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Entomophthorales (Fungi, Entomophthoromycota) attacking Coleoptera with a key for their identification

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A key to 30 species of entomophthoralean fungi is provided. These 30 species are listed in an alphabetical order and characterized based on their original descriptions and amended with new data. A few incompletely described but probably new species are included as well as a few unclassified species mentioned as pathogens of Coleoptera. A list of the coleopteran families containing hosts of Entomophthorales is given to help with the identification.

Key words: Insect pathogenic fungi, Entomophthorales, species list, identification key, Coleoptera.

INTRODUCTION

The systematics of the arthropod-pathogenic fungi previously placed in the order Entomophthorales has dramatically changed since DNA-based data are applied (Humber 2012). A new phylum, Entomophthoromycota, has been erected. The family Neozygitaceae became separated from the order Entomophthorales and placed in the new class Neozygitomycetes, order Neozygitales. The other arthropod-pathogenic species remained in the order Entomophthorales, placed in the newly erected class Entomophthoromycetes (Humber 2012).

The last census of the arthropod-pathogenic Entomophthoromycota revealed 236 species (Keller 2008). Since then a few further species have been added. There is no key for the identification of all these species, but there are keys to identify Neozygites spp. and Entomophthora spp. (Keller 1997, 2002) as well as keys to identify species attacking aphids and brachycerous Diptera (Keller 2006, 2007a). Keys focusing on host taxa have shown to be better suited for practical purposes and help to improve the collaboration between insect mycologists and entomologists. The following key for the identification of entomophthoralean fungi attacking Coleoptera is a further step in this direction and gives interested scientists and especially coleopterologists the possibility to identify these fungi.

METHODS

The dichotomous key is based on original descriptions except *Conidiobolus* spp. (originally described from detritus) and the widespread *Zoophthora radicans* whose original description is very poor and has as type host *Pieris brassicae* (Lepidoptera). The key is followed by a thorough description of the species listed in alphabetical order. The bold numbers in brackets refer to the number of the species in this list.

An important microscopic criterium to separate *Conidiobolus* spp. (family Ancylistaceae) from Entomophthoraceae is the staining ability of the nuclei with lactophenol-aceto-orcein (LPAO).

Generally, species are described from fresh material or from material stored for a short term in ethanol. Occasionally, species are described from air-dried (herbarium) material, so-called exsiccatae. In this case we must be aware that air-drying leads to a shrinking of the conidia and probably also of other structures except the resting spores. Since most species of Entomophthorales are very host specific, the knowledge of the host insect is very important and represents a significant role in the key.

RESULTS

Most species attacking Coleoptera produce conidia as well as resting spores, either as zygospores or as azygospores. Some species produce both spore types in the same host individuum, others produce only one spore type in an individual host insect. A few species are known only in their conidial state and others only or predominantly in their resting spore state like species of *Tarichium* but also *Zoophthora rhagony-charum* and *Z. crassitunicata*. This fact is considered in the first step of the key. A branch leads to species known only or primarily in their resting spore stage while the other branch leads to species known only or predominatly in their conidial stage.

The key based on host genera as well as the key based on fungus characteristics refer to a species list which is arranged in alphabetical order and numbered consecutively.

KEY BASED ON HOST FAMILIES

In the following paragraph the coleopteran families which contains species attacked by Entomophthorales are listed alphabetically. The number in brackets after the fungus name refers to the species list given after the identification key.

Cantharidae: Entomophthora sp. (6),

Eryniopsis lampyridarum (8),

Pandora lipai (11),

Zoophthora crassitunicata (22), Zoophthora larvivora (24), Zoophthora rhagonycharum (27),

Zoophthora sp. 1 (29).

Carabidae: Erynia nebriae (7),

Furia zabri (9),

Tarichium jaczewskii (18).

Cerambycidae: Batkoa apiculata (1). Chrysomelidae: Batkoa apiculata (1),

> Pandora suturalis (14), Tarichium sp. (unclassified)

Curculionidae: Conidiobolus coronatus (3),

Conidiobolus osmodes (4), Pandora phyllobii (13), Tarichium cleoni (15),

Tarichium hylobii (17), Tarichium phytonomi (19), Tarichium punctatum (20), Zoophthora phytonomi (25).

Elateridae: Zoophthora anglica (21),

Zoophthora elateridiphaga (23).

Lagriidae: Entomophaga lagriae (5). Melolonthidae: Pandora brahminae (10).

Ptilodactylidae: Batkoa major (2).

Scirtidae: Staphylinidae: Zoophthora sp. 2 (30). Pandora philonthi (12), Zoophthora tachypori (28).

KEY TO FUNGUS SPECIES

1 1*	Only resting spores known or present. Conidia unknown or rare 24 Conidia present. Resting spores may be present as well 2
2 2*	Conidiophores simple. Conidia multinucleate
3*	Body of primary conidia spherical to subspherical, papilla prominent. Nuclei smaller than 3 μ m, stain not or only faintly in LPAO. Rhizoids absent. Hyphal bodies complex. Good growth in artificial media genus <i>Conidiobolus</i> 4 Primary conidia spherical to pyriform or with pointed apex. Nuclei larger than 3 μ m, stain deeply in LPAO. Rhizoids present or absent. Hyphal bodies spherical to elliptical or irregulary rounded 5
4	Primary conidia on average 50.5–53 x 38–40 μ m, varying largely in size, L/D = 1.30–1.34; papilla abruptly protruding, prominent, elongate. Resting spores are azygospores, on average 30.5–31.5 μ m, villose, spherical
4*	Primary conidia 25–37 x 22–30 μ m; papilla broad, obtusely tapered. Resting spores are zygospores, spherical to ellipsoid with a diameter of 13–37 μ m
5	Primary conidia with pointed apex and truncate papilla
5*	Primary conidia spherical to pyriform, prominent conical papilla. Rhizoids present or absent. Secondary conidia like primary or long-cylindrical, and born vertically on capillary conidiophores 6
6 6*	Body of primary conidia nearly spherical, papilla demarcated, pointed or rounded
7	Primary conidia 30–37 x 28–30 μ m, average 35 x 30 μ m, papilla pointed
7*	
8	Primary conidia 35–43 x 24–30 μ m, ovoid or broadly turbinate with 12–18 nuclei, papilla narrow conical. Secondary conidia like primary
8*	Conidia 20–37 x 14–30 μ m, average 35 x 15 μ m, less than 10 nuclei. Secondary conidia like the primary or long-cylindrical and born vertically on capil lary conidiophores
9	Rhizoids compound (pseudorhizomorph). Primary conidia elongate, cylindrical, subcylindrical or ellipsoid. Two types of secondary conidia: like primary or capilliconidia genus <i>Zoophthora</i> 16

9*	Rhizoids simple (monohyphal). Primary conidia ovoid to pyriform. Two types of secondary conidia: like primary or subspherical to ovoid 10
10 10*	Pathogen of Carabidae
11	Primary conidia ovoid, on average 25 x 14 μ m. Zygospores spherical, formed mostly on the surface of the host. Pathogen of larval Zabrus
11*	Conidia ellipsoidal to fusiform, asymmetrical, $28-37 \times 10-13 \mu m$. Resting spores hyaline to pale brown, developing outside the body of the host, spherical, $35-50 \mu m$ diameter. Pathogen of <i>Nebria Erynia nebriae</i> (7)
12	Pathogen of Melolonthidae. Primary conidia $18-22 \times 11-15 \mu\text{m}$
12*	Pathogen of other Coleoptera
13 13*	Pathogen of Cantharidae. Primary conidia 19–23 x 9–11 μ m <i>P. lipai</i> (11) Pathogen of other Coleoptera
14	Pathogen of Staphylinidae. Primary conidia 21–26 x 11–14 μ m
14*	Pathogen of other Coleoptera
15	Pathogen of Curculionidae. Primary conidia narrow ovoid, 19.5–23 x 10–12.5
15*	μ m, or ellipsoid, 23–31 x 11.5–14.5 μ m
16 16*	Primary conidia on average shorter than 24 μ m
17 17*	Primary conidia on average shorter than $18 \mu \text{m}$ Zoophthora sp. 1 (29) Primary conidia on average $18-24 \mu \text{m}$
18	Pathogen of adult Staphylinidae. Primary conidia 19–22 x 5.5–6.5 μm. Capilliconidia 20–25 x 5–5.5 μm
18*	Pathogen of other or unspecific Coleoptera
19 19*	Capilliconidia 17–22 x 4.5–6 µm
20	Pathogen of Curculionidae. Primary conidia 24–28 x 7–10 μm
20*	Pathogen of other Coleoptera
21	Pathogen of larval Catharidae. Primary conidia 40–42 x 8–9 μ m
21*	Pathogen of adult Cantharidae and Elateridae
22	Pathogen of Cantharidae. Primary conidia $31-32 \times 10 \mu m$, resting spores
22*	spherical, thick walled $41-44 \mu m$

23*	Primary conidia on average 27.6 x 9.8 μ m and an L/D-ratio of 2.5. Resting spores spherical, 27.6–34.5 μ m with an average of 31.1 μ m. Capilliconidia unknown
	25–46 μ m with an average of 31–38 μ m Z. elateridiphaga (23)
24*	Resting spores spherical to subsperical, $35-62 \mu m$, on average between 40 and 49 μm , with thick or double-layered walls, densely verrucose
24*	Average diameter of resting spores smaller than 40 μ m
25* 25*	Resting spores on average 45–49 μ m, spherical, double-layered wall, inner layer more or less hyaline, outer layer brown. Young resting spores contain 8–24 nuclei. Pathogen of adult <i>Rhagonycha</i> spp. (Cantharidae)
26 26*	Pathogen of larval Carabidae. Resting spores spherical, 28–46 μ m in diameter epispore dark brown
2727*	Pathogen of <i>Hypera</i> (<i>Phytonomus</i>) spp. Resting spores spherical, 26–38 μ m. brown
28	Resting spores $32-40 \mu m$, episporium with $3.5-6 \mu m$ long spines. Pathogen of <i>Bothynoderes (Cleonus) punctiventris</i>
28*	Resting spores $28-31 \mu m$, episporium with bulges and ridges. Pathogen of larvae and prepupae of <i>Hylobius abietis</i>

LIST OF FUNGAL SPECIES

1. Batkoa apiculata (Thaxter) Humber (1989)

Hyphal bodies nearly spherical. Conidiophores simple, sometimes with a tendency to become digitate, originating directly from the hyphal bodies. Primary conidia $30-37 \times 28-30 \,\mu\text{m}$, average $35 \times 30 \,\mu\text{m}$, nearly spherical with prominent papillate base terminating in a short, sharp and abrupt point. Secondary conidia like primary. Resting spores hyaline, spherical, $30-45 \,\mu\text{m}$ diameter, zygospores or azygospores, formed laterally or terminally from hyphae. Rhizoids long and conspicuous, terminating in an irregular disc-like expansion.

Hosts: Originally described from larval and adult Lepidoptera, numerous genera of Diptera (small flies and gnats), and adult leafhoppers (Homoptera) collected in the USA (Thaxter 1888). The following hosts among Coleoptera are mentioned: Haltica quercetorum (Chrysomelidae) collected in Poland (Bałazy 1993) and Rosalia alpina (Cerambycidae) collected in Switzerland (Keller, 2008).

2. Batkoa major (Thaxter) Humber (1989)

Hyphal bodies nearly spherical to elliptical. Conidiophores simple sometimes with a tendency to become digitate. Primary conidia nearly spherical, $55-60 \times 38-45 \mu m$; papilla smaller in proportion to the body of the conidium than in *B. apiculata*.

Host. Adult Ptilodactyla serricollis (Say) (Ptilodactylidae) collected in the USA.

3. Conidiobolus coronatus (Costantin) Batko (1964a)

Hyphal bodies irregular. – Conidiophores not or only slightly enlarged terminally. Nuclei not or only exceptionally staining in LPAO, very small, 2.4 μ m (2.0–3.0 μ m). – Primary conidia 50.5–53 x 38–40 μ m (34–74 x 24–58 μ m), L/D = 1.30–1.34, varying largely in size, conidial body spherical to subspherical; papilla abruptly protruding, prominent, elongate, sometimes without cytoplasmic content. - Secondary conidia like primary, other types not observed. – Resting spores 30.5–31.5 μ m (16-42 μ m), villose, spherical; developing terminally from hyphae. – Cystidia and rhizoids absent.

Hosts: The species is unspecific and can be isolated from soil, detritus and dead insects. It is known as primary pathogen of aphids (Homoptera). The data given above originate from *Ceutorhynchus napi* (Curculionidae) collected as larvae from soil before pupation (Keller 1987).

4. Conidiobolus osmodes Drechsler (1954)

Primary conidia from cultures isolated from *Hypera* (*Phytonomus*) variabilis Herbst (= H.postica (Gyll.)). Larvae are described by Ben-Ze'ev & Kenneth (1980) as follows: $21-42~\mu$ m long and $16-34~\mu$ m broad, average $29.2-34.3~x~23.1-27.2~\mu$ m, globose to ovoid; papilla broad, obtusely tapered, $2.5~x~7-10~\mu$ m. Secondary conidia like primary but smaller. Zygospores globose to ellipsoid with a diameter of $28-44~\mu$ m, average $34~\mu$ m. Resting spores from H.variabilis measured $27-44~\mu$ m, average $34.0~\mu$ m. According to King (1977) the primary conidia from culture measure $25-37~x~22-30~\mu$ m. The zygospores are usually formed in axial alignments with conjugating segments, globose to ellipsoidal with a diameter of $13-37~\mu$ m surrounded by smooth walls or by walls with weakly marked small ridges, wall thickness $2-6.5~\mu$ m. Cultures produce a characteristic odour of benzene hexachloride.

Hosts: The species was isolated from detritus and from dead insects. It is known as primary pathogen of *Hypera* (*Phytonomus*) spp. (Curculionidae) (Ben-Ze'ev & Kenneth 1980).

Remarks: Ben-Ze'ev & Kenneth (1980) consider Tarichium punctatum Garbowski and T. phytonomi Jaczewski as identical with C. osmodes.

5. Entomophaga lagriae Bałazy (1993)

Hyphal bodies 7–15 nucleate, subspherical with a diameter of $28-35 \mu m$ or irregularly ovoid to ellipsoid up to $80 \times 15-20 \mu m$, germinate with one or two hyphae $9-10 \mu m$ thick. Conidiophores unbranched, conidiogenous cells claviform $65-102 \times 16-21 \mu m$. Primary conidia $35-43 \times 24-30 \mu m$, ovoid or broadly turbinate with regularly semispherically rounded top parts, with 12-18 nuclei, papilla narrow con-

ical or somewhat obtuse, 9–11.5 μ m wide. Secondary conidia like primary. Resting spores unknown.

Host: Lagria hirta L. (Lagriidae) collected in Switzerland.

6. Entomophthora sp. (Eilenberg 1987)

Primary conidia (17–) 21.6–24.4 (–29) x (13–) 17.1–19.9 (–24) μ m, L/D = 1.23–1.28, with 8–17 nuclei. Secondary conidia (16–) 15.9 (–21) x (16–) 19.3 (–24) μ m, L/D = 1.21. Resting spores probably azygospores (39–) 44.5 (–50) x (31–) 40.4 (–40) μ m. Rhizoids absent.

Host: Adult *Rhagonycha fulva* (Scopoli) (type host) and *Cantharis livida* L. (Cantharidae), collected from June to August on grass and lower vegetation of a hedge in Denmark.

7. Erynia nebriae (Raunkiaer) Humber & Ben Ze'ev (1981)

Conidiophores branched, septate, hyaline, club-like enlarged, $11-15~\mu m$ diameter. Conidia ellipsoidal to fusiform, asymmetrical, often slightly curved, $28-37~\mu m$ long, $10-13~\mu m$ broad, hyaline, smooth. Resting spores hyaline to pale brown, developing outside the body of the host, spherical, $35-50~\mu m$ diameter.

Host: Nebria brevicollis (F.) (Carabidae) collected in Sealand, Denmark.

Remarks: According to the index of fungi (http://www.indexfungorum.org) Erynia nebriae is an invalid name. Consequently, the name Entomophthora nebriae given by Raunkiaer (1893) is still valid, although there is no doubt that the species does not belong to Entomophthora. It is certainly a member of the subfamily Erynioideae but the data given in the original description do not allow to attribute the species to a genus. Therefore, we do not validate the name but consider Erynia nebriae as more appropriate.

Below in the paragraph «unclassified fungi», we mention a fungus as *Erynia* sp. found on the same host species, unfortunately with unprecise data. The two species are probably identical.

8. Eryniopsis lampyridarum (Thaxter) Humber (1984a)

Conidia 20–37 x 14–30 μ m, average 35 x 15 μ m, regular ovoid, slightly tapering towards the apex, with an abrupt slightly papillate base, content granular without larger oil globules. Secondary conidia like the primary or more commonly long-cylindrical, rounded at either end and born vertically on capillary conidiophores. Resting spores unknown. Host fixed to leaves by its mandibles.

Hosts: Adult Chauliognathus pensylvanicus (De Geer) (Cantharidae) collected in the USA.

9. Furia zabri (Rozsypal ex Ben-Ze'ev & Kenneth) Humber (1989)

Hyphal bodies are about 11 μ m thick and richly branched with a larger number of nuclei. The hemolymph contains fragmented mycelium, spherical and lobular shapes are present. Cystidia up to 300 μ m long, the flask-shaped base has a diameter of 40–50 μ m. Conidiophores branched. Primary conidia ovoid, 25 x 14 μ m, maximum 29 x 18 μ m. Zygospores spherical, formed mostly on the surface of the host. Rhizoids present.

Host: Larvae of *Zabrus tenebrioides* Goeze (Carabidae) collected in Moravia, Czech Republic.

10. Pandora brahminae (Bose & Metha) Humber (1989)

Conidiophores branched. Rhizoids monohyphal with a diameter of $14-24~\mu m$, endings with disc-like holdfast. Primary conidia ovoid, $18-22~x~11-15~\mu m$, tapering to a papillate base. Secondary conidia like primary. Resting spores zygospores, formed inside the host at the same time as the conidia, hyaline to light brown, $22-39~\mu m$, average $29~\mu m$, thick walled; episporium spiny, cannot be separated by pressure.

Host: Adult *Brahmina* sp. (Melolonthidae), collected in Uttar Pradesh, India. Dead beetles fixed with mouthparts and rhizoids to leaves of chestnut trees.

11. Pandora lipai (Bałazy, Eilenberg & Papierok) Keller in Keller & Petrini (2005)

Hyphal bodies irregularly elongate, hyphae-like, $50-70 \times 7-12 \mu m$, sometimes branched. Conidiophores $7-10 \mu m$ thick, richly branched. Primary conidia narrow ovoid to somewhat clavate, (18.5-) 19.5-23 $(-24) \times (8.5-)$ 9-10.5 $(-11) \mu m$, papilla slightly convex, $3.8-5 \mu m$ wide. Secondary conidia ovoid, shorther but of similar thickness as primary ones, $14.5-17.5 \times 8.5-10.5 \mu m$, strongly narrowing towards the base closed by semispherical papilla $2.5-3.5 \mu m$ wide. Cystidia numerous, oblong conical, $150-250 \mu m$ long, $10-17 \mu m$ thick at the level of the conidiogenous layer, $4.5-7 \mu m$ thick at the blunt tips. Rhizoids monohyphal terminated with wide, flat disc-like holdfast with uneven margins. Resting spores known only from cultures; regularly globose, diameter $20-33 \mu m$ and $2.3-3.0 \mu m$ thick walls; epispore minutely rough, brown.

Hosts: Cantharis livida L., C. rustica Fallen, Malthinus flaveolus (Herbst), and Rhagonycha lignosa (Müller) (Cantharidae) collected between end of May and mid June in Poland and Denmark.

Remarks: Pandora lipai is possibly a species complex or a species that shows a wide variation in conidial dimensions. Keller (2007b, 2012) found two groups of fungi attributed to *P. lipai* in a mixed host population consisting of Ancistronycha (Cantharis) abdominalis (F.) and A. (C.) erichsonii Bach. One fungus group had primary conidia measuring (22–) 23.9–25.1 (–28) x (11–) 12.3–13.6 (–15) μ m (L/D = 1.80–2.05) and the other one had primary conidia measuring (9.5–) 17.6–19.0 (–21) x (9.5–) 10.1–10.9 (–12) μ m (L/D = 1.74). The dimensions of the conidia of the two fungus groups clearly differ from each other but they both slightly overlap with those given in the original description. Further investigations are needed to clarify the situation.

12. Pandora philonthi (Bałazy) Keller in Keller & Petrini (2005)

Hyphal bodies irregularly elongate, 40– 250×15 – $25 \mu m$. Conidiophores 7– $9.5 \mu m$ thick, richly branched, grow in intersegmental junctions, mouth parts and between articles of legs and antennae. Terminal conidiogenous cells mostly flask-shaped about 25 x 13 μm . Primary conidia ellipsoid (19–) 21–26 (–28) x (10.5–) 11–14 (–14.5) μm , rarely ovoid, slightly but abruptly narrowed at the bases, forming very short overpapillar neck; papillae of rather distinctly arcuate outline or semiglobose,

 $5-6.5\,\mu\mathrm{m}$ wide. Secondary conidia similar, mostly ovoid, smaller. Few cystidia scattered in area of intensive conidiation, rather short, up to 120 $\mu\mathrm{m}$ long and about $10-14\,\mu\mathrm{m}$ thick at the base, unmarkedly tapering to obtuse tip. Rhizoids monohyphal, ribbon-like, $8-10\,\mu\mathrm{m}$ wide, terminated with irregularly rounded reticulate holdfasts, $20-40\,\mu\mathrm{m}$ in diameter, grow mostly in thoracic part of the host's body. Resting spores unknown.

Host: Philonthus sp. (Staphylinidae), collected in Poland in forests and on agricultural land.

13. Pandora phyllobii (Bałazy) Keller in Keller & Petrini (2005)

Hyphal bodies irregularly elongate, often with branches and outgrowths, about $20-130 \times 7-21 \,\mu\text{m}$. Conidiophores $6-9.5 \,\mu\text{m}$ thick typically branched in apical part. Conidiogenous cells cylindrical or clavate, $22-28 \times 10-12.5 \,\mu\text{m}$. Primary conidia narrow ovoid, $19.5-23 \times 10-12.5 \,\mu\text{m}$, or ellipsoid, $23-31 \times 11.5-14.5 \,\mu\text{m}$, basal part conically attenuated towards small papilla, about $4 \,\mu\text{m}$ wide. Secondary conidia short ovoid or almost subglobose with small papillae strongly protruding. Rhizoids monohyphal with terminal disc-like holdfast with unevenly sinuous margins. Cystidia $180-400 \,\mu\text{m}$ long, $9-11 \,\mu\text{m}$ wide at the base, slightly attenuate upwards. Resting spores unknown.

Host: Adult Phyllobius sp. (Curculionidae), collected in Poland in June.

14. Pandora suturalis (Ben-Ze'ev) Humber (1989)

Hyphal bodies short hyphal segments, up to 120 μ m long, usually not branched, plurinucleate. Conidiophores digitately branched with 3–7 conidiogenous cells. Primary conidia ovoid or ellipsoid, most of them of subpapillate type, 14.3–24.6 x 8.0–16.6 μ m, average 17.5 x 10.6 μ m, L/D ratio on average 1.67; usually with 2–3 vacuoles; papillae usually less than half of the conidial diameter. Secondary conidia pyriform or ovoid-pyriform, 13.2–15.5 x 9.7–11.5 μ m, average 14.3 x 11.0 μ m, L/D ratio on average 1.3. Cystidia 15–20 μ m at the base and about 150–200 μ m long, tapering. Rhizoids abundant, emerging in fascicles that appeared as pseudorhizomorphs, but diverged into individual, monohyphal threads, up to 35 μ m wide, sometimes branching in the middle, with dichotomically lobed holdfasts.

Host: Adult Lochmaea suturalis (Thomson) (Chrysomelidae), collected in Scotland near Edinburgh.

Remarks: Data taken from exsiccata.

15. Tarichium cleoni (Wize) Lakon (1915)

The following description is taken from Keller *et al.* (2009). Resting spores 32.2–40.1 (28–47) μ m, spherical to subspherical, red in mass and light brown in microscopic preparations, with regularly arranged $3.5–6.0~\mu$ m long spines. The endospores have a diameter of 21.2–23.6 (18–28) μ m, the spore wall measures on average $3.5–4.0~\mu$ m. Endospores and epispores are tightly connected. In the light microscope the two walls appear clearly separated. The diameter of the inner wall measures 16.8–17.9 (14–21) μ m.

Host: Bothynoderes [= Asproparthenis] (Cleonus) punctiventris (Germar) (Curculionidae) collected in the Ukraine.

16. Tarichium coleopterorum (Petch) Bałazy (1993)

Rhizoids pseudorhizomorph emerging from two points on the lower surface of the body of the insect. The resting spores were dark brown, thick-walled (up to $6 \mu m$), densely verrucose, globose, $35-50 \mu m$ diameter, or broadly oval, $48-52 \times 44-46 \mu m$, or sometimes pyriform, $56 \times 44 \mu m$.

Host: Unidentified Coleoptera collected in England.

Remarks: The spherical resting spores resemble those of *Zoophthora crassitunicata* and *Z. rhagonycharum*.

17. Tarichium hylobii Keller, Weiser & Wegensteiner (2009)

Mature resting spores measure $28.1-31.1~(24-36)~\mu\text{m}$, spherical to subspherical, grey in mass and light brown in microscopic preparations. In the light microscope the silhouette appears sinuous. The electron microscope shows irregularly undulating bulges and ridges. In the light microscope the separation between endospore and epispore is not clear. The diameter of the inner wall measures $19.4-20.2~(16-25)~\mu\text{m}$.

Host: Larvae or prepupae of *Hylobius abietis* (L.) (Curculionidae). The material originated from a closed pupal cell collected near Prague, Czech Republic.

18. Tarichium jaczewskii Zaprometov (1928)

Resting spores zygo- or azygospores, spherical, $28-46 \mu m$ in diameter, with almost smooth or verruculous two-layered epispore $4.5-7 \mu m$ thick, dark brown in colour. The infected larvae become black, dry, mummified and brittle.

Host: Larvae of Zabrus gibbosus (Zimm.) (Carabidae) collected at Samarkand in 1926 and at Katta-Kurgan in 1928 (former USSR). T. jaczewskii is possibly the resting spore state of Furia zabri (Ben-Ze'ev & Kenneth 1982).

19. Tarichium phytonomi Jaczewski in Zaprometov (1928)

The following data are taken from MacLeod & Müller-Kögler (1970). Resting spores zygo- or azygospores, spherical, $32-36 \mu m$ in diameter. Epispore dark brown, $2.6-3.9 \mu m$ thick with a few irregularly scattered warts that are $1.3-2.6 \mu m$ high.

Host: Larvae of Hypera (Phytonomus) variabilis [sic] (Curculionidae) collected in Taschkent (former USSR).

Remarks: As MacLeod & Müller-Kögler (1970) stated, the name is illegitimate as a later homonym of *Zoophthora phytonomi* (Arthur) Batko (1964b). Ben-Ze'ev & Kenneth (1980) considered *T. phytonomi* as the resting spore state of *Conidiobolus osmodes* and as conspecific with *T. punctatum*.

20. Tarichium punctatum Garbowski (1927)

The following data are taken from MacLeod & Müller-Kögler (1970). Resting spores spherical, 26–37.5 μ m in diameter, smoky dark in colour. Spore wall 2–3 μ m thick with tiny spots that give it a punctate appearance.

Host: Larvae of Hypera (Phytonomus) variabilis [sic] (Curculionidae) collected in Poland. Ben-Ze'ev & Kenneth (1980) considered T. punctatum as the resting spore state of Conidiobolus osmodes and as conspecific with T. phytonomi.

21. Zoophthora anglica (Petch) Humber (1989)

Petch (1943) described this species based on fungi found on the following hosts: *Plateumeris* sp. (Chrysomelidae), *Agriotes sputator* (L.) (Elateridae), *Lochmaea suturalis* (Thomson) (Chrysomelidae), and *Cantharis* sp. (Cantharidae) collected in England. He described the fungus as follows: Primary conidia narrow oval or subfusoid, sometimes slightly bent, with a broad truncate papilla, $22-27 \times 11-13 \mu m$, secondary conidia of the same shape but shorter, $18-21 \times 10-11 \mu m$. Rhizoids are produced from the ventral surface and the sides. The conidiophores in fully developed examples extend in a continuous sheet from the sides of the body to the substratum, but in general they do not spread over the elytra or only partially along their outer edges.

Ben-Ze'ev (1986) re-examined the air-dried material and found that it contained more than one fungus species and that the description is a mixture of different fungi. He separated it according to the host species. The fungus from *Agriotes sputator* had primary conidia measuring $16.7-33.4 \times 8.0-13.8 \mu m$, with an average of 27.6 x 9.8 μm and an L/D-ratio of 2.5. Most nuclei were ellipsoidal and measured $4.6 \times 6.8 \mu m$. The spherical resting spores measured $27.6-34.5 \mu m$ with an average of $31.1 \mu m$. The spore wall was $1.2-2.3 \mu m$ thick. Secondary conidia, neither type Ia nor capilliconidia were present. He found the fungus to be identical with *Z. elateridiphaga* and considered the latter as a synonym of *Z. anglica*.

The two fungi are indeed closely related. Nevertheless, there are differences between them, which were discussed by Keller (1991). They justify to consider the two species as distinct.

Hosts: Adult Agriotes sputator (L.) (Elateridae) collected in England.

22. Zoophthora crassitunicata Keller (1980)

Rhizoids pseudorhizomorph. Conidiophores sparingly branched, oligonucleate. Primary conidia (25–) 31.4–32.1 (–36) x (8.5–) 9.8 (–12) μ m, L/D = 3.2–3.3, subcylindrical to slightly fusiform, papilla distinct, conical. Capilliconidia 33–39 x 8–9 μ m, fusiform curved to banana-shaped. Resting spores (35–) 41.2–44.7 (–56) μ m, spherical, double walled, inner wall hyaline, episporium brown, about as thick as inner spore wall, densely and regularly covered with minute knobs, predominantly binucleate, but up to 8 nuclei observed, formed inside the host.

Host and symptoms: Adult cantharid beetle, probably Malthodes sp. (Cantharidae). Wings of the host insect closed when the fungus sporulated.

Remarks: The dimensions of the thick-walled resting spores match those of Tarichium coleopterorum. The surface structure as well is similar, «densely verrucose» (T. coleopterorum) and «densely and regularly covered with minute knobs» (Z. crassitunicata). A difference concerns the shape of the resting spores. Those of Z. crassitunicata were all spherical while some of T. coleopterorum were oval or pyriform. In spite of the large similarities some doubts concerning a conspecificity of the two species remain.

E. crassitunicata was hitherto known only from the type locality (Rickenbach, Switzerland, canton Zurich). Recently, it was found on a cantharid beetle (probably *Malthodes* sp.) at Fischingen (Switzerland, canton Thurgau).

23. Zoophthora elateridiphaga (Turian) Ben-Ze'ev & Kenneth (1980)

Rhizoids pseudorhizomorph on ventral side of thorax between the legs, holdfasts disc-like, or unspecialised and sometimes united to form a layer. Hyphal bodies elongate with (5–) 9–12 (–22) nuclei; nuclei measuring on average 5.1–5.7 μ m. Conidiophores branched, terminally slightly enlarged. Primary conidia (24–) 27.5–31.6 (–36) x (7–) 8.8–11.4 (–13) μ m, L/D ratio 2.51–3.52, cylindrical, papilla distinct, conical. Secondary conidia similar to primary, (21–) 25–25.7 (–30) x (7–) 8.6–9.9 (–12) μ m, L/D = 2.5–3.0, or capilliconidia (27–) 31.4–35.5 (–42) x (6–) 6.7–7.5 (–9) μ m, L/D = 4.53–4.86, fusiform to banana-like; length of capillary tube (67–) 86–90 (–109) μ m. Resting spores formed inside the host, (25–) 31.2–37.7 (–46) μ m, spherical, hyaline, smooth; zygospores or azygospores, young resting spores with (14–) 18–21 (–29) nuclei measuring 4.9–5.0 μ m. Fully developed but broken resting spores contained (6–) 10 (–14) nuclei.

Hosts: Adult Agriotes sputator (L.) (type host), A. lineatus (L.) (Elateridae) collected in Switzerland. Recently, Grabenweger (pers. comm.) reported heavy epizootics in laboratory rearings of A. lineatus, A. obscurus and A. sputator at Reckenholz, Zurich.

24. Zoophthora larvivora Bałazy (1993)

Mycelium inside host's body consists of almost equally narrow hyphae 7–11 μ m thick, rarely as separate hyphal segments up to 40 μ m long. Conidiophores 6–8 μ m thick, digitately branched, terminal conidiogenous branches cylindric or indistinctly clavate 32–47 x 7.5–11.5 μ m. Primary conidia cylindric with obtuse ends or with distal parts weakly, steadily narrowing towards blunt apex, (35–) 40–42 (–49.5) x (7.5–) 8.5–9 (–10.7) μ m, L/D ratio commonly exceeding 4.5. Secondary conidia, resting spores and cystidia unknown. Few rhizoids, pseudorhizomorph.

Host: A single larva of an unidentified Cantharidae collected in Poland.

25. Zoophthora phytonomi (Arthur) Batko (1964b)

Hyphal bodies branched, non-septate, colourless, $9-12 \mu m$ in diameter. Rhizoids on the ventral surface. Hymenium over the whole surface except the head. Conidiophores branched at the base, as thick as mycelium. Primary conidia oblong, colourless, $24-28 \times 7-10 \mu m$. Resting spores not observed.

Host: Larval *Hypera punctata* (F.) (syn.: *Brachyptera zoilus* (Scop.)) (type host) collected in the USA. Dead insects fixed on top of plants. Further hosts are *H. postica* (Gyll.) (syn.: *H. variabilis*) (Curculionidae).

26. Zoophthora radicans sensu lato (Brefeld) Batko (1964a)

Hyphal bodies hyphae-like. Conidiophores on average 6–8 μ m thick, branched with nuclei measuring 4.7 (4–5.5) μ m, conidiogenous cells terminally enlarged to 7–11 μ m. Primary conidia 15.5–22.5 x 6.3–8.4 μ m (13–28 x 5–10 μ m), L/D = 2.41–2.98, subcylindrical to subfusiform straight or slightly bent; papilla usually rounded; diameter of nuclei 4.0–4.6 (3–5.5) μ m. Secondary conidia similar to primary, 11.9–13.2 x 6.9–7.1 μ m (10–16 x 6–9 μ m), L/D = 1.67–1.88, or capilliconidia 17.3–21.8 x 4.6–5.9 μ m (15–24 x 4–7.5 μ m), L/D = 3.23–4.18, fusiform, slightly bent or straight, apically rounded; length of capillary tube 42.5–58.8 μ m (30–81

 μ m). Resting spores 24.5–27.2 μ m (20–33 μ m), spherical, hyaline, smooth. Rhizoids abundant, emerging ventrally or latero-ventrally, pseudorhizomorph or monohyphal with disc-like ending. Cystidia not observed. The data given above are taken from Keller (1991). According to Bałazy (1993), the primary conidia measure (17.5–) 19.5–22.5 (–27.5) x (4.7–) 5.5–6 (–6.5) μ m with an L/D ratio of 3.5–4.5.

Hosts: Many species of the insect orders Plecoptera, Heteroptera, Homoptera, Diptera, Hymenoptera and Lepidoptera. Type host is *Pieris brassicae* (L.) (Pieridae, Lepidoptera).

Remarks: The original description is very poor and a redescription has never been done. Therefore, it is very difficult to separate morphologically similar fungi from the type species. Consequently, Zoophthora radicans seems to be an unspecific species, but should be considered as a species complex. Bałazy (1993) has tried to split the complex based on tiny morphological differences but mainly by their hosts. Genetic markers should be used to prove the correctness of this separation.

So far, there are no confirmed reports of *Z. radicans* attacking Coleoptera. However, Lakon (1919) mentioned a report of Bail who observed an epizootic among *Nebria brevicollis* (L.) (Carabidae) at Jäschkental (now Jaškowa Dolina near Gdansk, Poland) caused by *Entomophthora sphaerosperma* which is a synonym of *Z. radicans*. As listed below in the paragraph «unclassified fungi», this fungus could also be identical with *Erynia* sp. reported from the same host species.

27. Zoophthora rhagonycharum (Bałazy) Keller (2007)

Rhizoids pseudorhizomorph, numerous, mainly emerging from the ventral side of the abdomen, endings unspecialised or with disc-like holdfast. Hyphal bodies in living hosts filamentous usually unbranched, with 7–16 nuclei with a diameter of 6–9.5 μ m. Conidia unknown. Resting spores (33–) 45.4–48.8 (–62) μ m, spherical, double-layered wall; inner layer more or less hyaline, outer layer (episporium) brown with minute knobs at the surface. Young resting spores contain 8–24 nuclei with a diameter of 5–6 μ m.

Host: Adult *Rhagonycha lignosa* (Müller) (type host) collected in Poland and *R. fulva* (Scopoli) (Cantharidae) collected in Switzerland.

Remarks: The average dimensions of the resting spores are within the range of the extreme dimensions of those of *Tarichium coleopterorum* although at the upper limit. Nevertheless, an identity of the two species cannot be excluded.

Fitton (1982) observed a fungus occurring epizootically in populations of *R*. *fulva* at Silwood Park in England. The fungus was identified at the Commonwealth Mycological Institute as *Entomophthora coleopterorum*. However, the host and the symptoms described by Fitton make it very probable that the observed fungus is *Z*. *rhagonycharum*. At least, his observations are a strong indication that *Tarichium* (*Entomophthora*) *coleopterorum* and *Z. rhagonycharum* might be identical.

28. Zoophthora tachypori Bałazy (1993)

Hypal bodies elongate, $25-80 \times 9-15 \mu m$, often with short outgrowths and branchlets. Conidiophores $6.5-12 \mu m$ thick, richly digitately branched; ultimate sporogenous branches about $20-24 \mu m$ long, cylindric or slightly widened near the top, $6-7 \mu m$ thick. Primary conidia cylindric, seldom somewhat subfusiform, $(18-)19.5-21.5(-22) \times 5.5-6(-6.5) \mu m$. Secondary conidia like primary or capilliconi-

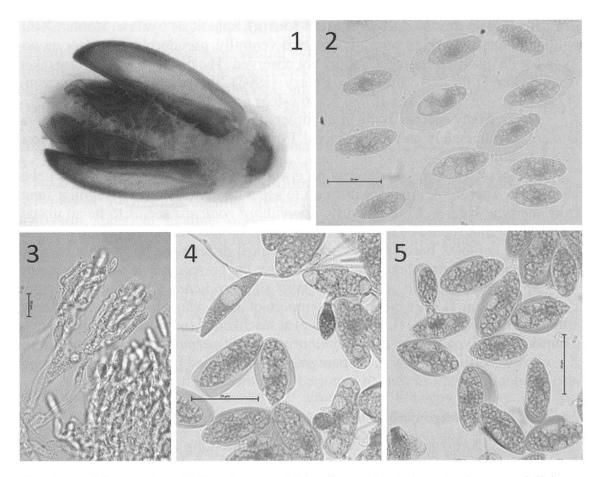


Plate 1. Zoophthora sp. 2 ex Elodes minuta. — 1: Mycelium on beetle (nat. size 5 mm); — 2: Primary conidia with typical, separated outer wall; — 3: Branched conidiophores; — 4: Primary conidia, a detached capilliconidum (left upper corner) and two developing type I secondary conidia; — 5: Primary conidia and a developing type I secondary conidium (left upper corner). — Bars in figs 2–5 represent $20 \ \mu m$. (Photos: R. Wegensteiner).

dia, 20–25 x 5–5.5 μ m, oblong fusiform. Capillary tube 40–50 μ m long. Cystidia conical, 30–80 (–120) μ m long and 8–12 μ m thick at the conidial layer. Pseudorhizomorphs growing from thoracic parts, monohyphal rhozoids produde from abdominal sternites. Resting spores unknown.

Host: Adult Tachyporus spp. (Staphylinidae) collected in Poland.

29. *Zoophthora* sp. 1 (Keller, 2012)

Rhizoids compound with common disc-like holdfast, lateral parts sometimes splitting into thinner compound rhizoids which are further divided into monohyphal holdfasts. Hyphal bodies hyphae-like, branched or unbranched with a diameter of (5-) 6.5 (-8) μ m (n = 25). Conidiophores branched with a diameter of 5–6 μ m. Primary conidia (13–) 15.6 (-17) x (5-) 5.9 (-6) μ m, L/D = 2.65 (n = 25), narrow fusiform to ellipsoidal, bitunicate, papilla blunt, separated by an indistinct bulge from the body of the conidium. Cystidia slender, tapering, basal part faintly stained with a diameter of 5–6 μ m, terminal parts slightly enlarged and darker stained. Secondary conidia and resting spores not present.

Host: Unidentified species of Cantharidae (Coleoptera), probably *Malthodes* sp. collected at Fischingen, canton Thurgau, Switzerland.

Remarks. The fungus was collected in early July on the underside of a leaf of *Corylus avellana* L. about 1.5 m above ground on the shore of the brook Murg at an altitude of about 650 m. The fungus is considered as a new species but the material is too incomplete to give a formal description.

30. Zoophthora sp. 2 (Plate 1, figs. 1–5)

The wings of the host were slightly opened, when the fungus sporulated (fig. 1). Rhizoids compound. Conidiophores branched (fig. 3). Primary conidia (20–) 22.8–23.4 (–26) x (9–) 10–10.5 (–12) μ m, L/D = 2.17–2.34, subcylindric to slightly ellipsoidal, bitunicate; papilla indistinctly demarcated from the conidial body, conical with rounded end (figs. 2, 4 and 5). Secondary conidia like primary but shorter (fig. 5), or capilliconidia 26–27 x 6.5–7.5 μ m (n = 3), L/D = 3.8, elongate fusiform and slightly bent, banana-like, usually with a single large vacuole (fig. 4).

Host: Elodes minuta L. (Scirtidae).

Location: Berglsteinersee, 714 m altitude, 3.8 km NE of Rattenberg, Kramsach, Tirol, Austria. The material was collected on June 19, 2011 by C. Tkaczuk and identified by the author. The fungus is probably an undescribed species.

Unclassified fungi

Entomophthora telaria Giard (1888)

This entomophthoralean fungus was recorded as pathogen of *Rhagonycha melanura* F. (Cantharidae) in northern France near Fécamp. Giard did not give any data of the fungus and described only the symptoms. According to him the fungus is characterized by a large membrane which covers the body of the host and fixes it to the substrate. The hyphae emerging from the host's body seemed to be united by a rubberlike secretion which looks like a cloth. The infected beetles were fixed to the underside of leaves of *Galeopsis tetrahit* L. The cadavers were always placed parallel to the median vein with the head towards the stem.

From the symptoms described we can suppose that this fungus is close to *Pandora lipai* but this assumption needs verification.

Entomophthora carpentieri Giard (1888)

This fungus was found by Mr. Carpentier near Amiens in northern France infecting Agriotes sputator L. (Elateridae). Giard described the symptoms very precisely and in the author's opinion there is no doubt that the fungus is identical with Zoophthora elateridiphaga (Turian) Ben-Ze'ev & Kenneth. Giard especially noticed the strong compound rhizoids unknown till then among entomophthoralean fungi. Therefore, he proposed Lophorhiza as a new genus for this fungus. However, the name was apparently overlooked or forgotten and has never been used by other authors. The genus name Zoophthora now generally accepted for species with compound rhizoids was proposed by Batko (1964a) who was obviously not aware of the existence of an older genus name.

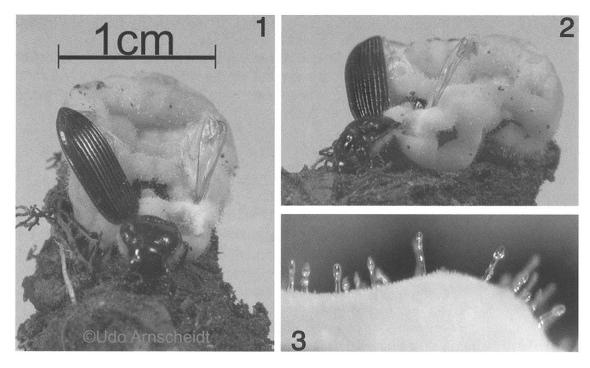


Plate 2. Erynia sp. ex Nebria brevicollis. — 1: Front view of the infected beetle with fully sporulating fungus; — 2: Lateral view of the same beetle (same magnification); — 3: Macrophotograph showing structures considered as cystidia towering above the sporulating fungus layer (unknown magnification). (Photos: U. Arnscheidt).

Erynia sp. (Plate 2, figs. 1–3)

A fungus collected on 17.11.2011 on two specimens of adult *Nebria* cf. *brevicollis* in Germany by Mr. Udo Arnscheidt was provisionally identified as Erynia sp. by the author. The identification is based on photos and measurements sent to the author by Mr. Arnscheidt. The photos showed extremely swollen cadavers, when the fungus sporulated, the wings were spread (figs. 1–2). Close-up photos showed structures which were interpreted as cystidia (fig. 3). These were powerful, often with an enlarged ending. Such strong cystidia are typical for Erynia spp. That's why the fungus was provisionally attributed to this genus. Unfortunately, the measurements of the conidia did not differentiate between primary conidia and conidia of higher orders and probably included also other structures. The average dimension of conidia considered as primary ones was calculated (based on photos) to be about 23–25 x 13 µm with an L/D ratio of 1.8–2.0. The largest conidium measured 34 x 16.5 μ m, the length is within the range of the primary conidia of Erynia nebriae whose conidia measure $28-37 \times 10-13 \mu m$ with an L/D ratio distinctly above 2. Considering the identity of the host and the similarities of the conidia an identity of the two fungi cannot be excluded.

Erynia sp was found in a forest called Hoersterholz, near Bochum, Germany, altitude 120 m, coordinates: 51°26′24.60 N; 7°8′52.14 E. The two sporulating ground beetles were on the soil in a forest dominated by *Fagus sylvatica* L. The two cadavers were found at a distance of 50 cm from each other.

Tarichium sp.

This fungus was found in the state of New York, USA, as pathogen of adult *Diabrotica barberi* Smith & Lawrence (Chrysomelidae) (Naranjo & Steinkraus, 1988). The infected beetles had a swollen abdomen and raised elytra. The resting spores produced inside the body of the host were smooth-walled and spherical with a mean diameter of $27.2 \pm 2.8 \, \mu \text{m}$ and contained 8–14 nuclei with a mean diameter of $5.8 \pm 2.0 \, \mu \text{m}$. Cystidia and rhizoids were absent. Size and structure of the nuclei allowed to attribute the species to the family Entomophthoraceae.

DISCUSSION

Most of the species listed above are well described. Only a few of them are doubtful or lack a formal description due to missing details or for other reasons. Doubtful species are *Tarichium coleopterorum* (Petch) Bałazy, *T. jaczewskii* Zaprometov, *T. phytonomi* Jaczewskii in Zaprometov and *T. punctatum* Garbowski.

According to the Index Fungorum (http://www.speciesfungorum.org) T. coleopterorum is an invalid name. Petch (1932) described the species as Ento-mophthora coleopterorum which is still the valid name. Nevertheless, T. coleopterorum refers to the fact that the fungus is known only in its resting spore state. Later on Petch (1944) found a conidial state on other host species (larval Coleoptera and Sitones flavescens Marsch. (= Sitona obsoletus (Gmelin)) and attributed it to E. coleopterorum, although he was in doubt of the conspecificity of the two fungi. These conidial measured $32-44 \times 8-14 \mu m$. However, the correct specific attribution of the conidial state remains unsolved (Ben-Ze'ev 1986). As discussed under Z. rhagonycharum, there are indications that T. coleopterorum might be identical with this species.

A possible synonymy of *T. jaczewskii* Zaprometov with *Furia zabri* has been discussed by Ben-Ze'ev & Kenneth (1982), however, an identity of the two species has not been proven. On the other hand Ben-Ze'ev & Kenneth (1980) gave good evidence, that *T. phytonomi* Jaczewski in Zaprometov and *T. punctatum* Garbowski are not only identical but also the resting spore stage of *Conidiobolus osmodes*. Due to remaining doubts they did not formally synonymize the three species.

Zoophthora sp. 1 (nr. 29) and Zoophthora sp. 2 (nr. 30) are incompletely known but supposed to be new species. Pandora lipai (nr. 11) is possibly a species complex. These three species need further investigations to clarify the situation. Entomophthora sp. (nr. 6) is well characterized and represents without doubt a new species. However, a formal description is still missing.

Although Coleoptera is the order with the highest number of decribed species, comparably low is the number of Entomophthorales known to attack these insects. Only eleven families are known as hosts of Entomophthorales, Cantharidae and Curculionidae are the preferred ones. Reasons for the relative scarcity of these fungi in Coleoptera are the unawareness of entomologists, the often inconspicuous symptoms of infections and characteristics of the Coleoptera like the strongly sclerotized body, which is supposed to act as a barrier to fungus infections. Therefore it is not surprising that larvae and soft-skinned adults like Cantharidae are the preferred hosts. Nevertheless, Entomophthorales can infect strongly sclerotized beetles like adult Elateridae and are even able to cause epizootics among them (Keller, 1994).

Entomophthorales and their role in the population dynamics of insects are still too less known. The key provided in this paper hopefully will animate coleopterists, other entomologists and insect mycologists to keep an eye out for these interesting fungi and thus contribute to a better knowledge of the diversity of Entomophthorales and their ecological importance.

ZUSAMMENFASSUNG

Käfer sind die artenreichste Insektenordnung. Trotzdem sind im Vergleich zu anderen Insektenordnungen nur wenige Arten von Entomophthorales bekannt, die Käfer infizieren. Gründe dafür sind unter anderem die mangelnde Bekanntheit dieser Pilze bei Entomologen, die oftmals undeutlichen Symptome von Infektionen sowie käferspezifische Merkmale wie das ausgeprägte und wahrscheinlich vor Infektionen schützende Exoskelett.

Die vorliegende Arbeit erfasst 30 Arten von Entomophthorales, darin eingeschlossen drei formal nicht beschriebene. Der dichotome Schlüssel erlaubt die Bestimmung dieser 30 Arten vorwiegend anhand von Primärkonidien und Wirtsarten. Aber auch dem Umstand, dass relative viele Pilzarten nur in der Dauersporenform bekannt sind, wird Rechnung getragen. Dem Bestimmungsschlüssel geht eine Zusammenstellung voraus, bei der die einzelnen Pilzarten elf Käferfamilien zugeordnet sind. Dies erleichert in vielen Fällen die Bestimmung.

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