert (1980). *E. blunckii* was allocated by Batko (1966b) to the subgenus *Erynia*, based on Lakon's (1935) description of club-shaped cystidia. Zimmermann's (1978) detailed description and a personal communication accompanied by unpublished photographs shows clearly that both the pseudocystidia and the rhizoids of this species are not considerably thicker than its conidiophores (8.0-10.5 μm), the pseudocystidia are round-ended but not club-shaped and the rhizoids end in differentiated holdfasts. These characters justify the transfer of this species to the subgenus *Neopandora*. *E. delphacis* was not mentioned by Batko in any of his articles and is allocated to this subgenus here. This species does not possess rhizoids, otherwise being morphologically almost identical with *E. neoaphidis*, from which it differs in the rate of growth in culture and in its ability to attack leaf- and plant-hoppers in addition to aphids, which are hosts for both species (Shimazu, 1977; Humber, 1981a).

Entomophthora zabrii Rozsypal (1951, *nomen nudum*) was regarded by Batko (1964b) as the conidial stage of *Tarichium jaczewskii* Zaprometov in Jaczewski & Jaczewski 1931 (cited by Batko, 1964b), and was placed by him in the new combination: *Zoophthora jaczewski* (Zaprometov in Jaczewski) Batko. With the publication of his subgeneric treatment of *Zoophthora*, Batko (1966a, b) allocated this species to the subgenus *Erynia*, apparently on the grounds of its very wide pseudocystidia (50.0-60.0 μm at the base). In their recent treatment of *Erynia*, Humber and Ben-Ze'ev (1981) diverged in the acceptance of Batko's (1964b) synonymy, one of them (R.A.H.) accepting it as the new combination: *Erynia jaczewski* (Zapr. in Jacz. & Jacz.) Humber.

We hold the different position, close to that expressed by Benjamin (1979) that in the ENTOMOPHTHORALES, as in most ZYGOMYCETES, classification, at least up to and including the generic level, is performed according to features-criteria of the anamorphs. Moreover, it is difficult to conclude what exactly are the teleomorphs of species producing azygospores or those of species in which resting spores were not conclusively described as either zygo- or azygospores. The genus *Tarichium* Cohn 1875 was defined as producing azygospores, therefore it cannot be considered as a genus comprised of the teleomorphs of species with lacking or unknown anamorphs, and is therefore considered in the present classification as a form-genus for species with unknown anamorphs (see part I). Thus, synonymies of anamorphic entomophthoralean species with *Tarichium* species can be unequivocally validated only when *Tarichium* species are found to produce conidial stages - either in the natural hosts or in artificial culture. Even in such situations, as that in which *Tarichium hylemiae* Lakon 1935 was shown to be the resting spore stage of one of the two known species of *Strongwellsea* Batko & Weiser (*S. castrans* Batko & Weiser and *S. magna* Humber: Wilding, 1975; Humber, 1976), none of the two known species could be synonymized as "*S. hylemiae*", despite the apparent priority of the latter name, since the species are distinguishable only in their conidial form, the resting spore stages being morphologically identical (Humber, 1976).

The following situation exemplifies even better the difficulties of pursuing "chronologic priority" when conidial species are placed in synonymy under earlier specific epithets of *Tarichium*. --*Entomophthora* (*Tarichium*) *punctata* Garbowski 1927 (cited here from MacLeod and Müller-Kögler, 1970) was described from dark, rough-walled resting spores

with a diameter of 26-37.5 μm , found in dead larvae of the alfalfa weevil, *Hypera postica* (= *Phytonomus variabilis*) in Poland and the U.S.S.R. The fungus from the U.S.S.R. was described at first as *Tarichium phytonomi* Jaczewski (Jaczewski in Zaprometov, 1928, cited in MacLeod and Müller-Kögler 1970) to show the connection, assumed by its author, with *Entomophthora phytonomi* Arthur 1886 (now: *Erynia phytonomi* (Arthur) Humber et al. in Humber and Ben-Ze'ev, 1981). However, *E. (T.) phytonomi* was placed in synonymy under *E. (T.) punctata* by MacLeod and Müller-Kögler (1970) because the connection with *E. phytonomi* was not proved, and the epithet *phytonomi* was preoccupied. Ben-Ze'ev and Kenneth (1980) found morphologically similar resting spores in larvae of *Hypera postica* (= *H. variabilis*) in Israel, but succeeded to isolate from infected larvae a *Conidiobolus*, *C. osmodes*, which proved to be pathogenic to *Hypera* larvae and to artificially infected houseflies, as well as to aphids (see refs. in part I). Harcourt et al. (1974, 1981) also found similar resting spores in larvae of *H. postica* in Ontario. In 1974 they thought these resting spores to belong to *Entomophthora phytonomi*. In 1981, however, they found that *H. postica* larvae were attacked by two different *Erynia* species, *E. phytonomi* with characteristic conidia and smooth-walled, hyaline resting spores, and a yet unnamed *Erynia* species, differing from *E. phytonomi* in both conidial morphology, and in being the one possessing dark, rough-walled resting spores, identical with those found by them in 1974 and similar to those described as *Tarichium punctata* or to those of *Conidiobolus osmodes*. Both *C. osmodes* (Ben-Ze'ev and Kenneth, 1980) and *Erynia* sp. (D. Tyrrell, pers. comm.) were proved to produce resting spores in *H. postica* larvae inoculated artificially with conidia, and in both cases the resting spores resembled *T. punctata* in dimensions and morphology.

Are there two, three or four species with similar resting spores attacking *Hypera* larvae? Supposing that there are only two such species, *C. osmodes* Drechsler 1954 and the yet unnamed *Erynia* sp., the name *T. punctata* appears to have priority over both. Since *T. punctata* does not exist in cluture, how can it ever be proved which of the two species, belonging to different genera and families, should be put in synonymy under the specific name *punctata*?

The logical conclusion must be that all specific names based on synonymies between *Tarichium* species and anamorphic entomophthoralean species, on the grounds of resting spore similarity and/or host identity, have to be regarded as

nomina dubia, including *Erynia jaczewskii*. Consequently, *E. zabrii* is validated here by a Latin description.

ERYNIA ZABRII Rozsypal ex Ben-Ze'ev & Kenneth,
sp. nov.

SYNONYM: *Entomophthora zabrii* Rozsypal,
Sbornik Česk. Acad. Zeměd. 24: 85-94. 1951
(nomen nudum).

Corpora hyphalia sphaerica vel lobulata; hyphae multinucleatae, ramosae, 11.0 μm med. diam. Conidiophori bifurcate ramosi. Conidia primaria uninucleata, ovoidea, papillata (secundum Lakoni [1919] classificationem), med. 25.0 x 14 μm, max. 29.0 x 18.0 μm, saepissime ad polos bivacuolata, ratione longitudinis ad diametrum = ca. 1.8. Conidia secundaria (typo I) non vidi, capilliconidia desunt. Pseudocystidia 300.0 μm longa, gradatim angustata, conidiophoris non latiora, base bulbosa 50.0-60.0 μm diam. excepta. Sporae perdurantes et intra et extra hospitis corpus formatae, atrobrunneae, sphaeroideae, 33.0-40.0 μm diam., laeves vel verrucosae, pariete crasso. Hospes ad substratum rhizoideis affixus. Hospes typicus: Zabrus tenebrioides (Coleoptera: Carabeidae) larvae.

Hyphal bodies are spheroidal or lobular, hyphae are multinucleate, ramified, 11.0 μm av. width. Conidiophores are bifurcately branched. Primary conidia are uninucleate, ovoid, of the papillata-type according to Lakoni's (1919) classification, av. 25.0 x 14.0 μm, max. 29.0 x 18.0 μm, usually polarly bivacuolate, approx. length/diameter ratio = 1.8. Secondary conidia (of type I) not observed, capilliconidia absent. Pseudocystidia are 300.0 μm long, tapering, not wider than the conidiophores except for the bulbous bases (which measure 50.0-60.0 μm in diameter). Resting spores are produced both inside and outside the host's body (on its surface) and are dark-brown, smooth or verrucose, thick walled, 33.0-40.0 μm in diameter. The host is affixed to the substrate by rhizoids. Pathogen of *Zabrus tenebrioides* larvae.

Type: the description and figures 2-12 in: Rozsypal, J., *Sbornik Českosl. Acad. Zeměd. 24: 85-94. 1951.*

We allocate this species to the subgenus *Neopandora*, excluding it from subgen. *Erynia* since only the bases of its pseudocystidia are considerably wider than the conid-

iophores, whereas subgen. *Erynia* is characterized by pseudocystidia wider than the conidiophores over their whole length. Moreover, the pseudocystidia of *E. neoaphidis*, the type species of subgen. *Neopandora*, have wide, bulbous bases as well.

E. myrmecophaga was allocated to this subgenus (under its former name, *Pandora*) by Bařazy and Sokořowski (1976), the characteristics of its pseudocystidia and rhizoids being described in detail by Loos-Frank and Zimmermann (1976). Humber (1981b) found that the descriptions of this species by different authors from different countries (Turian and Wuest, 1969; 1977 - Switzerland; Bařazy and Sokořowski, 1976 - Poland; Loos-Frank and Zimmermann, 1976 - F. R. Germany) related to two species of *Erynia*, both attacking ants but differing in conidial dimensions and rhizoid structure. The Swiss fungus was redescribed as *Erynia myrmecophaga* while the new species described from Poland and F. R. Germany was named *E. formicae* (Humber, 1981b). The rhizoids and pseudocystidia of *E. formicae*, as described by Humber and Bařazy (in Humber, 1981b), are characteristic for the subgenus *Neopandora*, while the presence of rhizoids in *E. myrmecophaga* appears as doubtful, and no pseudocystidia were reported.

3. The Subgenus *Zoophthora*

The characters used by Batko to distinguish between species of the subgenus *Zoophthora* and those belonging to the other subgenera of the genus *Zoophthora* were conidial shape, conidial plasmatic structure, nuclear shape and affinity to cotton-blue, rhizoids aggregated into pseudorhizomorphs and, least important, production of capilliconidia. The last feature was apparently considered by Batko (1966a, b) as correlated to the other features, but not essential, as implied by his allocation of species in the subgenus *Z. (Zoophthora)*. Of the ten listed species (Batko, 1966b) only four were known to produce capilliconidia. The remaining six species produced pseudorhizomorphs and only one of them was proved latter to produce capilliconidia: *Erynia phytonomi* (Arthur) Humber et al. (Ben-Ze'ev and Kenneth, 1980; Humber and Ben-Ze'ev, 1981). We expressed our doubts (Ben-Ze'ev and Kenneth, 1979) whether all species allocated by Batko to the subgenus *Zoophthora* belong there, and our intention to emend the diagnosis of this subgenus:

ERYNIA Nowakowski subgen. *ZOOPHTHORA* (Batko)
Ben-Ze'ev & Kenneth, emend. et comb. nov.

SYNONYMS: *Zoopthora* subgen. *Zoopthora* Batko, *Acta Mycol.* 2: 16, figs. 1-3, 1966.

= *Zoopthora* Batko *sensu* Remaudiere and Humber, *Mycotaxon* 11: 269-321.

= *Zoopthora* Batko subgen. *Pandora* Batko, *Acta Mycol.* 2: 18-19, 1966, excl. descr. et specimen.

Primary conidia are elongate and belong to the papillata-sporangiata type (according to Lakon's (1919) classification), their cytoplasm is without large vacuoles. Secondary conidia are of Types Ia and II (capilliconidia). Germ-conidia (known in two species, *E. canadensis* and *E. radicans**), arising on germ-conidiophores from germinating resting spores, are of Type I. Pseudocystidia are as thick as conidiophores, present in some species, absent in others. Rhizoids are monohyphal and pseudorhizomorphs, both usually with differentiated holdfasts, usually both kinds present together. Resting spores are budded from hyphal bodies or hyphal segments and are produced after apparent conjugations in some cases or without conjugations in others. Parasites of different insect orders.

The species allocated to this subgenus are:

- 1) *Erynia radicans* (Brefeld 1870) Humber *et al.* in Humber and Ben-Ze'ev, 1981 - subgeneric type;
- 2) *E. aphidis* (Hoffm. in Fres. 1858) Humber & Ben-Ze'ev, 1981 (= *Zoopthora aphidis* *sensu* Rem. & Henn. 1980);
- 3) *E. canadensis* (MacLeod *et al.* 1979) Humber & Ben-Ze'ev, 1981;
- 4) *E. crassitunicata* (Keller 1980) Humber & Ben-Ze'ev, 1981;
- 5) *E. elateridiphaga* (Turian 1978) Humber *et al.* in Humber and Ben-Ze'ev, 1981;
- 6) *E. geometralis* (Thaxter 1888) Humber & Ben-Ze'ev, 1981;
- 7) *E. lanceolata* (Keller 1980) Humber & Ben-Ze'ev, 1981;
- 8) *E. occidentalis* (Thaxter 1888) Humber & Ben-Ze'ev, 1981;
- 9) *E. orientalis* (Ben-Ze'ev & Kenneth, 1981) Humber *et al.* in Humber and Ben-Ze'ev, 1981;
- 10) *ERYNIA PETCHII* (Ben-Ze'ev & Kenneth) Ben-Ze'ev & Kenneth, comb. nov. BASIONYM: *Zoopthora petchi* Ben-Ze'ev & Kenneth, 1981, *Entomophaga* 26: 140-141, figs. 10-17.
- 11) *E. phalloides* (Batko 1966) Humber & Ben-Ze'ev, 1981;
- 12) *E. phytonomi* (Arthur 1886) Humber *et al.* in Humber and Ben-Ze'ev, 1981.

Five of the twelve listed species, Nos. 1, 6, 8, 11 and 12, were allocated to this subgenus by Batko (1966a,b).

*D. Perry, in preparation, personal communication (photographs).

Species Nos. 2, 3 and 5 were added by Ben-Ze'ev (1980). *E. orientalis* and *E. petchii* were added to subgen. *Zoophthora* by Ben-Ze'ev and Kenneth (1981a, b, respectively), and the species *E. crassitunicata* and *E. lanceolata* are allocated to this subgenus in the present paper.

Batko (1966b) included in subgenus *Zoophthora* five species which do not produce capilliconidia: *Zoophthora americana*, *Z. creatonoti*, *Z. forficulae*, *Z. bullata* and *Z. nebriae*. Four of these five species were transferred to *Erynia* by Humber and Ben-Ze'ev (1981), while *Entomophthora forficulae* was considered by them a doubtful species. Batko's reasons for allocating these species to subgen. *Zoophthora* were, apparently, their conidial shapes and production of pseudorhizomorphs. We prefer to keep these species outside any of *Erynia*'s subgenera, in a group devoid of subgeneric status, but comprised of species belonging to *Erynia*, *Erynia sensu lato*.

In the twelve species of *Erynia* producing capilliconidia and classified by us in subgen. *Zoophthora*, seven species were described as producers of both monohyphal rhizoids and pseudorhizomorphs: *E. radicans* (Ben-Ze'ev and Uziel, 1979); *E. canadensis* (MacLeod et al., 1979); *E. geometralis* (Thaxter, 1888); *E. occidentalis* (Ben-Ze'ev, 1980); *E. petchii* (Ben-Ze'ev and Kenneth, 1981b); *E. phal-loides* (Ben-Ze'ev, 1980); *E. phytonomi* (Ben-Ze'ev and Kenneth, 1980). Only pseudorhizomorphs were described in *E. elateridiphaga* (Remaudière et al., 1976), and only monohyphal rhizoids in *E. aphidis* (Remaudière and Hennebert, 1980). In *E. crassitunicata* and *E. lanceolata* the rhizoids were mentioned as present but were not described (Keller, 1980), while in *E. orientalis* rhizoids remain unobserved (Ben-Ze'ev and Kenneth, 1981a). A quite strong correlation is apparent from the above enumeration, between production of capilliconidia and production of both monohyphal rhizoids and pseudorhizomorphs. This correlation justifies the classification of species which possess the correlated features, in a separate subgenus. A species of *Erynia* that produces capilliconidia can be safely allocated to subgen. *Zoophthora* if only one kind of rhizoids is present and even if no rhizoids were observed, since there cannot be any mistake in identifying capilliconidia. However, the evolutionary possibility may exist, in which species derived from the common ancestor of subgenus *Zoophthora* might have lost the ability to produce capilliconidia. Such species might still be classified in this subgenus, if the other two characteristics are found to be correlated, e.g., if both pseudo-

rhizomorphs and monohyphal rhizoids are present, or even if only pseudorhizomorphs are found. In such a case the circumscription of subgen. *Zoophthora* will have to be emended accordingly. However, since pseudorhizomorph-like structures or even aggregations of abundant monohyphal rhizoids can be mistaken as pseudorhizomorphs, more careful identification of these structures is necessary. The four above-mentioned species excluded here from the subgenus *Zoophthora* are species in which the rhizoids appear to be, but have not been definitely identified as pseudorhizomorphs. Another species in which capilliconidia were not observed but which possesses unmistakable pseudorhizomorphs is *Erynia creatonoti* Yen ex Humber 1981(b). However, we keep this species in *Erynia sensu lato* as well, at least until such species are reencountered and thorough searches for capilliconidia are carried out. *E. phytonomi*, known for almost a century, was found to possess capilliconidia only recently (Ben-Ze'ev and Kenneth, 1980) and this may happen to other species as well.

4. The Subgenus *Furia* Batko 1964

This monotypic subgenus proposed by Batko (1966b) was typified by *Empusa virescens* Thaxter 1888, and was placed in synonymy with *Erynia* Nowak., together with the other subgenera of *Zoophthora* except subgen. *Zoophthora*, by Remaudière and Keller (1980). Three features-criteria were used by Batko (1966b) to characterize this subgenus:

"Conidia mostly of the epapillata type ... Conidiophores irregularly ramified, apical parts of the particular branchings separated from conidiophore by septa and bottlenwise distended. Pseudocystides absent."

We do not accept this subgenus on the following grounds: the conidia of *E. virescens* resemble those of other species of *Erynia*, particularly in the subgenera *Erynia* and *Neopandora*; the epapillate shape of conidia in one species cannot be considered as a subgeneric feature-criterion. The situation would have been different if there were more species characterized by this feature and by other correlated ones. The description of the conidiophores of *E. virescens* does not differ from that of conidiophores in other species of *Erynia* - some are irregularly ramified, all have septa separating the conidiogenous apical cells from the branches, some have bottlenwise distended conidiogenous cells. Contrary to Batko's claim that pseudocystidia are absent, Thaxter (1888, fig. 261) des-

cribed and figured "...structural similarity [with *E. neoaphidis*] indicated by the peculiar germination of the hyphal bodies already described in the last named form" (called by Thaxter *Empusa aphidis*). It is known at present that the "spherical hyphal bodies" thought by Thaxter (1888) to produce conidiophores, were pseudocystidial initials, located in the center of a group of conidiophores (Brobyn and Wilding, 1977). The finding of similar structures in *E. virescens* strongly suggests that this little-known species does possess pseudocystidia that were overlooked by Thaxter. Batko did not include features of the rhizoids in his description of *Z. (Furia)*, since these were not seen or described - except for being mentioned by Thaxter (1888): "Host attached to substratum by rhizoids?" In a later description, by Bucher and MacLeod (1974), rhizoids were mentioned as present, but were not described. To summarize: this monotypic subgenus was based on an incompletely described species, the lack of details concerning the subgeneric features-criteria rendering this taxon unacceptable. *E. virescens* is thus classified in *Erynia sensu lato*.

5. Incompletely Described *Erynia* species: *Erynia sensu lato*

Species that clearly belong to the genus *Erynia* by virtue of their bitunicate, uninucleate conidia borne on multicellular, usually ramified conidiophores, but which lack adequate descriptions of subgeneric features-criteria, cannot be placed in one of the three subgenera of *Erynia* and are therefore referred to as *Erynia sensu lato*. The species listed in this section were found and described only once, or continue to be poorly or inadequately described, without mention of the type and dimensions of secondary conidia or type and dimensions of their rhizoids and pseudocystidia.

These species include the following:

- 1) *Erynia americana* (Thaxter 1888) Rem. & Henn. 1980 - secondary conidia are of Type I, dimensions unmentioned; capilliconidia unmentioned; pseudocystidia absent; rhizoids monohyphal, apparently aggregated in a pseudorhizomorph-like structure.
- 2) *E. aquatica* (Anderson & Ringo ex Anderson & Anagnostakis 1980) Humber 1981(a) - described as lacking both pseudocystidia and rhizoids and producing secondary conidia of Type I only.

- 3) *E. bullata* Thaxter & MacLeod in Humber 1981 (b) - secondary conidia (any type) and pseudocystidia were not observed; rhizoids as in *E. americana*.
- 4) *E. coleopterorum* (Petch 1932) Humber & Ben-Ze'ev 1981 - in Petch's (1943) description of the conidial stage, secondary conidia (any type) were not mentioned. The primary conidia were assumed by Humber and Ben-Ze'ev (1981) to be bitunicate and uninucleate from the conjecture of the other features criteria. Its pseudocystidia and pseudorhizomorphs are like in *Erynia* subgen. *Zoophthora*.
- 5) *E. creatonoti* Yen ex Humber 1981 - secondary conidia (any type) were not mentioned; pseudocystidia were only mentioned as rarely present; pseudorhizomorphs are tubular, ending in funnel-like holdfasts, like in subgen. *Zoophthora*.
- 6) *E. crustosa* (MacLeod & Tyrrell 1979) Humber & Ben-Ze'ev 1981 - secondary conidia (any type) were not mentioned; pseudocystidia and rhizoids were not observed, although the authors mentioned that larvae are held on the substrate by the contraction of the prolegs and "...possibly by hyphae which protrude from the prolegs and ventral surface and may have an adhesive effect."
- 7) *E. henrici* (Molliard 1918) Humber & Ben-Ze'ev 1981 - the primary conidia were assumed by Humber and Ben-Ze'ev (1981) to be bitunicate and uninucleate from the conjecture of the other features-criteria; the type of secondary conidia is unknown; pseudocystidia and monohyphal rhizoids were mentioned but not described.
- 8) *E. myrmecophaga* Turian & Wuest ex Humber 1981 (b) has secondary conidia of Type I only; the monohyphal rhizoids described by Turian and Wuest (1977) are unlike any other such rhizoids in *Erynia* and were omitted from the new description provided by Humber (1981b); pseudocystidia are absent. Humber (1981b) regards the description of this species as "fragmentary".
- 9) *E. nebriae* (Raunkiaer 1892) Humber & Ben-Ze'ev 1981 - is in the same position as *E. coleopterorum* and *E. henrici*, except that pseudocystidia were not mentioned either.
- 10) *E. virescens* (Thaxter 1888) Rem. & Henn. 1980 - was discussed in the previous section.
- 11) *ERYNIA SCIARAE* (Olive) Ben-Ze'ev & Kenneth, comb. nov.
 BASIONYM: *Empusa sciarae* Olive, Bot. Gaz. (Crawfordsville), 41: 196, Pl. 14, figs. 1-9, 12-21, 27-29. 1906.
NON Entomophthora montana (Thaxter) Lakon, Z. Angew. Entomol. 5: 161-216. 1919, combination proposed again

by Gustafsson, *Lantbrukshögskolans Ann.* 31: 155-156, fig. 104-105. 1965.

This species was placed twice in synonymy under *E. montana* due to the different interpretations of the genus *Entomophthora* by the abovementioned authors (*Entomophthora sensu* Nowakowski vs. *Entomophthora* Fres. respectively, see Fig. 1 in Ben-Ze'ev and Kenneth, 1982). Both synonymies were based on similarity of conidial shape and dimensions and on the occurrence of both species on small dipterous insects. However, *E. montana* is easily recognized as a member of the subgenus *Erynia* by its conspicuous pseudocystidia. *E. sciarae* was described in considerable detail by Olive (1906), without any mention of pseudocystidia. Since Olive's description cannot be considered as less detailed than Thaxter's (1888) or Gustafsson's (1965) descriptions of *E. montana*, we have to conclude that *E. sciarae* does not possess pseudocystidia, or that its pseudocystidia are far less conspicuous than these of *E. montana*. Consequently the two species have to be considered as separate ones. *E. sciarae* is placed in *Erynia sensu lato* since capilliconidia and pseudocystidia were not seen, the rhizoids being only mentioned as "numerous". Furthermore, this species was not redescribed since its original description, and appears therefore to be a rare one.

This concludes, for the present, the list of species allocated to each of the *Erynia* subgenera and to the section *Erynia sensu lato*.

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REFERENCES

- Bařazy, S. and Sokořowski, A. (1977). Morphology and biology of *Entomophthora myrmecophaga*. *Trans. Br. Mycol. Soc.* 68: 134-137.
- Batko, A. (1964a). On the new genera: *Zoophthora* gen. nov., *Triplosporium* (Thaxter) gen. nov. and *Entomophaga* gen. nov. (Phycomycetes: Entomophthoraceae). *Bull. Acad. Polon. Sci., Ser. Sci. Biol.* 12: 323-326.
- Batko, A. (1964b). Some new combinations in the fungus family Entomophthoraceae (Phycomycetes). *Bull. Acad. Polon. Sci., Ser. Sci. Biol.* 7: 403-406.
- Batko, A. (1966a). A new aphidicolous fungus from Poland *Zoophthora phalloides* sp. nov. (Entomophthoraceae). *Acta Mycol.* 2: 7-13.
- Batko, A. (1966b). On the subgenera of the fungus genus *Zoophthora* Batko 1964 (Entomophthoraceae). *Acta Mycol.* 2: 15-21.
- Ben-Ze'ev, I. (1980). Systematics of entomopathogenic fungi of the "sphaerosperma group" (Zygomycetes: Entomophthoraceae) and their prospects for use in biological pest control. Ph.D. dissertation, Hebrew University of Jerusalem.
- Ben-Ze'ev, I. and Kenneth, R. G. (1979). *Zoophthora erinacea* sp. n. (Zygomycetes: Entomophthoraceae), a fungal parasite of aphids. *Mycotaxon* 10: 219-232.
- Ben-Ze'ev, I. and Kenneth, R. G. (1980). *Zoophthora phytonomi* and *Coinidiobolus osmodes* (Zygomycetes: Entomophthoraceae), two pathogens of *Hypera* species (Col.: Curculionidae) coincidental in time and place. *Entomophaga* 25: 171-186.
- Ben-Ze'ev, I. and Kenneth, R. G. (1981a). *Zoophthora orientalis* sp. nov. a fungal pathogen of *Aphis citricola* (Homoptera: Aphididae), and two new combinations of other species of Entomophthoraceae. *Phytoparasitica* 9: 33-42.
- Ben-Ze'ev, I. and Kenneth, R. G. (1981b). *Zoophthora radicans* and *Zoophthora petchii* sp. nov. (Zygomycetes: Entomophthorales), two species of the "sphaerosperma group" attacking leaf-hoppers and frog-hoppers (Homoptera). *Entomophaga* 26: 131-142.
- Ben-Ze'ev, I. and Kenneth, R. G. (1982). Features-criteria of taxonomic value in the Entomophthorales: I. A revision of the Batkoan classification. *Mycotaxon* 14: 393-455.
- Ben-Ze'ev, I. and Uziel, A. (1979). *Monellia costalis* (Fitch), a new host for *Zoophthora radicans* (Brefeld) Batko and *Entomophthora planchoniana* Cornu (Zygomycetes: Entomophthoraceae) in Israel. *Phytoparasitica* 7: 159-167.
- Benjamin, R. K. (1979). Zygomycetes and their spores. In: THE WHOLE FUNGUS (ed. B. Kendrick) Vol. 2. National Museum of Natural Sciences, Ottawa, Canada.
- Brobyn, P. J. and Wilding, N. (1977). Invasive and developmental processes of *Entomophthora* species infecting aphids. *Trans. Br. Mycol. Soc.* 69: 349-366.
- Bucher, G. E. and MacLeod, D. M. (1974). Rediscovery of *Tarichium megaspermum* (Entomophthoraceae) in Canadian cutworms (Noctuidae). *J. Invertebr. Pathol.* 23: 157-163.
- Gustafsson, M. (1965). On species of the genus *Entomophthora* Fres. in Sweden. I. Classification and distribution. *Lantbrukshögskolans Ann.* 31: 103-212.
- Harcourt, D. G., Guppy, J. C., MacLeod, D. M. and Tyrrell, D. (1974). The fungus *Entomophthora phytonomi* pathogenic to the alfalfa weevil *Hypera postica*. *Can. Ent.* 106: 1295-1300.

- Harcourt, D. G., Guppy, J. C., MacLeod, D. M., and Tyrrell, D. (1981). Two *Entomophthora* species associated with disease epizootics of the alfalfa weevil, *Hypera postica* (Coleoptera: Curculionidae), in Ontario. *The Great Lakes Entomologist* 14: 55.
- Humber, R. A. (1976). The systematics of the genus *Strongwellsea* (Zygomycetes: Entomophthorales). *Mycologia* 68: 1042-1060.
- Humber, R. A. (1981a). An alternative view of certain taxonomic criteria used in the Entomophthorales (Zygomycetes). *Mycotaxon* 13: 191-240.
- Humber, R. A. (1981b). *Erynia* (Zygomycetes: Entomophthorales): validations and new species. *Mycotaxon* 13: 471-480.
- Humber, R. A. and Ben-Ze'ev I. (1981). *Erynia* (Zygomycetes: Entomophthorales): emendation, synonymy and transfers. *Mycotaxon* 13: 506-516.
- Keller, S. (1980). Two new species of the genus *Zoophthora* Batko (Zygomycetes Entomophthoraceae): *Z. lanceolata* and *Z. crassitunicata*. *Sydowia Ann. Mycol. Ser. 2*, 33: 167-173.
- Lakon, G. (1919). Die Insektenfeinde aus der Familie Entomophthoraceen. *Z. Angew. Entomol.* 5: 161-216.
- Lakon, G. (1935). Entomophthoraceen - Studien I-IV. *Z. Angew. Entomol.* 21: 89-95.
- Loos-Frank, B. and Zimmermann, G. (1976). Über eine dem *Dicrocoelium*-Befall analoge Verhaltensänderung bei Ameisen der Gattung *Formica* durch einen Pilz der Gattung *Entomophthora*. *Z. Parasitenk.* 49: 281-289.
- MacLeod, D. M., and Müller-Kögler, E. (1970). Insect pathogens: species originally described from their resting spores mostly as *Tarichium* species (Entomophthorales: Entomophthoraceae). *Mycologia* 62: 33-66.
- MacLeod, D. M. and Tyrrell, D. (1979). *Entomophthora crustosa* n. sp. as a pathogen of the forest tent caterpillar, *Malacosoma disstria* (Lepidoptera: Lasiocampidae). *Can. Ent.* 111: 1137-1144.
- MacLeod, D. M., Tyrrell, D. and Soper, R. S. (1979). *Entomophthora canadensis* n. sp., a fungus pathogenic on the woolly pine needle aphid, *Schizolachnus piniradiatae*. *Can. J. Bot.* 57: 2663-2672.
- Nowakowski, L. (1881). O grupie owadomorków (Empusaceae). *Zienn. III Zjazdu Lek. Przynr. Polak. Kraków., Sekc. Bot.* 6: 67.
- Nowakowski, L. (1883). Entomophthoreae. Przyczynek do znajomości pasorzytnych grzybków sprawiających pomór owadów. *Pamiętn. Wydz. Akad. Umiej. w. Kraków.* 8: 153-183.
- Olive, E. W. (1906). Cytological studies on the Entomophthoreae. I. The morphology and development of *Empusa*. *Bot. Gaz.* 41: 192-208.
- Petch, T. (1932). A list of the entomogenous fungi of Great Britain. *Trans. Br. Mycol. Soc.* 17: 170-178.
- Petch, T. (1943). Notes on entomogenous fungi. 193. *Entomophthora coleopterorum* Petch (p.88). *Trans. Br. Mycol. Soc.* 26: 81-93.
- Remaudière, G. and Hennebert, G. L. (1980). Révision systématique de *Entomophthora aphidis* Hoffm. in Fres. Description de deux nouveaux pathogènes d'aphides. *Mycotaxon* 11: 269-321.
- Remaudière, G. and Keller, S. (1980). Révision systématique des genres d'Entomophthoraceae à potentialité entomopathogène. *Mycotaxon* 11: 323-338.
- Remaudière, G., Keller, S., Papierok, B. and Latgé, J.-P. (1976). Considérations systématiques et biologiques sur quelques espèces d'*Entomophthora* du groupe *sphaerosperma* pathogènes d'insectes (Phycomycètes: Entomophthoraceae). *Entomophaga* 21: 163-177.

- Rozsypal, J. (1951). Příspěvek k biologickému boji proti škůdcům obilí (nový parazit larev hrbáče osenního) *Sborn. Českosl. Akad. Zeměd.* 24: 85-94.
- Shimazu, M. (1977). Infectivity of *Entomophthora delphacis* (Entomophthorales: Entomophthoraceae) to the cotton aphid, *Aphis gossypii* (Hemiptera: Aphididae). *Appl. Entomol. Zool.* 12: 200-201.
- Thaxter, R. (1888). The Entomophthoraeae of the United States. *Mem. Boston Soc. Nat. Hist.* 4: 133-201
- Turian, G. and Wuest, J. (1969). Mycoses à Entomophthoracées frappant des populations de fourmis et de drosophiles. *Mitt. Schweiz. Entomol. Ges.* 42: 197-201.
- Turian, G. and Wuest, J. (1977). Description complémentaire de *Zoophthora* (*Entomophthora*) *myrmecophaga* Turian & Wuest, agent d'une mycose chez *Serviformica fusca* L. *Mitt. Schweiz. Entomol. Ges.* 50: 285-289.
- Wilding, N. (1975). Wheat bulb fly: Infection by *Strongwellsea castrans* and *Entomophthora hylemia*. *Rept. Rothamsted exp. Stn. for 1974, Pt. 1*: 108.
- Zimmermann, G. (1978). *Entomophthora blunckii* an Kohlschaben (*Plutella maculipennis*). Isolierung und neue Beschreibung. *Entomophaga* 23: 181-187.

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MYCOLOGICAL AND LICHENOLOGICAL IMPLICATIONS OF CHANGES IN THE CODE OF NOMENCLATURE ENACTED IN 1981

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SUMMARY

The adoption of a uniform 1753 starting-point date for all fungi, coupled with privileged status for the names in Persoon's 'Synopsis Methodica Fungorum' and in Fries's 'Systema Mycologicum,' leads to simplification in author citation and to disappearance of most of the formulations which use 'ex' between authors' names. This and other changes enacted at the 1981 International Botanical Congress are discussed in some detail, and areas of the Code of Nomenclature that still appear to require attention are noted.

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INTRODUCTION

Very possibly no International Botanical Congress since that of Cambridge in 1930 (which saw adoption of the 'type concept' and which thus sounded the death-knell of the unfortunate 'American Code of Botanical Nomenclature') has had more far-reaching importance to mycologists and lichenologists than that of the 1981 Sydney Congress.

It is the purpose of this paper to view some of these changes from a personal, biased, and unofficial position, with the hope that the opinions expressed here will allieviate some of the understandable anxiety with which all changes in the International Code of Botanical Nomenclature are felt by a large segment of the botanical public. It is my firm belief that most of the changes that affect mycologists/lichenologists are indeed changes for the better, simplifications, more rational solutions, guidelines to a more consistent application of the articles ('rules') and recommendations that comprise the Code. That our job is not completed (and probably never will be!) is not unexpected. The changes enacted at Sydney will unquestionably require us to formally conserve some few generic names. These I shall not comment on here, since they are even now being addressed by the Committee on Fungi of the International Association for Plant Taxonomy (IAPT). But there are still doubtful areas of the Code which must be addressed, some of which were recognized at Sydney and resulted in establishment of IAPT Special Committees asked to report to the next Congress. In the final section of this paper I comment upon these briefly, and call attention to specific problems of real concern to mycologists/lichenologists that need immediate attention by the IAPT Committee on Fungi.

I. CHANGES IN STARTING-POINT DATES FOR FUNGI (ART. 13)

At the 1910 (Brussels) Congress, later starting points for non-fossil fungi were introduced, tied to Persoon's Synopsis Methodica Fungorum (1801) for Uredinales, Ustilaginales, and Gasteromycetes, and to Fries's Systema Mycologicum (1821-1832) for 'Fungi caeteri,' except for Myxomycetes and Lichens, these both tied to Linnaeus's Species Plantarum (1753) in common with most other plants. The ambiguity of how to handle the 1821-1832 date-spread, and the later decision that Fries's Elenchus Fungorum (1828) was to be considered an integral part of the Systema, were only partially solved by adoption of a starting-point date (1 Jan. 1821) for Fungi caeteri at the 1950 Stockholm Congress.

The Sydney Code now starts the nomenclature of all fungi with 1753, but affords a special protected status to names adopted ('sanctioned') by Persoon in his 1801 work and by Fries in his 5-volume 1821-1832 opus. I have already commented at length on these provisions in another article (Korf, 1982a), and shall not repeat that material here except in briefest outline.

What the Sydney Code has done is to maintain the protection desired for Persoon's and Fries's names by those who adopted the texts at the 1910 and 1950 Congresses; it also stripped nomenclatural significance from a large number of works published in the 1821-1832 period in particular. The adoption in 1950 of a starting-point date (1 Jan. 1821) for Fungi caeteri gave immense nomenclatural importance to many minor, insignificant, hard-to-find, local

floras and compilations. Works by Hooker, Purton, Mérat, St.-Amans, and others, rightfully forgotten for over a century but elevated by the 1950 decision to dizzying heights of nomenclatural significance, lost that significance in 1981. These volumes can now be returned to the bookshelves to gather the dust they deserve.

Two works will retain immense nomenclatural (and taxonomic) significance, the very two selected by our colleagues in 1910, Persoon's Synopsis and Fries's Systema. Both have been reprinted, are available as well in microform, and have a respected history. The arbitrary dates of publication assigned these by the 1950 Congress (31 Dec. 1801 for the Synopsis, 1 Jan. 1821 for volume 1 of the Systema) no longer have any special interest to us. What now concerns us primarily is whether Persoon or Fries sanctioned any particular name or epithet¹ by adopting it in the appropriate work.

Myxomycetes continue to have a 1753 starting point, and are not considered to be Fungi caeteri. Lichens, which until now enjoyed a simple 1753 starting point, now must be considered in reference to whether Fries sanctioned any applicable name (even if he did not recognize it as a lichenized fungus), for if so it will now have special priority and typification status.²

II. NEAR DISAPPEARANCE OF THE 'ex' FORMULATION BETWEEN AUTHORS' NAMES (REC. 46E, ART. 13)

The use of the connective 'ex' between authors' names has two, quite contradictory, uses under the Code. One is specified in Rec. 46C, the other in Rec. 46E. Both will continue to apply to a few fungi, but the great majority of such citations in the past 30 years in publications on fungi apply to post-1753 and yet pre-1801 or pre-1821 names that were 'revalidated' after the respective later starting-point dates. All such "ex" formulations, such as "Bull. ex Mérat," "Pers. ex Pers.," "Hedw. ex St.-Amans," "Nees ex Fr.," will now disappear. One of two new formulations, either " : Pers." or " : Fr.," will very often replace these. For cases of continued use with fungi of "ex" under Recs. 46C and 46E, see Korf (1982a).

III. SANCTIONED NAMES AND THEIR AUTHOR CITATIONS (ART. 13)

Under the new provisions, a name adopted by Persoon in the Synopsis or by Fries in the Systema (for the respective groups) is treated as sanctioned, i.e., given a unique status under the Code with no parallel in any other group of plants.

¹ Beginning with the 1950 Stockholm Congress, the Code has spelled out that the "names" in Fries's Systema (including the Elenchus) have a kind of 'conserved' status, in that they take precedence over all synonymous or homonymous names. It is clear that workers have interpreted the Code's use of "names" in this Article to include also "epithets." Many of my arguments here are predicated upon my belief that the Code intends to protect epithets as well as names. Otherwise much of the nomenclature that has been proposed since 1953 would be technically not validly published. This is a case of imprecise use of "names" by the Code (such as the Code has used words like "genera" in places where it means "names of genera"). I shall return to this later (Korf, 1982b).

² If there are any lichenized rusts, smuts, or gasteromycetes, the special status of their names would devolve on Persoon, not Fries, of course.

Although the starting point for nomenclature is now 1753, any sanctioned name or epithet attains a special priority status (at its own rank) over any earlier homonymous or synonymous name, whether mentioned by the sanctioning author or not. Thus when Fries sanctioned Peziza brunnea Alb. & Schw. 1805 in the Systema, he took away the priority of P. brunnea Batsch 1783, an earlier homonym. Likewise when Fries sanctioned Peziza applanata (Hedw. [1801]) Alb. & Schw. [1805], he listed as a synonym the earlier P. depressa Pers. [1796], which thereby lost its normal priority status to the name Fries adopted. Neither of these particular cases represent any change from the 1950 Code's requirements. What is new is that this same priority status is now extended to the names sanctioned in Persoon's Synopsis, and to lichens in both treatments.

A second feature that makes sanctioned names unique is their unusual method of typification, discussed below in Section VII-B.

The new Code provides for a system of indicating a sanctioned name or epithet by use of a formula following the original author's name, ": Pers." or ": Fr.," an expansion of the formulation proposed by Donk (1961) for indicating that Fries had sanctioned a revalidated name (often revalidated by some other author after 1 Jan. 1821 before Fries treated it in the Systema). Under the new Code, if the sanctioning author has adopted a name or epithet (at any rank), the ": Pers." or ": Fr." may (or, many believe, should) follow the original author's name. Thus we will have Peziza brunnea Alb. & Schw. : Fr., a legitimate name. (There will also be an illegitimate name, P. brunnea Batsch [1783] non P. brunnea Alb. & Schw. [1805]: Fr., based on a different type specimen, of course.)

Other names might take such formulations as Peziza bulbosa (Hedw. : Fr.) Pers., a species described by Hedwig as Octospora bulbosa in 1801, transferred later that year to Peziza by Persoon, and sanctioned in 1822 by Fries in volume 2 of the Systema. Note that the ": Fr." is always attached to the original author, even though in this instance Fries also treated the species in Peziza. It is not to be written P. bulbosa (Hedw.) Pers. : Fr., since it is Hedwig's epithet and not Persoon's combination which was sanctioned, and when the epithet is transferred to a third genus, it is "(Hedw. : Fr.)" that will transfer.

It should be rigidly borne in mind that ": Pers." or ": Fr." does not signify either at what rank or under what particular generic name an epithet in question may have been sanctioned. It merely acts as a warning flag to indicate that "this name or epithet³ has both special priority status and special typification status."

IV. NAMES OF PLEOMORPHIC FUNGI (ART. 59)

Undoubtedly one of the thorniest articles of the Code for mycologists to apply has been Art. 59, dealing with pleomorphic fungi. It is little consolation to realize that all of its past problems lie at the doorstep of mycologists themselves, for they have been responsible for the wording from the first. The Sydney Code adopts wholly new wording, that proposed by the IMA Subcommittee on Art. 59 as adopted by the IAPT Committee for Fungi and Lichens. "Perfect" and "imperfect" states are now replaced by teleomorph and anamorph,

³ I am of course aware that only names, and not epithets, have types, but since epithets exist only as parts of names, I will not labor the argument further.

and the concept of holomorph is introduced. There are new and clearer solutions to the application of names. Teleomorphic names continue to have priority over anamorphic names. The name of the teleomorph is still also the name to be applied to the holomorph. When an anamorphic fungus is wrongly described under a teleomorphic generic name, we now know how to handle that problem and the transfers from that name. Or when an anamorphic name is proposed for a teleomorphic type specimen, whether or not we can transfer such a name to a teleomorphic genus is now detailed here.

The changes in Art. 59 are far too complex to spell out here. Those interested will find the texts adopted at Sydney published in Taxon 28: 426, 1979 as Proposition 19, and in Taxon 28: 427, 1979 as Props. 19bis, 20, and 21. (One change was the substitution of "morph" for both "form of propagation" and for "form" where these words appeared in that last proposal.)

That we may not even now be through tinkering with Art. 59 seems possible to me. Probably the problem of "ana-holomorphic" names, so exquisitely discussed by Weresub (1979), should be left outside the provisions of the Code. What has been achieved at Sydney is unquestionably a major advance over the morass of special exceptions, often contradictory, that Art. 59 previously represented.

V. ON AUTONYMS (ARTS. 19, 22, 26) AND THE DELETION OF THE '-OIDES' AND '-OPSIS' PROHIBITIONS (ART. 21)

Those who were dismayed by the introduction of the concept of autonyms (names created automatically even without formal mention) in the Code some years ago may not be happy with the Sydney decisions to continue the practice, and to extend the provisions under which they arise. Those autonym rules which were previously (Art. 22.1) restricted to the type subgenus and type section of a genus now apply to all subdivisions of a genus containing the type species. (The type subsection of Hygrocybe is now to be called Hygrocybe subsect. Hygrocybe, and to be used without an author citation for the subsectional epithet, instead of Hygrocybe subsect. Conicae Sm. & Hesl.) Though the number of infrageneric taxa used in mycology is generally small, in agarics, in particular, new autonyms are now called for in place of many established subsections, stirpes, etc. The change has the virtue of symmetry, if not of stability of nomenclature. Such an autonym acquires automatic priority over the name of equivalent rank that has established it. Autonyms previously (Art. 19.4) had no priority.

The prohibition of subdivisions of genera repeating the name of the genus with the prefix "Eu-" has been retained, but the previous prohibition of repeating the generic name with the termination "-opsis" or "-oides" was deleted at Sydney (Art. 21.3).

The Editorial Committee considering the exact wording of the autonym articles as amended at Sydney undoubtedly had its hands full, for in retrospect it is not all that clear to me just how some of these provisions will apply. When the printed Code appears (within the year it is hoped), we will be better able to assess the damage done or the advances made.

VI. CONSERVATION AND REJECTION OF SPECIFIC NAMES (ARTS. 14, 69)

Though conservation of specific names has been a cause célèbre

in botanical nomenclature since the earliest days, it was surreptitiously introduced⁴ via the back door at the 1975 Leningrad Congress. Art. 69, previously a toothless statement about nomina ambigua, was revised there to provide for a list of nomina rejicienda for names "widely and persistently used for a taxon not including its type." An immediate flood of 35 proposals for rejecting species names (and a single proposal on a generic name) was noted by the time of the Sydney Congress.

At Sydney the inevitable happened - those who have so long supported species conservation succeeded in passing that proposal by exceeding (just!) the 60% affirmative vote necessary, and Art. 14 has now been amended to allow conservation of the names of species. These conserved names are restricted to "names of species of major economic importance." The hope is that this restriction will stem a flow of proposals for species of less than "major economic" importance. (Those with long memories or a sense of history may recall that there were assurances - when that concept was adopted - that the lists of conserved generic names would be short: how much of the volume we now call our Code is devoted to those lists of conserved generic names?)

If, for example, we were to discover an older, legitimate name for a species of such economic importance as Saccharomyces cerevisiae or Puccinia graminis we might be able to invoke Art. 69 to list the competing name as rejected, or could propose S. cerevisiae or P. graminis for conservation under Art. 14. Are there imperilled names for fungal species of "major economic" importance? Though I know of no immediate examples, we have the mechanism in place to retain them and to gain stability even at species rank.

VII. TYPIFICATION: MANY FACETS

It is becoming more and more clear that the foundation of our whole nomenclatural system lies in typification. Several significant advances were made at Sydney in applying the type concept in unambiguous (if not always logical) ways. Mycologists can claim some credit to contributing to several of these improvements, especially through the IMA's Subcommittee on Types of Generic Names with Misapplied Type Species Names. Their deliberations were fully considered by the IAPT Special Committee on Generic Names that reported to the Congress (that Committee had co-opted two members of the IMA Subcommittee to help them).

VII-A. LIVING TYPES (ART. 9)

Though an IMA Subcommittee reported itself in favor of provisions to allow a 'living type culture' to serve as nomenclatural type for certain fungi and other microorganisms, the IAPT Special Committee for Fungi and Lichens reported against such provisions, and they were not enacted at Sydney. Instead, the sanctity of a dried-down culture or specimen as holotype was reaffirmed, and a new Recom-

⁴ Mycologists have never admitted publically that we, alone, have had species (and even infraspecific) conservation for many years by virtue of the special priority status given to the names in Fries's Systema under Art. 13. At Sydney we added those in Persoon's Synopsis for names of rusts, smuts, and gasteromycetes.

mendation to Art. 9 will be inserted suggesting that "Whenever practical, in addition to the non-living holotype, a living culture prepared from the holotype specimen before preservation of newly proposed fungal and algal taxa should be deposited with a reputable culture collection." Since bacteriologists have "type cultures," it is understandable that mycologists and phycologists may feel "left out" by this prohibition (even with their cultures deposited in, e.g., the American Type Culture Collection!).

What have been called "type cultures" of fungi and algae should really be called "subcultures of the holotype collection" (if, indeed, they are even that much). The type, for nomenclatural purposes, is a dried-down culture or a specimen on deposit in some herbarium. Designation of a living culture as type will still not suffice for valid publication of a new taxon (Art. 9.5), and names so proposed will not be validly published until an acceptable holotype specimen is designated in print.

Not all data is lost on drying, as some opponents of the status quo would have us believe; our current technology already allows access to much information on the chemistry and biology of long-dead, even fossil structures. Dried specimens may certainly change slightly (and, even, predictably) over time. Living "types" would always be subject to mutation and to unpredictable change, and are thus a poor nomenclatural base.

VII-B. TYPIFICATION OF SANCTIONED NAMES (ARTS. 7, 13)

As noted above in Section III, the names and epithets sanctioned by Persoon and by Fries not only have special priority status, but special typification status as well.

When a name is adopted in the sanctioning work, we are compelled to look at that name through the eyes of the sanctioning author. The aim is always to attain stability, and above all to retain the stability that application of later starting points may have achieved over the past 70+ years.

Let us be quite frank about the status of old (say 1753 to 1820) names of fungi. For almost none of these are there extant holotype specimens. Even if we are lucky enough to find authentic specimens, in very few cases can we definitely state that such a specimen is actually "part of the original material" on which a name is based. Most often all we have is an illustration and/or a description. To typify such names under the Code someone will need to propose a neotype in nearly all cases known to me.

Let us also examine what has happened since 1910 when we introduced later starting points for fungi, established on the basis that Persoon and Fries had made some sense out of the chaos of their past; we intended thenceforth to build our nomenclature on that foundation. (Recall that this was done before the type concept had been accepted.) When we look to the Persoon herbarium in Leiden for type specimens of his own or of others' species, we learn that most of the specimens on deposit are from Persoon's late period in Paris, and that very few can qualify as holotypes. Often several species are represented under a single name in his herbarium. Even the Fries herbarium at Uppsala has few specimens that are unequivocally holotypic. So, again, even to typify a name "in the sense of" Persoon or Fries requires, most often, careful neotypification.

The unique feature of typification of sanctioned names is that we gain the possibility to typify names in a sense which best pre-

serves current usage. This is accomplished by virtue of provisions which have us select a type not only in accordance with the protologue of the original publishing author, but also in accordance with whatever (and all) additional material was added⁵ by the sanctioning author.

By adopting an early name, the sanctioning author necessarily included the type of that name in his concept unless he explicitly excluded the holotype. (Such explicit exclusion will almost never, I believe, be found to have occurred with fungi. This pragmatic approach is in keeping with that adopted at Sydney for generic names, as discussed in greater detail below in Section VII-D.)

The sanctioning author very often will have grossly expanded the concept of the taxon. The sanctioned use of the name then includes all diagnoses, illustrations, specimens, etc. of his own description, notes, etc., all those of the references to added synonyms, as well as all those of the original publication, from any of which a type can be selected to retain current usage. In most cases a neotype specimen can be designated to fit that current usage.

I believe that the new wording does something not fully understood by the Committees that proposed it: it strips away 'holotype' status from 'original' material of all sanctioned names, for these must be typified in accordance with the new provisions, i.e., as seen through the filter of the Persoon and Fries works. Such 'holotypes,' if found, would retain, at best, status as possible lectotypes of a ": Pers." or ": Fr." sanctioned name, in my view. The newly appointed Committee on Lectotypification (see Section VIII-A below) may wish to look into this unusual case!

Since Persoon and Fries were very often correct in their interpretations, this should cause little consternation. If indeed 'holotypes' of sanctioned material surface, and they differ greatly from current usage, they can, I believe, be ignored, and some other lectotype (or even neotype⁶) be designated. After all, we have tried to build on the nomenclature and taxonomy of Persoon and Fries for over 70 years. Now we have the procedure for doing so.

VII-C. TYPES OF NAMES OF PLEOMORPHIC FUNGI (ART. 59)

I call attention to the exact wording of proposals in Taxon which provide the revised wording of Art. 59 as adopted in Sydney (see above, Section IV). In briefest outline: (1) if a type specimen of an Ascomycete or Basidiomycete is teleomorphic (bears asci/basidia),

⁵ The wording adopted at Sydney expressed this as the "protologue of the sanctioning author," which is an expansion of the definition of "protologue" (everything associated with the 'original' publication of a name) that seems unwarranted; the Editorial Committee will surely adjust the terminology. What was meant was that everything, new and old, mentioned by the sanctioning author was to be considered when typification is attempted.

⁶ But a neotype cannot be designated if any of the 'original material' is available! We are on the horns of a dilemma. (I suspect I would be laughed out of the nomenclatural community were I to suggest the need for still another type term, "sanctotype" or the like, for neotypes or lectotypes of sanctioned names. If I am right, there will be very few, if any, such cases in any event.)

the name can be transferred to any teleomorphic genus, even is proposed originally in an anamorphic ('imperfect') genus, and can act as the name of a holomorph ('whole fungus'); (2) if a type specimen is anamorphic, its name can be transferred to another anamorphic genus even if described originally in a teleomorphic genus, but it cannot serve as the name of a teleomorph or of a holomorph. For exact wording and examples of how this works see 59.6 of Proposition 19bis in Taxon 28:427, 1979, as adopted at Sydney.

VII-D. TYPES OF FAMILIAL, INFRAFAMILIAL, GENERIC, AND INFRAGENERIC NAMES (ART. 10)

One of the most important decisions to be reached at Sydney concerns typification of generic (and, thus, of other supraspecific) names. Though previous Codes have held that the type of a specific or infraspecific name was a specimen, "the type of a name of a genus or any taxon between genus and species is a species."

The Sydney Code has changed that, for now it reads, for the underlined words above, "... is the type of the name of an included species." That is, we now have generitype specimens.

It is now possible to apply the Code to the thorny problem of what to do about generic names proposed on a named species where it turns out that the named species had nothing to do with the material in hand, i.e., it was a misapplied species name. An example may make the point easier to follow:

In 1932 Imai proposed the new generic name Neogyromitra on the basis of Japanese material before him, which he identified as the North American species, Helvella caroliniana Bosc. He provided in addition a photograph of the characteristic, apiculate spores. In 1938 he discovered that Bosc's species has ovoid, non-apiculate spores, and that he had obviously misidentified his material, which he now redetermined as H. gigas Krombh., a European species with apiculate spores; he proposed that the correct name for the type species of his genus was N. gigas, not N. caroliniana as he had claimed 6 years earlier. (It may well be that Imai had an Asian species, neither H. caroliniana nor H. gigas, before him.)

What, then, is the type of the generic name Neogyromitra? When the Code specified that the type of a generic name was a "species," which species, that in front of Imai (maybe H. gigas, maybe an unnamed Japanese species), or H. caroliniana, the species he claimed he had?

Two solutions to the dilemma were possible. One, termed the "idealistic" approach, would hold that the material Imai saw and actually illustrated and described, must represent the "species," and that one should then select a 'type' for the generic name from among Imai's materials, i.e., a lectotype specimen for the very possibly unnamed species growing in Japan. Such a lectotypification would have to be followed by later workers. The second solution, called the "pragmatic" approach, would hold that it is impossible to determine precisely what taxonomic circumscription Imai had in mind in 1932 when he proposed N. caroliniana as the name of his species, except that one point is certain: since he based his name on Bosc's species, he necessarily included the type specimen of Bosc's name within the conceptual circumscription (or, otherwise, would obviously not have adopted that name). It is this second, "pragmatic," approach which prevailed at Sydney. The type of the generic name Neogyromitra is the type of the name of its named type

species, Bosc's, i.e., a type specimen never seen nor consulted by Imai, and one which we believe has no close relationship to Imai's generic description, his specific description, nor his photographs! The generic description/diagnosis has now almost no importance: what is critical is the identity of the named type species.

Those of us who labored for many years on resolving the problem of misapplied names could have accepted either of the two alternatives above; what was intolerable was the doubt about which way to proceed. The pragmatic approach is now the rule, and though it will surely necessitate additional proposals for conservation of generic names, it is at least far easier to apply, and will require far less work on the part of taxonomists, than the idealistic approach would have entailed.⁷

VIII. UNSOLVED PROBLEMS AND UNFINISHED BUSINESS

Though one might fervently wish that the Code has now been modified to produce a thoroughly workable document, and that we ought not try to doctor it further until we can assess how well this newest version works, the truth is that the Code is still imperfect, still offers confusion instead of instruction in several areas. Some problems were already evident at Sydney, and the machinery was set in motion to attack these (see Section VIII-A, below). Others that I perceive and one that has been pointed out to me by colleagues are noted here, and surely deserve the attention of the IAPT's Committee on Fungi. There are now 15 members of that Committee, each pledged to work hard during the coming five years; three more members will be added by appointment from the IMA at the Third International Mycological Congress in Tokyo, in 1983. Perhaps subcommittees of that Committee could be formed to address specific points, much as the IMA's Subcommittees of its Nomenclature Secretariat functioned to bring matters to a head at Sydney. Those who wish to call the Committee's attention to particular problem areas should feel free to contact the Chairman of the IAPT Committee on Fungi, Dr. Lennart Holm, Institute for Systematic Botany, University of Uppsala, Box 541, S-751 21 Uppsala, Sweden, or the Secretary of that Committee, Prof. Ronald H. Petersen, Department of Botany, University of Tennessee, Knoxville, TN 37916, USA.

⁷ One worry about the pragmatic approach still nags me. It could lead to an intentional introduction of fictitious specific names. Were I about to propose a new generic name, might I be tempted to avoid designating an "old" species as its type, but rather propose a "new" species name for that species as its type? The generic name would thus be tied to the type specimen of my new species (in my herbarium), and not to the type specimen of an old name in someone else's herbarium. Next month, or next year, I could report my "discovery" that my new species is really a synonym of the older species, make the needed transfer of that to my new genus, and then ignore my new species name (except that forever the type of that generic name would reside in my herbarium, not in the herbarium where the type specimen of the correct species name resides). Donk (1959) forsook such problems when he designated as the type of his new generic name *Cellypha*: "Typus: *Cyphella* sp. = C. Bas 1519...TYPE SPECIES. - *Cyphella goldbachii* Weins. (in the sense indicated below). Genitype specimen: C. Bas 1519..." Donk carefully avoided creating a new name for the species he wanted as type of his genus; will others be as careful?

VIII-A. THREE SPECIAL COMMITTEES ESTABLISHED

The members of the Sydney Congress debating proposed changes in the Code found themselves quite unable to reach logical conclusions in three areas, and appointed three Special Committees to address these and to prepare reports for possible action at the next (Berlin) International Botanical Congress. These are: (1) a Special Committee on Lectotypification, with particular reference to Arts. 8 and 72; (2) a Special Committee on Effective and Valid Publication, with special reference to Arts. 29, 33, 37, and Rec. 37B, in light of our rapidly changing methods of publication; and (3) a Special Committee on Orthography, with special reference to Arts. 64, 73, and 75. Additional changes in the Code in these three areas are clearly to be expected.

VIII-B. TAXONOMIC CONFUSION AND SANCTIONING WORKS

It is always regrettable when taxonomic considerations enter into the Code of Nomenclature for taxonomy is not its business. For example, what differentiates a lichen from a non-lichenized fungus is a taxonomic (or biologic) decision, not a nomenclatural one. One bright light is that though in previous Codes a serious problem existed because of the different starting-point dates for lichens (1753) and for fungi (here mostly 1821), adoption of a uniform 1753 starting point has resolved these problems. For borderline cases where it is uncertain whether a taxon is lichenized or not, or whether some populations exist lichenized, others not, a single name at both generic and specific ranks will now apply.

What has not been fully solved, however, is that we still must make taxonomic decisions, since we have merely substituted two sanctioning works (Persoon's and Fries's) where we previously had two starting-point dates. What, indeed, is a "Gasteromycete"? Is the *Russula*-like *Macowanites*, which fails to discharge its basidiospores from its somewhat distorted gills, an agaric to be seen through Fries's filter or a Gasteromycete to be seen through Persoon's? Is *Phleogena* with transversely septate basidia and non-discharged basidiospores borne within a peridium a Gasteromycete or a jelly fungus? Or do such fungi have two different sanctioning works depending on the viewpoint of the taxonomist?

Worse, to my mind, is the desire for precision that has led the Code to specify Persoon's work as the sanctioning one for "Uredinales, Ustilaginales, and Gasteromycetes." What is a 'modern' taxonomist to do who also recognizes an order Phragmidiales among the rusts, and the orders Tilletiales and Graphiolales among the smuts? By virtue of our decisions about ordinal limits do we change from "Uredinales" to "Fungi caeteri," from "Ustilaginales" to "Fungi caeteri," changing sanctioning author in the process? Surely that was never intended! It would have been better, perhaps, to give Persoon the "rusts, smuts, and gasteromycetes," and that is how I shall interpret the present rigid wording of the Code.⁸

⁸ The problem was even worse when we had later starting-point dates. The change to a uniform 1753 date is an improvement, but the folly of having taxonomic considerations affect our application of nomenclatural rules still will cause us difficulties in the future. We would have been wise, perhaps, to adopt a single sanctioning work, but we do have a history of 70 years of work dividing the responsibility for early taxonomy of fungi

A fairly minor but irritating problem arises when a sanctioning author has synonymized two taxa that happen to have the same epithet. Taxonomic confusion may arise over which of the two names was actually sanctioned. I intend to return to this point in a later paper (Korf, 1982b).

VIII-C. WHAT ABOUT 1801 (PERSOON) FOR HYPHOMYCETES?

Few mycologists are unaware of the current division among Hyphomycete workers in regard to which starting-point date they were using for that group of fungi. Though the official starting point for these Fungi caeteri has been tied to Fries's *Systema* since 1910, it was Hughes (1958, 1959) in particular who showed that adoption of a Friesian starting point leads to great difficulties, and that it would be far preferable to start the nomenclature of Hyphomycetes with Persoon. Hughes's (1959) formal proposal to change the starting point was defeated at the 1959 (Montreal) Congress, in part because of uncertainty as to whether such a change might not better encompass other Fungi Imperfecti as well. Despite this, Hughes and a very large number of active students who have followed him have intentionally continued to treat these fungi as though their nomenclature begins with 1801.

Even today, with the starting point pushed back to 1753 for all fungi, it will be necessary under the Code to view Hyphomycetes through Fries's filter as sanctioned Fungi caeteri, not through the probably preferable Persoon filter. It is quite intolerable that we should have a large segment of our taxonomy, including several major compilations of Hyphomycetes, based on a brazen, intentional disregard of the Code. Surely Hyphomycete workers should be able to decide at this point whether that group should now be moved from Fungi caeteri and listed instead with Uredinales, Ustilaginales, and Gasteromycetes.⁹

Perhaps before the Berlin Congress we can get agreement as to whether Persoon or Fries would be the more appropriate filter for Hyphomycetes; at the same time, the question should be raised about a possible change for all Fungi Imperfecti.¹⁰ I thus challenge my colleagues who work on Hyphomycetes or on Coelomycetes to undertake the necessary nomenclatural studies forthwith.

VIII-D. TRANSFERS OF SANCTIONED NAMES AND REFERENCE TO THE BASIONYM REQUIRED BY ART. 33.2

The change in starting point to 1753 for those fungi which had

between Persoon and Fries. Upsetting that dichotomy might have had more serious consequences than those nagging problems that remain.

⁹ The same problem alluded to in Section VIII-B would then arise again, of course, for 'Hyphomycetes' is a taxonomic group, and the Code rules on nomenclature, not taxonomy. When is a Hyphomycete a Hyphomycete, when a Coelomycete? Borderline problems do exist, and merely wishing they would go away will not successfully dispose of them.

¹⁰ It is at least possible to delimit Fungi Imperfecti in taxonomic terms fairly precisely, in comparison to Hyphomycetes.

a later starting point raises a conflict with Art. 33.2 of the Code that was not fully addressed by the IMA Subcommittee or by the IAPT Committee on Fungi and Lichens:

33.2 A new combination, or an avowed substitute (*nomen novum*), published on or after 1 Jan. 1953, for a previously and validly published name is not validly published unless its basionym (name-bringing or epithet-bringing synonym) or the replaced synonym (when a new name or epithet is proposed) is clearly indicated and a full and direct reference given to its author and original publication with page or plate reference and date. Bibliographic errors of citation do not invalidate the publication of a new combination.

The Editorial Committee has been made aware of problems (1) to (4) below, and presumably will take some remedial action on Art. 33.2, such that these may be treated as mere bibliographic errors, by virtue of prompt action by Professor Petersen as Secretary of the IAPT Committee on Fungi. Items (5) and (6) have apparently not been brought to their attention, and are presumably matters of substance more than merely editorial, in any case.

(1) Because of changes at the 1950 Congress, a starting-point date of 1801 or 1821 was to be used for new combinations or avowed substitutes. This was technically in effect from 1 Jan. 1953 until the end of August 1981.

Any name published before those later starting points which were in every other respect validly published may be considered, for our discussion, as "devaluated" names. What most workers construed (I believe correctly) as the "original publication" of such devaluated names was the first valid publication (i.e., "revalidation") after the starting-point date. It was not the intent at Sydney to remove validity from combinations made from 1953 to 1981 which cited such revalidated names as the place of "original publication," when this was done in full compliance with the provisions of the 1950-ff Codes.

(2) Because of the changes at Sydney, the new starting point is retroactively in effect from the end of August, 1981. No provision was made there to allow time for workers to adjust to citing the pre-1801 or pre-1821 original publication rather than the revalidated name they would have cited under the 1950-ff Codes. It was certainly not the intent to rule against papers in press, and Art. 33.2 will need to protect these by allowing application of the old rules well beyond August 1981.

(3) One abominable procedure is actually recommended as a practice by Rec. 46E (my candidate for most pernicious of all recommendations in the Code!): it permits deletion from citations (and thus from basionym references!) of a pre-starting-point author's name and the 'ex' that connects it to the validating author's name. That recommendation permitted a species to be cited, e.g., as *Peziza tuberosa* Bull. ex Mérat, or as *P. tuberosa* Mérat, the latter submerging all reference to Bulliard's 1791 treatment, placing the burden of taxonomy and nomenclature on Mérat's floristic listing in 1821.

It was thus possible under the 1950-ff Codes to transfer that species to another genus with the author citation "(Mérat) comb. nov." and with bibliographic reference only to Mérat's book. Under today's Code, Mérat's mere use of this name, long before well-

established in the literature, has no interest at all, and is certainly not "direct reference ... to ... original publication." Clearly those authors who attempted to follow the Code and were deceived by Rec. 46E ought not to be penalized.

(4) Art 33.2 has also a problem of interpretation in wording. When it was pointed out on the floor of the Sydney Congress that the editors of both the Index Kewensis and the Index of Fungi interpreted "page or plate reference" to invalidate transfers in which a page-spread was used, there were hoots of ridicule and disbelief from the delegates. The editor of the Index of Fungi has even stated the policy in print (Sutton, 1981).

A proposed change from "page or plate reference" to "page or pages or plate reference, as appropriate" was defeated, since those voting apparently agreed with the Congress' Rapporteurs that "page" here is an adjective, not a noun, and does not connote number of pages. The silliness of the Kew position is demonstrated by the fact that a reference to page "739" when it should have been, say, "639," is correctable as a bibliographic error under the provisions of the article (and is so corrected by the Kew compilers), while a reference to pages "639-641" for a description and discussion on those three successive pages is treated by them as not valid. Before deciding that it is necessary to recombine a name indicated as "not validly published" in the Index of Fungi, mycologists would be well-advised to see if it was a page-spread in citation that misled the editors of that otherwise excellent and invaluable compilation.

(5) Another problem arises with revalidated names, but does not concern those who followed the 1910-1935 Codes. An example will again help. Since Fries accepted Peziza tuberosa in the Systema (in volume 2, published in 1822), almost all mycologists held that the species was correctly cited as P. tuberosa Bull. ex Fr. (some earlier Codes also allowed this as "[Bull.] Fr."), or even (under that miserable Rec. 46E, again), as P. tuberosa Fr. After the 1950 Code established a starting-point date (1 Jan. 1821 for this group) rather than a starting-point book, such a citation was technically incorrect if someone else had taken up the name between 1 Jan. 1821 and when Fries treated it in the 2nd or 3rd volume of the Systema or in the Elenchus during the 1822-1832 period.

Thus it was that Mérat's second edition of a flora of the Paris region achieved a fame and importance neither intended for it by its author when he compiled the species, nor deserved. But if an author (after 1953) has erroneously transferred P. tuberosa Fr. 1822 instead of P. tuberosa Mérat 1821, was this really an error or should Art. 33.2 be modified to protect that transfer based on a misunderstanding of starting-point date vs. starting-point book? The question needs attention before the next Congress.

(6) Another interesting question is how one should best transfer a sanctioned name. Since Bulliard published Peziza tuberosa in 1791, after the 1753 starting point, we can surely transfer this as "(Bull.) comb. nov.," and should cite Bulliard's reference in full. We could also transfer this as "(Bull. : Fr.) comb. nov.," with the Bulliard page or plate reference. That would give our readers the added information that Fries treated this epithet at some rank and in some genus sometime between 1821 and 1832 in the Systema, and, even more important, that it has sanctioned status (special priority and

special typification). We surely do not need to cite the Fries reference in full, since ": Fr." always means "see the Systema."

But would it be possible to give only the Fries page reference for a "(Bull. : Fr.) comb. nov." new combination, on the grounds that Fries's sanctioning is critical in priority and in typification and also his treatment carries reference back to Bulliard's use? I would again plead for leniency, at least until some future date, during which time full reference to either the original publication or to the sanctioning author's publication would be considered adequate. I believe we should initiate a study to determine whether the either/or formulation would be appropriate to include in Art. 33 on a permanent basis. Or should, at some future date, reference to the sanctioning author be a requirement? After all, most mycologists will have the two sanctioning works at their disposal; many fewer will have access to the original, old literature to check pages and plate numbers there.

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LITERATURE CITED

- DONK, M. A. 1959. Notes on 'Cyphellaceae'. - *l. Persoonia* 1: 25-110.
- DONK, M. A. 1961. The citation of authors of revalidated names. *Taxon* 10: 66-69.
- HUGHES, S. J. 1958. Revisiones Hyphomycetum aliquot cum appendice de nominibus rejiciendis. *Canad. j. Botany* 36: 727-836.
- HUGHES, S. J. 1959. Starting point of nomenclature of Hyphomycetes. *Taxon* 8: 96-103.
- KORF, R. P. 1982a. Citation of authors' names and the typification of names of fungal taxa published between 1753 and 1832 under the changes in the code of nomenclature enacted in 1981. *Mycologia* 74: 250-255.
- KORF, R. P. 1982b. Sanctioned epithets, sanctioned names, and cardinal principles in ": Pers." and ": Fr." citations. (MS in preparation for *Mycotaxon*.)
- SUTTON, B. C. 1981. [Review of] Genera of Hyphomycetes. *Trans. Brit. Mycol. Soc.* 77: 224-225.
- WERESUB, L. K. 1979. On the question of naming pleomorphic anamorphic fungi. In B. Kendrick [ed.], *The Whole Fungus* 2: 689-709. National Museum of Natural Sciences, National Museums of Canada, and the Kananaskis Foundation.

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LATERISPORA BREVIRAMA, A NEW HYPHOMYCETE ON SCLEROTIA OF SCLEROTINIA MINOR

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SUMMARY

A new dematiaceous hyphomycete on sclerotia of Sclerotinia minor is illustrated and described as Laterispora brevirama. It is distinctive because each determinate stable conidiogenous cell gives rise terminally to a short hyaline branch and laterally to an erect, long, thin, appendaged phragmospore from a single fixed conidiogenous locus. The fungus sometimes produces a Selenosporella state.

In previous papers we (Uecker et al., 1978, 1980) described two new dematiaceous hyphomycetes that attack the sclerotia of species of Sclerotinia. One of these, Sporidesmium sclerotivorum Uecker et al. [= Teratosperma sclerotivorum (Uecker et al.) Hughes (1979), as T. sclerotivora], has been found in fields at Beltsville, Maryland, at Vineland and Cedarville, New Jersey, and in Oswego County, New York. The other, Teratosperma oligocladum Uecker et al., has been collected from fields near Salinas

and Tulelake, California. From the New Jersey, Beltsville, and Salinas fields we have discovered another dematiaceous hyphomycete on sclerotia and are unable to place it in any previously described taxon. We describe it here as a new genus containing a single species.

Terminology used in this paper follows the recommendations of Kendrick (1971) with regard to conidial development. Names of herbaria are abbreviated according to the Index Herbariorum (Holmgren et al., 1981).

Laterispora Uecker, Ayers, et Adams, gen. nov.

Cellula conidiogena discreta, determinate stabilis, appendicem terminalem et locum conidiogenum singularem fixum ferens. Conidium erectum, dematiaceum, phragmoseptatum, holoblasticum, lateraliter e cellula conidiogena productum.

Conidiogenous cell discrete, determinate stable, bearing a terminal appendage and a single fixed conidiogenous locus. Conidium erect, dematiaceous, phragmoseptate, holoblastic, produced laterally from the conidiogenous cell.

Etymology: L., *latus*, *lateris* = of the side; *spora* = spore.

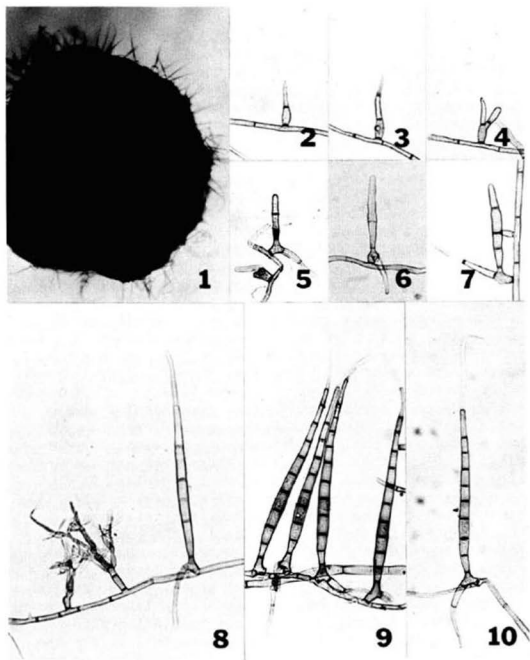
Typus generis: Laterispora brevirama Uecker, Ayers, et Adams

Laterispora brevirama Uecker, Ayers, et Adams, sp. nov.

Coloniae super Sclerotinia minoris sclerotia efformatae. Hyphae 4-6 μm latae, pallide vel aureo-brunneae vel mediocriter brunnescentes. Cellula conidiogena discreta, lateraliter ex hypha exoriens, anguste doliiformis, levis, determinate stabilis, terminata ab extensione determinata hyalina plerumque cellulis duobus vel tribus composita. Conidium erectum, 70-140 x 6-7 μm , 7-12-phragmoseptatum, gradatim angustatum, aureo-brunneum vel mediocriter brunnescens, leve, ad basim truncatum, ad apicem appendicem rectam elongatam hyalinam, singulariter in loco conidiogeno singulo fixo proferens, parietis evolutione holoblastica.

Holotypus BPI 71918; isotypi in DAOM, NY, et IMI.

Colonies developing superficially on the surface of sclerotia of Sclerotinia minor (Fig. 1). Hyphae 4-6 μm wide, light or golden brown to mid brown. Conidiogenous cell discrete, arising laterally from hypha, narrowly barrel-shaped, smooth, determinate stable, terminated by a



Figs. 1-10. *Laterispora brevirama*. (All figures X350 unless otherwise stated.) Fig. 1. Conidia on sclerotium of *Sclerotinia sclerotiorum*, X40. Fig. 2. Conidiogenous cell with short terminal appendage. Fig. 3. Conidiogenous cell with short lateral conidiogenous locus. Fig. 4. Young conidium initial already delimited by a septum. Fig. 5. One-septate conidium initial with dark brown structures in base. Fig. 6. One-septate conidium initial, elongating terminally. Fig. 7. Three-septate conidium initial. Fig. 8. Mature conidium with hyaline terminal appendage; *Selenosporella* state on same hypha. Figs. 9, 10. Mature conidia.

determinate hyaline extension usually composed of two or three cells. Conidium erect, 70-140 x 6-7 μm , 7-12-phragmoseptate, gradually becoming narrower, golden brown or medium brown, smooth, truncate at the base, with a straight, hyaline, elongate appendage at the apex, produced singly on a single fixed conidiogenous locus, development of the wall holoblastic.

Etymology: *L.*, *brevis* = short, *ramus* = branch.

Techniques for isolation of the fungus are the same as those described for *Teratosperma oligocladium* (Ayers and Adams, 1981). *Laterispora brevirama* grows slowly as a compact, dark brown mycelium on cornmeal agar and on glucose-glutamine agar devised for *Sporidesmium sclerotivorum* (Barnett and Ayers, 1981). Conidial production in vitro is infrequent. Cultivation of the fungus in vivo on sclerotia of *Sclerotinia minor* Jagger has so far been successful only when sclerotia inoculated with *Sporidesmium sclerotivorum* or *Teratosperma oligocladium* are subsequently inoculated with *L. brevirama*. Thus far, *L. brevirama* has been observed in nature only on sclerotia in association with *S. sclerotivorum* or *T. oligocladium*.

Laterispora brevirama is unique because it produces single, erect conidia from single, fixed conidiogenous loci on lateral, determinate stable conidiogenous cells that bear short, hyaline, determinate terminal branches (Figs. 2-10). Other distinctive characters are its long, thin, phragmoseptate, appendaged conidia (Figs. 9, 10); its possession of a distinctive *Selenosporella* state (Fig. 8); and its habit on sclerotia of *Sclerotinia minor*.

By observing conidiogenous cells that bear mature spores, it would be difficult to determine whether the position of the conidium was terminal or lateral. But a study of the younger developmental stages (Figs. 2-7) shows that the conidiogenous cell develops as a lateral outgrowth of an assimilative hypha and that a terminal hyaline appendage is present on the conidiogenous cell before the conidium begins to form. Most of the appendages consist of two cells, but one-, three-, and four-celled appendages also occur. A short protrusion from the side of the conidiogenous cell (Fig. 3) heralds the conidium, which is set off by a septum (Fig. 4) when the conidium is still very small. Further elongation of the conidium appears to be apical (Figs. 5, 6), with new septa being constructed in acropetal sequence as the conidium elongates. Intercalary septum formation also occurs. The thick brown structures shown in the base of the conidium in Fig. 5 were observed in only a few conidia.

When *L. brevirama* was first isolated (1977), a *Selenosporella* state developed on the same hyphae (Fig. 8) or on different hyphae than the *Laterispora* state. We saw the *Selenosporella* state, photographed it, assumed that it would be available in the future, and did not retain either cultures or slides. Since then, we have not found the *Selenosporella* state again. Even reisolation of the fungus from soil samples from the original fields failed to yield the *Selenosporella* state. Consequently, the holotype and isotype specimens do not bear the *Selenosporella* state of *L. brevirama* but they do bear the *Selenosporella* state of *Sporidesmium sclerotivorum*. This is unavoidable because, as previously mentioned, *L. brevirama* grows on sclerotia only when the sclerotia have already been invaded by either *S. sclerotivorum* or *Teratosperma oligocladium*. Fortunately, the *Selenosporella* states of *L. brevirama* and *S. sclerotivorum* are readily distinguishable on the basis of conidial size and shape: conidia of the *Selenosporella* state of *L. brevirama* are usually 11-13 x 0.8-1 μm and cylindrical to falcate whereas those of the *Selenosporella* state of *S. sclerotivorum* are usually 7-9 x 0.8-1.0 μm and banana-shaped.

The substrate utilized by *L. brevirama* has not yet been determined. The fungus could be pathogenic on the sclerotia, further requiring something provided by *Sporidesmium* or *Teratosperma*; it could be mycoparasitic upon *Sporidesmium* or *Teratosperma*; or it could be merely a fastidious organism whose nutritional tolerances are extremely narrow.

Bulbils measuring about 50 μm in diameter have been observed on some of the filter paper cultures but it is not certain that they are produced by *L. brevirama*. Bulbils in the same size range are also produced by both *Sporidesmium* and *Teratosperma*, and because the culture is mixed the bulbils could be produced by the other member of the culture.

We have not been able to find a dematiaceous hyphomycete that produces conidia in a manner similar to *L. brevirama*. Because of the importance attributed to the conidial apparatus by present-day taxonomists, we believe that the new fungus deserves generic status.

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LITERATURE CITED

- Ayers, W. A., and P. B. Adams. 1981. Mycoparasitism of sclerotial fungi by Teratosperma oligocladium. Can. J. Microbiol. 27: In Press.
- Barnett, E. A., and W. A. Ayers. 1981. Nutritional and environmental factors affecting growth and sporulation of Sporidesmium sclerotivorum. Can. J. Microbiol. 27: 685-691.
- Holmgren, P. K., W. Keuken and E. K. Schofield. 1981. Index Herbariorum. I. The herbaria of the world. 7th ed. Regnum Veg. 106:1-452.
- Hughes, S. J. 1979. Relocation of species of Endophragmia auct. with notes on relevant generic names. New Zealand J. Bot. 17:139-188.
- Kendrick, B. 1971. Conclusions and recommendations. pp. 253-262. In Kendrick, B. (ed). Taxonomy of Fungi Imperfecti. U. of Toronto Press, Toronto, 309 pp.
- Uecker, F. A., W. A. Ayers, and P. B. Adams. 1978. A new hyphomycete on sclerotia of Sclerotinia sclerotiorum. Mycotaxon 7:275-282.
- Uecker, F. A., W. A. Ayers, and P. B. Adams. 1980. Teratosperma oligocladium, a new hyphomycetous mycoparasite on sclerotia of Sclerotinia sclerotiorum, S. trifoliorum, and S. minor. Mycotaxon 10:421-427.

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BLASTOSCHIZOMYCES PSEUDOTRICHOSPORON, GEN. ET SP. NOV.

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The genus *Trichosporon*, originally described by Behrend (1890), is characterized by the formation of true hyphae, pseudohyphae, blastoconidia, and arthroconidia (Carmo-Sousa, 1970). Isolates recovered from clinical specimens in our and other laboratories resembled this genus superficially in forming budding cells and arthroconidialike structures, but detailed microscopic examination revealed that the "arthroconidia" actually arose as annelloconidia. As a result of these findings we propose a new genus and species to accommodate these *Trichosporon*-like isolates.

MATERIALS AND METHODS

Test Organisms. Thirteen *Trichosporon*-like isolates and the type *Trichosporon capitatum* (CBS 2364) were maintained at 27°C on modified Sabouraud dextrose agar slants (MSDA; 2% dextrose, 1% neopeptone, and 2% agar) and transferred to fresh medium at monthly intervals. Inocula for all morphologic and physiologic studies were obtained from slants incubated at 27°C for 72 h.

Morphology by Light Microscopy. Each isolate was grown on malt-extract agar and on cornmeal + 1% Tween 80 agar. Colony morphologies were examined after 3 and 14 days' incubation at 27°C. The microscopic morphology was evaluated by a slide culture technique, with cornmeal + Tween 80 agar incubated at 27°C.

Morphology by Electron Microscopy. Two isolates (425 and 425A) were examined by scanning and transmission electron microscopy. To obtain the thin agar cultures required for these investigations, each isolate was grown in a Coleman perfusion chamber (Salkin and Robertson, 1970). The gasket and one cover slip were placed on the inverted upper housing unit in a 60-mm glass petri dish, and the three components were autoclaved as a unit (Fig. 1). The other cover slip and support ring and the lower housing unit were autoclaved in a second petri dish. Molten, sterile cornmeal agar with 1% Tween 80 was layered over three-quarters of the first cover slip to the depth of the gasket. A portion of growth from a 72-h MSDA culture was then cut lightly into the surface of the solidified agar. The chamber was assembled aseptically and incubated at 30°C for 48 h.

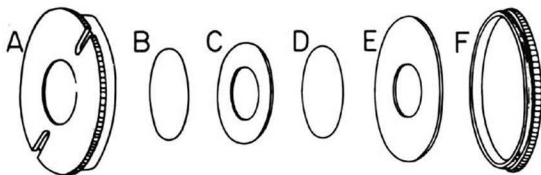


Fig. 1. Coleman perfusion chamber; A, upper metal housing unit; B & D, glass cover slips; C, gasket; E, metal ring; F, lower housing unit.

At the appropriate stage of development, as determined by microscopic examination, the chamber was disassembled, and the agar disk (approximately 1-mm thick and 2-cm in diameter) was removed. For both scanning and transmission studies the disk was initially fixed for 1-4 h in 2% glutaraldehyde buffered to pH 7.1 with 0.1 M cacodylate. The samples were then washed in buffer, postfixed in 1% osmium tetroxide for 1 h, and dehydrated in a graded ethanol series. In the scanning investigations the samples were then critical-point-dried with liquid carbon dioxide as the transition fluid, mounted on aluminum stubs with conductive paint, sputter-coated with gold, and examined in an Etec scanning electron microscope.

In the transmission studies the dehydrated samples were flat-embedded in Epon-Araldite on glass cover slips. The embedding substrate was removed with hydrofluoric acid and the samples were examined by phase-contrast microscopy (Moore, 1975). Suitable fungal material in the desired plane of orientation was excised, mounted on Epon pegs, and trimmed, and serial thick (0.25 μm) sections were made with a Sorval Mt-2B microtome (Rieder, 1981). The sections were collected on Formvar-coated, slotted grids, stained in 2.5% aqueous uranyl acetate (60°C, 120 min) followed by lead citrate (23°C, 30 min), and examined in an AEI EM7 MK II 10 high-voltage electron microscope operated at 800 KV with an objective aperture of 20 μm .

Biochemical Tests. Assimilation of carbon and nitrogen sources and fermentation of carbohydrates were determined for each isolate and for the *T. capitatum* type strain by the Wickerham procedures (van der Walt, 1970). Test cultures were incubated at 30°C and read at weekly intervals for growth, i.e., turbidity. In addition, the API 20C assimilation test (Analytab Products, Plainview, NY), consisting of 19 dehydrated substrates and a negative control, was

performed according to the manufacturer's instructions.

Urea Hydrolysis Test. A portion of growth of each isolate was removed with a sterile transfer wire from a 72-h MSDA slant, streaked onto the surface of a Christensen urea agar slant, incubated at 27°C, and read after 3 and 7 days for color change of the pH indicator.

Temperature Tolerance Test. A portion of growth of each isolate was removed with a sterile transfer wire from a 72-h MSDA slant and streaked onto the surface of two MSDA slants. One slant was then incubated at 37°C and the other at 45°C; both were read for growth after 7 days.

Vitamin Utilization Test. Vitamin-Free Yeast Base (Difco), prepared as per manufacturer's instructions, was dispensed, 5 ml per tube, into 20 X 150-mm disposable glass screw-capped culture tubes. A portion of growth sufficient to prepare a Wickerham 1+ suspension was removed from a 72-h MSDA slant and transferred to 5 ml of sterile water. With a sterile pipette 0.1 ml of this suspension was removed and added to the Vitamin-Free Yeast Base. The tubes were incubated at 27°C and read for growth, i.e., turbidity, at weekly intervals. In related tests thiamine or biotin (10 µg/ml) was added to the Vitamin-Free Yeast Base to determine the effect of each vitamin on growth.

Splitting of Arbutin. A portion of growth from a 72-h MSDA slant of each isolate was streaked with a sterile transfer loop over the surface of an arbutin agar plate. The plate was incubated at 30°C and read weekly for color change.

Fast Blue B Test. A chilled Fast Blue B solution comprising 1 mg of Fast Blue B salt (ICN Pharmaceuticals, Inc., Plainview, NY) per ml of 0.1M Tris-HCl (Fisher Scientific Co., Fair Lawn, NJ) adjusted to pH 7.0 was freshly prepared for each test. One ml of the solution was added to 1-, 2-, and 3-week old MSDA cultures of each isolate. In a positive reaction the colonies turned red within 1-2 min at room temperature.

TAXONOMIC PART

Division: Fungi Imperfecti

Form Class: Blastomycetes

Blastoschizomyces Salkin, Gordon, Samsonoff et Rieder, gen. nov.

Mycelium bene evolutum laeve hyalinum. Cellulae conidiogae annellidiformes hyphoideae hyalinae laeves, ex hyphis fertilibus exorientes. Annelloconidia hyalina laevia, interdum schizolytice divisa. Blastoconidia ex annelloconidiis exorientia Pseudohyphae interdum adsunt. Fermentatio nulla.

Species typica: *Blastoschizomyces pseudotrichosporon*. Salkin, Gordon, Samsonoff et Rieder.

Mycelium well developed, smooth, hyaline. Conidiogenous cells are annellides, hyphalike, hyaline, smooth, arising from fertile

hyphae. Anelloconidia hyaline, smooth; may undergo schizolytic division. Blastoconidia developing from annelloconidia. Pseudohyphae may be formed. Fermentation absent.

Type species: *Blastoschizomyces pseudotrichosporon* Salkin, Gordon, Samsonoff et Rieder.

Blastoschizomyces pseudotrichosporon Salkin, Gordon, Samsonoff et Rieder, sp. nov.

Notulis sub genere descriptis distinguenda.

On malt-extract agar at 27°C, colonies 25 mm in diameter after 14 days. Surface flat to slightly raised in the center. Colonies glabrous, dry, ground-glass in appearance with regular margins, white to off white in color.

On cornmeal agar with Tween 80 at 27°C, colonies 25 mm in diameter after 14 days. Surface convoluted with rhizomorphous ridges radiating from a raised center. Colonies glabrous, glossy to shiny with radiating mycelial fringes, white to off white in color. Hyphae hyaline, smooth, and 2.5-5.0 µm in diameter. Anellides hyaline, smooth, hyphalike, 3.0-80.0 X 2.5-5.0 µm, developing near septum from the main growing axis. Anelloconidia hyaline, smooth, oblong with truncate to obtuse base, 6.3-20.0 X 2.5-5.0 µm, accumulating in clusters around anellides. Anelloconidia may undergo schizolytic division and/or form secondary conidia. Pseudohyphae may also be present (Fig. 2-6). Physiologic characteristics, identical to those of *T. capitatum*, are summarized in Table 1. Fast Blue B Test negative.

Habitat: Man

Holotype: M46-67, isolated from sputum, Albany, New York

Permanently preserved specimens and lyophilized cultures deposited in the Fungal Herbarium, Science Service, New York State Department of Education, Albany, New York. Living and lyophilized cultures deposited in the American Type Culture Collection, Rockville, Maryland (accession number ATCC 46132).

Figs. 2-6. Fig. 2. Phase-contrast micrograph of annelloconidium of *B. pseudotrichosporon* (arrow) developing from annellidic conidiogenous cell (arrow) at apex of side branch. Fig. 3. Later stage in conidium development. Anelloconidium illustrated in Fig. 2 has undergone schizolytic division (arrow) as new annelloconidium develops from conidiogenous cell (arrow). Fig. 4. Scanning electron micrograph of annelloconidium development showing annellations (arrow) and zone of proliferation (zp). Fig. 5. High-voltage transmission electron micrograph of conidiogenous cell showing annellations (arrows). Fig. 6. Conidiogenous cell from Fig. 5, shown at higher magnification.

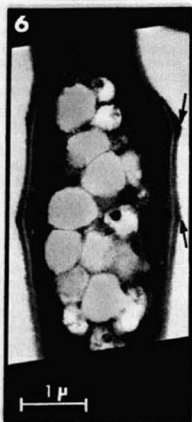
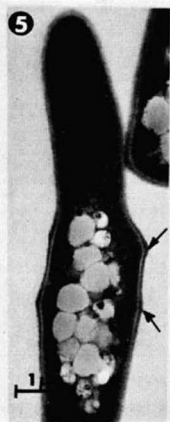
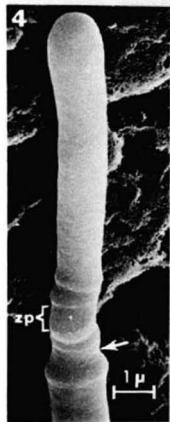
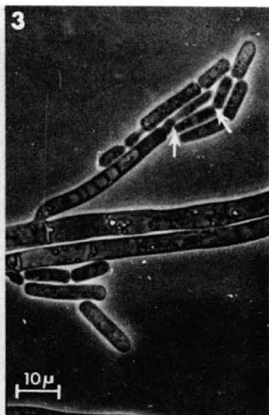


Table 1. Physiologic Characteristics of *B. pseudotrichosporon*

Test	Result	
Growth on MSDA at:		
37°C		+
45°C		+
Growth on Mycosel		+
Hydrolysis of Urea		-
Splitting of Arbutin		-
Growth in vitamin-free medium		-
Vitamin stimulating growth		
Thiamine		+
Biotin		-
Fermentation of:		
Glucose		-
Maltose		-
Sucrose		-
Lactose		-
Trehalose		-
Assimilation of potassium nitrate		-
Assimilation of:	API 20C	Wickerham
L-Arabinose	-	ND ^a
Cellobiose	-	-
Dextrose	+ (100) ^b	+ (100)
Erythritol	ND	-
Galactose	+ (53)	+ (100)
Glucitol	-	ND
Glycerol	+ (100)	ND
Inositol	-	-
2-Ketogluconate	-	ND
Lactose	-	-
Maltose	-	-
Melezitose	-	-
Melibiose	-	-
α-Methyl-D-glucoside	-	ND
Raffinose	-	-
Ribitol	-	ND
Ribose	ND	-
Rhamnose	ND	-
Sucrose	-	-
Trehalose	-	-
Xylitol	-	ND
Xylose	-	-

^a Not done as part of test procedure

^b Numbers within parentheses indicate percent positive isolates

DISCUSSION

Oblong conidia collecting in rows or clumps at the ends of hyphal branches in the present isolates simulate arthroconidia described in *Trichosporon* species. The similarity is enhanced by the formation of buds from the conidia. These morphologic problems are compounded by the isolates' physiologic characteristics, which are indistinguishable from those of *T. capitatum*. However, our examination of the type strain of *T. capitatum* revealed the presence of arthroconidia. In contrast, the percurrent proliferation of the conidiogenous cells and their extension during conidiogenesis, as shown in our light and electron micrographs, clearly demonstrate that the apparent arthroconidia in our isolates are actually annelloconidia. The subsequent proliferation of the annelloconidia by equal or unequal schizolytic division, with occasional bud formation, results in clumps of conidia at the ends of branches. This combination of annelloconidial formation with subsequent schizolytic division and budding has not been described in any other member of the eumycota. Hence a new genus and species, *Blastoschizomyces pseudotrichosporon*, are required to accommodate the isolates.

Although repeated schizolytic division of annelloconidia was noted in all isolates, the presence and extent of budding was variable. In several instances three to five buds developed serially from a single proliferating point on an annelloconidium. The morphology of the proliferating zone and the manner in which the buds were formed indicated an enteroblastic process. In these isolates the annelloconidium was acting as an annellidic conidiogenous cell, as has been described in several yeasts (Cole and Samson, 1979).

In each instance the conidiogenous cells was situated at the apex of a branch which had developed off the main axis directly below the septum. Often the branch separated from the main axis as conidia were forming at its apex, and conidial development continued on the isolated branches. Alternatively, the branches separated from the axis acted as conidia, in that the entire branch underwent repeated schizolytic division.

The Fast Blue B color reaction has been used to establish the ascomycetous (negative reaction) or hemibasidiomycetous (positive reaction) affinities of imperfect yeasts (van der Walt and Hopsu-Havu, 1976). The negative response of all isolates of *B. pseudotrichosporon* indicates that the new genus is related to the Ascomycotina.

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LITERATURE CITED

- Behrend, G. 1890. Ueber trichomycosis nodosa. Berlin Klin. Wochenschr. 27:464-467.
- Carmo-Sousa, L. do. 1970. Genus 11. *Trichosporon* Behrend, p. 1309-1352. In J. Lodder (ed.), The yeasts, a taxonomic study, 2nd ed. North-Holland Publishing Co., Amsterdam.
- Cole, G. T., and R. A. Samson. 1979. Patterns of development in conidial fungi. Pittman Pub. Ltd., London, England.
- Moore, M. J. 1975. Removal of glass coverslips from cultures flat embedded in epoxy resins using hydrofluoric acid. J. Microsc. 104:205-207.
- Rieder, C. L. 1981. Thick and thin serial sectioning for the three-dimensional reconstruction of biological ultrastructure, p. 215-249. In J. N. Turner (ed.), Methods in cell biology, vol. 22, Academic Press, New York.
- Salkin, I. F., and J. A. Robertson. 1970. Use of a tissue culture chamber for developmental studies of aquatic phycomycetes. Arch. Mikrobiol. 70:157-160.
- van der Walt, J. P. 1970. Criteria and methods used in classification, p. 34-113. In J. Lodder (ed.), The yeasts, a taxonomic study, 2nd ed. North-Holland Publishing Co., Amsterdam.
- van der Walt, J. P., and V. K. Hopsu-Havu. 1976. A colour reaction for the differentiation of ascomycetous and hemibasidiomycetous yeasts. Antonie Van Leeuwenhoek 42:157-163.

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REVUE DES LIVRES

par

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HOW TO KNOW THE NON-GILLED MUSHROOMS, par A.H. SMITH, Helen V. SMITH & Nancy S. WEBER, in Pictured Key Nature Series, 2e édition, 324 p., 340 f., 18x23 cm, reliure spirale, 1981. Wm. C. Brown Co. Publ. Dubuque, Iowa, USA.

Ce guide et celui que les mêmes auteurs ont déjà publié en 1979 sur les champignons à lamelles (How to know the gilled Mushrooms) font un ensemble couvrant quelque 1600 espèces de champignon.

Ce guide propose à l'amateur des clés de terrain permettant l'identification des espèces communes de morille, chaterelle et bolet, sans l'aide du microscope. Mais en outre et surtout il propose au mycologue plus averti des clés précises, basées sur des caractères microscopiques, pour la détermination des espèces Nord-américaines connues. Parmi les Ascomycotina, ce sont des Sphaeriales (*Xylaria*, *Cordyceps*, *Hypomyces*), des Helotiales (Geoglossacées, Scotiacées), des Pezizales (Pezizacées, Morchellacées, Helvellacées, Sarcosomatacées etc.) des truffes (*Tuber*); parmi les Basidiomycotina, ce sont des Tremellales, des Aphyllophorales clavarioides, cantharelloïdes, hydnoïdes et poroïdes, des Agaricales tubiformes (p.140-224), des Gasteromycètes et des truffes basidiosporées (*Leucogaster*, *Hymenogaster*, *Melanogaster*, *Rhizopogon*, etc.). Chaque espèce a sa description complète, et certaines (330) son illustration, insérée dans la clé.

FUNGORUM RARIORUM ICONES COLORATAE. PART. XII. NEW, RARE AND INTERESTING SPECIES OF *ENTOLOMA*, par E. ARNOLDS et M. NOORDELOOS, p.1-36, pl. col. 89-96, f. 1-25, 8°, broché, 1981. J. Cramer, FL 9490 Vaduz.

Vingt-cinq espèces d'*Entoloma* du Nord-ouest de l'Europe sont décrites, illustrées et dépeintes. Les noms de 8 d'entre elles ont été récemment publiés comme nouveaux par l'un des auteurs dans *Persoonia* 10:283-300, 1979 et 10:427-534, 1980.

NUTRITIONAL REQUIREMENTS OF *LACTARIUS* SPECIES AND CULTURAL CHARACTERS IN RELATION TO TAXONOMY, par A.J.P. OORT, 96 p., 27 f., 4 pl. col., 8°, broché, dos papier, 1981. Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, afd. Natuurkunde, 2e série, v. 76. North-Holland Publ. Cy, Amsterdam. Prix US \$ 29.75, DFL 70.-

Bien que les recherches sur les champignons mycorrhizogènes aient débuté il y a plus de 50 années en Suède avec Melin, peu a été réalisé sur les Lactaires. L'objectif de l'auteur est d'apporter une étude de base

sur les possibilités de culture des Lactaires pour en comprendre les exigences physiologiques. Après un chapitre d'introduction et un autre sur la méthode appliquée, l'auteur caractérise ses souches d'espèces dans un troisième chapitre et analyse leurs besoins spécifiques en azote et en vitamines dans un quatrième chapitre. Enfin il pose la question de la correspondance entre les différences culturales et physiologiques observées et les distinctions taxonomiques. Il est clair que cette étude contribue au développement de recherches sur la mycorhization par les Lactaires, sur la réponse de la mycoflore forestière aux amendements chimiques et sur la production en monoculture d'espèces comestibles. La méthode d'investigation de l'auteur est aussi en elle-même un aspect intéressant de cette étude.

Comme je l'ai mentionné par ailleurs, l'emploi de clés dichotomiques est souvent fastidieux. En effet, nombreuses d'entre elles, dites "dichotomiques", ne le sont pas vraiment. En effet la dichotomie procède "par divisions et subdivisions binaires" (P. Robert, Dictionnaire de la langue française, 1978) de telle sorte que chaque branche est à nouveau bifurquée. Or, les clés "dichotomiques" apparaissent souvent, en tout ou en partie, "sorioïdes" (cyme unipare). On y trouve en effet la répétition de bifurcations unipares, l'une des branches aboutissant à une espèce, l'autre branche seule étant bifurquée à nouveau de manière unipare. Cette autre branche est souvent indiquée "not as above". Pareille clé oblige le chercheur à éliminer une par une, un grand nombre d'espèces souvent très rares ou particulières, avant de trouver l'espèce commune qu'il a en main.

Quoiqu'il en soit, ce livre ne peut manquer d'être utile et ne peut que pousser le mycologue débutant à travailler de manière précise et à faire usage du microscope, d'ailleurs devenu indispensable à toute identification sérieuse.

COMPENDIUM OF POTATO DISEASES, par W. J. HOOKER, éditeur, in The Disease Compendia Series, (n°6), 125 p., 106 f., 87 pl. col. 4°, broché, 1981. The American Phytopathological Society, 3340 Pilot Knob Road, St Paul, Minnesota 55121. Prix US\$ 11.00.

Les Compendia sur les maladies des plantes cultivées de l'American Phytopathological Society nous sont maintenant bien connus pour leur qualité de texte et d'illustration et leur contenu scientifique précis mis au service de la pratique de la défense des végétaux. Déjà les maladies du soja (1975), du froment (1977), de la luzerne (1979), du maïs (1980) et du coton (1981) ont été publiés.

Ce Compendium sur les maladies de la pomme de terre est particulièrement fouillé dans un texte en petits caractères et documenté d'une excellente iconographie. Les maladies sont non par organe mais par agent causal. Trente quatre maladies de nature fongique sont décrites. La classification et la nomenclature des champignons sont assez bonnes. On notera qu'à côté de *Phytophthora infestans*, on trouvera aussi le *Phytophthora erythroseptica*, et d'autres, la cause de la pourriture rose. On ne voit pas pourquoi le nom *Stemphylium consortiale* est préféré à *Ulocladium consortiale* bien plus correct, de même *Sclerotinia fuckeliana* au lieu de *Botryotinia fuckeliana*, ces genres étant en chaque cas si clairement distincts.

COMPENDIUM OF ELM DISEASES, par R.J. STIPES et R.J. CAMPANA, ed., in The Disease Compendia Series, (n°7), 96 p., 106 f., 198 pl. col. 4°, broché, 1981. The American Phytopathological Society, 3340 Pilot Knob Road, St Paul, Minnesota 55121. Prix US\$ 11.00.

Le Compendium des maladies de l'orme donne, comme il faut s'y attendre, une large place à l'*Ophiostoma ulmi*, la cause de "la" maladie de l'orme, mais il envisage aussi 28 autres maladies d'origine fongique, sans compter les pourritures fongiques du bois. Les maladies sont ici classées par type de symptômes. La nomenclature des champignons est aussi correcte que possible. Cependant le nom *Phymatotrichum omnivorum* est maintenu, incorrigible, alors que *Phymatotrichum* est synonyme de *Botrytis* et que le genre *Phymatotrichopsis* a été créé en 1973 avec *P. omnivora*, pour type.

ECOLOGY AND COENOLOGY OF MACROFUNGI IN GRASSLANDS AND MOIST HEATHLANDS IN DRENTHÉ, THE NETHERLANDS, PART I. INTRODUCTION AND SYNECOLOGY, par Eef ARNOLDS, in *Bibliotheca Mycologica* v. 83, 410 p. 45 f., 14 tableaux en pochette, 8°, relié toilé, 1981. J. Cramer, 9490 Vaduz, Lichtenstein. Prix DM 96.- (souscription), 120.-.

Cet important travail, dont ce livre est la première partie, relate les observations accumulées par l'auteur de 1974 à 1977, dans le Nord-est des Pays-Bas, dans 64 sites différents. Plus de 370 espèces furent relevées. Dès le début de l'ouvrage, l'auteur rejette la terminologie proposée par Darimont pour la mycosociologie (voir *Mycotaxon* IV(1):312) et préfère adopter une terminologie analogue à celle de la phytosociologie et l'écologie végétale, y substituant le préfixe "myco" au préfixe "phyto". L'auteur aussi préfère le terme "mycocénologie" au terme "mycosociologie", afin d'écarter l'idée de l'existence d'une relation entre les espèces fongiques d'une même cénose. L'auteur caractérise ensuite chaque association végétale par sa mycoflore d'espèces caractéristiques, différentielles, constantes, dominantes et productrices. De même, il caractérise les associations dans des habitats particuliers tels le bois, les excréments. Il étudie enfin les similitudes entre les différentes mycocénoses. En guise de conclusion de cette première partie, l'auteur montre l'importance des observations mycocénologiques dans la Protection de la nature, pour la détection des espèces rares, l'observation des modifications apportées par les fertilisants dans la mycoflore et l'influence des pratiques culturales sur le maintien de la mycocénose.

NATIONAL WORK CONFERENCE ON MICROBIAL COLLECTIONS OF MAJOR IMPORTANCE TO AGRICULTURE, University of Maryland, College Park, Maryland, March 12-14, 1980, by M. ROGOSA éd., 52 p., 8°, relié toilé, 1981, The American Phytopathological Society, 3340 Pilot Knob Road St Paul, MN 55121, USA. Prix US \$ 6.50.

Voir disparaître des collections uniques de microorganismes, phytopathogènes ou autres, outil de travail de chercheurs isolés, par suite d'une absence de reconnaissance institutionnelle à quelque niveau que ce soit, est regrettable. La conférence, réunie par la Société Américaine de Microbiologie, a donc confirmé la nécessité de maintenir certaines souches de microorganismes selon des critères définis, et établit les conditions de caractérisation et de conservation. Elle insiste sur la nécessité d'établir les catalogues des collections et un système de communication entre collections. Elle reconnaît l'urgent besoin d'un support financier des collections. Les 40 participants de la Conférence décident de créer un Comité de Conseil et de Planification qui résultera de la formation à l'échelle nationale de pareils comités.

Encore reçus:

CATALOGUE OF CULTURES. BACTERIA, MYCOPLASMAS, VIRUSES, FUNGI, par M. KOCUR éd., 3e édit., 630 p., 8°, 1975. Czechoslovak Collection of Microorganisms, J.E. Purkyně University, 66243 Brno, Czechoslovakia. (The Fungi, par L. Marvanova, p. 499-587.)

CATALOGUE OF YEAST CULTURES, par Anna KOCKOVA-KRATOCHILOVA, 324 p. 8°, relié toilé, 1977. Slovak Academy of Sciences. Veda Publ., Bratislava, Czechoslovakia. Prix Kčs 28.-. (Répertoire des cultures qui existent dans 7 collections tchécoslovaques. Une application de la taxonomie numérique aux levures, avec 14 clés d'identification.)

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ERRATA, VOLUME FOURTEEN

- 14(1) cover 1, line 18: for synnemetal read synnematal
 28: for Pseudoallescheria read Pseudallescheria
 cover 2, line 30: for Basidiomycetes read Basidiomycetes
 37: for Gloeocystidiellum read Gloeocystidium
 47: for Tilachidiopsis read Tilachlidiopsis
 page 14, line 13: for Spatularia read Spathularia
 31: for juglandis read juglandis
 pages 94-100: throughout correct endings of epithets:
 from Ps. africanum to Ps. africana
 from Ps. angustum to Ps. angusta
 from Ps. desertorum to Ps. desertarum
 from Ps. ellipsoideum to Ps. ellipsoidea
 from Ps. fusoideum to Ps. fusoidea
 page 178, line 8: for C. simplex read Codinaea simplex
 193, lines 36, 38: for syzigii read syzygii
 194, line 2: for anonicola read annonicola
 24: for cercropiae read cecropiae
 46: for crinosporium read crinisporium
 195, line 32: for mikanium read mikanum
 196, line 20: for T. read Trichomerium
 38: for clitorae read clitoriae
 200, line 20: for vagae read javae
 201, line 34: for stuhlmanniana read stuhlmanniana
 204, line 18: for crinisporum read criniporum
 212, line 21: for clitorae+ read clitoriae+
 39: for crinosporum read criniporum
 229, line 17: for calvatum read clavatum
 243, line 18: for floccocephla read floccocephala
 258, line 41: for Helicodencron read Helicodendron
 280, line 12: for Cjepomyces read Cejpomyces
 291, line 17: for Botryohypchnus read Botryohypochnus
 295, line 31: for Haploti- read Haplotri-
 297, line 48: for Bryobasidium read Botryobasidium
 398, note 19: for Erinia read Erynia
 410, col. 5: for ERINIA read ERYNIA
 429, line 3: for chlamidosporus read chlamydosporus
 22: for humicolus read humicola
 431, line 22: for rhyzosporus read rhyso-sporus
 437, line 1: for Tiletia-like read Tilletia-like
 9: for T. read Triplosporium

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