Arthropod-pathogenic Entomophthorales of Switzerland. I. *Conidiobolus, Entomophaga* and *Entomophthora*

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Introduction

The Entomophthorales include the most important pathogens of many species of Arthropods. There are numerous reports of epizootics in pest insect populations, but also in populations of harmless and beneficial species. They are adapted to a high degree to their hosts and this is expressed in their pathological, biological and ecological characteristics. They usually possess a high specificity, pathogenicity and virulence. Multiplication and colonisation may be very rapid and they are able to survive unfavourable conditions.

Considering these attributes and abilities it is not surprising that these fungi increasingly attract the interests of insect mycologists and plant protectionists. They possess without doubt an enormous potential which could be used in the regulation of populations of pest and vector arthropods. Important prerequisits for their practical use are a knowledge of the species, host-pathogen-interactions and host range as well as ecological and physiological attributes.

Since the first description of an arthropod-pathogenic Entomophthorales by Cohn (1855) many publications on morphology and pathology of these fungi have appeared. Here reference is made to only 3 monographs which are still considered as standard publications: Thaxter (1888), Lakon (1919) and Macleod (1963). More recent papers concerning their occurrence in geographically limited regions concern the Entomophthorales of Sweden (Gustafson, 1965), Great Britain (Waterhouse & Brady, 1982) and Israel (Ben-Ze'Ev et al., 1984).

Up to date there are only a few sporadic observations on these fungi from Switzerland, e. g. by Lebert (1857), Winter (1881), Turian (1957, 1960), Turian & Wuest (1969) and Carl (1975). In the present paper the author describes those species from Switzerland collected by himself or sent for identification. In addition to morphological and cytological data, observations on distribution, seasonal occurrence, epizootiology and culturing are given. The species described include those mentioned earlier from Switzerland with the excep-

tion of *Conidiobolus carpentieri* (GIARD) REMAUDIÈRE & KELLER (TURIAN, 1957).

Methods

a. Collection and preparation of the material

Arthropods that had succumbed to mycosis were usually collected together with their support. When this was impossible they were loosened with a pair of tweezers, placed in small plastic containers and transported to the laboratory. Numerous samples were desiccated. The preparation of the material followed the same day or within a few days. Small cadavers like mites or thrips were directly mounted on slides. Larger cadavers were placed on the surface of water in small Petri dishes. The projected conidia were collected on a slide placed 1–4 mm above the cadaver.

The collection of secondary conidia of type I (BEN-ZE'EV & KENNETH, 1982) took place in the same way as that of primary ones: a slide with primary conidia was placed in a humid chamber. The projected conidia were collected on a second slide placed about 2 mm above. Secondary conidia of type II (capilliconidia) were often produced in this situation on the lower slide. However, they were usually also collected from the water surface on which the cadaver had been placed, often together with secondary conidia of type I.

The cadavers usually remained on the water surface for 8–16 hours and were then transferred to 70% (v/v) ethanol and stored until preparation took place. Numerous samples were removed from the water surface and dried as herbarium material.

b. Stains

Conidia and cadavers were mounted in lactophenol-cottonblue (LPCB) (0.1% cotton blue) or in lactophenol-aceto-orcein (LPAO) composed of the two following solutions: solution 1: lactophenol (LP) (ROMEIS, 1968): 20 g crist. phenol, 20 ml lactic acid, 10 ml glycerol, 20 ml dist. water. Solution 2: aceto-orcein (AO): 1 g orcein powder solved in 100 ml 50% acetic acid (v/v). These two solutions were used in the following compositions: 1 part LP + 1 part AO (suitable for nuclear staining in the genera *Conidiobolus, Entomophaga, Neozygites, Eryniopsis*), 2–3 parts LP + 1 part AO (suitable for nuclear staining in the genera *Entomophaga, Entomophthora, Eryniopsis, Erynia, Zoophthora).*

The FEULGEN reaction stain (FRS) proved to be a suitable stain for nuclei in conidia of practically all considered species (ROMEIS, l. c.). In some species of Entomophthora good nuclear staining results were obtained with the method of GIEMSA (ROMEIS, l. c.). This method was applied using whole cadavers instead of projected

conidia. For the FRS and Giemsa methods fixation is needed prior to the staining process. This results in a shrinking of both the conidia and the nuclei. Both methods especially the FRS eliminate the cytoplasmic content of the conidia, the remaining stained nuclei appear on a clear background which facilitates the counting of nuclei. For this purpose the FRS is recommended for species of the genera *Conidiobolus*, *Entomophaga* and *Entomophthora*.

For histological sections the cadavers stored in ethanol were fixed in BOUIN's fixative, embedded in plastic (JB4), sectioned in 4 µm sections and stained with haematoxilin (ROMEIS, l. c.).

c. Isolation and cultivation

Two methods were used to isolate the fungi: small insects like aphids were briefly dipped in 70% ethanol and subsequently disinfected in sodium-hypochlorate with about 2% active chlorine for 2 minutes. After washing twice in sterile water the cadavers were placed on the culture medium. The second method was used for larger insects as well as aphids. Cadavers were placed, usually without previous disinfection of their surface, in small sterile Petri dishes containing water, humid filter paper or humid cotton plugs. A cover glass placed above the cadaver collected the projected conidia which subsequently were removed with a piece of medium and inoculated into the culture tube.

4 media were used for isolation and culturing of the fungi: (1) Sabouraud-dextrose-agar (SDA), (2) SDA enriched with egg yolk (1 egg yolk per 200 ml SDA) (SDAEY), (3) 1 part egg yolk diluted with 1 part milk, coagulated at 80° C for 70 minutes (EYM) and (4) the *Entomophthora*-complete medium (EMC) developped by BEN-ZE'EV (pers. comm.). The conidia and resting spores measured usually originated from the first, second or third subculture.

d. Presentation of the results

Measurements of fungal structures were made from preparations mounted in LPCB or LPAO using a magnification of x500. Measurements and counts of nuclei were made, if not otherwise stated, from preparations mounted in LPAO using a magnification of x1250. For these measurements only nuclei appearing more or less spherical were considered. It must be noted that an error of about 0.2–0.3 µm resulted due to the resolution power of the microscope and the often indistinct margins of the nuclei.

All counts and measurements were based, if not otherwise stated, on 50 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 number of these series is

given after the range of the mean values, the range of the extreme values (in brackets) and the ratio length/diameter (L/D). Single measurements of fungal structures are rounded to 1 µm, those of nuclear diameters to 0.5 µm.

Systematics

The order Entomophthorales differs from the other orders of the Zygomycotina by the active projection of the single conidia and the tendency to parasitism mainly of insects and small soil-inhabiting organisms. A detailed description is given by BENJAMIN (1979). According to their biology they can be placed in 3 groups: (1) Saprobes, (2) parasites of tardigrades, nematodes, tabanid larvae, algae and fern gametophytes, and (3) parasites of arthropods, mainly insects. This classification, however, is without taxonomic importance.

The saprobes are placed in the genera *Basidiobolus* and *Conidiobolus*. The latter, however, contains some insect pathogenic species. Both genera were recently revised, *Basidiobolus* by COREMANS-PELSENEER (1974) and *Conidiobolus* (without the typical insect pathogenic species) by KING (1976 a, b). The species of the second group were reviewed by TUCKER (1981) and attributed to 6 genera.

The arthropod pathogenic species were, until recently, placed in the genera *Massospora* and *Entomophthora* (MACLEOD, l. c.). In contrast to *Massospora*, which represents a homogenous group (reviewed by SOPER, 1974) the genus *Entomophthora* with the then accepted definition formed a morphologically very heterogenous group without a sound delimitation of the genus *Conidiobolus*. Propositions by BATKO (1964 a, b, 1966) and by BATKO & WEISER (1965) to split this genus into several genera and subgenera were not immediately followed but formed the basis for the revisions carried out by REMAUDIÈRE & HENNEBERT (1980), REMAUDIÈRE & KELLER (1980), HUMBER (1981, 1984 a) and BEN-ZE'EV & KENNETH (1982). These revisions appear controversial at first sight, because different emphasis were placed on different characteristics. The results, however, look very similar. The generic classification chosen for this presentation is a synthesis of the different points of view, considered in the light of the author's own research.

Following HUMBER (1984 b) the order Entomophthorales consists of 3 families: the Basidiobolaceae, Ancylistaceae and Entomophthoraceae, differing in nuclear characteristics and organisation of the thalli. Following this classification all of the genera listed below would belong in the Entomophthoraceae except the genus *Conidiobolus* (Ancylistaceae).

Descriptions of the Swiss material

The following genera and species are presented:

Part I: *Conidiobolus apiculatus, C. coronatus, C. major, C. obscurus, Entomophaga aulicae, E. batkoi, E. conglomerata, E. domestica* sp. nov., *E. gigantea, E. grylli, E. limoniae* sp. nov., *E. papillata, E. tenthredinis, Entomophthora brevinucleata, E. culicis, E. helvetica, E. muscae, E. planchoniana, E. schizophorae* sp. nov., *E. trinucleata* sp. nov.

Part II: *Erynia aquatica, E. athaliae* sp. nov., *E. blunckii, E. bullata, E. conica, E. curvispora, E. dipterigena, E. ellisiana, E. gammae, E.* cf. *magna, E. minutospora, E. myrmecophaga, E. neoaphidis, E. ovispora, E. rhizospora, E. variabilis, E. virescens, Eryniopsis caroliniana, Neozygites adjarica, N. fresenii, N. microlophii* sp. nov., *N. parvispora, N. turbinata, Zoophthora anglica, Z. aphidis, Z. crassitunicata, Z. lanceolata, Z. phalloides, Z. radicans, Z. viridis* sp. nov., *Tarichium rhagonycharum.*

Key to the described genera of Entomophthorales

1. Only resting spores known; species incertae sedis *(Tarichium)*
1*. Conidia known 2
2. Primary conidia uninucleate, bitunicate; elongate pyriform, fusiform or cylindrical. Conidiophores usually branched. Rhizoids usually present 3
2*. Primary conidia with more than 1 nucleus, unitunicate; campanulate, spherical, pyriform, ellipsoidal or subcylindrical. Conidiophores unbranched. Rhizoids present or absent 4
3. Primary conidia pyriform, fusiform or subcylindrical; papilla smoothly rounded, not clearly demarcated from conidial body. Secondary conidia like primary or spherical with or without small apical point ..... *Erynia*
3*. Primary conidia fusiform or cylindrical; papilla conical, pointed or rounded, demarcated from conidial body by a collar. Secondary conidia like primary or sickle- to crescent-shaped on long, slender capillary ..... *Zoophthora*
4. Primary conidia with apical point, containing 2 to about 40 nuclei. Halo around projected primary conidia ..... *Entomophthora*
4*. Primary conidia without apical point. No halo around projected conidia 5
5. Primary conidia elongate with about 5–15 nuclei; papilla usually indistinct, rounded. Secondary conidia either like primary or fusiform to subcylindrical on relatively short conidiophore .... *Eryniopsis*
5*. Primary conidia spherical to pyriform 6

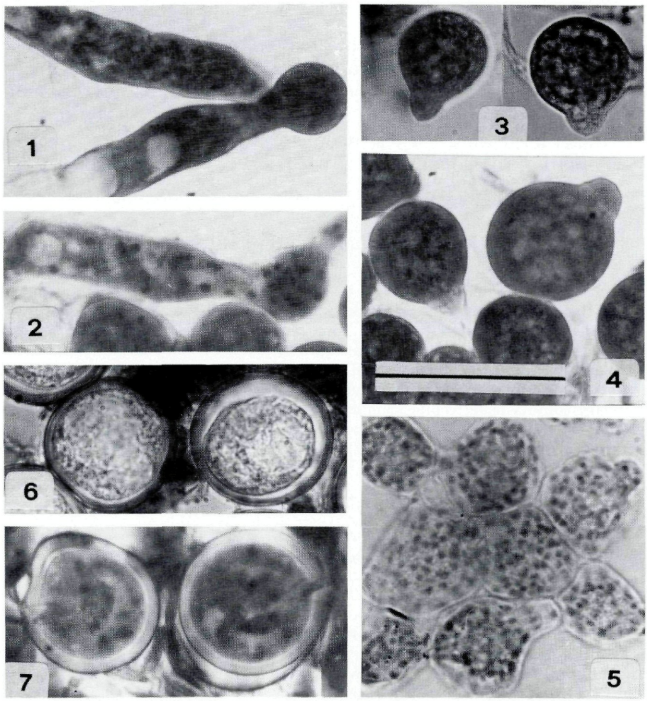


Plate 1: figs. 1–7: *Conidiobolus apiculatus*. 1. Conidiophores. – 2. Conidiophore showing nuclei (LPAO). – 3. Primary conidia with pointed papilla. – 4. Primary conidia with rounded papilla. – 5. Primary conidia with nuclei (Feulgen reaction stain). – 6. Resting spores. – 7. Burst resting spores showing numerous nuclei (LPAO). – Bar in fig. 4 represents 50 μm, figs. 1–7 same magnification.

6. Primary conidia relative small, spherical with flattened papilla or rarely Montgolfière-shaped with more rounded papilla, 4–8 nuclei. Secondary conidia like primary or amygdalliform on long, slender, distally bent capillary. Resting spores ellipsoidal to subspherical, dark ..... *Neozygites*

6*. Primary conidia relative large, subspherical, pyriform; more than 8 nuclei on average; papilla rounded or pointed 7

7. Nuclei small, not or weakly staining in LPAO, on average more than 50 per conidium ..... *Conidiobolus*

7*. Nuclei large, more or less deeply staining in LPAO, on average more than 10 per conidium ..... *Entomophaga*

Conidiobolus BREFELD (1884)

Untersuch. Gesammtg. Mykol. 6: 35–78

Hyphal bodies irregular, producing single conidiophore or resting spore. Conidiophores unbranched, with or without terminal enlargement; nuclei staining weakly or not in LPAO, on average smaller than 3.0 µm. Primary conidia unitunicate, spherical with rounded or conical papilla with or without point; nuclei small, stain distinctly with the FRS, very numerous, on average between 50–100 per conidium. Secondary conidia usually like primary, produced on short lateral secondary conidiophore; sometimes microconidia around primary conidia; capilliconidia, in some species only, fusiform to elliptical. Resting spores spherical, hyaline, surrounded by thin episporium, or villose. Rhizoids present or absent, cystidia very rare. Rapid growth on standard media.

Type species: *Conidiobolus utriculosus* BREFELD, l. c.: 37.

Key to described species of *Conidiobolus*

1. Rhizoids present 2
1*. Rhizoids absent 3
2. Primary conidia on average 40–45 × 34–39 µm; resting spores on average 40–45 µm; rhizoids numerous, vigorous; on Homoptera Cercopidae ..... *major* (3)
2*. Primary conidia on average 35–39 × 29–32 µm; resting spores on average 35–38 µm, single rhizoids; on different hosts ..... *apiculatus* (1)
3. Primary conidia on average 34–44 × 28–36 µm; resting spores smooth, on average 34–38 µm; on Homoptera Aphididae, Callaphididae, Lachnidae ..... *obscurus* (4)
3*. Primary conidia on average 50–53 × 38–40 µm; resting spores villose, on average 30–32 µm; on different hosts ..... *coronatus* (2)

1. *Conidiobolus apiculatus* (THAXTER) REMAUDIÈRE & KELLER (1980) – Pl. 1: figs. 1–7

Mycotaxon 11: 330.

Bas.: *Empusa apiculata* THAXTER (1888). Mem. Boston. Soc. nat. Hist. 4: 163–164, figs. 62–75.

Hosts. – Adults of different species of Diptera including *Psila rosae* F. (Psilidae); larvae of Hymenoptera Tenthredinidae.

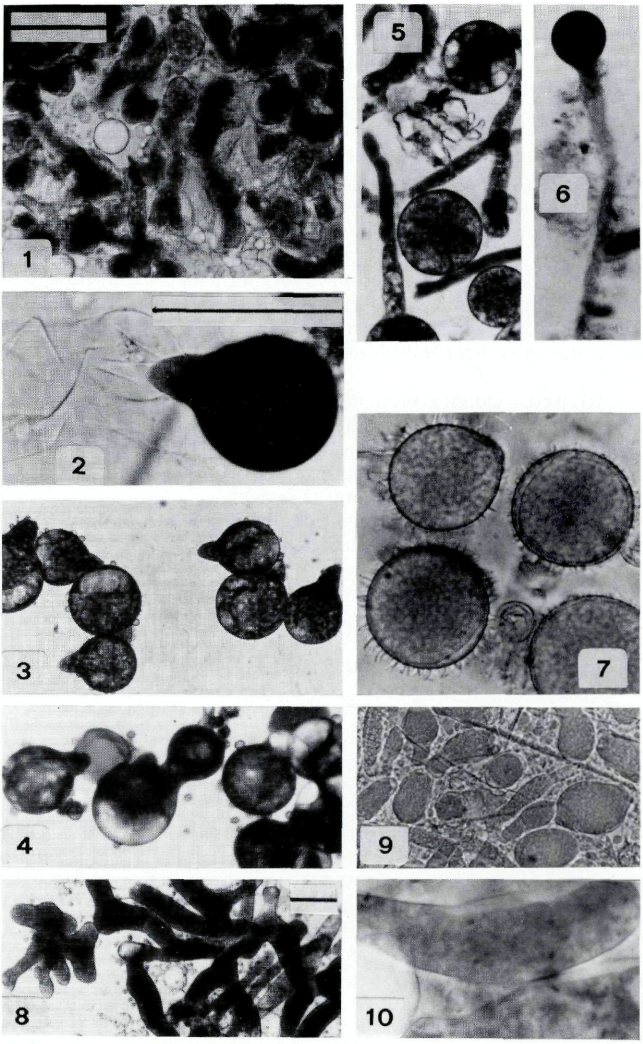


Plate 2: figs. 1–10: *Conidiobolus coronatus*. 1. Hyphal bodies from insect. – 2. Fully developed primary conidium on conidiophore. – 3. Primary conidia. – 4. Formation of secondary conidia. – 5. Resting (villose) spores developing terminally on hyphae. – 6. Germinating villose spore with germ conidium. – 7. Villose spores. – 8. Hyphal bodies from EYM-cultures. – 9. Hyphal bodies from SDAEY-cultures. – 10. Hyphal body showing nuclei (LPAO). – Bar in figs. 1, 2, 8 represents 50 μm; figs. 1, 3–6; 2, 7, 10; 8–9 same magnification.

Symptoms. – Diseased insects attached to substrate by rhizoids.

Rhizoids monophyphal. – Conidiophores with very many nuclei (figs. 1–2), staining weakly in LPAO, diameter 2.6–2.7 µm (2.0–3.5 µm) (2 series), arranged like pearls on a string in narrow basal portion, irregularly distributed in terminal portions. – Primary conidia 35.5–38.5 × 29–32 µm (28–47 × 23–41 µm), L/D = 1.17–1.21 (3 series). Papilla conical, ending rounded or pointed. Tend to germinate quickly, sometimes before projection (figs. 3–5). – Secondary conidia like primary, produced on short conidiophore. – Resting spores probably azygospores, hyaline, surrounded by thin episporium derived from hyphal wall (figs. 6 and 7). Diameter 35.5–38 µm (30–41 µm) (2 series). Often together with conidia on the same host individual. Many nuclei (fig. 7). – Cystidia absent.

Culture. – Quick growth on SDA, SDAEY, EYM. Conidia 47.5–50.5 × 43–44.5 µm (42–59 × 36–52 µm, L/D = 1.11–1.13 (2 series). Resting spores 40.7 µm (32–51 µm) (1 series). Diameter of nuclei in mycelium 2.5–2.6 µm (2.0–3.5 µm) (2 series), diameter of nuclei in conidia (FRS) 1.5 µm (1.5–2.0 µm) (1 series).

Distribution. – Siblingen SH, Hallau SH, Oberhallau SH, Watt ZH. The *Psila rosae* examined originated from Denmark, sent for identification by J. EILENBERG.

Remarks. – The species seems to be rare. It was found occasionally on single individuals in late summer and autumn.

2. *Conidiobolus coronatus* (COST.) BATKO (1964 e) – Pl. 2: figs. 1–10

Entomophaga 2: 129–131.

Bas.: *Boudierella coronata* COSTANTIN (1897). Bull. Soc. Mycol. France 13: 38–43.

Host. – *Ceutorhynchus napi* (Coleoptera, Curculionidae).

Symptoms. – Infected weevil larvae in the soil, covered with a white to greyish mycelial mat.

Rhizoids absent. – Hyphal bodies irregular (fig. 1). – Conidiophores not or only slightly enlarged terminally. Nuclei not or only exceptionally staining in LPAO, very small, 2.4 µm (2.0–3.0 µm) (1 series). – Primary conidia 50.5–53 × 38–40 µm (34–74 × 24–58 µm), L/D = 1.30–1.34 (4 series), varying largely in size; papilla prominent, elongate, sometimes without cytoplasmic content (figs. 2 and 3). – Secondary conidia like primary (fig. 4), other types not observed. – Resting spores 30.5–31.5 µm (16–42 µm) (4 series), villose, spherical (fig. 7); developing terminally from hyphae outside (exclusively?) the host (fig. 5). May germinate immediately to form germ conidium on rather long conidiophore (fig. 6). – Cystidia absent.

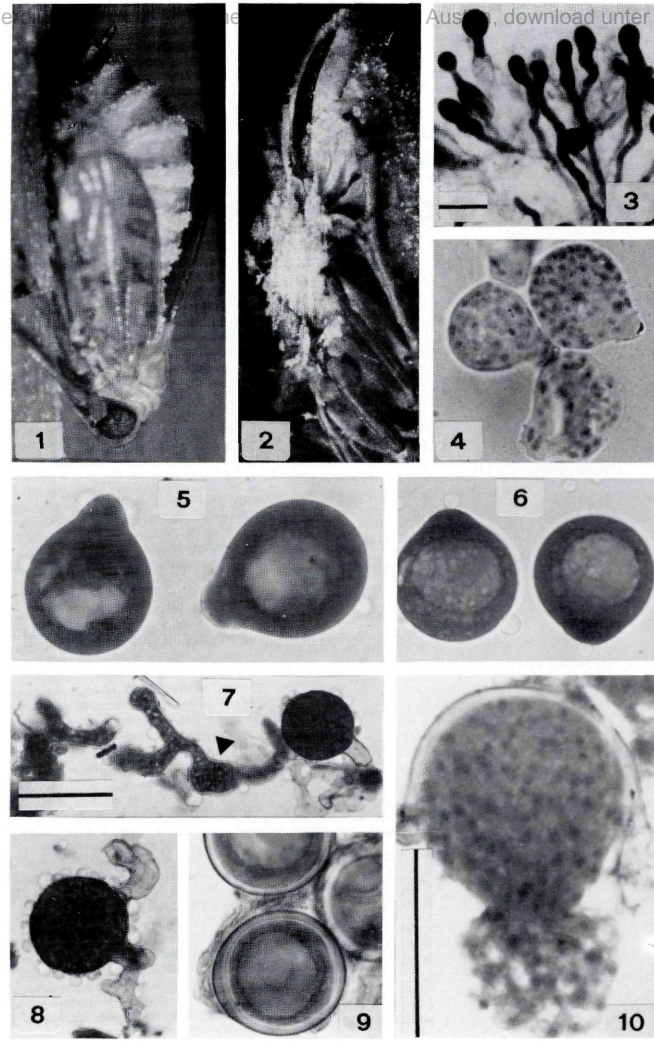


Plate 3: figs. 1–10: *Conidiobolus major*. – 1. Diseased cercopid attached to plant, with conidiophores emerging in bands along intersegmental membranes (about 12 × nat. size). – 2. Diseased cercopid with rhizoids on the ventral side (abouth 20 × nat. size). – 3. Conidiophores. – 4. Primary conidia showing nuclei (Feulgen reaction stain). – 5, 6. Primary conidia showing papillae of different shapes. – 7. Initiation of resting spore formation (arrow) and young resting spore developing terminally on hypha. – 8. Young resting spore developing laterally from hypha. – 9. Mature resting spores. – 10. Burst mature resting spore showing nuclei (LPAO). – Bar in figs. 3, 7, 10 represents 30 μm; figs. 4–6, 9–10; 7–8 – same magnification.

Culture. – Very quick growth on SDA, SDAEY, EYM. Conidia 44–56 × 35–46.5 µm (30–73 × 21–63 µm), L/D = 1.21–1.27 (5 series).

Distribution. – Zürich–Reckenholz.

Remarks. – Larvae of *C. napi* were collected by placing infested rape stalks in boxes with laboratory soil. The larvae left the stalks and entered the soil for pupation where they all (about 30 specimens) succumbed to the disease within a few days. Date of collection: June 8, 1984.

C. coronatus is considered to live mainly as a widespread soil saprophyte. Nevertheless the species is known to cause diseases in insects, but also in mammals including humans. Strains of different origins including saprobes and pathogens proved to be pathogenic for aphids, but their virulence showed marked differences (PAPIEROK, 1985).

3. *Conidiobolus major* (THAXTER) REMAUDIÈRE & KELLER (1980) – Pl. 3: figs. 1–10

Mycotaxon 11: 331.

Bas.: *Empusa apiculata* var. *major* THAXTER (1888). Mem. Boston. Soc. nat. Hist. 4: 164–165, figs. 71–73.

Hosts. – Homoptera Cercopidae, several undetermined species.

Symptoms. – Diseased insects brown, fixed to plants by rhizoids, head downwards, wings sometimes slightly opened (fig. 1).

Rhizoids numerous, emerging ventrally on thorax and abdomen, monohyphal with disk-like holdfast, often forming a compact layer (fig. 2). – Hyphal bodies filamentous, thick, short; nuclei small, staining weakly in LPAO, measuring 2.6–2.7 µm (2.5–3.5 µm) (2 series). – Conidiophores (fig. 3) penetrating host cuticle at intersegmental membranes and pleura to form white mycelial bands (fig. 1); nuclei in histological sections measuring 1.7 µm (1.5–2.5 µm) (1 series). – Primary conidia 40–45 × 33.5–38.5 µm (34–56 × 28–51 µm), L/D = 1.17–1.20 (6 series), subspherical to broadly pyriform; papilla broad, short, tip rounded (figs. 5 and 6). Contain numerous vacuoles of varying size and many very small nuclei (fig. 4), measuring (FRS) 1.3 µm (1.0–2.0 µm) (1 series). – Secondary conidia 40–45 × 34.5–40 µm (29–55 × 25–48 µm), L/D = 1.10–1.16 (1 series). – Resting spores 38–43.5 µm (32–50 µm), probably azygospores, developing terminally or laterally from hyphae (fig. 7 and 8), spherical, hyaline (fig. 9); formed in presence of conidia. – Cystidia absent.

Culture. – Quick growth on SDA, SDAEY, EYM, ECM. – Primary conidia 48–59 × 42–53.5 µm (40–77 × 34–70 µm), L/D = 1.10–1.16 (10 series). Colonised medium not discolored.

Distribution. – Zürich–Reckenholz, Watt ZH, Boppelsen, Oberlunkhofen, Ottenbach, Alterswilen TG, Randengebiet SH, Neunkirch SH.

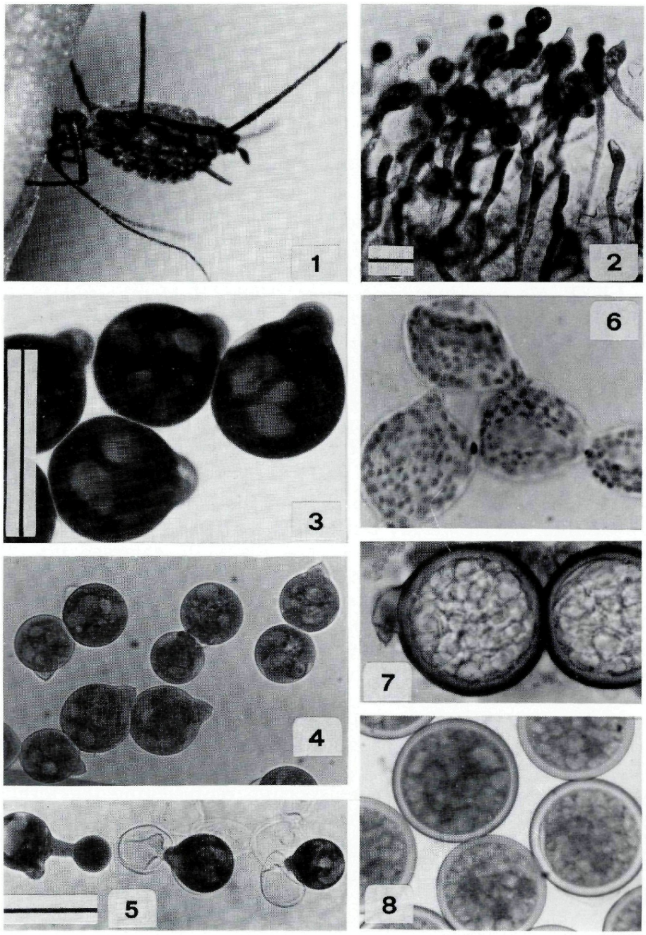


Plate 4: figs. 1–8: *Conidiobolus obscurus*. 1. Diseased *Megoura viciae* fixed to plant by proboscis (about 8 × nat. size). – 2. Conidiophores. – 3. Primary conidia with rounded papilla. – 4. Primary conidia with pointed papilla. – 5. Formation of secondary conidia. – 6. Primary conidia showing nuclei (Feulgen reaction stain). – 7. Resting spore with remains of hypha. – 8. Mature resting spores. – Bar in figs. 2, 3, 5 represents 50 μm, figs. 3, 6–8; 4–5 same magnification.

Remarks. – The species is widespread and common in autumn, sometimes causing epizootics.

4. *Conidiobolus obscurus* (HALL & DUNN) REMAUDIÈRE & KELLER (1980) – Pl. 4: figs. 1–8

Mycotaxon 11: 331.

Bas.: *Entomophthora obscura* HALL & DUNN (1957). Hilgardia 27; 162–163, figs. 4–5.

Hosts. – Homoptera Aphidina: *Acyrthosiphon pisum* HARRIS, *Aphis fabae* SCOP., *A. urticata* F., *Cavariella theobaldi* GILLETTE & BRAGG, *Dactynotus jacea* L., *Drepanosiphum acerinum* WALKER, *Macrosiphum euphorbiae* THOMAS, *M. funestum* MACCHIATI, *M. rosae* L., *Megoura viciae* BUCKTON, *Metopolophium dirhodum* WALKER, *M. festucae* THEOB., *Microlophium evansi* THEOB., *Rhopalosiphum padi* L., *Sitobion avenae* F., *Tuberolachnus salignus* GMELIN.

Symptoms. – Infected aphids brown, attached to plants by proboscis, head downwards (fig. 1). Host keeps its shape when sporulating.

Rhizoids absent. – Hyphal bodies irregular, subovoid to hyphae-like; nuclei weakly but clearly staining in LPAO. – Conidiophores terminally more or less distinctly enlarged (fig. 2); penetrate host cuticle to cover the whole body with the exception of some head and thoracic parts. – Primary conidia 33.5–44 × 28–36 µm (29–53 × 23–47 µm), L/D = 1.16–1.27 (11 series), body spherical, papilla medium-sized, tip rounded, sometimes pointed (figs. 3 and 4). Contain numerous vacuoles of varying size and very many small nuclei (fig. 6), on average about between 50 and 100, measuring (FRS) 1.4–1.8 µm (1.0–2.5 µm) (2 series). – Secondary conidia 32.5 × 30 µm (29–41 × 24–35 µm), L/D = 1.09 (1 series) (fig. 5). – Resting spores 34–38 µm (27–48 µm) (6 series), spherical, hyaline, surrounded by thin episporium representing the former hyphal wall (figs. 7 and 8); formed inside host in presence or absence of conidia. – Cystidia absent.

Culture. – Quick growth on SDA, SDAEY, EYM. – Conidia 41.5–45.5 × 37–40 µm (34–55 × 29–48 µm), L/D = 1.13–1.16 (5 series). Diameter of nuclei (FRS) 1.8 µm (1.5–2.5 µm) (1 series), and 1.5 µm (1.0–2.0 µm) (1 series) in histological sections.

Remarks. – *C. obscurus* is a very common and widespread aphid pathogen. The tendency to cause epozootics is present but not as pronounced, compared with *Erynia neoaphidis* REM. & HENN. (KELLER & SUTER, 1980). The species occasionally forms rhizoids emerging from around the mouthparts (BROBYN & WILDING, 1977).

Discussion

The genus Conidiobolus was revised by KING (1977). He listed 27 species including the occasional insect pathogens *C. coronatus, C. osmodes. C. pseudococcus* and *C. thromboides*. REMAUDIÈRE & KELLER (1980) listed a further 11 species of the genus, all entomogenous. 6 of these 11 species are transferred in this paper to the genus *Entomophaga*. The systematic positions of two of the 11, *C. carpentieri* (GIARD) and *C. tipulae* (FRES.) and of the following species with conidioboloid characteristics listed by MACLEOD & MÜLLER-KÖGLER (1973): *E. blissi* (LAKON), *E. destruens* (WEISER & BATKO) (very probably a species of *Conidiobolus*), *E. dysderci* (VIEGAS), *E. jassi* (COHN), *E. kansana* HUTCHISON and *E. thaxteri* (BRUMPT) remain unclear. Two other species of this group, *E. thaxteriana* and *E. virulenta*, were demonstrated to be identical with *C. obscurus* and *C. thromboides* respectively (REMAUDIÈRE & al., 1979; LATGÉ & al., 1980).

The genus now comprises 30 recognised species, the 27 listed by KING (1977) plus *C. apiculatus, C. major* and *C. obscurus*. The systematic status of the 8 other insect pathogens mentioned above remains unclear.

Entomophaga BATKO (1964 a)

Bull. Acad. Polon. Sci., cl. II, ser. Sci. Biol. 12: 325–326.

Hyphal bodies spherical, subspherical or irregular, each producing a single conidiophore or azygospore. Conidiophores unbranched, with more or less distinct terminal enlargement. Nuclei staining distinctly in LPAO, usually larger then 3 µm on average; diameter of nucleolus abouth 1/3–1/2 of that of the nucleus. Primary conidia unitunicate, spherical to pyriform; papilla conical, rounded or pointed; nuclei larger than those of Conidiobolus, staining distinctly in FRS and LPAO; numerous, on average between 10 and about 100. Secondary conidia like primary, produced on short lateral secondary conidiophore. Resting spores spherical, smooth, usually hyaline. Rhizoids present or absent. Cystidia absent. Most species grow on standard media.

Type species: *Entomophaga grylli* (FRES.) BATKO, l.c.: 326.

Bas.: *Entomophthora grylli* FRESENIUS (1856). Bot Zeitg. 14: 883.

Key to described species of *Entomophaga*

1. Rhizoids present 2
1*. Rhizoids absent or uncertain 4
2. Rhizoids without specialised holdfast. Primary conidia pyriform with prominent papilla. On aquatic Nematocera ..... *papillata* (8)
2*. Rhizoids with specialised holdfasts. Primary conidia spherical without prominent papilla. On terrestrial insects 3
3. Primary conidia on average 32–38 × 29–34 µm, mainly on small Diptera ..... *domestica* (4)
3*. Primary conidia on average 48–52 × 40–47 µm, on Limoniidae .... *limoniae* (7)

4. On Arachnida Opiliones. Primary conidia on average 41–44 × 32–34 µm ..... *batkoi* (2)
4*. On dipterous insects 5
4**. On other insects 6
5. On aquatic Nematocera. Primary conidia on average 41–48 × 29–34 µm with less than 30 nuclei on average ..... *conglomerata* (3)
5*. On Tipulidae. Primary conidia on average 87–99 × 70–85 µm with more than 50 nuclei on average ..... *gigantea* (5)
6. On larvae of Lepidoptera. Primary conidia on average 30–33 × 20–22 µm with 10–13 nuclei on average ..... *aulicae* (1)
6*. On Saltatoria Acridiidae. Primary conidia on average 36–41 × 27–31 µm with 25–28 nuclei on average ..... *grylli* (6)
6**. On larvae of Hymenoptera Tenthredinidae. Primary conidia on average 49–53 × 35–42 µm with more than 30 nuclei on average ..... *tenthredinis* (9)

1. *Entomophaga aulicae* (Reichardt in Bail) Humber (1984) – Pl. 5: figs. 1–7

Mycotaxon 21: 270.

Bas.: *Empusa aulicae* Reichardt in Bail (1869). Schriften Naturf. Ges. Danzig, n. s. 2 (2): 3.

Host. – Unidentified lepidopteran larvae.

Symptoms. – Dead caterpillars fixed usually to upper parts of grass leaves by contraction of the hindlegs. Last body segments in upright position, anterior portion of the body hanging downwards (fig. 1).

Rhizoids absent. – Hyphal bodies spherical, subspherical or elongate (fig. 2). – Conidiophores: Diameter of nuclei 4.8–4.9 µm (4.5–6.0 µm) (2 series) and 2.9–3.4 µm (2.5–4.5 µm) (4 series) in histological sections (fig. 3). – Primary conidia 29.5–32.5 × 20–22 µm (24–44 × 17–30 µm), L/D = 1.46–1.57 (6 series), pyriform to obovate; papilla broad, rounded, not distinctly delimited from the body of the conidium (fig. 4). Number of nuclei 10–13 (7–18) (4 series, 25 each), diameter (FRS) 3.0 µm (2.5–3.5 µm) (1 series) (fig. 5). – Secondary conidia (fig. 6) 24.5–28 × 18–21.5 µm (18–33 × 13–25 µm), L/D = 1.31–1.38 (4 series). – Resting spores (fig. 7) 29–31 µm (22–38 µm) (6 series), spherical to supspherical, hyaline.

Culture. – Growth on EYM at first bacteria-like, slimy, glossy. Aerial mycelium light grey-brown to greyish. Diameter of colonies after 15 days at 20° C 50–65 mm. Growth on SDAEY not bacteria-like, colonies white, distinctly delimited, diameter after 15 days at 20° C 35–45 mm. Colonised medium not discolored. Conidia 36–42.5 × 26–33 µm (24–62 × 15–51 µm), L/D = 1.30–1.48 (6 series).

Remarks. – The species was found once on October 4, 1979, in a meadow near Oberhallau SH causing an epizootic. It was observed that, before death, many of the infected caterpillars span a small web to which they were fixed by their hindlegs when dying.

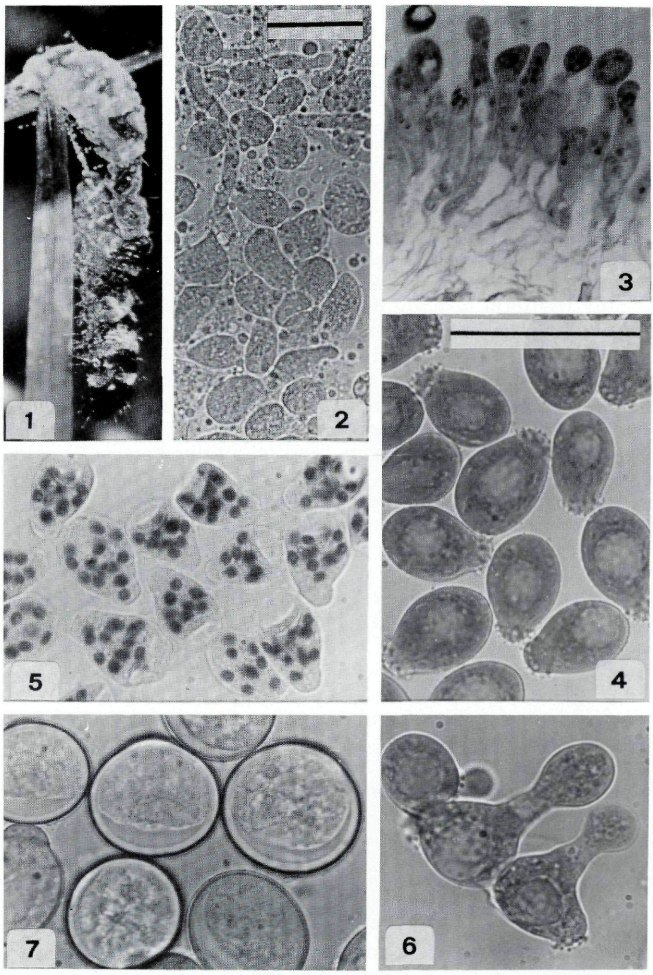


Plate 5: figs. 1–7: *Entomophaga aulicae*. 1. Diseased caterpillar hanging from grass blade. Note the light mycelial bands (ca. 5 × nat. size). – 2. Protoplasts/hyphal bodies. – 3. Conidiophores in histological section. – 4. Primary conidia. – 5. Primary conidia with nuclei (Feulgen reaction stain). – 6. Formation of secondary conidia. – 7. Resting spores. – Bar in figs. 2 and 5 represents 50 µm, figs. 2–3; 4–7 same magnification.

2. ***Entomophaga batkoi*** (BALAZY) KELLER comb. nov. – Pl. 6: figs. 1–7

Bas.: *Entomophthora batkoi* BALAZY (1978). J. Invertebr. Pathol. 31: 278.
Syn.: *Conidiobolus batkoi* REMAUDIÈRE & KELLER (1980). Mycotaxon 11: 330.

Host. – Oligolophus tridens C.L. KOCH (Arachnida, Phalangiidae).

Symptoms. – Infected harvestmen clasping the upper parts of plants, usually grass leaves, with their long legs (fig. 1).

Rhizoids absent. – Hyphal bodies (fig. 2) subspherical to irregular, about 25–70 nuclei staining distinctly in LPAO and measuring 4.2–4.3 µm (3.5–5.0 µm) (2 series), and 2.9–3.1 µm (2.5–4.0 µm) (1 series) in histological sections. – Primary conidia (fig.4) 40.5–44 × 32–34 µm (34–51 × 27–42 µm), L/D = 1.22–1.30 (6 series), broadly pyriform, usually with single prominent vacuole; papilla conical, rounded, often asymmetric, not delimited from conidial body. – Secondary conidia (fig. 5) 36–42 × 30–35.5 µm (32–50 × 24–42 µm), L/D = 1.16–1.23 (5 series); papilla small, short, conical, often asymmetric and pointed. – Resting spores (fig. 7) 34–39.5 µm (29–44 µm) (5 series), probably azygospores, spherical, hyaline; present in all cadavers in different numbers. – Cystidia absent.

Distribution. – Siblingen SH, Neunkirch SH, Bommen TG, Boppelsen ZH, Watt ZH.

Culture. – Isolation through projected conidia only on SDAEY after external disinfection on the host. Grows very slowly on SDAEY. After a few transfers the fungus stopped growing. – Conidia 49–56.5 × 42–46.5 µm (41–74 × 33–64 µm), L/D = 1.16–1.21 (2 series). No growth on EYM.

Remarks. – The species is rather common in open forests, along borders of forests and hedges, often causing epizootics. It was collected between July 25 and September 12.

3. ***Entomophaga conglomerata*** (SOROKIN) KELLER comb. nov. – Pl. 7: figs. 1–3

Bas.: *Entomophthora conglomerata* SOROKIN (1877). Beitr. Biol. Pflanzen 2: 388–393, Pl. 13, figs. 1–11.
Syn.: *Conidiobolus conglomeratus* REMAUDIÈRE & KELLER (1980). Mycotaxon 11: 330.

Hosts: Chironomidae (Diptera, Nematocera).

Symptoms: Infected midges attached to substratum by rhizoids or floating on water, mycelium white to grey.

Rhizoids uncertain. – Hyphal bodies simple, rounded. – Conidiophores: Number of nuclei 22–28 (14–51) (3 series), diameter of nuclei 4.6–4.8 µm (4–5.5 µm) (4 series) (fig. 1). – Primary conidia (fig. 2) 41–48 × 29.5–34 µm (30–61 × 21–46 µm), L/D =

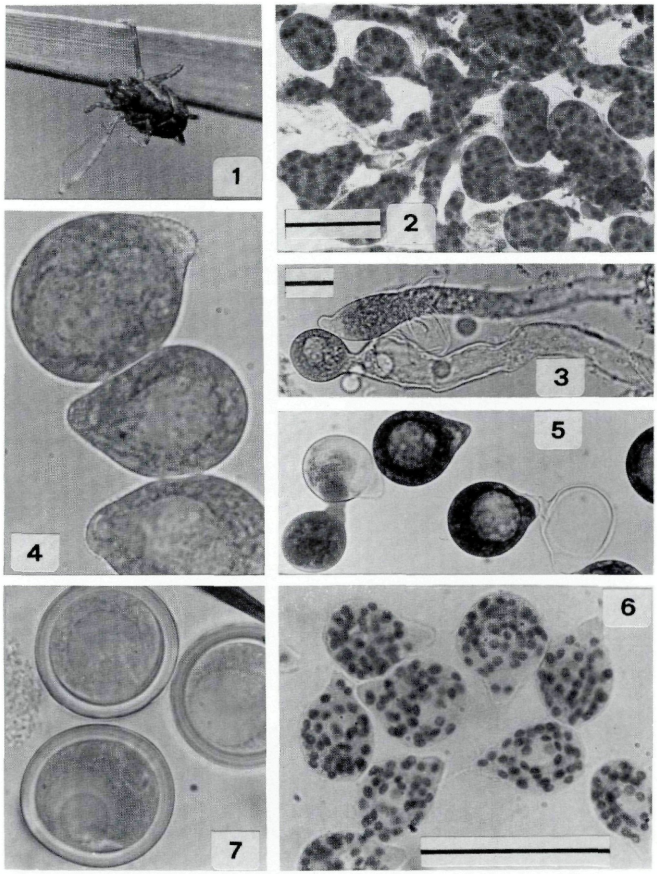


Plate 6: figs. 1–7: *Entomophaga batkoi*. 1. Diseased harvestmen hanging from grass blade (ca. 3 × nat. size). – 2. Hyphal bodies with nuclei (LPAO). – 3. Conidiophores. – 4. Primary conidia. – 5. Formation of secondary conidia. – 6. Primary conidia with nuclei (Feulgen reaction stain). – 7. Resting spores. – Bar in figs. 2, 3 and 6 represents 50 µm; 2, 5; 4, 6–7 same magnification.

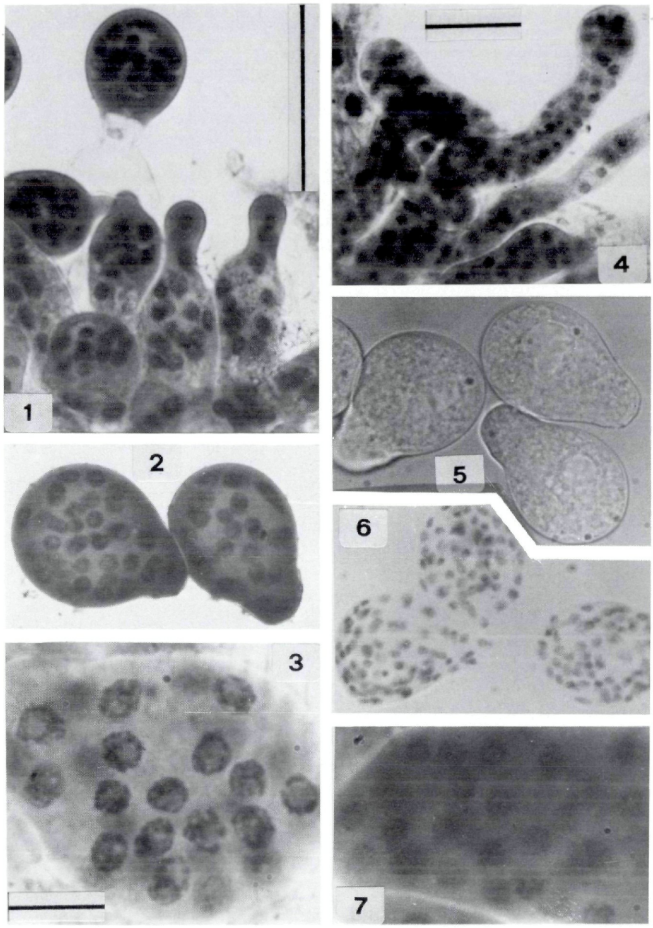


Plate 7: figs. 1–3: *Entomophaga conglomerata*. 1. Conidiophores with nuclei at different stages of development. – 2. Primary conidia with nuclei. – 3. Nuclei in primary conidium. All LPAO. – Figs. 4–7: *Entomophaga papillata*. 4. Conidiophores with nuclei (LPAO). – 5. Primary conidia. – 6. Primary conidia with nuclei (Feulgen reaction stain). – 7. Nuclei in conidiophore (LPAO). – Bar in figs. 1 and 4 represents 50 µm, that in fig. 3 10 µm; 1, 2, 5, 6; 3 and 7 same magnification.

1.34–1.41 (6 series), pyriform; papilla distinct, tip rounded. Number of nuclei 22–26 (11–36) (2 series), diameter of nuclei 4.2–4.5 µm (3.5–5 µm) (3 series), and 3.2 µm (2.5–4 µm) (1 series) in histological sections. – Secondary conidia 27–35 × 21–27.5 µm (22–41 × 17–34 µm), L/D = 1.28–1.31 (3 series). – Resting spores and cystidia absent.

Distribution: Stammheim ZH.

Remarks: The species seems to be rare. It was collected in a wooden barrel filled with water between August 11 and September 10. The species was associated with *Entomophthora culicis, Erynia conica* and *Entomophaga papillata.*

4. *Entomophaga domestica* KELLER, sp. nov. – Pl. 8: figs. 1–9

Conidia primaria (30–)33–38(–46) × (25–)29–34(–41) µm, sphaerica, distincta papilla acuminata vel rotundata praedita. Conidia secundaria habitu primariis similia. Conidiophora simplicia, apicaliter inflata, 10–33 nucleis diametro 3–5 µm impleta. Corpora hyphalia subsphaerica, rotundata vel curta, crassa, mycelio similibus structuris composita. Rhizoidea mononemata, discoideis appressoriis terminata. Sporae cystidiaque absunt. In Dipteris, Helvetia. Holotypus ZT no. 401–407, Cotypi K et BPI.

Hosts. – Diptera: Sciaridae (type host), Psycodidae, Chloropidae (*Oscinella frit* L., *Chlorops pumilionis* BJERK.), Coleoptera (*Coccinella septempunctata* L., *Propylaea quatuordecimpunctata* L.).

Symptoms. – Infected insects fixed to support by rhizoids (fig. 1).

Rhizoids monohyphal, stout, emerging ventrally from thorax and abdomen, ending with disk-like holdfast (fig. 2). – Hyphal bodies subspherical or composed of simple, rounded structures, sometimes thick, short, hyphaelike. Nuclei staining distinctly in LPAO (fig. 3). Number of nuclei 18–20 (10–28) (3 series) with a diameter of 3.5–3.7 µm (3–5 µm) (4 series). 1(–2) nucleoli per nuclei with a diameter of 1.5–2.5 µm. Nuclei sometimes dividing. – Conidiophores (figs. 4 and 5) unbranched, terminally anlarged; 20 (11–33) nuclei (1 series) with a diameter of 3.7–3.8 µm (3–5 µm). No nuclear division observed. Penetrate cuticle of the host at intersegmental membranes and pleura to form white to greyish mycelial bands. – Primary conidia 33.5–38 × 29–33.5 µm (30–46 × 25–41 µm), L/D = 1.11–1.21 (12 series), body spherical; papilla distinct, tip rounded or pointed (figs. 6 and 7). – Secondary conidia similar to primary ones, 29 × 24 (27–33 × 22–28 µm) (1 series) (fig. 9). – Resting spores and cystidia absent.

Culture. – Quick growth on SDA, SDAEY, EYM and ECM. – Primary conidia 37–42 × 31–36.5 µm (30–51 × 25–46 µm), L/D = 1.12–1.19 (6 series). No resting spores observed. Nuclei in mycelium

measuring 3.2–3.9 µm (3–5 µm) (2 series) and 2.6 µm (2.5–3 µm) stained with FRS.

Distribution. – Zürich-Reckenholz (type locality), Neunkirch SH, Hausener Seen ZH.

Remarks. – The species closely resembles *C. apiculatus*. *E. domestica* has nuclei staining deeply in LPAO, especially in hyphal bodies and conidiophores; its nuclei are larger and about half the number of those of *C. apiculatus*. The two species further differ in isoenzymatic patterns (LATGÉ & BOUCIAS, 1984). The strains refered to there as numbers 1316–1319 represent *E. domestica*, and strain nrs. 698, 706, 877, 905 and 1027 *C. apiculatus*.

The species is found throughout the year in the glasshouse on sciarid midges. From time to time it attacks other insects in culture, e.g. coccinellid beetles and larvae (no sporulation on larvae) and frit flies. In the latter case it is not completely clear whether infection occurred in the glasshouse or whether infective material was brought in from the field with plants containing frit fly larvae. The fungus was also occasionally found in fields on *Chlorops pumilionis* and on unidentified small flies.

5. ***Entomophaga gigantea*** (KELLER) KELLER comb. nov.

Bas.: *Entomophthora gigantea* KELLER (1978). Sydowia, Ann. Mycol. Ser. II, 31: 89, figs. 6–19.

Syn.: *Conidiobolus giganteus* REMAUDIÈRE & KELLER (1980). Mycotaxon 11: 331.

Host. – *Tipula paludosa* MEIG. (Diptera, Tipulidae).

Symptoms. – Legs of diseased insects clasping upper parts of grasses and other meadow plants.

Rhizoids absent. – Hyphal bodies usually bizarre, amoeboid or hyphae-like. – Conidiophores penetrate host cuticle at intersegmental membranes and pleura of whole body. Nuclei staining distinctly in LPAO, their diameter being 4.1 µm (3.5–5 µm) (1 series). – Primary conidia 87–98.5 × 70.5–84.5 µm (57–123 × 46–105 µm), LD = 1.16–1.25 (6 series), spherical; papilla clearly demarcated from conidial body, conical, rounded. Nuclei in histological sections measuring 3.2 µm (3–4 µm) (1 series). About 50–100 nuclei on average. – Secondary conidia 76 × 65.5 µm (65–88 × 57–76 µm), L/D = 1.16 (1 series, n = 25). – Resting spores 58.5–70 µm (47–93 µm) (3 series), spherical, hyaline, smooth; developing from amoeboid hyphal bodies or terminally on hyphae.

Culture. – Quick growth on SDA, SDAEY, EYM. Diameter of colonies on SDAEY and EYM (20° C, 7 days) 60–100 mm. Colonies on EYM coarsly folded, on SDAEY with abundant white-greyish-brownish aerial mycelium. – Conidia 86.5–101 × 74.5–89 µm

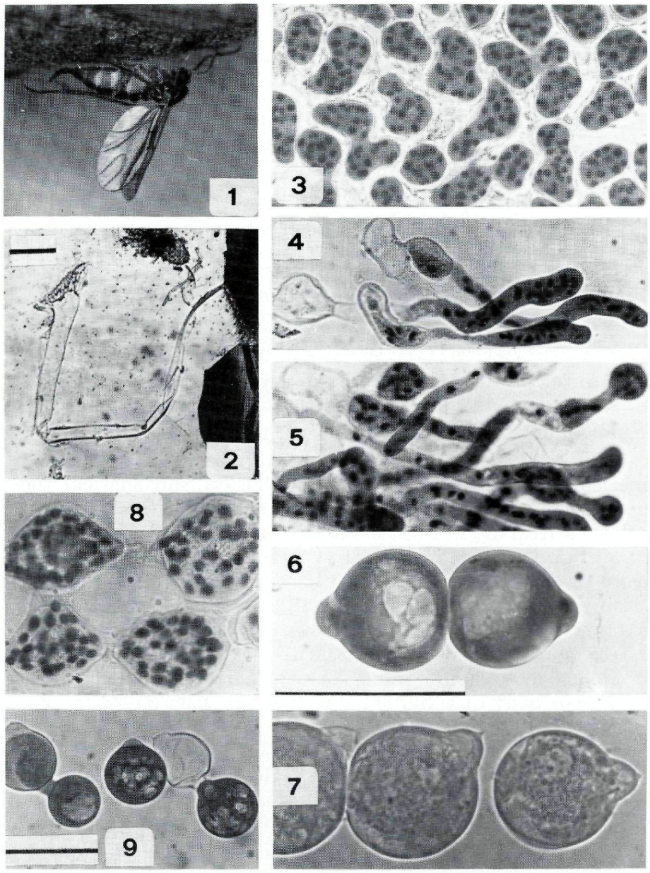


Plate 8: figs. 1–9 *Entomophaga domestica*. 1. Diseased sciarid midge attached to underside of leaf. – 2. Rhizoid. – 3. Hyphal bodies with nuclei. (LPAO). – 4, 5. Germinating hyphal bodies developping to conidiophores and conidia respectively, nuclei visible. – 6. Primary conidia with rounded papilla. – 7. Primary conidia with pointet papilla. – 8. Primary conidia with nuclei (Feulgen reaction stain). – 9. Formation of secondary conidia. – Bar in figs. 2, 6 and 9 represents 50 μm. 3–5 and 9; 6–8 same magnification.

(70–137 × 57–131 µm), L/D = 1.13–1.16 (6 series). – Resting spores 79.5–87 µm) (3 series).

Distribution. – Zürich-Reckenholz, Alterswilen TG, Nussbaumen TG.

Remarks. – The fungus was found on single individuals of *T. paludosa,* often in mixed infections with *Eryniopsis caroliniana,* never causing epizootics. It was collected between August 25 an September 12. Figures and more detailed informations are given in the original description (KELLER, 1978).

6. *Entomophaga grylli* (FRES.) BATKO (1964 a) – Pl. 9: figs. 1–8

Bull. Acad. Pol. Sci., cl. II, Sér. sci. biol. 12, 325.

Bas.: *Entomophthora grylli* FRESENIUS (1856): Bot. Zeitg. 14, 883.

Hosts. – Saltatoria, Acrididae: Several undetermined species.

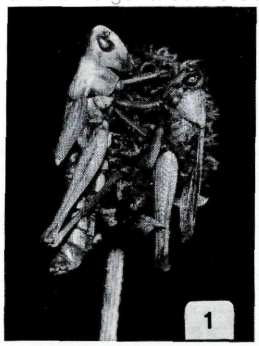
Symptoms. – Infected grasshoppers fixed to upper parts of meadow plants by contraction of legs, head upwards (fig. 1).

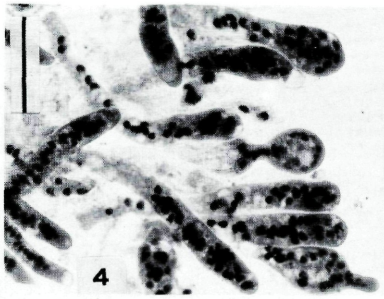
Rhizoids absent. – Hyphal bodies developing from nearly spherical protoplasts (fig. 2), usually spherical, subspherical, sometimes irregular (fig. 3). Nuclei deeply staining in LPAO; 26 (13–33) nuclei (1 series) with 4.3 µm (4–5.5 µm) diameter. – Conidiophores (fig. 4) penetrating host cuticle at intersegmental membranes and pleura of whole body to for light brownish mycelial bands. Nuclei measuring 4.7 µm (4.5–5.5 µm) (1 series) and 3.4–3.5 µm (3–4.5 µm) (3 series) in histological sections. – Primary conidia (fig. 5) 36–41 × 26.5–30.5 µm (33–47 × 23–38 µm), L/D = 1.29–1.41 (7 series), pyriform to obovate; papilla broad, conical, rounded, not clearly demarcated from body of conidium. Number of nuclei 25–28 (11–39) (5 series, 20 each) (fig. 6), diameter of nuclei (FRS) 2.5 µm (2–3.5 µm) (1 series). – Secondary conidia 28.5–30 × 22–23.5 µm (23–36 × 17–32 µm), L/D = 1.26–1.31 (2 series). – Resting spores (figs. 7 and 8) 38.5–41 µm (32–47 µm) (6 series), probably azygospores, spherical, hyaline, smooth. Young resting spores with 18–65 nuclei. As spore matures nuclear number decreases (fig. 7). Diameter of nuclei in young resting spores 4.3–4.8 µm (4–5.5 µm) (2 series).

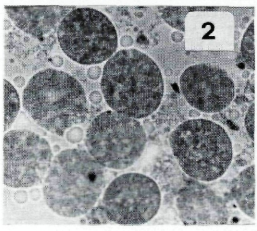
Culture: – Isolation on EMC succeeded, but fungus stopped growing after first transfer.

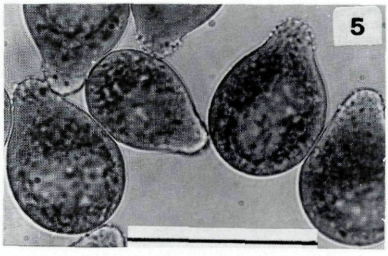
Distribution. – Silblingen SH, Oberhallau SH, Watt ZH, Sonogno TI.

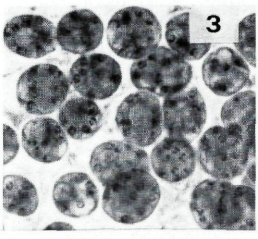
Remarks. – The fungus was found on extensively cultivated meadows, often causing epizootics. Sampling dates were beween July 31 and October 6. The fungus is further reported from St. Moritz GR by FRESENIUS (1858).

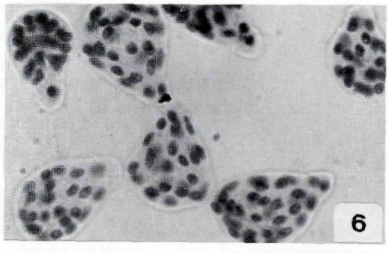


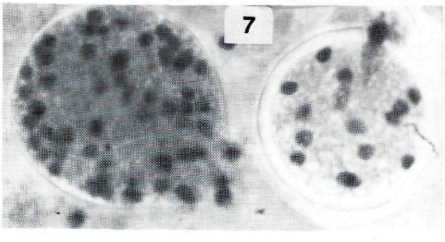












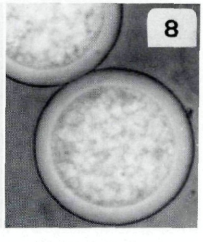


Plate 9: figs. 1–8: *Entomophaga grylli*. 1. Diseased grasshoppers on flower at top of plant stem (ca. 1.5 × nat. size). – 2. Protoplasts. – 3. Hyphal bodies with nuclei visible (LPAO). – 4. Conidiophores with nuclei (LPAO). – 5. Primary conidia. – 6. Primary conidia with nuclei (Feulgen reaction stain). – 7. Young (left) and mature (right) resting spores. Note reduction of number of nuclei during maturation (LPAO). – 8. Mature resting spores. – Bar in figs. 4 and 5 represents 50 µm; 2–4; 5–8 same magnification.

7. ***Entomophaga limoniae*** KELLER sp. nov. – Pl. 10: figs. 1–12

Conidia primaria (38–)48–52(–58) × (32–)40–47(–55) µm, sphaerica, papilla rotundata praedita, 15–56 nucleos continentia. Conidia secundaria habitu primariis similia. Conidiophora simplicia, corpora hyphalia irregulares, rhizomata mononemata, fortia, rhizoidiis formae specialis terminata. Sporae cystidiaque absunt. In Limonia tripunctata F. (Dipteris, Nematoceris). Holotypus ZT, no. 850702/I–III, Cotypi K and BPI.

Hosts. – Diptera, Limoniidae: *Limonia tripunctata* F. (type species) and related species in the same habitat.

Symptoms. – Infected insects fixed to the underside of leaves with rhizoids (fig. 1).

Rhizoids with 25–45 µm (20–55 µm) diameter, monohyphal, powerful, emerging ventrally from thorax and abdomen, terminally often branched, ending with a specialised holdfast of various types (figs. 2–5): bifurcate, fingerlike, with numerous minute branchings or disk-like. Endings of 2 or more rhizoids sometimes united. Contain many nuclei. – Hyphal bodies (figs. 6 and 7) subspherical or composed of simple, rounded structures. Nuclei deeply staining in LPAO. 30 (18–44) nuclei per hyphal body (1 series) with 4.5 µm (3.5–6 µm) (2 series) diameter. – Conidiophores (figs. 9 and 10) unbranched, terminally often strongly enlarged, elongate conical bud before formation of conidia; sometimes without prominent terminal enlargement. Number of nuclei 20–42 (15–63) (4 series), diameter of nuclei 4.5–4.8 µm (4–6 µm) (2 series). Nuclei in basal portions arranged like pearls on a string, in the enlarged terminal portions distributed in the cytoplasm. Nuclei sometimes arranged in pairs, but no nuclear divisions observed. – Primary conidia 47.5–52 × 40.5–47 µm (38–58 × 32–55 µm), L/D = 1.10–1.22 (6 series), spherical to broadly pyriform; papilla medium-sized, slightly conical to rounded, tip rounded. Contain numerous vacuoles. Number of nuclei 20–39 (15–56) (2 series) (figs. 11 and 12). – Resting spores and cystidia absent.

Culture. – Grows on SDAEY, EYM and ECM. – Conidia 50–59 × 44–53 µm (30–69 × 25–62 µm), L/D = 1.11–1.15 (3 series). – Resting spores produced in EYM 42–47.5 µm (30–58 µm) (2 series), spherical, hyaline, surrounded with thin episporium.

Distribution. – Tägerwilen TG (type locality), Felben TG, Hausener Seen ZH, Etzelkofen BE.

Remarks. – The morphology of *E. limoniae* closely resembles that of *C. major*. The two species differ slightly in conidial dimensions but distinctly in the staining ability of the nuclei and by their number and dimensions and by the host.

The species was collected between June 9 and July 3 along brooks at the border of forests or flanked with bushes and trees, on

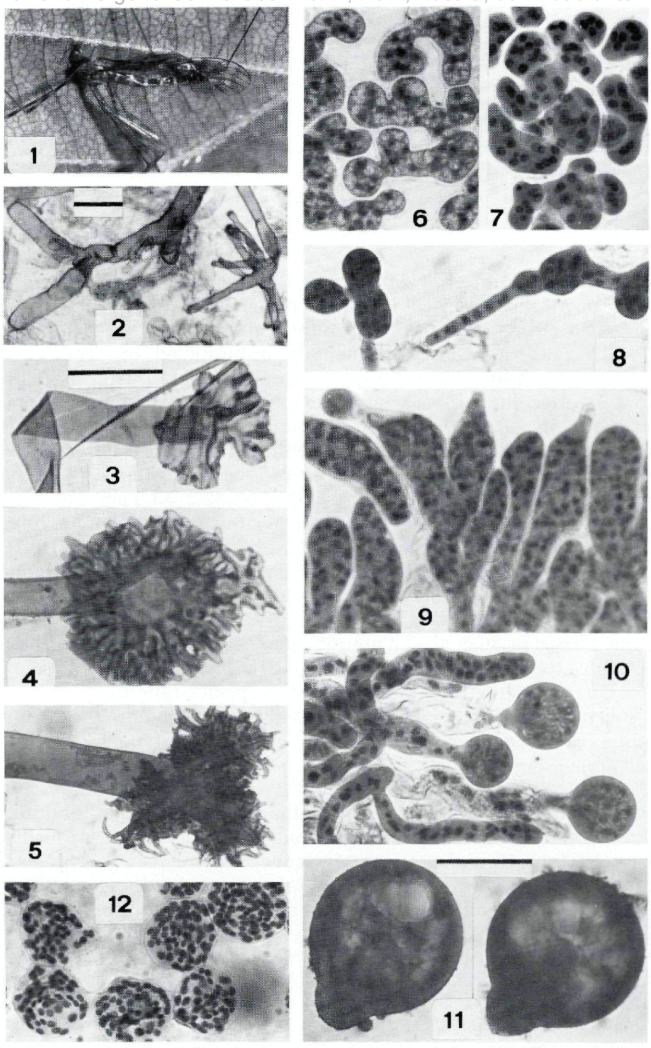


Plate 10: figs. 1–12: *Entomophaga limoniae*. 1. Diseased *Limonia tripunctata* attached to underside of leaf (ca. 2 × nat. size). – 2–5. Endings of rhizoids showing different holdfasts. – 6. Young vacuolised hyphal bodies, nuclei becoming visible. – 7. Mature hyphal bodies with nuclei. – 8. Germinating hyphal bodies. – 9. Conidiophores. – 10. Formation of primary conidia. – 11. Primary conidia. (All LPAO). – 12. Primary conidia with nuclei (Feulgen reaction stain). – Bar in figs. 2 and 3 represents 50 μm, that in fig. 11 25 μm; 2 and 5; 3, 4, 6,–10, 12 – same magnification.

the underside of leaves of *Urtica dioica* L., *Spiraea ulmaria* L., *Corylus avellana* L., and *Prunus padus* L. The fungus attacked single insects only; it was never observed to cause an epizootic.

8. ***Entomophaga papillata*** (THAXTER) KELLER comb. nov. – Pl. 7; figs. 4–7

Bas.: *Empusa papillata* THAXTER (1888). Mem. Boston Soc. nat. Hist. 4; 166–167, figs. 82–90.

Syn.: *Conidiobolus papillatus* REMAUDIÈRE & KELLER (1980). Mycotaxon 11; 331.

Hosts. – Diptera, Nematocera: Chironomidae, Simuliidae.

Symptoms. – Infected midges attached to substratum by rhizoids or floating on water. Mycelium white to grey.

Rhizoids monohyphal, usually unbranched but sometimes with short terminal branchings, no specialised holdfast. – Hyphal bodies mycelium-like, vacuolised. Nuclei staining weakly but distinctly in LPAO, border of nuclei distinct. Diameter of nuclei 3–3.4 µm (2.5–4 µm) (3 series). – Conidiophores (fig. 4) terminally often strongly enlarged. Diameter of nuclei 3.2 µm (3–4 µm) (1 series). – Primary conidia 47–52.5 × 32.5–35.5 µm (38–59 × 26–45 µm), L/D = 1.41–1.49 (6 series), pyriform; papilla long, prominent, rounded or slightly pointed (fig. 5). Nuclei staining in LPAO, number estimated to be usually between 50–80. Diameter of nuclei 2.5–2.6 µm (2.5–3 µm) (2 series), in histological sections 1.7–2 µm (1.5–2.5 µm) (3 series) and FRS 2 µm (1.5–2.5 µm) (1 series). – Secondary conidia 36.5 × 27.5 µm (32–41 × 23–33 µm), L/D = 1.33 (1 series). – Resting spores and cystidia absent.

Culture. – Attempts to isolate the species failed.

Distribution. – Hallau, Trasadingen, Frauenfeld, Stammheim, Hausener Seen ZH, Pramagnon/Pouta Fontana VS (coll. G. RABOUD).

Remarks. – The species is more frequent than *E. conglomerata* and widely distributed. It was usually found on single individuals and once causing an epizootic among simuliids. It was collected between June 15 and October 24. Concerning nuclear numbers and dimensions the species shows some affinities with the genus *Conidiobolus*. But the nuclear structure, as indicated by light microscopic examinations, is considered to be of the entomophagian type.

9. *Entomophaga tenthredinis* (FRES.) BATKO (1964c) – Pl. 11: figs. 1–7

Bull. Acad. Pol. Sci. Cl. II, Sér. Sci. Biol. 12: 404.

Bas.: *Entomophthora tenthredinis* FRESENIUS (1858). Abhandl. Senckenb. Naturf. Ges. 2: 205, figs. 51–58.

Hosts. – Hymenoptera, Tenthredinidae: Several unidentified species.

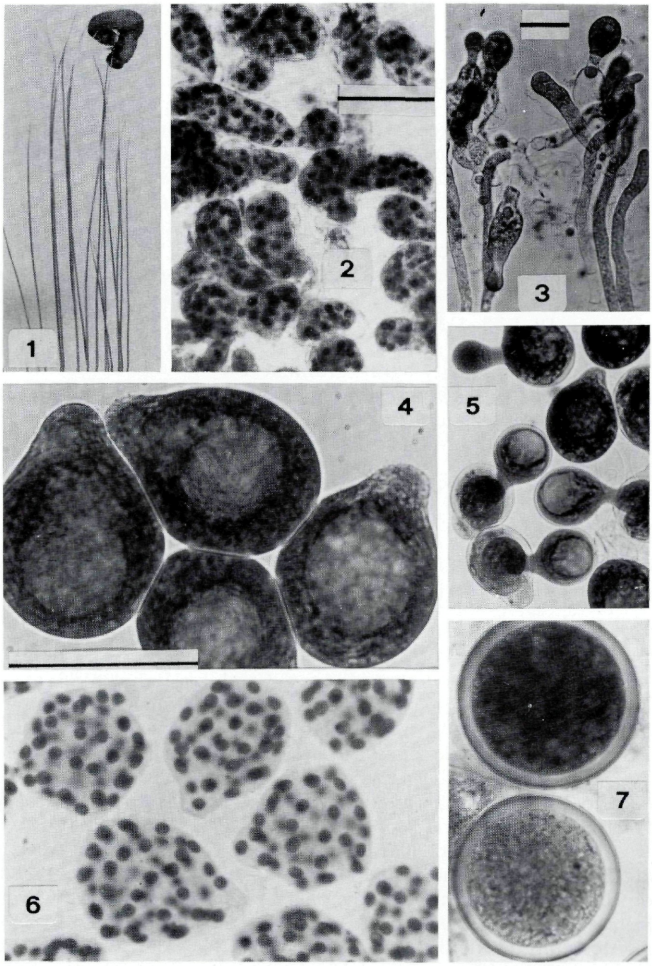


Plate 11: figs. 1–7: *Entomophaga tenthredinis*. 1. Diseased sawfly larva in typical position on top of awn of rye. (ca. nat. size). – 2. Hyphal bodies with nuclei (LPAO). – 3. Conidiophores with developing conidia. – 4. Primary conidia. – 5. Formation of secondary conidia. – 6. Primary conidia with nuclei (Feulgen reaction stain). – 7. Resting spores. – Bar in figs. 2–4 represents 50 µm; 2 and 5; 4, and 7 – same magnification.

Symptoms. – Diseased sawfly larvae at top of plants (cereals, grass leaves) fixed by their mandibules, coiled, head downwards (fig. 1).

Hyphal bodies subspherical to irregular, nuclei deeply staining in LPAO (fig. 2). – Conidiophores (fig. 3) penetrate body of the host everywhere except the head to form a light brown to brown cover. Diameter of nuclei 4.8–4.9 µm (3.5–6 µm) (2 series). – Primary conidia 48.5–53.5 × 35–41.5 µm (40–65 × 32–53 µm), L/D = 1.28–1.48 (8 series), pyriform to obovate; papilla broad, conical, rounded, often asymmetrical, not clearly delimited from conidial body (fig. 4); usually single prominent vacuole. 29–78 nuclei (n = 38) with a diameter (FRS) of 3 µm (2.5–4 µm) (1 series) (fig. 6). – Secondary conidia (fig. 5) 44.5–52.5 × 34.5–43.5 µm (36–67 × 29–51 µm), L/D = 1.19–1.38 (11 series). – Resting spores 48.5–52 µm (42–62 µm) (6 series), spherical, smooth (fig. 7). Content in young spores dark, at maturity lights, granular.

Culture. – Slow growth on SDAEY and EYM. – Conidia 51.5–71.5 × 41–58.5 µm (44–91 × 34–79 µm), L/D = 1.20–1.25 (7 series). – Resting spores absent.

Distribution. – Zürich-Reckenholz, Zürich-Waid, Frauenfeld, Iselisberg TG, Alterswilen TG, Randen SH.

Remarks. – The species is frequent, often causing epizootics in meadows as well as in cereal fields. It was collected between June 23 and August 24. Detailed data on this fungus are also given by Zimmermann & Huger (1984).

Discussion

The genus *Entomophaga* was defined by Batko (1964a) to include arthropod-pathogenic species with conidioboloid characters and lacking rhizoids. Morphologically similar species were included in the genus *Culicicola* Nieuwland (1916) together with the rhizoid producing species of the genus *Entomophthora* (Batko, 1964b). This classification proved to be unsatisfactory and was not followed by insect mycologists.

Since there are no clear morphological characteristics to separate *Entomophaga* and *Conidiobolus*, Remaudière & Keller (1980) considered Entomophaga as synonym of *Conidiobolus*. However, Humber (1981) and Ben-Ze'ev & Kenneth (1982) showed that the two genera could be distinguished cytologically by nuclear size and structure. From the practical point of view using only the light microscope it is not always easy to separate them. In most species the size of the nuclei is an unequivocal criterium. However, the nuclei of *E. papillata* overlap in size with those of species of *Conidiobolus*. The nuclear structure as expressed by the staining ability of

the nuclei in aceto orcein, too, must be considered as intermediate in this species.

It is noteworthy that *E. domestica* and *C. apiculatus* as well as *E. limoniae* and *C. major* are morphologically very similar differing practically only in the number and size of nuclei. The first pair has as a further common characteristic a wide host spectrum. These facts could be of some importance with respect to evolutionary aspects.

The genus at present comprises 10 species: the 9 listed above and *E. tabanivora* (ANDERSON & MAGNARELLI) HUMBER (1984c). BATKO (1964c) included 4 further species. Two of them, *E. obscura* and *E. thaxteriana* were demonstrated to be identical (REMAUDIÈRE & al., 1979) and transferred to *Conidiobolus* by REMAUDIÈRE & KELLER (1980). The systematic position of *E. saccharina* (GIARD, 1888) and *E. kansana* (HUTCHISON, 1962) is uncertain, the latter probably belongs to *Entomophaga.*

Entomophthora FRESENIUS (1856)

Bot. Zeitung 14, 883.

Hyphal bodies usually homogenous and regular, spherical, subspherical or elliptical. Germinate with single germ tube. Conidiophores unbranched, terminal portion enlarged. Primary conidia campanulate, appearing unitunicate, bi- to multinucleate; nuclei large, deeply staining in LPAO. Projected conidia surrounded by a halo. Secondary conidia similar to primary ones, apical point often absent or weakly developed, formed on short secondary conidiophore laterally from primary conidia. Projected secondary conidia not surrounded by a halo. Resting spores spherical, hyaline or surrounded with dark episporium. Rhizoids present or absent, cystidia absent. Some species grow on standard media.

Type species: *Entomophthora muscae* (COHN) FRESENIUS, l.c., figs. 1–4.

Bas.: *Empusa muscae* COHN (1855). Hedwigia 1: 60.

Key to described species of *Entomophthora*

1. Rhizoids present or indistinctly developed on mouthparts of Sciaridae, pathogens of Diptera Nematocera and Homoptera Aphidina 2
1*. Rhizoids absent or limited to proboscis of flies, pathogens of Diptera Brachycera and Cyclorrhapha and Heteroptera 5
2. Conidia with 3–13 nuclei, mean diameter of nuclei less than 4 µm, pathogens of Aphidina and Cecidomyiidae 3
2*. Conidia with 2–4 (rarely 5) nuclei, mean diameter of nuclei more than 4 µm, pathogens of Nematocera 4
3. Conidia with 15–22 × 12–19 µm with 4–12 nuclei, hyphal bodies elliptical; in Aphididae, Callaphididae ..... *planchoniana* (5)
3*. Conidia 11–19 × 9–16 µm with 3–13 nuclei, hyphal bodies spherical; in Cecidomyiidae ..... *brevinucleata* (1)
4. Conidia 12–16 × 9–12 µm with 2 (very rarely 3) nuclei; mainly in Culicidae and Chironomidae ..... *culicis* (2)
4*. Conidia 16–22 × 12–17 µm with 2–4 (rarely 1–5) nuclei; in Sciaridae ..... *trinucleata* (7)

5. Conidia with 18–22 × 15–18 µm with 8–13 nuclei; in Miridae ..... *helvetica* (3)
5*. Pathogens of Diptera 6
6. Conidia with less than 8 nuclei, mean diameter of nuclei larger than 4.5 µm (LPAO); in Schizophora ..... *schizophorae* (6)
6*. Conidia with more than 8 nuclei, mean diameter of nuclear smaller than 4.5 µm (LPAO); in Brachycera and Cyclorrhapha ..... *muscae* (4)

1. *Entomophthora brevinucleata* KELLER & WILDING (1985)

Entomophaga 30: 56, Pl. 1–3.

Hosts. – Diptera, Cecidomyiidae: *Sitodiplosis phalaridis, Contarinia pisi, Mycodiplosis* sp. and several undetermined species.

Symptoms. – Infected midges fixed to the underside of leaves by rhizoids, the wings spread outwards.

Rhizoids usually monohyphal, often irregularly flattened along much of their length and sometimes fused in pairs distally; some, especially those emerging from te mouthparts, joined together in bundles, ending without specialised holdfast, 6–9 µm in diameter, exceptionally 5–14 µm. – Hyphal bodies 27–28.5 × 22 µm (19–40 × 15–30 µm) (2 series), subspherical to elliptical, present at the moment of the death of the host; germinate with single germ tube to form usually the conidiophore, or to form to well defined types of transitional bodies: type A 46.5–51.5 × 8.5–11 µm (34–73 × 6–14 µm) (3 series), rod-shaped; type B 25.5 × 19.5 µm (22–31 × 17–24 µm) (1 series), subovoid, formed under the cuticle of the host. – Conidiophores developed either from hyphal bodies or from type A transitional bodies. – Primary conidia 11–19 × 8.5–16 µm (10–22 × 8–19 µm), L/D = 1.14–1.29 (10 series) with more or less prominent apical point, base slightly convex. 4–10 (3–13) nuclei (10 series) with 2.7–3.1 µm (2.5–4 µm) diameter (4 series). – Secondary conidia 12.5–15 × 10.5–12 µm (11–17 × 9–14 µm) (2 series). – Resting spores and cystidia absent.

Culture. – No attempt was made to isolate the species.

Distribution. – Neunkirch SH, Oberhallau SH, Nussbaumen TG, Stammheim ZH, Zürich-Reckenholz, Watt ZH, Solothurn.

Remarks. – The first host species recorded were *Sitodiplosis mosellana* from *Phalaris arundinacea, Mycodiplosis* sp. and an unidentified midge from *P. arundinacea*. Recently *S. mosellana* from *P. arundinacea* was described as a distinct species *S. phalaridis* (ABBASS, 1986).

In the meantime numerous other host were collected but with the exception of *Contarinia pisi* not yet identified, mainly on *Triticum aestivum, Medicago sativa, Quercus robur, Fagus silvaticus, Phragmites communis, Echinochloa crus-galli, Chenopodium* spp. and other weed in arable land. The species is obviously common;

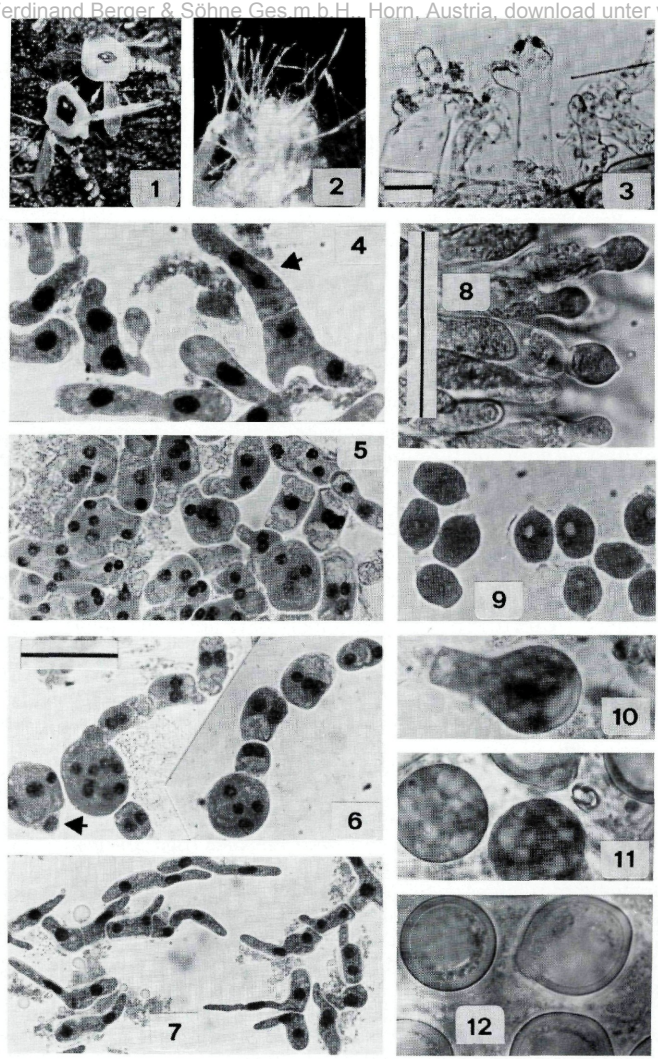


Plate 12: figs. 1–12: *Entomophthora culicis*. – 1. Diseased midges (ca. 3 × nat. size). – 2. Rhizoids on ventral side of thorax (ca. 15 × nat. size). – 3. Endings of rhizoids. – 4. Hyphal bodies. Arrow indicates division of nucleus. – 5. Young oligonucleate hyphal bodies. – 6. Oligonucleate hyphal bodies developing by budding to usually binucleate hyphal bodies arranged in chains. Arrow indicates beginning of budding. – 7. Germinating hyphal bodies often arranged in chains. – 8. Developing conidia. – 9. Primary conidia. – 10. Young resting spore developing terminally from hypha. – 11. Immature resting spores. – 12. Mature resting spores. – Bar in figs. 3, 6 and 8 represents 50 µm; 5–7; 4, 8–12 – same magnification.

epizootics were repeatedly observed on midges on *Phalaris arundinacea* and on *Chenopodium album*.

2. *Entomophthora culicis* (BRAUN) FRESENIUS (1858) – Pl. 12: figs. 1–12

Abhandl. Senckenberg. Naturf. Ges. 2: 206, pl. 9, figs. 44–45.

Bas.: *Empusa culicis* BRAUN (1855): Algarum unicellularum genera nova et minus cognita, praemissis observationibus de algis unicellularibus in genere. W. Engelmann, Lipsiae, 105.

Hosts. – Diptera, Nematocera: Culicidae, Chironomidae.

Symptoms.–Infected insects fixed to support by rhizoids. Sporulating mycelium white, greyish, yellowish, brownish or greenish, covers small insects completely, on larger insects along intersegmental membranes and pleura (fig. 1).

Rhizoids ventral on thorax and abdomen, numerous, monohyphal, vigorous, 20–50 µm in diameter, ending without specialised holdfast or with small branchings (figs. 2–3). – Hyphal bodies at an early stage of development subspherical with up to 8 nuclei; smaller hyphal bodies with 1–3 nuclei produced by budding, often arranged in lines, developing to binucleate, ellipsoidal to rod-shaped hyphal bodies measuring 34.5 × 16 µm (24–44 × 12–22 µm) (1 series) (figs. 4–6). Germinate with single germ tube (fig. 7). Larger hyphal bodies with up to 16 nuclei considered as mother cells of rhizoids. – Conidiophores terminally 8–12 µm in diameter, 2 nuclei with 4.8–5.4 µm (4.5–6 µm) diameter (3 series). – Primary conidia (fig. 9) 12.5–14 × 9–11 µm, (11–16 × 7–12 µm), L/D = 1.17–1.41 (8 series) with distinct apical point, often prominent central vacuole. 2 (rarely 3) nuclei, often in polar positions, measuring 4.9–5 µm (4.5–5.5 µm) (2 series). – Secondary conidia without prominent apical point. – Resting spores 25–25.5 µm (21–28 µm) (2 series), spherical to slightly ellipsoidal, rare; probably azygospores, formed from terminal swellings of hyphae, the many small vacuoles progressively fusing to single vacuole as spore wall thickens (figs. 10–12).

Culture. – Grows on EYM and SDA, but better on SDAEY. Diameter of colonies on SDAEY (21 days, 20° C) 30–50 mm. Colonies flat or slightly vaulted, folded or honeycomb-like, white, grey or slightly greenish. Medium not discolored. Conidia 15.5–19 × 11–14 µm (12–22 × 10–16 µm), L/D = 1.36–1.46 (6 series). Resting spores absent.

Distribution. – Trasadingen, Hallau, Neunkirch SH, Bommer Weiher TG, Frauenfeld, Nussbaumen TG, Stammheim, Hausener Seen ZH, Katzensee ZH, Pramagnon/Pouta Fontana VS (coll. G. RABOUD).

Remarks. – The species is very common from May till October, often causing epizootics. Usually very close to water (lakes, rivers,

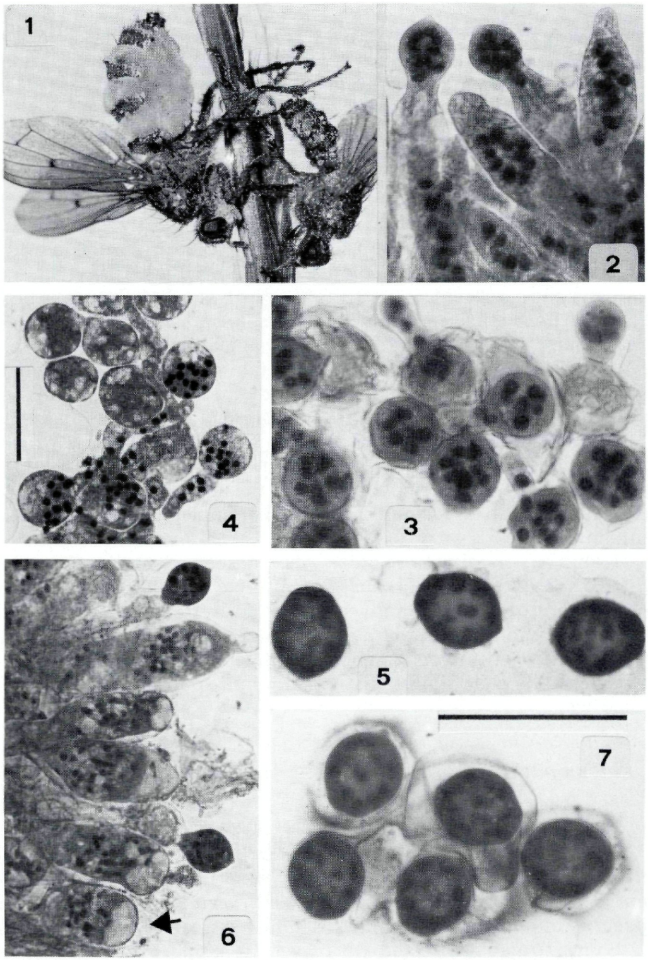


Plate 13: figs. 1–7: *Entomophthora muscae*. 1. Diseased flies with fungus in full sporulation (left) and at the end of sporulation (ca. 4 × nat. size). – 2–3: 10–11 nucleate group: – 2. Conidiophores. – 3. Primary conidia. – 4–5. 15–19 nucleate group: – 4. Protoplasts (nuclei unstained) and hyphal bodies with nuclei stained. – 5. Primary conidia. – 6–7: 19–22 nucleate group from syrphids: – 6. Transitional body (arrow), conidiophores and developing conidia. – 7. Primary conidia. All LPAO. – Bar in figs. 4 and 7 equals 50 µm; figs. 4, 6; 2, 3, 5, 7 same magnification.

brooks, rainwater container etc.), host attached immediately above the water level or some centimeters higher, on walls, stones, stakes, boards, treetrunks etc., sometimes floating on water.

3. *Entomophthora helvetica* KELLER & BEN-ZE'EV (1985)

Can. J. Bot. 63,1471.

Host. – Heteroptera, Miridae: *Notostira elongata.*

Symptoms. – Infected insects predominantly last instar nymphs on grass leaves, head downwards, fixed by proboscis and legs. The whole insect body colonised by the fungus.

Rhizoids absent. – Conidiophores distally enlarged, 11–23 µm, 8–15 nuclei. – Primary conidia 18–22 × 15–17.5 µm (16–24 × 12–19 µm), L/D = 1.18–1.3 (6 series), apical point weakly developed, basal papilla broad; content granular, often with a prominent vacuole. 8–13 (6–18) nuclei with 2 µm diameter (Giemsa stain). — Secondary conidia 14–15.5 × 11–14 µm (12–18 × 10–18 µm), L/D × 1.09–1.23 (5 series) on short conidiophore. – Resting spores spherical, only immature stages found in a single cadaver.

Culture. – All attempts to isolate the species failed.

Distribution. – Neunkirch SH, Siblingen SH, Zürich-Rekkenholz.

Remarks. – Hyphal bodies were described earlier (KELLER, 1981; BEN-ZE'EV & al., 1985) based on a single host individual reared in the laboratory. The data given there appear doubtful in the light of recent findings in comparative pathobiology. – The fungus was collected between August 25 and September 12; it appeared irregularly in usually wet habitats with *Agropyron* sp. sometimes causing epizootics.

4. *Entomophthora muscae* (COHN) FRESENIUS (1856) – Pl. 13: figs. 1–7

Bot. Zeitung (Berlin) 14: 883

Bas.: *Empusa muscae* COHN (1855a). Hedwigia 1: 60.

Hosts. – Diptera, Cyclorrhapha: *Delia kullensis* R., *D. planipalpis* STEIN, *Musca domestica* L., *Scopeuma (Scatophaga) stercorarium* L., *Melanostoma mellinum* L., *M. scalare* F., *Platycheirus clypeatus* MG. and several underdermined species.

Symptoms. – Infected flies fixed to support with proboscis and legs, wings usually spread latero-dorsally (fig. 1).

Rhizoids absent (see discussion). – Protoplasts spherical to subspherical, nuclei not staining in LPAO (fig. 4). – Hyphal bodies 23.5–37 × 20.5–31.5 µm (18–48 × 17–38 µm) (9 series), spherical to subspherical, developing from protoplasts, present during the period when the host dies. Nuclei deeply staining in LPAO,

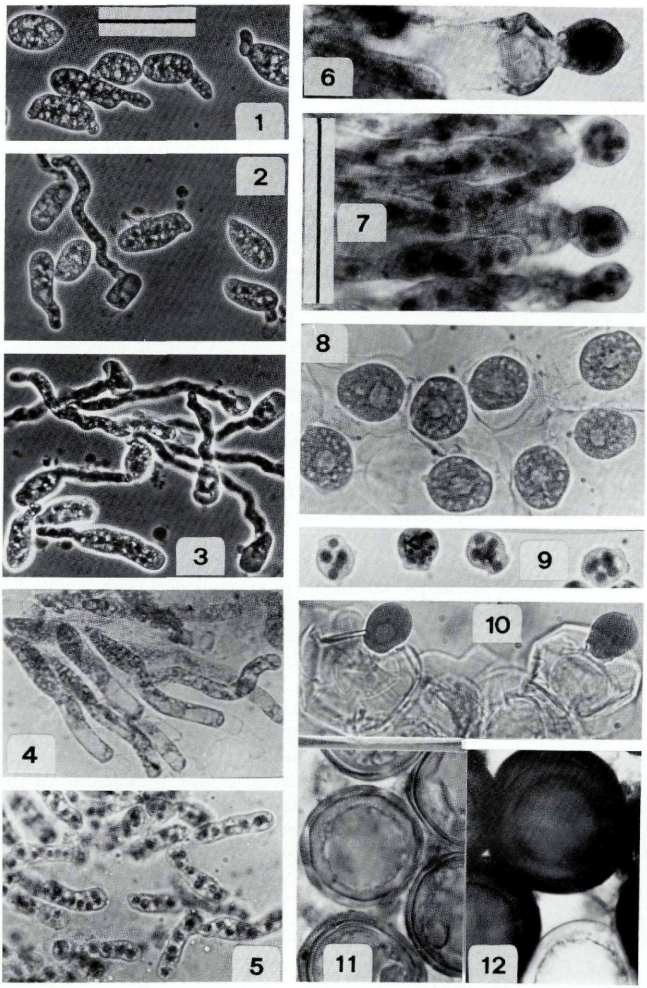


Plate 14: figs. 1–12: *Entomophthora planchoniana*. 1–3. Hyphal bodies in different phases of germination (phase contrast). – 4. Developing conidiophores. – 5. Transitional bodies of type A. – 6, 7. Developing conidia with nuclei (7). – 8. Primary conidia. – 9. Primary conidia with nuclei (Feulgen reaction stain). – 10. Formation of secondary conidia. – 11. Immature resting spores. – 12. Mature resting spores. – Bar in figs. 1 and 7 represents 50 μm; 1–5; 6–12 – same magnification.

diameter on average 4–4.5 µm (5 series). Germ tube 6–12 µm diameter. – Conidiophores (figs. 2 and 6) terminally enlarged, penetrating the host cuticule at the intersegmental membranes and pleura. 10–25 (7–32) nuclei (18 series) with a diameter of 3.7–4.5 µm (3–5.5 µm) (11 series). – Primary conidia 22.5–32.5 × 18–27.5 µm (21–36 × 16–30 µm), L/D = 1.15–1.33 (19 series) (figs. 3, 5 and 7). Apical point and papilla well developed. 10–22 (6–30) nuclei per conidium (19 series) with a diameter of 2.8–4.2 µm (2.5–5 µm) (14 series), or 2.4 µm (FRS) and 2.7 µm in histological sections (1 series each). – Secondary conidia 17.5–24.5 × 14–17.5 µm (16–30 × 12–19 µm), L/D = 1.22–1.39 (7 series), apical point weakly developed. – Resting spores and cystidia absent.

Culture. – Attempts to isolate the species on SDAEY and EYM failed.

Distribution. – Very widespread and common species.

Remarks. – Cohn (1855a, b) was the first to describe this fungus from the house fly, *Musca domestica*, under the generic name Empusa. Fresenius (1856) transfered it to *Entomophthora*. The same fungus from the same host was also described by Lebert (1857) under the name *Myiophyton cohnii*. Giard (1888) described *Entomophthora syrphi* from *Melanostoma mellinum* and *E. scatophagae* from *Scatophaga merdaria (= S. stercoraria)*. All three are considered to be synonyms of *E. muscae*.

E. muscae as defined here consists of 3 groups differing mainly in the number of nuclei per conidium (Keller, 1984). The group with *D. kullensis* as host has on average 10–11 nuclei, the second group with the other non-syrphid hosts has 15–19, and the third group with the syrphids as hosts has 19–22; the nuclei of the latter group are also smaller than those of the first two groups. Further investigations are needed to demonstrate whether a division of this taxon into species corresponding to these groups is justified. Ideally, host specificity tests should be used to provide further information about the significance of the nuclear numbers. Some indications of this kind were given by Wilding (1970, cited in Brobyn & Wilding, 1983). Additional investigations should determine the exact nature of the existing syntype material of *E. muscae*.

5. *Entomophthora planchoniana* Cornu (1873) – Pl. 14: figs. 1–12

Bull. Soc. Bot. France 20: 189.

Hosts. – Homoptera, Aphidina: *Aphis fabae* Scop. on *Evonymus europaeus,. A. sambuci* L., *Cavariella aegopodii* Scop., *C. theobaldi* Gillette & Bragg, *Drepanosiphum acerinum* Walker, *D. platanoides* Schrank, *Dactynotus jaceae* L., *Macrosiphum funestum*

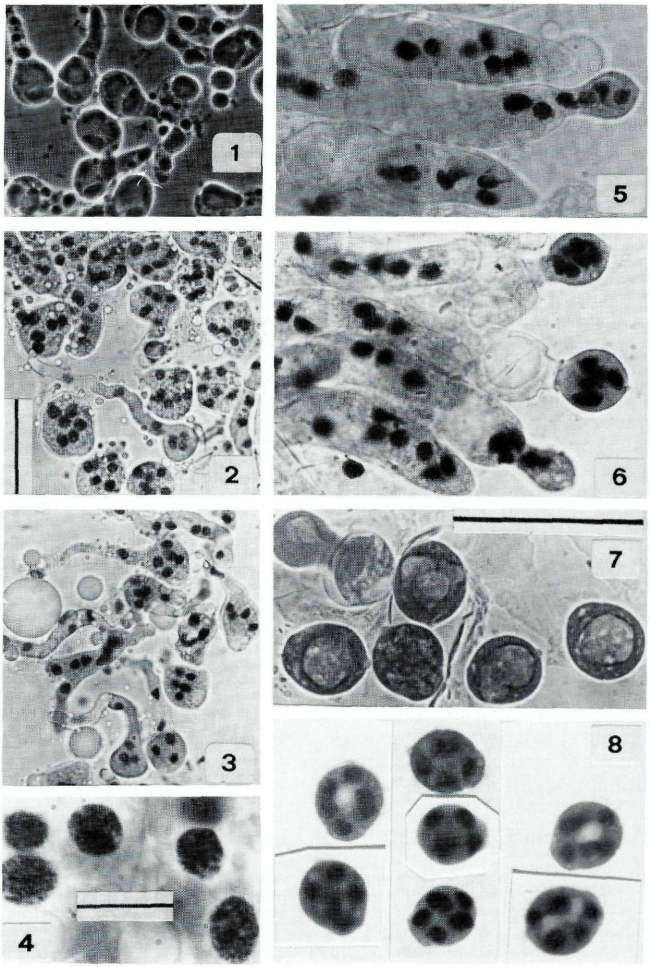


Plate 15: figs. 1–8: *Entomophthora schizophorae*. 1. Protoplasts. – 2, 3. Hyphal bodies with nuclei. – 4. Nuclei in conidiophore. – 5, 6. Formation of primary conidia. – 7. Primary conidia and formation of secondary conidium (upper left). – 8. Primary conidia with nuclei. All LPAO. – Bar in figs. 2 and 7 represents 50 μm, that in fig. 4 10 μm; 1–3; 5–8 – same magnification.

MACCHIATI, *M. rosae* L., *M. silvaticum* MEIER, *Metopolophium dirhodum* WALKER, *Microlophium evansi* THEOBALD, *Phorodon humuli* SCHRANK, *Rhopalomyzus lonicerae* SIEBOLD, *Rhopalosiphum padi L.*, *Sitobion avenae* F.

Symptoms. – Infected aphids light-brown to dark-brown depending on the colour of the host, fixed with rhizoids. Limited swelling before sporulation, sporulation in the dorsal region of the abdomen.

Hyphal bodies. – Regular, ellipsoidal to short rod-shaped, 29.5–31.5 × 15.5–17.5 µm (22–51 × 12–19 µm), L/D = 1.81–1.91 (2 series), cytoplasm with many smaller and larger vacuoles, 5–8 (3–12) nuclei (5 series) with 3.9–4.4 µm (3.5–5 µm) diameter (2 series); germinate with single germ tube (figs. 1–3). Conidiophores distally enlarged, 15–17 µm (12–21 µm) diameter (2 series), 7–8 (5–10) nuclei (4 series) with 3.6 µm (3–4.5 µm) diameter (1 series) (figs. 6 and 7). – Primary conidia 15.5–19.5 × 12.5–16 µm (15–23 × 11–19 µm), L/D = 1.21–1.39 (7 series), apical point and papilla not prominent, cytoplasm granular with numerous vacuoles (fig. 8), 6–8 (4–11) nuclei (4 series) with 3.3–3.5 µm (3–4.5 µm) diameter (2 series), or 2.5–2.8 µm (FRS) and 2.8 µm in histological preparations. – Secondary conidia 13.5–16 × 10.5–11.5 µm (12–18 ×10–13 µm), L/D = 1.19–1.4 (4 series), apical point weakly developed, usually with single central vacuole. – Resting spores 31–37.5 µm (27–42 µm) (6 series) including episporium, hyaline with dark-brown, uneven episporium, produced in absence of conidia (figs. 11 and 12).

Culture. – Attempts to isolate the fungus failed.

Distribution. – Widespread species.

Remarks. – The species seems to prefer relatively dry habitats like loose plant communities, tall plants, bushes and trees, often causing epizootics; does not occur in dense, humid crops. It is able to hibernate in the hyphal body stage producing a modified type of hyphal body (KELLER, 1987).

6. ***Entomophthora schizophorae*** KELLER & WILDING sp. nov. – Pl. 15: figs. 1–8

Conidia primaria (16–)18–24(–25) × (12–)14–19(–22) µm, campanulata, (3–)4–7(–9) nucleos (4–)5(–6) µm diametro continentia. Conidia secundaria habitu primariis similiar. Conidiophora simplicia, Corpora hyphalia sphaerica vel subsphaerica, 18–36 × 16–30 µm. Rhizoidea, cystida sporaeque absunt. In Dipteris Schizophoris. Holotypus ZT, no. 830630/18–21, Cotypi K et BPI.

Hosts. – Diptera, Schizophora: *Delia platura* Mg. (type host), *Psila rosae* F., *Pollenia rudis* F.

Symptoms. – Diseased flies fixed to plants with proboscis and legs.

Rhizoids absent (see discussion). – Protoplasts (fig.. 1) spherical to subspherical, nuclei not staining in LPAO; present before death of the host. – Hyphal bodies 21–28.5 × 18–23.5 µm (18–36 × 16–30 µm), L/D = 1.15–1.22 (4 series), spherical to subspherical, formed from protoplasts in the period of dying of the host; nuclei in LPAO distinctly staining, 4.9–5 µm (4.5–6.5 µm) diameter (2 series); germinate with single germ tube (figs. 2 and 3). – Conidiophores enlarged in the terminal portion to a diameter of 17–18 µm (13–23 µm) (2 series) (figs. 5 and 6). 4–7 (2–9) nuclei (7 series) with 5.2–5.3 µm (4.5–6.5 µm) diameter (4 series). Penetrate cuticle of the host at intersegmental membranes and pleura to form white to greyish mycelium bands. – Primary conidia (figs. 7 and 8) 18.5–24 × 13.5–19.5 µm (16–25 × 12–22 µm), L/D = 1.19–1.37 (14 series), apical point and papilla distinct but not prominent. 4–7 (3–9) nuclei (15 series) with 4.8–5 µm) (4–6 µm) diameter (5 series), or 3.3 µm when stained with FRS and 3.6 µm in histological sections. – Secondary conidia 15–16.5 × 12–13 µm (13–18 × 11–15 µm), L/D = 1.25–1.27 (3 series), with indistinct apical point, produced laterally on short conidiophore from the primary conidia. – Resting spores and cystidia absent.

Culture. – Diameter of colonies on EYM in 3 weeks at 20°C 15–20 mm, slightly sunken, rosette-like with coarse but not deep folds. On SDAEY (3 weeks, 20° C) 10–20 mm, dome-like with dense, fine, shallow folds, colonies sharply delimited from uncolonised medium, medium not discolored.

Distribution. – Stammheim ZH (type locality), Trasadingen SH, Neunkirch SH, Zürich-Reckenholz, Watt ZH.

Remarks. – The species has been attributed to *Entomophthora muscae* (KELLER, 1984), but differs by the smaller conidia and larger nuclei, and particularly by the smaller number of nuclei per conidium.

The species is common from June till October in prairies and arable land, where infected flies usually hang on tall plants emerging above the canopy of the crop, epizootics are not rare. *Delia brassicae* BOUCHÉ is reported from England as a further host (WILDING, pers. comm.).

7. ***Entomophthora trinucleata*** KELLER sp. nov. – Pl. 16: figs. 1–9

Conidia primaria (16–)17–18(–22) × (12–)14–15(–18) µm, campanulata, acumine apicali distincto, 2–4(–5) nucleos 5–6.5 µm diametro continentia. Conidia secundaria habitu primariis similia. Conidiophora simplicia, rhizomata mononemata. Sporae cystidiaque absunt. In Dipteris Sciaridis. Holotypus ZT, no. 851028/I–V, Cotypi K et BPI.

Hosts. – Diptera, Sciaridae: undetermined species (type host).

Symptoms. – Infected insects fixed to underside of leaves by rhizoids emerging from mouthparts, presence of rhizoids sometimes indistinct. Rhizoids monohyphal without specialised holdfast (fig. 1), 5–12 µm diameter. – Hyphal bodies at an early stage elongate, oligonucleate, producing mono- or binucleate hyphal bodies by budding (figs. 2 and 3), these developing usually to 2, 3 or 4 nucleate, spherical, subspherical, elongate or irregular hyphal bodies (figs. 4–6) measuring 20–26 × 15–22 µm (18–36 × 13–27 µm) (3 series; 19, 21, 33 measurements); nuclei deeply staining in LPAO. – Conidiophores developing from 3 (1–5) nucleate hyphal bodies, distally enlarged (fig. 7), penetrate host cuticle at intersegmental membranes and pleura to form white to greyish bands of mycelium. – Primary conidia (fig. 8) 17.5–18 × 14–15 µm (16–22 × 12–18 µm), L/D = 1.19–1.25 (6 series), apical point distinct but not prominent. 3 (2–5) nuclei with 5.6–5.9 µm (5–6.5 µm) diameter. – Secondary conidia without distinct apical point (fig. 9) – Resting spores and cystidia absent.

Culture. – No attempt to isolate the fungus.

Distribution. – Zurich-Reckenholz (type locality), Siblingen SH, Schleitheim SH.

Remarks. – *E. trinucleata* differs from *E. culicis* mainly by the dimensions of conidia and nuclei and the number of nuclei/conidium. It differs from *E. brevinucleata* mainly by number and dimension of the nuclei. It differs from *E. schizophorae* by the rhizoids, the shape of the hyphal bodies, the dimensions of the conidia and the number of nuclei.

The species was found in the second half of October in sciarid midges attached to leaves of *Zea mays* and *Brassica rapa* var. *rapa*.

Discussion

The genus was treated monographically by Macleod & al. (1976). The following 5 species were included: *E. culicis, E. erupta, E. muscae, E. planchoniana* and *E. weberi*. At present 11 species are described, 7 of them treated in this paper. The remaining 4 species are *E. erupta* (Dustan) Hall (1959), *E. israelensis* Ben-Ze'ev & Zelig (1984), *E. thripidum* Samson & al. (1979) and *E. weberi* Lakon ex Samson & al. (l.c.).

In addition to the characters given in the definition of the genus other common characteristics exist; these include the hyphal bodies which are, as far as known, of a simple, homogenous shape, spherical or elliptical depending on the species. The number of nuclei remains more or less constant from te hyphal body stage to the conidium. Nevertheless observations in some species demonstrated that the whole set of nuclei does not always enter the conidium

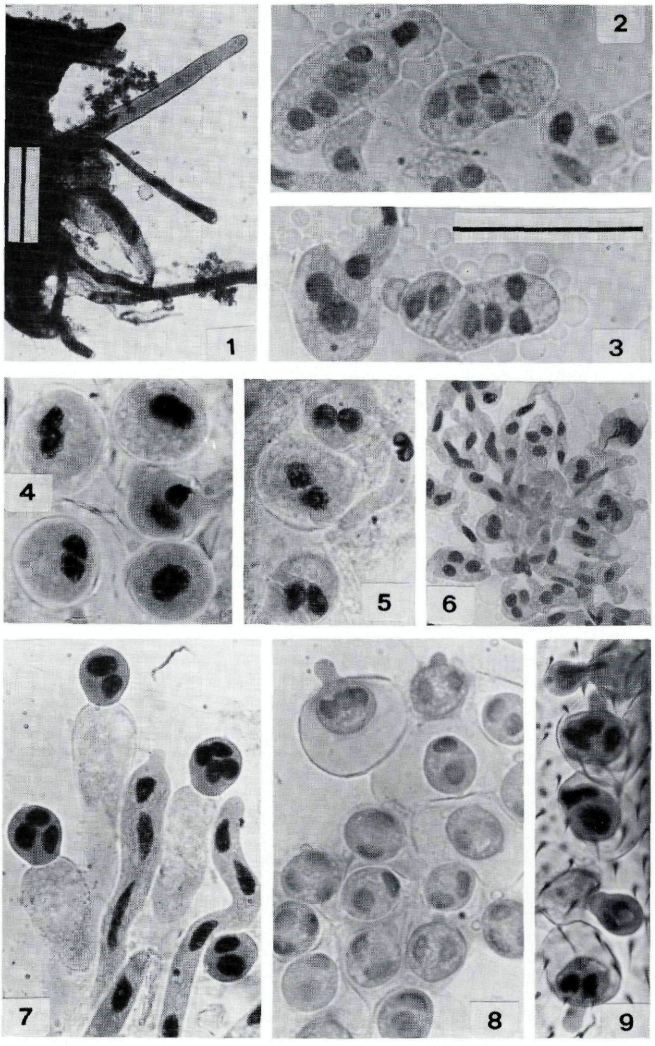


Plate 16: figs. 1–9: *Entomophthora trinucleata*. 1. Rhizoids emerging from mouthparts. – 2, 3. Oligonucleate hyphal bodies developing usually to 2-nucleate hyphal bodies by budding. – 4, 5. Bi- and 3-nucleate hyphal bodies. – 6. Germinating 2- to 4-nucleate hyphal bodies. – 7. Formation of primary conidia. – 8. Primary conidia. – 9. Formation of secondary conidia. – Bar in figs. 1 and 3 represents 50 µm; 1 and 6; 2–5, 7–9 – same magnification.

during its formation, one or more nuclei remaining in the conidiophore together with part of the cytoplasm. Division of nuclei were never observed either in the hyphal bodies or in the conidiophores. The size of the nuclei varies during the development. The smallest nuclei are those in the conidia probably due to concentration of the nuclear material.

Transitional bodies, first described in *E. brevinucleata* (KELLER & WILDING; 1985) also exist in other species of the genus. They were observed in *E. planchoniana* and in *E. muscae* mainly from Syrphidae. These structures obviously develop by the interruption of the formation of conidiophores. It is assumed that they have a certain function in the survival of the fungus during short periods of unfavourable climatic conditions.

E. muscae (and/or *E. schizophorae*) is reported to produce rhizoids from the proboscis of infected hosts (BALAZY, 1984; EILENBERG, 1985). According to recent findings (EILENBERG & al., 1986) the halo aroud projected primary conidia is formed by the ruptured outer conidial membrane and not by cytoplasmic material as described by previous authors (e.g. MACLEOD & al., l.c.).

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