Keys to the identification of the arthropod pathogenic genera of the families Entomophthoraceae and Neozygitaceae (Zygomycetes), with descriptions of three new subfamilies and a new genus

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The family Entomophthoraceae is subdivided into three subfamilies. The Entomophthoroideae subfam. nov. is characterised by conidia which are produced on conidiophores and forcibly projected. The conidiophores are unbranched and the conidia bi- to multinucleate. The Erynioideae subfam. nov. is also characterised by conidia which are produced on conidiophores and are forcibly projected, but the conidiophores are branched and the conidia are mononucleate. The Massosporoideae subfam. nov. has conidia produced in chambers within a mycelial mass and are passively detached. A new genus, *Apterivorax* sp. nov. is described in the family Neozygitaceae. It comprises species which neither have capilliconidia nor resting spores. Keys to the subfamilies and to the genera as well as lists of genera and species belonging to the two families are provided.

Key words: Entomophthoraceae, Neozygitaceae, Entomophthoroideae, Erynioideae, Massosporoideae, *Apterivorax*, new taxa, identification keys, species list.

In the past three decades the systematics of the order Entomophthorales has undergone considerable changes. The order as established by Humber (1989) consisted of six families, Ancylistaceae, Basidiobolaceae, Completoriaceae, Entomophthoraceae, Meristacraceae and Neozygitaceae. The arthropod-pathogenic species are placed in the families Ancylistaceae (genus *Conidiobolus*), Entomophthoraceae and Neozygitaceae. Only one entomopathogenic species, *Meristacrum milkoi* (Dudka & Koval) Humber (1981), pathogen of larval Tabanidae (Diptera) exists in the family Meristacraceae. The other species of this family are obligate pathogens of nematodes and tardigrades. The family Basidiobolaceae contains a single genus, *Basidiobolus*, with four species, occurring as saprobes

in soil and on excrements. The only species of Completoriaceae is an obligate intracellular parasite of fern gametophytes.

Cavalier-Smith (2002) proposed a new classification. He excluded the Basiodobolaceae from the order Entomophthorales to place it in the class Bolomycetes. He separated the other families of the Entomophthorales from the Zygomycetes and placed them in the class Zoomycetes together with five other orders including the Laboulbeniales which, however, are true Ascomycetes. Benny & al. (2002) did not follow this proposal and treated the Entomophthorales as Zygomycetes. Nevertheless, the exclusion of the Basidiobolaceae is justified by the results of recent genetic investigations (Jensen & al., 1998; Nagahama &. al., 1995). Also, the taxonomic position of the Completoriaceae is uncertain (Humber, 1989) as well as that of the Neozygitaceae (Benny & al., 2002). The Zoomycetes (Cavalier-Smith, 2002) and especially the Neozygitaceae are considered to be the ancestors of microsporidia (Freimoser, 2000). Further changes in respect to the classification of the Entomophthorales and its families can be expected.

In recent years the knowledge of the species belonging to the families Entomophthoraceae and Neozygitaceae has strongly increased, as the use of cytological and molecular criteria allowed the researchers new taxonomic, systematic and phylogenetic interpretations of relationships. The new information collected now justifies the emendation of existing and the erection of new taxa. The aims of this paper are: To give the families Entomophthoraceae and Neozygitaceae a clear and logical structure by describing three new subfamilies and a new genus, to facilitate the identification, to provide a list of species of Entomophthoraceae and Neozygitaceae described so far and to address research needs.

Taxonomic concept

The two families Entomophthoraceae and Neozygitaceae consist exclusively of arthropod-pathogenic species.

The family Entomophthoraceae is defined by the following characteristics (Humber, 1989): Early vegetative stages mycelial, hyphal bodies spherical to rounded, with or without cell wall, or fusoid to catenate or irregularly shaped, amoeboid with or without cell wall. The nuclei with a diameter of (3–) 5–12 µm, contain much condensed chromatin that stains usually readily with aceto-orcein. The nucleolus is not prominent. The conidiophores are simple, dichotomously or digitally branched (Fig. 1). The primary conidia are uni- or bitunicate (Fig. 2), forcibly discharged, mono- to multinucleate, and one or two, rarely three types of secondary conidia are produced. Resting spores are zygospores or azygospores, formed as

lateral or terminal buds connected to parental cell by a narrow isthmus, multinucleate, hyaline or coloured, with the episporium smooth or ornamented.

Humber (1989) also characterised the familiy Neozygitaceae as follows: Vegetative growth as globose or rod-shaped hyphal bodies with or without cell wall. The nuclei are small, about 3–5 µm diameter with a central, ovoid nucleolus, the condensed chromatin is inconspicuous and stains poorly in aceto-orcein or other nuclear stains. The conidiophores are simple. The primary conidia are unitunicate, forcibly discharged by papillar eversion, slightly melanised, with 4 (5) or 7–11 nuclei, and their papilla is truncate or small. Usually two types of secondary conidia occur, one resembling the primary ones, the other being smoky capilliconidia with a terminal haptor. Resting spores are usually zygospores that bud from a conjugation bridge between conjugating hyphal bodies and receive one nucleus from each gametangium (thus becoming binucleate); they are ovoid with a smooth surface or globose to subglobose with a rough surface, and form a mature epispore strongly melanized and readily detached from the endospore. Resting spores germinate directly to produce secondary-type capilliconidia on capillary germ conidiophore.

The genera of the family Entomophthoraceae are very heterogeneous, but they can be assigned to three groups of rather homogenous genera. We propose to describe these three groups as subfamilies. The only genus in the family Neozygitaceae is heterogenous and consists of two groups of species which we propose to separate by the erection of a new genus.

Taxonomic descriptions and keys

1. Entomophthoraceae

The family consists of three groups of genera. The first group is characterised by unbranched conidiophores and multinucleated, forcibly ejected conidia and the second one by branched conidiophores and mononucleate, forcibly ejected conidia. The third one lacks conidiophores, the conidia are mono-, bi- to multinucleate and passively detached. These three groups are described here as new subfamilies.

The form-genus *Tarichium* Cohn (1875) consists of species known only from their resting spore stage. The genus is usually included in the family Entomophthoraceae although some individual species may belong to other families. As the taxonomic position of

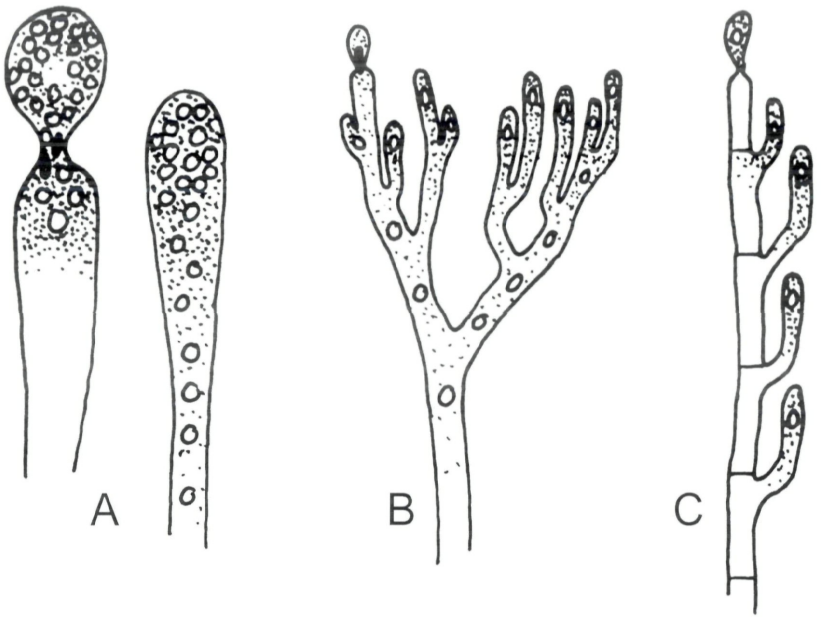


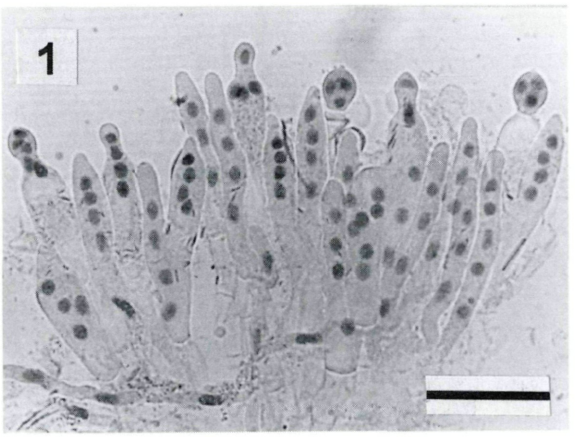
Fig. 1. Conidiophores branching. – A: unbranched; B–C: branched. B: digitally branched; C: dichotomously branched.

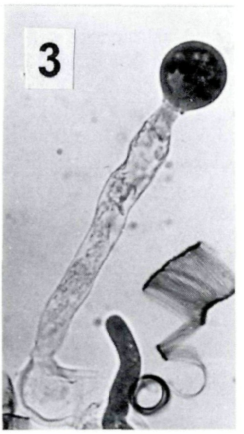
the species included in this genus is far from being satisfactorily solved, this genus is not treated here.

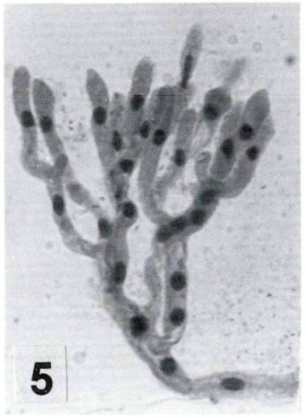
Key to subfamilies (Plate 1)

1 Conidia produced on conidiophores. Conidia forcibly projected 2
1* Conidia produced in chambers within a mycelial mass, passively detached . . . . . *Massosporoideae* (1.3)
2 Conidiophores unbranched, conidia bi- to multinucleate (Plate 1, Figs. 1–4) . . . . . *Entomophthoroideae* (1.1)
2* Conidiophores branched, conidia mononucleate (Plate 1, Figs. 5–7) . . . . . *Erynioideae* (1.2)

Plate 1. – Unbranched conidiophores with multinucleate conidia (Figs. 1–4), digitally (Figs. 5-6) and dichotomously (Fig. 7) branched conidiophores with mononucleate conidia (Figs. 5–7): 1. *Entomophthora schizophorae*; 2. *E. muscae*; 3. *Entomophaga apiculata*; 4. *E. grylli*; 5. *Zoophthora elateridipahaga*; 6. *Pandora blunckii*; 7. *Furia ellisiana*. Lactophenol-aceto-orcein (LPAO). Bar in Fig. 1 represent 50 µm, all same magnification.







1.1. **Entomophthoroideae subfam. nov.** S. Keller

Corpora vegetativa primo curte hyphalia, baculiformia, ellypsoidea, globosa vel subglobosa, irregulariter rotundata vel amoeboidea, parietibus cellularibus praedita vel nuda. Conidiophora non ramosa, in apicibus expansa, collo conidia primaria formanti praedita. Conidia primaria motu cellulae conidiogenae expulsa, unitunicata, globosa, subglobosa, pyriformia, cilindrico-elongata vel campanulata apice acuto, binucleata vel multinucleata. Nuclei diam. 3-6 µm mensi. Conidia secundaria habitu distincta vel indistincta, motu cellulae conidiogenae expulsa. Sporae perdurantes globosae vel subglobosae, hyalinae vel episporio fusco praeditae, probabiliter azygosporae. – Cystidia absentia, rhizoidea monohyphalia vel absentia.

Species pathogenae insectorum vel Phalangiidarum (Arachnidum).

Genus typicum: *Entomophthora* Fresenius, Bot. Zeitung 14, 882. 1856.

Early vegetative stages short hyphae-like, rod-shaped, ellipsoid, globose to subglobose, irregularly rounded or irregularly shaped amoeboid, with or without cell walls. Conidiophores unbranched, terminally enlarged, forming a neck to produce primary conidia. Primary conidia actively discharged, unitunicate, globose, subglobose, pyriform, elongate cylindrical or campanulate with pointed apex, bi- to multinucleate. Nuclei with an average diameter of 3–6 µm. One or two types of secondary conidia formed , actively discharged. Resting spores globose to subglobose, hyaline or with dark epispore, probably azygospores. Cystidia absent, rhizoids monohypyhal or absent. Obligate pathogens of insects and Phalangiidae (Arachnida).

Type genus: *Entomophthora* Fresenius, Bot. Zeitung 14, 882. 1856.

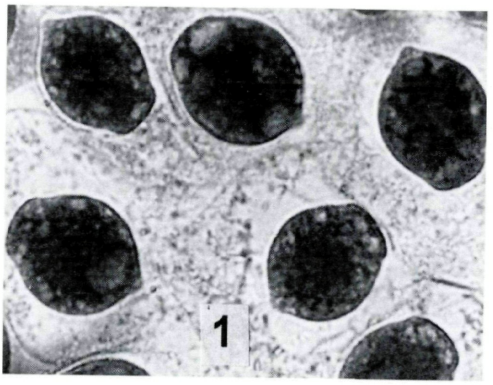
The subfamiliy Entomophthoroideae includes the four genera *Batkoa, Entomophaga, Entomophthora* and *Eryniopsis*.

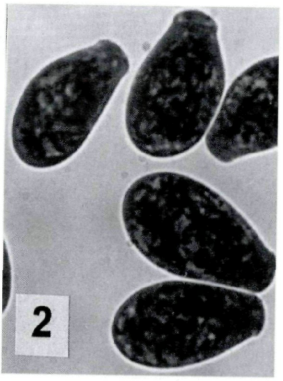
Key to genera (Plate 2)

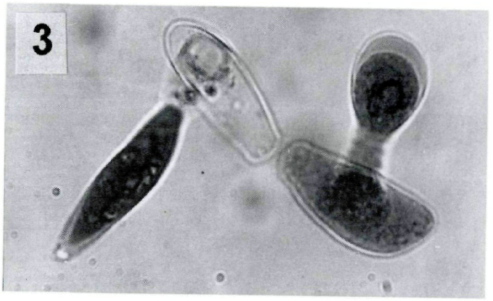
1 Primary conidia bell-shaped (campanulate) (Plate 2, Fig. 1), apical point prominent or indistinct, bi- to multinucleate. Rhizoids monohyphal or absent . . . . . *Entomophthora* (1.1.3.)

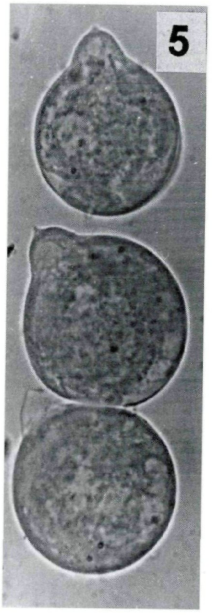
1* Primary conidia elongate, pear-shaped, ovoid or spherical to subspherical. Rhizoids monohyphal or absent 2

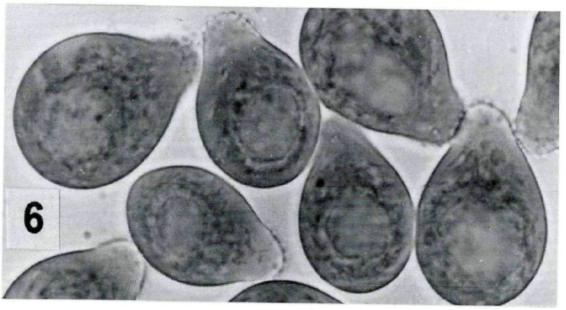
Plate 2. Entomophthoroideae. – Types of conidia. 1. *Entomophthora muscae*; 2. *Eryniopsis caroliniana*, primary conidia; 3. *Eryniopsis caroliniana*, two types of secondary conidia; 4. *Batkoa limoniae*; 5. *B. apiculata*; 6. *Entomophaga grylli*; 7. *E. conglomerata* with nuclei visible (LPAO). Figs. 1–6: Lactophenol-cottonblue (LPCB). Bar in Fig. 7 represent 50 µm, all same magnification.











2 Primary conidia elongate, pear-shaped to ovoid, less than 10 nuclei per conidium on avergae (Plate 2, Fig. 2). Two types of secondary conidia (Plate 2, fig. 3). Rhizoids absent . . . . . *Eryniopsis* (1.1.4.)

2* Primary conidia spherical, subspherical, pear-shaped to ovoid, more than 10 nuclei per conidium on average. Rarely two types of secondary conidia. Rhizoids present or absent 3

3 Primary conidia spherical to subspherical, papilla demarcated from conidial body (Plate 2, Figs. 4–5). Secondary conidia like primary. Rhizoids present or absent . . . . . *Batkoa* (1.1.1.)

3* Primary conidia pear-shaped to ovoid, papilla smoothly joining the conidial body (Plate 2, Figs. 6–7). Secondary conidia like primary or elongate on long slender conidiophore. Rhizoids absent . . . . . *Entomophaga* (1.1.2.)

1.1.1. *Batkoa* Humber, Mycotaxon 34, 446. 1989.

Hyphal bodies short, hyphae-like, irregularly rounded to elongate, subspherical, composed of rounded portions or amoeboid-like. They contain about 10-100 nuclei. Nuclei stain readily with aceto-orcein. Aceto-orcein stained nuclei with a diameter of 3.5–4.6 µm. – Conidiophores unbranched. – Primary conidia in most species separated into a nearly spherical conidial body and a prominent papilla, rarely *Entomophaga*-like; papilla conical or semi-circular, sometimes prolonged, ending rounded, rarely pointed. – Secondary conidia of only one type and resembling the primary ones, produced on a short thick secondary conidiophore arising laterally of primary conidia. – Resting spores spherical, hyaline. – Cystidia absent. Rhizoids monohyphal, thick, with specialised ending; absent in some species. Obligate entomopathogens.

Type species: *Batkoa apiculata* (Thaxter) Humber (1989)

Other species included:
B. amrascae S. Keller & Villacarlos in Villacarlos & Keller (1997)
B. dysderci (Viégas) Humber (1989)
B. gigantea (S. Keller) Humber (1989)
B. limoniae (S. Keller) S. Keller comb. nov. Basionym: *Entomophaga limoniae* Keller, Sydowia 40, 146. 1987.
B. major (Thaxter) Humber (1989)
B. papillata (Thaxter) Humber (1989)

1.1.2. *Entomophaga* Batko emend Humber, Mycotaxon 34, 447. 1989.

Vegetative cells usually wall-less protoplasts during early stages of development. – Hyphal bodies spherical, subspherical

or irregularly rounded or composed of rounded structures, containing about 10–70 nuclei. Nuclei stain readily with aceto-orcein. Aceto-orcein stained nuclei with a diameter of 4.2–5.0 µm. – Conidiophores unbranched. Primary conidia pyriform, the conidial body joining the papilla smoothly; papilla prominent, rounded. – Secondary conidia like primary produced on a short, thick secondary conidiophore arising laterally of primary conidia or elongate fusiform to ellipsoid produced on long, slender secondary conidiophore. – Resting spores spherical, hyaline. – Cystidia and rhizoids absent. Obligate entomopathogens.

Type species: *Entomophaga grylli* (Fresenius) Batko (1964a)

Other species included:
E. aulicae (Reichardt in Bail) Humber (1984b)
E. batkoi (Bałazy) Keller (1987)
E. bukidnonensis Villacarlos & Wilding (1994)
E. calopteni (Bessey) Humber (1989)
E. conglomerata (Sorokin) Keller (1987)
E. diprionis Bałazy (1993)
E. kansana (Hutchison) Batko (1964b)
E. lagriae Bałazy (1993)
E. maimaiga Humber, Shimazu & Soper in Soper & al. (1988)
E. ptychopterae (Keller & Eilenberg) Hajek & al. (2003)
E. pyriformis (Thoizon) Bałazy (1993)
E. saccharina (Giard) Batko (1964b)
E. tabanivora (Anderson & Magnarelli) Humber (1984b)
E. tenthredinis (Fresenius) Batko (1964b)
E. tipulae (Fresenius) Humber (1989)
E. transitans (Keller & Eilenberg) Hajek & al. (2003)

Excluded species (*nomina nuda*):
E. macleodii Humber (1992)
E. praxibulii Humber (1992).
E. asiatica Humber (1992)

More details on of the origin of the excluded species are given by Carruthers & al. (1997).

1.1.3. *Entomophthora* Fresenius, Bot. Zeitung 14, 882. 1856.

Vegetative cells either protoplasts or hyphal bodies. – Hyphal bodies usually regular, spherical to subspherical, elliptical or subrectangular, sometimes irregularly rounded, germinating with single germ tube. Nuclei stain distinctly in lactophenol-aceto-

orcein (LPAO), diameter on average 2.5–6 µm. – Conidiophores unbranched, terminal portion enlarged. – Primary conidia campanulate, outer wall ruptures after discharge, projected conidia therefore surrounded by a halo, bi- to multinucleate (Plate 1, Figs. 1-2; Plate 2, Fig. 1). – Secondary conidia similar to primary ones, apical point often indistinct, formed laterally from primary conidia on a short secondary conidiophore. Projected secondary conidia not surrounded by a halo. – Resting spores spherical, hyaline or surrounded with a dark episporium. – Rhizoids present or absent, monohyphal or joined to form bundles in the basal portion, in some Diptera restricted to mouthparts, without specialized endings. – Cystidia absent when conidia are produced, may be abundant in presence of resting spores. Obligate entomopathogens.

Type species: *Entomophthora muscae* (Cohn) Fresenius (1856).

Other species included:
E. brevinucleata Keller & Wilding (1985).
E. byfordii S. Keller (2002).
E. chromaphidis Burger & Swain (1918).
E. culicis (Braun) Fresenius (1858).
E. erupta (Dustan) Hall (1959).
E. ferdinandii S. Keller (2002).
E. grandis S. Keller (2002).
E. helvetica Keller & Ben-Ze'ev in Ben-Ze'ev, Keller & Ewen (1985).
E. israelensis Ben-Ze'ev & Zelig (1984).
E. leyteensis Keller & Villacarlos in Villacarlos & al. (2003).
E. philippinensis Villacarlos & Wilding (1994).
E. planchoniana Cornu (1873).
E. rivularis Keller, Niell & Santamaria in Keller (2002).
E. scatophagae Giard (1888).
E. schizophorae Keller & Wilding in Keller (1987).
E. simulii Keller (2002).
E. syrphi Giard (1888).
E. thripidum Samson, Ramakers & Oswald (1979).
E. trinucleata Keller (1987).
E. weberi Lakon ex Samson in Samson & al. (1979).

Keller (2002) provided a key to these species which includes a further, not yet formally described species from *Rhagonycha fulva* (Coleoptera, Cantharidae) (Eilenberg, 2002). The paper also addresses possible synonymies of *E. brevinucleata* and *E. israelensis* and of *E. chromaphidis* and *E. planchoniana*. Molecular studies done with species of this genus basically confirmed the species concept. Dif-

ferences were found between the studied species except between *E. muscae* and *E. sactophagae* (Jensen, 2001). However, the slight morphological differences and the different host range justifiy a separation of the two species.

1.1.4. *Eryniopsis* Humber, Mycotaxon 21, 258–259. 1984.

Hyphal bodies subglobose, ovoidal or irregularly rounded. – Conidiophores unbranchedor with few branchings. – Primary conidia ovoid, ellipsoidal or elongate fusiform with 4–10 nuclei on average. Usually two types of secondary conidia, either type Ia and type Ib, or type Ia and type II (Plate 2, Fig. 3; Figs. 2 and 3), both produced laterally from primary conidia on thick secondary conidiophores (types Ia and Ib) or on elongate slender or capillary tube (type II) Resting spores spherical, hyaline, smooth; unknown in some species. – Cystidia absent. – Rhizoids in most species absent, or monohyphal without specialised holdfast. Obligate entomopathogens.

Type species: *Eryniopsis lampyridarum* (Thaxter) Humber (1984a).

Other species included:
E. caroliniana (Thaxter) Humber (1984a).
E. longispora (Bałazy) Humber (1984a).

The genus is heterogenous. Investigations using PCR-RFLP demonstrated that two species previously placed in this genus are closely related with species of the genus *Entomophaga* to which they were transfered while *E. caroliniana* showed a different molecular pattern (Hajek & al., 2003).

1.2. **Erynioideae subfam. nov.** S. Keller

Corpora vegetativa primo globosa vel subglobosa, breviter baculiformia ad hyphalia, ramosa vel non ramosa, parietibus cellularibus praedita vel nuda, oligonucleata vel multinucleata. Nuclei corporum hyphalium in liquido dicto lactophenolo acetoorceinico valde colorati diam. 4-9 µm mensi. Conidiophora ramosa, unum solum conidium ad apicem formantia. Conidia primaria motu cellulae conidiogenae expulsa, bitunicata, subglobosa, ovoidea vel ellypsoidea, cilindrica vel fusiformia vel conico-elongata, in specibus aquaticis tetraradiata, papilla rotundata vel subconica praedita. Conidia secundaria varia, duobus vel pluribus formibus. Sporae perdurantes multinucleatae, zygosporae vel azygosporae globosae vel subglobosae, hyalinae vel coloratae, episporio laevi vel ornato, unicam hypham germinativam formantes. Rhizoidea monohyphalia, composita, peudorhizomorpha vel absentia. – Cystidia praesentia vel absentia.

Species pathogenae insectorum vel Phalangiidarum (Arachnidum).

Early vegetative stages spherical, subspherical, short rod-shaped to hyphae-like, branched or unbranched, with or without cell wall, oligonucleate to multinecleate. Nuclei in hyphal bodies deeply staining in lactophenol-aceto-orcein, average diameter 4–9 µm. – Conidiophores branched producing a single conidium at the end of each branch. – Primary conidia actively discharged, bitunicate, subglobose, ovoid, ellipsoid, cylindrical, spindle-shaped or elongate conical, or tetraradiate in waterlogged species; papilla rounded or sub-conical. At least two types of secondary conidia. – Resting spores multinucleate, zygospores or azygospores, spherical to subspherical, hyaline or coloured, endospore smooth or ornamented, germinate with single germ tube. Rhizoids monohyphal, compound pseudorhizomorph or absent. – Cystidia present or absent. Obligate pathogens of insects and Phalangiidae (Arachnida).

Type genus: *Erynia* (Nowakowski ex Batko) Remaudière & Hennebert (1980).

The subfamiliy Erynioideae consists of the six genera *Erynia, Furia, Orthomyces, Pandora, Strongwellsea* and *Zoophthora*.

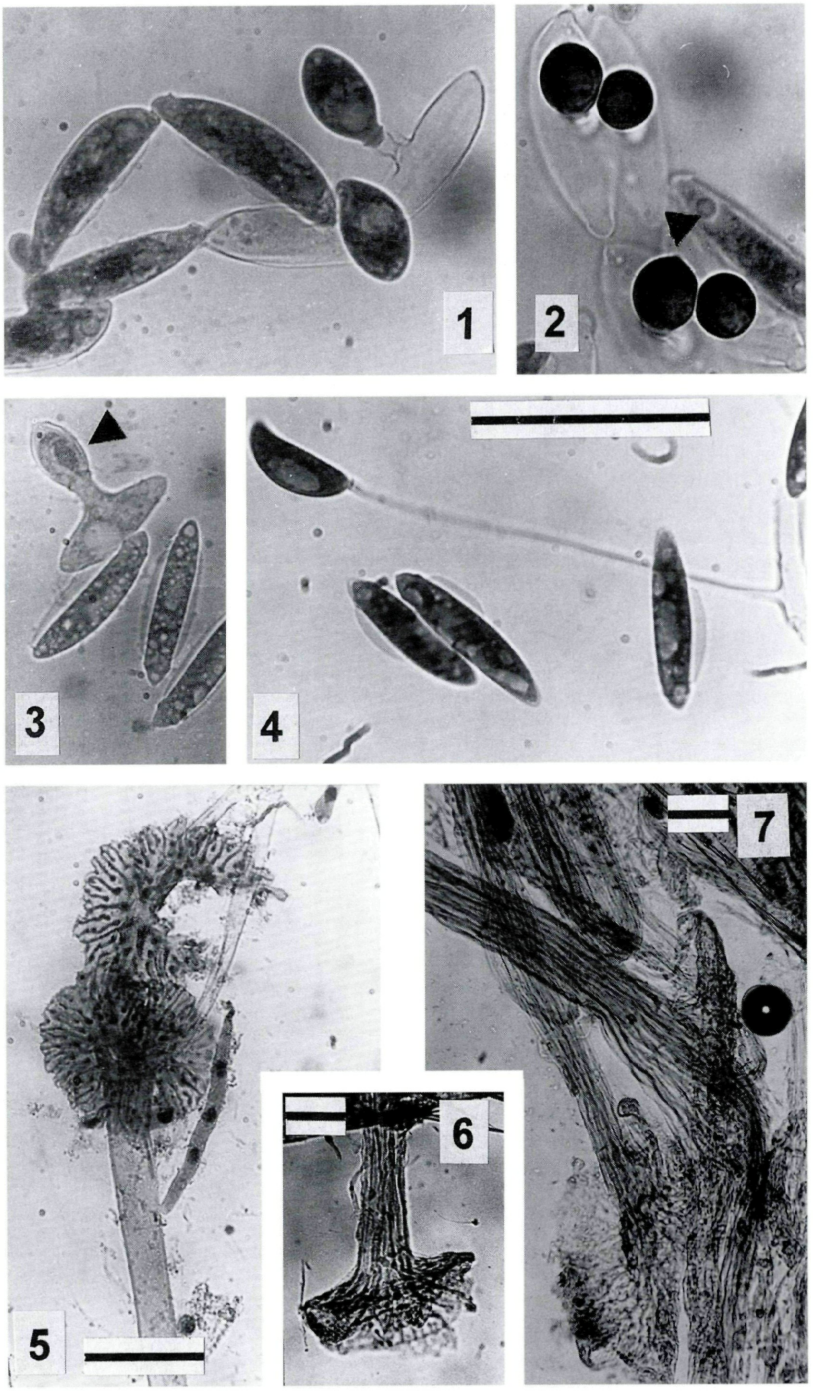
Key to genera (Plates 3, 4; Fig. 3)

1 Conidia produced on the body surface of the host. Conidiophores branched, rhizoids present 2

1* Conidia produced in the abdomen of living flies and projected through 1–2 circular holes on the ventral side. Conidiophores unbranched, rhizoids absent . . . . . *Strongwellsea* (1.2.5.)

2 Secondary conidia either spherical to subspherical or resembling the primary ones (Plate 3, Figs. 1–2). Rhizoids monohyphal (Plate 3, Fig. 5) 3

Plate 3. Erynioideae. – Types of secondary conidia (Figs. 1–4) and rhizoids (Figs. 5–6). 1–2. *Erynia rhizospora*: 1. Primary conidia (left) and secondary conidia resembling the primary ones (type Ia secondary conidia) (right). 2. Secondary conidia of the globular type (type Ib secondary conidia). Note pointed apex (arrowhead). 3–4. *Zoophthora phalloides*: 3. Primary conidia and developing conidium of type Ia. 4 (arrowhead). Primary conidia and capilliconidium (type II secondary conidium). 5. Two rhizoids of *Pandora blunckii*, one with circular (disc-like), the other with semi-circular holdfast (ending). 6. Single compound rhizoid (pseudorhizomorph) of *Zoophthora radicans* with disc-like holdfast (side view). 7. Cluster of compound rhizoids of *Z. radicans* with holdfasts. LPCB. Bar in Fig. 4, 5, 6 and 7 represent 50 µm, Figs. 1-4 same magnification.



2* Secondary conidia either resembling the primary ones or produced on capillary tube (Plate 3, Figs. 3–4). Rhizoids monohyphal and compound pseudorhizomorphs (Plate 3, Figs 6–7) 5

3 Hyphal bodies spherical to subsperical (Plate 4, Fig.1). Condiophores digitally branched (Fig. 1B). Rhizoids at least twice as thick as conidiophores, without specialised holdfast. Cystidia long, at least twice as thick as conidiophores (Plate 4, Fig. 6) . . . . . *Erynia* (1.2.1.)

3* Hyphal bodies irregular, rhizoids with specialised holdfasts . . 4

4 Hyphal bodies irregularly subspherical, spherical to hyphoid. Conidiophores dichotomously (Plate 1, Fig.7; Fig. 1C) or indistinctly digitally branched. Rhizoids not thicker as conidiophores, holdfast sucker-like or with thin, irregular terminal branches. – Cystidia as thick as conidiophores, tapering . . . *Furia* (1.2.2.)

4* Hyphal bodies irregular, short hyphae-like (Plate 4, Figs. 2–4). Condiophores digitally branched (Fig 1B). Rhizoids 2–3 times thicker as conidiophores, holdfast discoid or irregularly spreading. – Cystidia 2–3 times thicker as conidiophores, tapering (Plate 4, Fig. 7). . . . . *Pandora* (1.2.4.)

5 Primary conidia short ovoid with prominent papilla. Capillary conidiophore either emerging from the conidial body or axially through the papilla of primary conidia. Capilliconidia with small basal papilla after dispersal. Rhizoids monohyphal, holdfast absent. . . . . *Orthomyces* (1.2.3.)

5* Primary conidia cylindrical to slightly fusiform, papilla conical (Plate 3, Figs. 3–4). Capillary conidiophore emerging laterally from the primary conidia (Plate 3, Fig. 4). Capilliconidia without basal papilla. Compound rhizoids with specialised holdfast (Plate 3, Figs. 6–7) usually accompanied by monohyphal rhizoids . . . . . *Zoophthora* (1.2.6.)

1.2.1. *Erynia* (Nowakowski ex Batko) Remaudière et Hennebert, Mycotaxon, 11, 301. 1980.

Hyphal bodies spherical, subsperical or irregularly rounded, oligo- to multinucleate, germinating with a single germ tube. – Conidiophores branched. – Primary conidia elongate pyri-

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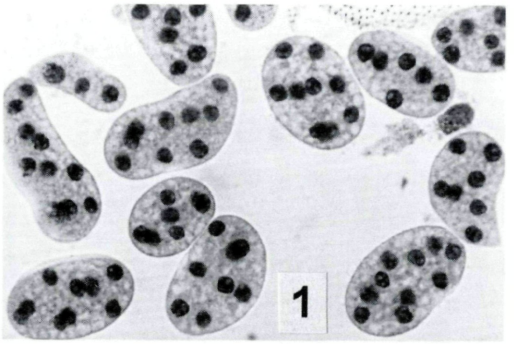
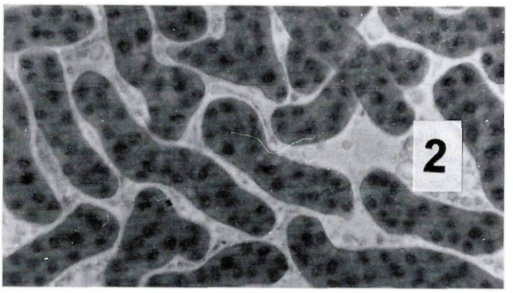
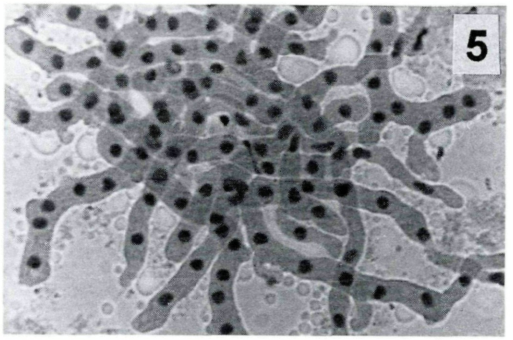
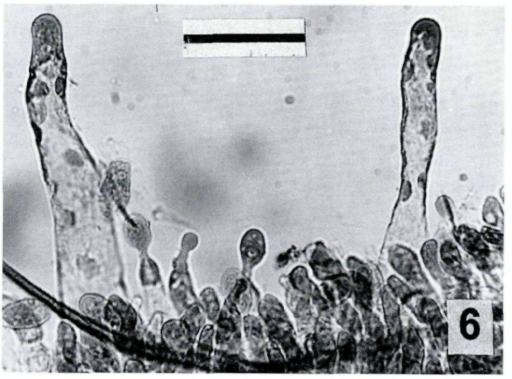
Plate 4. Erynioideae. – Types of hyphal bodies (Figs. 1–5) and cystidia (Figs. 6–7). 1. Erynia-type of *Erynia conica*: spherical to elongate subspherical; 2-4: Pandora-type: irregularly rod-shaped to short hyphae-like. 2. *Pandora gammae*; 3. *P. athaliae*; 4. *P. neoaphidis*; 5. Zoophthora-type of *Zoophthora elateridiphaga:* mycelium-like; 6. *Erynia ovispora*; 7. *Pandora blunckii*. LPAO. Bar in Fig. 6 represent 50 µm, all same magnification.









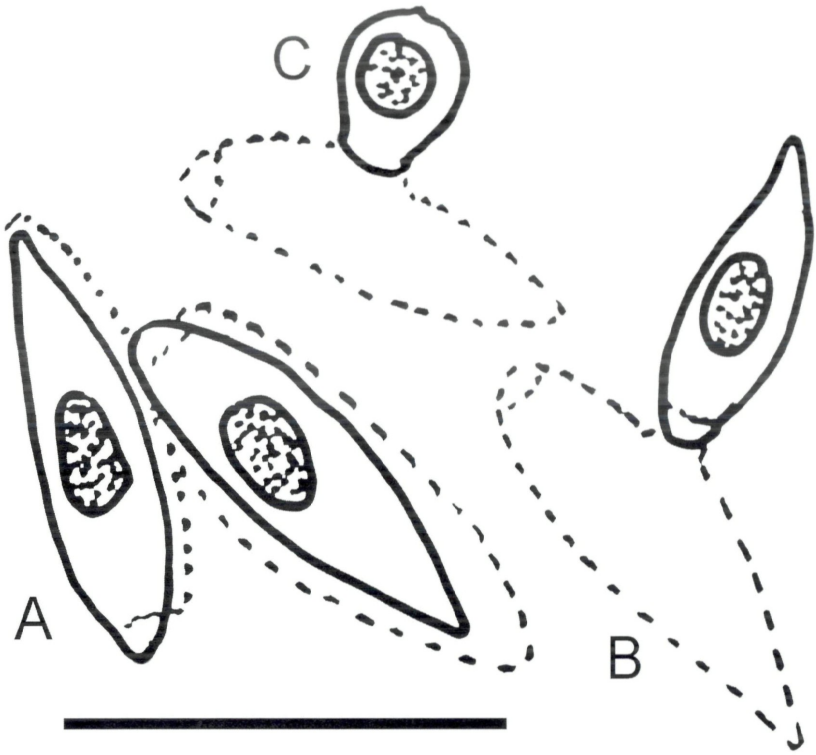


Fig. 2. Erynioideae (*Erynia conica*). – Primary (A) and secondary conidia of type Ia (B) and type Ib (C). Outer wall of primary conidia partially separated. Bar: 50 µm.

form, ovoid, ellipsoid, fusiform, often curved; papilla rounded. Two types of secondary conidia, type Ia resembling the primary condia, type Ib with spherical conidial body and distinct papilla as defined by Ben-Ze'ev & Kenneth (1982), often with indistinct apical point, both types forcibly discharged. Capilliconidia absent. Waterlogged species may produce tetraradiate conidia. – Resting spores spherical to subspherical. – Cystidia present, at least twice as thick as conidiophores, long. – Rhizoids monohyphal, at least twice as thick as conidiophores, terminal holdfast enlarged, with finger-like outgrowths or indistinct. Obligate pathogens of insects.

Type species: *Erynia ovispora* (Nowakowskii) Remaudière & Hennebert (1980).

Other species included:
E. aquatica (Anderson & Anagnostakis) Humber (1989).
E. chironomi (Fan & Li) Fan & Li (1995).
E. conica (Nowakowski) Remaudière & Hennebert (1980).
E. curvispora (Nowakowski) Remaudière & Hennebert (1980).
E. delpiniana (Cavara) Humber (1981).
E. erinacea (Ben-Ze'ev & Kenneth) Remaudière & Hennebert (1980).
E. gigantea Li, Chen & Xu (1990).
E. gracilis (Thaxter) Remaudière & Hennebert (1980).
E. henrici (Molliard) Humber & Ben-Ze'ev (1981).
E. plecopteri Descals & Webster (1984).
E. rhizospora (Thaxter) Remaudière & Hennebert (1980).
E. sepulchralis (Thaxter) Remaudière & Hennebert (1980).
E. variabilis (Thaxter) Remaudière & Hennebert (1980).

1.2.2. *Furia* (Batko) Humber, Mycotaxon 34, 450. 1989.

Hyphal bodies irregularly subspherical to hyphoid, germinating with a single germ tube. – Conidiophores digitally or dichotomously branched. – Primary conidia ovoid, obpyriform, subcylindrical or obclavate, straight or slightly bent. Two types of secondary conidia, type Ia resembling the primary condia, type Ib with spherical conidial body and distinct papilla, often with indistinct apical point, both types forcibly discharged. Capilliconidia absent. – Resting spores spherical, hyaline or coloured or absent. – Cystidia as thick as conidiophores, unbranched, tapering apically. – Rhizoids monohyphal, not thicker than condiophores, terminal holdfast with few, irregular short branches, not strongly differentiated. Obligate pathogens of insects.

Type species: *Furia virescens* (Thaxter) Humber (1989).

Other species included:
F. americana (Thaxter) Humber (1989).
F. creatonoti (Yen in Humber) Humber (1989).
F. crustosa (McLeod & Tyrrell) Humber (1989).
F. ellisiana (Ben-Ze'ev) Humber (1989).
F. fujiana Huang & Li (1993).
F. fumimontana (Bałazy) S. Keller comb. nov.
Bas.: *Zoophthora fumimontana* Bałazy, Flora of Poland. Fungi, Vol. 24, Entomophthorales, 166. 1993.
F. gastropachae (Raciborski) S. Keller comb. nov.
Bas.: *Empusa (Entomophthora) gastropachae* Raciborski, Kosmos 35 (7-9), 775. 1910.

F. ithacensis (Kramer) Humber (1989).
F. montana (Thaxter) Humber (1989).
F. neopyralidarum (Ben-Ze'ev) Humber (1989).
F. pieris (Li & Humber) Humber (1989).
F. sciarae (Olive) Humber (1989).
F. shandongensis Wang, Lu & Li (1994).
F. triangularis (Villacarlos & Wilding) Li, Fan & Huang (1998).
F. vomitoriae (Rozsypal) Humber (1989).
F. zabri (Rozsypal ex Ben-Ze'ev & Kenneth) Humber (1989).

1.2.3. *Orthomyces* Steinkraus, Humber and Oliver, J. Invertebr. Pathol. 72, 7. 1998.

Conidiophores branched, conidiogenous cells short and blocky. – Primary conidia uninucleate, bitunicate, forcibly discharged by papillar eversion. – Secondary conidia either like primary on a short, broad conidiophore, forcibly discharged, or formed on a capillary conidiophore, globose (or otherwise distinct from primary one), with small basal papilla after dispersal. Capillary conidiophores either emerging from the conidial body or axially through the papilla. – Cystidia slightly thicker than vegetative hyphae at the level of the hymenium, tapering. – Rhizoids slightly thicker than vegetative hyphae, numerous, simple or sparingly branched, tapering, holdfast absent. Obligate pathogen of insects.

Type species: *Orthomyces aleyrodis* Steinkraus, Humber & Oliver, in Steinkraus & al. (1998).

No other species are described. An unidentified species is known from the Philippines (Villacarlos & Mejia, 2004).

1.2.4. *Pandora* Humber, Mycotaxon 34, 451. 1989.

Hyphal bodies as short hyhae, unbranched or with few branches, oligo- to multinucleate. – Conidiophores digitally branched. Primary conidia ovoid, obpyriform, subcylindrical or obclavate, straight or slightly bent. Two types of secondary conidia, type Ia resembling the primary condia, type Ib with spherical conidial body and distinct papilla, often with indistinct apical point, both types forcibly discharged. Capilliconidia absent. – Resting spores spherical, hyaline or coloured, episporium smooth or ornamented; unknown in several species. – Cystidia 2–3 times thicker than conidiophores, tapering apically. – Rhizoids monohyphal, 2–3 times thicker than conidiophores, highly vacuolated, terminal hold-

fast discoid or irregularly branched. Obligate pathogens of insects and Phalangicidae (Arachnida).

Type species: *Pandora neoaphidis* (Remaudière & Hennebert) Humber (1989).

Other species included:

P. aleurodis (Bałazy & Manole) S. Keller, comb. nov.
Bas.: *Zoophthora aleurodis* Bałazy & Manole, Flora of Poland. Fungi, Vol. 24, Entomophthorales, 176-177. 1993.

P. athaliae (Li & Fan) Li, Fan & Huang (1998).

P. bibionis Li, Huang & Fan (1997).

P. blunckii (Lakon ex Zimmermann) Humber (1989).

P. borea (Fan & Li) Li, Huang & Fan (1997).

P. brahminae (Bose & Metha) Humber (1989).

P. bullata (Thaxter & McLeod in Humber) Humber (1989).

P. cicadellis (Li & Fan) Li, Fan & Huang (1998).

P. dacnusae (Bałazy) Humber (1989).

P. delphacis (Hori) Humber (1989)

P. dipterigena (Thaxter) Humber (1989).

P. echinospora (Thaxter) Humber (1989).

P. formicae (Humber & Bałazy in Humber) Humber (1989).

P. gammae (Weiser) Humber (1989).

P. gloeospora (Vuillemin) Humber (1989).

P. heteropterae (Bałazy) S. Keller comb. nov.
Bas.: *Zoophthora heteropterae* Bałazy, Flora of Poland. Fungi, Vol. 24, Entomophthorales, 188–189. 1993.

P. kondoensis (Milner in Milner, Mahon & Brown) Humber (1989).

P. lipae (Bałazy, Eilenberg & Papierok) S. Keller comb. nov.
Bas.: *Zoophthora lipae* Bałazy, Eilenberg & Papierok, Flora of Poland. Fungi, Vol. 24, Entomophthorales, 192–193. 1993.

P. minutospora (Keller) S. Keller comb. nov.,
Basionym: *Erynia minutospora* Keller, Sydowia, 46, 42. 1994.

P. muscivora (Schroeter) S. Keller comb. nov.
Bas.: *Entomophthora muscivora* Schroeter, Kryptogamen-Flora von Schlesien, III, 14. Lief., 223. 1886.

P. myrmecophaga (Turian & Wuest in Humber) S. Keller comb. nov.
Bas.: *Erynia myrmecophaga* Turian & Wuest in Humber, Mycotaxon 13, 475. 1981.

P. nouryi (Remaudière & Hennebert) Humber (1989).

P. phalangicida (Lagerheim) Humber (1989).

P. philonthi (Bałazy) S. Keller comb. nov.
Bas.: *Zoophthora philonthi* Bałazy, Flora of Poland. Fungi, Vol. 24, Entomophthorales, 197–198. 1993.
P. phyllobii (Bałazy) S. Keller comb. nov.
Bas.: *Zoophthora phyllobii* Bałazy, Flora of Poland. Fungi, Vol. 24, Entomophthorales, 199. 1993.
P. poloniaemajoris (Bałazy) S. Keller comb. nov.
Basionym: *Zoophthora poloniaemajoris* Bałazy, Flora of Poland. Fungi, Vol. 24, Entomophthorales, 180. 1993.
P. shaanxiensis Fan & Li (1994).
P. suturalis (Ben-Ze'ev) Humber (1989).
P. terrestris (Gres & Koval) S. Keller comb. nov.
Basionym: *Entomophthora terrestris* Gres & Koval, Microbiol. J. (Kiew) 44, 68. 1982.
P. uroleuconii Barta & Cagan (2003).

1.2.5. *Strongwellsea* Batko and Weiser, J. Invertebr. Pathol. 7, 455–463. 1965.

Hyphal bodies simple, rarely branched, uni- or oligonucleate. – Conidophores unbranched, uninucleate. – Primary conidia uninucleate, bitunicate, obovoid, ellipsoidal to subcylindrical; papilla flattened to slightly rounded. Two types of secondary conidia, either rounded or like primary. – Resting spores orange, spherical to ovoid; episporium covered with broad spines. – Cystidia and rhizoids absent. Infection restricted to abdomen, causing one, sometimes two nearly circular holes on the ventral side through which conidia are projected. No hole when resting spores are present. Obligate pathogens of muscoid flies.

Type species: *Strongwellsea castrans* Batko & Weiser (1965).

Other species included:
S. magna Humber (1976).

Additional six species are known, but not yet formally described (Eilenberg, 2002).

1.2.6. *Zoophthora* Batko. Bull. Acad. Pol. Sci., Ser. Sci.Biol. 12, 323–324. 1964a

Hyphal bodies hyphae-like or short, irregularly rod-shaped. Nuclei stain distinctly in LPAO, mean diameter 4–8 µm. – Conidiophores branched with terminal enlargement. – Primary conidia bitunicate, elongate, cylindrical to slightly fusiform;

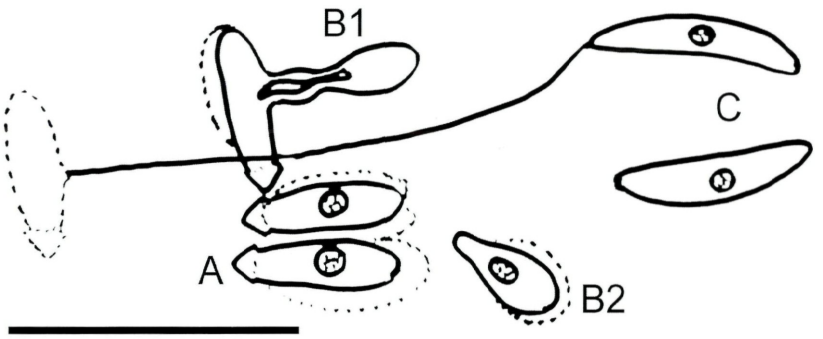


Fig. 3. Erynioideae. – Primary (A) and secondary conidia of type Ia (B1, formation; B2 projected) and type II (C) (capilliconidium) developing and detached (*Zoophthora elateridiphaga*). Outer wall of primary conidia partially separated. Bar: 50 µm.

papilla conical, pointed or sometimes rounded, separated from the conidial body by a raised collar. – Secondary conidia similar to primary, formed on a short, thick conidiophore, or falciform to banana-like, formed on a long, slender capillary tube. – Resting spores spherical, hyaline, brown or black, episporium smooth or ornamented. – Rhizoids pseudorhizomorph and monohyphal, with or without special holdfast, rarely absent. – Cystidia rare or absent. Obligate pathogens of insects.

Type species: *Zoophthora radicans* (Brefeld) Batko (1964a)

Other species included:
Z. anglica (Petch) Humber (1989).
Z. anhuiensis (Li) Humber (1989).
Z. aphidis (Hoffmann in Fresenius) Remaudière & Hennebert (1980).
Z. arginis Bałazy (1993).
Z. autumnalis Bałazy (1993).
Z. bialoviezensis Bałazy (1993).
Z. brevispora Bałazy (1993).
Z. canadensis (MacLeod, Tyrrell & Soper) Remaudière & Hennebert (1980).
Z. crassispora Bałazy (1993).
Z. crassitunicata Keller (1980).
Z. elateridiphaga (Turian) Ben-Ze'ev & Kenneth (1980).
Z. falcata Bałazy (1993).

Z. forficulae (Giard) Batko (1964b).
Z. geometralis (Thaxter) Batko (1964b).
Z. giardii Bałazy (1993).
Z. humberi (Aruta & Carillo) Bałazy (1993).
Z. ichneumonis Bałazy (1993).
Z. lanceolata Keller (1980).
Z. larvivora Bałazy (1993).
Z. miridis Bałazy & Mietkiewski in Bałazy (1993).
Z. nematoceris Bałazy (1993).
Z. obtusa Bałazy (1993).
Z. occidentalis (Thaxter) Batko (1964b).
Z. orientalis Ben-Ze'ev & Kenneth (1981).
Z. opomyzae Bałazy & Mietkiewski in Bałazy (1993).
Z. pentatomis (Li) Li, Fan & Huang (1998).
Z. petchii Ben-Ze'ev & Kenneth (1981).
Z. phalloides Batko (1966).
Z. phytonomi (Arthur) Batko (1964b).
Z. psyllae Bałazy (1993).
Z. tachypori Bałazy (1993).
Z. viridis Keller ex Keller (1994).

1.3. **Massosporoideae subfam. nov.** S. Keller

Conidia globosa, ovoidea, ellypsoidea vel fusiformia, 1-6 nucleis praedita, non motu proprio cellulae conidiogenae espulsa. Sporae perdurantes globosae, ornatae, incoloratae vel pallide fuscae ad fuscae cum coacervatae. Cystidia et rhizoidea absentia. Species in corpore hospitis abdomen solum incolentes, conidiis et sporis perdurantibus e fissura in segmentibus abdominalibus hospitis viventis liberatae.

Species pathogenae adultorum Homopterum Cicadidarum.

Conidia globose, ovoid, ellipsoid or fusiform, with 1–6 nuclei; passively detached. – Resting spores globose, ornamented, light or yellow brown to brown in mass. – Cystidia and rhizoids absent. Infection limited to abdomen, conidia and resting spores liberated by sloughing off of the abdominal segments of the living host. Obligate pathogens of adult Homoptera Cicadidae.

Type genus: *Massospora* Peck *emend.* Soper, Mycotaxon 1, 15–16. 1974.

The subfamily Massosporoideae is so far monogeneric. No molecular work has yet been done and the taxonomic position of these fungal group is uncertain.

Type species: *Massospora cicadina* Peck (1879).

Other species included:
M. carineta Soper (1974)
M. diceroprocta Soper (1974)
M. diminuta Soper (1974)
M. dorisiana Soper (1974)
M. fidicina Soper (1974)
M. levispora Soper (1974)
M. ocypetes Soper (1974)
M. platypedia Soper (1974)
M. spinosa Ciferri, Machado & Vital (1957)
M. tettigates Soper (1974)

2. Neozygitaceae

The family consists of two groups.

One group is characterized by two types of secondary conidia, one resembling the primary one and the other produced on long, slender capillary tubes (capilliconidia). The resting spores are brown, spherical to ellipsoidal and surrounded with a dark episporium. The resting spores are zygospores with the exception of *N. tetranychi* . They attack insects and mites.

The other group is characterised by having only one type of secondary conidia resembling the primary ones, and by the lack of resting spores. They attack mites and collembolans. All species have been so far placed in one genus, *Neozygites*. The differences between the two groups, however, justify the description of a new genus for the second group.

Key to genera

1 Secondary conidia resembling the primary ones or capilliconidia. Resting spores spherical spherical to ellipsoid, with dark episporium ..... *Neozygites* (2.1)
1* Secondary conidia globose. Capilliconidia and resting spores absent ..... *Apterivorax* (2.2)

2.1. *Neozygites* Witlaczil, Arch. F. Mikr. Anat. 24, 599–603. 1885.

Vegetative growth as globose or rod-shaped hyphal bodies, cell wall present or absent. Nuclei with an average diameter of 2.5–4 µm, staining weakly in aceto-orcein. – Conidiophores unbranched. – Primary conidia forcibly discharged, unitunicate, subspherical, ovoid, elongate ovoid to fusiform, papilla truncate or small, contain on average 3–8 nuclei. – Secondary conidia either resembling the primary ones or produced on long slender capillary

tube. Capilliconidia passively detached, amygdaliform, falciform or cucumber-like, smoky, finely ornamented. – Resting spores zygospores, rarely azygospores, developing from the conjugation bridge of two hyphal bodies that contain each twice the number of nuclei as the hyphal bodies forming conidia. One nucleus from each hyphal body enters the developing zygospore. Mature resting spores spherical to subspherical or ellipsoidal, binucleate, epispore brown or black, smooth or ornamented. The resting spores germinate either with short thick germ tube to produce a spherical germ conidium or with a long, slender capillary tube to form a capillary germ conidium. – Rhizoids absent, only in rare cases present (*N. floridana* and *N. tanajoae* when resting spores are present), cystidia absent. Obligate pathogens of small insects and mites.

Type species: *Neozygites fresenii* (Nowakowski) Remaudière & S. Keller (1980).

Other species included:
N. abacaridis Mietkiewski & Bałazy (2003).
N. acaridis (Petch) Milner (1985).
N. cinarae S. Keller (1997).
N. cucumeriformis Mietkiewski & Bałazy in Bałazy (1993).
N. floridana (Weiser & Muma) Remaudière & S. Keller (1980).
N. fumosa (Speare) Remaudière & S. Keller (1980).
N. heteropsyllae Villacarlos & Wilding (1994).
N. lageniformis (Thaxter) Remaudière & S. Keller (1980).
N. lecanii (Zimm.) Remaudière & S. Keller (1980).
N. microlophii S. Keller (1991).
N. parvispora (MacLeod & Carl) Remaudière & S. Keller (1980).
N. tanajoae Delalibera, Humber & Hajek (2004).
N. tetranychi (Weiser) Remaudière & S. Keller (1980).
N. turbinata (Kenneth) Remaudière & S. Keller (1980).

The genus consists of two groups as pointed out by Keller (1997). One group is characterised by spherical hyphal bodies, ellipsoidal resting spores with smooth episporium and capillary germ conidia and the other by rod-shaped hyphal bodies, spherical resting spores with ornamented episporium and subspherical germ conidia. Not all species can be attributed to either group due to missing data. Further investigations may lead to the erection of separate genera for these groups.

An undescribed species has recently been reported from Antarctica attacking the oribatid mite *Alaskozetes antarcticus* (Bridge & Worland, 2004).

2.2. ***Apterivorax* gen. nov.** S. Keller

Corpora hyphalia sphaerica ad subsphaerica, 3–4 nucleos continentia. Nuclei 2.5–3 µm, pallide in liquido dicto acetoorceinico colorati. Conidiophora non ramosa. Conidia primaria ovoidea vel pyriformia. Conidia secondaria forma una, conidiis primariis similia. Capilliconidia, rhizoidea, cystidia atque sporae perdurantes absentia.

Species semper pathogenae acarum et insectorum apterigotorum.

Hyphal bodies spherical to subspherical with 3–4 nuclei. Nuclei 2.5–3 µm, weakly staining in aceto-orcein. – Conidiophores unbranched. – Primary conidia ovoid, pyriform to elogated. – Secondary conidia of only one type, resembling the primary ones. – Capilliconidia, rhizoids, cystidia and resting spores absent. Obligate pathogens of collembolans and mites.

Type species: *A. sminthuri* (S. Keller & Steenberg) S. Keller comb. nov.

Bas.: *Neozygites sminthuri* S. Keller & Steenberg, *Sydowia* 49: 22, 1997.

Etymology: The name refers to the hosts which are wingless arthropods (apterygote insects, mites).

Other species included:

A. acaricida (Petch) S. Keller comb. nov.

Bas.: *Neozygites acaricida* (Petch) S. Keller & Milner in Keller, Sydowia 49: 136, 1997.

Additional species belonging to this new genus have recently been detected on Collembola but have not yet been formally described (Dromph & al., 2001). All species of this genus are poorly known. The generic description is mainly based on absence of capilliconidia and resting spores. The value of these characters can only be demonstrated with increased knowledge of the species. However, the preference of these species for extraordinary arthropod hosts, the Collembola, which live in an environment unusual for arthropod-pathogenic Entomophorales is another strong argument to include them in a separate genus. Nevertheless, further criteria including molecular data should be used for a unequivocal definition of the genus.

Discussion

The description of three subfamilies within the family Entomophthoraceae separates three morphologically clearly distinct

groups. The three subfamilies differs from the "two-lines" system presented for this fungus group by Humber (1984c). He placed *Eryniopsis, Erynia* (in the broad sense) and *Strongwellsea* in one line and *Entomophaga, Neozygites, Entomophthora* and *Massospora* in another line. *Neozygites* was later one placed in the new family Neozygitaceae (Ben-Ze'ev & al., 1987).

The genera in the subfamily Entomophthoroideae are well separated with the exception of *Batkoa* and *Entomophaga*. The criteria for the separation of these two genera are not unequivocal. Further investigations are needed to clarify the taxonomic position of the genus *Batkoa* and its delimitation. *Batkoa papillata*, for instance, has conidia with the typical shape of those found in the genus *Entomophaga*, but has rhizoids which are absent in all species of the latter genus.

Within *Entomophaga E. ptychopterae* and *E. transitans* are noteworthy. They produce two types of secondary conidia typical for *Eryniopsis* and described only for *Entomophaga tipulae* by Bałazy (1993). However, his description differs slightly from the original one and may refer to a new species. Recent molecular investigations have revealed the close relationship of *E. ptychopterae* with other species of *Entomophaga* and justifiy the attribution of the species with two types of secondary conidia but otherwise typical *Entomophaga*-like structures to the genus *Entomophaga*. (Hajek & al. 2003).

Within the subfamily Erynioideae the genera *Erynia, Furia* and *Pandora* (*Erynia sensu lato*; Remaudière & Keller, 1980; Keller, 1991) cannot be clearly separated. One criterium used to separate *Erynia* from the other two genera were the secondary conidia, which are of two types in *Erynia* and of only one type resembling the primary conidia in the other two genera (Humber, 1989). In the meantime, however, it has been demonstrated that species of all three genera may produce two types of secondary conidia, a type resembling the primary conidia (type Ia) and a more or less spherical type (type Ib) (Ben-Ze'ev & Kenneth, 1982). Other structures that are used to separate the three genera include the cystidia (diameter, shape), the rhizoids (diameter and type of holdfast) and the hyphal bodies (shape, number and size of nuclei) (Humber, 1989). For many species, if not for the majority, these structures are unknown or only partly known so that the inclusion of many species in one of these genera must be considered doubtful. In this paper the attribution of the species to one of these three genera follows Humber (1989) and Bałazy (1993) or accepts the generic placement given in the original descriptions.

Hyphal bodies, cystidia and rhizoids allow to separate *Erynia* from the other two genera. *Furia* and *Pandora*, however, are very closely related and a clear separation is almost impossible. The

structures and dimensions used for their separation are unknown or incompletely known for many species and no definitions are given where measurements of conidiophores and of the very variable cystidia and rhizoids have to be taken. Collection of additional samples, subsequent investigations of the fungal structures, definitions of the morphometric data, the use of enzyme patterns (Wilding & al., 1993) and the application of molecular methods will help to conclusively assess whether or not all three genera are justified and where doubtful species have to be placed. All other genera in this subfamily are clearly defined and can be easily separated from each other.

The systematic of the arthropod-pathogenic Entomophthorales is primarily based on morphological and cytological data. The overview presented in this paper demonstrates the limits of this approach and allow to define the five most critical areas where research is needed to confirm or deny the present classification. These critical areas are the following: Within the Entomophthoroideae the relationship between *Batkoa* and *Entomophaga* needs clarification; the same applies for *Erynia, Furia* and *Pandora* within the Erynioideae. Molecular methods should be used to attribute the species of the form-genus *Tarichium* to the proper genera. The forth area concerns *Massospora* whose taxonomic position is uncertain. The fifth area concerns Neozygitaceae where additional criteria may help to clarify relationships within the genus *Neozygites* and to improve the definition of the genus *Apterivorax*. The use of biochemical and especially molecular methods can substantially contribute to the understanding of the relationships in the treated fungus families and especially within the addressed areas and thus contribute to a sound classification of the arthropod-pathogenic Entomophthorales.

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