The genus *Entomophthora* (Zygomycetes, Entomophthorales) with a description of five new species

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Twenty two species of *Entomophthora* are listed, and a key for their identification is provided. Five new species are described, namely *E. byfordii* from Sciaridae, *E. ferdinandi* from Anthomyiidae, *E. grandis* from large Syrphidae, *E. rivularis* from Plecoptera and *E. simulii* from Simuliidae. Data on life cycles, morphology and cytology obtained from personal collections are included.

Keywords: *Entomophthora*, Entomophthorales, entomopathogenic fungi, taxonomy, life cycles, identification, key.

The generic name *Entomophthora* Fresenius was given by Fresenius (1856) to a fungus described by Cohn (1855) as *Empusa muscae* Cohn, arguing that the name *Empusa* was already occupied by an orchid genus. The two names were subsequently used synonymously until Brefeld (1877) used these names to define two different genera. Nowakowski (1881) then characterized the genus *Entomophthora* by branched conidiophores and the genus *Empusa* by unbranched ones. He described two new genera, *Erynia* Nowakowski (type species: *E. ovispora* Nowakowski) and *Lamia* Nowakowski [type species *L. culicis* (Braun) Nowakowski] to separate the species with rhizoids. He placed all species in one family, Entomophthoreae. In the following year Nowakowski (1882) placed *E. ovispora* again in the genus *Entomophthora*. Thaxter (1888) in the first monograph on this fungus group did not accept this classification and placed all species in the genus *Empusa*, however, with *Entomophthora* and *Triplosporium subgen. nov.* (type species: *E. fresenii* Nowakowski) as subgenera. In his classification Lakon (1919) defined three genera: *Empusa* and *Lamia* with unbranched conidiophores, the latter with cystidia and rhizoids, and *Entomophthora* with branched conidiophores and rhizoids.

The confusion and the debate on the terminology continued until Batko (1964a, b, c, d) presented his new classification of the arthropod-

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pathogenic Entomophthorales. He defined *Entomophthora muscae* as the type species of the genus, with *Empusa* consequently becoming a synonym (same type species) (Batko, 1964a). However, his definition of the genus *Entomophthora* was still unsatisfactory, placing species with the typically campanulate primary conidia in two different genera, namely *Entomophthora* and *Culicicola* Nieuwland (type species *C. culicis* Braun). Nieuwland considered the latter to be the valid genus name arguing that *Lamia* Nowakowski was already occupied (Batko, 1964b; Nieuwland, 1916). Finally, Remaudière & Keller (1980) defined the genus *Entomophthora* in the present and generally accepted sense.

The first overview of this group with campanulate primary conidia was given by MacLeod & al. (1976) referring to "... Entomophthorales with *E. muscae*-like conidia ..." They listed five species. Remaudière & Keller (1980) added another species. Keller (1987a) listed 11 species and Bałazy (1993) added two further ones. The present paper lists 22 species. This increase in species number demonstrates not only the increasing interest in this group of fungi but also an improved knowledge of the taxonomic background, life cycles and molecular biology of these species.

Material and methods

The fungal material examined consist largely of personal collections or of material sent to the author either prepared and mounted on slides, or stored in ethanol or as exsiccati. Where no material was available, data were taken from the literature or from personal communications.

Fungal material was mounted in lactophenol-cotton blue (LPCB) or in lactophenol-aceto-orcein (LPAO) as described by Keller (1987a). All measurements and counts were based, if not otherwise stated, on 50 objects per individual host, designated as one series. From each fungus species and origin, usually more than one series was studied to assess variation. The number of 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).

For practical reasons but also due to the high specificity the key for the identification of the species of *Entomophthora* was set up based on hosts. It proved to be very difficult to construct a clear key based on fungal structures alone.

Results

Life cycle

Basically the life cycle can be divided into a conidial cycle and a resting spore cycle (Fig. 1). The former serves to the propagation and

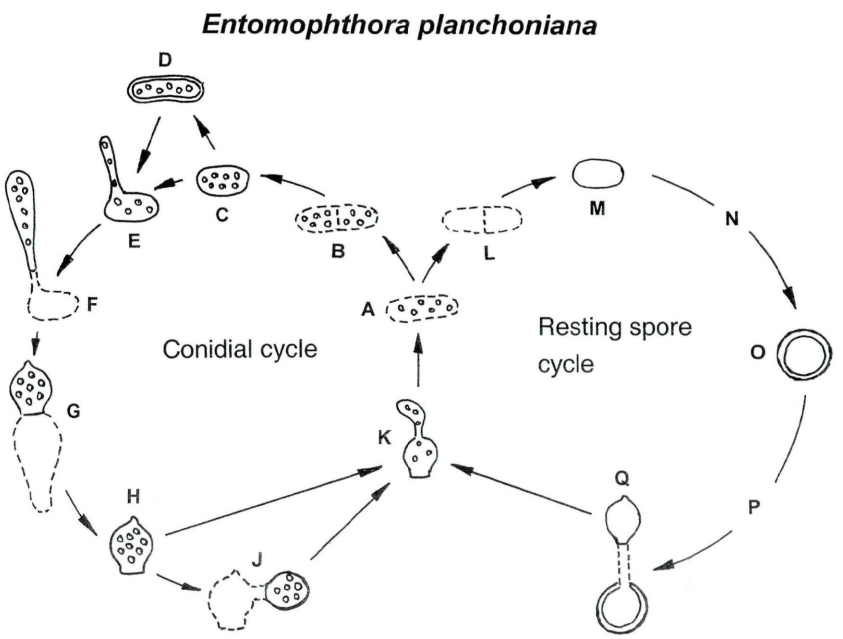


Fig. 1. Life cycle of *Entomophthora planchoniana*. – A–K: Conidial cycle. – A. Tubular protoplast. – B. Protoplast dividing by binary fission. – C. Hyphal body. – D. Overwintering hyphal body. – E. Germinating hyphal body. – F. Formation of conidiophore. – G. Formation of primary conidium. – H. Primary conidium. – J. Formation of secondary conidium. – K. Germinating primary or secondary conidium with penetration peg. – L–Q: Resting spore cycle. – L. Protoplast dividing by binary fission. – M. Hyphal body. – N. Formation of resting spore. – O. Resting spore. – P. Formation of germ tube. – Q. Supposed formation of germ conidium. Note: Resting spores are known, but details on their formation and their germination are unknown.

spread of the disease, the latter to the survival of unfavourable conditions. Infections are always due to conidia which adhere to the cuticle and form a penetration tube. Penetration through the host cuticle leaves usually a triangular hole (Brobyn & Wilding, 1983). The multiplication within the host either takes place by protoplasts or by hyphae. These structures colonise the abdomen or, more commonly, the whole body of the host. The depletion of nutrients stops vegetative growth. The hosts of most species die at this stage. Normally, hyphal bodies immediately start to form a single conidiophore, occasionally they may turn to a thick-walled overwintering stage (known only from *E. planchoniana*). The conidiophores penetrate the host cuticle, obviously with mechanical pressure, and form the primary conidium, which is actively projected. Upon landing a halo consisting of the ruptured outer wall is produced. Within a few hours a secondary condium is formed laterally on the primary one and

projected. The secondary conidia are considered to be more virulent than the primary ones.

The resting spore cycle is supposed to start in the same way as the conidial cycle. It is unknown at which stage resting spore formation is induced and if there are changes at the nuclear level. Resting spores are described as azygospores, however, their mode of formation has never been observed in detail. They germinate with a single germ tube (Thomsen & al., 2001). The formation of the germ conidium has never been observed, but we may assume that only a single one is produced.

Fungal structures

Studies on the early development of species of the genus *Entomophthora* are rare. Knowledge is based on sporadic observations. According to these observations, protoplasts may be the typical stage of early development. In *E. muscae, E. scatophagae* and *E. planchoniana* they are either tubular or rounded. In comparison, *E. byfordii* and probably also *E. culicis* grow vegetatively as hyphae which segregate later on into the hyphal bodies with the species-specific number of nuclei.

The hyphal bodies are simple rounded structures, either regular or variable. Most regular ones are spherical, subspherical or ellipsoidal. Examples are *E. philippinensis, E. planchoniana, E. scatophagae* and *E. syrphi*. The variable ones include elongate, ovoid, club-shaped, amoeboid or subrectangular structures. Examples are *E. byfordii, E. culicis, E. erupta* and *E. muscae*. Hyphal bodies normally multiply by binary fission, rarely by budding as in *E. trinucleata* or by segregation from hyphae as described from *E. byfordii* and *E. culicis*. Modified hyphal bodies are known to be the overwintering stage in *E. planchoniana* (Keller, 1987b).

The hyphal bodies germinate with a single germ tube which develops into the conidiophore. They are always unbranched. Rarely single branchings may occur but there are no reports that more than one conidium develops from a single conidiophore. They penetrate the host cuticle usually at the intersegmental membranes resulting in a typically banded appearance of the host. Soft-skinned insects are normally ruptured at the dorsal part of the abdomen. The conidiophores enlarge terminally and form the primary conidium. Sometimes the conidiophores stop their growth below the host cuticle and form transitional bodies. These subrectangular to rod-shaped structures are considered to be able to survive short periods of dryness or other unfavourable conditions (Keller & Wilding, 1985).

All primary conidia have an apical point that is typical for this genus. It is prominent in some species and less prominent in others. Statistically there are no differences in the number of nuclei between

the primary conidia and the conidiophores, although occasionally nuclei may remain in the conidiophore. The primary conidia are forcibly ejected by a mechanism which is described as the "spore-cannon" mechanism in contrast to the other genera of Entomophthoraceae, where the primary conidia are projected by papillar eversion (Humber, 1989). Upon landing the outer membrane separates into several layers and expands to form a halo around the conidium. The mucus between the wall layers takes part in the adhesion of the spore to the substrate (Eilenberg & al., 1986). Sometimes the primary conidium forms a germ tube through the apex, but normally they germinate laterally to form a secondary conidium.

The secondary conidia are similar to the primary ones although slightly smaller. However, they differ from the primary ones in several aspects. The apical point is reduced, sometimes hardly visible or even missing, the papilla is more rounded, the cytoplasma is more homogenous and the nuclei stain weaker with LPAO, the discharge is by papillar eversion and upon landing no halo of any kind is produced. There is always only one type of secondary conidia. Secondary conidia germinate with germ tubes normally through the apex. Tertiary conidia exist but are rare (Mullens & Rodriguez, 1985; Eilenberg, pers. comm.). In *E. muscae* it has been demonstrated that secondary conidia are much more infective than the primary ones (Bellini & al., 1992).

Cystidia have never been observed in this genus, except when resting spores are formed (Thomsen & al., 2001). Rhizoids exist in several species. They are monohyphal. In some species some of them may join to form bundles in the basal portion (e.g., *E. brevinucleata* and *E. byfordii*). They never have specialised endings. *E. planchoniana* produces a peculiar type of rhizoid which by the appearance and the mode of formation must be considered as modified conidiophores (Plate 6, figs. 6–7). Although sometimes described as pseudorhizomorphs or compound rhizoids (Ben-Ze'ev & Uziel, 1979) they distinctly differ from this type of rhizoid which is delimited to the genus *Zoophthora*. Rhizoids are very abundant in *E. culicis* and formed over the whole ventral side of the host. Normally rhizoids are not abundant and are confined to the ventral side of the thorax and the head or even to the mouthparts. Brachyceran flies are fixed to the substrate by their proboscis. This is partly attributed to secretions but also to fungal structures which may penetrate the rostrum and act as rhizoids (Bałazy, 1984).

Resting spores are known from several species. They are described as azygospores. However, their mode of formation *in vivo* is unclear. Under *in vitro* conditions, *E. schizophorae* produced resting spores in the germ tubes arising from hyphal bodies, either at their ends or intercalary (Eilenberg & Bresciani, 1990). The resting spores

germinate with a single thick germ tube. However, the formation of germ conidia was not observed (Thomsen & al., 2001).

Description of the genus

Vegetative cells either as protoplasts or hyphal bodies. – Hyphal bodies usually regular, spherical to subspherical, elliptical or subrectangular, sometimes irregularly rounded. They germinate with single germ tube. – Nuclei stain distinctly in LPAO, diameter on average 2.5–6 µm. – Conidiophores unbranched, terminal portion enlarged. – Primary conidia campanulate, outer wall ruptures after discharge, projected conidia therefore surrounded by a halo, bi- to multinucleate. – Secondary conidia similar to primary ones, apical point often indistinct, 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, monohyphal or joined to form bundles in the basal portion, in some Diptera restricted to mouthparts, without specialized endings. – Cystidia absent when conidia are produced, may be abundant in presence of resting spores. – Parasites of insects.

Type species: *Entomophthora muscae* (Cohn) Fresenius, Bot. Zeitung 14: 882. 1856.

Key to species

1. Pathogen of Hemimetabola 2
1*. Pathogen of Holometabola 9

2. Pathogen of Homoptera or Heteroptera 3
2*. Pathogen of other Hemimetabola 4

3. Pathogen of Heteroptera 5
3*. Pathogen of Homoptera 6

4. Pathogen of Thysanoptera. Primary conidia 10–15 × 8–12 µm with 2–4 nuclei . . . . . 20. *E. thripidum*
4*. Pathogen of Plecoptera. Primary conidia 22–29 × 18–23 µm with 11–13 nuclei . . . . . 15. *E. rivularis*

5. Primary conidia 17–23 × 11–16 µm with 3–5 nuclei. Sporulation from living host. On larval and adult Miridae . . . . 6. *E. erupta*
5*. Primary conidia 18–22 × 15–18 µm with 8–13 nuclei. On larval *Notostira elongata* (Miridae) . . . . . 9. *E. helvetica*

6. Pathogen of Aphididae 7
6*. Pathogen of other Homoptera 8

7. Primary conidia 11–14 × 10–11 µm with 4–6 nuclei. Resting spores 30 µm. . . . . 4. *E. chromaphidis*
7*. Primary conidia 15–20 × 12-16 µm with 5–9 nuclei. Resting spores 31–38 µm . . . . . 14. *E. planchoniana*

8. Pathogen of Aleurodidae. Primary conidia 12–16 × 12–13 µm with 3–4, rarely 5 nuclei. . . . . 11. *Entomophthora* sp. 2
8*. Pathogen of Psyllidae. Primary conidia 15–18 × 13–16 µm with 4–5 nuclei . . . . . 13. *E. philippinensis*

9 Pathogen of other Holometabola 10
9*. Pathogen of Diptera 11

10. Pathogen of Coleoptera Cantharidae. Primary conidia 22–24 × 17–20 µm with 8–17 nuclei . . . . . 3. *Entomophthora* sp. 1
10*. Pathogen of Rhaphidides Rhaphididae. Primary conidia 12–18 × 11–16 µm with 4–6 nuclei . . . . . 22. *E. weberi*

11. Pathogen of Nematocera 12
11*. Pathogen of Brachycera 17

12. Pathogen of Sciaridae 13
12*. Pathogen of other Nematocera 14

13. Primary conidia 15–16 × 12–14 µm with 5–9 nuclei with a diameter of 3–4 µm. Rhizoids abundant on ventral side . . . . . 2. *E. byfordii*
13*. Primary conidia 17–18 × 14–15 µm with 3 nuclei with a diameter of 5.5–6 µm. Rhizoids from mouthparts . . . . . 21. *E. trinucleata*

14. Pathogen of Cecidomyiidae 15
14*. Pathogen of other Nematocera 16

15. Primary conidia 11–19 × 9–16 µm with 4–10 nuclei. . . . . 1. *E. brevinucleata*
15*. Primary conidia 17 × 13 µm with 4 nuclei. . . . 10. *E. israelensis*

16. Primary conidia 12–14 × 9–11 µm with 2 nuclei. On Culicidae, Chironomidae and Simuliidae . . . . . 5. *E. culicis*
16*. Primary conidia 24–26 × 18–21 µm with 14–15 nuclei. On Simuliidae . . . . . 18. *E. simulii*

17. Pathogen of Syrphidae 18
17*. Pathogen of other Brachycera 19

18. Pathogen of larger syrphids. Primary conidia 30–32 × 24–26 µm with 31 (22–47) nuclei with a diameter of 3.5–3.6 µm. . . . . 8. *E. grandis*

18*. Pathogen of smaller syrphids. Primary conidia 28–32 × 21–27 µm with 19–22 (14–30) nuclei with a diameter of 2.8–3.4 µm . . . . . 19. *E. syrphi*

19. Primary conidia with less than 13 nuclei on average 20

19*. Primary conidia with more than 13 nuclei on average 21

20. Primary conidia 19–21 × 15–17 µm with 4–5 nuclei with a diameter of 4.9–5.0 µm. Hyphal bodies spherical to subspherical, 21–23 × 18–20 µm . . . . . 17. *E. schizophorae*

20*. Primary conidia 23–27 × 18–23 µm with 10–11 nuclei with a diameter of 3.9–4.0 µm. Hyphal bodies subspherical 23–26 × 21–23 µm . . . . . 7. *E. ferdinandi*

21. Primary conidia 27–31 × 20–24 µm with 15–20 nuclei with a diameter of 3.9–4.4 µm. Hyphal bodies subspherical to broadly ovoid, 33–39 × 24–32 µm . . . . . 12. *E. muscae*

21*. Primary conidia 28–29 × 22–23 µm with 17–18 nuclei with a diameter of 3.8-4.2 µm. Hyphal bodies subspherical 30–33 × 26–30 µm . . . . . 16. *E. scatophagae*

Description of the species

1. *Entomophthora brevinucleata* S. Keller & Wilding, Entomophaga 30: 56. 1985.

The species has subspherical to elliptical hyphal bodies. The primary conidia measure on average 11.2–18.9 × 8.7–15.8 µm and contain on average of 4.1–9.6 nuclei with a mean diameter of 2.7–3.1 µm (all data from type host). The rhizoids are monohyphal, sometimes basically joined to form bundles. Transitional bodies were described for the first time from this species. They are considered as a development stage able to survive adverse conditions for a limited time. Transitional bodies are also found in other species of *Entomophthora*. Resting spores are unknown. Additional morphological details are given in Tab. 1.

The species attacks adult gall midges (Diptera, Cecidomyiidae). It was originally described from *Sitodiplosis mosellana* on *Phalaris arundinaceae, Mycodiplosis* sp. and an unidentified midge on *Phalaris arundinacea*. In the meantime the first (type) host was described as a distinct species *S. phalaridis* (Abbass, 1986), which became the new type host. *E. brevinucleata* is obviously a common pathogen of gall midges. It was found on numerous other hosts but, with the

exception of *Contarinia tritici* and *C. pisi,* not yet identified. They were mainly collected on *Triticum aestivum, Zea mays, Medicago sativa, Quercus robur, Fagus sylvatica, Salix* spp., *Phragmites communis, Echinochloa grus-galli* and *Chenopodium* spp.

The species is known from Switzerland, Great Britain, Italy (Keller, unpubl.), Poland (Bałazy, 1993) and Spain (Niell, 1999; Niell & Santamaria, 2001). It is closely related to *E. israelensis* (Ben-Ze'ev & Zelig, 1984) from which it differs mainly by overall size of the primary conidia (16.8 × 13.1 µm, L/D = 1.28 for *E. israelensis* and 14.8 × 12.4 µm, L/D = 1.20 for *E. brevinucleata)* and the average number of nuclei per conidium (3.7 for *E. israelensis* versus 4.1–9.6 for *E. brevinucleata*). The relationship between these two species is comparable to that of *E. planchoniana* and *E. chromaphidis*. However, a more detailed study on the variability of the characters of *E. israelensis* may reveal the identity of the two species.

2. ***E. byfordii*** S. Keller, **sp. nov.** – Pl. 1, figs. 1–7.

Rhizoidea mononemata e partibus buccalibus emergentia. Conidiophora simplicia. Conidia primaria (13–)15–16(–18) × (11)12–14(–16) µm, campanulata, 5–9 nucleos 3–4.5 µm diametro continentia. Conidia secundaria habitu primariis similia. Cystidia et sporae perdurantes absunt.

In *Bradysia* sp. (hospite typico) (Diptera: Sciaridae).

Holotypus ZT, Conthey Valais, coll. et leg. S. Keller, X 1999, nos. 87-2, 87-7, 87-8, 87-23, 87-27. Paratypi K et BPI.

Rhizoids monohyphal, cell walls thickened and slightly brown, with a diameter of 8.2 (6–12) µm (1 series), emerging from the mouthparts and from the ventral side of the thorax, surrounded by a mucous mass, nuclei concentrated in the terminal portion, without specialised holdfast, endings sometimes slightly enlarged (Fig. 1). – Hyphal bodies irregularly rounded, ovoid-elongate or rod-shaped, straight or slightly bent, sometimes branched, developed by binary or rarely multiple fission from short hyphae-like structures. They contain 6.9–7.7 (4–11) nuclei with a diameter of 3.7–3.9 (3–5) µm (2 series). They germinate with single germ tube with a diameter of 7.1 (6–8.5) µm (1 series) (Figs. 2–3). – Conidiophores unbranched with 6.6–6.9 (4–9) nuclei (4 series) with a diameter of 3.7 (3–4.5) µm (2 series), terminal diameter 13.0 (11–16) µm (1 series) (Fig. 4–5). – Primary conidia 15.1–16.1 (13–18) µm × 12.3-13.5 (11–16) µm, L/D = 1.18–1.22 (5 series), with small apical point. They contain 6.9 (5–9) nuclei (1 series) with a diameter of 3.5–3.6 (3–4.5) µm (2 series) (Fig. 6). – Secondary conidia 12–13 × 10–12 µm, L/D = 1.14 (1 series, n = 10) (Fig. 7). – Cystidia and resting spores absent.

Tab. 1. – Data of fungal structures of *Entomophthora* spp. attacking large flies (Diptera: Brachycera). Measurements in µm, PC = primary conidia, SC = secondary conidia, HB = hyphal bodies

Fungal species	Fungal structure	Host species[1]	Length L		Diameter D		L/D	Nuclei (mean values)		Reference
			average	min–max	average	min–max		number	diameter	
E. grandis	PC	*Episyrphus balteatus*[2]	30.6–32.1	28–35	24.4–25.3	20–28	1.25–1.27			Keller, this paper
		Eupeodes corollae	29.6–32.0	27–35	23.6–25.4	21–29	1.26–1.27	24.7–31[3]	3.2–3.6	
		Scaeva pyrastri	31.8	29–35	26.2	24–28	1.21	23.8[3]		
	SC	*E. balteatus*[2]	24.1–24.3	22–27	19.0–19.5	18–22	1.25–1.29			
		S. pyrastri	24.2	22–27	18.7	17–21	1.29			
E. syrphi	PC	*Melanostoma mellinum*[2]	27.5–32.3	24–36	20.7–27.3	18–30	1.18–1.33	18.6–22.2	2.8–3.4	Keller, this paper
		Herina frondescentiae	28.6–30.8	25–34	22.7–24.5	19–28	1.22–1.29	19.2–21.7[3]		
	SC	*M. mellinum*	21.9–24.3	18–30	17.2–17.6	15–19	1.27–1.39			
		H. frondescentiae	23.0	21–29	17.6	16–19	1.31			
	HB	*M. mellinum*	37.0	25–48	31.3	23–38	1.18			
E. scatophagaeee	PC	*Scatophaga stercoraria*[2]	27.9–28.7	25–32	21.6–23.2	19–28	1.23–1.31	15.2–18.3	3.8–4.2	Keller, this paper Steinkraus & Kramer (1988)
		Delia planipalpis	25.3–28.9	23–33	20.7–23.7	18–28	1.20–1.24	15.1–18.5	3.4–4.0	Keller, this paper
	SC	*S. stercoraria*[2]	18.9–20.9	17–23	15.3–17.1	13–19	1.20–1.23			
		D. planipalpis	20.3–21.0	17–24	16.6–17.3	15–19	1.22			

Tab. 1 (cont.). – Data of fungal structures of *Entomophthora* spp. attacking large flies (Diptera: Brachycera). Measurements in µm, PC = primary conidia, SC = secondary conidia, HB = hyphal bodies

Fungal species	Fungal structure	Host species[1]	Length L		Diameter D		L/D	Nuclei (mean values)		Reference
			average	min–max	average	min–max		number	diameter	
E. muscae	PC	*Musca domestica*[2]	26.9–31.1	21–35	20.4–24.2	16–29		15.2–20.2	3.9–4.4	Keller et al., 1999
		Drosophila spp.	26.0–27.6	23–30	21.1–21.6	18–24		15.3–15.9	4.4	Keller, this paper
		Empididae	26.4–28.5	23–33	21.7–22.9	17–27		17.9	4.0	Keller, this paper
	SC	M. domestica[2]	19.3–24.2	16–28	15.1–19.1	12–23				Keller et al., 1999
		Drosophila spp	20.6–21.9	18–23	16.7–17.8	16–19				Keller, this paper
		Empididae	20.2–21.7	18–24	16.3–17.9	15–21				Keller, this paper
	HB	*M. domestica*[2]	33.0–38.8	24–54	23.5–31.6	17–41	1.18–1.49	14.9–18.9	4.4–4.7	
		Drosophila spp.	34.0–37.8	27–46	29.5–31.0	24–36	1.15–1.22	15.5	4.5	
E. ferdinandi	PC	*Delia kullensis*[2]	22.7–26.6	21–30	17.9–22.7	16–27	1.15–1.27	9.8–11.2	3.9–4.0	Keller 1984, this paper
	SC	*D. kullensis*[2]	17.7–17.8	16–19	13.9–14.0	12–17	1.27			
	HB	*D. kullensis*[2]	23.3–26.4	18–31	20.6–22.7	17–28	1.12–1.17	10.0–10.3	4.0–4.3	
E. schizophorae	PC	*Delia platura*[2]	18.9–21.1	18–23	14.9–17.1	13–19	1.23–1.27	4.3–4.6	4.9–5.0	Keller, 1987a
		Psila rosae	18.3–20.9	16–24	13.6–16.4	12–19	1.27–1.37	4.4–5.1	4.8–4.9	Keller, 1984
		Musca domestica	18.9–20.5	18–22	13.8–16.4	12–18	1.25–1.37	4.1–5.5	5.3	Keller et al., 1999
		Pollenia rudis	21.5–23.9	19–25	17.2–19.4	15–22	1.19–1.27	5.6–6.6	5.0	Keller, 1984
		Platypalpus sp.	18.6–18.9	17–21	14.1–15.0	12–18	1.26–1.32	4.0–4.2	4.9–5.0	Keller, this paper
	SC	*D. platura*[2]	15.0–16.5	13–18	12.0–13.1	11–15	1.25–1.27			
		M. domestica	14.6	12–16	12.0	10–13	1.22			
		Platypalpus sp.	15.8–16.3	15–18	12.7–12.9	11–16	1.24–1.26			
	HB	*D. platura*[2]	21.0–22.7	18–28	18.2–19.5	16–23	1.15–1.16		4.9–5.0	

[1] For details see under the corresponding fungal species; [2] Type host; [3] including data from conidiophores

Host. – Diptera, Sciaridae: *Bradysia* sp.

Symptoms. – Diseased midges fixed with rhizoids on the underside of leaves of apple trees.

Distribution. – Switzerland: Conthey, Canton Valais (type locality); Jenaz, Canton Graubünden; Gächlingen, Canton Schaffhausen.

Etymology of specific epithet. – The specific epithet refers to W. J. Byford who mentioned the species first but considered it to be *E. planchoniana* (Byford & Reeve, 1969).

The species was collected in September-October mainly in plantations of apple trees (Conthey, Gächlingen), rarely on old scattered apple trees (Jenaz). At Conthey the disease had occurred epizootically. Numerous fresh and old cadavers of midges were found on the underside of the leaves. The conidia and the nuclei match the description of *E. planchoniana*, from which, however, it can easily be separated by the hyphal bodies and the rhizoids. It differs from *E. trinucleata*, which attacks sciarid midges as well, mainly by number and size of the nuclei.

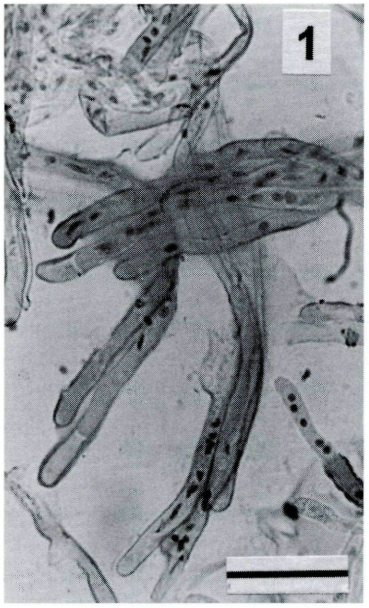
3. *Entomophthora* sp. 1 Eilenberg (in prep.).

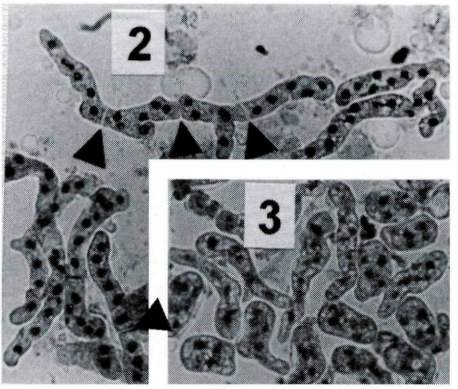
The species attacks adult *Rhagonycha fulva* (type host) and *Cantharis livida* (Coleptera, Cantharidae) in Denmark. The diseased beetles were attached with their mandibles to grass or lower vegetation, the elytra more or less spread.

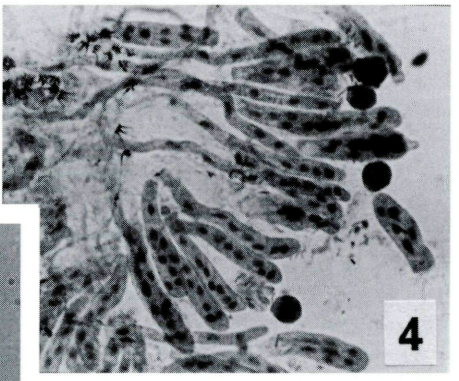
Primary conidia 21.6–24.4 (17–29) × 17.1–19.9 (13-24) µm; L/D = 1.23–1.28, with 8–17 nuclei. – Secondary conidia 19.3 (16–21) × 15.9 (16–24) µm; L/D = 1.21. – Resting spores probably azygospores, 44.5 (39–50) × 40.4 (31–44) µm. – Rhizoids absent.

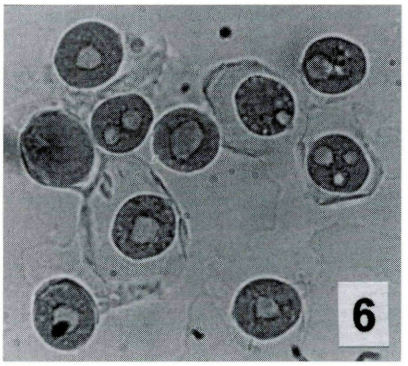
The species was collected from June to August on grass and lower vegetation of a hedge. Transmission of the disease to Diptera failed. The species was attributed to the *E. muscae*-complex (Eilenberg & al., 1987). However, it differs by morphological and cytological characters, by the host and by molecular pattern from other species of the genus (Jensen & Eilenberg, 2001)

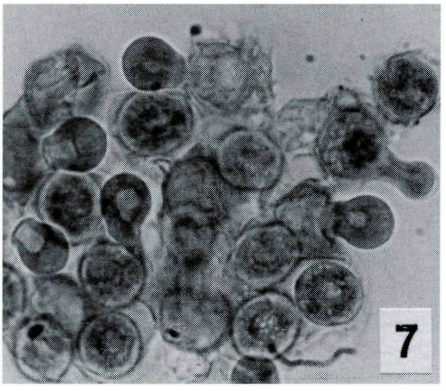
Plate 1. – Figs. 1–7: *Entomophthora byfordii* sp. nov. from *Bradysia* sp. – 1. Rhizoids, partly joined to bundles. – 2. Hyphae with nuclei from living hosts. Arrowheads show septa, where the hyphae separate to form hyphal bodies. – 3. Hyphal bodies with nuclei. – 4–5. Conidiophores with nuclei and developing and fully developed conidia. – 6. Primary conidia, some with halo formed by the ruptured outer wall. – 7. Formation of secondary conidia (arrowhead). – 1–5: LPAO; 6–7: LPCB. – Bars in Figs. 1 and 5 = 50 µm, Figs. 1–4 and 5–7 same magnification.

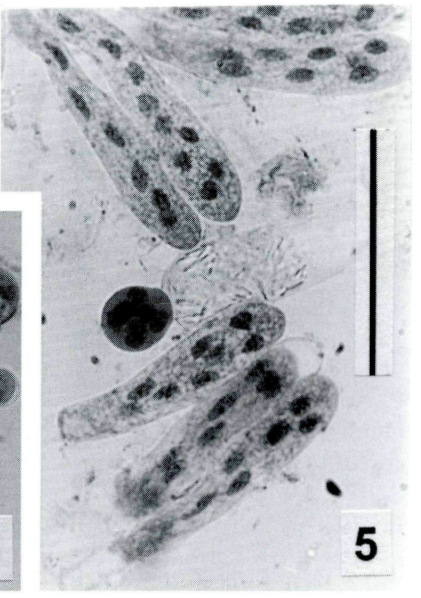












4. *E. chromaphidis* Burger & Swain, J. Econ. Ent. 11: 278–288. 1918.

The species was originally found as a pathogen of the walnut aphid *Chromaphidis juglandicola* (Kalt.) (Homoptera, Aphididae) (type host) in California. The primary conidia measure 11–14 × 10–11 µm and contain a single large oil globule. The resting spores are azygospores, brown, with a diameter of 30 µm. The host is fixed with rhizoids. Another host species mentioned by Burger & Swain, *Psocus* sp. (Psocidae) must be considered as doubtful. Humber & Feng (1991) identified the species from *Schizaphis graminum, Metopolophium dirhodum* and *Sitobion avenae* from Idaho and Washington. The conidia measured 12–16 × 10–14 µm and contained 4–6 nuclei. The rhizoids are described as pseudorhizomorphs as for *E. planchoniana*. The same authors attributed a fungus with similar conidial dimensions described as *E. planchoniana* by Holdom (1983) from Queensland, Australia, to *E. chromaphidis*.

E. chromaphidis is very closely related to *E. planchoniana*. The latter varies widely in conidial sizes and nuclear numbers (Tab. 3). Nevertheless there is only an overlap with the nuclear number but not with the morphological data and the nuclear dimensions given by Humber & Feng (1991) for *E. chromaphidis*. These authors also report that they could isolate the small-spored fungus from USA but not the large-spored one from Europe. Further, the two species are geographically separated. However, genetic analysis could not separate *E. planchoniana* from material provided by Humber & Feng (Jensen & Eilenberg, 2001; Freimoser & al., 2001). Based on the available data *E. chromaphidis* must be considered a valid species.

5. *E. culicis* (Braun) Fresenius, Abhandl. Senckenb. Naturf. Ges. 2: 205, figs. 51–58, (1858).

≡ *Empusa culicis* Braun, *Algarum unicellularum genera nova et minus cognita*. Lipsiae: 105. 1855.

≡ *Lamia culicis* (Braun) Nowakowski, Pam. Akad. Umiej., Wydz.Mat. Przyr. 8: 173. 1883.

≡ *Culicicola culicis* (Braun) Nieuwland, Am. Midl. Nat. 4: 378. 1916.

≡ *Myiophyton culicis* (Braun) von Arx, The genera of fungi p. 51. 1970.

The species attacks adult midges of the families Culicidae, Chironomidae and Simuliidae (Diptera, Nematocera). Hosts not belonging to Nematocera must be considered doubtful. Numerous rhizoids develop ventrally on the thorax and abdomen, monohyphal with a diameter of 20–50 µm, without specialised endings. Hyphal bodies are ellipsoid to short rod-shaped 34.3. (24–44) × 16.1 (12–22) µm, L/D = 2.13 (1 series) , binucleate, often arranged in chains. They germinate with a single germ tube which forms an unbranched

conidiophore with a terminal diameter of 8–12 µm. According to Fresenius the primary conidia have a length of 11.8 µm. Personal measurement revealed a dimension of 12.7–14.0 (11–16) × 9.1–11.0 (8–12) µm, L/D = 1.17–1.41 (6 series), binucleate with distinct apical point. Secondary conidia are like the primary ones but without prominent apical point. Resting spores are spherical to slightly ellipsoidal, smooth 24.9–25.3 (21–28) µm. Cystidia are absent.

The species can easily be identified by the bi-nucleate conidia. It is very common and often causes epizootics in wet habitats, usually close to water. It was regularly found in large quantities on wooden support in ponds and on walls at the border of brooks. It is known from Europe, North America and Asia.

6. *E. erupta* (Dustan) Hall, J. Ins. Pathol. 1: 48. 1959.

≡ *Empusa erupta* Dustan (1924), Proc. Acad. Entomol. Soc. 9: 31. 1924.

The species attacks larvae and adults of the familiy Miridae (Heteroptera): *Lygus communis* var. *novaescotiensis* (type species), *L. pabulinus*, *Adelphocoris lineolatus*., *Irbisia solani* and *Plagiognathus* sp. According to the data and illustrations given in the original description (Dustan, 1924), the hyphal bodies are ellipsoidal to short club shaped and germinate with a single germ tube. The unbranched conidiophores produce the conidia which measure 17–23 × 15–18 µm. The secondary conidia are 14.3 × 13.2 µm. The resting spores are spherical, light brown and smooth with a diameter of 33–36 µm. They are asexually formed at the end of specialised hyphal tubes arising from the hyphal bodies and growing out through the integument to the surface of the abdomen. The infection is confined to the abdomen and sporulation of the fungus takes place while the host is still moving around.

Ben-Ze'ev & al. (1985) studied fungal material from histological sections (Ewen, 1966) and from type material which contained only resting spores. They gave the following amendments: Hyphal bodies ovoid or short allantoid, 12.6–18.8 µm wide. Primary conidia 17–23 × 11–16 µm with 3–5 nuclei (the authors also mentioned mononucleate conidia, which must be considered doubtful, possibly due to counts from histological sections). Resting spores are spherical to subspherical, 30.9–40.1 µm, with 1–3, usually 2 nuclei. All resting spores contained a large spherical oil droplet. Spore wall 3.4–6.9 µm thick, covered with a brown, rather smooth, removable episporium with a thickness of 1.2–3.4 µm. Rhizoids and cystidia are absent. The species is known only from North America.

The species is related to *E. helvetica* from which it differs mainly by the pathobiology and by the number and the size of the nuclei.

7. ***E. ferdinandi*** S. Keller, **sp. nov.** – Plate 2, Figs. 1–4.

Corpora hyphalia (18–)23–26(–31) × (17–)21–23(–28) µm, subsphaerica vel ellipsoidea. Conidiophora simplicia. Conidia primaria (21–)23–27(–30) × (16)18–23(–27) µm, campanulata, (6–)10–11(–16) nucleos 3.5–5 µm diametro continentia. Conidia secundaria habitu primariis similia. Rhizoidea, cystidia et sporae perdurantes absunt.

In *Delia kullensi* (hospite typico) (Diptera: Anthomyiidae) et *Drosophila* sp. (Diptera: Drosophilidae).

Holotypus ZT, Neunkirch SH, coll. et leg. S. Keller, VI-VII 1983, nos. 62-1, 62-7, 62-30, 62-31. Paratypi K et BPI.

Hyphal bodies subsperical to slightly ellipsoidal 23.3–26.4 (18–31) × 20.6–22.7 (17–28) µm, L/D = 1.12–1.17 (3 series), containing 10.0–10.3 (8–16) nuclei (3 series) with a diameter of 4.0–4.3 (3.5–5.0) µm (2 series) and germinate with single germ tube with a diameter of 7.7–8.0 (6–10) µm (3 series) (Figs. 1–2). – Conidiophores unbranched with 10.1–10.3 (7–14) nuclei with a diameter of 4.0–4.3 (3.5–5.0) µm (3 series) (Fig. 3). – Primary conidia 22.7–26.6 (21–30) × 17.9–22.7 (16–27) µm, L/D = 1.15–1.27 (7 series), distinct apical point. They contain 9.8–11.2 (6–16) nuclei (6 series) with a diameter of 3.9–4.0 (3.5–5.0) µm (2 series) (Fig. 4). – Secondary conidia similar to the primary, 17.7–17.8 (16–19) × 13.9–14.0 (12–17) µm, L/D = 1.27 (2 series). – Rhizoids, cystidia and resting spores absent.

Host. – Diptera, Anthomyiidae: *Delia kullensis* (type host), *Drosophila* sp.

Symptoms. – Diseased flies attached to substrate fixed with proboscis, wings spread laterally.

Distribution. – Switzerland: Neunkirch (Widen), Canton Schaffhausen (type locality).

Etymology of specific epithet. – In honour of Ferdinand Cohn, who described the first species of the familiy Entomophthoraceae. Cohn's given name was chosen since the family name is already occupied by *Myiophyton cohnii* (Lebert, 1857), a synonym of *Entomophthora muscae*.

The species was collected at the end of June when it caused an epizootic among its host. Numerous dead flies were attached to nettles (*Urtica dioica*) in a small, light forest. A fungus found on *Drosophila* sp. at Zurich-Reckenholz was considered to belong to this species, although the conidia were slightly smaller [22.5 (18–25) × 17.3 (15–19) µm, L/D = 1.30] and contained 11.8 (8–16) nuclei with a diameter of 3.8 (3.5–4.5) µm.

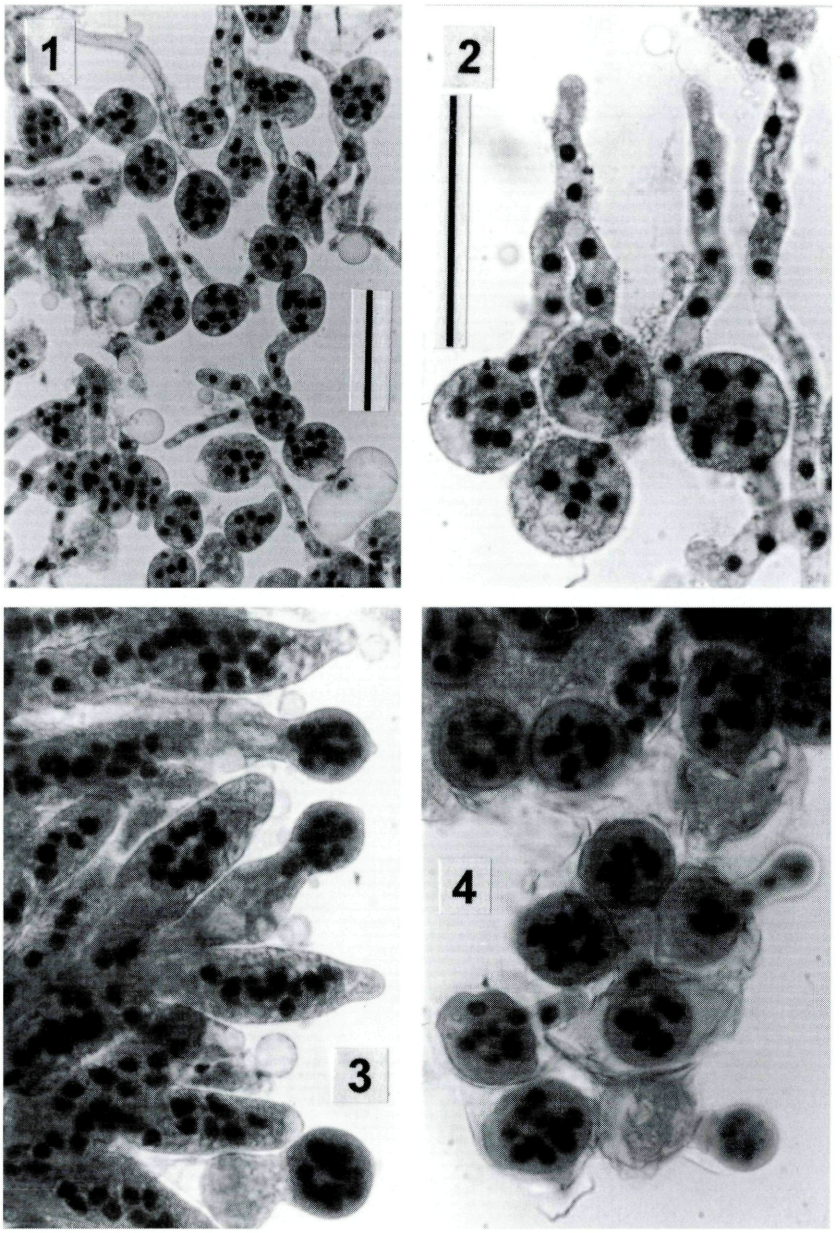


Plate 2. – Figs. 1–4: *Entomophthora ferdinandi* from *Delia kullensis*. – 1–2. Hyphal bodies with nuclei. – 3. Conidiophores with developing conidia and nuclei. – 4. Primary and developing secondary conidia. LPAO. - Bars in Figs. 1 and 2 = 50 µm, Figs. 2–4 same magnification.

The species corresponds to group B of the *E. muscae* complex (Keller, 1984). It can be separated clearly from *E. schizophorae* and *E. muscae* by the number of nuclei. It further differs from *E. muscae* by the different hyphal bodies (Tab. 2). The species is also known from Denmark infecting the anthomyiid fly *Botanophila fugax*. *In vivo* isolates of this origin were recently successfully used to induce resting spore formation in *Musca domestica*. The resting spores are globose and hyaline and measured on average 35 µm with a range of 30–40 µm (Thomsen & al., 2001).

8. ***E. grandis*** S. Keller, **sp. nov.**

Corpora hyphalia sphaerica, subsphaerica vel ovoidea. Conidiophora simplicia. Conidia primaria (27–)30–32(–35) × (20–)24–26(–29) µm, campanulata, (22–)31(–47) nucleos 3–4.5 µm diametro continentia. Conidia secundaria habitu primariis similia. Rhizoidea, cystidia et sporae perdurantes absunt.

In *Episyrpho balteato* De Geer (hospite typico), *Eupeodes corollae* F., *Scaeva pyrastri* L. (Diptera: Syrphidae).

Holotypus ZT, Hallau (Canton Schaffhausen), coll. et leg. S. Keller, VII 1984, no 88-23.

Hyphal bodies spherical, subspherical or ovoid, germinate with single germ tube. – Conidiophores unbranched with 23.8–29.0 (14–42) nuclei with a diameter of 3.2–4.0 (3.0–5.0) µm (3 series each). – Primary conidia 29.6–32.0 (27–35) × 23.6–26.2 (20–29) µm, L/D = 1.21–1.27 (5 series), apical point not prominent, with 31 (22–47) nuclei (1 series) with a diameter of 3.5–3.6 (3.0-4.5) µm (2 series). – Secondary conidia similar to the primary 24.2–24.3 (22–27) × 18.7–19.5 (17–22) µm, L/D = 1.25–1.29 (2 series), apical point indistinct or missing. – Rhizoids, cystidia and resting spores absent.

Hosts. – Diptera, Syrphidae: *Episyrphus balteatus* (type host), *Eupeodes corollae, Scaeva pyrastri*.

Symptoms. – Dead hoverflies fixed to flowers or to the underside of leaves by their proboscis. The fungus sporulates along the intersegmental membranes and the pleurae.

Distribution. – Switzerland: Hallau, Canton Schaffhausen (type locality), Solothurn, Stammheim and Rafz, Canton Zurich.

Etymology of specific epithet. – Refers to the large size of the conidia and of the other fungal structures.

Single individuals of diseased insects were occasionally found. Although the hosts were sometimes present in high densities, epizootics as for *E. syrphi* were never observed. The species was collected from June to August. It closely resembles *E. syrphi*, but its structures are larger and have more and larger nuclei.

Tab. 2. – Data of fungal structures of *Entomophthora* spp. attacking Diptera Nematocera. Measurements in µm, PC = primary conidia, SC = secondary conidia, HB = hyphal bodies

Fungal species	Fungal structure	Host species[1]	Length L		Diameter D		L/D	Nuclei (mean values)		Reference
			average	min–max	average	min–max		number	diameter	
E. simulii	PC	*Simulium lineatum*[2]	24.2–26.2	21–30	17.9–20.6	16–24	1.26–1.35	13.8–14.8[3]	3.6–3.8	Keller, this paper
	SC	*S. lineatum*	18.1–19.9	15–24	14.6–15.9	12–22	1.19–1.26			
	HB	*S. lineatum*	36.3	27–45	24.6	18–30	1.48	12.2–13.8	3.7–4.3	
E. byfordii	PC	*Bradysia* sp.[2]	15.1–16.1	13–18	12.3–13.5	11–16	1.18–1.22	6.6–6.93	3.3–3.6	Keller, this paper
	HB	*Bradysia* sp	Irreg.					6.9–7.7	3.7–3.9	
E. brevinucleata	PC	*Sitodiplosis phalaridis*[2]	11.2–17.4	10–22	8.7–15.8	8–19	1.14–1.29	4.1–9.6	2.7–3.1	Keller & Wilding (1985).
	SC	S. phalaridis	12.5–15.1	11–17	10.3–12.1	9–14	1.21–1.25			
	HB	S. phalaridis	27.2–28.3	19–40	22.0–22.1	15–30	1.24–1.28			
E. israelensis	PC	Cecidomyiidae[2]	16.8	15–20	13.1	11–16	1.28	3.7		Ben-Ze'ev & Zelig, 1984
	SC	Cecidomyiidae	12.8	10–14	11.2	10–11.3	1.14			
E. trinucleata	PC	Sciaridae	17.5–18.0	16–22	14.0–15.0	12–18	1.19–1.25	2.7–3.4	5.6–5.9	Keller, 1987a
	HB	Sciaridae	23.6–26.0	19–36	20.1–21.9	16–27	1.17–1.18			
E. culicis	PC	Nematocera	12.7–14.0	11–16	9.1–11.0	9–12	1.17–1.41	2	4.8–5.4[3]	Keller, 1987a
	DS	Nematocera			24.9–25.3	21–28				

[1] For details see under the corresponding fungal species; [2] Type host; [3] including data from conidiophores

9. *E. helvetica* S. Keller & Ben-Ze'ev in Ben-Ze'ev, Keller & Ewen, Canad. J. Bot. 63: 1471–1472. 1985.

The species attacks larvae of *Notostira elongata* Geoffr. (Heteroptera, Miridae) (type species). Dead insects are fixed to grasses by their proboscis or, especially those that had recently died, by their clasping legs, head downwards. The hyphal bodies are subspherical, ovoid or claviform and measure 27.1–27.3 (22–24) × 18.6–21.0 (15–24) µm. The unbranched conidiophores contain 8–15 nuclei. The primary conidia measure 18.0–22.0 (16–24) × 14.8–17.5 (12–19) µm, L/D = 1.18–1.30, apical point present, but indistinct. They contain 6–18, usually 8–13 nuclei, 11 being the most frequent number. Secondary conidia like primary, apical point indistinct or missing, 13.8–15.5 (12–18) × 11.2–14.1 (10–18) µm, L/D = 1.09–1.23. Structures resembling immature resting spores were spherical and measured 23–32 µm. Cystidia and rhizoids are absent.

The species was originally identified as *E. erupta* (Keller, 1981) due to the nearly identical dimensions of the fungal structures and the same systematic position of the host. A re-examination of North American material revealed differences in the number and the diameter of the nuclei (Ben-Ze'ev & al., 1985). *E. helvetica* is known only from Switzerland. The hyphal bodies were originally described as hypha-like. A re-examination of the material showed that they belonged to *Zoophthora viridis* Keller, another entomophthoralean species which attacks the same host.

10. *E. israelensis* Ben-Ze'ev & Zelig, Mycotaxon 21: 463–474. 1984.

The species attacks unidentified adult gall midges (Diptera, Cecidomyiidae). Dead insects were found on young leaves of orange and grapefruit trees. They were fixed with monohyphal rhizoids protruding among the mouthparts and, later on, from the abdomen, unspecialised endings. The wings were held in an upright position. Hyphal bodies pyriform to ovoid, sometimes cylindric with rounded ends. Unbranched conidiophores with 3–6 (average 4.4) nuclei. The primary conidia measured 16.8(15–20) × 13.1(11–16) µm and contained 3–5 (average 3.7) nuclei. Secondary conidia like primary, 12.8(10–14) × 11.2(10–11) µm. Cystidia and resting spores absent. The criteria to separate *E. israelensis* from *E. brevinucleata* are given under this species. *E. israelensis* is known only from Israel.

11. *Entomophthora* sp. 2 Villacarlos & Keller, in Villacarlos & al., (submitted to J. Invertebr. Pathol.).

The species attacks adult whiteflies *Tetraleurodes acaciae* (Homoptera, Aleurodidae) on *Gliricida sepium*. The rhizoids are

monohyphal and emerge ventrally from head and thorax, rarely from the abdomen, ends rounded, sometimes with short extensions. The hyphal bodies are subsperical to oblong with 3–5 nuclei. Condiophores unbranched. The primary conidia measure 12.3–15.5 (12–18) × 11.9–12.8 (10–14) µm and have a distinct apical point. They contain 3–4, rarely 5 nuclei with a diameter of 2–3 µm. The secondary conidia are 11–14 × 10–12 µm. Resting spores and cystidia were not observed. Between 35–117 conidia per host are produced. The species is known only from the Philippines, where the host was recently introduced.

12. *E. muscae* (Cohn) Fresenius, Bot. Zeitung 14: 882. 1856.

≡ *Empusa muscae* Cohn, Hedwigia 1: 60. 1855.
= *Myiophyton cohnii* Lebert, Neue Denkschr. Allg. Schweiz. Gesellsch. Ges. Naturwiss. 15: 1–48. 1857.

The species was originally described as a pathogen of the house fly *Musca domestica* L. (Diptera, Muscidae) (type host). For a long time all fungi of the *E. muscae*-type attacking larger flies were attributed to this species (MacLeod & al., 1976). Based on conidial dimensions and nuclear characteristics, Keller (1984) pointed out that it was indeed a species complex. The species was recently redescribed (Keller & al., 1999) supporting the hypothesis that Cohn (1855, 1875) was dealing with two species, *E. muscae* and *E. schizophorae*. The species is known to attack other adult flies of the families Drosophilidae and Empididae (Tab. 1) (Keller, unpublished). Steenberg & al. (2001) reported the species from *Hydrotaea irritans, Phaonia perdita, Spilogona dispar, Myospila meditabunda* (all Muscidae) and *Platycheirus clypeatus* (Syrphidae).

Infected insects are fixed to the substrate by their proboscis. The hyphal bodies develop from tubular protoplasts and are subspherical to broadly ovoid, measuring 33–39 (24–54) × 24–32 (17–41) µm (L/D = 1.18–1.49) and contain 15–19 (10–24) nuclei. Until the host's death the hyphal bodies are able to multiply by budding as shown by Keller et al. (1999). In this case the mother cell forms a narrow protrusion from which a narrow drop-like daughter cell develops. Immediately after separation the mother cell has a tapering, pointed protrusion. The daughter cell turns into a spherical or ovoid hyphal body with usually 4–6 nuclei. At rare occasions the daughter cells are budded off without this narrow protrusion. At death immature hyphal bodies with 1 to about 8 nuclei are still present.

The terminal enlargement of the unbranched conidiophores measure on average 23–30 µm and contain 15.7–20 (10–27) nuclei

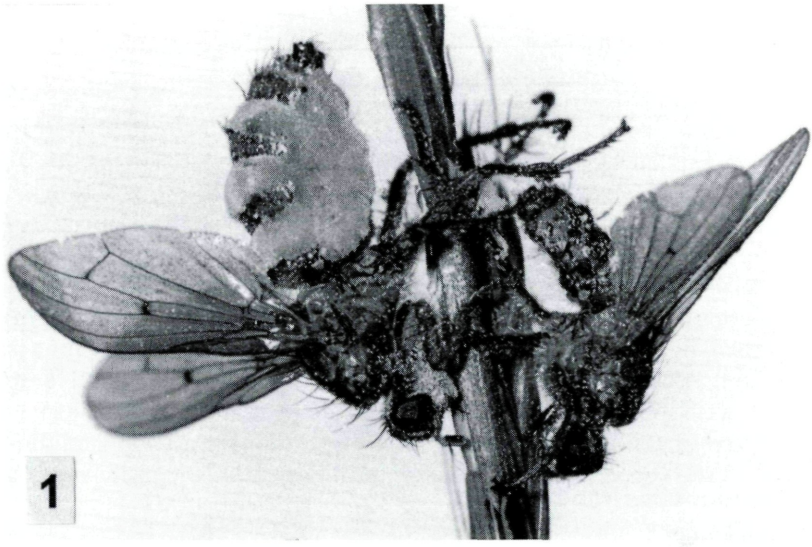
with a mean diameter of 3.6–4.7 µm. The primary conidia have a distinct apical point and measure 26.9–31.1(24–35) × 20.4–24.2(16–29) µm and contain 15.2–20.2(10–27) nuclei with a diameter of 3.9–4.4(3.5–5.5) µm. The secondary conidia are like the primary and measure 19.3–24.2(16–28) × 15.1–19.1(12-23) µm, apical point indistinct. Cystidia are absent. Hyphae in the mouthparts may act as rhizoids. Resting spores from *Delia radicum* are spherical and measure 39.4(34–44) µm (Thomsen & Eilenberg, 2000). They have never been reported from *Musca domestica*.

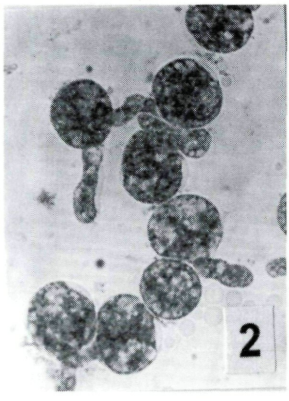
The species is closely related to *E. syrphi* and *E. scatophagae*, but inhabits generally other hosts. *E. muscae* can clearly be separated from the former mainly by the larger and fewer nuclei. It differs from the latter by the shape of the hyphal bodies. *E. muscae* has predominantly irregularly rounded subspherical to broadly ovoid ones while those of *E. scatophagae* are predominantly regularly spherical to subspherical (Plate 3, figs. 2–3). The justification to consider them as distinct species is also supported by the host specificity. In transmission experiments Steinkraus & Kramer (1988) were unable to infect *M. domestica* with *E. scatophagae*, while Steenberg & al (2001) achieved a low percentage (6.4%) of infected house flies. PCR-techniques did not reveal significant differences between *E. muscae* and *E. scatophagae* (Jensen, 2001).

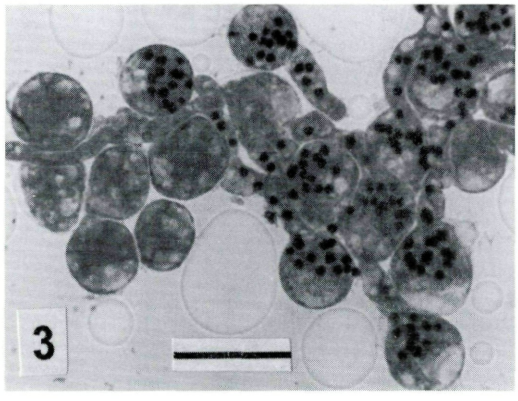
13. *E. philippinensis* Villacarlos & Wilding, Mycol. Res. 98(2): 161–163. 1994.

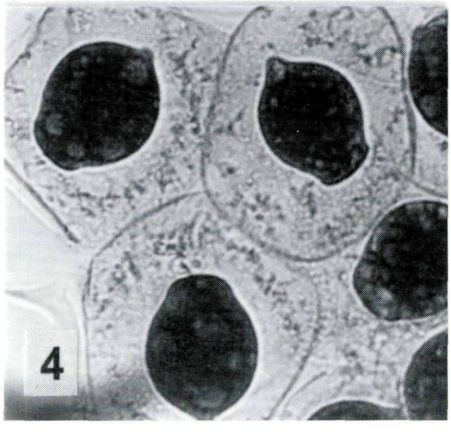
The species attacks adults of *Heteropsylla cubana* Crawford (Homoptera: Psyllidae) (type host). The infected insects were fixed to the substrate by the proboscis, the presence of rhizoids is suspected but unconfirmed. The hyphal bodies are spherical, 14–18.5 µm in diameter to ellipsoidal, 14–20.5 × 12.5–17.5 µm. Conidiophores unbranched and club-shaped. The primary conidia have a prominent apical point and a broad base. They measure on average 15–17.5 × 13–15.5 µm and contain predominantly 4–5 nuclei with mean dimensions of 2.5 × 3 µm. The secondary conidia are like the primary and measure on average 12.5 × 10 µm. Cystidia and resting spores absent. The species is known only from the Philippines.

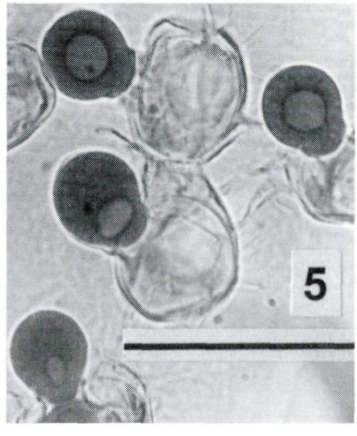
Plate 3. – Figs. 1–5: *Entomophthora scatophagae* from *Scatophaga stercoraria*. – Diseased flies fixed with proboscis and legs to the inflorescence of a grass. Two cadavers, with fully sporulating fungus (left) and at the end of sporulation (right). Ca. 7 × nat. size. – 2. Structures considered as protoplasts developing to hyphal bodies. 3. Young (nuclei not stained) and mature hyphal bodies with stained nuclei, some with germ tube. – 4. Primary conidia with halo formed by the ruptured outer wall. – 5. Secondary conidia on the remnants of the primary conidia. 2–3: LPAO; 4–5: LPCB. – Bars in Figs. 3 and 5 = 50 µm, Figs. 2–3 and 4–5 same magnification.











14. *E. planchoniana* Cornu, Bull. Soc. Bot. France 20: 189. 1873.

= *Myiophyton planchoniana* (Cornu) von Arx, The genera of fungi, p. 51. 1970.

Cornu (1873) originally found the species on aphids on elder. Since *Aphis sambuci* is the most common species on elder in western Europe, this species is very likely to be the type host (Remaudière, pers. comm.). Cornu (1873) gave no additional data on the fungus. The species attacks nymphs and adults of numerous aphid species of different families (Homoptera, Aphidoidea) (Tab. 3). The life cycle of the species is described in Fig. 1. Vegetative growth by tubular or elongate ellipsoid protoplasts with a diameter of 14.6 µm (10–21 µm) (1 series) and a variable length of 36–78 µm. They multiply by binary division. They normally contain 4–11 nuclei, but nuclear numbers up to 18 were observed. Hyphal bodies rather regular, ellipsoidal to short rod-shaped, 29–32 × 15–18 µm with 5–8(3–12) nuclei. Conidiophores unbranched with 4–8 nuclei, terminal enlargement measuring 15–17 µm. Primary conidia 15–20 × 12–16 µm with 6–8(4–11) nuclei, distinct apical point. Secondary conidia 13–16 × 10–12 µm on short lateral conidiophore. Resting spores spherical, 31–38 µm with 18.6(15–25) nuclei, episporium uneven, dark brown. Cystidia absent. Rhizoids joined in bundles, contain cytoplasm and resemble conidiophores, without specialised holdfast (Plate 6, Figs. 6–7). The species is known to overwinter in the form of specialised hyphal bodies which are rod-shaped to club-shaped and measure 47–49(29–68) × 16–17(12–21) µm (Keller, 1987b).

The species shows some variation between host species especially concerning the number of nuclei per conidium (Tab. 3). Conidiophores and primary conidia from the type host contain 5.3–6.3 nuclei, those from *Rhopalosiphum padi* 7.1–7.5 (Tab. 4). However, the dimensions of the conidia from all hosts lie within the range of 16–19.5 × 12–16 µm. The size of the conidia is a good criterion to separate *E. planchoniana* from the other aphid pathogenic species of this genus, *E. chromaphidis*. There is some confusion about the rhizoids. They have been described as pseudorhizomorphs (Ben-Ze'ev & Uziel, 1979) as in the genus *Zoophthora* or as pseudorhizomorph-like structures (Ben-Ze'ev & Kenneth, 1982). However, there are fundamental differences between the two types. In *Zoophthora* they are specialised, compound rhizoids. The individual hyphae grow parallel and are fixed together to form a single, tube-like structure with a common specialised holdfast. At maturity cytoplasm is not visible. *E. planchoniana* has rhizoids that resemble the conidiophores in shape and dimensions. They are filled with cytoplasm and do not form specialised holdfasts. Like the conidiophores they emerge in bundles and are not fixed together. The similarity

Tab. 3. – Data of fungal structures of *Entomophthora planchoniana* originating from different hosts collected in north-eastern Switzerland. Measurements in µm. PC = primary conidia, SC = secondary conidia, RS = resting spores, HB = hyphal bodies (Keller, unpublished).

Fungal structure	Host species	Number of series. Dimension/ nuclei	Length		Diameter		Nuclei average values	
			average	min-max	average	min-max	number	diameter
PC	*Aphis sambuci*[1]	5/6	16.1–18.1	15–21	13.3–14.9	12–17	5.3–6.3[2]	3.8
	Rhopalosiphum padi	2/6	18.0–19.5	16–22	13.8–15.8	12–19	7.1–7.5[2]	3.3–3.5
	Sitobion avenae	1	18.3	16–23	13.1	11–18		
	Drepanosiphum platanoides	2	17.7–19.3	16–22	14.4	12–16		
	Chaitophorus capreae	5/5	16.1–18.6	15–22	13.1–15.3	12–18	5.1–8.6[2]	3.9–4.0
	Tuberculatus annulatus	2/3	16.1–16.8	14–18	12.1–13.2	11–15	4.7–5.0[2]	
SC	*R. padi*	2	13.3–14.0	12–16	10.7–11.7	10–13		
	S.avenae	1	15.9	13–18	11.4	10–13		
	C. capreae	1	12.7	11–15	10.4	10–12		
RS	*A. sambuci*[1]	1			37.5	30–42		
	Phorodon humuli	5			31.1–35.4	27–39		
HB	*A. sambuci*[1]	1/1	31.0	25–39	16.1	13–18	5.3	
	R. padi	2/4	29.4–31.5	22–51	15.4–17.4	12–19	5.5–7.6	

[1] type host; [2] including conidiophores

with conidiophores is striking and there are good reasons to consider them as modified conidiophores. There are no other species in this genus with similar rhizoids except the closely related *E. chromaphidis*.

The species is widely distributed and is one of the most important aphid pathogenic Entomophthorales.

15. ***E. rivularis*** S. Keller, M. Niell & S. Santamaria, **sp. nov.** – Figs. 11–12 in Niell & Santamaria (2001).

Conidiophora simplicia. Conidia primaria 24.5(22–29) × 20.1(18–23) µm, campanulata, acumine apicali distincto, 11–13 nucleos 3–3.5 µm diametro continentia. Conidia secundaria habitu primariis similia. Sporae perdurantes, rhizoidea et cystidia absunt.

In Plecoptera indet. (hospite typico).

Holotypus ZT, Fogars de Montclús, Santa Fé del Montseny, Barcelona, Spain, coll. et leg. M. Niell, VI 1998, nos. BCB-Ent. 903-905.

Conidiophores simple, yellowish green, protruding between tergites. – Primary conidia campanulate with distinct apical point, 24.5(22–29) × 20.1(18–23) µm, L/D = 1.22. They contain 11–13 nuclei with a diameter 3–3.5 µm. – Secondary conidia similar to primary, 19.3(16–21) × 15.5(13–18) µm, L/D = 1.17. – Resting spores, rhizoids and cystidia absent.

Host. – Undetermined adult Plecoptera.

Distribution. - Fogars de Montclús, Santa Fé del Montseny, Barcelona, Spain.

Etymology of specific epithet. – Referring to the collection place in a small river.

The species was found only once on an undetermined species of Plecoptera on a stone in a river some centimeters above the water level. This habitat is unusual for a species of *Entomophthora*. The other species of this genus attacking a "water insect", *E. simulii*, is usually found 1–2 m above the water level. *E. rivularis* shows also morphological similarities with *E. simulii*, but the two species can clearly be distinguished by the size of the primary conidia.

16. *E. scatophagae* Giard, Bull. Sci. France Belgique 19: 308. 1888. – Plate 3, Figs. 1–5.

Type host of the species is the dung fly *Scatophaga stercoraria* L. (Diptera, Scatophagidae) (Fig. 1). Giard (1888) gave no further data on the fungus. So far only a single species of *Entomophthora* was found to attack the dung fly which can, therefore, be considered as *E. scatophagae*. The species was also found on *Delia planipalpis* Stein (Diptera: Anthomyiidae) (Keller, 1984). Data from the original host are as follows (Keller, unpubl.; Steinkraus & Kramer, 1988):

Vegetative growth as rounded or elongate protoplasts (Fig. 2). – Hyphal bodies spherical to subspherical, rarely ellipsoidal, 30.4–32.6(24–39) × 26.3–29.9(22–36) µm, L/D = 1.09–1.20. They contain 15.6–20. (12-24) nuclei with a diameter of 4.1–4.5(3.5–5.0) µm (Fig. 3). – Unbranched conidiophores are terminally enlarged to 23.6(18–30) µm and contain 16.9–17.2(13–22) nuclei with a diameter of 3.9–4.5(3.0–5.5) µm. – Primary conidia 28.4–28.7(27–31) × 22.1–23.2(20–28) µm with pronounced apical point, containing 17.0–18.3(14–23) nuclei with a diameter of 3.8–4.2(3.0–5.0) µm (Fig. 4). – Secondary conidia like primary, 20.0 × 17.7 µm, apical point indistinct or missing (Fig. 5). – Cystidia and resting spores absent.

Bałazy (1993) mentioned hyphae in the mouthparts which may function as rhizoids. Data from *D. planipalpis* are listed in Tab. 1. Resting spores are spherical and measure on average 41.3–46.5 µm with a range of 38–51 µm (Thomsen & Jensen, 2002)

The species is known from Europe and North America. It was found to cause epizootics usually in spring and in autumn. Both sexes are affected. The species is closely related to *E. syrphi* and *E. muscae*. Details for their separation are given under *E. muscae*.

17. *E. schizophorae* Keller & Wilding in Keller, Sydowia 40: 160–161. 1987a.

The species attacks adults of several fly species belonging to the families Anthomyiidae, Calliphoridae, Psilidae, Muscidae and Hybotidae (Diptera): *Delia platura* Meig. (type host), *D. brassicae* Bouché, *D. florilega* Zetterstedt, *Chaemapsila rosae* F., *Musca domestica* L., *Pollenia rudis* F. and *Platypalpus* sp. (Keller, unpublished). With the exception of the latter they all belong to the section Schizophora, which led to the specific epithet. Steenberg & al. (2001) reported *Phaonia incana*, *Helina* spp. *Myospila meditabundis* (all Muscidae) and *Bellardia viarum* (Calliphoridae) as further hosts. The infected flies are fixed to plants with their proboscis, which contain hyphae that may act as rhizoids. Data from the type host are as follows:

Hyphal bodies spherical to subspherical, 21.0–22.7(18–28) × 18.2–19.5(16–23) µm. – Conidiophores unbranched. – Primary conidia 18.9–21.1(18–23) × 14.9–17.1(13–19) µm containing 4.3–4.6(3–6) nuclei with a diameter of 4.9–5.0(4.0–6.0) µm. – Secondary condia like primary, 15.0–16.5(13–18) × 12.0–13.1(11–15) µm. – Cystidia and resting spores unknown.

Data from other host are summarised in Tab. 1.

The species is known from Europe and North America. Until 1984 it has been attributed to *E. muscae* and many reports of this species may indeed refer to *E. schizophorae*. The species is clearly characterised by the number and the size of the nuclei and by the hosts. The fungi found on *Delia* spp., *P. rosa*, *M. domestica* and *Platypalpus* sp. are very similar while those from *P. rudis* have slightly larger conidia and more nuclei (Tab. 2). However the present knowledge is considered insufficient to separate them as distinct species. In transmission experiments the species could not be transmitted to *Hydrotaea irritans* and *Haematobia irritans* (Muscidae) (Steenberg & al., 2001). Eilenberg & al. (2001) found that the species can overwinter in living *P. rudis*.

18. ***E. simulii*** S. Keller, **sp. nov.** – Pl. 4, figs. 1–7.

Rhizoidea mononemata e partibus buccalibus emergentia. Corpora hyphalia (27–)36(–45) × (18–)25(–30) µm, subspherica vel irregularia. Conidiophora simplicia. Conidia primaria (21–)24–26(–30) × (16–)18–21(–24) µm, campanulata, acumine apicale distincto, (10–)14–15(–20) nucleos 3–4.5 µm diametro continentia. Conidia secundaria habitu primariis similia. Cystidia absunt.

In *Simulio (Wilhelmia) lineato* Mg. (hospite typico) (Diptera: Simuliidae).

Holotypus ZT, Rüdlingen (Canton Schaffhausen), coll. et leg. S. Keller, VIII 1999, nos. 86-9, 86-16, 86-29, 86-30, 86-36. Paratypi K et BPI.

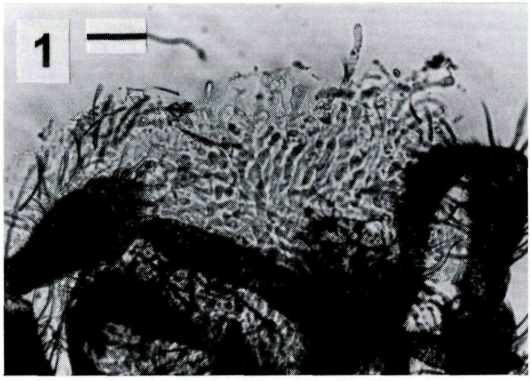
Rhizoids monohyphal, emerging from mouthparts, without specialized holdfasts (Fig. 1). – Protoplasts subspherical to tubular (Fig. 2). – Hyphal bodies 36.3(27–45) × 24.6(18–30) µm, L/D = 1,48 (1 series), subspherical, elongate ellipsoidal ovoidal or irregularly rounded, sometimes slightly bent, containing 12.2–13.8(8–21) nuclei with a diameter of 3.7–4.3(3–5) µm (2 series) and germinating with a single germ tube (Fig. 3). – Conidiophores unbranched with 13.8–14.4(10–21) nuclei with a diameter of 3.7–3.9(3–5) µm (2 series) (Fig. 4). – Primary conidia 24.2–26.2(21–30) × 17.9–20.6(16–24) µm, L/D = 1.26–1.35 (4 series) with distinct apical point, containing 14.8(10–20) nuclei (1 series) with a diameter of 3.6–3.8 (3–4.5) µm (2 series) (Fig. 5). – Secondary conidia similar to the primary, 18.1–19.9(15–24) × 14.6–15.9(12–22) µm, L/D = 1.19–1.26 (4 series, n = 16–50), apical point absent or indistinct (Fig. 6). – Cystidia absent.

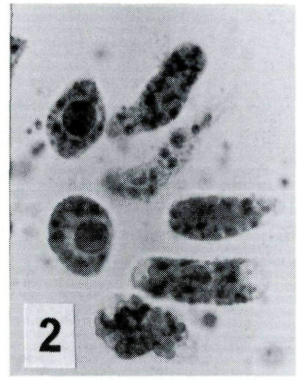
Host. – Diptera, Simuliidae: *Simulium (Wilhelmia) lineatum* Mg., adults.

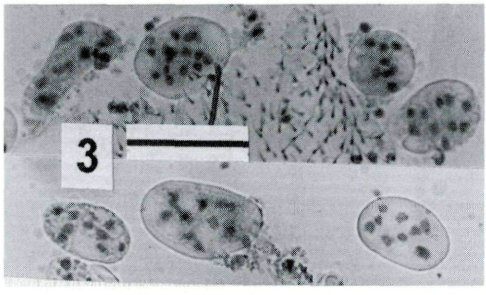
Symptoms. – Diseased simuliids on various plants (e.g. *Rubus* sp., *Fraxinus* sp., *Evonymus europaeus*, grasses) at the border of the Rhine river up to about 2 m above water level, fixed with proboscis on underside of leaves. The sporulation of the fungus is limited to the dorsal part of the abdomen, the central body parts are bent dorsally and the wings join above the thorax.

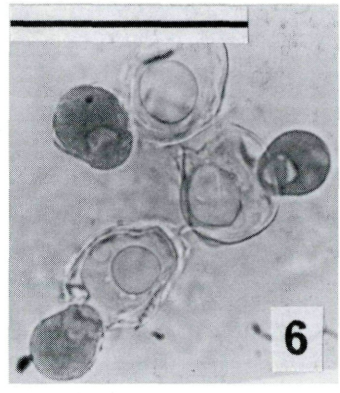
Distribution. – Switzerland: Rüdlingen (SH), northern border of the Rhine (type locality).

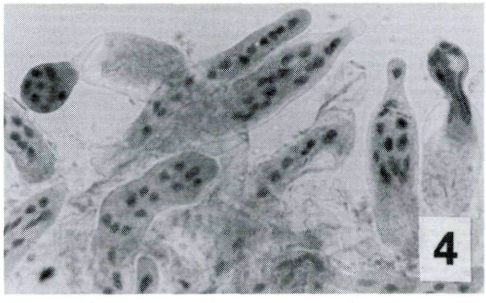
Plate 4. – Figs. 1–7: *Entomophthora simulii* sp. nov. from *Simulium lineatum*. – 1. Rhizoids emerging from the mouthparts. – 2. Structures considered as protoplasts. – 3. Hyphal bodies. – 4. Conidiophores with developing conidia. – 5. Primary conidia with halo formed by the ruptured outer wall. – 6. Secondary conidia on the remnants of the primary conidia. – 7. Unknown structures interpreted as developing resting spores. 1, 6–7: LPCB; 2-5: LPAO. – Bars in Figs. 1, 3 and 6 = 50 µm, Figs. 2–4, 7 and 5–6 same magnification.

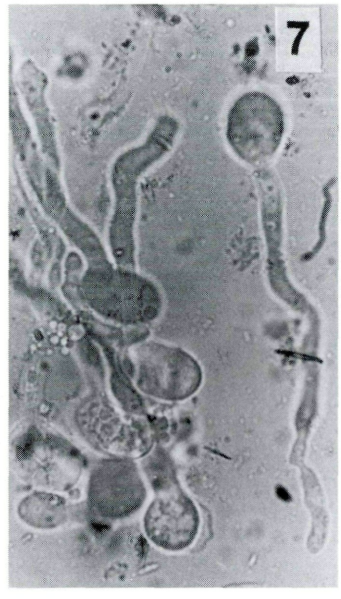


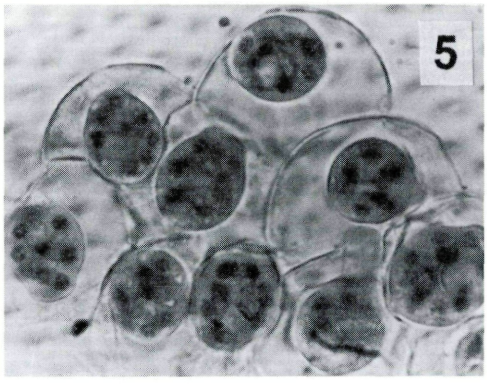












Etymology of specific epithet. – Suggesting the genus of the host from which the fungus was collected.

The species was collected in the first half of August 1999. Numerous dead simuliids were fixed to those parts of plants which hang over a concrete wall limiting the border of the river. Only one cadaver contained subsperical, ellipsoidal to ovoid structures, sometimes with thickened cell wall. They measured 31.1(24–38) × 24.9(19–29) µm, L/D = 1.25 (1 series) and were believed to be developing azygospores (Fig. 7).

The species resembles *E. muscae* from which it can be separated mainly by the smaller conidia, the number and the diameter of the nuclei and the host.

19. *E. syrphi* Giard, Bull. Sci. France Belgique 19: 308. 1888. – Plate 5, figs. 1–5.

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

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, 37.0 × 31.3 (25–48 × 23–38) µm (1 series), germinate with single germ tube with a diameter of 10.2 (8–12) µm (1 series) (Fig. 1). The germ tubes form either the transitional bodies (Fig. 2–3) or directly the conidiophores. – Conidiophores unbranched, terminally enlarged to a diameter of 22.7–27.3 (18–39) µm (2 series), containing 18–21(–25) (11–32) nuclei (8 series) with a diameter of 3.7–4.1 (3.0–5.0) µm (3 series) (Fig. 4). – Primary conidia 27.5–32.3 × 20.7–27.3 µm (24–36 × 18–30 µm), L/D = 1.18–1.33 (6 series) with 19–22 (14–30) nuclei (6 series) with a diameter of 2.8–3.4 (2.5–4.0) µm (5 series), distinct apical point; papilla flat to slightly rounded (Fig. 5). – Secondary conidia 21.9–24.3 × 17.2–17.6 µm (18–30 × 15–19 µm), L/D = 1.27–1.39 (3 series), like primary but without apical point (Fig. 5). – Resting spores spherical measuring on average 37.5–40.2 µm with a range of 36–43 µm (Thomsen & Jensen, 2002; in press). – Rhizoids and cystidia absent.

The species is known from several European countries, sometimes causing epizootics among populations of *Melanostoma* spp. and *Platycheirus* spp.

A note on a species of *Entomophthora* attacking syrphids in France was presented by Cornu & Brongniart (1878). In a later paper

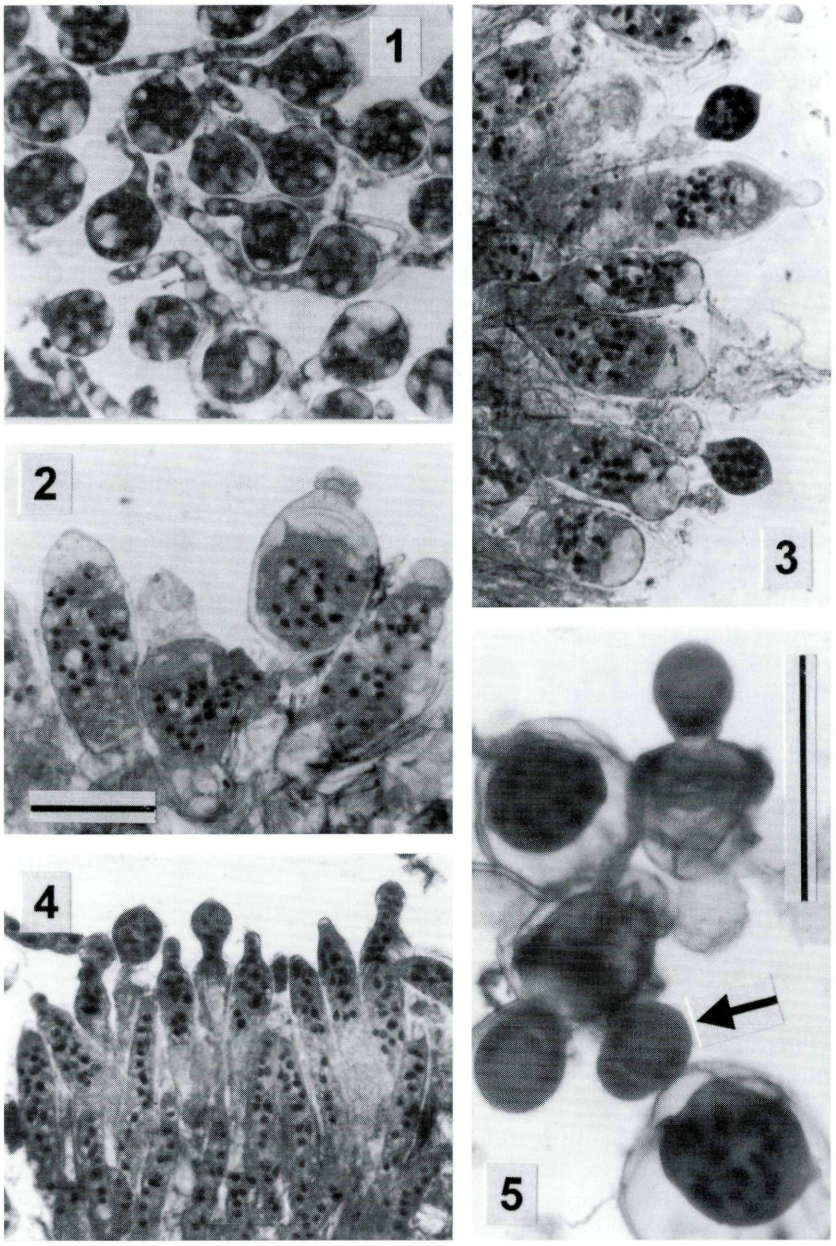


Plate 5. – Figs. 1–5: *Entomophthora syrphi*. – 1. Hyphal bodies. – 2. Transitional bodies. – 3. Transitional bodies with developing conidia. – 4. Normal conidiophores with developing conidia. – 5. Two primary conidia with the germ tube starting to grow, two secondary conidia on the remnants of the primary ones and a projected secondary conidium (arrow). – LPAO. – Bars in Figs. 2 and 5 = 50 µm, Figs. 1–4 same magnification.

(Cornu & Brongniart, 1880) the host was identified as *Syrphus mellinus*, which leaves no doubt that they collected the fungus later on described as *E. syrphi*.

A fungus with identical dimensions was found on adult *Herina frondescentiae* L. (Diptera, Otitidae) and attributed to *E. syrphi* (Tabs. 1 and 2). Steenberg & al. (2001) reported the species from *Phaonia perdita* (Muscidae) and they were able to transmit the fungus from this host to the house fly (*Musca domestica*). In the light of the present knowledge this note must be taken with care. Muscidae have so far not been mentioned as hosts of *E. syrphi*. The study implies that either pathotypes of *E. syrphi* or an undescribed species exist.

20. *E. thripidum* Samson, Ramakers & Oswald, Can. J. Bot. 57: 1317–1323. 1979.

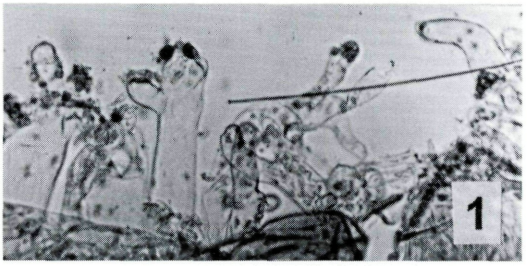
The species was described from *Thrips tabaci* Lind. (Thysanoptera, Thripidae) (type host). The hyphal bodies are cylindrical, simple or irregularly branched. Condiophores are simple, more or less cylindrical, slightly tapering towards the base. The primary conidia measure 10–15 × 8–12 µm. They have a distinct apical point and contain 2–4 nuclei. The secondary conidia resemble the primary ones but with indistinct apical point. They measure 9–12 × 7-9 µm. Rhizoids, cystidia and resting spores are absent.

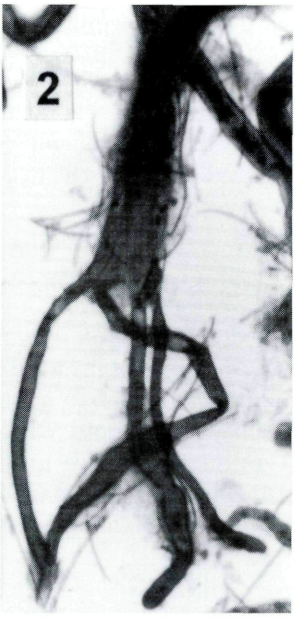
The species was originally described from larval and adult thrips attacking glasshouse crops in the Netherlands, where it caused epizootics. Freimoser & al. (2000) reported the occurrence in Germany and isolated the fungus in liquid media. The protoplasts were tubular. Transferred on solid media they produced conidia which measured 15.5 × 10.9 µm and contained 3–6 nuclei.

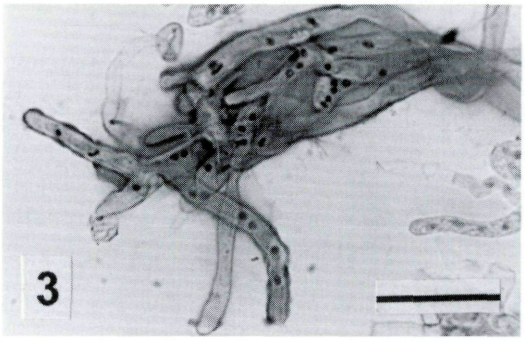
21. *E. trinucleata* S. Keller, Sydowia 40: 161–162. 1987a.

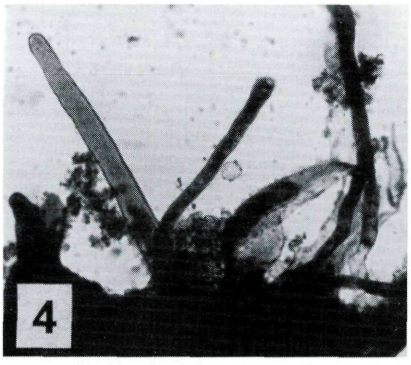
The species attacks unidentified adult Sciaridae (Diptera: Nematocera). Infected insects are fixed to the underside of leaves of annual crop plants with rhizoids. The rhizoids protrude from the mouthparts and are monohyphal without specialised endings. The hyphal bodies develop by budding and are spherical, subspherical or elongate, measuring on average 20–26 × 15–22 µm and contain 2–4 nuclei. The conidiophores are unbranched. The primary conidia measure 17.5–18(16–22) × 14–15(12–18) µm and contain usually 3,

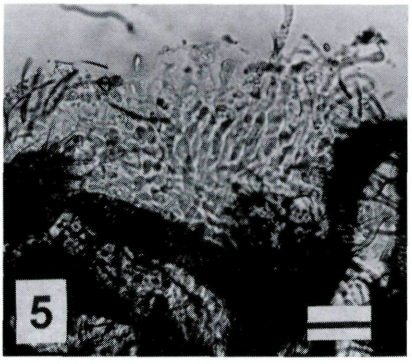
Plate 6. – Figs. 1–7: Rhizoids from *Entomophthora* spp. – 1. *E. culicis*. – 2. *E. brevinucleata*. – 3. *E. byfordii*. – 4. *E. trinucleata*. – 5. *E. simulii*. – 6-7. *E. planchoniana*. 2–4: LPAO; 1 and 5–7: LPCB. – Bars in Figs. 3, 5 and 7 = 50 µm, Figs. 1,5; 2–4 and 6–7 same magnification.

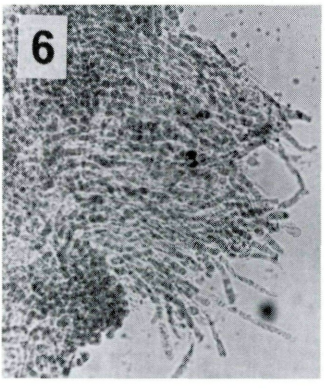


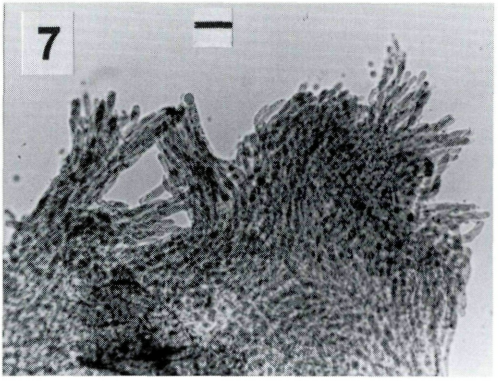












rarely 2 or 4 nuclei with a mean diameter of 5.6–5.9 µm. Secondary conidia like primary, but without distinct apical point. Cystidia and resting spores absent.

The species is clearly characterised by the three, rarely two or four, large nuclei per conidium. It is known from Switzerland and Poland (Bałazy, 1993).

22. *E. weberi* Lakon ex Samson, Can. J. Bot. 57: 1322. 1979.

≡ *Empusa weberi* Lakon, Z. ang. Ent. 26: 518. 1939.

This species attacks larvae of *Raphidia ophiopsis* L. (Neuropteroidea, Raphidiidae) (type host). Diseased insects fixed with contracted legs to substrate. Hyphal bodies are spherical, subspherical or amoeboid with 4–6(–10) nuclei (taken from the Figs. 1–12). Conidiophores are unbranched. Conidia measure 16(12–18) × 13(11–16) µm, with a broad base and sharply pointed apex, usually with 6 nuclei. Rhizoids, cystidia and resting spores absent.

The species was originally described from Germany. The fungus colonises only the abdominal parts of the host and sporulates while the host is still moving around. A single specimen was collected by C. Lienhard in southern Switzerland (St. Leonhard, Canton Valais). The examination of the air-dried material revealed the following data: The primary conidia measured 19.4 × 15.8 µm (L/D = 1.23) and contained 6 (5–9) nuclei with a diameter of 4.1 µm. The differences in the dimension of the primary conidia may be due to the fact that Lakon based his description on histological sections.

Discussion

The genus *Entomophthora* was recently reviewed by Bałazy (1993). He listed 13 species. Since then 9 new species have been described so that the genus now comprises 22 species. Furthermore, the knowledge on morphology and life cycles of some species was elucidated.

The genus consists of a morphologically homogenous group of fungi. Only the rhizoids (presence/absence) and shape and mode of development of the hyphal bodies show some variation. That is why the identification of the species on morphological data alone proved difficult and species complexes remained undetected until nuclear numbers and nuclear sizes were introduced into the taxonomy (Keller, 1984). This new tool widened the range of the identification criteria and enabled separation between closely related species. Nevertheless, there are no characters within this genus which would

allow us to subdivide it into groups, as was possible in the genus *Neozygites* (Keller, 1997).

Recently molecular methods were developed and introduced in the identification of Entomophthorales with special reference to the genus *Entomophthora* (Jensen, 2001; Jensen & Eilenberg, 2001). They confirmed the classical concept based on morphological and cytological data. Further, the data revealed a wide genetic variation within species, assuming that species still could be species complexes. Jensen & al. (2002) applied PCR-techniques to study the intraspecific variation of *E. muscae*. They revealed nearly no genetic variation between isolates from the same host irrespective of sampling dates and localities. On the other hand they found a wide variation between the isolates from different hosts. These findings imply that obviously no genetic exchange between the isolates from different host takes place. This is a strong indication that only the isolates from the type host should be considered as the "true" species, in the case of *E. muscae*, the "true" host is thus *M. domestica*. In addition, it implies a high host specificity of these isolates and that no exchange of genetic material occurs, even not in the resting spores, which develop as azygospores. The question arises as to why these fungi are so successful in their evolution in spite of such a narrow genetic base. There is no doubt that these new tools will substantially improve our knowledge and our understanding of these fungi. Not only taxonomy but also ecology, population biology and genetic will benefit from them.

In spite of this increase in taxonomic criteria the knowledge of the host is still an important criterion. It is based in the generally accepted assumption that these fungi are specific to a limited range of host species. This is one reason why the key was based on hosts. The other one has practical reasons since it proved difficult to give a dichotomous key on morphological and cytological criteria alone. It may also enable non-specialists to apply the key to an advanced point.

Most hosts of the genus *Entomophthora* belong to Diptera (12 species out of 22) and Hemiptera. Only four species, *Entomophthora* sp. 1, *E. rivularis, E. thripidum* and *E. weberi*, are known to attack hosts of other orders. This situation reminds us of the genus *Neozygites* which exclusively attacks Homoptera (8 out of 15 species), other small insects and mites (Keller, 1997). It can be speculated that the specificity of *Neozygites* spp. may be due to the capilliconidia. In the case of *Entomophthora* we have no clue to explain the preference for Diptera.

Transmission experiments have shown that the known host range can be enlarged under laboratory conditions (Steenberg & al., 2001). Usually such conditions are characterised by a high infection

pressure on stressed hosts. They produce results which differ from observations under natural conditions. Corresponding observations were made with *Entomophaga maimaiga*. Under natural conditions only a few species of the family Lymantriidae were found infected, while under laboratory conditions members of several other families could be infected (Hajek & al., 1995, 1996). It might be helpful to define the natural hosts as primary or ecological hosts and those attacked only under high infection pressure and/or artificial situations as secondary or physiological hosts. Secondary hosts are not only more resistant but may inhibit sporulation of the fungus. Under natural situations in a stable, we observed an epizootic among *M. domestica* caused by *E. muscae*. The sympatric biting fly *Stomoxys calcitrans* (Muscidae), which represented about 40% of the fly population was only exceptionally found dead with symptoms of an entomophthoralean infection. Sporulation did not occur although dissection revealed the presence of decaying vegetative stages attributed to *E. muscae* (Keller, unpubl.).

Resting spores are known from *Entomophthora* sp. 1, *E. chromaphidis*, *E. culicis*, *E. erupta*, *E. muscae*, *E. planchoniana*, *E. scatophagae* and *E. syrphi*. Structures considered to be developing resting spores were observed in *E. helvetica* and in *E. simulii*. Resting spore formation was induced in the house fly infected under laboratory conditions with isolates attributed to *E. ferdinandi* (Thomsen & al., 2001). Resting spores with known mode of formation are described as azygospores.

Resting spores from the other species are unknown. Other overwintering structures are described only from *E. planchoniana*. Therefore the question arises about how these species overwinter. In the case of *E. muscae* ecological investigations lead to the hypothesis that not only the main host species (*M. domestica*) but other host species like *Delia* spp. may be responsible for overwintering of the fungus (Steenberg & al., 2001; Thomsen & Eilenberg, 2000).

There are further collections of fungi which belong to the genus *Entomophthora*. Eilenberg & al. (1987) found a species on *Torymus druparum* (Hymenoptera, Torymidae). It had the same morphological, cytological and molecular characteristics as *E. muscae*, but the authors hesitated to attribute the fungus to this species due to the host, which belongs to another insect order. Keller (unpubl.) collected *Bibio marci* (Diptera, Bibionidae) and *Micropeza corrigiolata* (Diptera, Micropezidae) infected with *Entomophthora* sp. Another fungus found on *Hilara* sp. (probably *fuscipes*) (Diptera, Empididae) with primary conidia measuring 22–23 × 17–18 µm and 12–13 nuclei per conidium (Keller, unpubl.) may represent a new species. In all cases the available data did not allow identification of the fungus or to attribute it to a known species.

Several species of the genus *Entomophthora* are known to cause epizootics and thus are important agents in the natural regulation of insect populations. All species with the ability to cause epizootics among pest insects are considered to be candidates for biological control. This is especially true for house fly control with *E. muscae* or *E. schizophorae*, for thrips control with *E. thripidum* and for aphid control with *E. planchoniana*. So far, only attempts to control *M. domestica* with *E. muscae* and *E. schizophorae* have been undertaken, but no effective method to achieve control has been developed (Kuramoto & Shimazu, 1997; Six & Mullens, 1996; Steinkraus & al., 1993). An obstacle is the difficulty to produce large quantities of the fungus *in vitro*. Freimoser (2000) and Freimoser & al. (2000) recently developed a culture medium which allowed the *in vitro* production of *E. thripidum*, which is a first step to overcome this difficulty. However, much more research is needed to exploit the potential of these fungi.

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