Redescription of *Entomophthora muscae* (Cohn) Fresenius

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Entomophthora muscae (Zygomycetes, Entomophthoraceae) is redescribed from its type host, the house fly (*Musca domestica* L.), based on several collections from Switzerland and from Denmark. The species has subspherical, ellipsoidal, kidney-shaped or rounded hyphal bodies measuring 24–54 × 17–41 µm with 10–24 nuclei (average 15–19). Conidiophores are unbranched and contain 10–27 nuclei (average 15–20). The primary conidia measure on average 27–31 × 20–24 µm with a length/diameter ratio of 1.20–1.32 and 10–27 nuclei (average 15–20). The secondary conidia measure on average 19–24 × 15–19 µm with a length/diameter ratio of 1.20–1.33. These data correspond with the type material deposited in herbaria. They do not correspond with the data given in the original description which is assumed to concern *E. schizophorae*, which was also found as a pathogen of *M. domestica* during these investigations. Detailed data on morphology, including intraspecific variability of *E. muscae* are given.

Keywords: Entomophthorales, *Entomophthora muscae*, redescription, morphology, *Musca domestica*.

Entomophthora muscae (Cohn) Fresenius (1856) is the first described species of an insect pathogenic Zygomycete. It became the type species of a genus, a family and an order. This pathogen of the house fly, *Musca domestica* L., was originally described as *Empusa muscae* (Cohn, 1855a; 1855b). Fresenius (1856) subsequently transferred the species to the new genus *Entomophthora*, arguing that the name *Empusa* was already used for an orchid genus. Similar reasons may have led to the description of the same fungus as *Myiophyton cohnii* Lebert (1857). Since then the morphology of this pathogen has been repeatedly described. MacLeod & al. (1976) summarised the available data on this species, demonstrating wide variation in morphology and the host range.

Keller (1984), on the basis of nuclear numbers and sizes pointed out that *E. muscae* was in fact a complex of species. The members of

the complex, referred to as *E. muscae* s.l., are: *E. schizophorae* Keller & Wilding *in* Keller (1987) with 4–8 nuclei per conidium, *E. scatophagae* Giard (1888), amended by Steinkraus & Kramer (1988), with 15–18 nuclei, *E. muscae* with 15–20 nuclei, and *E. syrphi* Giard (1888) with 19–22 nuclei. A recent study on the molecular biology of the genus *Entomophthora* has supported the validity of *E. schizophorae* and *E. syrphi* as species distinctly separated from *E. muscae* (Jensen & Eilenberg, 1999).

It remains unsolved, however, to what extent the other species are sufficiently clearly separated from each other and what the nature of the "real" *E. muscae* originally described from *M. domestica* is. This is mainly due to the fact that the herbarium material is in a poor state. Balazy (1993) gave the following remarks on it: "Four specimens of the house fly (*Musca domestica*) overgrown by the fungus were deposited in the WRSL herbarium with the following label '1873. *Empusa muscae* Cohn nov. gen. et spec. Hedwigia N. 10..'. The mycelium is in poor condition and only few primary conidia of the dimension range (24–)26.5 × 29.5(–31) × (18.5)22–24(–25) µm have been found among numerous secondary ones". Humber in a letter to the senior author (4. 9. 1984), gave the following information on syntype material from Kew and Wrozlaw: "The Kew material has conidia that are 20.3 × 15.9 µm and contain ca. 16–18 nuclei. ... the Wrozlaw syntype was hard to interpret ..., but two conidia definitely contained 12 and 13 nuclei. Whether these two syntype specimens are in complete agreement might be debatable, but the 4-8 nuclear class is not the real *E. muscae*".

It is noteworthy that Cohn gave two descriptions of *E. muscae*. In the original description (Cohn, 1855a) he gave the mean length of the primary conidia as 21 µm. In his second description (Cohn, 1875) the primary conidia are described with a mean length of 25 µm. The first description would match that of *E. schizophorae*. However, the existing type material excludes such an identity due to the larger conidia of the WRSL material and the greater number of nuclei. This second description obviously corresponds to the deposited material. To overcome the uncertainty about the identity of *E. muscae* we present in this paper a re-description of the species based on several collections of infected house flies from Switzerland and from Denmark.

Material and methods

Collection sites

The Swiss material was collected in several cow stables. One collection site (CH 1) is located at Burgrain-Alberswil in the canton

of Lucerne, central Switzerland. The other site (CH 2) is located at Guntmadingen/Stammheim in north-eastern Switzerland. The two sites are about 80 km apart. More material (CH div) was collected at five locations east of Zurich and at Arenenberg south of Lake Constance. Living flies were sampled with a sweep net and placed in groups of 8–15 individuals in plastic boxes measuring $12 \times 10 \times 7$cm covered with cotton gauze. A cotton plug soaked with a saccharose solution was added as food. The flies were kept for 5 days (CH 1) and for 3 days (CH 2), respectively. Infected flies were removed once or twice a day dependent on the material needed for the investigations.

In Denmark, flies were collected from cow stables from two organic farms (DK 1 and 3) and from two traditional farms (DK 2 and 4) of which one stable (DK 2) also housed pigs. The farms were situated in northern and central Zealand and the maximum distance between the farms was 35 km. On all farms, the infection level was high at the time of sampling. Flies were brought to the laboratory and *in vivo* cultures were started by a modification of the method described by Kramer & Steinkraus (1981). Four cadavers (DK 1 and 2; August–September, 1996) or one cadaver (DK 3 and 4; September, October, 1998) were used as inoculum.

Preparation, staining, measurements

Swiss material. – Living flies showing symptoms of the disease or flies with sporulating fungus were mounted in their fresh state in lactophenol-aceto-orcein (LPAO) as described by Keller (1987). This material was mainly used to count and measure nuclei, but also to measure hyphal bodies, diameter of conidiophores and primary conidia. Only nuclei that appeared to be spherical were measured. Primary conidia were collected on slides placed 1–2 mm above a single sporulating cadaver placed on water. Secondary conidia were obtained in the same way but for a prolonged collection time, allowing the primary conidia to produce secondary ones. Conidia were mounted in lactophenol-cotton-blue (LPCB).

Danish material. – Due to the *in vivo* cultures, it was possible to study flies half way through the incubation time, dying flies (sitting in the characteristic position with outstretched wings and legs, but still alive) and flies very early in sporulation (immediately after the first conidia were detected on a glass slide placed above the cadaver). These stages were placed in 70% ethanol for the measurement of hyphal bodies. Primary and secondary conidia as well as conidiophores were collected from the same cadaver. Primary conidia were collected by placing a cadaver between slides in a humid chamber.

For secondary conidia a glass slide was placed for one hour 2 mm above a slide with primary conidia. Germination of the secondary spores was reduced by collecting at room temperature for about 4 hours, thereafter placing the glass slides at 16 °C until the next day, followed by mounting in lactophenol-cotton-blue (0.001%). Although secondary conidia were collected on six slides per cadaver, only about half of the cadavers gave more than 50 secondary conidia.

Nuclei were counted from primary conidia mounted in DAPI (5 µl/ml) in fluorescence microscopy at 400 × magnification (filter 0.5; violet; excitation 395-440). Furthermore, counts were made from conidiophores taken from cadavers kept in 70% ethanol. The size of primary and secondary conidia mounted in lactophenol-cotton-blue was measured with an Olympus Provis microscope supplemented with an Oly-Lite computer-based system for morphometrics. All measurements and counts were based, if not otherwise stated, on 50 objects per individual host, designated as one series. From each collection site, usually more than one series was studied to assess variation. A t-test was used to compare length and diameter of the primary and secondary conidia and of the number of nuclei in primary conidia of the collections from Denmark and Switzerland.

Results

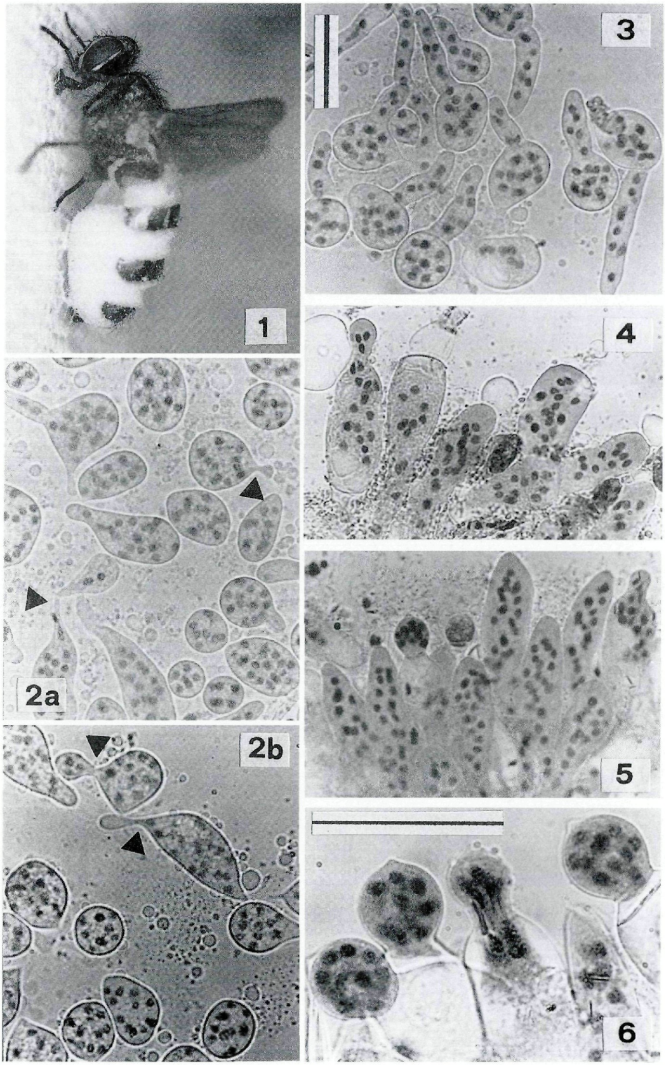
The examination of the material revealed two species of *Entomophthora, E. muscae* (Figs. 1–8) and *E. schizophorae* (Figs. 9–12).

Morphology of *E. muscae*

Symptoms. – Infected flies hang on the gauze of the rearing container, fixed with legs and proboscis, wings latero-dorsally spread (Fig. 1). In stables the dead flies were attached to walls, windows or other supports.

Vegetative growth by tubular protoplasts which become rounded at the end of multiplication. – Mature hyphal bodies subspherical, subellipsoidal, subovoid to kidney-shaped, rarely spherical, 33.0–38.8 (24–54) × 23.5–31.6 (17–41) µm, L/D = 1.18–1.49

Figs. 1–6. *Entomophthora muscae* from *Musca domestica*. – 1. Infected house fly fixed to support with legs and proboscis (about 6 × natural size). – 2. Hyphal bodies 1–2 hours before death of the host. – 3. Germinating hyphal bodies about one hour after death of the host. – Conidiophores. – 4. Developing conidiophores stunted below the host cuticle to form transitional bodies. – 5. Conidiophores with developing primary conidia. – 6. Developing primary conidia. – Bars in Figs. 3 and 6 = 50 µm. 2–5 and 6: same magnification.



(10 series) and contain 14.9–18.9 (10–24) nuclei (8 series) with a diameter 4.4–4.7 (4–5.5) µm (5 series) (Fig 2). They germinate with a single germ tube which develops to form the conidiophore (Fig. 3). – Developing conidiophores may become stunted below the host cuticle to form transitional bodies (Keller & Wilding, 1985) (Fig. 4). Conidiophores unbranched, terminally enlarging, 23.2–30.2 (18–39) µm (6 series), contain 15.7–20 (10–27) nuclei (16 series) with a diameter of 3.6–4.7 (3–5.5) µm (9 series) (Fig. 5). – Primary conidia campanulate with distinct apical point and broad base, 26.9–31.1 (21–35) × 20.4–24.2 (16–29) µm, L/D = 1.20–1.32 (27 series), with 15.2–20.2 (10–27) nuclei (16 series) with a diameter of 3.9–4.4 (3.5–5.5) µm (8 series) (Figs. 6–7). – Secondary conidia 19.3–24.2 (16–28) × 15.1–19.1 (12–23) µm, L/D = 1.20–1.33 (20 series), produced on short germ tube laterally from the primary conidia, apical point indistinct, with prominent central vacuole (Fig 8). – Resting spores and cystidia not observed. – Hyphae with rounded endings sometimes grew out from the proboscis and may act as rhizoids. Detailed data on morphology and number and size of nuclei are given in Tab. 1 and Tab. 2.

Tab. 1. – Dimensions in (µm) of fungal structures of *E. muscae* collected at different localities. – PC = primary conidia, SC = secondary conidia, CP = conidiophore (terminal enlargement), HB = hyphal bodies, n = number of series measured.

Origin	Structure	n	Length (L)		Diameter (D)		L/D
			mean	min–max	mean	min–max	
CH 1	PC	7	27.0–29.8	24–34	21.7–24.2	19–27	1.20–1.25
	SC	3	21.6–22.4	19–25	17.5–18.4	16–22	1.22–1.24
	CP	2			25.9–30.2	19–39	
	HB	2	36.4–36.5	24–52	25.5–29.3	21–36	1.24–1.43
CH 2	PC	4	27.7–28.9	25–33	22.6–23.2	19–28	1.22–1.25
	SC	4	21.4–22.9	18–25	17.7–18.9	16–22	1.20–1.22
	CP	2			27.2–27.3	21–34	
	HB	5	34.1–38.8	25–54	25.4–31.6	19–41	1.18–1.49
CH div	PC	3	27.9–29.2	25–31	21.6–23.3	19–25	1.26–1.29
	SC	1	22.7	21–25	18.4	16–22	1.23
DK 1	PC	3	27.2–28.6	21–31	21.8–22.5	16–26	1.24–1.30
	SC	3	22.5–23.1	19–27	18.0–18.8	16–23	1.22–1.25
	HB	3	33.0–35.8	24–47	23.5–26.3	17–35	1.26–1.49
DK 2	PC	3	26.9–30.8	24–35	20.4–24.0	18–29	1.25–1.32
	SC	3	19.3–22.1	16–27	15.1–18.4	12–22	1.20–1.28
DK 3	PC	3	28.5–28.9	25–32	22.3–23.6	19–27	1.22–1.28
	SC	3	21.9–23.3	19–27	17.5–19.1	15–22	1.22–1.26
DK 4	PC	4	29.3–31.1	25–35	22.4–24.0	20–28	1.24–1.29
	SC	3	23.1–24.2	19–28	18.0–18.3	14–23	1.27–1.33
	CP	2			23.2–25.3	18–30	

The primary and secondary conidia from the Danish material measured on average 29.1 × 23.7 and 22.4 × 17.8 µm, respectively. They tended to be slightly larger than those from Switzerland which measured on average 28.3 × 22.9 µm and 22.0 × 18.1 µm, respectively. Primary conidia from the Danish material contained on average 16.7 nuclei, those from Swiss material 17. However, no significant differences either in the size of the conidia or in the number of nuclei per conidium between the Danish and the Swiss material were found.

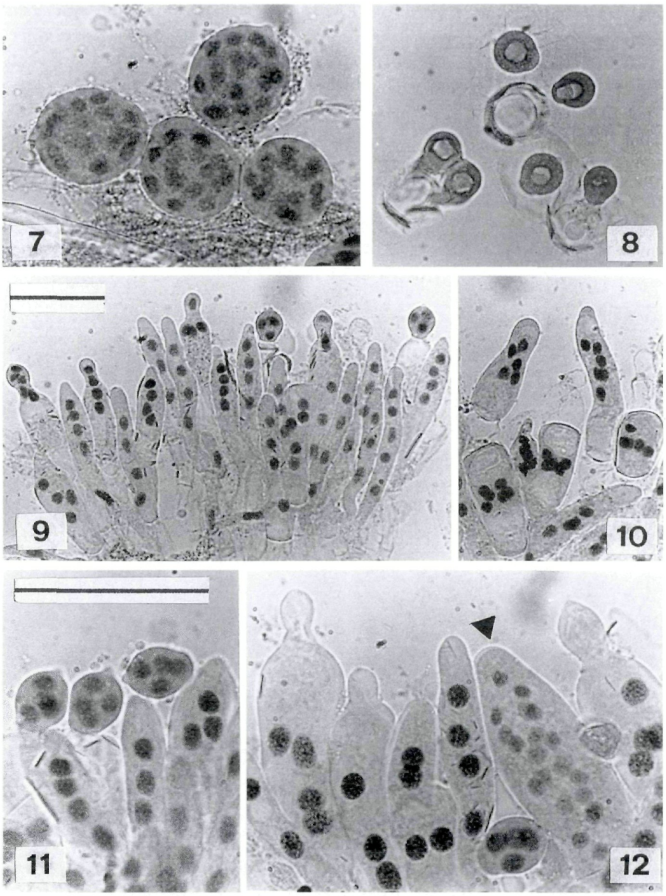
Table 2. – Number and dimensions (in µm) of nuclei in fungal structures of *E. muscae*.– HB = hyphal bodies, CP = conidiophore, PC = primary conidia, n = number of series measured.

Origin	Structure	Number of nuclei			Diameter of nuclei		
		n	mean	min–max	n	mean	min–max
CH 1	PC	3	15.4–19.2	11–24	4	4.1–4.4	3.5–5.5
	CP	6	15.8–20.0	10–27	4	3.6–4.7	3–5.5
	HB	3	16.9–18.0	10–23	3	4.4–4.7	4–5.5
CH 2	PC	1	16.0	12–21	2	4.0	3.5–5
	CP	5	15.7–17.4	11–23	2	4.3–4.6	3.5–5
	HB	5	14.9–18.9	10–24	2	4.6–4.7	4–5.5
CH div	CP	3	16.7–19.0	10–23	2	4.7	4–5.5
DK 1	PC	3	15.2–16.8	10–25			
DK 2	PC	3	15.2–20.2	11–27			
DK 3	PC	3	16.6–17.0	12–24			
DK 4	PC	3	15.9–17.0	11–23	2	3.9–4.0	3.5–5
	CP	2	16.1–18.2	11–24	1	4.3	4–5

Morphology of *E. schizophorae*

Infected flies show the same symptoms as caused by *E. muscae* (Fig. 1). – Conidiophores are unbranched and contain 4.1–5.6 (3–7) nuclei with a diameter of 6.0–6.1 (5.5–7.0) µm (3 series) (Figs. 9–12). – Primary conidia with prominent apical point, 18.9–20.5 × 13.8–16.4 µm (18–22 × 12–18 µm), L/D = 1.25–1.37 (4 series), contain 4.1–5.5 (3–6) nuclei (2 series) measuring 5.3 (5–6.5) µm (1 series) (Fig. 11). – Secondary conidia 14.6 × 12.0 (12–16 × 10–13) µm, L/D = 1.22 (1 series), apical point flattened, not prominent, cytoplasm below apical point often bright.

The species is easy to distinguish from *E. muscae* by number and size of the nuclei (Fig. 12).



Figs 7–8. – *Entomophthora muscae* from *Musca domestica*: – 7. Projected primary conidia. – 8. Developing and projected secondary conidia together with two primary ones. – Figs. 9–12. *Entomophthora schizophorae* from *Musca domestica*. – 9. Conidiophores and developing primary conidia. – 10. Conidiophores developing from transitional bodies. – 11. Conidiophores and primary conidia. – 12. Conidiophores of *E. schizophorae* and *E. muscae* (arrowhead). Note the difference in number and size of nuclei (mixed infection). – Bars in Figs. 9 and 11 = 50 µm. 8–10, 7 and 11–12 same magnification.

Tab. 3. – Data of fungal structures of *Entomophthora muscae* originating from *Musca domestica*. Measurements in µm, PC = primary conidia, SC = secondary conidia.

Fungal structure	Collection	Length		Diameter		number of nuclei	Reference
		average	min–max	average	min–max	min–max	
PC	orig. description	21	19–27		15–21		Cohn, 1855a[a]
		25	22–33				Cohn, 1875
	type material	27.9	24–31	23.1	18–27		Balazy, 1993 and pers. comm.
	type material					12–18	Humber, pers. comm.
	Lebert	25	20–30				Lebert, 1857
	Jaczewski		20–30		18–25		from MacLeod & al., 1976
	Batko	23	19–30	18	14–24		from MacLeod & al., 1976
	Ba_azy		20–32		15–28	10–22	Balazy, 1993
	Keller	27.0–29.8	24–34	21.6–24.2	19–28	11–24	this paper
	Kalsbeek	26.9–31.1	21–35	20.4–24.0	16–29	10–27	this paper
SC	type material	22.5	19–28	17.5	16–24		Balazy, 1993 and pers. comm
	Keller	21.4–22.9	18–25	17.5–18.9	16–22		this paper
	Kalsbeek	19.3–24.2	16–28	15.1–19.1	12–23		this paper

[a] Original measurements given in Prussian lines. Translation into micrometers was done according to MacLeod & al., 1976

Discussion

Until recently *E. muscae* has been considered a pathogen with a wide host range among higher dipterans. MacLeod & al. (1976) reported it from *M. domestica* (Muscidae), at least from three species of Anthomyiidae, two species of Calliphoridae, a species each of Drosophilidae, Sarcophagidae and Scatophagidae, and at least four species of Syrphidae. Empididae (Balazy, 1984) and Psilidae (Eilenberg, 1985) were reported as further hosts. As soon as nuclei were used as taxonomic criteria (Keller, 1984) it became clear that this wide host range was partly due to different species. Nuclear numbers and diameters enabled the description of a new species, *E. schizophorae* Keller & Wilding (Keller, 1987) and the separation of the synonymised species *E. syrphi* Giard (1888). Nevertheless the real nature of *E. muscae* remained unclear.

In recent years several studies on epizootiology and host-pathogen interactions with *M. domestica* were carried out. Originally the authors were not aware that they were making their investigations with a species complex (Kramer & Steinkraus, 1987; Mullens & al., 1987). However, in later studies they specified their isolates: For instance, Bellini & al. (1992) used a 4–8 nucleate and a 12–18 nucleate isolate and Kalsbeek (in preparation) studied the epizootiology of *E. muscae s.s.* and *E. schizophorae* in more than 15 farms. For future investigations, particularly with respect to the control of stable fly populations with Entomophthorales, it will be crucial to know the identity of the fungi involved.

The confusion that has so far been prevailing has now been cleared. Collections of house flies at several locations in Denmark and Switzerland revealed two species of *Entomophthora* which attack the house fly, *M. domestica*: *E. muscae* and *E. schizophorae*. The material from the two countries proved to be identical. The two species can easily be distinguished by the size of the conidia and the number and size of the nuclei. The data obtained allowed us a thorough redescription of *E. muscae*. They also support the hypothesis that Cohn observed two species, first *E. schizophorae* (Cohn, 1855a) and later *E. muscae* (Cohn, 1875). Since the existing type material (designated 1873 by Cohn) has priority over the description we have to consider it as the legal base for the re-description.

The dimensions of primary and secondary conidia obtained during this investigation correspond precisely with the data from the type material provided by Balazy (1993 and pers. comm.) (Tab. 3). Mean values for primary conidia from other authors, however, tended to be smaller, while the range corresponds to our findings (Tab. 3). This correspondence also includes the number of nuclei as pointed out by Humber (pers. comm.). Although there are no addi-

tional fungal structures for further comparisons we have no doubts about the identity of the two fungi.

There are still some unknown steps in the life cycle of *E. muscae*. We are not sure about the infective stage. It is assumed that both primary and secondary conidia can infect the house fly through any part of the cuticle, but there are data demonstrating that secondary conidia can infect with a dose 100–200 fold lower than primary ones (Bellini & al.,1992). Vegetative growth occurs by tubular protoplasts. A few hours before the host dies they turn into rounded, strongly vacuolised hyphal bodies. Subsequently the vacuoles disappear. At this stage some hyphal bodies show narrow cytoplasmic protrusions with one or few nuclei which may become tied up and explain the presence of small, oligonucleate, rounded hyphal bodies, which do not develop into conidiophores. The mechanism of protoplast multiplication remains unclear.

Resting spores were not found in our material, which corresponds to the observation of Cohn (1855a, 1855b, 1875) and Lebert (1857). In later studies some authors described them as spherical with a diameter of 30 µm or oval (30 × 21 µm; Goldstein, 1923). Resting spores of *E. muscae* s. l. from the host *Delia radicum* (Anthomyiidae) had a diameter of 33.6–44.0 µm (Thomsen, 1999). In both examples it remains unclear as to which species the resting spores belong. Further, Thomsen (1999) could infect *M. domestica* with "*E. muscae* type B" (Keller, 1984) from *Botanophila fugax* (Anthomyiidae) and the resting spores subsequently formed in *M. domestica* measured 30.4–40 µm.

Balazy (1984) reported the presence of rhizoids emerging from the proboscis. Our observations confirmed the presence of fungal structures on the mouth parts. They never ended with specialised holdfasts known from other species of Entomophthoraceae. The proboscis was fixed to the substrate by secretions and it is unknown whether these fungal structures really support fixation or even serve as rhizoids.

E. muscae and *E. scatophagae* are very similar. They differ by their natural host, the colour of the conidia (those of *E. scatophagae* are more yellowish according to Steinkraus & Kramer, 1988) and by the consistently spherical hyphal bodies of *E. scatophagae* (Keller, unpubl.). Concerning host specificity, Steinkraus and Kramer (1988) could not transfer *E. scatophagae* to other dipterans, while Steenberg (pers. comm.) was able to infect *M. domestica*. Thus, the differentiation between the two species needs further studies.

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