Arthropod-pathogenic Entomophthorales from Switzerland. III. First additions

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Twenty-nine species of arthropod-pathogenic Entomophthorales new to Switzerland are described. Nine are described as new species, namely *Batkoa hydrophila* from Plecoptera, *Conidiobolus caecilius* from Psocoptera, *Entomophaga antochae* from Limoniidae (Diptera), *E. thuricensis* from Cicadellidae (Homoptera), *Erynia fluvialis* from midges (Diptera), *E. tumefacta* from Muscidae (Diptera), *Eryniopsis rhagonidis* from Rhagionidae (Diptera), *Pandora longissima* from Limoniidae (Diptera) and *Strongwellsea pratensis* from Muscidae (Diptera). *Pandora americana*, *P. sciarae, Zoophthora aphrophorae* and *Z. rhagonycharum* are new combinations. Eleven species are first records since the original description. The list of species recorded from Switzerland amounts to 90 species representing 38 % of the world-wide known species of arthropod-pathogenic Entomophthorales.

Part I of this monograph (Keller 1987) treated the genera *Conidiobolus, Entomophaga* [including the species later transferred on to the new genus *Batkoa* Humber (1989)], and *Entomophthora*. Part II (Keller 1991) treated the genera *Erynia sensu lato* (now subdivided into the genera *Erynia, Furia* and *Pandora*), *Eryniopsis*, *Neozygites, Zoophthora* and *Tarichium*. So far 51 species including 8 new ones have been listed. A species described as new, *Entomophaga domestica*, was shown to be identical with *Entomophaga apiculata* (Humber 1989) and *Erynia athaliae* Keller (1991) proved to be identical with *E. athaliae* Li & Fan (1991), later transferred to the genus *Pandora* (Li *et al*. 1998) and is considered a synonym of the latter.

In the meantime 10 new species from Switzerland have been recorded or described as new species: *Entomophaga lagriae* (Bałazy 1993), *Erynia echinospora* (Keller 1993), *Entomophaga transitans* (Keller & Eilenberg 1993), *Entomophthora byfordii, E. ferdinandii, E. grandis, E. simulii, E. weberi* (Keller 2002), *Neozygites cinarae* (Keller 1997), and *N. remaudierei* (Keller 2006).

The following 61 species from Switzerland have been recorded hitherto and are listed here: *Batkoa* (4 species): *B. apiculata, B. gigantea, B. limoniae* and *B. papillata. Conidiobolus* (4 species):

C. cercopidis, C. coronatus, C. obscurus and *C. pseudapiculatus*. *Entomophaga* (6 species)*: B. aulicae, E. batkoi, E. conglomerata, E. grylli, E. lagriae*, *E. tenthredinis* and *E. transitans*. *Entomophthora* (12 species)*: E. brevinucleata, E. culicis, E. byfordii, E. ferdinandii, E. grandis, E. helvetica, E. muscae, E. planchoniana, E. schizophorae, E. simulii, E. trinucleata* and *E. weberi*. *Erynia (sensu lato)* (17 species)*: E. aquatica, E. athaliae, E. blunckii, E. bullata, E. conica, E. curvispora, E. dipterigena, E. echinospora, E. ellisiana, E. gammae, E. minutospora, E. myrmecophaga, E. neoaphidis, E. ovispora, E. rhizospora, E. variabilis* and *E. virescens*. *Eryniopsis (*1 species*): E. caroliniana*. *Neozygites* (7 species)*: N. cinarae, N. floridana, N. fresenii, N. microlophii, N. parvispora, N. remaudierei* and *N. turbinata*. *Strongwellsea* (1 species)*: S. castrans* (listed as *Erynia castrans* (Keller 1991). *Tarichium* (1 species): *T. rhagonycharium*. *Zoophthora* (7 species): *Z. aphidis, Z. crassitunicata, Z. elateridiphaga, Z. lanceolata, Z. phalloides, Z. radicans* and *Z. viridis*.

In this study nine new species are described and 19 described species are new records from Switzerland. Morphological and ecological data are provided and discussed in the context of published data.

Methods

The methods are described in detail by Keller (1987) and the most important procedures and abbreviations are reported here.

Stains: Conidia and cadavers were mounted in lactophenol-cotton blue (LPCB) (0.1 % cotton blue), lactophenol-aniline-blue (LPAB) (1 % aniline blue) or in lactophenol-aceto-orcein (LPAO) (0.25 % – 0.5 % orcein).

Cultures: Two media were used for isolation and culture of the fungi: (1) Sabouraud-dextrose-agar (SDA) enriched with egg yolk (1 egg yolk per 200 mL) (SDAEY) and (2) the *Entomophthora*-complete medium (EMC) developed by Ben-Ze'ev (pers. comm.). This medium consists of dextrose, yeast extract, casein hydrolysate, tryptophan, a solution of eleven salts and a solution of nine vitamins. Attempts to isolate and cultivate the fungi were limited to a few species.

Counts and measurements: If not otherwise stated, all counts and measurements were based on 50 objects per individual host; to assess variability several collections from each fungal species were examined. The number of collections (series) is given after the range of the mean and extreme values (in brackets) and the length/diameter ratio (Q).

Genera and species are listed in alphabetical order. The Swiss cantons are given with the official Swiss abbreviations. Collections

from isolated geographical locations are defined with coordinates originating from Swisstopogeodata (Anonymus 2006).

Results

1. ***Batkoa hydrophila*** Keller **sp. nov.** – Pl. 10, Figs. 1, 2.

Rhizoidea mononemata, partibus terminalibus non evolutis, amplificata vel ramosa. Conidiophora simplicia 14–23 nucleos continentia. Conidia primaria 24–40 x 17–33 µm, pyriformia vel ovoidea. Papilla distincta, elongata. Conidia secundaria habitu primariis similia, 24–26 x 17–20 µm, saepe e non dimissis conidiis primariis orientia. Sporae perdurantes spherical, (25) 29.4 (34) µm. Cystidia absunt.

In hospite indeterminato Plecopterum.

Holotypus. – ZT, Helvetia, (Fischingen TG), coll. et leg. S. Keller, 4 Aug 2004, no. 98–7.

Host. – *Leuctra* sp. (Plecoptera, Leuctridae).

Symptoms. – Dead adult insects fixed to stones in small prealpine rivers immediately above the water level. Sporulation from white mycelial bands along intersegmental membranes of the whole body but most pronounced on thoracic part.

Rhizoids monohyphal, numerous, endings unspecialised, enlarged or branched. – Conidiophores unbranched with a terminal diameter of (13) 16 (18) µm (n = 10), containing (14) 19 (23) nuclei (n = 14). – Primary conidia (24) 30.4–34.6 (40) x (17) 22.5–26.4 (33) µm, Q = 1.27–1.36 (5 series, n = 25), elongate pyriform to ovoid with one to several vacuoles, papilla prominent, extended, endings rounded or slightly flattened, basal diameter 10–11 µm (Plate 10, Figs. 1, 2). Some primary conidia started to germinate before projection. – Secondary conidia like primary, (24) 25.0 (26) x (17) 18.5 (20) µm (1 series, n = 5), often formed on unprojected primary conidia. – Immature resting spores spherical, (25) 29.4 (34) µm, granular, type of formation unclear. – Cystidia absent.

Etymology of specific epithet. – Refers to the habitat of the species.

Distribution. – Switzerland, Fischingen TG, coordinates 715960/251130, on stones in the river Murg (type locality) and Steg/Fischenthal ZH in the brook Fuchslochbach at an altitude of 750 m, coordinates 714960/245850.

Distinguishing characters. – *B. hydrophila* resembles *B. apiculata* but it is distinguished by the narrower conidia, the more pronounced papilla, the host and the habitat. From related species existing in an aquatic environment (*B. papillata, Entomophaga conglomerata*) it is clearly separated by the smaller conidia and the different host.

2. ***Batkoa major*** (Thaxter) Humber (1989)

Host. – *Tipula vernalis* M. (Diptera, Tipulidae)

Symptoms. – Infected insect fixed with clasped legs to pods of oilseed rape (*Brassica napus*) plants growing at the border of the field.

Primary condia (48) 60.4 (82) x (36) 48.4 (61) µm, Q = 1.25 (1 series), papilla usually broad and flat. The nuclei in the conidiophores had a diameter of (5) 5.2 (6) µm (1 series).

Distribution. – Zurich-Reckenholz (ZH).

The conidia nearly matche the dimensions given by Thaxter (1888) and they are larger than those of *B. limoniae* (Keller, 1987). However, the limited data do not allow identifying the species unequivocally.

3. ***Conidiobolus caecilius*** Keller **sp. nov.** – Plate 1, Figs. 1–7.

Rhizoidea mononemata, plerumque ex parte ventrali thoracis orientia, saepe irregulariter vel digitate ramosa, amplificationibus terminalibus praedita sine hapteronibus specialibus. Corpora hyphalia curta, hyphis similia, irregularia, multinucleata. Nuclei 3.0–3.5 µm diametro. Conidiophora simplicia. Conidia primaria 24–42 x 23–38 µm, sphaerica, prominenti papilla praedita, multinucleata. Conidia secundaria habitu primariis similia, 27–38 x 21–31 µm. Sporae perdurantes et cystidia absunt.

In Caecilio flavido Stephens (Hospite typico) and Caecilio sp. (Psocopteribus, Caeciliidis).

Holotypus. – ZT, Helvetia, Zurich-Reckenholz, coll. et leg. S. Keller, 21 Oct 1999, no 80–75. Paratypi K.

Host. – *Caecilius flavidus* Stephens (Psocoptera, Caeciliidae) (type species) and *Caecilius* sp.

Symptoms. – Dead Psocoptera fixed with rhizoids to the underside of leaves of bushes and young trees, mainly *Prunus padus* L., wings spread, thus showing the bright yellow abdomen.

Rhizoids monohyphal with a diameter of (7) 12.5 (21) µm (1 series), emerging mainly from the ventral side of the thorax, with terminal enlargement or simple branchings but without specialised holdfast (Plate 1, Fig. 7). – Hyphal bodies short, hyphae-like, irregular, multinucleate. Nuclei stain weakly in LPAO and measure (3) 3.2 (3.5) µm (1 series) (Plate 1, Figs. 1–2). – Conidiophores unbranched, terminally slightly enlarged ("shoulders") with a diameter of (17) 19.4 (24) µm (1 series), nuclei weakly stained, measuring 3.2 (3.0–4.0) µm (1 series) (Plate 1, Figs. 3–4). – Primary conidia (24) 32.1–38.1 (42) x (23) 26.8–31.9 (38) µm, Q = 1.11–1.25 (6 series), conidial body spherical, papilla prominent, rounded or slightly pointed, rarely flattened, multinucleate with single prominent vacuole or several smaller vacuoles (Plate 1, Fig. 5). – Secondary conidia

like primary, (27) 30.5 31.0 (38) x (21) 24.3–25.0 (31) µm, Q = 1.24–1.26 (2 series) formed on short, lateral conidiophores, sometimes with apical point (Plate 1, Fig. 6). – Resting spores and cystidia not observed.

Culture. – Quick growth on ECM. Primary conidia measure (28) 32.1–36.5 (44) x (23) 26.5–30.7 (39) µm, Q = 1.19–1.22 (2 series).

Etymology of specific epithet. – Suggesting the genus of the host from which the fungus was first collected.

Distribution. – Switzerland: Zurich-Reckenholz (ZH) (type locality), Neunkirch (Widen), SH.

Distinguishing characters. – *B. caecilii* closely resembles *Conidiobolus pseudapiculatus* (Keller 1991) from which it differs mainly by the larger, faintly stainable nuclei, the stronger papilla and the host. Gustafsson (1965) mentions *Entomophthora apiculata* as a pathogen of an unidentified Psocoptera and of other insects. He gives three dimensions for primary conidia but without stating from which host they originated. Although one of these measurements matches the description of *C. caecilius* it remains unknown whether the two species are identical.

The species was collected in the second half of October, predominantly on adult Psocoptera, exceptionally on larvae. Primary conidia picked up from water surface germinated only to produce secondary conidia. None produced "sterile" germ tubes or other types of secondary conidia.

4. ***Entomophaga antochae*** Keller **sp. nov** – Plate 2, Figs. 1–4.

Corpora hyphalia sphaerica vel subspherica, 31 x 30 µm. Conidiophora simplicia, 22–24 nucleos continentia. Conidia primaria 35–40 x 25–28 µm, pyriformia. Conidia secundaria habito primariis similia, 31–34 x 24–25 µm vel elongata, curvata, 44–46 x 18–19 µm. Sporae perdurantes sphaericae, hyalinae, laeves, 31–47 µm. Rhizoidea et cystidia absunt.

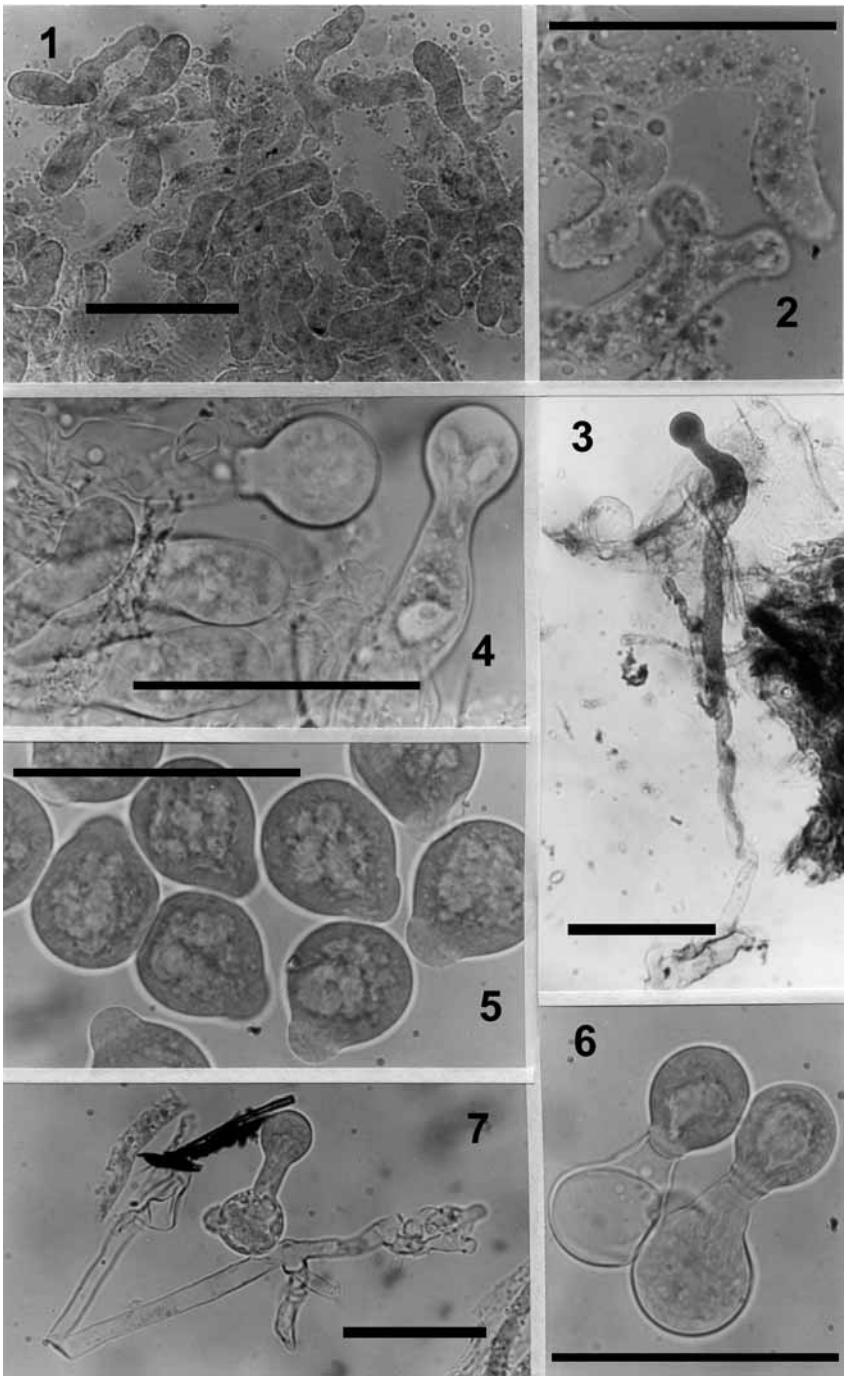
In Antocha vitripenni (M.) (hospite typico) (Dipteris, Limoniidis).

Holotypus. – ZT, Helvetia, Ruedlingen (SH), coll. et leg. S. Keller, 15 Jun2004, no 91-8. Paratypi K et PBI.

Host. – *Antocha (Antocha) vitripennis* (Meigen, 1830) (Diptera, Limoniidae).

Symptoms. – Cadavers fixed with the legs to a concrete wall bordering the Rhine river about 10–30 cm above the water level.

Hyphal bodies spherical to subspherical, (28) 31.0 (35) x (28) 30.1 (35) µm (1 series), germinating with a single germ tube (Plate 2, Fig. 1). The nuclei in the hyphal bodies have a diameter of 5.2 $\pm$ 0.4 µm (1 series). – Conidiophores unbranched with (13) 22.1–24.0 (37) nuclei with a diameter of 4.3 $\pm$ 0.44 µm (2 series) (Plate 2, Fig. 2). – Primary conidia pyriform (33) 35.3–39.5 (45) x (21) 24.9–28.0



(31) µm, L/D = 1.39–1.56 (6 series), usually with a single large vacuole (Plate 2, Fig. 3). – Secondary conidia either resembling the primary ones, (29) 30.8–34.4 (39) x (22) 24.4–24.8 (30) µm (2 series) often with apical point or elongate, curved, apex rounded, (39) 43.8–45.9 (56) x (15) 17.8–19.2 (23) µm, L/D = 2.28–2.58 (2 series), usually with a single large vacuole (Plate 2, Fig. 4). The length of the conidiophore of type Ia secondary conidia is 8–11 µm and that of the elongate type 30–38 µm. – Resting spores spherical, hyaline, smooth, immature ones with a diameter of 41.0 $\pm$ 3.17 µm (34–47 µm), mature measuring 37.3 $\pm$ 4.06 µm (31–47 µm) (1 series each). – Rhizoids and cystidia absent.

Distribution. – Switzerland, Rüdlingen SH (type locality), coordinates 685800/270200.

Etymology. – The specific epithet refers to the host genus on which the fungus was collected.

Distinguishing characters. – The species is closely related to *E. ptychopterae* and *E. transitans*. It can be separated mainly by the shape of the elongate secondary conidia and by the host.

The species was collected in June 2004 in large amounts, on insects fixed to a concrete wall bordering the river Rhine. The wall was exposed southwards but shaded by trees.

A few specimens of the same host were collected in 2003 at the same locality. The fungus seen on these specimens differs in some respects from the description given above, as the conidiophores contained only 14.4–16.4 nuclei (3 series) with the same diameter. The primary conidia were slightly broader (35.7–39.9 x 27.2–31.7 µm; L/D = 1.26–1.31 – 2 series). The elongate type of secondary conidia measured 35.1–36.5 x 16.6–20.2 µm; L/D = 1.75–2.11 (3 series); type Ia secondary conidia were rare. That the fungi from the two samples belong to the same species is uncertain.

A fungus corresponding to the description given above was identified as *E. tipulae* by Bałazy (1993). Because of the different hosts and ecological circumstances we prefer to describe this fungus as a new species (see also discussion of *E. tipulae*).

5. ***Entomophaga thuricensis*** Keller **sp. nov.** – Plate 3, Figs. 1–10.

Corpora hyphalia sphaerica vel ellipsoidea, 41–43 x 38–40 µm, 32–51 nucleos 4.0–6.0 µm diametro continentia. Conidiophora simplicia 21–52 nucleos continentia. Conidia primaria 42–59 x 30–47 µm, pyriformia. Papilla distincta, asym-

Plate 1. *Condiobolus caecilius*: **1.** Hyphal bodies. **2.** Hyphal bodies with faintly stained nuclei. **3.** Condiophore with empty hyphal body (bottom) and developing conidium (top). **4.** Formation of primary conidia. **5.** Projected primary conidia. **6.** Formation of secondary conidia. **7.** Rhizoid and germinating conidium. Bars 50 µm.

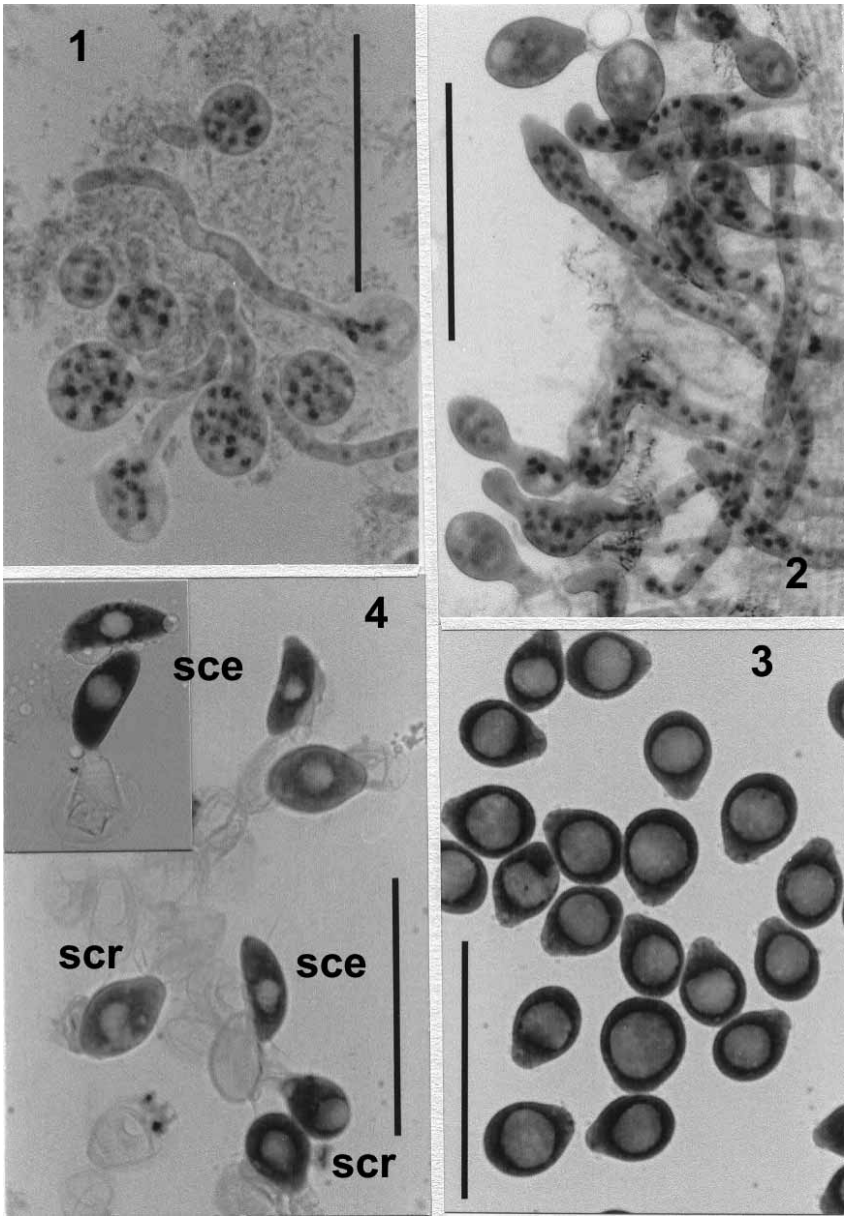


Plate 2. *Entomophaga antochae*: **1.** Germinating hyphal bodies with nuclei. **2.** Conidiophores with nuclei and formation of primary conidia. **3.** Primary conidia with prominent vacuole. **4.** Secondary conidia of the rounded (scr) and the elongate type (sce). Bars 100 μm.

metrica. Conidia secundaria habito primariis similia, 38–54 x 28–47 µm. Sporae perdurantes sphaericae, hyalinae, laeves, 38–53 µm. Rhizoidea et cystidia absunt.

In *Cicadella viridi* L. (hospite typico) (Homopteribus, Cicadellidis).

Holotypus. – ZT, Helvetia, Zurich-Affoltern (regione Katzensee, ZH), coll. et leg. S. Keller, 13 Sep 1999, no 79–53, Paratypi K et PBI.

Host. – *Cicadella viridis* L. [Homoptera, Cicadellidae (Jassidae)] (type host).

Symptoms. – Dead insects fixed to plants with inserted proboscis, head upwards, wings slightly spread, white mycelial bands along intersegmental membranes when the fungus sporulates.

Hyphal bodies spherical to slightly ellipsoidal, 41.5–43.2 x 38.5–39.9 µm (2 series), pyriform when germination starts; contain (32) 41 (51) nuclei (1 series) with a diameter of (4) 4.5-4.9 (6) µm (2 series). Nuclei deeply staining in LPAO (Plate 3, Figs. 1 and 3). – Conidiophores unbranched, terminally enlarged to 33.8–35.0 µm, with (21) 38–39 (52) nuclei (2 series) with a diameter of 4.3 µm (1 series) (Plate 3, figs 2–3). – Primary conidia (42) 49.1–51.9 (59) x (30) 35.8–38.2 (47) µm, Q = 1.36–1.41 (5 series), pyriform, apex rounded, multinucleate, usually one to three vacuoles; papilla prominent, usually asymmetrical, rounded or slightly flattened (Plate 3, Fig. 4). – Secondary conidia like primary, (38) 44.6–49.1 (54) x (28) 35.2–40.7 (47) µm, Q = 1.21–1.27 (4 series), apex rounded, sometimes with indistinct apical point, usually single central vacuole; papilla less prominent than in primary conidia (Plate 3, Figs. 5–6). – Resting spores spherical, hyaline, smooth, (38) 42.0–47.0 (53) µm (3 series) with (19) 39 (57) nuclei (1 series) (Plate 3, Figs. 9–10); young resting spores measure (45) 51.1 (61) µm with (49) 70 (126) nuclei with a diameter of (4) 4.5 (5) µm (1 series) (Plate 3, Figs. 7–8). – Rhizoids and cystidia absent.

Culture. – Conidia projected from insects and transferred to culture tubes with ECM produced secondary conidia but no growth occurred.

Distribution. – Switzerland: Zurich, Allmend Katzensee ZH (type locality).

Etymology. – The specific epithet refers to Zurich in reminiscence of an IOBC-workshop on Entomophthorales in 1993, during which part of the material described here was collected.

The species was collected between end of August and end of October. Some specimens were found at the border of the lake Katzensee by members of the IOBC-working group "Insect pathogens and insect parasitic nematodes" during a workshop on Entomophthorales held in Zurich from 9–10 September 1993. The majority of the material was collected in the following years in a wet meadow (Allmend Katzensee) where the dead insects were mainly fixed to small reed plants (*Phragmites australis* Cav.). It was striking

that living *C. viridis* concentrated on plants with one or more infected hosts.

Resting spores were predominantly found at the end of the collection period. They are considered as zygospores produced by the fusion of two hyphal bodies. During this process the cytoplasmic content of a hyphal body enters the other hyphal body leaving an empty envelope (Plate 3, Figs. 7–8). These observations of zygospore formation are supported by nuclear numbers. Young resting spores contained on average 70 nuclei which is nearly twice the average number of nuclei present in hyphal bodies. The number of nuclei in resting spores decreases during maturation.

Primary conidia projected on slides sometimes germinated with up to five germ tubes. Occasionally the same primary conidium produced sterile germ tubes and a secondary conidium (Plate 3, Fig. 6). On these slides some exceptionally small conidia were observed (29–35 x 21–25 μm, Q = 1.4; 1 series, n = 13) reminiscent of microconidia. However, there are no direct observations of their formation.

Entomophaga thuricensis is a typical member of the *E. grylli*-group having spherical to ellipsoidal hyphal bodies, pyriform conidia, deeply staining nuclei and lacking rhizoids. It can be separated from these species mainly by the number of nuclei and the host species. Under natural conditons the species must be considered as non-infective for grasshoppers. Among a population of these insects living in high density in the same environment during an epizootic caused by *E. thuricensis*, not a single infected grasshopper was found.

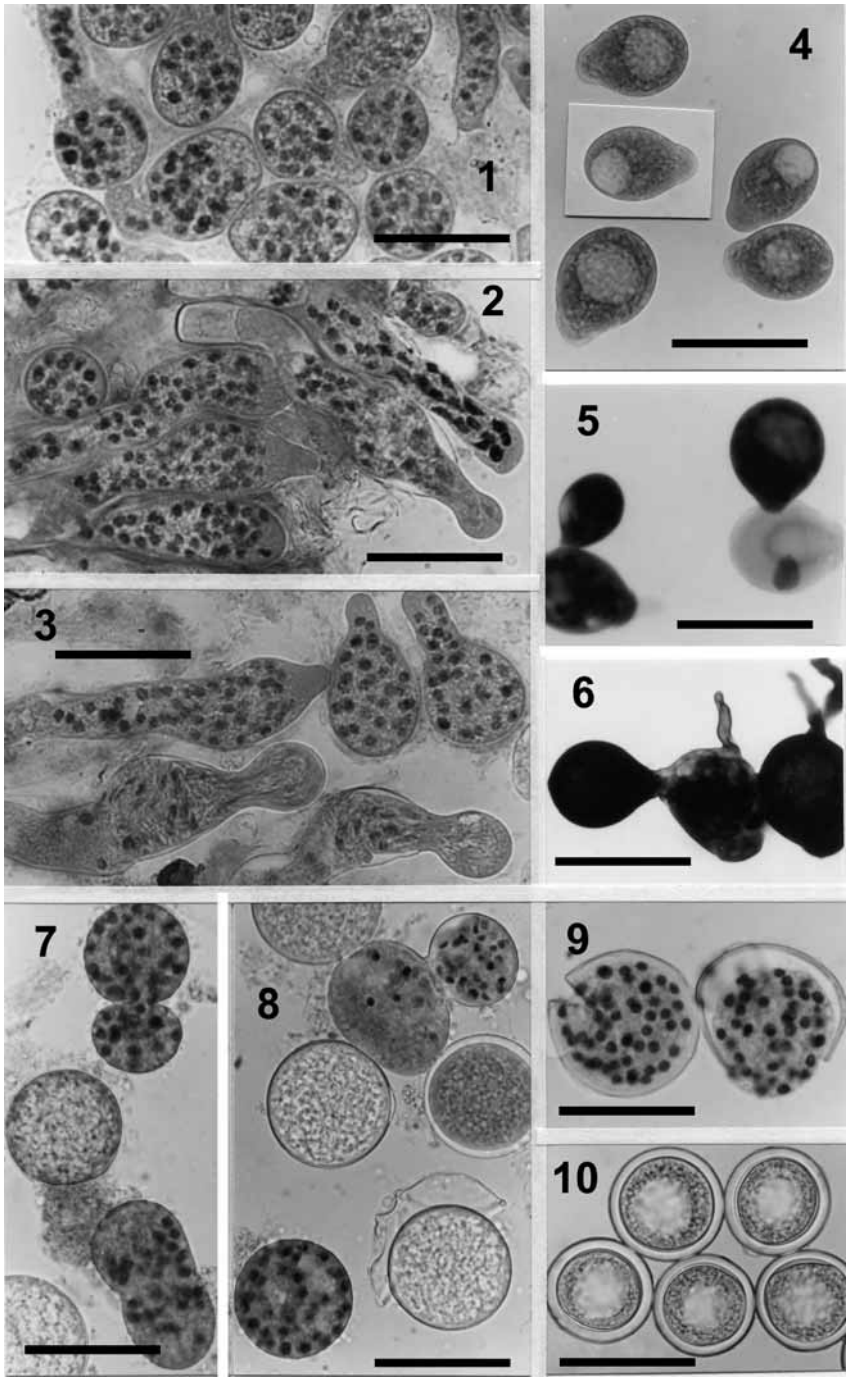
6. ***Entomophaga tipulae*** (Fresenius) Humber (1989)

Host. – Diptera, Tipulidae: *Tipula (Acutipula) luna* Westhoff, and unidentified species.

Symptoms. – Dead adult tipulids fixed with clasped legs to a leaf of *Phragmites australis* (Cav.) and *Aegopodium podagraria* L. respectively.

Hyphal bodies spherical (27) 35.7 (42) μm (1 series) or subspherical. – Conidiophores unbranched with (17) 25–28 (37) nuclei (2 series) with a diameter of (4.5) 5.1 (6.0) μm (1 series), nuclei deeply stain in LPAO. – Primary conidia (31) 35.5–41.9 (50) x (23)

Plate 3. *Entomophaga thuricensis*: **1.** Hyphal bodies with nuclei. **2.** Conidiophores with nuclei. **3.** Two germinating hyphal bodies and three tips of conidiophores with developing conidia. **4.** Projected primary conidia with vacuole. **5.** Developing secondary condia. **6.** Formation of secondary conidium with indistinct apical point; the two primary conidia with thin "sterile" germ tubes. **7., 8.** Formation of resting spores. **9.** Young resting spores with nuclei. **10.** Mature resting spores. Bars 50 μm.



26.9–29.8 (41) µm, Q = 1.32–1.46 (3 series), pyriform to ovoid, papilla often slightly asymmetrical, rounded, nuclei with a diameter of (3.5) 4.3 (5.0) µm (1 series). – Secondary conidia like primary, (31) 35.0 (39) x (24) 26.5 (30) µm, Q = 1.32 (1 series, n = 16). – Resting spores spherical, hyaline, (33) 36.0 (44) µm (1 series), young spores with about 30–50 nuclei. – Rhizoids absent, cystida not observed.

Distribution. – Burgrain/Willisau LU, Rickenbach ZH.

Fresenius (1858) found the species on a larger adult *Tipula* in the middle of May, "sitting dead and without wings on reed". He described the length of the conidia to be 33–40 µm. The data from the own collection match nicely the original description. However, the identity remains still uncertain, because other similar fungi are known from related species. The one described by Balazy as *E. tipulae* is considered a new species (see *E. antochae*), as the morphological data are similar but host and ecological data do not correspond.

Thaxter (1888) mentioned a similar fungus from Tipulidae under the name *Empusa conglomerata*, being aware, however, that there were some differences between his fungus and *Entomophthora conglomerata* Sorokin (1877). Brumpt (1940) believed to have found Thaxter's *E. conglomerata* on mosquitoes and described the species (invalidly) as *Empusa thaxteri*. According to Thaxter (1888) the conidia measure on average 32 x 23 µm, which does not match the data given for *E. tipulae*. Brumpt (1940) gives a wide variation of dimensions which covers those for *E. tipulae* but does not help to classify his fungus. Another reason to consider Thaxter's and Brumpt's fungi as different from *E. tipulae* are the ecological circumstances under which the species were originally found. Fresenius (1858) found *E. tipulae* on a larger adult tipulid on reed whereas Thaxter (1888) and Brumpt (1940) found their fungus on adults and larvae of tipulids and culicids respectively among moss in water or floating on water.

The species was found in June and July. Slight differences were observed between the material from *Phragmites* and from *Aegopodium*, the latter tended to have larger conidia. However, no differences were found in the number of nuclei. The tipulid from reed contained thin-walled, young resting spores together with conidia.

Entomophtora tipulae is a typical member of the *E. grylli*-group. The morphological and cytological data do not allow one to separate it from *E. grylli*. The only difference is the host. It also closely resembles *Eryniopsis transitans* (Keller & Eilenberg, 1993) and *Batkoa limoniae* (Keller in Keller & Petrini 2005). It can be distinguished from the former by the number of nuclei and by the secondary conidia (two types present with *E. transitans*) and from the

latter by the shape of the hyphal bodies and conidia and the presence of rhizoids.

The fungus described as *Entomophthora* cf. *thaxteri* by Descals and Webster (1984) has larger conidia than *E. tipulae* and can therefore not be considered as identical with this species (Humber, 1989).

7. ***Entomophthora rivularis*** Keller *et al.* in Keller (2002). – Plate 6, Figs. 5–6.

Host. – *Siphonoperla* sp., probably *S. torrentium* (Pictet) (Plecoptera, Chloroperlidae).

Symptoms. – Infected stoneflies loosly fixed to leaves of bushes 1–2 m above the water level of a small river.

Hyphal bodies subspherical to subellipsoidal (27) 35 (42) x (24) 27.6 (30) µm (n = 8) with (11) 15.2 (20) nuclei with a diameter of (3) 3.5 (4) µm (1 series, n = 25). – Conidiophores with long tapering neck (Plate 6, Fig. 5). – Primary conidia (22) 25.2–25.9 (29) x (18) 19.8–21.1 (23) µm, Q = 1.23–1.27 (2 series, n = 25), campanulate (Plate 6, Fig. 6). – Secondary conidia like primary without distinct apical point, (17) 19.7–20.8 (22) x (12) 15.8–16.1 (18) µm (2 series, n = 25).

Distribution. – Three host specimen were collected on June 28, 2005, at Fischingen, TG, along the river Murg at an altitude of 670 m, coordinates 715960/251130. The data match those given in the original description that was based on a single specimen of an unknown Plecoptera.

8. ***Entomophthora scatophagae*** Giard (1888).

Host. – *Scopeuma (Scatophaga) stercorariorum* L. (Diptera, Scatophagidae)

Symptoms. – Infected dung flies fixed to upper parts of plants (often grasses) with proboscis and clasped legs, head usually downwards, wings spread latero-dorsally.

Hyphal bodies subspherical (24) 30.4–32.6 (39) x (22) 26.3–29.9 (36) µm, Q = 1.09–1.20 (5 series), contain (12) 15.6–20.1 (24) nuclei with a diameter of (3.5) 4.1–4.5 (5) µm (2 series). Germinate with a single germ tube with a diameter of (7) 8.7–9.9 (12) µm (4 series). – Unbranched conidiophores terminally enlarged to (18) 23.6 (30) µm. They contain (13) 16.9–17.2 (22) nuclei with a diameter of (3) 3.9–4.5 (5.5) µm. – Primary conidia (25) 27.9–28.5 (32) x (19) 21.6–22.8 (28) µm, Q = 1.23–1.31 (6 series) with pronounced apical point; they contain (13) 15.2–16.1 (21) nuclei. – Secondary conidia (17)

18.9–20.9 (23) x (13) 15.3-17.1 (19) *m, Q = 1.20-1.23 (4 series), apical indistinct or missing. – Cystidia and resting spores absent.

Distribution. – The species is very common in northern and central Switzerland. It was found to cause epizootics mainly in spring and in autumn. A fungus matching this description was found on *Delia planipalpis* Stein (Diptera, Anthomyiidae) (Keller 1984).

9. ***Entomophthora syrphi*** Giard (1888).

Hosts. – *Melanostoma mellinum* L., *M. scalare* F., *Platycheirus clypeatus* Meig. (Diptera, Syrphidae)

Symptoms. – Infected hoverflies fixed to plants (often flowering Plantago lanceolata and grasses) with proboscis and clasped legs, head downwards, wings spread latero-dorsally.

Protoplasts spherical to subspherical, nuclei not staining in LPAO. – Hyphal bodies spherical to subspherical, (25) 37.0 (48) x (23) 31.3 (38) µm (1 series), germinate with single germ tube with a diameter of (8) 10.2 (12) µm (1 series). – Conidiophores unbranched, terminally enlarged to a diameter of (18) 22.7–27.3 (39) µm (2 series), contain (11) 18–25 (32) nuclei (8 series) with a diameter of (3) 3.7–4.1 (5.0) µm (3 series). – Primary conidia (24) 27.5–32.3 (36) x (18) 20.7–27.3 (30) µm, Q = 1.18–1.33 (6 series) with (14) 19–22 (30) nuclei (6 series) with a diameter of (2.5) 2.8–3.4 (4.0) µm (5 series), distinct apical point; papilla flat to slightly rounded. – Secondary conidia (18) 21.9–24.3 (30) x (15) 17.2–17.6 (19) µm, Q = 1.27–1.39 (3 series), like primary but without apical point. – Resting spores, rhizoids and cystidia absent.

Distribution. – The species is widely distributed in northeastern Switzerland. Epizootics were observed at Hallau (SH), Stammheim (ZH), Hausener Seen (ZH) and Frauenfeld (TG).

MacLeod *et al.* (1976) treated the species as *E. muscae*. They considered the description given by Giard (1888) as invalid "... since he failed to describe the fungus.". Data collected since then lead to the conclusion that *E. syrphi* must be considered as a distinct species (Bałazy 1993, Keller 1984). It is well defined by its type host, *Melanostoma mellinum* L. So far no other entomophthoralean fungus is known to attack this syrphid species.

Entomophtora syrphi differs from the other members of the *E. muscae*-complex mainly by the larger number of nuclei per conidium, the smaller nuclei and the hosts (Keller 1984). The species is common from July to September. It sometimes causes epizootics especially in meadows, at borders of brooks and along forest paths. Since its hosts predominantly feed on pollen, the intestine of diseased insects is often filled with pollen grains (diameter in two specimens 30–42 µm and 23–45 µm respectively) associated with micro-

organisms (yeast?) measuring 6–11 x 2.5–5 µm. The pollen grains have been misinterpreted as spores (Turian, 1957). The fungus sometimes produces transitional bodies as defined by Keller & Wilding (1985).

A fungus found on *Herinia frondescentiae* L. (Diptera, Otitidae) at Zurich-Affoltern (ZH) matches the description given for *E. syrphi*. The primary conidia measure (25) 28.6–30.8 (34) x (19) 22.7–24.5 (28) µm, Q = 1.22–1.26 (3 series) and contain (15) 19 (24) nuclei (1 series). – The secondary conidia measure (21) 23.0 (29) x (16) 17.6 (19) µm, Q = 1.31 (1 series, n = 22). – The conidiophores contain (15) 20–22 (32) nuclei (3 series) with a diameter of (3.5) 3.7 (4.5) µm (2 series). The fungus was found in June and July in a wet meadow. The host flies were mainly attached to the lower surface of leaves of reed (*Phragmites australis* (Cav.). The morphological and cytological data do not allow separating this fungus from *E. syrphi*. The only difference concerns the host species.

10. ***Erynia fluvialis*** Keller **sp. nov.** – Plate 4, Figs. 1–3.

Rhizoidea monohyphalia, hapteronibus specialibus non praedita. Conidiophora digitate ramosa. Conidia primaria 17–24 x 7–11 µm, uninucleata, bitunicata, elongate obovoidea, curvata. Conidia secundaria habito primariis similia, 13–16 x 7–10 µm, vel subsphaerica, dein 10–12 x 7–10 µm. Cystidia longa imponentiaque. Sporae perdurantes absunt.

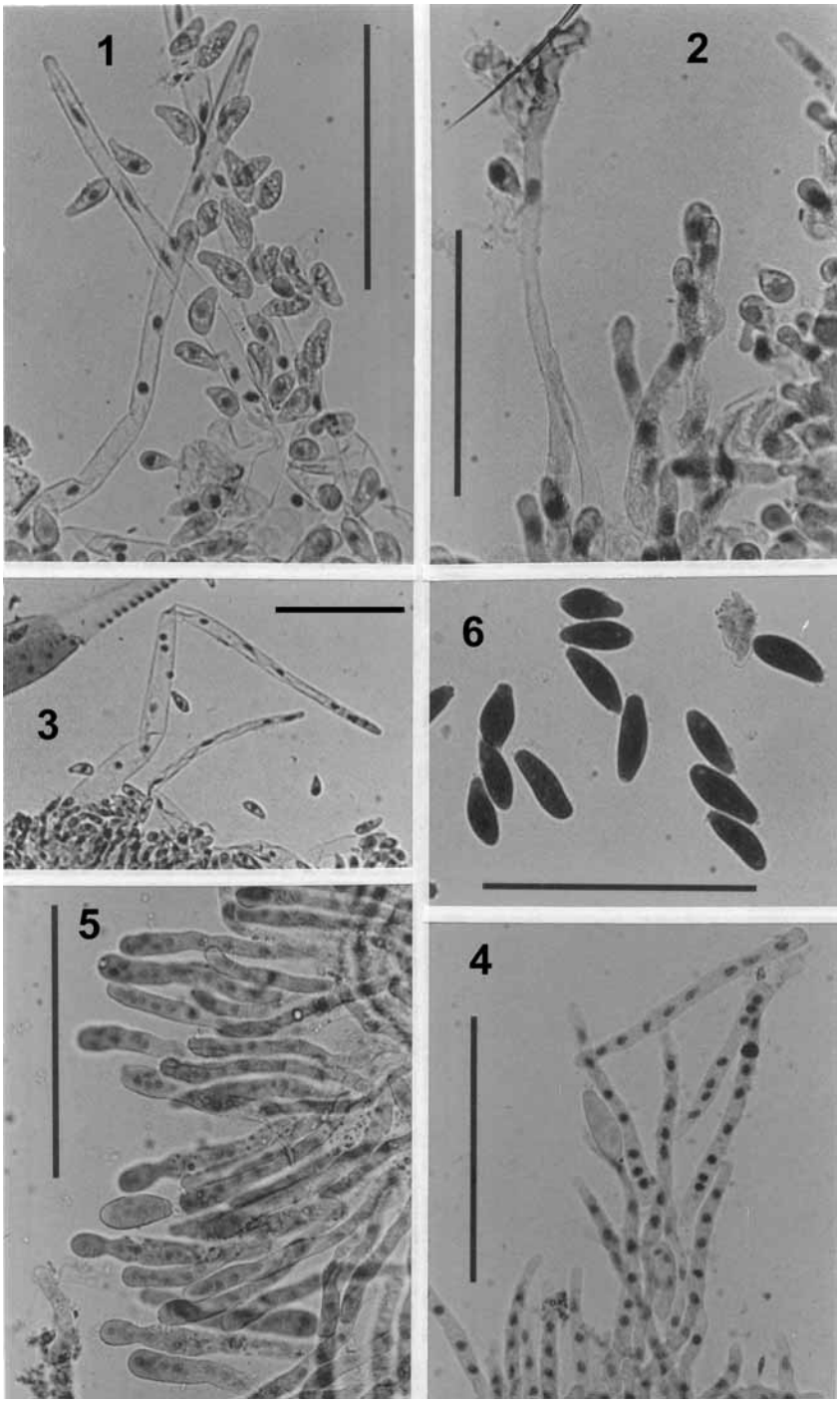
In nematocerum specie incognita (hospite typico) (Dipteribus, Nematoceris).

Holotypus. – ZT, Helvetia (Steg/Fischenthal ZH), coll. et leg. S. Keller, 3 Jul2006, no 99-60. Paratypi K.

Host. – Unidentified species of tiny midges (Diptera, Nematocera).

Symptoms. – Infected insects attached to stones in small rivers immediately above the water level, wings spread.

Rhizoids monohyphal with a diameter of 6–19 µm (n = 18), terminally enlarged, with a few outgrowths or simple root-like hyphae (Plate 4, Fig. 2). – Hyphal bodies (empty shells) subsphaerical, ellipsoidal to short rod-shaped, 26–38 x 20–28 µm (n = 9). – Conidiophores branched. – Primary conidia (17) 19.2–20.8 (24) x (7) 8.4–9.4 (11) µm, Q = 2.19–2.43 (5 series, n = 25), bitunicate, elongate obovoid, curved, largest diameter close to the apical part, usually with single vacuole, papilla narrow with a diameter of 3.5–4 µm (Plate 4, Fig. 1). – Type Ia secondary conidia (13) 14.6 (16) x (7) 8.5 (10) µm, Q = 1.73 (1 series, n = 25); type Ib secondary conidia (10) 11.1 (12) x (7) 8.8 (10) µm, Q = 1.27 (1 series, n = 25). – Cystidia powerful and reaching a length of up to 300 µm above the conidial layer, tapering, basal diameter (15) 21.4 (33) µm and apical diameter (6) 6.5 (8) µm (1 series, n = 25) (Plate 4, Fig. 3). – Resting spores absent.



Etymology of specific epithet. – The name refers to the habitat in which the fungus has been collected.

Distribution. – Switzerland, Steg/Fischenthal (ZH) in the brook "Fuchslochbach", 750 m a.s.l., coordinates 714960/245850 (type locality) and Fischingen (TG) in the river Murg, 670 m a.s.l., coordinates 715960/251130.

Distinguishing characters. – The species has the same shape of primary conidia as *Erynia variabilis*. The conidia, however, are distinctly smaller and have also a smaller lengh/diameter-ratio than those of *E. variabilis* which measure on average 25 x 8 µm (Thaxter 1888).

The species was collected between end of June and end of August. It is a typical member of *Erynia* with simple hyphal bodies and powerful cystidia. It was found associated with *E. gracilis* (often on the same type of host) and *E. conica*. Usually, the infected insects, tiny midges, were found in groups of up to about 20 individuals on the shady side of stones laying in the water. The wings had a length of 0.8-0.9 mm and are considered to belong to species of Sciaridae (B. Merz, pers. comm.).

11. ***Erynia gracilis*** (Thaxter) Humber (1989). – Plate 5, Figs. 1–5.

Host. – Small unidentified midges, about 2–3 mm long (Diptera, Nematocera).

Symptoms. – Dead insects fixed on stones and branches at the water level to some cm above the water level of a small pre-alpine river. Mycelium white or grey sometimes with a distinct violet touch.

Rhizoids monohyphal with a diameter of (8) 14.9-16.8 (34) µm (2 series, n = 25), at the end gradually enlarging, endings branched, bulbous, sucker-like or corkskrew-like (Plate 5, Fig. 1). – Hyphal bodies subspherical to elongate, (23) 30.8-32.3 (45) x (19) 25.0–28.0 (36) µm, Q = 1.15–1-22 (4 series, n = 25) with (6) 8.3 (12) nuclei (1 series, n = 18). – Conidiophores branched, terminal enlargement (7) 7.3–9.0 (11) µm (2 series, n = 15 and 25). – Primary conidia (24) 30.1–39.0 (46) x (6) 7.6–8.6 (10) µm, Q = 3.50–5.10 (4 series, n = 25), elongate, curved to slightly sickle-shaped, largest diameter in basal half (Plate 5, Figs. 3–4). In contact with water rocket-like stellate primary conidia with a length of (27) 31.3 (38) µm (1 series, n = 25) are produced (Plate 5, Fig. 5). – Secondary conidia like primary (Plate

Plate 4. 1–3. *Erynia fluvialis*: **1.** Primary conidia and cystidia. **2.** Rhizoid (rh) with holdfast (hf). **3.** Cystidia. Bars 100 µm. 4–6. *Eryniopsis rhagionidis*: **4.** Young conidiophores with nuclei. **5.** Conidiophores with developing primary conidia. **6.** Primary conidia. Bars 100 µm.

5, Fig. 3) or nearly spherical. – Cystidia rare, basal diameter 17–34 µm tapering to 10–13 µm (n = 9) (Plate 5, Fig. 2). – Restings spores absent.

Distribution. – Fischingen TG, in the river Murg at an altitude of 670 m, coordinates 715960/251130, and Steg ZH in the Fuchslochbach at an altitude of 750 m, coordinates 714960/245850. The species was collected between end of June and early August.

This is the first record of this species since its original description from the eastern USA. The conidia vary widely but match the dimensions given in the original description. However, the dimensions given by Thaxter do not correspond to those of his drawings which show distinctly more slender conidia. The material examined contained only very few secondary conidia, but both types were present. The observation that cystidia are rare is in agreement with Thaxter's. In addition to the description given by Thaxter the mycelial mass was either white or grey with a distinct violet touch. The colour may depend on the host. The species was often associated with *Erynia conica* (Plate 5, Fig. 4) and with a species described above as *E. fluvialis*. The species produces primary stellate or aquatic conidia with a mean length of 31.3 µm. They are produced under water or in contact with on the tapered end of a conidiophore and resemble small rockets. The central part consists of a rounded body with the nucleus and a lancet-like protrusion in the conidial axis. At the base four smaller pointed outgrowths are arranged regularly (Plate 5, Fig. 5).

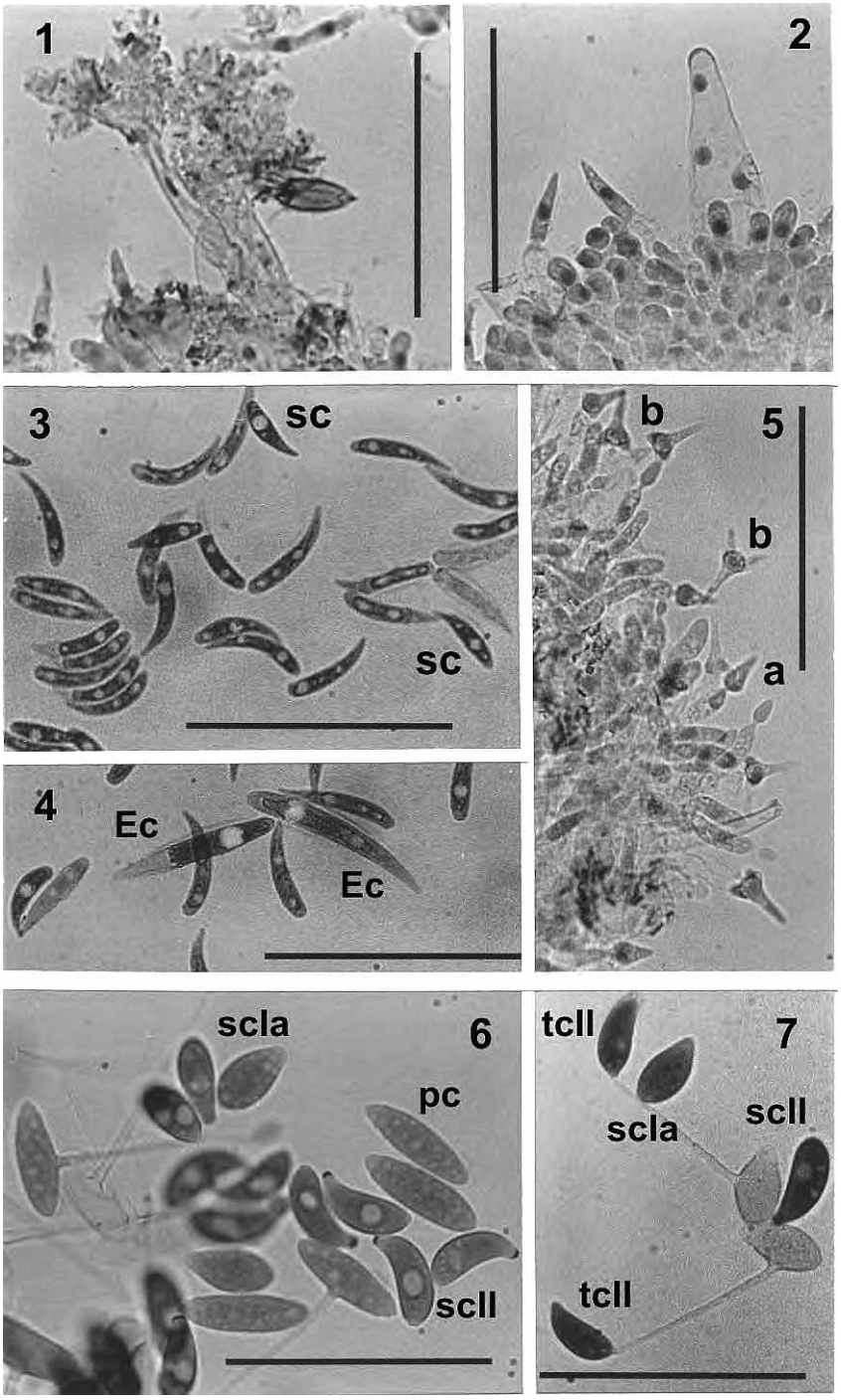
12. ***Erynia plecopteri*** Descals & Webster (1984). – Plate 6, Figs. 1–4.

Host. – Unidentified species of Nemouridae (Plecoptera).

Symptoms. – Dead insect fixed on the shady side of stones immediately above the water level, wings slightly spread, abdomen covered with brown mycelium, thorax with brown bands of mycelium along the intersegmental membranes.

Primary conidia (25) 29.0–31.1 (36) x (12) 13.2–14.1 (18) µm, Q = 2.05–2.28 (2 series), elongate pyriform, largest diameter in apical half, usually with several vacuoles; papilla protruded, rounded (Plate 6, Fig. 1). – Secondary conidia of type Ia measured (19) 21.6 (24)

Plate 5. 1–5. *Erynia gracilis*: **1.** Three rhizoids with specialised holdfast. **2.** Cystidium. **3.** Primary and secondary (sc) conidia. **4.** Primary conidia together with two primary conidia of *Erynia conica* (Ec). **5.** Aquatic conidia: a. developing, b. detached. Bars 100 µm. 6–7. *Zoophthora petchii*: **6.** Primary conidia (pc) and secondary coninida of type Ia (scIa) and of type II (scII, capilliconidia). **7.** Secondary conidia of type Ia (scIa) and type II (scII) and two tertiary conidia of type II (tcII) produced from type Ia secondary conidia. Bars 50 µm.



x (12) 13.6 (16) µm, L/D = 1.58 (1 series), those of type Ib were present but rare. – Cystidia powerful with a basal diameter of (20) 26.4 (34) µm tapering to (10) 11.5 (13) µm at the apex. (1 series, n = 18) (Plate 6, Fig. 2). – Resting spores (zygospores) develop from two conjugating short hyphae-like hyphal bodies (Plate 6, Fig. 4). Mature resting spores spherical, (28) 30.2–32.1 (35) µm, (2 series), yellow to brownish, surrounded with brown and stiff mycelium with a diameter of (5) 6.1 (9) µm (Plate 6, Fig. 3). Parts of this mycelium form root-like structures connected with the resting spores.

Distribution. – Fischingen TG, on stones in the river Murg at an altitude of 670 m.

A few infected Plecoptera were collected in early July. One of them contained sporulating mycelium and developing zygospores. Two cadavers contained mature resting spores; they were surrounded by brown, stiff mycelium as known from *E. rhizospora* (Thaxter 1888) and also mentioned in the original description of *E. plecopteri*. The fungus was assigned to this species although the fungal structures are slightly smaller than those described by Descals & Webster (1984).

On a single Plecoptera, Nemouridae at the same locality and in the same environment a similar species with distinctly smaller conidia was collected with the following morphology: Primary conidia (16) 18.7 (21) x (8) 9.1 (10) µm, Q = 2.06 (1 series, n = 25), mononucleate, bitunicate, elongate ellipsoid, largest diameter in the centre or slightly in the apical part, usually one prominent vacuole, sometimes two, papilla rounded. Type Ia secondary conidia (13) 14.3 (16) x (8) 9.1 (10) µm, Q = 1.58 (1 series, n = 25). Rhizoids and cystidia present, resting spores absent.

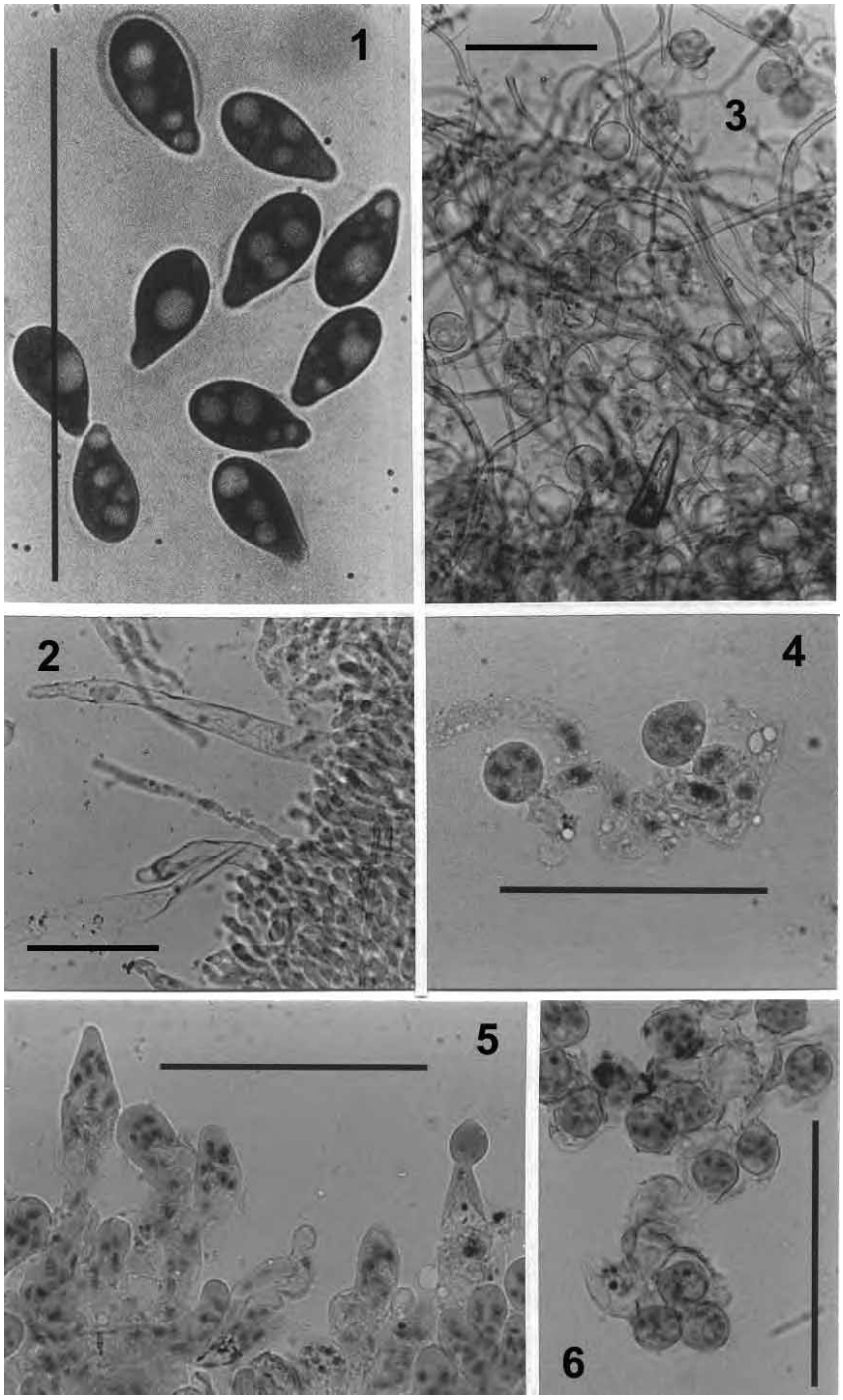
13. ***Erynia tumefacta*** Keller **sp. nov.** – Plate 7, Figs. 1–8.

Latin diagnosis. Rhizoidea imponentia, apicibus ramosa, hapteronibus specialibus non praedita. Protoplasti sphaerici vel subsphaerici, irregulariter rotundati vel ameboidei, valde vacuolati. Corpora hyphalia subsphaerica, 33–82 x 25–65 µm 8–28 nucleos 5–7 µm diametro continentia. Conidiophora digitate ramosa. Conidia primaria 24–35 x 11–16 µm, uninucleata, bitunicata, elongate ovoidea vel ellipsoidea, in medio vel parte apicali amplissima. Conidia secundaria habito primariis similia, 19–28 x 12–17 µm, vel subsphaerica, dein 17–19 x 12–16 µm. Cystidia abundant, longa imponentiaque. Sporae perdurantes absunt.

In Poliete lardaria Fabr. (hospite typico) (Dipteribus, Muscidis).

Holotypus. – ZT, Helvetia (Wattwil/Feldbach, SG), coll. et leg. S. Keller, 10 Aug 1994, no 83–68. Paratypi K et BPI.

Plate 6. 1–3. *Erynia plecopteri*: **1.** Primary conidia. **2.** Cystidia. **3.** Young resting spores embedded in thin and stiff hyphae. **4.** Developing resting spores with nuclei. Bars 100 µm. 5–6. *Entomophthora rivularis*: **5.** Conidiophores with tips becoming conical when primary conidia are formed. **6.** Projected primary conidia embedded in typical halo. Bars 100 µm.



Host. – *Polietes lardaria* Fabr. (Diptera, Muscidae).

Symptoms. – Cadavers attached with rhizoids to wet stones, moss and wood in a brook and along its borders, mainly 0-40 cm above the water level, but also to the walls and ceiling of a concrete bridge. The abdomen of sporulating cadavers was strongly swollen and completely covered by a white fungus layer; on head and thorax. The fungal growth was limited to mycelial bands along the intersegmental membranes. When cadavers were removed they usually broke between thorax and abdomen. Moribund but still living flies attached with rhizoids at the tip of the abdomen. When removing this flies the tip of the abdomen usually broke making visible a yellow mass of fungal material.

Rhizoids usually powerful and branched at the end, without specialised holdfast (Plate 7, Fig. 7). – Protoplasts spherical, subspherical, irregularly rounded or amoeboid, strongly vacuolised, in early stages nuclei not or only weakly staining in LPAO, in later stages deeply staining, multiplication probably by budding rather than by binary fission. Cells contain (3) 8 (15) nuclei with a diameter of (5) 6.1 (7) µm (1 series) (Plate 7, Fig. 1). – Hyphal bodies predominantly subspherical, (33) 44.0–57.5 (82) x (25) 38.1–52.1 (65) µm, (3 series) with (8) 15–20 (28) nuclei (4 series) with a diameter of (5) 5.7–5.9 (7) µm (2 series), germinating with single germ tubes (Plate 7, Fig. 2). – Conidiophores at base unbranched with a diameter of (10) 14.2 (18) µm (1 series, n = 30), digitately branched at terminal portion, shoulders with a diameter of (8) 10.6 (12) µm (1 series) (Plate 7, Figs. 3–4). – Primary conidia (24) 28.9–30.6 (35) x (11) 12.3–14.6 (16) µm, Q = 2.04–2.43 (6 series), uninucleate, bitunicate, elongate ovoid to ellipsoid, largest diameter in the middle or in apical portion, outer membrane separated except at papilla, large central vacuole; papilla rounded, slightly displaced from central axis, often separated from the body of the conidium with a slight bulge, where the outer membrane is attached (Plate 7, fig 5). – Secondary conidia of two types (Plate 7, fig 6): usually like primary, (19) 23.8–24.2 (28) x (12) 12.9–14.5 (17) µm, Q = 1.67–1.84 (3 series), developing laterally from primary conidia, outer membrane separated except at papilla, large vacuole, papilla distinctly narrower than that of primary conidia, often asymmetrical; or occasionally more rounded with indistinct apical point, (17) 17.8 (19) x (12) 13.9 (16) µm, Q = 1.28 (1 series, n = 20), large central vacuole, more intensely stained with LPCB than the other type of secondary conidia. – Cystidia abundant, powerful and long, endings usually enlarged, rarely bifurcate, diameter at the level of the conidial layer (19) 36.4 (53) µm and at the tip (10) 14.1 (24) µm (1 series, n = 30). – Resting spores not observed.

Culture. – Good growth on EMC. Mycelium white to dirty-white, felt-like with flocky to bush-like outgrowths around the

inoculation point, fold to honeycomb-like. Abundant projection of conidia. Primary conidia (24) 27.5-29.7 (38) x (12) 12.9–14.4 (17) µm, Q = 2.03–2.14 (4 series).

Distribution. – Switzerland, Wattwil (SG): Along the brook Feldbach, altitude of 870 m (type locality) and Fischingen (TG) along the river Murg.

Etymology of specific epithet. – The name refers to the fact that infected flies are strongly swollen.

The species was first collected by the end of July and sent to the author by C.Lienhard with the remark that diseased flies were abundant. This was still the case when own collections were carried out in the mid of August.

The species is a typical member of genus *Erynia* Humber (1989). This group is characterised by globular hyphal bodies, powerful cystidia and rhizoids without differentiated holdfasts.

From the same host (reported as *Polyetes lardaria)* Cavara (1899) described *Entomophthora delpiniana,* later transferred to *Erynia* by Humber (1981). This fungus has branched conidiophores, the conidia are obovate with rounded apex, 14–16 x 6–8 µm with a single nucleus measuring 3.5–4 µm, secondary conidia like the primary, the azygospores pyriform, 40–46 x 23–32 µm, the cystidia 260–300 x 20–26 µm, sometimes with bifurcate ending. The two fungi share identical characters such as the habitat, the host species, the strongly swollen appearance and the powerful, sometimes bifurcate cystidia. However, the dimensions of the conidia clearly separate these two fungi, also when considering that Cavara's material was shrunk and he took the germinating hyphal bodies as resting spores.

Polietes lardaria is on a list of fly species suspected to transmit *Mycoplasma conjunctivae*, the agent of infectious keratoconjunctivitis of small domestic and wild ruminants (Degiorgis & al., 1999).

14. ***Eryniopsis rhagionidis*** S. Keller **sp. nov.** – Plate 4, Figs. 4–6.

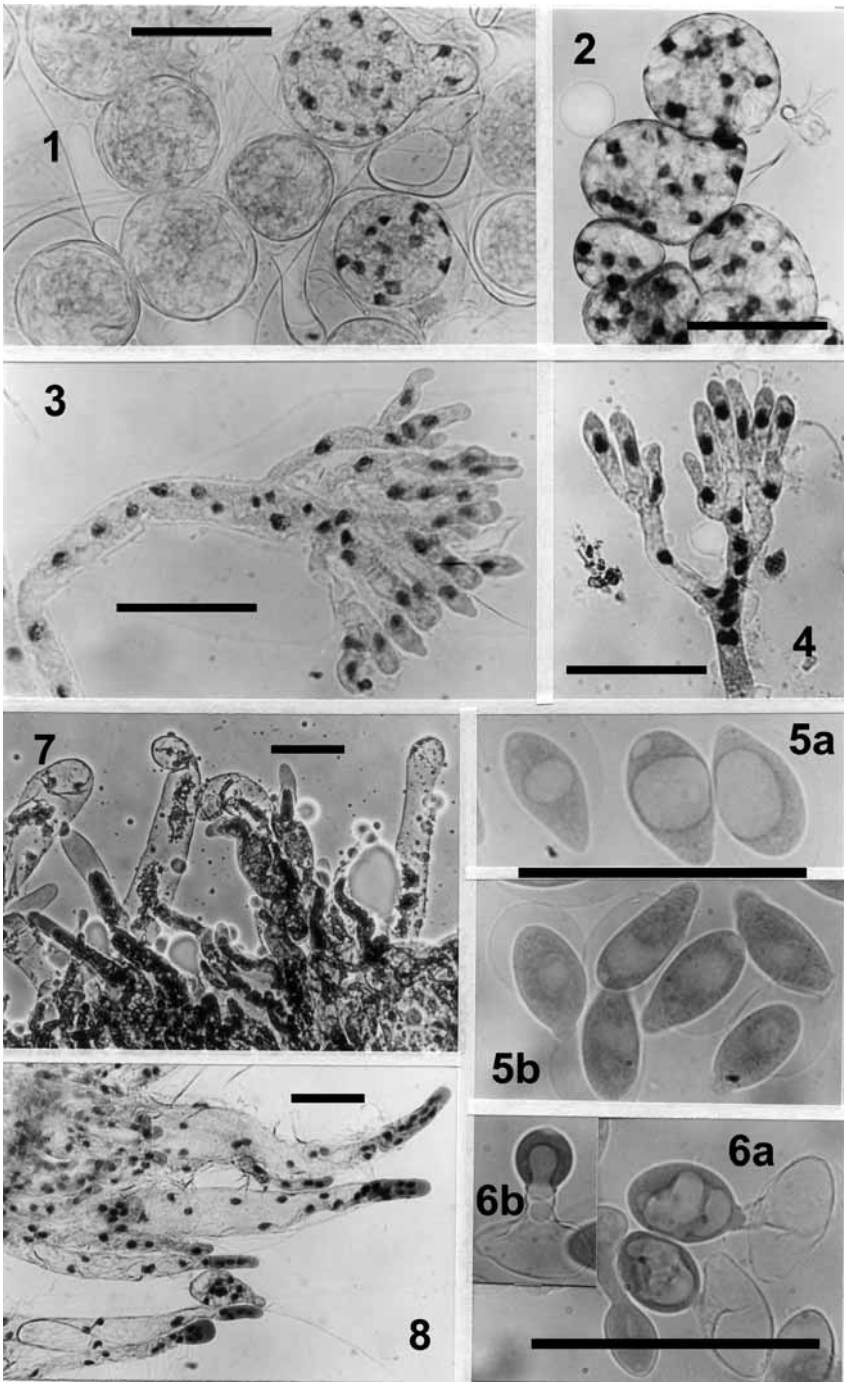
Corpora hyphalia, 25–49 x 16–19 µm. Conidiophora simplicia. Conidia primaria 27–35 x 10–17 µm, elongate subcylindrica vel subellipsoidea, asymmetrica, 7–11 nucleos continentia. Conidia secundaria habito primariis similia vel obovata, 22–25 x 11–13 µm. Cystidia, rhizoidea et sporae perdurantes absunt.

In Rhagionidarum hospite indeterminato. (hospite typico) (Dipteribus, Rhagionidis).

Holotypus ZT, Helvetia (Fischingen, Murg, TG), coll. et leg. S. Keller, 14 Jul 2005, no 93-1.

Host. – Unidentified species of Rhagionidae (Diptera).

Symptoms. - Cadavers fixed with the legs clasped around a twig about 150 cm above the water level of a small river.



Hyphal bodies (25) 34.9 (49) x (16) 18.1 (19) µm, sub-rectangular to short rod-shaped, rarely elongate-subspherical. – Conidiophores unbranched with a terminal diameter of (11) 12.5 (13) µm (1 series, n = 25) (Plate 4, Figs. 4–5). – Unprojected primary conidia measure (27) 29.9 (34) x (12) 13.6 (17) µm, Q = 2.2 (1 series), projected primary conidia measure (27) 31.2 (35) x (10) 12.0 (13) µm, Q = 2.61 (1 series, n = 25), elongate subcylindrical to subellipsoidal, with (7) 8.4 (11) nuclei with a diameter of (4) 4.5 (5) µm (1 series, n = 25), nuclei stain weakly with LPAO; asymmetric, largest diameter in the center or in the apical part; papilla indistinct (epapillate according to Lakon 1939) (Plate 4, Fig. 6). – Secondary conidia either resembling primary ones or elongate ovoid, (22) 23.2 (25) x (11) 12.4 (13) µm (1 series, n = 25). – Cystidia, rhizoids and resting spores absent.

Distribution. – Switzerland, Fischingen TG, river Murg at an altitude of 67o m. The species was collected mid July.

Distinguishing characters. - The species is closely related to *E. caroliniana* from which it can be separated by the number of nuclei and by the host.

A fungus matching the description given above from an unidentified fly had primary conidia measuring (25) 31.4 (39) x (10) 12.3 (16) µm, Q = 2.55 (1 series, n = 50). The elongate secondary conidia measured 38.9 $\pm$ 5.8 x 9.3 $\pm$ 0.6 µm, Q = 4.18 (n = 9).

15. ***Pandora americana*** (Thaxter) Keller **comb. nov.**

Basionym. – *Entomopthora americana* Thaxter, Mem. Boston Soc. Nat. Hist. 4: 179–180 (1888).

Synonyms. – *Zoophthora americana* (Thaxter) Batko emend. Balazy ex Humber (1993); *Erynia americana* (Thaxter) RemaudiÍre & Keller (1980); *Furia americana* (Thaxter) Humber (1989).

Host. – *Pollenia* cf. *vespillo* (Diptera, Calliphoridae) and unidentified calliphorid flies.

Symptoms. – Infected flies fixed to plants with spread wings.

Hyphal bodies short mycelium-like. – Conidiophores branched. – Primary conidia (27) 30.1–30.3 (35) x (13) 15.9–16.3 (19) µm, Q = 1,84–1,91 (2 series) ellipdoidal with distinct papilla; usually with single prominent vacuole. – Secondary conidia type Ia (22) 24.3 (27) x (15) 16.4 (19) µm, Q = 1.48 (1 series), usually

Plate 7. *Erynia tumefacta*: **1.** Protoplasts. **2.** Hyphal bodies. **3., 4.** Conidiophores. **5.** Different shapes of primary conidia, broad (a) and narrow (b). **6.** Secondary conidia of type Ia (a) and type Ib (b). **7.** Rhizoids with unspecialised endings. **8.** Cystidia. Bars 50 µm.

asymmetrical; secondary conidia type Ib (17) 18.4 (19) x (15) 16.4 (19) µm, Q = 1.13 (1 series) with indistinct apical point. – Rhizoids monohyphal with disc-like holdfast.

Distribution. – Stammheim (ZH) and Cazis (GR). Since resting spores were absent, the species cannot be identified unequivocally. However, material collected during an epizootic in northern Italy (Eraclea Mare, Veneto) and identified as *Erynia americana* (Keller 1993) contained resting spores and conidia, the latter with identical morphology as described here. Therefore, the Swiss material was attributed to this species. Previous records of *Pandora (Erynia) bullata* from Switzerland (Keller 1991) possibly should be attributed to *P. americana*.

16. ***Pandora cicadellis*** (Li & Fan) Li, Fan & Huang (1998)

Host. – Unidentified cicadellids (Homoptera, Cicadina)

Hyphal bodies short hyphae-like with a diameter of 11–16 µm with 4–10 nuclei (n = 15), nuclei with a diameter of 6.5 ± 0.58 µm. – Conidiophores branched. – Primary conidia (19) 20.6–26.3 (30) x (8) 10.1–12.0 (13) µm, Q = 2.02-2.20 (4 series). – Secondary conidia type Ia 18–23 x 8–11 µm, Q = 2.07 (n = 5); secondary conidia type Ib (14) 16.0–16.3 (18) x (10) 11.1.–11.5 (13) µm, Q = 1.42-1.47 (3 series). – Cystidia slender. – Rhizoids monohyphal with a diameter of (7) 11.3 (17) µm (n = 15).

Distribution. – Widen/Neunkirch (SH) and Watt (ZH). The species was collected in September in meadows bordering forests.

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

Hosts. – *Cantharis* (*Ancistronycha) abdominalis* (F.), *C. (A.) erichsonii* Bach, (Coleoptera, Cantharidae).

Symptoms. – Whole ventral side of infected beetles firmly attached to the underside of leaves of bushes and trees by numerous rhizoids. Wings closed also when the fungus is sporulating. Sporulation mainly around pronotum and from the parts of the abdomen not covered by the wings.

Hyphal bodies short mycelium-like, bent, branched or unbranched, with (10–) 17–18 (–28) nuclei (2 series, n = 25). – Primary conidia (22) 23.9–25.1 (28) x (11) 12.2–13.6 (16) µm, Q = 1.80–2.05 (6 series, n = 25), usually with 1-2 prominent vacuoles, papilla 6–7 µm broad, distinct, asymmentric. – Secondary conidia (16) 17.4–18.1 (19) x (11) 12.2–12.3. (13) µm, Q = 1.43-1.46 (2 series, n = 25). – Rhizoids monohyphal with a diameter of (6) 13.6 (23) µm.

Distribution. – Fischingen (TG), Steg/Fischenthal (ZH) (*C. erichsonii* and *C. abdominalis*) and Wyler/Innertkirchen (BE) (*C. abdominalis*).

All infected beetles included in the description above were collected between end of June and early August along small rivers about 1.5–3 m above ground. The dimensions given above are slightly larger than those given by Balazy (1993). On a single individual distinctly larger primary conidia measuring (27) 27.9 (30) x (17) 18.2 (19) µm, Q = 1.53 (1 series) were produced. From another unidentified cantharid species narrow primary conidia measuring (23) 27.5 (31) x (10) 11.9 (13) µm, Q = 2.32 (1 series) were obtained. The secondary conidia measured (18) 21.7 (25) x (12) 13.0 (16) µm, Q = 1.67. The differences in dimensions may be related to different host species but it cannot be excluded, that different species are involved. *P. lipai* was originally described as *Zoophthora lipai* from *Rhagonycha lignosa* and transferred to *Pandora* with the incorrect spelling "*lipae*" (Keller & Petrini 2005). Other hosts mentioned in the original description are *Cantharis livida, C. rustica* and *Malthinus flaveolus* (Balazy 1993).

18. ***Pandora longissima*** Keller, **spec. nov.** – Plate 8, Figs. 1–5.

Rhizoidea monohyphalia. Corpora hyphalia hyphis similia, 12–20 µm diametro, 30–130 µm longa, 2–10 nucleos 6–8 µm diametro continentia. Conidiophora digitate ramosa. Conidia primaria 78–81 x 11–12 µm, uninucleata, bitunicata, elongata, latissima in inferiore parte, ad apicem acuminata, recta vel curvata. Conidia secundaria habito primariis similia, 55–57 x 11–12 µm, vel subsphaerica, dein 19–20 x 15–16 µm. Cystidia rara, basali diametro 12–14 µm. Sporae perdurantes absunt.

In Limoniidarum insecto (hospite typico) (Dipteribus, Limoniidis).

Holotypus ZT, Helvetia (Lengnau, Surb, AG), coll. et leg. S. Keller, 8 Jul 2004, no 100-3.

Host. – *Antocha (Antocha) vitripennis* (Meigen, 1830) (Diptera, Limoniidae).

Etymology of specific epithet. – The name refers to the very long primary conidia.

Symptoms. – Cadavers attached with rhizoids on the shadow side of a thick wooden stake in a brook 10 to 30 cm above the water level. They could easily be removed.

Hyphal bodies short hyphae-like, unbranched or with single branch with an average diameter of (12) 15.5 (21) µm and a length varying between 30 and 130 µm (1 series, n = 25). They contain on average (2) 5.5 (10) nuclei with a diameter of (6) 7.4 (8) µm (1 series, n = 25) (Plate 8, Figs. 1–2). Multiplication by binary fission, rarely by budding. – Conidiophores digitally branched. Terminal diameter before formation of conidia 10–13 µm (Plate 8, Fig. 3). – Primary

conidia (68) 78.1–80.9 (100) x (10) 11.0–11.6 (13) µm, L/D = 6.97–7.07 (2 series, n = 25), slender, elongate, uninucleate, bitunicate; largest diameter in basal half, tapering towards the apex, straight or slightly bent. The conidia contain a single nucleus in central portion and 2–3 vacuoles, the largest vacuole close to the papilla or sometimes in the apical portion. Papilla subtriangular to rounded. Outer membrane partially separated (Plate 8, Figs. 4–5). – Two types of secondary conidia produced laterally on primary conidium, usually in the central portion, sometimes in the apical portion (Plate 8, Figs. 4–5). Undetached conidia of type Ia measure on average (45) 55.1–57.0 (70) x (10) 10.8–11.6 (13) µm, Q = 4.92–5.08 (2 series, n = 25), largest diameter in the basal half, distinctly bent. Type Ib secondary conidia measure on average (18) 18.9–19.9 (22) x (14) 14.9–15.6 (17) µm, Q = 1.27 (2 series, n = 25), conidial body nearly spherical with distinct papilla and sometimes with indistinct apical point. They may produce tertiary type Ia conidia that are strongly bent. – Cystidia rare with a diameter at the conidial level of about 12–14 µm. – Few monohyphal rhizoids with a diameter of 12–30 µm, tapering towards the end. – Resting spores not observed.

Distribution. – Switzerland, Endingen (AG), river Surb, coordinates 665700/264740.

Distinguishing characters. – The species is closely related to *E. conica* from which it is clearly separated by the shape of the hyphal bodies, the larger conidia and the host.

Two cadavers and a living host were collected on July 8, 2004. The two cadavers were fixed on the shaded side of a wooden stake together with thousands of small midges which had succumbed to *Erynia variabilis* and a few larger midges infected with *E. conica*.

19. ***Pandora philonthi*** (Balazy) Keller & Petrini (2005)

Host. – Unidentified species of staphilinid beetles (Coleptera, Staphylinidae).

Symptoms. – The species was collected in a pitfall trap. Two infected adult beetles were fixed with rhizoids to the wall of the collection vial.

Primary conidia (18) 20.9-23.4 (27) x (11) 13.4–13.9 (17) µm, Q = 1.57–1.68 (2 series), ovoid to ellipsoid, slightly asymmetric, usually with single prominent vacuole; papilla broad. – Secondary conidia type Ia (17) 19.6 (24) x (13) 14.5 (17) µm, Q = 1.35 (1 series). – Rhizoids monohyphal.

Distribution. – Klettgau (SH)

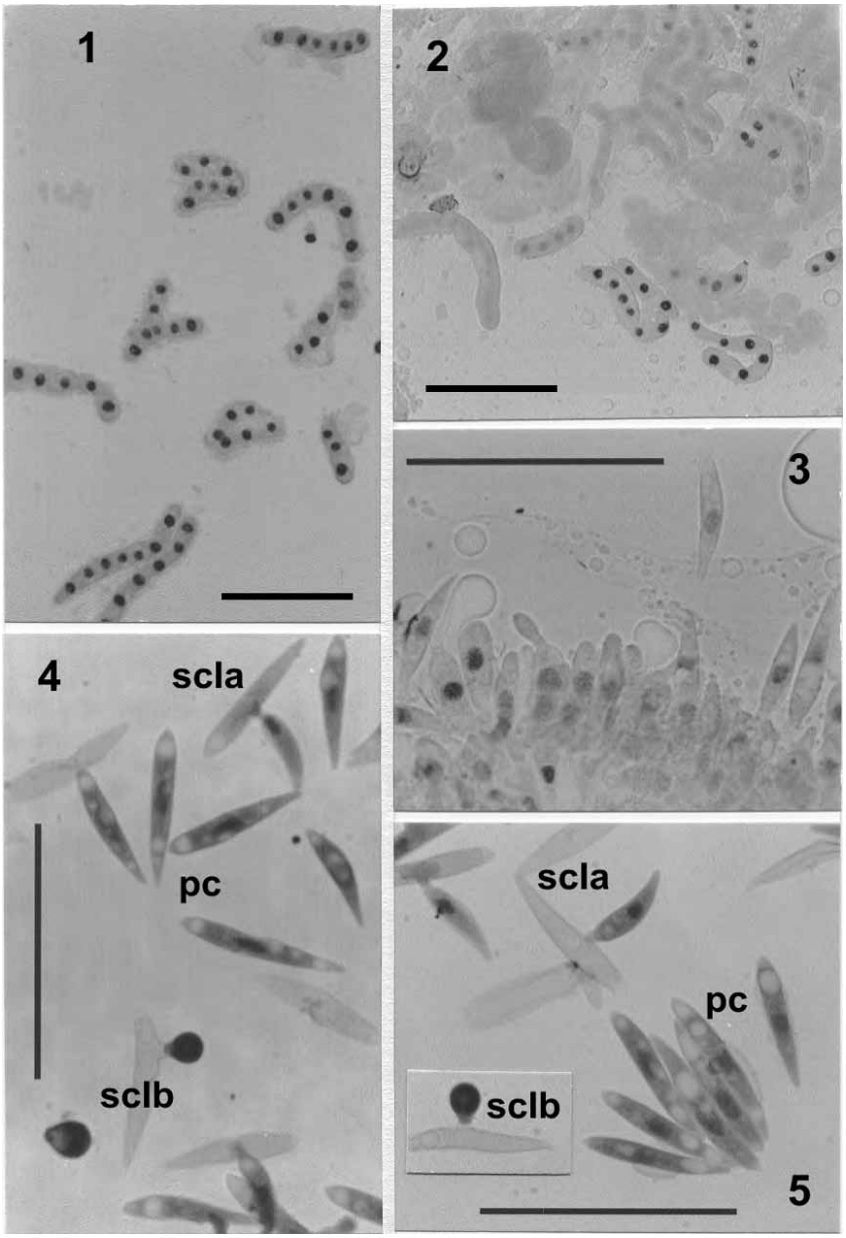


Plate 8. *Pandora longissima*: **1.** Hyphal bodies with nuclei. **2.** Protoplasts and hyphal bodies. **3.** Formation of primary conidia. **4., 5.** Primary conidia (pc) and secondary conidia of type Ia (scIa) and type Ib (scIb). Bars 100 μm.

20. ***Pandora sciarae*** (Olive) Keller **comb. nov.** – Plate 9, Figs. 1–7

Basionym. – *Empusa sciarae* Olive, Bot. Gaz. 41: 196. 1906.
Synonym. - *Furia sciarae* (Olive) Humber (1989)

Host. – *Bradysia* sp. (Diptera, Sciaridae).

Symptoms. – Infected midges fixed with rhizoids to the underside of leaves of fruit trees with wings spread.

Rhizoids with a diameter ranging from 7–21 µm, endings strongly branched, root-like to disc-like (Plate 9, Figs. 6–7). – Hyphal bodies short rod-shaped to short hyphae-like with a diameter of 10–18 µm, sometimes arranged in chains; contain 5–11 nuclei. – Conidiophores branched (Plate 9, fig 3). – Primary conidia (17) 19.6–21.8 (25) x (12) 14.9–16.6 (18) µm, Q = 1.25–1.42 (4 series), elongate subspherical, ellipsoid to subcylindrical; papilla narrow, small, asymmetrical (Plate 9, Figs. 4–5). – Two types of secondary conidia, those of type Ia measuring (17) 18.3–18.4 (21) x (13) 14.5–14.7 (17) µm, Q = 1.25–1.26 (2 series) (Plate 9, Fig. 5). – Cystidia with basal diameter ranging from 6–14 µm, not tapering, largest diameter sometimes short before apex (Plate 9, Fig. 2). – Resting spores absent.

Distribution. – Switzerland, Conthey (VS), and Burgrain, Alberswil (LU).

The data matches the description of *E. sciarae* Olive and and the fungus was therefore attributed to this poorly known species. It was collected from end of September to end of October in apple plantations. Sciarid larvae, which are also attacked by this species, were not investigated.

21. ***Strongwellsea pratensis*** S. Keller, **sp. nov.** – Plate 10, Figs. 3–7.

Conidiophora simplicia, mononucleata, terminaliter inflata. Conidia primaria 25–30 x 11–12 µm, bitunicata, elongate pyriformia vel subcylindrica. Cystidia, rhizoidea et sporae perdurantes absunt.

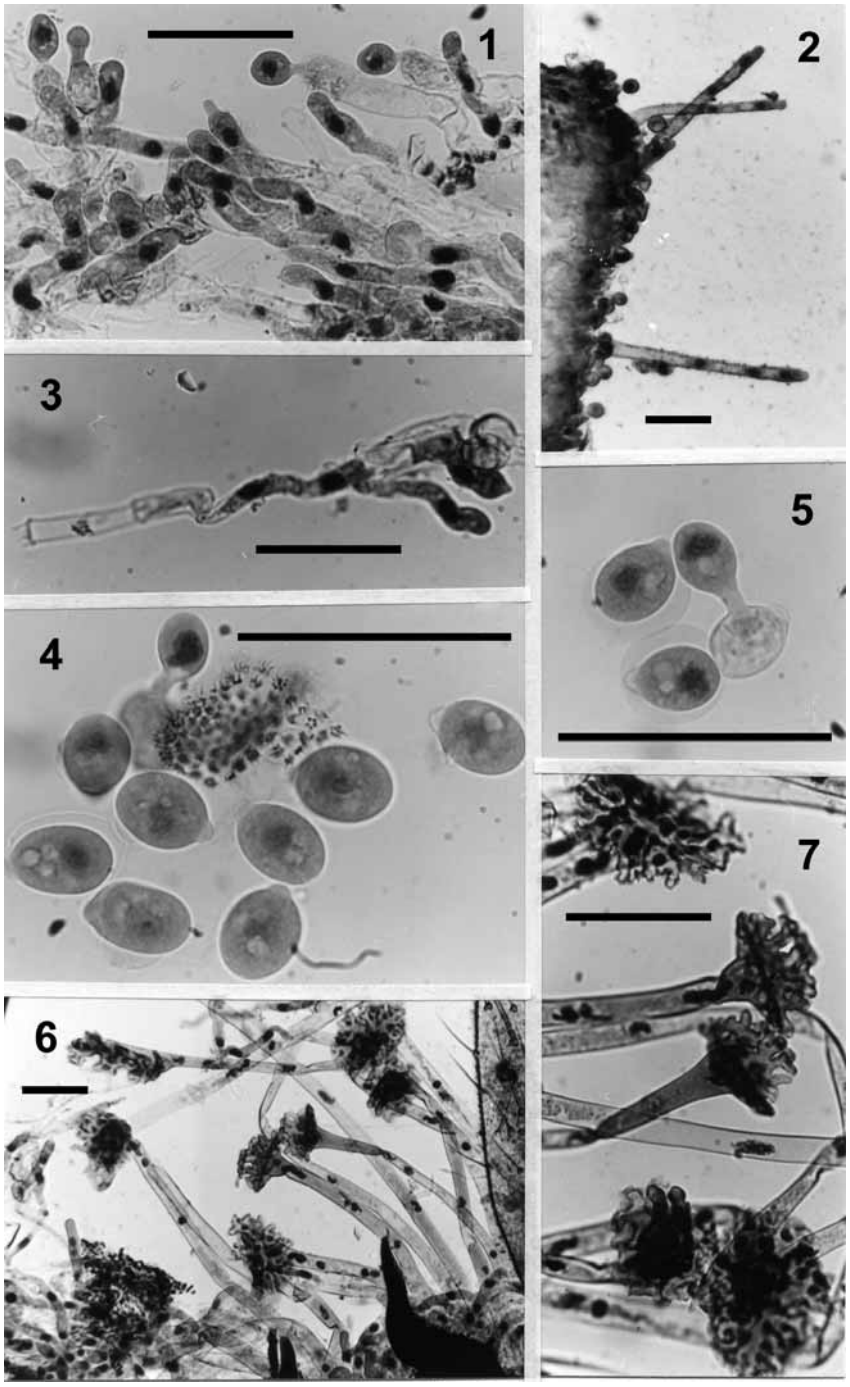
In Coenosia albicorni M. (hospite typico) (Dipteribus, Muscidae).

Holotypus ZT, Helvetia, Berg am Irchel, ZH, coll. et leg. S. Keller, 20 Jun 1994, no 68–42.

Host. – *Coenosia albicornis* Meigen [= *C. lineatipes* (Zett.)], (Diptera, Muscidae).

Etymology of specific epithet. – The name refers to the habitat where the infected flies where collected.

Plate 9. *Pandora sciarae*: **1.** Formation of primary conidia. **2.** Cystidia. **3.** Conidiophore. **4.** Primary conidia. **5.** Two primary conidia and formation of a secondary conidium of type Ia. **6., 7.** Rhizoids with disc-like endings. Bars 50 µm.



Symptoms. – The flies were collected in yellow Moerike-traps filled with 4 % sodium-hypoclorite. The infected flies were easily recognised by the presence of a hole on the ventral part of the abdomen.

Hyphal bodies in flies before the development of the typical hole hyphae-like, unbranched with (1) 5.0 (14) nuclei (1 series) measuring (7) 8.1–8.8 (10) µm (2 series). Some larger tubular, unbranched vesicles may contain up to 50 nuclei (Plate 10, Fig. 3). – Conidiophores unbranched, mononucleate, terminally enlarged (Plate 10, Fig. 5). – Primary conidia (24) 25.5-29.6 (33) x (11) 11.4–12.3 (13) µm, Q = 2.24–2.40 (3 series), mononucleate, bitunicate, elongate pyriform to subcylindrical, largest diameter usually in apical half (Plate 10, figs 6-7). – Secondary conidia and resting spores not present in the examined material.

Distinguishing characters. – The species resembles *S. castrans* and *S. magna*. It can be separated from the former by the larger Q-ratio and from the latter by the shorter conidia. It differs from both species by the host.

The species was collected in the frame of ecological investigations comparing the biodiversity in farms with high and low input (Keller & Häni 2000). It was collected in a meadow of a single low-input farm. In the same material a species of *Hydriella*, probably *H. griseola* (Diptera, Ephydridae) was found infected with a species of *Strongwellsea*. However, the fungus was in poor condition and could not be identified.

22. ***Zoophthora aphrophorae*** (Rostrup) Keller **comb. nov.**

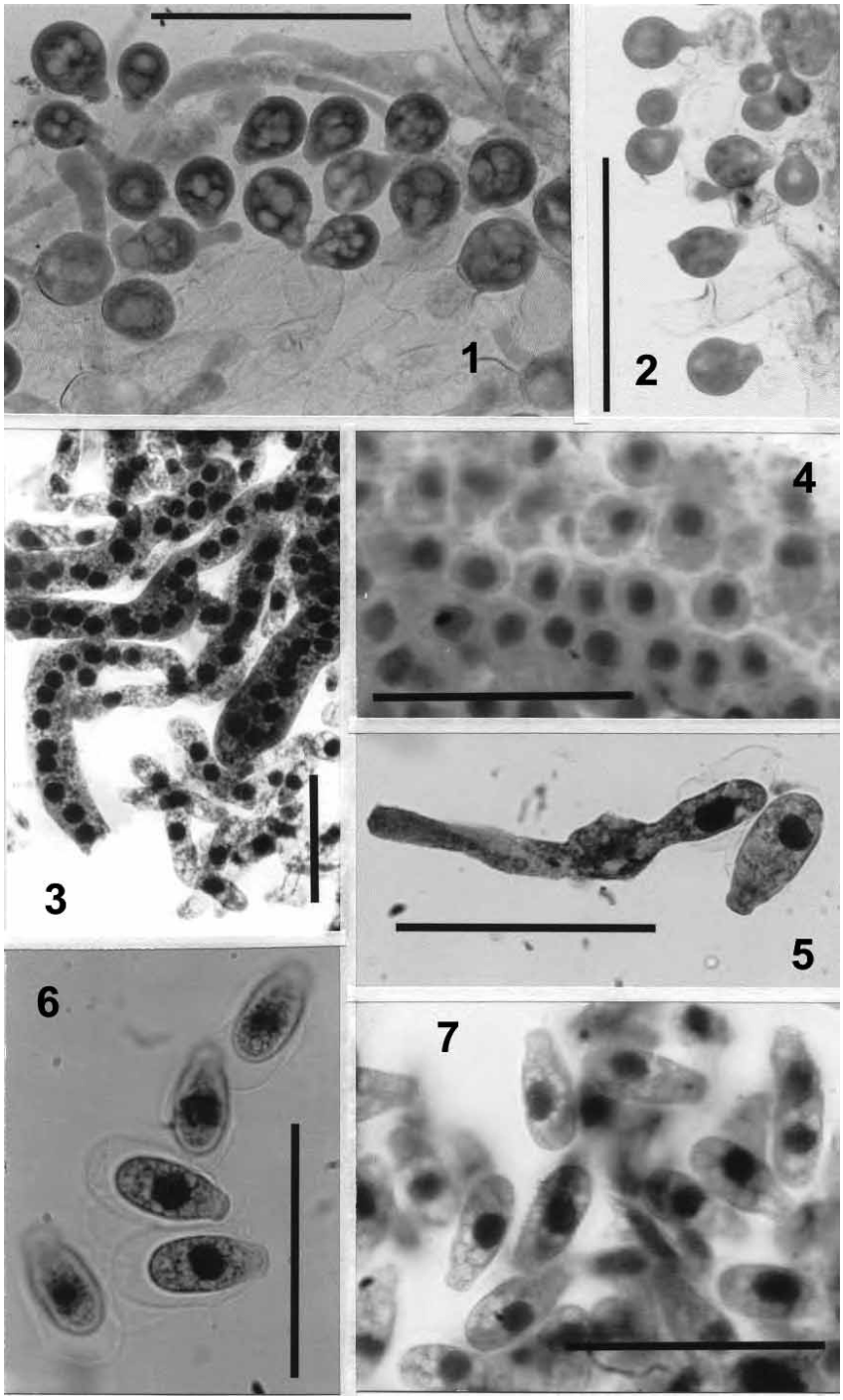
Basionym. – *Entomophthora aphrophorae* Rostrup, Botanisk Tidsskrift 20: 127–128 (1895)

Host. – Unidentified cicadellids (Homoptera, Cicadina).

Symptoms. – Infected insects fixed to the underside of leaves of *Salix* sp.

Rhizoids pseudorhizomorph. – Primary conidia (16) 18.2–18.3 (22) x (5) 6.1–6.7 (9) µm, Q = 2.73–2.98 (2 series, n = 50). Capilliconidia (16) 18.0 (21) x (4) 4.8 (6) µm, Q = 3.73 (1 series, n = 50). Length of the capillary tube (36) 42.5 (48) µm (1 series, n = 50).

Plate 10. 1–2. *Batkoa hydrophila*: **1.** Primary conidia. **2.** Formation of primary conidia. Bars 100 µm. 3–7. *Strongwellsea pratensis*: **3.** Multinucleate structures (developing hyphal bodies?). **4.** Mononucleate cell layer (differentiated hyphal bodies?). **5.** Mononucleate, unbranched conidiophore with developing conidium and projected primary conidium. **6., 7.** Primary conidia with separated outer membrane (5). Bars 50 µm.



Distribution. – Reckenholz-Zurich (ZH)

Two specimens were collected in October. The species has smaller conidia than *Z. radicans* and differs in many aspects from *Z. petchi* Ben-Zeév & Kenneth (1981). Although it has slightly narrower primary conidia it was attributed to *Z. aphrophorae*.

23. ***Zoophthora ichneumonis*** Bałazy (1993)

Hosts. – Unidentified species from Ichneumonidae and Torymidae.

Symptoms. – Infected insects fixed to the underside of leaves of deciduous trees and bushes, wings spread.

Rhizoids pseudorhizomorph. – Primary conidia (16) 17.5–21.6 (28) x (5) 6.1–7.2 (9) µm, Q = 2.65–3.17 (5 series). – Secondary conidia of type Ia (149 15.6 (17) x (6) 7.0 µm, Q = 2.24 (1 series). Capilliconidia (16) 17.8 (19) x (4) 5.3 (6) µm, Q = 3.34 (1 series). – Resting spores spherical, hyaline, smooth, (19) 26.1–26.4 (30) µm (2 series). – Nuclei in hyphal bodies with a diameter of (4) 4.7 (5.5) µm.

Distribution. – Zurich-Reckenholz (ZH), Watt (ZH) and Fischingen (TG). The material was collected between June and September.

24. ***Zoophthora miridis*** Bałazy (1993)

Host. – *Dicyphus pallidus* (H.-S.) (Heteroptera, Miriade).

Symptoms. – Dead insects fixed to the underside of leaves of *Lamium* sp.

Rhizoids pseudorhizomorph. – Primary conidia (14) 17.2–19.7 (25) x (6) 6.7–7.5 (9) µm, Q = 2.47–2.67 (6 series). – Secondary conidia of type Ia (10) 11.9–13.2 (16) x (6) 6.9–7.1 (9) µm, Q = 1.67–1.88 (3 series). Capilliconidia (16) 17.7–18.9 (23) x (4) 4.6–5.5 (6) µm, Q = 3.23–4.10 (3 series). Length of the capillary tube (30) 42.5–53.1 (67) µm (3 series). – Resting spores spherical, hyaline, smooth, (21) 24.5–25.0 (30) µm (2 series).

The species grows well on Sabouraud-egg yolk media. Primary conidia produced on this medium measure (14) 17.4–18.7 (23) x (6) 6.2–6,9 (9) µm, Q = 2.56–2.92 (6 series).

Distribution. – Hausener Seen (ZH).

Although the species differs slightly from the original description of *Z. miridis* it has been attributed to this species because of the identical host species.

25. ***Zoophthora nematoceris*** Bałazy (1993)

Host -.- Undetermined species of Sciaridae (Diptera).

Symptoms. – Dead insect fixed to the underside of leaves of bushes, wings spread.

Rhizoids pseudorhizomorph. – Primary conidia (15) 17.7–18.3 (19) x (5) 5.8–6.5 (7) µm, Q = 2.73–3.14 (4 series, n = 25). Capilliconidia (14) 16.3–19.3 (22) x (4) 4.4–4.9 (6) µm, Q = 3.36–3.95 (4 series, n = 25). Length of the capillary tube (36) 55.3–59.7 (82) µm (2 series, n = 25). Resting spores spherical, hyaline, smooth, (23) 27.3 (34) µm (1 series, n = 25).

Although it originates from the same host group as *Z. nematoceris*, the species differs slightly in the size of the capillary conidia as well as in the length of the capillary tubes.

26. ***Zoophthora occidentalis*** (Thaxter) Batko (1964).

Host. – *Acyrthosiphon pisum, Rhopalosiphum padi* (Homoptera, Aphididae).

Rhizoids pseudorhizomorph. – Primary conidia measured on average 33.1–38.2 x 6.9–8.7 µm (Q = 4.0–5.5) (9 series). – Capilliconidia 24.1–25.0 x 7.7–8.9 µm (Q = 2.73–3.15) (5 series) and the capillary tube had a mean length of 98–108 µm.

Distribution. – Klettgau (SH).

The species is closely related to *Z. phalloides*. A possibile identity of the two species has been discussed by Balazy (1993) and Keller (2006).

27. ***Zoophthora petchii*** Ben-Ze'ev & Kenneth (1981). – Plate 5, Figs. 6–7.

Host. – unidentified larger cicadellid species (Homoptera, Cicadellidae).

Symptoms. – Adult insect fixed with rhizoids to the underside of a leaf, wings closed, also when sporulating.

Rhizoids pseudorhizomorph. – Primary conidia (25) 27.9 (33) x (7) 7.7 (9) µm, Q = 3.63 (1 series, n = 25), elongate subcylindrical, papilla conical and clearly demarcated (Plate 5, Fig. 6). – Secondary conidia of two types (Plate 5, Figs. 6–7). Type Ia secondary conidia (17) 18 (19) x (8) 9.2 (10) µm, Q = 1.95 (1 series, n = 25), obovoid. Capilliconidia (18) 19.6 (21) x (6) 7.4 (9) µm, Q = 2.65 (1 series, n = 25), banana-shaped with rounded base and bent apical part, ending with ring-like structure, usually with single prominent vacuole (Plate 5, Figs. 6). Capillary tube (31) 42.8 (52) µm long (1 series, n = 25). Type Ia secondary conidia produced tertiary

capilliconidia of similar shape as the secondary capilliconidia but with more pointed base and apex (Plate 5, Figs. 7).

Distribution. – Fischingen TG, river Murg.

The species was found mid July fixed to the underside of a leaf on the border of a samll river. It was attributed to *Z. petchii* due to the peculiar shape of the capilliconidia although the dimensions are slightly larger than those given in the original description. However, the original description was based on exsiccata which are known to characteristically shrink.

28. ***Zoophthora psyllae*** Bałazy (1993).

Host. – *Trioza urticae* (Homptera, Psyllidae)

Symptoms. – Infected insects fixed to stem and underside of leaves of *Urtica dioica*, adults also to the stem. White mycelium emerges along the intersegmental membranes.

Hyphal bodies hyphae-like. – Primary conidia (14) 17.5–19.2 (24) x (6) 6.8–7.4 (10) µm, Q = 2.41–2.78 (6 series). – Capilliconidia (16) 18.2–19.7 (22) x (5) 5.4–5.7 (7) µm, Q = 3.23–3.83 (6 series). Length of the capillary tube (37) 51.0–56.3 (81 µm) (3 series). – Resting spores spherical, hyaline, smooth, (21) 24.5–25.0 (30) µ m (2 series).

The species grows well on Sabouraud-egg yolk media. Primary conidia produced on this medium measure (16) 18.3 (23) x (7) 8,3 (10) µm, Q = 2.20 (1 series). Capilliconidia measure (16) 18.6–19.8 (24) x (5) 5.5–5.8 (7) µm, Q = 3.38–3.41 (2 series).

Distribution. – Neunkirch (Widen) (SH), Watt (ZH), Zurich-Reckenholz (ZH).The species is very common on *Tioza urticae* (Homoptera, Psyllidae) often causing epizootics in autumn.

A similar fungus was collected from another species of Psyllidae, *Psyllopsis fraxinicola* (Foerster) attached to the underside of laeves of *Fraxinus excelsior*. The primary conidia measured (18) 19.8–21.1 (24) x (6) 7.0–8.1 (8) µm, Q = 2.53–2.93 (4 series, n = 25). The capilliconidia measured (18) 20.7–22.0 (24) x (5) 5.6–6.1 (7) µm, Q = 3.40–3.83. The type Ia-secondary conidia measured (14) 15.0 (16) x (8) 8.7 (10) µm, Q = 1.72 (1 series, n = 25).

29. ***Zoophthora rhagonycharum*** Keller **comb. nov.**

Basionym. – *Tarichium rhagonycharum* Bałazy. Bull. Acad. Pol. Sci., Ser. Sci. Biol. 29: 223–224. 1982.

The presence of typical characters of the genus *Zoophthora* (hyphae-like hyphal bodies, compound rhizoids) justify the transfer

of this species to the genus *Zoophthora*. The species was found on *Rhagonycha fulva* (Coleoptera, Cantharidae) and has been reported earlier from Switzerland (Keller 1991).

Distribution. – Boppelsen (ZH), Klotener Ried (ZH).

Discussion

This research adds 29 species of arthropod-pathogenic Entomophthorales to the list of records from Switzerland and brings its number to 90 species. This represents 38 % of the described species (45 % if the form-genus *Tarichium* is not considered). Nine species are new to science. A single one is from the agricultural environment and the others originate from natural habitats. Three species are new combinations and 11 species first records since the original description; among them, *Entomophthora rivularis* (known only from a single specimen, Keller 2002), *Erynia gracilis* (no records since Thaxter 1888), *Pandora cicadellis* (known only from China, Li & Fan 1998) and *Zoophthora aphrophorae* (no records since Rostrup 1895) are noteworthy.

Many collections are not included in this paper because they could not be attributed to a species. Most of these belong to the *Entomophaga tipulae*-group, the *Erynia ovispora*-group and the *Zoophthora radicans*-group. The difficulties with the attribution to a given species show that classical taxonomy based on morphology and cytology has reached its limits and does no longer allow one to distinguish species. It may also suggest that these groups of fungi or the arthropod-pathogenic Entomophthorales in general are in a complex and dynamic evolutionary process.

Future work based on genetic markers may help to define and delimit species. Nevertheless, there is stil enough to do for classical taxonomists. There are still many habitats which are not or only incompletely explored and harbour doubtless many further undescribed species. Thus, molecular and classical taxonomy are expected to yield additional information in the survey of Entomophthorales.

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