

## Entomophthorales attacking aphids with a description of two new species

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Twenty-nine species belonging to eight genera of Entomophthorales attacking aphids are listed, and a summary table is provided outlining the main hosts. Two species, *Neozygites remaudierei* affecting *Myzocallis coryli* (Callaphidinae) and *Neozygites slavi* affecting *Slavum esfandiarii* (Pemphiginae), are described as new species. Keys are provided to identify the fungal genera and the species within the genera. All species are described using data from the literature and the author's own observations; type hosts and geographical distributions are given. Suggestions for future research on better identification of the aphid pathogenic species are provided.

Key words: Homoptera, Zygomycetes, identification keys, *Neozygites remaudierei*, *Neozygites slavi*.

More than 5300 species of aphids are described worldwide (Remaudière & Remaudière 1997). They are small insects but their specialised way of life makes them important members of ecosystems. Within a short time they can build up enormous biomass that provides food for many predatory animals, parasitic insects and pathogenic organisms, mainly fungi. Furthermore, honeydew produced in abundance by aphids is another important source of food for numerous insects including honey bees. Most aphid species are innocuous but some are serious pests directly affecting crop yields through feeding on plants and also transmission of diseases.

The fungi of the Entomophthorales are important aphid antagonists. They have a tendency to occur epizootically and to reduce aphid densities dramatically (Keller & Suter 1980, Nielsen 2002, Steinkraus *et al.* 1995, Wilding & Perry 1980). Therefore, they are not only effective natural regulation factors but have substantial potential for microbial control (Pell *et al.* 2001). So far only a few studies have considered these fungi for aphid control (Pell *et al.* 2001). Knowledge of the biology and taxonomy of aphid pathogenic

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Entomophthorales is a prerequisite for researchers working in this field and also for those conducting broader ecological investigations. Entomophthorales are often overlooked or neglected by entomologists and by highlighting this fact new species may be discovered in the future, especially in forest ecosystems, and in tropical and subtropical regions which have yet to be thoroughly explored.

A few papers have appeared listing species of the aphid pathogenic Entomophthorales. Keller (1977) summarised the species which are common on arable crops in central Europe, Zimmermann (1978), and Humber (1991) listed all species known but since these publications several new species have been described and many new hosts recorded. Furthermore, general biology and life cycles have been studied in more detail and are now better understood (Eilenberg 2002, Keller 1997, 2002). The fungal structures of all species are basically the same, but they differ in shape, size, and in the number and size of nuclei. This paper describes two new species, summarises all species described from aphids and includes new data from recent research on morphology and host range. It also provides keys to the genera and to all species known to attack aphids.

### **Material and methods**

Most species of Entomophthorales listed are aphid specialists, but some, like most species of *Conidiobolus*, have a wider host range or have also been isolated from detritus. Most of the information presented is from the published literature, but some is new data from investigations following the methods described in previous publications (Keller 1987, 1991). Counts and measurements made by the author are based on 25 objects per individual host, designated as 1 series. From each fungus species there are usually several such series to give an impression of the variability.

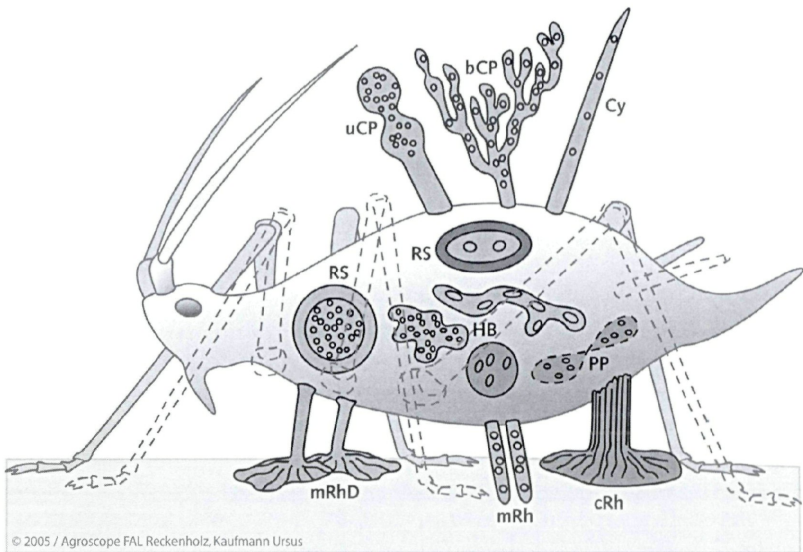
The type hosts are only given for aphid specialists. The geographical distribution of non-specific Entomophthorales is related only to aphids, and the host range includes only species that were naturally infected thus representing the ecological host range. Genera and species are listed in alphabetical order. Dimensions or counts in the description of species give the range of mean values or are taken from the original descriptions; those in brackets are the minimal and maximal values. Dimensions given in the keys are mean values.

Genera and species are listed in alphabetical orders and consecutively numbered. These numbers are given in the keys in brackets after the corresponding genus or species. The fungal structures are described and illustrated elsewhere (Keller & Petrini



2005). Photographs and drawings of the most common aphid pathogenic species are given by Wilding & Brady (1984), Bałazy (1993) and Keller (1987, 1991, 1997). The term “obligate entomopathogen” means, that the fungi can multiply only in living arthropods under natural conditions. It does not exclude growth on or in artificial media.

For a better understanding the fungal structures used for identification are shown in Fig.1. They can be separated by structures formed inside the host (protoplasts, hyphal bodies, resting spores) and by structures formed on the outside of the host (rhizoids with or without specialised holdfasts [endings], cystidia, conidiophores, conidia). The dimensions are given as averages together with minima and maxima. The length (L) of the conidia include the papilla and is given together with the diameter (D). Where appropriate, the length/diameter quotient (Q) is given. The primary conidia are typified according to Lakon (1919). The secondary conidia are typified according to Ben-Ze'ev & Kenneth (1982); type Ia resembles the primary ones, type Ib is spherical and type II is produced on a long, slender capillary tube. They are also known as capilliconidia.



**Fig. 1.** Entomophthoralean structures present inside the host and on the surface of the host. Projected conidia are not shown. PP: Protoplasts; HB: Hyphal bodies; RS: Resting spores (zygospores or azygospores); uCP: Unbranched conidiophores; bCP: Branched conidiophores; Cy: Cystidia; mRhD: monohyphal rhizoids with disc-like (specialised) holdfast; mRh: monohyphal rhizoids without specialised holdfast; cRh: compound rhizoid.

## Results

The aphid-pathogenic Entomophthorales are placed in the three families Ancylistaceae (genus *Conidiobolus*), Entomophthoraceae (genera *Batkoa*, *Entomophaga*, *Entomophthora*, *Erynia*, *Pandora*, *Tarichium* and *Zoophthora*) and Neozygitaceae (genus *Neozygites*). Twenty-nine species belonging to eight genera of Entomophthorales attacking aphid species are given in Table 1. Most of them are rare, some are only known from a single species or from the original description. Keys are provided to identify all genera with aphid pathogenic species and to identify the species in those genera which contain more than two aphid pathogenic species.

### Key to aphid pathogenic genera of Entomophthorales

- 1 Only resting spores known ..... *Tarichium* (8)
- 1\* Conidia produced ..... 2
- 2 Conidiophores unbranched; primary conidia spherical, subspherical, short-ovoid, cylindrical to fusoid or campanulate, bi- to multinucleate, unitunicate ..... 3
- 2\* Conidiophores branched, elongate ovoid, spindle-shaped, ellipsoid to cylindrical, mononucleate, bitunicate ..... 7
- 3 Primary conidia campanulate, bi- to multinucleate, hyphal bodies spherical, subspherical or short rod-shaped, cystidia absent, rhizoids monohyphal or absent. .... *Entomophthora* (4)
- 3\* Primary conidia spherical, subspherical to short-ovoid, bi- to multinucleate. .... 4
- 4 Primary conidia subspherical to short-ovoid, papilla broad with more or less flat base, usually 4 – 8 nuclei, secondary conidia like primary or capilliconidia. Resting spores spherical to ellipsoid, dark brown to black. Cystidia and rhizoids usually absent. .... *Neozygites* (6)
- 4\* Primary conidia spherical, subspherical, short-ovoid to pyriform; papilla prominent, semi-circular to cylindrical, with more than 20 nuclei. Cystidia absent, rhizoids present or absent. .... 5
- 5 Primary conidia spherical, subspherical, short-ovoid, papilla prominent, semi-circular to cylindrical, usually with more than 40 nuclei. Nuclei smaller than 3 µm, not or only weakly staining in lactophenol-aceto-orcein (LPAO). Hyphal bodies hyphae-like or irregular. .... *Conidiobolus* (2)
- 5\* Primary conidia spherical, subspherical, short-ovoid or pyriform, papilla prominent, semi-circular to elongate cylindrical, with less than 40 nuclei. Nuclei larger than 3 µm, staining in LPAO. Hyphal bodies spherical, subspherical, irregularly rounded to elongate or composed of rounded structures. .... 6

- 6 Primary conidia spherical to subspherical with about 20 nuclei on average, nuclei deeply stain in LPAO; papilla hemi-spherical. Hyphal bodies rounded or composed of rounded structures. Rhizoids monohyphal. . . . . *Batkoa* (1)
- 6\* Primary conidia pyriform with 20–30 nuclei, large extended papilla. Nuclei deeply staining in LPAO. Resting spores spherical, 12–25 µm, smooth, hyaline. Rhizoids absent. . . *Entomophaga* (3)
- 7 Primary conidia elongate, cylindrical to ellipsoid; papilla usually conical, demarcated with a slight bulge from the conidial body, cylindrical or rounded. Secondary conidia like primary or capilliconidia. Rhizoids thin, compound with specialised holdfast. . . . . *Zoophthora* (9)
- 7\* Primary conidia ovoid to elongate ovoid; papilla smoothly connected with conidial body, rounded. Secondary like primary or spherical to indistinctly campanulate; capilliconidia absent. Rhizoids thick and monohyphal. . . . . 8
- 8 Hyphal bodies globose; rhizoids without distinct terminal holdfast. . . . . *Erynia* (5)
- 8\* Hyphal bodies short hyphae-like, unbranched or branched; rhizoids with discoid or irregularly branched holdfast. . . . . *Pandora* (7)

1. *Batkoa* Humber, Mycotaxon 34: 446, 1989 (Entomophthoraceae).

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 finger-like or disc-like ending; absent in some species. Obligate entomopathogens.

Type species. – *Batkoa apiculata* (Thaxter) Humber (1989).

1.1. *Batkoa apiculata* (Thaxter) Humber, Mycotaxon 34: 446, 1989.

Basionym. – *Empusa apiculata* Thaxter, Mem. Boston Soc. Nat. Hist. 4: 163–164. 1888.

The species was originally described from Lepidoptera, Diptera and Hemiptera.



Hyphal bodies subspherical or composed of simple, rounded structures, sometimes thick, short and hyphae-like. Contain on average (10) 18–20 (28) nuclei with a diameter of 3.5–3.7  $\mu\text{m}$ , distinctly staining in LPAO. – Conidiophores unbranched, terminally enlarged. – Primary conidia 33–38  $\times$  29–34  $\mu\text{m}$ ,  $Q = 1.11–1.21$ , body spherical, papilla distinct, tip rounded or pointed. – Secondary conidia similar to primary ones, 29  $\times$  24  $\mu\text{m}$ . – Rhizoids monohyphal, stout, ending with disc-like holdfast.

Distribution. – The species is a common pathogen of numerous insect species belonging to different orders (Bałazy 1993). It has only been recorded as an aphid pathogen in Israel (Ben-Ze'ev, 1993, referred as *Conidiobolus apiculatus*) (Tab. 1).

**2. *Conidiobolus*** Brefeld, Unters. Ges. Mycol. 6: 35–78. 1884 (Ancylistaceae).

Hyphal bodies elongate, amoeboid or polymorphic, containing about 50–100 nuclei. Nuclei do not or only faintly stain with acetoorcein. Conidiophores unbranched. Primary conidia unilocular, globose to pyriform, papilla prominent, rounded or conical. Secondary conidia usually like primary, produced on a short, thick secondary conidiophore arising laterally from primary conidia. Resting spores spherical, hyaline or coloured, smooth or echinulate. Cystidia absent, rhizoids present or absent. Saprophytes in soil and organic detritus, parasites of higher fungi, pathogens of arthropods, exceptionally of warm-blooded animals and man (Bałazy 1993, King 1979, Ribes *et al.* 2000).

Type species. – *Conidiobolus utriculosus* Brefeld (1884).

#### Key to species of *Conidiobolus*

- 1 Primary conidia on average 50–53  $\times$  38–40  $\mu\text{m}$ ,  $Q = 1.30–1.34$ ; Resting spores with average diameter of 30–32  $\mu\text{m}$ , villose. . . . . *coronatus* (2.1.)
- 1\* Primary conidia smaller; resting spores spherical, usually smooth and hyaline. . . . . 2
- 2 Primary conidia 24–32  $\times$  17–27  $\mu\text{m}$ ; zygosporangia 15–27  $\mu\text{m}$ , globose, wall 1.5–2  $\mu\text{m}$  thick. . . . . *thromboides* (2.4.)
- 2\* Primary conidia and resting spores larger. . . . . 3
- 3 Primary conidia 33–44  $\times$  28–36  $\mu\text{m}$ ,  $Q = 1.16–1.27$ ; Resting spores 34–38  $\mu\text{m}$ , smooth. . . . . *obscurus* (2.2.)
- 3\* Primary conidia 25–37  $\times$  22–30  $\mu\text{m}$ ; zygosporangia 13–37  $\mu\text{m}$ , globose to ellipsoid, wall smooth or with indistinct ridges, 2–6.5  $\mu\text{m}$  thick. . . . . *osmodes* (2.3.)

**2.1. *Conidiobolus coronatus*** (Costantin) Batko, Entomophaga, Mém. Hors Ser. 2: 129. 1964a.

Basionym. – *Boudierella coronata* Costantin, Bull. Soc. Mycol. France 13: 40. 1897.

Hyphal bodies polymorphic. – Primary conidia on average  $50 - 53 \times 38 - 40 \mu\text{m}$ ,  $Q = 1.30 - 1.34$ , varying largely in size, conidial body spherical, papilla prominent, demarcated from conidial body, elongate conical. – Secondary conidia like primary or microconidia produced in large numbers on conidial surface. – Azygospores with average diameter of  $30 - 32 \mu\text{m}$ , villose, spherical. Isolated from different substrates including dead and living insects of different orders, it is also known to cause mycosis in warm blooded animals and man (King 1979, Thammayya 2000).

Distribution. – Worldwide on several aphid species (Tab. 1).

**2.2. *Conidiobolus obscurus*** (Hall & Dunn) Remaudière & Keller, Mycologia 31: 331. 1980.

Basionym. – *Entomophthora obscura* Hall & Dunn, Hilgardia 27: 162. 1957.

Important synonyms. – *Entomophthora thaxteriana* (Petch) Hall & Dunn (1957); *Entomophthora ignobilis* Hall & Dunn (1957).

Type host. – *Therioaphis maculata* (Buckton)

Hyphal bodies polymorphic, subovoid to hyphae-like. – Primary conidia on average  $33 - 44 \times 28 - 36 \mu\text{m}$ ,  $Q = 1.16 - 1.27$ , conidial body spherical, papilla medium-sized, tip rounded, sometimes pointed, demarcated from conidial body. – Resting spores probably azygospores, average diameter  $34 - 38 \mu\text{m}$ , spherical, hyaline, smooth, formed inside the host in presence or absence of conidia. – Grows and sporulates well on artificial media. Although isolated also from soil this species is considered a specific pathogen of aphids, sometimes causing epizootics.

Distribution. – Worldwide but not reported from tropical regions. Pathogen of many aphid species from different subfamilies (Tab. 1).

Remarks. – *C. obscurus* belongs to among the most important entomophthoralean fungi attacking aphid species of agricultural importance (Barta 2004, Dedryver 1981, Hall & Dunn 1957, Keller & Suter 1980, Remaudière *et al.* 1981). In the older literature the species is mentioned as *Entomophthora thaxteriana* (Petch) Hall & Dunn. The species has been intensively studied in respect to use for aphid control (Latgé & Perry 1980, Hall & Dunn 1957).

**2.3. *Conidiobolus osmodes*** Drechsler, Am. J. Bot. 41: 571. 1954.

Vegetative hyphae branched, 4–12 µm thick. – Primary conidia 25–37 × 22–30 µm, globose to ovoid, papilla tapering. – Zygosporangia with a diameter of 13–37 µm, globose to ellipsoid, wall smooth or with indistinct ridges, 2–6.5 µm thick. – Isolated from different substrates including dead and living insects. – Characteristic odour of benzene hexachloride is usually produced in cultures.

Distribution. – Australia, Europe, North America, Israel from several aphid species (Tab. 1).

**2.4. *Conidiobolus thromboides*** Drechsler, J. Wash. Acad. Sci 43: 38. 1953.

Synonym. – *Entomophthora virulenta* Hall & Dunn (1957).

Vegetative hyphae moderately branched, 6–13 µm thick. – Primary conidia 24–32 × 17–27 µm, globose to pyriform, with several large globules, papilla short, obtuse, smoothly joining conidial body. – Zygosporangia with a diameter of 15–27 µm, globose, wall smooth 1.5–2 µm thick. – Isolated from different substrates including dead and living insects.

Distribution. – Asia, Australia, Europe, North America and South Africa on several aphid species (Tab. 1).

**3. *Entomophaga*** Batko, Bull. Acad. Pol. Sci., Ser.Sci. Biol. 12: 325–326. 1964 c. (Entomophthoraceae).

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 from 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 (1964 c)



**3.1. *E. pyriformis*** (Thoizon) Bałazy, Flora of Poland, Fungi Vol. 24, Entomophthorales, 119. 1993.

Basionym. – *Entomophthora pyriformis* Thoizon, Entomophaga 12 : 303 – 307. 1967.

Type host. – *Rhopalosiphum insertum* Walk.

The original description of this fungus was made from fungal structures obtained from cultures. The primary conidia measure on average  $25 \times 19 \mu\text{m}$ ,  $Q = 1.32$ , pyriform with prominent papilla. The dimensions vary widely as well as the length/diameter ratio. They contain 20–30 nuclei. Secondary conidia are like the primary but more variable in shape and sometimes spherical. Resting spores spherical with an average diameter of  $19 \mu\text{m}$ , smooth and hyaline. Diseased insects contain short hyphal sections which are more or less branched. Dead aphids are brown-red before the fungus grows out and turn to yellow-brown as the conidiophores appear. These are described as branched which is in contrast to the genus description and therefore doubtful. Cystidia and rhizoids are absent, infected aphids fixed with proboscis.

Humber (1992) treated the species as a synonym of *C. thromboides* while Bałazy (1993) placed it in the genus *Entomophaga* which is justified by the number of nuclei.

Distribution. – The species is known from France and Russia from a single aphid species (Tab. 1).

**4. *Entomophthora*** Fresenius, Bot. Zeitung 14: 882. 1856 (Entomophthoraceae).

Vegetative cells either protoplasts or hyphal bodies. – Hyphal bodies usually regular, spherical to subspherical, elliptical or subrectangular, sometimes irregularly rounded, germinating with a single germ tube. Nuclei stain distinctly in lactophenol-aceto-orcein (LPAO), diameter on average  $2.5 - 6 \mu\text{m}$ . – 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).

**4.1. *Entomophthora chromaphidis*** Burger & Swain, J. Econ. Ent. 11: 278 – 288. 1918.

Type host. – *Chromaphidis juglandicola* (Kalt.)

Primary conidia  $11 - 14 \times 10 - 11 \mu\text{m}$ , contain a single large oil globule. – Resting spores are azygospores, brown, with a diameter of  $30 \mu\text{m}$ . – Host fixed with rhizoids.

Humber & Feng (1991) identified the species from *Schizaphis graminum*, *Metopolophium dirhodum* and *Sitobion avenae* from Idaho and Washington. The conidia measured  $12 - 16 \times 10 - 14 \mu\text{m}$  and contained 4 – 6 nuclei. The rhizoids are described as pseudo-rhizomorphs as for *E. planchoniana*. The same authors attributed a fungus mentioned as *E. planchoniana* by Holdom (1983) from Queensland, Australia, to *E. chromaphidis*.

This species was originally found as a pathogen of the walnut aphid *Chromaphidis juglandicola* (Kalt.) (Homoptera, Aphididae) in California. Another host species mentioned by Burger & Swain (1918), *Psocus* sp. (Psocidae) must be considered as doubtful. *E. chromaphidis* is very closely related to *E. planchoniana*. The latter varies widely in conidial sizes and nuclear numbers (Keller 2002). Nevertheless there is only an overlap with the nuclear number but not with the morphological data and the nuclear dimensions given by Humber & Feng (1991) for *E. chromaphidis*. These authors also report that they could isolate the small-spored fungus from USA but not the large-spored one from Europe. On the other hand, genetic analysis could not separate *E. planchoniana* from material provided by Humber & Feng (Jensen & Eilenberg 2000). Based on these data *E. chromaphidis* must be considered to be a valid species.

Distribution. – The species is known only from a few sites in USA and Australia from a few aphid species (Tab. 1).

**4.2. *Entomophthora planchoniana*** Cornu, Bull. Soc. Bot. France 20: 189. 1873.

Type host. – *Aphis sambuci* L.

Vegetative growth by tubular or elongate ellipsoid protoplasts with a diameter of  $(10) 14.6 (21) \mu\text{m}$  (1 series) and a variable length of  $36 - 78 \mu\text{m}$ . They multiply by binary division and normally contain 4 – 11 nuclei but nuclear numbers up to 18 were observed. – Hyphal bodies rather regular, ellipsoidal to short rod-shaped,

29–32 × 15–18 µm with (3) 5–8 (12) nuclei (3 series). – Conidiophores unbranched with 4–8 nuclei, terminal enlargement measuring 15–17 µm. – Primary conidia 15–20 × 12–16 µm with (4) 6–8 (11) nuclei (20 series), distinct apical point. – Secondary conidia 13–16 × 10–12 µm on short lateral conidiophore. – Resting spores spherical, 31–38 µm with (15) 18.6 (25) nuclei (1 series), episprium uneven, dark brown. – Cystidia absent. – Rhizoids monohyphal but joined in bundles, contain cytoplasm and resemble conidiophores, without specialised holdfast. – The species is known to overwinter in the form of specialised hyphal bodies which are rod-shaped to club-shaped and measure (29) 47–49 (68) × (12) 16–17 (21) µm (2 series) (Keller 1987).

The species shows some variation especially concerning the number of nuclei per conidium while the dimensions of the conidia lie within the range of 16–19.5 × 12–16 µm. The size of the conidia is a good criterion for separating it from the other aphid pathogenic species of this genus, *E. chromaphidis*. There is some confusion concerning the rhizoids. They have been described as pseudorhizomorphs or pseudorhizomorph-like structures as in the genus *Zoophthora* (Ben-Ze'ev & Uziel 1979, Ben-Ze'ev & Kenneth 1982). However, there are fundamental differences between the two types: In *Zoophthora* they are specialised structures and the individual hyphae that form the rhizoids are connected to a single structure with a common, specialised holdfast. At maturity cytoplasm is not visible. In contrast, *E. planchoniana* has rhizoids with a shape and dimension resembling those of conidiophores. They are filled with cytoplasm and do not form specialised holdfasts. Like the conidiophores they emerge in bundles and there are good reasons to consider them as modified conidiophores. There is no other species in this genus with similar rhizoids except *E. chromaphidis*.

Distribution. – Worldwide. The species has a wide host range, causes often epizootics and belongs the most important aphid pathogenic Entomophthorales (Barta 2004, Remaudière *et al.* 1981) (Tab. 1).

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

Hyphal bodies spherical, subspherical or irregularly rounded, oligo- to multinucleate, germinating with a single germ tube. Conidiophores branched. Primary conidia elongate pyriform, ovoid, ellipsoid, fusiform, often curved; papilla rounded. Two types of secondary conidia, type Ia resembling the primary conidia, 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 tetradiate 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).

**5.1. *Erynia erinacea*** (Ben-Ze'ev & Kenneth) Remaudière & Hennebert, Mycotaxon 11: 302. 1980.

Basionym. – *Zoophthora erinacea* Ben-Ze'ev & Kenneth, Mycotaxon 10: 219 – 232. 1979.

Type host. – *Aphis craccivora* Koch.

The following description follows the original description. – Conidiophores digitate, 4.7 – 7.2  $\mu\text{m}$  diameter. Primary conidia 2.6 – 20.5  $\times$  7.1 – 13.4  $\mu\text{m}$ , symmetrical or slightly curved towards the base, turbinate to obovoid, broadly rounded apex, tapering uniformly toward a narrow base, small papilla, slightly prominent collar. – Secondary conidia like primary, 10.3  $\times$  6.3  $\mu\text{m}$ . – Resting spores mostly zygospores, spherical with a diameter of 27.7 – 37.1  $\mu\text{m}$ , wall 4 – 7.1  $\mu\text{m}$  thick with regularly echinulate, yellowish epispore. – Cystidia abundant, long and thick, 150 – 225 (– 500)  $\times$  16 – 40  $\mu\text{m}$ , occasionally bifurcated. – True rhizoids absent. Attached to substratum by proboscis.

Distribution. – The species is known only from Israel (Ben-Ze'ev 1993) from a few aphid species (Tab. 1).

**6. *Neozygites*** Witlaczil, Arch. F. Mikr. Anat. 24: 599 – 603. 1885. (Neozygitaceae).

Vegetative growth as globose or rod-shaped hyphal bodies, cell wall present or absent. Nuclei with an average diameter of 2.5 – 4  $\mu\text{m}$ , 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 each contain 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, episporium 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. tanaioae* when resting spores are present), cystidia absent. – Obligate pathogens of small insects and mites.

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

Key to aphid pathogenic species of *Neozygites*

- 1 Zygosporos subspherical,  $30.3 \times 28.8 \mu\text{m}$  with episporium, regularly postulated. Conidia unknown. . . . . *slavi* (6.6.)
- 1\* Zygosporos ellipsoidal, smooth. Conidia known. . . . . 2
- 2 Pathogen of Aphidinae on grass and herbs, rarely on bushes. Conidiophores and primary conidia with 3 – 5 nuclei. . . . . 3
- 2\* Pathogen of Lachninae and Callaphidinae on trees and bushes. Conidiophores and primary conidia with 4 – 10 nuclei. . . . . 4
- 3 Primary conidia  $18.2 - 21.5 \times 14.5 - 17.8 \mu\text{m}$ ,  $Q = 1.16 - 1.46$ , with usually 4 nuclei; capilliconidia  $19.7 - 27.2 \times 11.2 - 13.7 \mu\text{m}$ ,  $Q = 1.55 - 2.43$ . Capillary tube  $24 - 35 \mu\text{m}$  long. Resting spores  $29.7 - 41.1 \times 18.2 - 23.2 \mu\text{m}$ ,  $Q = 1.45 - 2.10$ . . . . . *fresenii* (6.2.)
- 3\* Primary conidia  $24.1 - 25.5 \times 17.6 - 18.8 \mu\text{m}$ ,  $Q = 1.33 - 1.38$ , with usually 5 nuclei; capilliconidia,  $30.1 - 33.6 \times 12.2 - 14.4 \mu\text{m}$ ,  $Q = 2.28 - 2.60$ . Capillary tube  $156 - 168 \mu\text{m}$  long. Zygosporos  $35.6 - 42.8 \times 20.2 - 23.3 \mu\text{m}$ ,  $Q = 1.68 - 1.99$ . . . . . *microlophii* (6.4.)
- 4 Primary conidia  $35 \times 20 \mu\text{m}$ , on aphids on *Betula* and *Corylis*. . . . . *lageniformis* (6.3.)
- 4\* Primary conidia smaller. . . . . 5
- 5 Conidiophores and primary conidia with 4 – 5 nuclei. Primary conidia  $24 - 31 \times 18.5 - 21 \mu\text{m}$ ,  $Q = 1.27 - 1.50$ . Capilliconidia  $32 - 34.5 \times 13.5 - 17 \mu\text{m}$ ; capillary tube of  $68 - 108 \mu\text{m}$  long. Resting spores  $34 - 36 \times 23 - 24 \mu\text{m}$ ,  $Q = 1.45 - 1.51$ . . . . . *cinarae* (6.1.)
- 5\* Conidiophores and primary conidia with more than 4 nuclei. . . 6
- 6 Primary conidia  $22.7 - 23.3 \times 19.7 - 20.4 \mu\text{m}$ ,  $Q = 1.14 - 1.15$ , conidia body nearly spherical, papilla flat. Capilliconidia,  $27.9 - 30.6 \times 13.8 - 15.3 \mu\text{m}$ ,  $Q = 2.00 - 2.07$ . Capillary tubes  $190 - 200 \mu\text{m}$  long. Conidiophores with 8 – 11 nuclei. . . . . *remaudierei* (6.5.)
- 6\* Primary conidia  $21.1 - 22.3 \times 16.1 - 17.1 \mu\text{m}$ ,  $Q = 1.29 - 1.35$ , pyriform to ovoid, tapering towards papilla, smoky except papilla, papilla narrow, rounded. Zygosporos  $32.0 - 34.6 \times 20.7 - 22.4 \mu\text{m}$ ,  $Q = 1.51 - 1.61$ . Capilliconidia absent. Conidiophores with 4 – 11 nuclei. . . . . *turbinata* (6.7.)

**6.1. *Neozygites cinarae*** Keller, Sydowia 49: 137 – 138. 1997.

Type host. – *Cinara pilicornis* (Hartig).

Hyphal bodies spherical, 20.5 – 22 (18 – 25)  $\mu\text{m}$ , or slightly subspherical with usually 4, sometimes 5 nuclei. – Primary conidia 24 – 31  $\times$  18.5 – 21  $\mu\text{m}$ ,  $Q = 1.27 - 1.50$ , ovoid to pyriform, papilla distinct, truncate or slightly rounded. – Capilliconidia 32 – 34.5  $\times$  13.5 – 17  $\mu\text{m}$ , short, almond-shaped, brownish, produced on slender capillary with an average length of 68 – 108  $\mu\text{m}$ . – Resting spores 34 – 36  $\times$  23 – 24  $\mu\text{m}$ ,  $Q = 1.45 - 1.51$ , ellipsoid, black, produced by fusion of two hyphal bodies, smooth surface. – Cystidia and secondary conidia of type I not observed.

Distribution. – The species is known from central Europe as a pathogen of *C. pilicornis* (Tab. 1).

Remarks. – Smirnoff & MacLeod (1973) described an epizootic in *Cinara curvipes* Patch on *Abies balsamea* L. in Canada caused by a species of Entomophthorales, but without giving morphological or cytological details. However, the illustrations clearly demonstrate that the fungus is a species of *Neozygites* closely related to *N. cinarae*. The number of nuclei in the conjugating hyphal bodies are indistinctly illustrated but estimated to be around eight which excludes an identity with *N. cinarae*.

**6.2. *Neozygites fresenii*** (Nowakowski) Remaudière & Keller, Mycotaxon 11: 332. 1980.

Basionym. – *Empusa fresenii* Nowakowski, Pam. Akad. Umiej. Krakow 8: 171 – 172. 1883.

Type host. – *Brevicoryne brassicae* L.

Protoplasts elongate, often comma-shaped, 4-nucleate, multiplication by binary fission. – Hyphal bodies spherical, 4-nucleate when forming conidia, 8-nucleate when conjugating to form zygospores. Sporogenous hyphal bodies 15.1 – 15.5  $\times$  14.1 – 14.8  $\mu\text{m}$ , spherical to slightly subspherical. Conidiophores terminally swollen. – Primary conidia 18.2 – 21.5  $\times$  14.5 – 17.8  $\mu\text{m}$ ,  $Q = 1.16 - 1.46$ , conidial body spherical to ovoid, papilla distinct, cylindrical, blunt or slightly rounded. – Secondary conidia like primary or capilliconidia, 19.7 – 27.2  $\times$  11.2 – 13.7  $\mu\text{m}$ ,  $Q = 1.55 - 2.43$ , almond-shaped. Capillary conidiophore with an average length of 24 – 35  $\mu\text{m}$ . – Resting spores 29.7 – 41.1  $\times$  18.2 – 23.2  $\mu\text{m}$ ,  $Q = 1.45 - 2.10$ , ellipsoid, dark brown to black with binucleate, germinate with slender capillary 135 – 188  $\mu\text{m}$  (73 – 220  $\mu\text{m}$ ) long. – Germ conidium 22.6  $\times$  11.9  $\mu\text{m}$ , almond-shaped.



Distribution. – The species is common world-wide including arctic and tropical regions (Keller 1997, Nielsen *et al.* 2001). It is a pathogen of many aphid species and an effective control agent of agriculturally important aphids (e.g. Barta 2004, Mejia *et al.* 2000, Steinkraus *et al.* 1991) (Tab. 1).

**6.3. *Neozygites lageniformis*** (Thaxter) Remaudière & Keller, Mycotaxon 11: 322. 1980

Basionym. – *Empusa* (*Triplosporium*) *lageniformis* Thaxter, Mem. Boston. Soc. Nat. Hist. 4: 169. 1888.

Type host. – Aphids on *Betula populifolia*.

Primary conidia on average  $35 \times 20 \mu\text{m}$ , maximum  $38 \times 30 \mu\text{m}$ , slightly smoky, flask-shaped, with truncate, hardly papillate base, apex rounded. – Secondary conidia like primary ones or almond-shaped and borne obliquely on capillary conidiophores. – Resting spores unknown.

Aruta and Carillo (1989) reported the species from Chile as a pathogen of *Myzocallis coryli*. According to them the primary conidia and the capillicondia measure (26)  $30.3$  (35)  $\times$  (17)  $19.4$  (24)  $\mu\text{m}$  and  $29 - 35 \times 16.5 - 18 \mu\text{m}$ , respectively.

Distribution. – USA and Chile from Callaphiniae (Tab. 1).

**6.4. *Neozygites microlophii*** Keller, Sydowia 43: 82 – 85. 1991.

Type host. – *Microlophium carnosum* Buckton.

Conidiogenous hyphal bodies spherical to subspherical,  $20.8 - 22.2 \times 19.9 - 21.4 \mu\text{m}$  with 4 or usually 5 nuclei, sporogenous hyphal bodies spherical,  $17.1 \times 17.5 \mu\text{m}$  with 10 (4 – 14) nuclei. – Primary conidia  $24.1 - 25.5 \times 17.6 - 18.8 \mu\text{m}$ ,  $Q = 1.33 - 1.38$ , with 4 or usually 5 nuclei, subspherical to pyriform. – Secondary conidia like primary,  $23.8 - 24.4 \times 15.3 - 15.5 \mu\text{m}$ , or almond-shaped capillicondia,  $30.1 - 33.6 \times 12.2 - 14.4 \mu\text{m}$ ,  $Q = 2.28 - 2.60$ . Capillary tube with an average length of  $156 - 168 \mu\text{m}$ . – Zygospores  $35.6 - 42.8 \times 20.2 - 23.3 \mu\text{m}$ ,  $Q = 1.68 - 1.99$ , ellipsoidal, dark brown to black. Resting spores germinate with capillary germ tube with an average length of  $315 \mu\text{m}$ . – Germ conidia  $29.4 \times 12.2 \mu\text{m}$ , almond shaped, similar to capillicondia produced by primary conidia.

Distribution. – This species is known from Switzerland and Poland as a pathogen of the nettle aphid *Microlophium carnosum* Buckton.

### 6.5. *Neozygites remaudierei* S. Keller sp. nov., Figs. 2 – 5

Latin diagnosis: Corpora hyphalia 17 – 23 × 16 – 23 µm, sphaerica. Conidiophora simplicia, 9 – 11 nucleos continentia. Conidia primaria (21) 23 (25) × (17) 20 (23) µm, subphaerica. Capilliconidia amygdaliformia (24) 28 – 31 (36) × (12) 14 – 15 (18) µm, hyphae capillares evolutae 116 – 295 µm longae. Rhizoidea et cystidia absunt.

In *Myzocalle coryli* (Goetze) (hospite typico) (Homoptera, Aphididae).

Holotypus. – HELVETIA: Belp (BE), coll. et leg. S. Keller, 26 May 1997 (ZT no. 89 – 4).

Hyphal bodies spherical to slightly subspherical, (17) 20 (23) × (16) 19.1 (23) µm,  $Q = 1.05$  (1 series), germinating with a single germ tube. – Conidiophores unbranched with (8) 9.3 (11) nuclei. Young conidiophores may stop their growth below the host cuticle; such stunted conidiophores are club-shaped or cylindrical, often connected with the hyphal body, and measure (37) 44.9 (58) × (12) 15.4 (18) µm (1 series) (Fig. 2). – Primary conidia (21) 22.7 – 23.3 (25) × (17) 19.7 – 20.4 (23) µm,  $Q = 1.14 – 1.15$  (2 series), body of the conidia nearly spherical, papilla flat (Figs. 3 – 4). – Secondary conidia similar to the primary, produced on short thick conidiophore or capilliconidia, (24) 27.9 – 30.6 (36) × (12) 13.8 – 15.3 (18) µm,  $Q = 2.00 – 2.07$  (3 series), almond-shaped, tapering towards the apex, brownish (Figs. 4 – 5). Capillary tubes (116) 192 – 197 (295) µm (3 series) with characteristic bend near the end. – Rhizoids and cystidia absent, resting spores not observed. – Diseased aphids attached to substrate by proboscis and remain in colonies on the underside of leaves of *Corylus avellana*.

Etymology. – In honour of Georges Remaudière who is not only a founder of the modern classification of the arthropod-pathogenic Entomophthorales but also an expert in aphid taxonomy and systematics and first author of the latest catalogue of the world's Aphididae.

Host. – Homoptera, Aphididae: *Myzocallis coryli* (Goetze) (type host).

Distribution and habitat. – Switzerland: Belp (BE) (type locality). The species was collected at the end of May 1997 along the shore of the river Aare on leaves of *Corylus avellana* above the water. The host colonies were loose, and only single individuals were infected.

Distinguishing characters. – *N. remaudierei* closely resembles *N. fresenii* in shape and dimensions. It can, however, be separated unequivocally by the number of nuclei and the much longer capillary tubes. Secondary conidia were almost exclusively produced as capilliconidia, secondary conidia of type Ia were very rare.

**6.6. *Neozygites slavi* S. Keller, sp. nov., Figs. 6 – 8**

Latin diagnosis: Sporae perdurantes zygosporae sphaericae ad subsphaericae, (28) 30.3 (35) × (25) 28.8 μm (33 μm) episporio incluso et (25) 28.7 (31) × (24) 26.7 (29) μm episporio excluso. Episporium pustulatum 2 – 3 × 2 μm, brunneum. Structurae aliae non visae.

In sexuparis *Slavi esfandiarii* Davatchi & Remaudière (hospitis typici) (Homopterorum: Aphididarum).

Holotypus. – IRAN: Ghazoin, coll. G. Remaudière 22 May 1955, det. S. Keller (ZT no. 89-50).

Zygosporae spherical to subspherical, (28) 30.3 (35) × (25) 28.8 (33) μm with and (25) 28.7 (31) × (24) 26.7 (29) μm without episporium. Episporium brown with regularly arranged knobs with a diameter of 2 – 3 μm and a length of about 2 μm. Other structures unknown.

Etymology. – Refers to the genus of the host.

Host and distribution. – Sexuparae of *Slavum esfandiarii* Davatchi & Remaudière (Pemphiginae, Fordini) (type host) collected from *Pistazia vera* on 22 May 1955 at Ghazoin, Iran.

Distinguishing characters. – *N. slavi* is the only aphid pathogenic species of *Neozygites* with spherical resting spores.

The species was recently discovered in the aphid collection of the Musée d'Histoire Naturelle in Paris (Remaudière, unpubl.) in a sexupara of *Slavum esfandiarii* Davatchi & Remaudière. The structures that resisted the preparation process show clearly the zygosporae (Figs. 6 – 7) and the remains of the zygosporae formation (Fig. 8) which is an unequivocal characteristic of this genus. The resting spores resemble those of *N. parvispora*, but are much bigger. The fungus was detected in only one specimen.

**6.7. *Neozygites turbinata* (Kenneth) Remaudière & Keller, Mycotaxon 11: 322. 1980**

Basionym. – *Entomophthora turbinata* Kenneth, Mycotaxon 6: 381 – 390. 1977.

Type host. – *Pterochloroides persicae* Cholodkovski

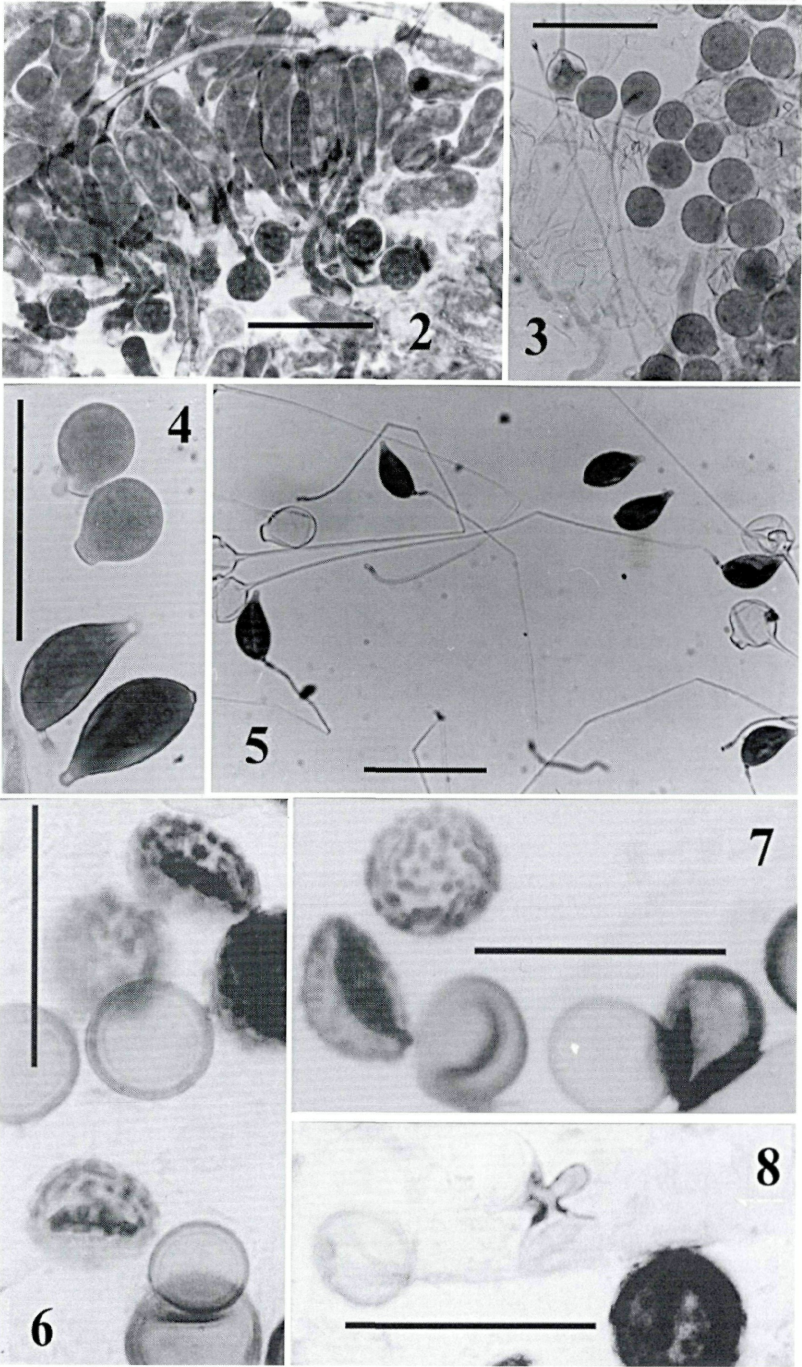
Conidiogenous hyphal bodies spherical to slightly ellipsoidal or ovoidal with an average dimensions of 21.1 × 17.4 μm and (4) 8 (11) nuclei. – Hyphal bodies producing resting spores are

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**Figs. 2 – 5. *Neozygites remaudierei*.** 2. Spherical hyphal bodies and young conidiophores stunt below the host cuticle. 3. Formation of primary conidia (left, with empty conidiophores) and primary conidia. 4. Primary conidia (up) and detached capilliconidia (below). 5. Capilliconidia and shells of primary conidia.

**Figs. 6 – 8: *Neozygites slavi*.** 6 – 7. Zygosporae with and without dark, ornamented episporium. 8. Remains of zygosporae formation. Bars represent 50 μm.





spherical with an average diameter of 17.4–17.8 µm and contain (6) 9–10 (16) nuclei. – Primary conidia 17.7–25.7 × 11.2–17.1 µm, pyriform, turbinate to obovoid, tapering uniformly toward a narrow base, smoky except papilla, papilla very small, rounded; conidia germinate through papilla. – Zygosporangia 32.0–34.6 × 20.7–22.4 µm, Q = 1.51–1.61, ellipsoidal, brown to black, smooth. – Germ conidia 31.7 × 9.4 µm, almond- to banana-shaped, produced on capillary tube with a length of (36) 52 (75) µm.

Distribution. – The species is reported from Israel from *Pterochloroides persicae* and from Switzerland from *Tuberolachnus salignus* (Tab. 1). The dimensions for the primary conidia originating from the two host species slightly differ. According to Kenneth (1977) they measure 17.7–25.7 × 11.2–16 µm, according to Keller (1991) 21.1–22.3 × 16.1–17.1 µm with a Q-ratio of 1.29–1.35. The dimensions of the resting spores overlap. They measure 31.6–44.2 × 15.8–25.3 µm (Kenneth, 1977) and 32.0–34.6 × 20.7–22.4 µm (averages), Q = 1.51–1.61 (Keller 1991).

**7. *Pandora*** Humber, Mycotaxon 34: 451. 1989 (Entomophthoraceae).

Hyphal bodies as short hyphae, 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 conidia, 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, epispore 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 holdfast discoid or irregularly branched. – Obligate pathogens of insects and Phalangicidae (Arachnida).

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

Key to aphid pathogenic species of *Pandora*.

- 1 Primary conidia 22 µm or longer. . . . . 2
- 1\* Primary conidia shorter. . . . . 3
- 2 Rhizoids present. . . . . *neoaphidis* (6.2.)
- 2\* Rhizoids absent. . . . . *uroleuconii* (6.5.)
- 3 Primary conidia 15.0–16.6 × 8.0–10.5 µm, resting spores hyaline and spherical, average diameter 24.9–30.4 µm. . . . *nouryi* (6.3.)
- 3\* Primary conidia on average longer than 17 µm. . . . . 4

- 4 Primary conidia  $16 - 24 \times 10 - 12 \mu\text{m}$ , resting spores absent. . . . .  
..... *kondoiensis* (6.1.)  
4\* Primary conidia  $18.9 \times 9.7 \mu\text{m}$ , resting spores  $31 \mu\text{m}$ . . . . .  
..... *terrestris* (6.4.)

**7.1. *Pandora kondoiensis*** (Milner in Milner, Mahon & Brown) Humber, Mycotaxon 34. 453, 1989.

Basionym. – *Erynia kondoiensis* Milner in Milner, Mahon & Brown, Austral. J. Bot. 31: 183. 1983.

Type host. – *Acyrtosiphon kondoi* Shinji.

Hyphal bodies hyphae-like, up to  $200 \mu\text{m}$  long, rarely branched. – Conidiophores digitate. – Primary conidia on average  $16 - 21 \times 10 - 12 \mu\text{m}$  when deriving from aphids and  $17 - 23 \times 11 - 14 \mu\text{m}$  from culture. – Secondary conidia like primary. – Resting spores unknown. – Cystidia present; rhizoids monohyphal, 10 – 20 in number, ending with sucker-like holdfast. Grows and sporulates well on artificial media.

Distribution. – The species is known only from Australia attacking *Acyrtosiphon kondoi* and from China attacking *Myzus persicae* (Fan *et al.* 1991) (Tab. 1). Experimentally, other aphid species can be infected. The species is very closely related to *P. neoaphidis*, from which it can be separated by the slightly smaller primary conidia, the lack of rosettes, and the longer and more branched hyphal bodies.

**7.2. *Pandora neoaphidis*** (Remaudière & Hennebert) Humber, Mycotaxon 34: 452. 1989.

Basionym. – *Erynia neoaphidis* Remaudière & Hennebert, Mycotaxon 11 : 307. 1980.

Type host. – *Nasonovia ribisnigri* Mosley.

Protoplasts and hyphal bodies filamentous, hyphae-like. – Hyphal bodies very variable  $32 - 260 \times 6 - 13 \mu\text{m}$ , branched or unbranched with (1) 5 – 6 (12) nuclei. Nuclei with a diameter of  $6 - 8 \mu\text{m}$ . Some hyphal bodies with much more nuclei probably develop to cystidia or rhizoids. – Conidiophores branched with  $6 - 10 \mu\text{m}$  diameter, terminally enlarged to a diameter of  $10 - 13 \mu\text{m}$ . – Primary conidia ovoid to ellipsoid with an average size of  $21 - 32 \times 11 - 14 \mu\text{m}$  ( $Q = 1.7 - 2.3$ ) when deriving from insects and  $21 - 37 \times 11 - 17 \mu\text{m}$  ( $Q = 1.6 - 2.6$ ) from cultures. – Two types of secondary conidia, one resembles the primary one, although smaller, the other subspherical,  $19 \times 16 \mu\text{m}$ ,  $Q = 1.2$ , sometimes with



pointed apex. – Cystidia develop from spherical mother cell with a diameter of 30–40 µm, basal diameter 12–16 µm, apical diameter 7–9 µm and a length of 120–240 µm, they contain 10–15 nuclei. – Rhizoids monohyphal, 15–30 in number, diameter 10–31 µm, on average 19 µm, ending with irregularly disk-like holdfast. – Resting spores unknown. Grows and sporulates on artificial media.

Distribution. – The species is known from all continents. It has the widest host range and attacks many aphid species belonging to different subfamilies (Tab. 1). In Central Europe it is the most important aphid pathogenic species of Entomophthorales often causing epizootics also among agriculturally important species (Barta 2004, Dedryver 1981, Keller & Suter 1980, Remaudière *et al.* 1981).

Remarks. – In the older literature the species is mentioned as *Entomophthora aphidis*. The use of this epithet erected by Hoffmann (in Fresenius 1858) for a fungus found on *Anoecia corni*, goes back to Nowakowski (1883) and Thaxter (1883) who misapplied the name for *P. neoaphidis* until Remaudière & Hennebert (1980) demonstrated that *E. aphidis* was, indeed, a species belonging to the genus *Zoophthora* and consequently described *P. neoaphidis* as a new species.

The structures of *P. neoaphidis* show some variability, especially the dimensions of the conidia. Further, the species can be isolated from most aphid species, while from a few other aphid species (*Brevicoryne brassicae*, *Impatiens asiaticum*) isolations on the same media failed (Keller 1991).

**7.3. *Pandora nouryi*** (Remaudière & Hennebert) Humber, Mycotaxon 34: 453. 1989.

Basionym. – *Erynia nouryi* Remaudière & Hennebert, Mycotaxon 11: 313. 1980.

Synonym. – *Entomophthora exitialis* sensu Gustafsson (1965).

Type host. – *Pemphigus bursarius* L. from roots of *Cichorium intybus*.

Hyphal bodies very variable 90–180 × 6–10 µm, branched or unbranched. Nuclei with a diameter of 4–6 µm. – Conidiophores branched, pillow-like appearance. – Primary conidia ovoid, 15.0–16.6 × 8.0–10.5 µm when deriving from insects and 18 × 11 µm from culture, papilla large, rounded to slightly flattened, joins smoothly conidial body. – Resting spores hyaline and spherical, average diameter 24.9–30.4 µm, with smooth and thick (4–6 µm) wall. – Cystidia rare, 70–140 × 8–11 µm, cylindrical. – Rhizoids monohyphal, present when conidia are formed, normally absent, when resting spores are formed.

Distribution. – The species is known from Europe and Israel from a few aphid species.

#### **7.4. *Pandora terrestris*** (Gres & Koval) Keller & Petrini (2005).

Basionym. – *Entomophthora terrestris* Gres & Koval, Microbiol. Journal (Kiev) 44: 64 – 69. 1982.

Type host. – *Pemphigus fuscicornis* (Koch) on sugar beet roots

Primary conidia  $18.9 \times 9.7 \mu\text{m}$ , ovoid, papilla distinct. Another type of primary conidia is formed from aphids dying on the soil surface or on beet root. They measure  $13.3 \times 8.3 \mu\text{m}$ . – Resting spores spherical with an average diameter of  $31 \mu\text{m}$ .

Distribution. – This species is known only from the environment of Kiev, Ukraine (type locality).

Remarks. – The identity of this species is uncertain. It resembles *P. nouryi* which was originally found on a congeneric host species, and the resting spores have similar dimensions. The presence of two types of primary conidia is confusing; however, their dimensions differ from *P. nouryi*. Nevertheless, the species should be studied in more detail to clarify the identity.

#### **7.5. *Pandora uroleuconii*** Barta & Cagan, Mycotaxon 11: 79 – 80. 2003.

Type host. – *Uroleucon (Uromelan) aeneum* Hille Ris Lambers.

Hyphal bodies hyphae-like, simple to ramified or irregular, oligokaryotic. – Conidiophores branched. – Primary conidia  $24.7 - 33 \times 11.6 - 17.2 \mu\text{m}$ ,  $Q = 1.79 - 2.25$ , ellipsoid, broadly ellipsoid to ovoid. Papilla rounded, centred on spore axis or slightly lateral. – Secondary conidia like primary,  $18.1 - 19.2 \times 9.3 - 9.6 \mu\text{m}$  or broadly ovoid,  $17.3 - 18.5 \times 9.6 - 10.2 \mu\text{m}$ . – Cystidia simple, tapering towards obtuse apex,  $12 - 20 \mu\text{m}$  diameter at the base and  $5 - 6 \mu\text{m}$  at the apex. – Rhizoids and resting spores absent. – Cadavers fixed to substrate by proboscis. No growth on standard media based on egg yolk.

Distribution. – The species is known only from Slovakia from the type host.

Remarks. – The species closely resembles *P. neoaphidis*. Its conidia are slightly larger but the most striking difference is the absence of rhizoids in *P. uroleuconii*, which is unusual in this genus. The lack of growth in standard media containing egg yolk cannot be taken as a criterion to separate the species from *P. neoaphidis* because although from most aphid species *P. neoaphidis* can be isolated and grown on such media, there are also a few aphid species from which *P. neoaphidis* cannot be isolated on these media (Keller 1991).

8. *Tarichium* Cohn, Beitr. Biol. Pflanz. 1: 58 – 86. 1870.

Resting spores, zygospores or azygospores; spherical, sub-spherical, ovoid, ellipsoid or irregularly rounded; thick-walled. Episorium hyaline or coloured, smooth, rough, echinulate or otherwise ornamented. Rhizoids present or absent. Pathogens of arthropods.

Type species. – *Tarichium megaspermum* Cohn (1870)

8.1. *Tarichium atospermum* (Petch) Bałazy, Flora of Poland, Fungi (Mycota) vol. 24: 256, 1993.

Basionym. – *Entomophthora atosperma* Petch, Trans. Brit. Mycol. Soc. 17: 172. 1932

Type host. – Unidentified Aphididae

Resting spores dark brown-black, globose, 38 – 45 µm, epispore covered with conical spines about 2 µm long. Host attached to substrate by a few hyaline hyphae. The species is known only from the type locality (Grassington, England).

9. *Zoophthora* Batko. Bull. Acad. Pol. Sci., Ser. Sci. Biol. 12: 323 – 324. 1964c.

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; 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, episorium 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 (1964c).

Key to aphid pathogenic species of *Zoophthora*

- 1 Resting spores black, spherical with a diameter of 34 – 47 µm. Primary conidia 25 – 32 × 9 – 13 µm, capilliconidia 20 – 27 × 8 – 12 µm. . . . . *aphidis* (9.2.)
- 1\* Resting spores hyaline or absent . . . . . 2
- 2 Primary conidia 25 µm long or shorter; Q below 3.2, capillary tube shorter than 45 µm . . . . . 3



- 2\* Primary conidia longer than 25  $\mu\text{m}$ , Q above 3.2, capillary tube longer than 45  $\mu\text{m}$  ..... 5
- 3 Pathogen of Lachninae. Primary conidia 25  $\times$  10  $\mu\text{m}$ ; capilliconidia 20  $\times$  8.5  $\mu\text{m}$  ..... *canadensis* (9.3.)
- 3\* Pathogen of other subfamilies ..... 4
- 4 Primary conidia 18 – 21  $\times$  6 – 7  $\mu\text{m}$ , Q = 2.7 – 3.2. Capilliconidia 19 – 20.5  $\times$  4.5 – 5.5  $\mu\text{m}$ , Q = 4.5: Capillary tube 38 – 43  $\mu\text{m}$  long. Resting spores 24 – 27  $\mu\text{m}$ . ..... *radicans* (9.7.)
- 4\* Primary conidia 24.7  $\times$  8.3  $\mu\text{m}$ , Q = 3.0, or 22.7  $\times$  11.6, Q = 2.0. Resting spores 26.6.  $\mu\text{m}$ . ..... *anhuiensis* (9.1.)
- 5 Primary conidia 27.1  $\times$  8.4  $\mu\text{m}$ , Q = 3.2 – 3.3. Capilliconidia 24.5 – 29.2  $\times$  5.5 – 10.3  $\mu\text{m}$ . Capillary tube 50 – 60  $\mu\text{m}$  long ..... *orientalis* (9.5.)
- 5\* Primary conidia longer than 30  $\mu\text{m}$  ..... 6
- 6 Primary conidia 30 – 35  $\times$  7 – 10  $\mu\text{m}$ . Capilliconidia 17 – 25  $\times$  6 – 8  $\mu\text{m}$ . Capillary tube 55 – 85  $\mu\text{m}$  long ..... *occidentalis* (9.4.)
- 6\* Primary conidia 29 – 40  $\times$  7 – 13  $\mu\text{m}$ . Capilliconidia 17 – 25  $\times$  7 – 9  $\mu\text{m}$ . Capillary tube 80 – 120  $\mu\text{m}$  long ..... *phalloides* (9.6.)

**9.1. *Zoophthora anhuiensis* (Li) Humber, Mycotaxon 34: 453. 1989.**

Basionym. – *Erynia anhuiensis* Li, Acta Mycologica Sinica 5: 1 – 6. 1986.

Type host. – *Myzus persicae* (Sulzer)

Conidiophores bifurcately branched. – Primary conidia long ellipsoid to oval with an average dimension of 24.7  $\times$  8.3  $\mu\text{m}$ , Q = 3.0, or obovoid, 22.7  $\times$  11.6  $\mu\text{m}$ , Q = 2.0. – Secondary conidia like the obovoid primary ones, capilliconidia not observed. – Cystidia as thick as conidiophores, basically widened to a diameter of 14 – 28  $\mu\text{m}$ . – Rhizoids with differentiated holdfasts. – Resting spores exogenic, globose, smooth, hyaline with an average diameter of 26.6.  $\mu\text{m}$ .

Distribution. – This species is known only from the type locality (Anhui province, Peoples Republic of China) where it caused an epizootic among *Myzus persicae*.

Remarks. – In agreement with Bałazy (1993) the attribution to the genus *Zoophthora* is not definite, since the presence of typical characters like capilliconidia and compound rhizoids are not mentioned.

**9.2. *Zoophthora aphidis* (Hoffmann in Fresenius) Remaudière & Hennebert, Mycotaxon 11: 304. 1980.**

Basionym. – *Entomophthora aphidis* Hoffmann in Fresenius, Abhandl. Senckenb. Naturf. Ges. 2: 208 – 209. 1858.

Type host. – *Anoecia corni* (F.)

Hyphal bodies hypha-like, branched,  $60 - 150 \times 6 - 10 \mu\text{m}$ , or irregularly rounded with 2–10 nuclei with an average diameter of  $4.6 - 5.5 \mu\text{m}$ . – Conidiophores branched, tending to segregate into mononucleate fragments. – Primary conidia on average  $25 - 32 \times 9 - 13 \mu\text{m}$ ,  $Q = 2.0 - 3.2$ , when deriving from aphids and  $32 - 38 \times 12 - 13 \mu\text{m}$  from culture, subcylindric to fusiform, apex rounded or conically tapering, papilla distinct, conical, rounded, sometimes pointed. – Secondary conidia like primary or capilliconidia with an average size of  $20 - 27 \times 8 - 12 \mu\text{m}$ ,  $Q = 1.9 - 3.2$ , asymmetrically fusoid to falciform, formed on long slender capillary tube with an average length of  $30 - 36 \mu\text{m}$ . – Resting spores spherical with an average diameter of  $34 - 47 \mu\text{m}$ , episporium dark brown to black with irregular indistinct ornamentation, separates easily from hyaline, smooth spore. Young resting spores contain on average 14–17 nuclei measuring  $6.3 - 7 \times 5 - 5.3 \mu\text{m}$ . – Cystidia absent when conidia are formed, but present when resting spores are formed. – Rhizoids monohyphal with a diameter of  $7 - 12 \mu\text{m}$ , sometimes arranged in parallel threads, endings unspecialised or enlarged, may be absent when resting spores are formed.

Resting spores germinate with up to three germ tubes. The individual germ tube is unbranched and measures  $145 - 350 \times 11 - 15 \mu\text{m}$ . The germ tubes are subdivided by cell walls. Individual cells produce laterally or terminally sessile germ conidia, resembling the primary conidia. Capillary germ conidia measure on average  $24.7 \times 11.6 \mu\text{m}$ . They are formed at the end of capillary conidiophores with an average length of  $67 \mu\text{m}$ , which develop from sessile germ conidia or directly from the germ tube (Keller 1991).

### 9.3. *Zoophthora canadensis* (MacLeod, Tyrrell & Soper) Remaudière & Hennebert, Mycotaxon 11: 301. 1980.

Basionym. – *Entomophthora canadensis* MacLeod *et al.*, Can. J. Bot. 57: 2663–2672. 1979.

Type host. – *Schizolachnus piniradiatae* (Davidson).

Hyphal bodies hyphae-like. – Conidiophores dichotomously or irregularly branched, segregating into uninucleate branchlets. – Primary conidia on average  $25.0 \times 10.0 \mu\text{m}$ , long-elliptical to nearly cylindrical, tapering slightly toward a rounded apex, papilla bluntly rounded, clearly defined from spore body. – Secondary conidia like primary or capilliconidia measuring on average  $20.0 \times 8.5 \mu\text{m}$ , fusiform-elliptical, formed on a capillary tube with a mean length of  $33 \mu\text{m}$ . – Resting spores described as azygospores, spherical with an average diameter of  $34 \mu\text{m}$ , episporium

verruculose to lightly rugulose, dark brown in mass, singly light reddish brown, produced from interlacing branching hyphae. – Cystida absent. – Infected aphids either attached by proboscis and/or clasping legs or by cylindrical, compound rhizoids with a digitally branched web-like holdfast.

**9.4. *Zoophthora occidentalis*** (Thaxter) Batko, Bull. Acad. Pol. Sci. Ser. Biol. 12: 404. 1964b.

Basionym. – *Entomophthora occidentalis* Thaxter, Mem. Boston. Soc. Nat. Hist. 4: 170 – 171. 1888.

Type host. – Aphids from *Betula populifolia*.

Conidiophores irregularly digitate. – Primary conidia on average  $35 \times 10 \mu\text{m}$ . – Secondary conidia like primary or long almond-shaped. – Resting spores spherical,  $20 - 35 \mu\text{m}$ , hyaline, smooth, borne laterally or terminally by budding from the hyphae. – Cystidia slender, slightly tapering. Host attached to substrate by numerous rhizoids.

According to Bałazy (1993) the conidiophores are  $5.5 - 7 \mu\text{m}$  thick, the conidiogenous cells are cylindric to clavate and measure  $27 - 40 \times 7.8 - 8.6 \mu\text{m}$ . The primary conidia measure  $30 - 35 \times 7 - 8.5 \mu\text{m}$ ,  $Q = 4.2$ , narrow spindle-shaped to almost cylindrical with conically convergent distal half, papillae conical or semiglobose. Capilliconidia  $17 - 25 \times 6 - 7.7 \mu\text{m}$ , thick almond-shaped, largest diameter in the basal half, or somewhat crescent-shaped. Capillary tubes  $55 - 85 \mu\text{m}$  long. Cystidia conical to cylindrical,  $7.5 - 15 \mu\text{m}$  thick at the base and  $5.5 - 6.5 \mu\text{m}$  at the apex, protruding to  $80 - 110 \mu\text{m}$  above the conidia layer. Resting spores spherical,  $24 - 30 \mu\text{m}$ , hyaline, smooth; walls  $3 - 3.5 \mu\text{m}$  thick.

Distribution. – The species is known from North and South America, Europe and Asia from several aphid species (Tab. 1).

Remarks. – There are several fungi with similar morphology and the attribution to *Z. occidentalis* is not always clear. Bałazy (1993) stated that the species shows some range of variability and that all material identified from aphids as “*Z. sphaerosperma*”, *Z. radicans*, *Z. occidentalis* and *Z. phalloides* should be revised. In a first step, however, the type material should be re-examined and the original description amended. This should also include the identification of the type host. See also remarks given under *Z. phalloides*.

**9.5. *Zoophthora orientalis*** Ben-Ze’ev & Kenneth, Phytoparasitica 9: 33 – 42. 1981.

Type host. – *Aphis citricola* v. d. Goot (syn.: *A. spiraeicola* Patch).



Conidiophores ramified, digitate, surrounding host's body in a continuous palisade. – Primary conidia on average  $27.1 \times 8.4 \mu\text{m}$ ,  $Q = 3.2 - 3.3$ , hyaline, narrow ellipsoid, mostly symmetrical. – Secondary conidia on average  $23.8 \times 9.1 \mu\text{m}$ ,  $Q = 2.6 - 2.7$ , similar to primary ones or capilliconidia,  $24.5 - 29.2 \times 5.5 - 10.3 \mu\text{m}$ , amygdaliform. – Capillary tube  $50.6 - 59.3 \mu\text{m}$  long. – Cystidia conical, tapering towards a bulbous apex. – Resting spores and rhizoids not observed.

Distribution. – The species is known only from Israel from the type host.

#### 9.6. *Zoophthora phalloides* Batko, Acta Mycol. 2: 7 – 23. 1966.

Type host. – *Microlophium evansi* Theob. (syn. *M. carnosum* Buckton).

Primary conidia  $40 \times 13$  ( $32 - 48 \times 11 - 14$ )  $\mu\text{m}$ , elongate cylindrical to elongate oval, sometimes curved with rounded tip, papilla broad, generally not narrower than conidium. – Secondary conidia similar to primary ones, or capilliconidia,  $18 \times 7 \mu\text{m}$  formed on capillary tubes with a length  $80 - 120 \mu\text{m}$ . – Cystidia rare, not thicker than conidiophores. – Rhizoids monohyphal or ramified, forming 2 – 4 pseudorhizomorphs.

Bařazy (1993) re-examined the type material. According to him the primary conidia measure on average  $28.5 - 29.5 \times 7.4 - 7.6 \mu\text{m}$  and differ distinctly from the data given by Batko. Unfortunately, Bařazy was unable to find other fungal structures in the type material.

According to Keller (1991 and unpubl.) the primary conidia from *M. carnosum* measured  $34.3 - 35.8 \times 9.3 - 10.2 \mu\text{m}$ ,  $Q = 3.44 - 3.80$ . From other aphid species (*A. pisum*, *R. padi*) the primary conidia measured on average  $33.1 - 38.2 \times 6.9 - 8.7 \mu\text{m}$  ( $Q = 4.0 - 5.5$ ), and the capilliconidia  $24.1 - 25.0 \times 7.7 - 8.9 \mu\text{m}$  ( $Q = 2.73 - 3.15$ ). Other data correspond with the original description, especially the length of the capillary tube, which measured on average  $98 - 108 \mu\text{m}$ .

Distribution. – This species is known from Europe and North America as a pathogen of several aphid species (Tab. 1).

Remarks. – There is some confusion about the identity of this species. Only a thorough redescription of the type material or material from type hosts collected at the type locality and a comparison with corresponding material from *Z. occidentalis* can clarify whether the two species are distinct or conspecific. Bařazy (1993) has drawn attention on the fact that the dimensions given in the original description do not agree with the dimensions given in the drawings. Another disagreement concerns the capilliconidia whose dimensions are not in relation to the primary conidia as they are within the other species of the genus.

**9.7. *Zoophthora radicans*** (Brefeld) Batko, Bull. Acad. Pol. Sci. Ser. Biol. 12: 324. 1964c.

Basionym: – *Empusa radicans* Brefeld, Bot. Zeitung 28: 186. 1870.

Type host. – *Pieris brassicae* (Lepidoptera) (Brefeld, 1870).

*Z. radicans* has a wide host range and attacks insects from different orders. Besides Lepidoptera the hosts of *Z. radicans* in the broad sense belong to the orders Plecoptera, Dermaptera, Heteroptera, Homoptera, Diptera, Trichoptera and Hymenoptera. The morphology is similar while the dimensions differ over a wider range. A differentiation on the basis of morphological data, therefore, is difficult. Nevertheless, some fungi from this group have been described as new species primarily characterized by the host (Bałazy 1993).

The following description is based on data obtained from different aphid species (Keller unpubl.). Hyphal bodies hyphae-like with (9) 14 (21) nuclei (1 series). – Conidiophores digitally branched. – Primary conidia 18.2 – 20.5 × 6.1 – 6.7 μm, Q = 2.7 – 3.2 (9 series), subcylindrical to subfusiform, straight or slightly bent, papilla usually rounded. – Secondary conidia like primary or capilliconidia, 18.9 – 20.4 × 4.4 – 5.6 μm, Q = 3.46 – 4.53 (6 series), elongate almond-shaped to banana-like, produced on a capillary tube with a length of (28) 38 – 43 (58) μm. – Resting spores spherical with a diameter of (21) 24.5 – 27.2 (33) μm (10 series), hyaline, smooth with (9) 15 – 19 (26) nuclei (3 series), produced laterally from hyphal bodies. – Rhizoids pseudorhizomorph and monohyphal with disc-like or finger-like ending.

Distribution. – Worldwide as a pathogen of many aphids species belonging to different subfamilies (Tab. 1).

**Tab. 1.** – Species of Entomophthorales attacking aphids (Aphididae). Mainly compiled from Balazy (1993), Barta (2004), Ben-Ze'ev (1993), Keller (1987, 1991, 2002 and unpublished data), ARSEF (2004), Hatting *et al.* (1999), Remaudière *et al.* (1981) and from the original descriptions. Aphid systematics follows Remaudière & Remaudière (1997).

Pathogen	Host	
	Subfamily	Species
<b><i>Conidiobolus</i></b>		
1. <i>C. coronatus</i>	Aphidinae	<i>Acyrtosiphon pisum</i> , <i>Aphis fabae</i> , <i>Brevicoryne brassicae</i> , <i>Metopolophium dirhodum</i> , <i>Rhopalosiphum maidis</i>
2. <i>C. obscurus</i>	Aphidinae	<i>Acyrtosiphon kondoi</i> , <i>A. loti</i> , <i>A. malvae</i> , <i>A. pisum</i> , <i>Amphorophora rubi</i> , <i>Aphis armata</i> , <i>A. fabae</i> , <i>Aulacorthum solani</i> , <i>Brachycaudus helichrysi</i> , <i>Brevicoryne brassicae</i> , <i>Cavariella aegopodii</i> , <i>Capitophorus horni</i> , <i>C. similis</i> , <i>Coloradoa achilleae</i> , <i>Cryptomyzus ballotae</i> , <i>Diuraphis noxia</i> , <i>Elatobium abietinum</i> , <i>Hyperomyzus lactucae</i> , <i>H. lamsanae</i> , <i>Impatiensinum asiaticum</i> , <i>Macrosiphum euphorbiae</i> , <i>M. prenanthis</i> , <i>Metopolophium dirhodum</i> , <i>Microlophium carnosum</i> , <i>Myzus ascalonicus</i> , <i>M. cerasi</i> , <i>M. ornatus</i> , <i>M. persicae</i> , <i>Nasonovia sp.</i> , <i>Rhopalosiphum maidis</i> , <i>R. padi</i> , <i>Sitobion avenae</i> , <i>S. fragariae</i> , <i>Tubaphis ranunculina</i> , <i>Uroleucon cirsii</i> , <i>U. tussilaginis</i>
	Myzocallidinae	<i>Therioaphis maculata</i>
3. <i>C. osmodes</i>		<i>Cavariella aegopodi</i> , <i>Hyperomyces picridis</i> , <i>Myzus ascalonicus</i> , <i>M. ornatus</i> , <i>Rhopalosiphum padi</i> , <i>Sitobion avenae</i> , <i>Uroleucon sp.</i>
4. <i>C. thromboides</i>	Aphidinae	<i>Aphis gossypii</i> , <i>Brevicoryne brassicae</i> , <i>Diuraphis noxia</i> , <i>Metopolophium dirhodum</i> , <i>Rhopalosiphum maidis</i> , <i>R. padi</i> , <i>Sitobion avenae</i>
	Myzocallidinae	<i>Therioaphis maculata</i>
<b><i>Batkoa</i></b>		
5. <i>B. apiculata</i>	Aphidinae	<i>Capitophorus inulae</i> , <i>Uroleucon sonchi</i>
<b><i>Entomophaga</i></b>		
6. <i>E. pyriformis</i>	Aphidinae	<i>Rhopalosiphum insertum</i>
<b><i>Entomophthora</i></b>		
7. <i>E. chromaphidis</i>	Aphidinae	<i>Acyrtosiphon kondoi</i> , <i>Metopolophium dirhodum</i> , <i>Sitobion avenae</i> , <i>Schizaphis graminum</i>
	Myzocallidinae	<i>Chromaphis juglandicola</i>



Table 1. Continued

Pathogen	Host	
	Subfamily	Species
8. <i>E. planchoniana</i>	Aphidinae	<i>Acyrtosiphon pisum</i> , <i>A. malvae</i> , <i>Amphorophora rubi</i> , <i>Aphis citricola</i> , <i>A. epilobii</i> , <i>A. fabae</i> , <i>A. frangulae</i> , <i>A. gossypii</i> , <i>A. pomi</i> , <i>A. rumicis</i> , <i>A. sambuci</i> , <i>A. spiraeicola</i> , <i>A. trifolii</i> , <i>A. umbrella</i> , <i>A. urticata</i> , <i>Aulacorthum solani</i> , <i>Brachycaudus</i> <i>helichrysi</i> , <i>B. lychnidis</i> , <i>B. rumexicolens</i> , <i>Brevicoryne brassicae</i> , <i>Capitophorus homi</i> , <i>C. inulae</i> , <i>Cavariella aegopodii</i> , <i>C. pastinacae</i> , <i>C. theobaldi</i> , <i>C. pastinacae</i> , <i>Corylobium</i> <i>avellanae</i> , <i>Cryptomyzus ribis</i> , <i>Capitophorus</i> <i>elaeagni</i> , <i>C. similis</i> , <i>Diuraphis noxia</i> , <i>Elatobium abietinum</i> , <i>Hayhurstia atriplicis</i> , <i>Hyalopteroides humilis</i> , <i>Hyalopterus pruni</i> , <i>Hyperomyces lactucae</i> , <i>H. lampsanae</i> , <i>Impatientinum asiaticum</i> , <i>Macrosiphoniella</i> <i>sp.</i> , <i>Macrosiphum euphorbiae</i> , <i>M. funestum</i> , <i>M. rosae</i> , <i>M. sylvaticum</i> , <i>Megoura viciae</i> , <i>Metopolophium dirhodum</i> , <i>M. festucae</i> , <i>Microlophium carnosum</i> , <i>Myzus ascalonicus</i> , <i>M. cerasi</i> , <i>M. ornatus</i> , <i>M. persicae</i> , <i>Ovatus</i> <i>crataegarius</i> , <i>Paramyzus heraclei</i> , <i>Periphyllus testudinaceus</i> , <i>Phorodon humuli</i> , <i>Rhopalomyzus loniceriae</i> , <i>Rhopalosiphum</i> <i>maidis</i> , <i>R. padi</i> , <i>Schizaphis graminum</i> , <i>Sitobion avenae</i> , <i>S. fragariae</i> , <i>Toxoptera</i> <i>aurantii</i> , <i>Tubaphis ranunculina</i> , <i>Uroleucon</i> <i>cirsii</i> , <i>U. hypochaeridis</i> , <i>U. jaceae</i> , <i>U. sonchi</i> , <i>U. tussilaginis</i>
	Drepanosiphinae	<i>Drepanosiphum acerinum</i> , <i>D. platanoidis</i>
	Chaitophorinae	<i>Chaitophorus populeti</i> , <i>C. capreae</i>
	Lachninae	<i>Tuberolachnus salignus</i>
	Myzocallidinae	<i>Monellia caryella</i> , <i>Eucallipterus tiliae</i> , <i>Myzocallis coryli</i> , <i>Tuberculatus annulatus</i>
	Pemphiginae	<i>Prociphilus xylostei</i>
<b><i>Erynia</i></b>		
9. <i>E. erinacea</i>	Aphidinae	<i>Aphis craccivora</i> , <i>A. fabae</i> , <i>A. gossypii</i> , <i>A. umbrella</i> , <i>Myzus persicae</i>
<b><i>Neozygites</i></b>		
10. <i>N. cinarae</i>	Lachninae	<i>Cinara pilicornis</i>
11. <i>N. fresenii</i>	Aphidinae	<i>Acyrtosiphon pisum</i> , <i>Aphis acetosa</i> , <i>A. citricola</i> , <i>A. craccivora</i> , <i>A. fabae</i> , <i>A. gossypii</i> , <i>A. nasturtii</i> , <i>A. rumicis</i> , <i>A. spiraeicola</i> , <i>A. umbrella</i> , <i>A. urticata</i> , <i>Brachycaudus cardui</i> , <i>Brevicoryne</i> <i>brassicae</i> , <i>Capitophorus elaeagni</i> , <i>Cavariella</i> <i>pastinacae</i> , <i>Elatobium abietinum</i> , <i>Hyalopterus pruni</i> , <i>Myzus persicae</i> , <i>Rhopalosiphum maidis</i> , <i>R. padi</i> , <i>Toxoptera</i> <i>aurantii</i> , <i>Uroleucon jaceae</i> , <i>U. sonchi</i>

Table 1. Continued

Pathogen	Host	
	Subfamily	Species
	Chaitophorinae	<i>Chaitophorus populiabae</i>
12. <i>N. lageniformis</i>	Myzocallidinae	<i>Myzocallis coryli</i> , <i>unid.</i>
13. <i>N. microlophii</i>	Aphidinae	<i>Microlophium carnosum</i>
14. <i>N. remaudierei</i>	Myzocallidinae	<i>Myzocallis coryli</i>
15. <i>N. slavi.</i>	Pemphiginae	<i>Slavum esfandiarii</i>
16. <i>N. turbinata</i>	Lachninae	<i>Pterochloroides persicae</i> , <i>Tuberolachnus salignus</i>
<b>Pandora</b>		
17. <i>P. kondoensis</i>	Aphidinae	<i>Acyrtosiphon kondoii</i> , <i>Myzus persicae</i>
18. <i>P. neoaphidis</i>	Aphidinae	<i>Acyrtosiphon loti</i> , <i>A. malvae</i> , <i>A. pelargonii</i> , <i>A. pisum</i> , <i>Amphorophora rubi</i> , <i>A. rumicis</i> , <i>Aphidula</i> sp., <i>Aphis craccivora</i> , <i>A. epilobii</i> , <i>A. fabae</i> , <i>A. frangulae</i> , <i>A. nasturtii</i> , <i>A. parietariae</i> , <i>A. pomi</i> , <i>A. rumicis</i> , <i>A. sambuci</i> , <i>A. urticata</i> , <i>Aulacorthum solani</i> , <i>Brachycaudus cardui</i> , <i>B. helichrysi</i> , <i>B. lychnidis</i> , <i>B. rumexicolens</i> , <i>Brachycorynella asparagi</i> , <i>Brevicoryne brassicae</i> , <i>Capitophorus elaeagni</i> , <i>C. horni</i> , <i>C. similis</i> , <i>Cavariella aegopodii.</i> , <i>Coloradoa achilleae</i> , <i>Corylobium avellanae</i> , <i>Cryptomyzus ballotae</i> , <i>C. ribis</i> , <i>Dactynotus formosanus</i> , <i>D. jaceae</i> , <i>Diuraphis noxia</i> , <i>Drepanosiphum platanoidis</i> , <i>Elatobium abietinum</i> , <i>Hyalopteroides humilis</i> , <i>Hyalopterus pruni</i> , <i>Hyperomyces lactucae</i> , <i>H. lamsanae</i> , <i>H. picridis</i> , <i>Impatiensinum asiaticum</i> , <i>Macrosiphoniella</i> sp., <i>Macrosiphum akebiae</i> , <i>A. albifrons</i> , <i>M. euphorbiae</i> , <i>M. funestum</i> , <i>M. prenanthidis</i> , <i>M. rosae</i> , <i>M. sylvaticum</i> , <i>Metopolophium dirhodum</i> , <i>M. festucae</i> , <i>Microlophium carnosum</i> , <i>Mindarus abietinus</i> , <i>Myzus ascalonicus</i> , <i>M. cerasi</i> , <i>M. nicotianae</i> , <i>M. ornatus</i> , <i>M. persicae</i> , <i>Paramyzus heraclei</i> , <i>Phorodon cannabis</i> , <i>P. humuli</i> , <i>Pleotrichophorus duponti</i> , <i>Rhopalomyzus lonicerae</i> , <i>Rhopalosiphum maidis</i> , <i>R. padi</i> , <i>Schizaphis graminum</i> , <i>Sitobion avenae</i> , <i>S. fragariae</i> , <i>Staticobium staticis</i> , <i>Tubaphis ranunculina</i> , <i>Uroleucon achilleae</i> , <i>U. aeneum</i> , <i>U. cirsii</i> , <i>U. formosanus</i> , <i>U. hypochaeridis</i> , <i>U. tussilaginis</i>
	Myzocallidinae	<i>Myzocallis coryli</i>
19. <i>P. nouryi</i>	Aphidinae	<i>Acyrtosiphon kondoii</i> , <i>A. fabae</i> , <i>A. umbrella</i> , <i>Brevicoryne brassicae</i>
	Pemphiginae	<i>Pemphigus bursarius</i>
	Myzocallidinae	<i>Therioaphis maculata</i>
20. <i>P. terrestris</i>	Pemphiginae	<i>Pemphigus fuscicornis</i>
21. <i>P. uroleuconii</i>	Aphidina	<i>Uroleucon aeneum</i>

Table 1. Continued

Pathogen	Host	
	Subfamily	Species
<b><i>Tarichium</i></b>		
22. <i>T. atospermum</i>	Aphididae	<i>Unidentified species</i>
<b><i>Zoophthora</i></b>		
23. <i>Z. anhuiensis</i>	Aphidinae	<i>Myzus persicae</i>
24. <i>Z. aphidis</i>	Aphidinae	<i>Rhopalosiphum padi</i>
	Anoeciinae	<i>Anoecia corni</i>
25. <i>Z. canadensis</i>	Lachninae	<i>Schizolachnus piniradiatae</i>
26. <i>Z. occidentalis</i>	Aphidinae	<i>Acyrthosiphon pisum</i> , <i>Aphis</i> sp., <i>Capitophorus similis</i> , <i>Hyperomyzus</i> <i>lactucae</i> , <i>Impatiatinum asiaticum</i> , <i>Macrosiphum euphorbiae</i> , <i>Sitobion fragariae</i>
27. <i>Z. orientalis</i>	Aphidinae	<i>Aphis citricola</i>
28. <i>Z. phalloides</i>	Aphidinae	<i>Acyrthosiphon loti</i> , <i>A. pisum</i> , <i>Aphis fabae</i> , <i>A. umbrella</i> , <i>Aulacorthum solani</i> , <i>Brachycaudus helichrysi</i> , <i>B. lychnidis</i> , <i>Brevicoryne brassicae</i> , <i>Capitophorus horni</i> , <i>Cavariella aegopodii</i> , <i>Coloradoa achilleae</i> , <i>Cryptomzus ballotae</i> , <i>Hyperomyzus</i> <i>lactucae</i> , <i>Macrosiphoniella</i> sp., <i>Macrosiphum rosae</i> , <i>Metopolophium</i> <i>dirhodum</i> , <i>M. festucae</i> , <i>Microlophium</i> <i>carosum</i> , <i>Myzu sascalonicus</i> , <i>M. ornatus</i> , <i>M. persicae</i> , <i>M. rannaculinum</i> , <i>Paramyzus</i> <i>heraclei</i> , <i>Rhopalosiphum padi</i> , <i>Sitobion</i> <i>avenae</i> , <i>S. fragariae</i> , <i>Tubaphis ranunculina</i> , <i>Uroleucon achilleae</i> , <i>U. sonchi</i>
29. <i>Z. radicans</i> s.l.	Aphidinae	<i>Acyrthosiphon pisum</i> , <i>Aphis fabae</i> , <i>A. gossypii</i> , <i>A. umbrella</i> , <i>Brachycaudus</i> <i>amygdalinus</i> , <i>Capitophorus</i> sp., <i>Diuraphis</i> <i>noxia</i> , <i>Hyperomyzus lactucae</i> , <i>Macrosiphum</i> sp., <i>Metopolophium dirhodum</i> , <i>Myzus</i> <i>persicae</i> , <i>Rhopalosiphum padi</i> , <i>Toxoptera</i> <i>aurantii</i> , <i>Uroleucon sonchi</i>
	Drepanosiphinae	<i>Drepanosiphum acerinum</i> , <i>D. platanoidis</i>
	Chaitophorinae	<i>Chaitophorus populialbae</i>
	Myzocallidinae	<i>Monellia caryella</i> , <i>Therioaphis maculata</i>

## Discussion

A total of 29 species is described, most of them are rare, and some are only known from a single species or from the original description (Tab. 1). Seventeen of the described species attack only aphids from a single subfamily, while two species attack aphids from more than two subfamilies. *Entomophthora planchoniana* is found on aphids of six subfamilies. *Zoophthora radicans* s.l. is known to attack four subfamilies. The two species have the lowest degree of specificity



among the aphid pathogenic species. However, it cannot be excluded that they consist of species complexes as earlier discussed in respect to *E. planchoniana* (Keller 2002). *Entomophthora planchoniana* has together with *C. obscurus*, *N. fresenii* and *P. neoaphidis* the highest impact on agriculturally important aphids in central Europe (Barta 2004, Keller & Suter 1980).

Species from eight genera attack aphids. However, it is noteworthy to mention that the two genera *Neozygites* and *Zoophthora*, which produce capilliconidia, contribute 14 species. This particular structure seems to be an advantage for the infection of aphids or for the infection of small hosts in general as is known from the genus *Neozygites* (Keller 1997).

Host preference or host specificity may vary from one geographical or climatic area to another. For example, *Z. radicans* has not been reported from Aphidinae from Europe until recently (Barta 2004, Keller this paper) but is frequently recorded in Israel. Furthermore, *Neozygites fresenii* was, in spite of significant investigations, never found on *Acyrtosiphon pisum* in Europe but recorded from Israel (Ben-Ze'ev 1993). The reasons for this difference are unknown. Future investigations may reveal that the fungi involved belong to different genotypes with different host preference or specificity.

The original descriptions of a few species are so poor (*N. lageniformis*) or imprecise (*E. chromaphidis*, *P. terrestris*, *Z. occidentalis*, *Z. phalloides*) that identifications and separations from similar species are often impossible. Redescriptions of incompletely known species should be done based on type material. If such material does not exist or does not allow a redescription an epitype should be designated. Species with wide morphological variation and/or a wide host range like *E. planchoniana* (Keller 2002), *P. neoaphidis* and *Z. radicans* should be further studied both morphologically and molecularly to assess whether they are single species or species complexes. Recently, *P. uroleuconii* was split from the *P. neoaphidis*-complex (Barta & Cagan 2004). The application of molecular markers will allow identifying and characterising the aphid-pathogenic species more accurately (Nielsen *et al.* 2001).

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