

Taxonomic considerations on some species of *Erynia* (Zygomycetes, Entomophthorales) attacking flies (Diptera)

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Species of *Erynia* recently collected in Europe on lauxaniid and calliphorid flies were identified as *E. echinospora* and *E. americana*. *Massospora richteri*, *Entomophthora lauxaniae* and *Tarichium pallidum* are considered as synonyms of *E. echinospora*. *Entomophthora* (*Tarichium*) *calliphorae* Giard, described twice with different dimensions given for the resting spores each time is considered as *nomen confusum*. However, the latter description of the resting spores corresponds with that given for those of *E. americana*. Taxonomic data obtained from type material of *E. americana*, *E. bullata*, *E. echinospora* and *E. montana* are presented and discussed.

Keywords: Insect-pathogens, taxonomy, morphology, Diptera, Calliphoridae, Lauxaniidae.

Within the genus *Erynia* (Nowakowski) Remaudière & Hennebert (1980) (Zygomycetes: Entomophthorales) there is a group of fly-pathogenic species with similar morphological characteristics and which cannot be readily distinguished. These include *E. americana* (Thaxter) Remaudière & Hennebert (1980), *E. bullata* Thaxter & Macleod in Humber (1981), *E. echinospora* (Thaxter) Remaudière & Hennebert (1980), *E. montana* (Thaxter) Remaudière & Hennebert (1980) described from North America and *Massospora richteri* Bresadola & Staritz (Staritz, 1892), *Entomophthora lauxaniae* Bubak (1903), *Tarichium pallidum* Roivainen ex Liro (1954) and *Entomophthora calliphorae*, form *Tarichium* Giard (1879), described from Europe.

According to Thaxter (cited in Povah, 1935) *E. americana* and *E. bullata* cannot be separated by their conidia; their resting spores, however, differ distinctly. *E. echinospora* has conidia smaller than the previous two species and its resting spores differ from those of *E. bullata* by the ornamentation of the episorium. The dimensions of the conidia of *E. montana* are similar to that of *E. echinospora*, and its resting spores are unknown.

The species described from Europe are known only by their original description which is scanty and limited mainly to the resting spores and the host species. The existing data suggest that some descriptions refer to the same fungus species. Bubák (1906) already concluded that *E. lauxaniae* Bubák (1903) was identical with *Massospora richteri*, which he subsequently transferred to *Entomophthora*. Handwritten remarks on the label of the type material show that he had the opportunity to compare the material. Bubák (1903) also noticed the similarity with *E. echinospora*, but denied an identity.

During the past years fungi were collected in Bulgaria and in Switzerland and identified as *E. cf. echinospora* (Markova, pers. comm.) and *E. richteri* (Keller, unpubl.). These collections proved to be identical and led to the hypophesis of a conspecificity of *E. richteri* with *E. echinospora*. Another fungus collected in Italy by Keller was identified as *E. americana*.

The material collected in Europe was compared with type material of the two species and of the related species *E. bullata* and *E. montana* with the aims of establishing and discussing conspecificities and clarifying the identification and classification of these organisms.

Material and methods

The fungal material examined is listed in Tab. 1. The type material consisted of *exsiccata*, two slides each with resting spores of *E. bullata* (nrs. 6424 and 6425) and of *E. echinospora* (both numbered 4309). Additional slides with resting spores and conidia were prepa-

Tab. 1. – Material examined.

Species of <i>Erynia</i> / <i>Tarichium</i>	Origin (Country)	Collection (designation)
<i>americana</i>	USA	FH acc. no. 4381 (Type)
	Italy	S. Keller (SK)
<i>bullata</i>	USA	FH acc. no. 4349 (Type)
		slide coll. nos. 6424, 6425 (Type)
	USA	N. Wilding (NW)
	Canada	Sault Ste. Marie (SM)
<i>echinospora</i>	USA	FH acc. no. 4309 (Type)
		2 slides no. 4309 (Type)
<i>cf. echinospora</i>	Bulgaria	G. Markova (GM)
<i>cf. richteri</i>	Switzerland	S. Keller (SK)
<i>lauxaniae/richteri</i>	Czech. Republic	F. Bubak/(BPI)
<i>pallidum</i>	Finland	Finnish Museum of Natural History (FMNH)
<i>montana</i>	USA	FH acc. no. 4418 (Type)

red. Conidia were mainly measured on wings of the host. The material from Europe was either prepared from freshly collected specimens (hyphal bodies, conidia) or specimens stored in 70% ethanol (v/v) (resting spores). Part of the Bulgarian material was air-dried (Tab. 3).

The fungal material was mainly mounted in lactophenol-cotton blue (LPCB), sometimes in lactophenol-aceto-orcein (LPAO) as described by Keller (1987). 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 were studied to assess variation. In addition to the measurements and counts the surface structure of resting spores was investigated by scanning electron microscopy (SEM).

Taxonomy

1. *Erynia americana* (Thaxter) Remaudière & Hennebert (1980), Mycotaxon 11, 301. – Pl. 1, Figs. 1–8.

Bas.: *Empusa* (*Entomophthora*) *americana* Thaxter (1888), Mem. Boston Soc. Nat. Hist. 4, 179–180.

Syn.: *Furia americana* (Thaxter) Humber (1989), Mycotaxon 34, 450.

The most relevant characters given in the original description concern the dimensions of the primary conidia and of the resting spores. They are given as 28–30 x 14 µm (maximum 35 x 15 µm) and 38–45 µm (maximum 50 µm) respectively. They do not completely match the data we obtained from either the type or our own material, but lie within the range, except for the maximum diameter of the resting spores (Tab. 2).

Based on our own observations the species can be described as follows:

Dead flies fixed by rhizoids to the underside of leaves of herbs, grasses and shrubs. Fresh cadavers with light brown to brown mycelial bands along the intersegmental membranes. These bands in older cadavers darker and rust-like coloured. – Rhizoids with a diameter of 6–30 µm, endings enlarged, branched or disk-like (Fig. 4). – Cystidia not observed. – Conidiophores terminally enlarged (“shoulders”) to 15.3 (12–19) µm (1 series). – Hyphal bodies subspherical, irregularly rounded, club-shaped, rod-shaped or irregularly elongate, with 3–20 nuclei (average 11) with a diameter of 6.5–6.7 (5.5–7.5) µm (2 series) (Figs. 1–2). – Primary conidia 28.7–30.8 (24–40) µm x 15.9–18.7 (13–25) µm, L/D = 1.64–1.93 (6 series); oblong ovoid, ellipsoid to subcylindrical, sometimes slightly bent; papilla broad (about 6 µm) rounded or nearly flat (Fig. 3). – Secondary conidia like primary, 25.2 (21–30) µm x 16.5 (13–18) µm, L/D = 1.53

Tab. 2. – Measurements of conidia and resting spores of *E. americana*, *E. bullata* and *E. montana* from different collections.

Species	Structure ¹	Collection	Number of series	Lenght L x (±s _x) Min – Max	Diameter D x (±s _x) Min – Max	L/D
<i>americana</i>	PC	Type	3	30.5–30.6 (2.4–2.8) 24–39	15.8–16.5 (1.2–1.3) 13–19	1.86–1.93
		SK	3	28.7–30.8 (1.7–2.2) 24–40	15.9–18.7 (1.3) 13–25	1.64–1.81
	SC (Ia)	SK	1 (n=38)	25.2 (1.9) 21–30	16.5 (1.4) 13–18	1.53
	SC (Ib)	SK	1 (n=20)	18.6 (0.9) 17–21	15.3 (1.1) 13–18	1.22
	RSepi	Type	3		35.6–37.3 (3.0–3.5) 29–42	
		SK	1		38.7 (3.4) 30–47	
<i>bullata</i>	PC	Type	4	30.9–32.4 (2.0–3.2) 25–41	15.3–17.0 (1.0–1.4) 13–21	1.91–2.05
		SM	4	26.8–33.0 (1.8–3.2) 23–39	14.1–16.0 (1.1–1.5) 12–18	1.81–2.06
	SC (Ia)	SM	1 (n=14)	24.9 (2.4) 21–29	14.0 (0.9) 12–16	1.78
	RSendo	Type	2		37.7–39.2 (2.6–3.4) 31–51	
		SM	3		40.0–41.0 (3.2–4.0) 31–52	
	RSepi	Type	2		48.4 (3.2–3.9) 42–61	
<i>montana</i>	PC	SM	3	48.4–52.8 (4.1–4.7) 38–62		
		Type	1 (n=33)	25.4 (1.4) 23–28	15.9 (1.0) 15–18	1.60

¹PC = primary conidia; SC (Ia) = secondary conidia type Ia (resembling primary conidia); SC (Ib) = secondary conidia type Ib [rounded with pointed apex (Ben-Ze'ev & Kenneth, 1982)]; RSendo = resting spores without episporium, RSepi = resting spores with episporium.

(1 series, n=38) or rounded with indistinct apical point, 18.6 (17–21) μm x 15.3 (13–18) μm , L/D = 1.22 (1 series, n=20). – Resting spores 35.6–38.7 (29–47) μm (4 series), spherical, smooth, yellowish. Broken resting spores contained 7–20 (average 12–13) nuclei (Figs. 5–8).

The European material was collected in July in two consecutive years in Northern Italy (Eraclea Mare, Veneto) on *Pollenia* sp. cf. *vespillo* (M.) (Calliphoridae). The dimensions of the primary conidia and of the resting spores correspond with those from type material (Tab. 2). Also the other characters match the original description.

2. ***Erynia bullata*** Thaxter & MacLeod in Humber (1981), Mycotaxon 13, 472. – Pl. 2, Figs. 1–3.

Syn.: *Pandora bullata* (Thaxter & MacLeod in Humber) Humber (1989), Mycotaxon 34, 452.

According to the data obtained from our own observations on type material and summarised in Tab. 2, the primary conidia measure 26.8–30.0 (23–41) μm x 14.1–17.0 (12–21) μm , L/D = 1.81–2.06 (8 series). The resting spores without episporium are 37.7–41.0 (31–52) μm and with episporium 48.4–52.8 (38–62) μm (5 series). There are no substantial differences between the material from the type collection and that provided by Sault Ste. Marie.

The species is unequivocally characterized by its resting spores. The episporium with its regularly arranged knobs is unique to this genus (Fig. 1). In a few specimens the knobs were terminally enlarged (Figs. 2, 3). A detailed description of this species is given by MacLeod et al. (1973).

3. ***Erynia echinospora*** (Thaxter) Remaudière & Hennebert (1980), Mycotaxon 11, 302. – Pl. 2, Figs. 4–11.

Bas.: *Empusa* (*Entomophthora*) *echinospora* Thaxter (1888), Mem. Boston Soc. Nat. Hist. 4, 180–181.

Syn.: *Pandora echinospora* (Thaxter) Humber (1989), Mycotaxon 34, 452.

Syn.: *Entomophthora richteri* (Bresadola & Staritz) Bubák (1906), Ann. Mycol. 4, 105.

Bas.: *Massospora richteri* Bresadola & Staritz (Staritz, 1892), Hedwigia 31, 41–42.

Syn.: *Entomophthora lauxaniae* Bubák (1903), Beiblatt zur Hedwigia 42, 100–101.

Syn.: *Entomophthora* (*Tarichium*) *pallida* (Roivainen ex Liro) MacLeod & Müller-Kögler (1970), Mycologia 62, 51–52.

Bas.: *Tarichium pallidum* Roivainen ex Liro (1954), Mycotheca Fennica, Schedae Fasc. 18, 96 (1953).

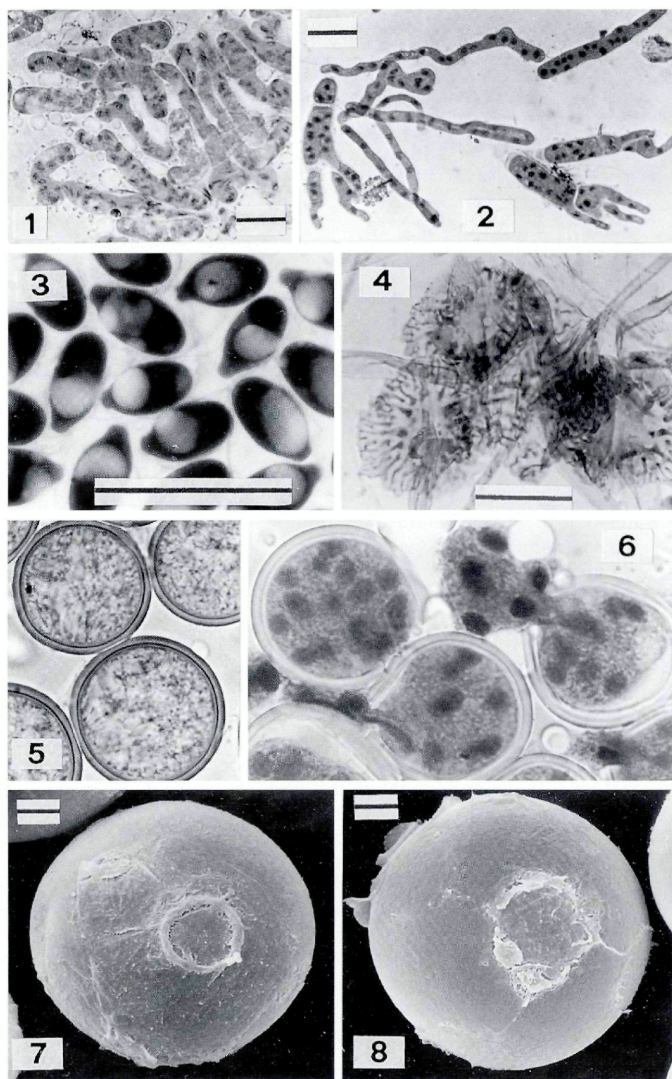


Plate 1. – 1-3: *Erynia americana*. – 1. Hyphal bodies with nuclei. – 2. Hyphal bodies developing to conidiophores. – 3. Primary conidia. – 4. Disk-like endings of rhizoids. – 5. Resting spores. – 6. Broken resting spores with nuclei. – 7, 8. Resting spores (SEM). – 1-7: Collection S. Keller. – 8: Farlow Herbarium (type material). – 1-6: LPAO. – Bars in figs. 1-4: 50 μ m; 3, 5, 6: same magnification. – Bars in figs. 7-8: 5 μ m.

Tab. 3. – Dimensions of conidia and resting spores of *E. echinospora* from different collections.

Structure ¹	Collection (see Tab. 1)	N ¹	Length L x (±s _x) Min – Max	Diameter D x (±s _x) Min – Max	L/D
PC	GM (exsiccata) (ethanol)	2	22.5 (1.8–1.9) 19–27	9.4–9.9 (0.8–0.9) 8–12	2.28–2.40
		1	24.7 (1.4) 22–27	11.9 (0.9) 10–13	2.07
RSendo	Type	5		29.6–38.7 (2.2–3.7) 24–46	
	GM	4		29.9–30.9 (2.4–3.1) 23–38	
	SK	6		30.7–35.0 (2.2–3.4) 24–42	
	BPI	4		32.2–34.9 (2.4–3.0) 25–41	
	FMNH	2		33.8–35.8 (2.6–2.7) 28–41	
RSepi	Type	3		42.2–46.7 (2.6–4.3) 35–54	
	GM	3		34.9–39.3 (2.9–3.2) 29–46	
	SK	6		37.5–41.3 (2.7–3.8) 30–48	
	BPI	4		36.7–42.5 (2.7–3.7) 30–53	
	FMNH	2		39.0–40.5 (3.1–3.5) 33–48	

¹ See table 2 for explanations

According to Thaxter (1888) the conidia measure 20–25 x 10–14 µm and the spherical resting spores 30–40 µm. Although not stated, we assume that this value includes the spinose episporium.

In Thaxter's material we did not find conidia. These were also absent in the type material of *E. lauxaniae* Bubák and of *T. pallidum* Rovainen ex Liro. Comparisons of material from different origins must therefore be based on resting spores. Our own measurements of resting spores without the episporium (endospores) (Tab. 3) corresponded with those of the type material. However, there was only an insignificant overlap of measurements when resting spores with episporium were compared. Possible reasons for this are given in the discussion. The surface structure showed some variability among the different origins. In some samples the spinose appendages (e. g. Fig. 4), in others the ridged ones dominated (e. g. Fig. 11). These differences, however, are not considered significant. The resting spores of all collections were characterized by a prominent hilum. Further, the dimensions of the primary conidia examined from the Bulgarian material match those given by Thaxter (1888).

The fly species serving as hosts all belong to the family Lauxaniidae. These are *Sapromyza longipennis*, type host of *E. echinospora*; *Lauxania aenea* (F.), type host of *E. lauxaniae*; *Calliopum aeneum* F., type host of *T. pallidum*; *Lyciella* sp., host of the Bulgarian material and *Lyciella* sp. cf. *pallidiventris* F. host of the Swiss material. *L. aenea* and *C. aeneum* are synonyms, with the latter being the valid name (G. Bächli, pers. comm.).

Based on these facts we consider *Massospora richteri* Bresadola & Staritz, *Entomophthora lauxaniae* Bubák and *Tarichium pallidum*

Roivainen ex Liro synonyms of *Erynia echinospora* (Thaxter) Remaudière & Hennebert. The fungus recently collected in Bulgaria and Switzerland is also attributed to this species. The additional data obtained during our investigations are included in the following amended description of *E. echinospora*.

Hosts. – Adult flies of the family Lauxaniidae. – Rhizoids abundant, monohyphal with disk-like endings. – Primary conidia 22.5 (19–27) μm \times 9.4–9.9 (8–12) μm , L/D = 2.28–2.40 from exsiccata (2 series) and 24.7 (22–27) μm \times 11.9 (10–13) μm , L/D = 2.07 (1 series) when stored in ethanol; obovate, rounded apex tapering to the papilla. – Resting spores 34.9–46.7 (29–54) μm (12 series), spherical; episorium with irregular spines and ridges, yellow to brownish. Endospore 29.6–38.7 (23–46) μm (15 series). – Young resting spores with 11 (6–16) nuclei with a diameter of 5.3 (5–6) μm (1 series).

Thaxter (1888) distinguished between external and internal resting spores. This distinction seems to be of minor or no importance. The existence of external resting spores is considered to be the result of the rupture of the host cuticle provoked by the pressure of the growing episorangial appendages. This interpretation is supported by the observation of Bubák (1903) that the yellow resting spore powder protruded from the abdomen of the host.

The European authors based their description on the resting spores only. They give a range of sizes which match those given above and in Tab. 3. Staritz (1892): 39–53 μm ; Bubák (1903): 28–50 μm ; Liro (1954): 30–38 μm). They described the colour as yellow to pale brown except Staritz (1892), who described it as reddish. The typical feature of the resting spores, however, is the spiny and ridged episorium which is nearly unique in the Entomophthorales attacking flies. Exceptions are *Strongwellsea castrans* and *S. magna*. Their resting spores are described as bright orange with spines (Humber, 1976). These species, however, differ not only in the colour of the resting spores, which might be considered a subjective criterium, but also in the distinctly larger nuclei (Keller, 1991) and the different taxonomic and ecological group of hosts.

4. *Erynia montana* (Thaxter) Remaudière & Hennebert (1980), Mycotaxon 11, 302.

Bas.: *Empusa* (Entomophthora) *montana* Thaxter (1888), Mem. Boston Soc. Nat. Hist. 4, 180.

Syn.: *Furia montana* (Thaxter) Humber (1989), Mycotaxon 34, 451.

E. montana was included in this study because of the conidia which are similar to those of *E. echinospora*. The shape, the diameter and consequently the L/D-ratio, however, are different (Tab. 2), as well as the host species. The resting spores are unknown.

Discussion

The three species originally described as *Massospora richteri*, *Entomophthora lauxaniae* and *Tarichium pallidum* are identical to *Erynia echinospora*. The data presented in this paper further allow a more detailed description of *E. echinospora*, of *E. americana* and *E. bullata*. The latter two species can easily be distinguished by their resting spores; a separation in the absence of resting spores, however, is difficult or even impossible as Thaxter (cited in Povah, 1935) already stated. Nevertheless it could be possible to separate them by (1) the number of nuclei per hyphal body or per resting spore, (2) the diameter of the nuclei and (3) the length/diameter-ratio of the conidia. The latter parameter for *E. americana* and for *E. bullata* was 1.64–1.93 and 1.81–2.06 respectively (Tab. 2) and suggests that *E. americana* has a lower L/D ratio than *E. bullata*. Recently the L/D ratio was used to attribute a species collected in Switzerland to *E. bullata* (Keller, 1991). Further it allows us to question the taxonomic position of a fungus collected 1936 by Linder and identified as *Entomophthora americana*, deposited in FH. The conidia of this fungus measure 31.4–32.9 (27–42) μm \times 14.1–15.3 (12–18) μm , L/D = 2.05–2.33 (2 series). However, the significance of this criterium for the separation of *E. americana* and *E. bullata* has yet to be proved. On the other hand it can be used to separate the conidia of *E. echinospora* and *E. montana*.

A separation of *E. bullata* and *E. echinospora* based on resting spores is unequivocal. *E. bullata* typically has knoblike, regularly arranged ornaments on the episporium. In some fly specimens the knobs are terminally enlarged to form a layer-like structure. *E. echinospora* also showed different degrees in the formation of the episporial ornamentations (Figs. 7–9). Young resting spores had only indications of spines and ridges (Fig. 9) whereas mature spores had stout spines and ridges. Age or degree of maturity of the resting spores obviously influence the ornamentation and the structure of the episporium. Accordingly, in *E. echinospora* the mean diameters of the whole spores do not overlap in the European and the American collections, whereas the mean diameters of the endospores (without episporium) correspond (Tab. 3). For taxonomic purposes the diameter of the endospore is a more precise measure than the diameter of the spore including the episporium.

A species which is probably identical with *E. americana* was described by Giard (1879) as "*Entomophthora calliphorae* forme *Tari-*

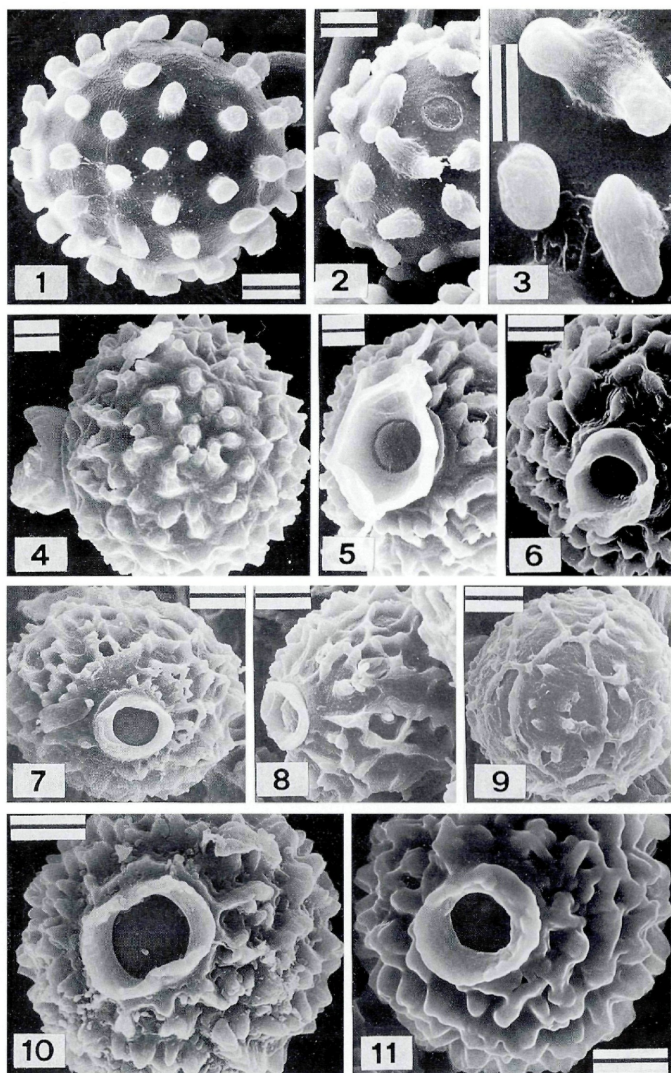


Plate 2. – 1-3: *Erynia bullata* (Farlow Herbarium, type material). – 1. Resting spore with typical knob-like ornamentations. – 2. Resting spore with some atypical knobs and hilum. – 3. A typical and two atypical knobs in detail. 4-11: *Erynia echinospora* from different collections. Note the prominent hilum. – 4-5. Farlow Herbarium (type material). – 6. Collection G. Markova. – 7-9: BPI (type material of *Entomophthora lauxania* Bubak). Note different ornamentation. – 10-11. Collection S. Keller. – SEM. – Bars in all figs.: 5 μ m.

chium". According to this description the smooth walled, yellowish resting spores measured 30 μm , which do not correspond with the average diameter of the material examined. Later Giard (1889) reported the diameter of the resting spores to be 35 μm which corresponds with the type material. Since no type material of *E. calliphorae* exists, it remains uncertain whether these two descriptions really refer to the same fungus species or to two different ones. We therefore should consider *E. calliphorae* a *nomen confusum*. Rozsypal (1966) mentioned a fungus under the same name with conidia measuring 20–24 x 11–13 μm and brown resting spores. This fungus, however, differs from *E. americana*. Another fungus closely related to *E. americana*, however, was described by Rozsypal (1966) as *Zoophthora vomitoriae* [= *Erynia vomitoriae* (Rozsypal) Remaudière & Hennebert]. In an earlier paper Rozsypal (1957) identified the same fungus as *Entomophthora americana*. The morphological data given in these two papers suggest the presence of three species: *E. americana* with conidia measuring 28–32 x 14–16 μm , *E. vomitoriae* with conidia measuring on average 37x17 μm and the doubtful *E. calliphorae* with conidia measuring 20–24 x 11–13 μm .

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