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Arthropod-pathogenic Entomophthorales of Switzerland. II. Erynia, Eryniopsis, Neozygites, Zoophthora and Tarichium

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KELLER, S. (1991). Arthropod-pathogenic Entomophthorales of Switzerland. II. Erynia, Eryniopsis, Neozygites, Zoophthora and Tarichium. – Sydowia 43: 39–122.

31 species of arthropod-pathogenic Entomophthorales are listed and described; 17 belongs to Erynia, 1 to Eryniopsis, 5 to Neozygites, 7 to Zoophthora and 1 to Tarichium. Erynia athaliae, E. minutospora, Neozygites microlophii, Zoophthora viridis and, in addition to part I, Conidiobolus cercopidis and C. pseudapiculatus are described as new species.

Keywords: taxonomy, insect pathogens, Zygomycetes, Entomophthorales.

In part I of this monograph (KELLER, 1987a) the genera *Conidiobolus* (4 species), *Entomophaga* (9 species), and *Entomophthora* (7 species) were treated. *Entomophaga domestica* S. KELLER, *E. limoniae* S. KELLER, *Entomophthora schizophorae* S. KELLER, and *E. trinucleata* S. KELLER were described as new.

Methods

The methods are described in detail by KELLER (1987a). For an easier understanding the most important procedures and abbreviations are repeated here.

Stains: Conidia and cadavers were mounted in lactophenol – cotton blue (LPCB) (0,1 % cotton blue) or in lactophenol-aceto-orcein (LPAO) (0,25 – 0,5 % orcein). The FEULGEN reaction stain (FRS) was used to stain the nuclei.

Cultivation: 4 media were used for isolation and culture of the fungi: (1) Sabouraud-dextrose-agar (SDA), (2) SDA enriched with egg yolk (1 egg yolk per 200 ml SDA) (SDAEY), (3) 1 part egg yolk diluted with 1 part milk, coagulated at 80C for 70 minutes (EYM) and (4) the *Entomophthora*-complete medium (EMC) developed by BEN-ZE'EV (pers. comm.)

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

Unless otherwise stated, the mean dimensions of conidia and resting spores are given in the keys.

Taxonomic part

1. Erynia

- Erynia (Nowakowski) Remaudière & Hennebert (1980). Mycotaxon 11:332–333.
 - Bas.: *Erynia* Nowakowski (1881). Dzienn. III Zjazdu Lek. Przyr. Polsk. Krakow 6:67.
 - Syn.: Erynia (Nowakowski ex Batko) Remaudière & Hennebert emend. Humber (1989) – Mycotaxon 34:448. Furia (Batko) Humber (1989). – Mycotaxon 34:450. Pandora Humber (1989). – Mycotaxon 34:451.

Hyphal bodies spherical, ellipsoidal, elongate, rod-shaped filamentous, rarely branched, or hyphae-like; oligo – or multinucleate, rarely mono-nucleate. – Nuclei large, deeply staining in LPAO. - Rhizoids monohyphal, endings rounded, branched, finger-, root- or disk-like. – Conidiophores branched, enlarged prior to the formation of conidia. – Primary conidia uninucleate, bitunicate, elongate, fusiform, conical, pyriform, ellipsoidal or ovoid, papilla rounded or conical. – Secondary conidia similar to primary or subspherical, tetraradiate in some "aquatic" species. – Resting spores spherical, hyaline or colored, smooth or ornamented. – Cystidia usually present, slender or powerful, tapering.

Most species grow on standard media.

Parasites of Insects and Opiliones.

Type species: Erynia ovispora (Nowakowski) Nowakowski (1881). – Djenn. III Zjazdu Lek. Przyr. Polsk. Krakow 6:67 Bas.: Entomophthora ovispora Nowakowski (1877). – Bot. Zeitg. 35:220

Key to described species of Erynia

1.	On hemimetabolic insect
1.*	On holometabolic insects 3
	2. On Dermaptera, primary conidia $27 \times 17 \mu m$, resting spores
	$27 - 36 \mu m$, wavy surface E. ellisiana (9)
	2.* On Heteroptera, Miridae, primary conidia 14 - 15 x 8 -
	8.5 μm <i>E. minutospora</i> (11)
	2.** On Homoptera, Aphididae, primary conidia 22 - 25 x 8.5 -
	15 μm <i>E. neoaphidis</i> (13)
3.	On Diptera
3.*	On other holometabolic insects
	4. Infected flies with abdominal hole, through which primary
	conidia are projected, these $33 - 37 \ge 17 - 19 \ \mu m$
	E. castrans (5)
	4.* Infected Diptera without abdominal hole
5.	On Nematocera whose immature stages develop in water. Dead
	insects attached to substrate close to water or floating on water
5.*	On other Diptera
	6. Primary conidia elongate conical, largest diameter in basal
	half. $45 - 72 \ge 10 - 12.5 \ \mu\text{m}$ E. conica (6)
	6.* Primary conidia elongate, ovoid to pyriform, largest diame-
	ter in apical half
7.	Primary conidia elongate pyriform, 31 – 43 x 11.5 – 16 µm
	E. aquatica (1)
7.*	Primary conidia elongate ovoid
	8. On Psychodidae. Primary conidia 19.5 - 26.5 x 10.5 -
	15.5 µm E. ovispora (14)
	8.* On other Nematocera. Primary conidia 32.5 – 39 x 11 –
	14 μ m E. curvispora (7)
	8.** Primary conidia $22 - 24.5 \ge 8 - 8.5 \ \mu\text{m}$ E. variabilis (16)
9.	Primary conidia $16 - 27 \ge 9 - 16 \mu m$, usually on smaller Diptera
	E. dipterigena (8)
9 *	Primary conidia $30 \times 15 \text{ µm}$ E bullata (4)
0.	10 On Jarval Lenidontera
	10 * On holometabolic insects other than Dinters and Lenidon-
	tera
11	Primary conidia $18 - 20.5 \times 9 - 10 \text{ µm}$ F blunckii (3)
11 1	Primary conidia $19 - 21 \ge 75 - 105$ µm resting spores dark
11.	brown to black $45 - 47 \times 41 - 44 \text{ µm}$ F gammag (10)
11 *	*Primary conidia $245 - 31 \times 13 - 16 \ \mu m$ F aircocone (17)
тт.	12 On Jarval Hymenontera Tenthredinidae Primary conidio
	$21 - 22 \times 9 - 11 \text{ µm}$
	$21 - 22 = 3 - 11 \mu m \dots \dots$

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12.* On adult Hymenoptera Formicidae. Primary conidia 19-20
x 12 μm <i>E. myrmecophaga</i> (12)
12.**On adult Trichoptera. Primary conidia 31 - 43 x 8.5 -
11 μm <i>E. rhizospora</i> (15)

1. Erynia aquatica (Anderson & Ringo ex Anderson & Anagnostakis) Humber (1981b). – Mycotaxon 13: 213. – Pl. 1: figs. 1–6.

Bas.: Entomophthora aquatica Anderson & Ringo ex Anderson & Anagnostakis (1980). – Mycotaxon 10: 350.

Host. - Diptera, Nematocera: Undetermined midges.

Symptoms. – Infected midges floating on the surface of water or attached to wood close above the water level. When sporulating the whole insect body is covered with a white conidiophore/conidia mass.

Rhizoids monohyphal, 18–50 μ m diameter, usually branched, sometimes with protuberances, endings often screw-like. – Conidiophores (fig. 3) branched, terminally with a diameter of 10 – 16 μ m, nuclei deeply staining in LPAO. – Primary conidia 31.1 – 43.0 x 11.6 – 16.1 μ m (24 – 51 x 9 – 19 μ m), (6 collections), L/D = 2.16 – 2.90, usually slightly bent; largest diameter in apical part, on slides the cytoplasmic content tends to withdraw from the apical region; papilla long, conical (fig. 4). – Secondary conidia similar to primary or rounded with indistinct apical point (fig. 5), the round form measuring 17.6 – 19.2 x 13.0 – 14.4 μ m (16 – 21 x 12 – 16 μ m) (2 collections), L/D = 1.33 – 1.45). – Resting spores not observed. – Cystidia powerful, diameter at the level of the conidia 17 – 46 μ m, at the tip 6 – 14 μ m, oligonucleate (figs. 1–2).

Culture. – Good growth on SDAEY, EYM and EMC. Conidia 48.5 x 16.9 μm (41 – 56 x 13 – 21 μm) (1 collection), L/D = 2.86. Resting spores 41.4 – 44.2 μm (30 – 61 μm) (4 collections), spherical, smooth, hyaline (fig. 6).

Distribution. – Pouta Fontana VS, Stammheim ZH, Hausener Seen ZH.

The species was occasionally found in ponds and small lakes as well as in a wooden barrel filled with water. It was collected between end of June and mid-October.

2. Erynia athaliae Keller sp.nov. – Pl. 2: figs 1–10.

Conidia primaria (17-)21-22 (-30) x (7-)9-11 (-15) $\mu m,$ elongata ellipsoidea. Conidia secundaria habitu primariis similia aut subglobosa apicaliter acuminata,

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Pl. 1. - 1-6: Erynia aquatica. - 1-2. Cystidia with nuclei. - 3. Conidiophore. 4. Primary conidia (phase contrast). - 5. Secondary conidium of the subspherical type. - 6. Resting spores from culture. - 7-8: Erynia bullata. - 7. Conidiophores. 8. Primary conidia. - All LPCB. - Bar in figs. 1 and 5: 50 μm; 1 - 3, 7; 4 - 6, 8 same magnification.

(13-) 15 – 16 (-19) x (9-) 10 – 12 (-15) µm. Sporae perdurantes zygosporae (24-) 31–35 (-42) µm, globosae, hyalinae, leves, 10 – 23 nucleos continentia. Cystidia elongata. Rhizoidea mononemata, numerosa, diametro 12 – 25 µm, basaliter ramificata. In Athalia rosae L. (hospite typico) (Hymenoptera: Tenthredinidae). Helvetia. Holotypus ZT, cotypi K et BPI.

Host. – Hymenoptera, Tenthredinidae: *Athalia rosae* L. (type host).

Symptoms. – Diseased larvae attached to leaves of the host plant, conidiophore/conidia layer grey, covers the whole insect (except ventral side) (fig. 1).

Rhizoids monohyphal, multinucleate, abundant on the ventral surface, $12 - 25 \mu m$ thick, endings with numerous terminal branchings, finger- or root-like (figs. 2-3). - Hyphal bodies simple irregular rod-like, sometimes branched, with 6 - 31 (-90) nuclei; nuclei deeply staining in LPAO, diameter 5.7 (5–7) μm (1 collection) (fig. 4). – Conidiophores branched, terminally ("shoulder") 8 – 12 μm diameter. – Primary conidia 21.2 – 22.0 x 9.3 – 10.8 μm $(17 - 30 \times 7 - 15 \text{ um})$ (6 collections), L/D = 1.96 - 2.36, elongate, slightly pyriform to subfusiform, sometimes slightly bent; papilla distinct broad, nearly flat (fig. 6). - Secondary conidia like primary or short ovoid to subspherical with apical point, 15.2-16.0 x $10.6 - 11.8 \mu m (13 - 19 \times 9 - 15 \mu m)$ (6 collections), L/D = 1.35 - 1.45, often with single prominent vacuole (fig. 7). - Resting spores zygospores developing laterally between two adjacent rod-shaped to filamentous hyphal bodies; $32.1 - 34.6 \,\mu\text{m} (24 - 42 \,\mu\text{m})$ (2 collections), hyaline, smooth, with 14 (10–23) nuclei (1 collection) (figs. 8–9). – Cystidia long, slender, slightly tapering, diameter at the level of the conidia 7 – 18 μ m, apical diameter 6 – 10 μ m (fig. 5).

Culture. – Good growth on SDAEY, EYM and EMC. Conidia $20.7 - 23.5 \ge 12.5 - 16.6 \ \mu m (17 - 33 \ge 11 - 25 \ \mu m)$ (6 collections), L/D = 1.36 - 1.77. Resting spores $31.0 - 33.0 \ \mu m$ (22 - 42 $\ \mu m$) (4 collections) (fig. 10).

Distribution. - Zürich-Reckenholz ZH.

The species was found twice to cause epizootics with very high mortalities (in a sample 89~% within 4 days after collection) among

^{Pl. 2. - 1-10: Erynia athaliae. - 1. Fungus sporulating from dead insects, projected conidia forming white zones around hosts (ca. 3 x nat. size). - 2. Rhizoids on the ventral surface shortly after insect death. 5 x nat. size). - 3. Rhizoids showing branched endings. - 4. Hyphal bodies with nuclei. - 5. Cystidia. - 6. Primary conidia. - 7. Secondary conidia. - 8. Formation of zygospore. - 9. Young zygospores with nuclei. - 10. Mature resting spores from culture. - 3, 4, 8, 9; LPAO, 5-7, 10: LPCB. - Bar in figs. 3 and 9: 50 µm; 3-5; 6-10 same magnification.}

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the third generation of its host on harvested and regrown rape fields. The resting spores were found in pre-pupae in their soil-cocoon. It was collected between end of August and beginning of October.

- Erynia blunckii (Lakon ex Zimmermann) Remaudière & Hennebert (1980). – Mycotaxon 11: 302. – Pl. 3: figs. 1–9.
 - Bas.: Entomophthora blunckii Lakon ex Zimmermann (1978). Entomophaga 23: 181–187.

Host. – Lepidoptera, Plutellidae: *Plutella maculipennis* CURT. Symptoms. – Diseased caterpillars attached to leaves of their host plant, light brownish when sporulating.

Rhizoids monohyphal, abundant on ventral surface, 10 - 25 (-35) µm diameter, disk-like holdfast (figs. 4–6). – Conidiophores branched, terminally slightly enlarged with a diameter of 7–10 µm (fig. 7). – Primary conidia 17.8 – 20.6 x 9.2 – 10.1 µm (16 – 23 x 7 – 12 µm) (2 collections), L/D = 1.76 – 2.23, slightly bent, elongate, papilla distinct (fig. 8). – Secondary conidia similar to primary. – Resting spores not observed. – Cystidia long and slender, diameter at the level of the conidia 8 – 13 µm, at the apex 4 – 7 µm (fig. 3).

Culture. – Good growth on ECM. Primary conidia $18.7 - 2\overline{1.3} \times 8.6 - 11.2 \ \mu\text{m} (16 - 24 \times 7 - 15 \ \mu\text{m}) (2 \text{ collections}), L/D = 1.90 - 2.17.$ Resting spores $28.4 \ \mu\text{m} (21.8 - 35.1 \ \mu\text{m}) (1 \text{ collection}), hyaline, smooth (fig. 9).$

Distribution. - Zürich-Reckenholz ZH.

The species was found on two caterpillars between mid-September and beginning of October. The species is described in detail by ZIMMERMANN (1978).

 Erynia bullata THAXTER & MACLEOD in HUMBER (1981a).- Mycotaxon 13: 472. - Pl. 1: figs. 7.

Hosts. – Diptera, Calliphoridae: *Pollenia* sp. cf. *vespillo* (M.). Symptoms. – Diseased fly attached to the underside of a leaf f a bush of *Salix* sp. Rhizoids readily visible. Brown mycelial bands

of a bush of *Salix* sp. Rhizoids readily visible. Brown mycelial bands along intersegmental membranes and pleura; abdomen more or less covered with a brown mat.

Rhizoids monohyphal, abundant ventrally and latero-ventrally; holdfasts disk-like. – Primary conidia 29.8 x 14.8 μm (27 – 34 x 13 – 18 μm) (1 collection), L/D = 2.01; slightly asymmetrical, elongate; papilla distinct, broad, truncate. – Resting spores and cystidia not found.



Pl. 3. - 1-9: Erynia blunckii. - 1. Young, probably multiplying hyphal bodies from living insect. - 2. Hyphal bodies with nuclei. - 3. Cystidia. - 4. Immature rhizoids with enlarged tips. - 5. Branched and unbranched rhizoid with endings starting to differentiate. - 6. Rhizoid with fully developed disk-like holdfast. - 7. Conidiophore. - 8. Primary conidia. - 9. Resting spores from culture. - All LPAO. - Bar in figs. 3 and 9: 50 µm; 2-5,7; 1, 6, 8-9 same magnification.

Culture. – Grows on SDAEY and EMC, Primary conidia $33.3 \times 18.2 \ \mu m \ (28 - 41 \times 13 - 27 \ \mu m) \ (1 \ collection), L/D = 1.82.$

Distribution. - Stammheim ZH.

The species was found once on August 25. According to THAXTER (cited in POVAH, 1935) the conidia of this species cannot be distinguished from the conidia of *E. americana*. Recent investigations (B. PAPIEROK, pers. comm.; S. KELLER, unpubl.) may indicate that the conidia of *E. americana* are slightly broader, resulting in a L/D-ratio of 1.6 - 1.8. The corresponding value for *E. bullata* is 2.1 (MACLEOD & al., 1973). Based on these data, which need further confirmation, the species was attributed to *E. bullata*.

Hosts. - Diptera, Anthomyiidae: unidentified species.

Symptoms. - Living flies with a ventral, abdominal hole with a diameter of about 1-2 mm, activity of the flies reduced. Infection restricted to the abdomen.

Rhizoids absent. – Hyphal bodies rounded, mono-rarely oligonucleate (fig. 1), diameter of nuclei 9.3 (8 – 10.5) μ m (1 collection). – Conidiophores unbranched, mononucleate, subcylindrical (fig. 2). – Conidia 33.0 – 37.1 x 17.1 – 19.4 μ m (29 – 41 x 15 – 22 μ m) (5 collections), L/D = 1.78 – 2.11, symmetrical, cylindrical, largest diameter in apical half, papilla distinct (fig. 3). – Secondary conidia like the primary. Resting spores not observed. – Cystidia absent.

Distribution. - Stammheim ZH, Zürich-Reckenholz ZH.

All specimen were collected between mid-August and mid-October in fields of *Brassica* spp. The species was originally described as *Strongwellsea castrans* BATKO & WEISER (1965). It is closely related to *E. magna* (HUMBER) REMAUDIÈRE & KELLER (1980). The dimensions of

Erynia castrans (Batko & Weiser) Remaudière & Keller (1980). – Mycotaxon 11: 333. – Pl. 4: figs. 1–3.

Bas.: Strongwellsea castrans BATKO & WEISER (1965). – J. Invertebr. Pathol. 7: 460–463.

^{Pl. 4. - 1-3: Erynia castrans. - 1. Mononucleate hyphal bodies differentiating into conidiophores. - 2. Conidiophores with developing conidia. - 3. Primary conidia. - 4-9: Erynia gammae. - 4. Noctuid larva killed by the disease (ca. 2 x nat. size). - 5. Hyphal bodies. - 6. Primary conidia. - 7. Secondary conidia. - 8. Zygospore formation. - 9. Mature resting spores. - 1-3, 5: LPAO; 6-9: LPCB. - Bar in figs. 1 and 6: 50 μm; 1, 5, 9: 2, 6-8 same magnification.}

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the conidia given above, indeed, match those given by HUMBER (1976) for *E. magna* but differ in their shape. His data listed for *E. castrans*, however, show that the dimensions of the conidia of the two species overlap. A further character used by HUMBER (1976) to distinguish the two species is the shape of the conidia. Whereas those of *E. castrans* have the largest diameter in their apical half, those of *E. magna* are largest in their basal half. Further the length/diameter ratio of fresh conidia is given as 1.7 - 2.1 for *E. castrans* and 2.2 - 2.4 for *E. magna*. The fungus described above better fits the description of *E. castrans* and is therefore attributed to that species.

 Erynia conica (Nowakowski) REMAUDIÈRE & HENNEBERT (1980). – Mycotaxon 11: 302. – Pl. 5: figs. 1–9; Pl. 6: figs. 1–4. Bas.: Entomophthora conica Nowakowski (1883). – Pamietn.

Wydz. Akad. Umiej. w. Krakow 8: 155–160.

 ${\tt Hosts.-Diptera, Chironomidae, Simuliidae:}$ unidentified species.

Symptoms. – Host attached to substratum just above the water level, rarely floating on the surface of water. Whole insect covered with grey or greenish fungal mat.

Rhizoids monohyphal (11-) 15-40 (-52) um diameter, holdfast simple, bifurcate, finger- or root-like, sometimes with lateral outgrowths (Pl. 6, figs. 1-4). - Hyphal bodies rounded with 6 - 8 (1 -14) (5 collections) nuclei, distinctly staining in LPAO, diameter of nuclei 7.0 – 9.0 µm (6 – 10.5 µm) (5 collections) (Pl. 5, fig. 1). – Conidiophores branched, terminally enlarged to a diameter of 13 - 20 μm. - Primary conidia 45.4 - 71.5 x 10.2 - 12.4 μm (36 -94 x 9 - 17 μ m) (10 collections) L/D = 3.8 - 6.7, widely varying in length, bent or straight, elongate, conical, largest diameter in basal half; papilla indistinct, rounded; diameter of nuclei 7.2 - 9.8 µm (5.5 – 12 µm) (3 collections) (Pl. 5, figs. 6–7). – Secondary conidia elongate, similar to primary, 37.5 - 46.6 x 10.9 - 13.2 μm (28 - 57 x 9 -16 μ m) (3 collections) L/D = 1.2 - 1.3 or rounded with apical point $17.2 - 19.6 \ge 13.7. - 15.8 \ \mu m \ (15 - 22 \ge 12 - 18 \ \mu m) \ (7 \ collections) \ L/D$ = 3.1 - 4.3 (Pl. 5, fig. 8). - Resting spores $40.1 - 49.4 \ \mu m \ (33 - 4)$ $62 \mu m$) spherical, hyaline with 21 - 24 (14 - 43) nuclei (2 collections) diameter of nuclei $7.5 - 8.0 \,\mu\text{m}$ ($6.5 - 10 \,\mu\text{m}$) (2 collections) (Pl. 5, figs. 4-5). - Cystidia prominent, diameter at the level of the conidia 16 -

Pl. 5. – 1–9: *Erynia conica.* – 1. Hyphal bodies with nuclei. – 2, 3. Cystidia. – 4. Resting spore (zygospore ?) formation. – 5. Young resting spores with nuclei. – 6. Typical primary conidia. – 7. Elongate primary conidia. – 8. Secondary conidia of the rounded and elongate type. – 9. Tetraradiate (stellate) conidia. – 1, 4, 5: LPAO; 2, 3, 6–9: LPCB.

[–] Bar in figs. 1, 3 and 9: 50 $\mu m;$ 2–3; 1, 4–5, 7–8; 6, 9 same magnification.

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 60μ m, at the apex $8 - 18 (-24) \mu$ m, more or less continuously tapering, apex sometimes slightly enlarged, 2 - 6 nuclei (Pl. 5, figs. 2–3).

Culture. – Good growth on SDAEY, EYM, EMC; colonies on SDAEY and EYM reach a diameter of 10 - 70 mm within 2 weeks with marked differences between isolates. Primary conidia $55.1 - 68.1 \times 10.4 - 14.8 \ \mu\text{m} (38 - 92 \times 9 - 18 \ \mu\text{m})$ (7 collections), L/D = 4,2 - 6.5, rounded secondary conidia $19.4 - 20.9 \times 15.8 - 16.9 \ \mu\text{m} (17 - 25 \times 13 - 22 \ \mu\text{m})$ (2 collections), L/D = 1.15 - 1.22.

Distribution. – Sonogno TI, Lenk BE, Pouta Fontana VS, Pramagnon VS, Ottenbach AG, Lengnau AG, Hausener Seen ZH, Stammheim ZH, Hallau SH, Trasadingen SH, Frauenfeld TG, Felben TG, Rüthi SG, Willsau LU.

The species occurs very frequently at borders of lakes, ponds, rivers and brooks. It was found between mid-May and end of October. The species can form stellate secondary conidia (Pl. 5, figs. 9).

- Erynia curvispora (Nowakowski) Nowakowski (1881). Dzienn. III Zjazdu Lek. Przyr.Polsk. Krakow. Sekc. Bot.6: 67–68. – Pl. 6: figs. 5–8.
 - Bas.: Entomophthora curvispora Nowakowski (1877). Bot. Zeitg. 35:217.

Hosts. - Diptera, Chironomidae: unidentified species.

Symptoms. – Dead midges fixed to substratum just above the water level, covered with a grey layer of fungal material.

R hizoids monohyphal with a diameter of $11 - 35 \mu m$, endings rounded, branched or root-like. – Primary conidia 32.4 - 39.3 x $11.3 - 14.0 \mu m (27 - 50 x 9 - 18 \mu m)$ (6 collections), L/D = 2.46 - 3.02, distinctly bent, elongate, largest diameter in the apical half, papilla distinct (fig. 7). – Secondary conidia rounded with apical point $15.2 - 16.4 x 12.2 - 13.1 \mu m (13 - 21 x 10 - 16 \mu m)$ (6 collections), L/D = 1.25 - 1.27, or resembling the primary ones, $25.4 x 11.4 \mu m (22 - 30 x 10 - 15 \mu m)$ (1 collection), L/D = 2.23 (fig. 8). – Cystidia prominent with a diameter at the level of the conidia of $18 - 40 \mu m$ more or less abruptly tapering to the apex (fig. 6).

Pl. 6. – 1–4: Erynia conica. – 1. Unspecialised rhizoids. – 2–4. Rhizoids with different tpyes of holdfasts. – 1, 2: Ethanol; 3, 4: LPAO. – 5–8: Erynia curvispora. – 5. Conidio-phores (Phase contrast). – 6. Cystidia. – 7. Primary conidia. – 8. Secondary conidia of the rounded and the elongate type. – 6–8: LPCB. – Bar in figs. 1, 6 and 8: 50 μ m; 1–4; 5–6; 7–8 same mangnification.

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Culture. – Good growth on SDAEY, EYM, and EMC. Primary conidia $32.8 - 47.2 \times 11.3 - 13.8 \ \mu m \ (29 - 63 \times 10 - 19 \ \mu m) \ (7 \ collections), L/D = 2.80 - 3.65, rounded secondary conidia 19.4 x 16.8 \ \mu m \ (16 - 24 \times 13 - 21 \ \mu m) \ (1 \ collection), L/D = 1.15.$

Distribution. - Hausener Seen ZH, Trasadingen SH.

The species was found along borders of lakes, ponds and brooks attached to wet wood or walls. It was collected between mid-August and end of October.

- Erynia dipterigena (THAXTER) REMAUDIÈRE & HENNEBERT (1980). Mycotaxon 11: 302. – PL. 7: figs. 1–6.
 - Bas.: *Empusa dipterigena* THAXTER (1888). Mem. Boston Soc. Nat. Hist. 4: 177.
 - Syn.: Empusa sciarae OLIVE (1906). Bot. Gaz. 41: 192-208.

Hosts. – Diptera, Sciaridae and unidentified smaller and rarely larger species.

Symptoms. – Dead host attached to substratum. Abdomen, sometimes whole insect covered with white fungal mat.

Rhizoids monohyphal with a diameter of 7 - 34 (-60) µm, ventrally and lateroventrally spreading, holdfast branched or disklike. – Hyphal bodies irregularly rod-shaped to filamentous, bent, sometimes branched, (fig. 1); 16 (9 - 28) nuclei with a diameter of 4.2 (4 - 5) µm (1 collection). – Primary conidia 15.4 - 26.6 x 8.7 - 15.9 µm (12 - 30 x 7 - 19 µm) (8 collections), L/D = 1.55 - 2.16, elongate, usually asymmetrical, often with 1 or 2 prominent vacuoles, widely varying dimensions; papilla distinct, rounded (figs. 3-5). – Secondary conidia 11.9 - 13.4 x 7.8 - 9.2 µm (10 - 16 x 6 - 10 µm) (3 collections), L/D = 1.45 - 15.6, like primary or more rounded with apical point (fig. 6). – Cystidia long, slender, diameter at the level of the conidia 6 - 15 µm, at the apex 4 - 7 µm, terminal portion sometimes slightly enlarged (fig. 2).

Culture. – Good growth on SDAEY, EYM, ECM. Primary conidia $18.7-28.1 \times 11.2-16.4 \ \mu m$ (16 – 31 \times 10 – 21 μm) (7 collections), L/D = 1.60 – 1.73. Resting spores 30.4 μm (25 – 35 μm) (1 collection), smooth, hyaline.

^{Pl. 7. - 1-6: Ergnia dipterigena. - 1. Hyphal bodies at an early developing stage with prominent oil globules. - 2. Cystidia. - 3-5. Primary conidia of different sizes. - 6. Secondary conidium of the rounded type. - 7-12: Ergnia myrmecophaga. - 7. Hyphal bodies with nuclei, partly arranged in chains. - 8. Formation of hyphal bodies. - 9. Primary conidia with many small oil doplets. - 10-12. Rhizoids with different types of holdfasts. - 2-6: LPCB; 1, 7-12: LPAO. - Bar in figs. 3, 7 and 10: 50 um; 10-11: 1-2, 7-8, 12: 3-6, 9 same magnification.}

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Distribution. – Happerswil TG, Zürich-Reckenholz, Watt ZH, Stammheim ZH, Ellikon-Rickenbach ZH, Trüllikon ZH, Osterfingen SH, Trasadingen SH, Hallau SH, Oberhallau SH, Neunkirch SH, Schleitheim SH, Seengen AG, Changins/Nyon VD, Sonogno TI.

The species is very common throughout the season. It was collected between end of May and mid-November at different habitats including borders of forests (on the underside of leaves), meadows, weeds but also in mushroom houses attacking Sciaridae. *E. dipterigena* shows a wide variation in the conidial size, encompassing that of *E. montana* (THAXTER, 1888) and *E. sciarae* (OLIVE, 1906). The closely related *E. americana* (THAXTER, 1888), which was found by the author on large numbers of flies in northern Italy (Eraclea Mare, Veneto), differs distinctly mainly by the symptoms and the larger conidia. *E. montana* can be distinguished from *E. dipterigena* by the shape of the conidia (broadly rounded apex), but no character was found to separate *E. dipterigena* and *E. sciarae*. We therefore consider the two species to be identical in contrast to the findings of MACLEOD & MÜLLER-KÖGLER (1973) who considered *E. sciarae* as identical to *E. montana*.

9. Erynia ellisiana BEN-ZE'EV (1986b). – Mycotaxon 27: 266. – Pl. 8: figs. 1–12.

Host. – Dermaptera, Forficulidae: Forficula auricularia L.

Symptoms.-Infected insects die in their hiding places. White mycelial bands along intersegmental membranes and protruding filaments.

Rhizoids monohyphal with poorly branched endings (figs. 6–7), usually few in number, sometimes arranged in small tufts. – Hyphal bodies rounded, elongate or irregularly rod-shaped with one to several nuclei (fig. 1); diameter of nuclei 6.9 (5.5 – 8) μ m (1 collection); germinate with single germ tube to form the conidiophore (fig. 2). – Young conidiophores segregate into mononucleate compartments, each of them forming a conidium (figs. 3–5). – Primary conidia 27.0 – 27.4 x 16.4 – 17.1 μ m (23–31 x 13–21 μ m) (L/D = 1.58 – 1.67) (2 collections), ovoid to pyriform, often with one prominent vacuole, papilla blunt to slightly rounded (fig. 10). –

Pl. 8. – 1–12: Erynia ellisiana. – 1. Hyphal bodies with nuclei. – 2. Hyphal bodies developing to conidiophores. – 3. Two conidiophores, one segregated into mononucleate fragments. – 4–5. Formation of conidiophores from mononculeate fragments. – 6–7. Rhizoids. – 8. Cystidium. – 9. Formation of primary conidia. – 10. Primary conidia. – 11. Formation of secondary conidium. – 12. Resting spores. – 1–3, 6–7: LPAO; 4–5, 8–12: LPCB. – Bar in figs. 2, 5 and 12: 50 µm; 1–4, 6–9; 10–12 same magnification.

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Secondary conidia similar to primary (fig. 11). – Resting spores $26.6 - 36.3 \ \mu m (27 - 45 \ \mu m)$ (2 collections), spherical, hyaline, surface slightly undulated (fig. 12). – Cystidia with a diameter of $14 - 31 \ \mu m$ at the base and $7 - 12 \ \mu m$ at the apex (fig. 8).

Distribution. – Zürich-Reckenholz ZH, Wädenswil ZH, Zizers GR.

The species was found at four occasions between beginning of July and mid-September in earwigs collected in an old web of *Yponomeuta* sp. on *Evonymus europaeus* and in cardboard strips mounted around apple tree trunks to collect larvae of the codling moth (*Cydia pomonella*). A further specimen containing resting spores originated from England and was kindly supplied by N. WILDING.

Although there is doubt about its generic position, the species differs from others in the genus by its mode of conidia formation. The mononucleate hyphal bodies form an unbranched conidiophore with a terminal conidium. The oligonucleate hyphal bodies grow out into unbranched germ "premature" conidiophores, which may segregate into mononucleate fragments. From these fragments, too, unbranched "mature" conidiophores arise forming a conidium each. Some of these conidiophores may give the impression of being unbranched.

 Erynia gammae (WEISER) GLARE & MILNER (1987). – Austr. J. Bot. 35: 72. – Pl. 4: figs. 4–9.

Bas.: Tarichium gammae WEISER (1965). – Ceské Mycol. 19: 203.

 ${\tt Hosts.}$ – Lepidoptera, Noctuidae: Autographa~gamma and unidentified related species.

Symptoms. – Dead caterpillars grey-brown to black, near the top of grass or herbs, the abdominal part behind the first pair of legs fixed to the plants, rest of the body hanging free (fig. 4).

Rhizoids with a diameter of $6 - 24 \,\mu\text{m}$ usually form a layer between the fixed part of the body and the plant. – Hyphal bodies elongate, rounded, straight or bent, unbranched, with 6 - 42 nuclei, diameter of nuclei: 5 (4.5 - 6) μm (1 collection) (fig. 5). – Primary

Pl. 9. - 1-3: Erynia minutospora. - 1. Rhizoids with holdfasts. - 2. Primary conidia. -3. Formation of secondary conidium. - All LPAO. - 4-9: Erynia virescens. - 4. Noctuid larva killed by the disease (ca. 2 x nat. size). - 5. Rhizoids (white spots) on the ventral surface of the posterior portion of the larva (ca. 10 x nat. size). - 6. Conidiophore divided into (mononuclear ?) fragments. - 7. Cystidium and formation of primary conidia. - 8. Primary conidia. - 9. Resting spores from culture. - All LPCB. - Bar in figs. 1, 7 and 8: 50 um; 1, 6; 2-3, 8-9 same magnification.

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conidia 18.9 – 20.9 x 7.7 – 10.4 µm (16 – 28 x 7 – 13 µm) (5 collections), L/D = 2.01 – 2.45, slightly asymmetrical; papilla distinct (fig. 6). – Secondary conidia 12.1 x 9.1 µm (11 – 16 x 9 – 11 µm) (1 collection), L/D = 1.33 (fig. 7). – Resting spores 45.6 – 46.3 x 41.5 – 43.4 µm (2 collections), spherical to subspherical when young, slightly compressed in the axis of the hylum when mature, diameter varying between 40 and 58 µm, black, ornamented (figs. 8–9). – Cystidia with a diameter of 8–14 µm at the level of the conidia and 6 – 8 µm at the apex.

Culture. – All attempts to isolate the fungus failed.

Distribution. – Zürich-Reckenholz ZH, Stammheim ZH, Rafz ZH, Oberhallau SH.

The fungus was found in meadows and pea fields between the end of June and end of October. Two epizootics were observed, one in a pea field at the end of June/beginning of July and the other in a meadow at the end of August.

The species was described originally by its resting spores only. MACLEOD & MÜLLER-KÖGLER (1970) placed it in the genus *Entomophthora* without formal transfer. HARPER & CARNER (1973) described the conidia and demonstrated the conspecificity with the resting spore state. However, the fungus was not formally placed in the correct genus until 1987 by GLARE & MILNER.

11. E. minutospora Keller sp.nov. - Pl. 9: figs. 1-3.

Conidia primaria (12-) 14 – 15 (-17) x (7-) 8 – 9 (-10) µm, ovoidea vel pyriformia, papilla rotunda praedita. Conidia secundaria primariis similia. Rhizoidea mononemata diametro 5 – 18 µm, basaliter ramificata. Cystidia et sporae perdurantes ignotae. In Trigonotylo ruficorni GEOFFR. (hospite typico) et Lygus spp. (Heteroptera: Miridae). Helvetia. Holotypus ZT.

Symptoms. - Dead insects attached to plants.

Rhizoids with a diameter of 5 – 18 μ m, endings root-like or undifferentiated (fig. 1). – Primary conidia 14.2 – 14.8 x 8.3 – 8.4 μ m (12 – 17 x 7 – 10 μ m), L/D = 1.70 – 1.75 (2 collections), ovoid to pyriform; papilla distinct, rounded (fig. 2). – Secondary conidia like primary (fig. 3).

Bar in figs. 1, 6 and 8: 50 µm; 1-2, 4-5; 3, 6-7; 8-10 same magnification.

Pl. 10. -1-10: *Erynia neoaphidis*. -1-2. Hyphal bodies from living aphids, with nuclei not (yet ?) staining (1) and with stained nuclei (2). -3-4. Rhizoids with disk-like holdfasts. -5. Histological section through a group of rhizoids with endings forming a layer (HE). -6. Cystidia. -7. Conidiophores. -8. Primary conidia. -9-10. Secondary conidia of the elongate (9) and the rounded type (10). -1-2: LPAC; 3-4, 6-10: LPCB.

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Distribution. - Losone TI (type locality).

Trigonotylus ruficornis were collected by sweep netting in maize fields. A single specimen succumbed to an *Erynia* sp. characterised by unusually small conidia which suggested the specific name.

Infected *Lygus* spp. collected in Czechoslovakia and kindly supplied by J. WEISER proved to be infected with the same species.

- Erynia myrmecophaga TURIAN & WUEST in HUMBER (1981a). Mycotaxon 13: 477. – Pl. 7: figs. 7–12.
 - Syn.: Erynia formicae Humber & Balazy in Humber (1981a). Mycotaxon 13: 475.

Hosts. – Hymenoptera, Formicidae: *Formica* (*Coptoformica*) *bruni* KUTTER and an unidentified species.

Symptoms. – Dead ants fixed at the top of grasses with mandibles and rhizoids, head downwards.

Rhizoids usually few in number, monohyphal with a diameter of $14 - 50 \ \mu\text{m}$, emerging ventrally mainly from the pro-/mesothorax region; holdfast branched, finger-, root- or disk-like (figs. 10-12). – Hyphal bodies spherical, subspherical, rod-shaped with a diameter of 12.7 (11 - 16) μm (1 collection) or irregularly elongate, straight or bent, rarely branched, sometimes arranged in chains (figs. 7-8); with 4 - 14 (-25) nuclei; diameter of nuclei 4.6 (3.5 - 5.5) μm (1 collection), nuclei with prominent nucleolus. – Primary conidia 19.2 – 20.3 x 11.8 μm ($16 - 25 \times 10 - 15 \mu\text{m}$) (2 collections), L/D = 1.62 – 1.72, slightly bent, papilla distinct (fig. 9). – Secondary conidialike primary. – Resting spores not observed. – Cystidia slender, tapering to an apical diameter of $6 - 8 \mu\text{m}$.

Distribution. - Genolier (Nyon) VD, Neunkirch SH.

The species was found between April and beginning of October. At Genolier (Bois de Chênes) it occurred epizootically and was considered to be responsible for the disappearance of *Formica bruni* in that region (MADDALENA & CHERIX, pers. comm.).

Pl. 11. – 1–9: Erynia ovispora. – 1. Diseased psychodid midge on moss with the fungus sporulating (ca. 8 x nat. size). – 2. Histological section through germinating hyphal bodies (HE). – 3. Young resting spores with nuclei. – 4. Cystidia and conidiophores. – 5. Conidiophores. – 6. Rhizoids with root-like holdfasts. – 7. Rhizoid with sucker or disk-like holdfast. – 8. Primary conidia. – 9. Formation of secondary conidia. – 2, 6: LPAO; 4, 5, 8, 9: LPCB; 7: Ethanol. – Bar in figs. 5, 7 and 9: 50 µm; 4–6; 2–3, 7; 8–9 same magnification.



TURIAN & WUEST (1969) discovered this fungus in the region of Geneva, which is only some kilometers away from Genolier. Their description (TURIAN & WUEST, 1977), however, is invalid because of the lack of a type designation. BALAZY & SOKOLWSKY (1977) reported the fungus from Poland. HUMBER (1981), however, considered the Polish material as different from the Swiss one and described a new species, *E. formicae* HUMBER & BALAZY. The present study based on topotypified material of *E. myrmecophaga*, demonstrates that there are no substantial differences between the two species. *E. formicae* must therefore be considered as synonym of *E. myrmecophaga*.

 Erynia neoaphidis REMAUDIÈRE & HENNEBERT (1980). – Mycotaxon 11: 307. – Pl. 10: figs. 1–10.

Hosts. – Homoptera Aphididae: Acyrthosiphon pisum Harris, Aphis fabae Scop., A. pomi De Geer, A. rumicis L., A. urticata F., Brevicoryne brassicae L., Cavariella sp., Cryptomyzus ribis L., Dactynotus jaceae L., Impatientinum asiaticum Nevs., Macrosiphum albifrons Essig, M. euphorbiae Thomas, M. funestum Macchiari, M. rosae L., M. silvaticum Meier, Metopolophium dirhodum Walker, M. festucae Theobald, Microlophium carnosum Buckton, Myzus persicae Sulzer, Phorodon humuli Schrank, Rhopalomyzus lonicerae Siebold, Rhopalosiphum padi L., Sitobion avenae F.

Symptoms. – Dead aphids light or dark brown depending on the colour of the living aphid, attached to plants within the aphid colonies. Whole body of the host covered with fungal mat.

Rhizoids monohyphal with a diameter of $10 - 30 \ \mu$ m, holdfast root- or disk-like, sometimes fused forming a layer (figs. 3–5). – Protoplasts and hyphal bodies filamentous, hyphal-like (figs. 1– 2). – Nuclei in hyphal bodies deeply staining in LPAO with a diameter of $6.7 - 7.0 \ \mu$ m (6 – 8 μ m) (3 collections) (fig. 2). – Conidiophores branched, terminally enlarged with a diameter of $10 - 13 \ \mu$ m (fig. 7). – Primary conidia 22.7 – 25.0 x 8.5 – 15.0 μ m (18 – 29 x 9 – 18 μ m) (10 collections), L/D = 1.60 – 2.38, slightly bent, papilla distinct, nuclei measuring $6.4 - 6.6 \ \mu$ m (5.5 – 8 μ m) (3 collections) (fig. 8). – Secondary conidia resembling the primary ones, 19.5 – 21.8 x 9.0 – 13.0 μ m (16 – 25 x 7 – 15 μ m) (9 collections), L/D = 1.56 – 2.17 (fig. 9), or more rounded with apical point, 15.3 – 18.4 x 11.0 – 13.8 μ m (13 – 21 x 10 – 16 μ m) (4 collections), L/D = 1.33 – 1.41 (fig. 10). – Cystidia emerging from large "mother cells", tapering, diameter at the conidial level 12 – 19 (-24) μ m and at the apex 5 – 10 μ m (fig. 6).

Culture. – Good growth on SDAEY, EYM and EMC. Conidia $32.9-37.9 \ x \ 21.1-22.2 \ \mu m \ (25-55 \ x \ 15-33 \ \mu m)$ (2 collections), L/D = 1.56-1.71.

Distribution. – The fungus is very frequent and widespread. It has been collected from many localities north and south of the Alps as well as in some alpine valleys up to a level of about 2000 m above sea level.

E. neoaphidis was found between April and December. It regularly causes epizootics among aphid populations in field crop (eg. alfalfa, pea, wheat) and is considered the most important aphid pathogenic fungus in Switzerland (KELLER & SUTER, 1980).

This species varies in morphological and in physiological aspects. Conidia from *B. brassicae* for example were distinctly broader $(14.1-15.0 \text{ versus } 10.5-12.3 \mu\text{m})$ and therefore had a distinctly smaller L/D ratio (1.60-1.66 versus 1.91-2.38). Further all attempts to isolate the fungus from *B. brassicae* and *I. asiaticum* failed using the same method to isolate it from other hosts.

 Erynia ovispora (Nowakowski) Nowakowski (1881). – Djenn. III Zjazdu Lek. Przyr. Polsk. Krakow 6: 67. – Pl. 11: figs. 1–9. Bas.: Entomophthora ovispora Nowakowski (1877). – Bot. Zeitg. 35: 220.

Hosts. – Diptera, Psychodidae: unidentified species.

Symptoms. – Dead midges attached to substrate just above the water level, wings spread, whole body covered with white to greyish fungal mat (fig. 1).

Rhizoids monohyphal with a diameter of 13 - 36 (-50) µm, endings rounded, branched, finger- or root-like (figs. 6–7). – Conidiophoresterminally enlarged to a diameter of 10 - 12 µm (fig. 5). – Primary conidia 19.6 - 26.6 x 10.6 - 15.4 µm (17 - 30 x 10 - 19 µm) (7 collections), L/D = 1.59 - 2.26, slightly bent, papilla distinct (fig. 8). – Secondary conidia resembling the primary ones or more rounded with apical point (fig. 9). – Resting spores 30,2 µm (25 -36 µm) (1 collection) (fig. 3). – Cystidia relatively numerous, powerful, slightly tapering, diameter at the level of the conidia 13 - 34 µm and 12 - 24 at the apex (fig. 4).

Culture. – Good growth on SDAEY, EYM, EMC. Primary conidia $28.4 - 30.5 \ge 18.9 - 21.0 \ \mu m \ (24 - 38 \ge 15 - 27 \ \mu m)$ (6 collections), L/D = 1.43 - 1.58.

Distribution. - Rickenbach ZH, Katzensee ZH, Tänikon TG.

E. ovispora is frequent along borders of lakes, ponds and brooks, where the infected midges are usually attached to wet stones and moss. The substrate probably modifies the shape of the endings of the

rhizoids. The species was collected between end of May and beginning of September.

- Erynia rhizospora (THAXTER) REMAUDIÈRE & HENNEBERT (1980). Mycotaxon 11: 302. – Pl. 12: figs. 1–11.
 - Bas.: *Empusa rhizospora* THAXTER (1888). Mem. Boston Soc. Nat. Hist. 4: 183.

Hosts. - Trichoptera, several unidentified species.

Symptoms. – Dead caddis flies attached to substratum just above the water level, wings laterally spread, whole body covered with white-greyish fungal mat (fig. 1).

Rhizoids monohyphal with a diameter of 11 - 35 (-80) μ m. endings rounded, branched, enlarged, sometimes with lateral outgrowths (figs. 8–10). – Nuclei in hyphal bodies and conidiophores deeply stain with LPAO, diameter of nuclei 7.0 (6 - 7.5) μm (1 collection). - Conidiophores branched, terminally enlarged with a diameter of $9 - 12 \mu m$ (fig. 4). – Primary conidia 31.2 - 42.9 x $8.6 - 11.0 \text{ um} (25 - 52 \times 9 - 13 \text{ um})$ (6 collections), L/D = 3.32 - 3.98. bent, largest diameter in the apical half, cytoplasmic content tends to draw back from the apex; papilla distinct, conical (fig. 5). - Secondary conidia similar to primary (fig. 6) 22.5 - 25.7 x 12.6 - 15.1 µm $(18 - 30 \times 11 - 17 \mu m)$ (3 collections), L/D = 1.70 - 1.74 or rounded with apical point (fig. 7) $13.3 - 15.3 \ge 11.3 - 12.8 \ \mu m \ (12 - 17 \ge 10 - 12.8 \ \mu m \ (12 - 12.8 \ \mu m \ (12 - 12.8 \ \mu \$ 15 μ m) (5 collections), L/D = 1.18 - 1.21. - Resting spores 50.8 μ m $(36-61 \text{ }\mu\text{m})$ (1 collection) spherical, light brown with brown episporium, produced on fine stiff, brown mycelium on the outside of the insect (fig. 11). - Cystidia prominent, long tapering, diameter at the level of the conidia $14 - 40 \,\mu\text{m}$ and $10 - 17 \,\mu\text{m}$ at the apex (figs. 2–3).

Culture. – Quick growth on SDAEY, EYM, ECM. Colonies reach a diameter of about 6 cm in 14 days at 20C on SDAEY, forming a compact, tough layer, aerial mycelium like cotton wool, voluminous, white. Primary conidia 37.8 – 43.3 x 10.5 – 13.1 μ m (30 – 58 x 9 – 21 μ m) (6 collections), L/D = 2.99 – 3.66. Elongate secondary conidia 25.0 – 29.5 x 13.1 – 15.2 μ m (21 – 35 x 10 – 16 μ m) (3 collections), L/D = 1.90 – 1.98; rounded secondary conidia 14.6 – 15.0 x 12.0 – 12.7 μ m (12 – 19 x 10 – 16 μ m) (3 collections), L/D = 1.18 – 1.21. Sometimes

Pl. 12. -1-11: *Erynia rhizospora.* -1. Diseased insect with the fungus sporulating (ca. 3 x nat. size). -2-3. Cystidia. -4. Conidiophore. -5. Primary conidia. -6-7. Secondary conidia of the elongate (6) and the rounded type (7). -8. Rhizoids fixed to a stone. -9-10. Rhizoids with different endings. -11. Sporogenous mycelium and resting spores. -2-7, 11: LPCB; 8-10: Ethanol. -Bar in figs. 2, 4 and 7: 50 µm; 2-3, 8-10; 4, 11; 5-7 same magnification.



the brown sporogenous mycelium developed, but resting spore formation was never observed.

Distribution. – Solothurn (Aare) SO, Rickenbach ZH, Hausener Seen ZH, Nussbaumer See TG, Felben TG.

The species is frequent along borders of lakes, ponds, rivers and brooks, causing sometimes epizooties. It was found between beginning of June and mid-September.

- Erynia variabilis (THAXTER) REMAUDIÈRE & HENNEBERT (1980). Mycotaxon 11: 302. – Pl. 13: figs. 1–8.
 - Bas.: *Empusa variabilis* Thaxter (1888). Mem. Boston Soc. Nat. Hist. 4: 183.

Hosts. - Diptera: unidentified very small midges.

Symptoms. – Dead midges attached to stones closely above the water level. Wings spread, body covered with fungal mat.

Rhizoids monohyphal with a diameter of 10 - 45 (-72) µm; ending branched regularly or irregularly enlarged, finger- or rootlike (figs. 4–5). – Hyphal bodies spherical to ellipsoid or elongate, with 10 - 15 (3 – 28) nuclei (3 collections), nuclei deeply staining in LPAO, diameter of nuclei 5.2 - 5.5 µm (4.5 – 6.0 µm) (3 collections, figs. 1–2). – Conidiophores branched, terminally enlarged with a diameter of 8 - 11 µm (fig. 6). – Primary conidia $22.0 - 24.3 \times 8.2 -$ 8.6 µm ($17 - 30 \times 7 - 11$ µm) (3 collections), L/D = 2.7 - 3.0, elongate, pyriform, asymmetrical; largest diameter in apical half; papilla distinct, rounded (figs. 7–8). – Secondary conidia like primary or rounded. – Cystidia long, slender, tapering, diameter at the level of the conidia 10 - 23 (-35) µm and 5 - 7 µm at the apex (fig. 3).

Distribution. - Trasadingen SH.

E. variabilis was found in large quantities on a single occasion on October 24, 1984 along the borders of a brook under a bridge. GUSTAFSON (1965) synonymised this species with *Erynia curvispora*, from which, however, it differs distinctly mainly by the size of the conidia and the shape of the cystidia. In contrast to THAXTER'S (1888) findings the dimensions of the conidia did not vary unusually.

Pl. 13. – 1–8: Erynia variabilis. – 1. Hyphal bodies with nuclei. – 2. Hyphal bodies germinating to conidiophores. – 3. Cystidium. – 4–5. Rhizoids with different types of holdfasts. – 6. Conidiophores. – 7. Formation of primary conidia. – 8. Primary conidia. – All LPAO. – Bar in figs. 1, 4 and 7: 50 µm; 1–3. 6; 4–5; 7–8 same magnification.



- Erynia virescens (Thaxter) Remaudière & Hennebert (1980). Mycotaxon 11: 302. – Pl. 9: figs. 4–9.
 - Bas.: *Empusa virescens* THAXTER (1888). Mem. Boston Soc. Hist. Nat. 4: 178.

Hosts. - Lepidoptera, Noctuidae: unidentified species.

Symptoms. – Dead caterpillars attached to the top of the plants (grass and herbs), body more or less straight, dark-brown to black or, when sporulating, grey (fig. 4).

Rhizoids in spots on the ventral side, monohyphal (fig. 5). – Young conidiophores with 4 – 19 nuclei, diameter of nuclei 5.8 (5 – 7) μ m (1 collection). – Primary conidia 24.7 – 30.9 x 13.3 – 16.2 μ m (22 – 42 x 10 – 18 μ m) (11 collections), L/D = 1.70 – 2.19, usually symmetrical, largest diameter in central portion; papilla slightly rounded (fig. 8). – Secondary conidia like primary 24.4 – 25.3 x 15.6 – 16.3 μ m (22 – 30 x 13 – 19 μ m) (3 collections), L/D = 1.54 – 1.56. – Cystidia few, tapering (fig. 7).

Culture. – Slow growth on EYM and ECM. Colonised EYMmedium stained brown to dark brown, producing resting spores only. Resting spores $33.8 - 39.8 \ \mu m (25 - 58 \ \mu m)$ (2 collections), spherical, sometimes with irregularities, brown to dark brown (fig. 9).

Distribution. – Neunkirch SH, Hallau SH, Oberhallau SH, Siblingen SH, Stammheim ZH, Zürich-Reckenholz ZH.

E. virescens is common but was never found in large numbers. It occurred between mid-April and beginning of October. *Tarichium megaspermum* Сонм (1870) is probably the resting spore state of this species. The resting spores produced in vitro more or less match its description, but infection experiments, to elucidate this suggestion, have not been done.

There are indications that the conidiophores may develop in a similar way as described for *E. ellisiana* (fig. 6).

Discussion

The genus as defined by REMAUDIÈRE & HENNEBERT (1980) and REMAUDIÈRE & KELLER (1980) comprises 42 species: the 17 listed above and the following 25:

- E. americana (Thaxter) Remaudière & Hennebert (1980)
- E. brahminae (Bose & Metha) Remaudière & Hennebert (1980)
- E. creatonoti YEN in HUMBER (1981a)
- E. crustosa (Macleod & Tyrrell) Humber & Ben-ze'ev (1981)

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- E. dacnusae BALAZY (1981)
- E. delphacis (HORI) HUMBER (1981b)
- E. delpiniana (CAVARA) HUMBER (1981b)
- E. echinospora (Thaxter) Remaudière & Hennebert (1980)
- E. erinacea (Ben-ze'ev & Kenneth) Remaudière & Hennebert (1980)
- E. glaeospora (Vuillemin) Remaudière & Hennebert (1980)
- E. gracilis (Thaxter) Remaudière & Hennebert (1980)
- E. henrici (Molliard) Humber & Ben-ze'ev (1981)
- E. ithacenis KRAMER (1981)
- E. kondoensis MILNER in MILNER & al. (1983)
- E. magna (Humber) Remaudière & Keller (1980)
- E. montana (Thaxter) Remaudière & Hennebert (1980)
- E. neopyralidarum BEN-ZE'EV (1982)
- E. nouryi Remaudière & Hennebert (1980)
- E. phalangicida (Lagerheim) Remaudière & Hennebert (1980)
- E. pieris Li & Humber (1984)
- E. plecopteri Descals & Webster (1984)
- E. sepulchralis (Thaxter) Remaudière & Hennebert (1980)
- E. suturalis BEN-ZE'EV (1987)
- E. vomitoriae (Rozsypal) Remaudière & Hennebert (1980)
- E. zabri Rozsypal ex Ben-ze'ev & Kenneth (1982b)

Three further species were listed in this genus: *E. calliphorae* (GIARD) REMAUDIÈRE & HENNEBERT (1980) is known only by its resting spores and belongs therefore to the form genus *Tarichium* (MACLEOD & MULLER-KÖGLER, 1970). It was found in the same host species as *E. vomitoriae* and they could be conspecific. *E. formicae* HUMBER & BALAZY in HUMBER (1981a) and *E. sciarae* (OLIVE) BEN-ZE'EV & KENNETH (1982b) are considered in this paper as synonyms for *E. myrmecophaga* and *E. dipterigena* respectively. Another species, *Entomophthora terrestris* GRES & KOVAL (1982) eventually also belongs to this genus.

Two species differ distinctly from the others: *E. castrans* and *E. magna* (HUMBER, 1976). They were originally placed in a separate genus, *Strongwellsea* BATKO & WEISER (1965), but REMAUDIÈRE & KELLER (1980) synonymized this genus with the genus *Erynia* because of the similar conidial morphology. A consideration of other factors (pathobiology, unbranched conidiophores, lack of cystidia and rhizoids), however, justifies a separate genus to include these two species.

With the exception of these two species, the genus consists of rather similar species. There are some criteria discussed below which suggest groups of related species but neither a single nor a combination of criteria was found to delimit groups unequivocally.

The early development stages (protoplasts and hyphal bodies). neglected in the past, are considered as important for the taxonomy and systematics of these fungi. But since they occur in the living or freshly dead host they are usually absent in material collected. In E. conica and E. variabilis the hyphal bodies are more or less spherical or ellipsoidal. The same is probably true for E. *ovispora* and E. rhizospora, where empty but collapsed hyphal bodies of similar shape were observed. In contrast to these rounded hyphal bodies, those of E. athaliae, E. blunckii, E. dipterigena and E. gammae were elongate, more or less rod-shaped. E. neoaphidis with its irregular. hyphal-like hyphal bodies represents another group. The size of the nuclei in the hyphal bodies is obviously not correlated with such groups but more with the size of the conidia. The number of nuclei in the hyphal bodies, which is assumed to correspond with the number of conidia produced per hyphal body, is a measure of the intensity of branching of the conidiophores. Mononucleate hyphal bodies were found exceptionally in E. conica and more often in E. ellisiana where consequently simple (unbranched) conidiophores must also occur occasionally. Apart from these exceptions all conidiophores are more or less intensively branched. The diameter before and after the branchings may vary but tends to become more constant in the apical portion (the "shoulders") from which the primary conidia develop.

Cystidia were found in most of the described species. They emerge from more or less voluminous "mother cells", and taper more or less abruptly or continuously toward the apex. Length and basal diameter vary widely, whereas the apical diameter is more constant. These characters are good criteria at the species level and also suggest groups of species within the genus. The "aquatic" species other than *E. variabilis* for example all have powerful cystidia with a broad base, whereas those of *E. athaliae, E. dipterigena, E. neoaphidis, E. variabilis* and others are long and slender.

All described species possess various numbers of rhizoids. An individual rhizoid has a more or less constant diameter throughout its length. The diameters of individual rhizoids emerging from the same host, however, vary widely and are therefore unsuitable for taxonomic and systematic purposes. The endings, however, may be group-specific. *E. blunckii, E. dipterigena* and *E. neoaphidis* e.g. usually produce typical disk-like holdfasts, whereas the closely related *E. athaliae* produces predominantly root-like ones. In many species, including the "aquatic" ones, there is a wide variation of the shapes of the endings. In *E. ovispora* for example the endings may be undifferentiated rounded, enlarged, branched, finger- or root-like. It is assumed that the substrate to which the host insect is attached influences the shape of the holdfasts.

The primary conidia with the exception of *E. conica* and *E. aquatica* are of very similar shape and do not offer characters for any delimitation. Two types of secondary conidia are known in *Erynia*: One type resembling the primary ones and the other is more or less spherical. These two types are striking in species with elongate primary conidia and less distinct in species with a length/diameterratio of up to 2 as e.g. in *E. neoaphidis*. Some aquatic species produce additionally stellate or tetraradiate conidia, which is probably not genetically but habitat-related.

The resting spores, unknown in many species, offer group-specific criteria by their surface (smooth or ornamented), by their colour and by the mode of formation; the latter, however, is often unknown.

In the last decade there have been attempts to subdivide this large genus into "frames" (BEN-ZE'EV & KENNETH, 1982a) or into subgenera (BEN-ZE'EV & KENNETH, 1982b). The recent attempt of Hum-BER (1989) to divide the genus Erynia as defined in this paper (excluding E. castrans and E. magna) into 3 genera (Erynia, Furia and Pandora) again clearly demonstrate the difficulties of such an intention. He used the criteria discussed above, which previously he himself had rejected (HUMBER, 1981b) as unsuitable for the characterisation of genera. In many cases he failed to give distinct definitions or circumscriptions and in some cases they are wrong (e.g. dimensions of nuclei, endings of rhizoids) or speculative (e.g. resting spores "assumed to germinate indirectly by formation of germ mycelium"). Applying these criteria HUMBER (1989) arrived at an arbitrary classification, which may well further confuse an already complex nomenclature. For example E. dipterigena and E. sciarae, which are considered as synonyms in this paper, are placed by Humber (1989) in different genera (Pandora and Furia, respectively). With our present knowledge at the species level such a classification cannot be accepted in the form presented.

2. Eryniopsis

Eryniopsis Humber (1984). - Mycotaxon 21: 258-259.

Hyphal bodies irregular, oligonucleate, nuclei relatively large, deeply staining with LPAO. – Conidiophores usually unbranched. – Primary conidia elongate, cylindrical to fusoid, oligonucleate, unitunicate; papilla distinct, sometimes indistinct. – Secondary conidia produced laterally from primary on relatively short conidiophore, resembling the primary ones or more or less rounded. – Resting spores spherical, smooth hyaline. – Rhizoids present or absent. – Cystidia unknown.

Parasites of insects.

Type species: Eryniopsis lampyridarum (Thaxter) Humber (1984). – Mycotaxon 21: 258–259.

> Bas.: *Empusa (Entomophthora) lampyridarum* THAX-TER (1888). – Mem. Boston Soc. Nat. Hist. 4: 169– 170.

Eryniopsis caroliniana (THAXTER) HUMBER (1984). – Mycotaxon 21: 259. – Pl. 14: figs. 1–11.

Bas.: *Empusa caroliniana* THAXTER (1888). – Mem. Boston Soc. Nat. Hist. 4: 167.

Hosts. - Tipula paludosa MEIG., T. vernalis MEIG.

Symptoms. – Dead adult insects fixed to taller plants (grass and herbs) by their crumbled legs, otherwise identical to living tipulids (fig. 1).

Rhizoids absent. - Hyphal bodies irregular, sometimes arranged in chains, 6 (3-10) nuclei (5 collections) stain in LPAO, measuring on average $5.2 - 5.6 \mu m (4.5 - 6.5 \mu m)$ (3 collections) (figs. 2-3). - Conidiophores usually unbranched, terminally slightly enlarged (figs. 4-5). - Primary conidia 27.7 - 42.6 x 11.9 - 15.2 μm $(22 - 51 \times 10 - 19 \mu m)$ (9 collections), L/D = 1.9 - 2.8, elongate, subcylindrical to fusoid, papilla sometimes indistinct, with 6-7 (4-10) nuclei (3 collections, figs. 6–8). Diameter of nuclei 4.2 – 4.5 µm (3 – 5 μ m) (3 collections) in LPAO and 3.1 – 3.2 in histological sections or FRS stain. - Secondary conidia elongate, slender, resembling primary $36.4 - 42.5 \ge 8.6 - 9.9 \ \mu m (30 - 55 \ge 7 - 13 \ \mu m)$ (7 collections). L/D = 3.7 - 4.5, or ovoid $21.3 - 28.6 \ge 11.9 - 18.4 \ \mu m (18 - 25 \ge 10 - 10.4 \ \mu m)$ 15 μ m) (8 collections), L/D = 1.55 - 1.83 (figs. 9-10); secondary conidia with 2-4 nuclei. - Conidiophores of elongate secondary conidia on average about 35 µm long, those of ovoid secondary conidia on average about 15 µm long. - Resting spores 33.6 - $40.7 \ \mu m \ (24 - 55 \ \mu m) \ (7 \ collections)$, spherical, smooth, hyaline (fig. 11). Young resting spores with 14-64 nuclei; diameter of nuclei 4.8 -5.1 $(4.5 - 6.0) \mu m$ (2 collections). - Cystidia absent.

Culture. – Grows very slowly on EYM, colonies brown with white pustules, colonised medium grey to yellow-brown. On SDA colonies reach a diameter of about 4 cm after 4 weeks at 20C,

Bar in figs. 2, 4 and 7: 50 $\mu m;$ 3–4, 8; 5–7, 9–11 same magnification.

Pl. 14. – 1–11: Eryniopsis caroliniana. – 1. Tipulids killed by the disease (ca. nat. size). – 2–3. Hyphal bodies from living host, partly arranged in chaines. – 4. Histological section through conidiophores (HE). – 5. Formation of primary conidia. – 6–7. Primary conidia of different shapes. – 8. Primary conidia with nuclei (FRS). – 9–10. Secondary conidia of two different types. – 11. Resting spores. – 2–3: LPAO; 5–7, 9–11: LPCB. –


mycelium grey to brownish, colonised medium not pigmented. Quikker growth on SDAEY, length of colonies after 4 weeks at 20°C about 5 cm, colonised medium brownish, mycelium white to light brown, velvet-like to fluffy, primary conidia $30.9 - 38.6 \ge 21.0 - 26.5 \ \mu\text{m}$ (21-47 $\ge 16 - 36 \ \mu\text{m}$) (4 collections), L/D = 1.35 - 1.78.

Distribution. – Zürich-Reckenholz ZH, Kloten ZH, Rickenbach ZH, Hausener Seen ZH, Oberlunkhofen AG, Klettgau SH, Randen SH, Alterswilen TG, Bommer Weiher TG, Lengwiler Weiher TG, Hüttwilen TG, Nussbaumen TG, Oberneunforn TG, Burgrain/Willisau LU.

The fungus is very common and widespread in north-eastern Switzerland, sometimes causing epizootics among *T. vernalis* in June and regularly causing epizootics among *T. paludosa* in August/September with mortalities of about 80 %. The number of nuclei in young resting spores varies widely. A sample contained 14 - 28 (n = 50), another 29 - 64 (n = 21). More details and illustrations are given by KELLER (1978).

Discussion

The genus *Eryniopsis* was established to include species with characters intermediate between *Entomophaga* and *Erynia/Zoophthora*. From the former it is distinguished mainly by the elongate conidia, the smaller number of nuclei/conidium and the formation of secondary conidia; from the latter two genera by the number of nuclei per conidium and the wall structure.

The genus consists of 3 species: *E. caroliniana, E. lampyridarum* and *E. longispora* (Balazy) Humber (1984), discussed by Humber (1984).

3. Neozygites

Neozygites WITLACZIL (1885). – Arch. f. Mikr. Anat. 24: 599–603

Syn.: Thaxterosporium BEN-ZE'EV & KENNETH in BEN-ZE'EV & al. (1987) – Mycotaxon 28: 323.

Neozygites WITLACZIL (1885) sensu BEN-ZE'EV & KENNETH in BEN-ZE'EV & al. (1987) – Mycotaxon 28: 322.

Hyphal bodies regular, spherical or short rod-shaped. – Conidiophores unbranched, with more or less distinct terminal enlargement. Nuclei in hyphal bodies and conidiophores staining distinctly in LPAO. – Primary conidia unitunicate, spherical, pyriform, or in the shape of a Montgolfière (hot air balloon), hyaline or light brown, papilla cylindrical or conical, usually 4 – 8 nuclei. Nuclei not or weakly staining in LPAO. – Secondary conidia like primary, produced on short lateral secondary conidiophores, or capilliconidia amygdaliform produced on long, slender capillary, light brown with terminal drop or haptor. – Resting spores zygospores produced by conjugation of two hyphal bodies, binucleate, spherical or ellipsoidal, episporium brown or black, smooth or ornamented. – Germ conidia corresponding to one of the two types of secondary conidia: spherical, hyaline on short thick germ tube or capilliconidia amygdaliform, brownish on long, slender capillary. – Cystidia absent, rhizoids usually absent.

No growth on standard media.

Pathogens of insects and mites.

Type species: *Neozygites fresenii* (Nowakowski) Remaudière & Keller (1980). – Mycotaxon 11: 331.

Bas.: Empusa fresenii Nowakowski (1883). – Pamietn. Wydz. Akad. Umiej.w. Krakow 8: 171–172.

Key to described species of Neozygites

1.	Pathogens of aphids, hyphal bodies spherical, resting spores		
	ellipsoidal		
1.*	Pathogens of mites or thrips, hyphal bodies elongate, resting		
	spores more or less spherical 4		
	2. Primary conidia $21 - 22 \ge 16 - 17 \mu m$, with more than 5-6		
	nuclei, smoky coloured, in the shape of a Montgolfière. On		
	Lachnidae N. turbinata (5)		
	2.* Primary conidia 4- or 5-nucleate, hyaline, spherical.On		
	Aphididae 3		
3.	Primary conidia $18 - 22 \ge 14 - 18 \ \mu m$, with 4 nuclei, capilliconi-		
	dia 20 – 27 x 11 – 14 μm on capillary shorter than 60 μm \ldots .		
	N. fresenii (2)		
3.*	Primary conidia 24 – 26 x 18 – 19 μ m, with predominantly 5		
	nuclei, capilliconidia $30 - 34 \ge 12 - 15 \ \mu m$ on capillary longe than $100 \ \mu m$ N. microlophii (3)		
	4. Primary conidia $14 \ge 12 \ \mu m$, capilliconidia $17 - 19 \ge 8 - 9 \ \mu m$,		
	resting spores $19 - 23 \ge 18 - 21 \ \mu m$. On mites $\dots \dots \dots$		
	N. floridana (1)		
	4.* Primary conidia 14 – 16 x 12 – 14 μ m, capilliconidia 18 – 20 x		
	$9 - 10 \mu m$, resting spores $17 - 19 \mu m$. On thrips		
	N. parvispora (4)		

- 1. Neozygites floridana (WEISER & MUMA) REMAUDIÈRE & KELLER (1980). -Mycotaxon 11: 331. Pl. 15: figs. 1–11.
 - Bas.: Entomophthora floridana WEISER & MUMA (1966). Florida Ent. 49: 155–157.
 - Syn.: Neozygites adjarica (TSINTSADZE & VARTAPETOV) REMAUDIÈRE & KELLER (1980). Mycotaxon 11: 331.
 - Bas.: Entomophthora adjarica TSINTSADSE & VARTAPETOV (1976). Bull. Acad. Sci. Georgian SSR 83: 465–468.

Host. – Acari, Tetranychidae: Tetranychus urticae Косн.

Symptoms.-Infected mites in their webs or on plant surface, brown when fungus producing conidia or black when resting spores present.

Rhizoids absent when the fungus forms conidia, sometimes present, when resting spores are present; monohyphal, threadlike with unspecialised endings (fig. 1). - Hyphal bodies rod-shaped, rarely with single branching, 3 – 5 nucleate, diameter of nuclei 3.3 – 3.8 μ m (3 – 4.5 μ m) (2 collections) (figs. 2–3). Hyphal bodies measuring $20.6 - 29.5 \ge 5.9 - 8.0 \ \mu m \ (15 - 41 \ge 5 - 10 \ \mu m)$ (6 collections). -Conidiophores unbranched with indistinct terminal enlargement (fig. 4). - Primary conidia 13.9 - 14.1 x 11.9 - 12.4 µm (12 - 16 x $11 - 15 \mu m$) (3 collections), L/D = 1.14 - 1.18, spherical; papilla distinct with a diameter of $5 - 6 \mu m$, blunt; 3 - 5 nucleate (fig. 5). -Secondary conidia like primary formed on short, relatively thick conidiophore $12.4 \ge 10.7 \ \mu m \ (11 - 13 \ge 10 - 12 \ \mu m) \ (1 \ collection), L/D$ = 1.16, or capilliconidia, almond-shaped on long capillary (fig. 6) $17.2 - 18.5 \ge 8.3 - 9.3 \ \mu m \ (15 - 22 \ge 7 - 11 \ \mu m) \ (3 \ collections), L/D =$ 1.99-2.25. - Resting spores 19.3-22.9 x 18.4-21.1 μm (16-25 x $16 - 24 \text{ \mum}$) (6 collections). L/D = 1.05 - 1.11, spherical to slightly ellipsoidal (fig. 8), formed by conjugation of two hyphal bodies (fig. 7). Resting spores germinate with relatively thick, long germ tube to form a spherical primary germ conidium (fig. 9) remaining on germ tube and forming a capilliconidium (figs. 10–11). – Cystidia absent.

Distribution. – Zürich-Reckenholz ZH, Watt ZH, Stammheim ZH, Alterswilen TG.

Pl. 15. – 1–11: Neozygites floridana. – 1. Rhizoids. – 2. Hyphal bodies, one dividing. – 3. Hyphal bodies with 3 and 6 nuclei, those with six dividing. – 4. Formation of primary conidia. – 5. Primary conidia and formation of one secondary conidium of type I. – 6. Formation of capilliconidium. – 7. Zygospore formation. – 8. Mature zygospores. – 9–11. Germination of zygospores. – 9. Formation of rounded primary germ conidium. – 10–11. Formation of secondary, capillary germ conidium, arrows indicate remains of primary germ conidia. – 1–2, 4–8: LPCB; 3, 9–11: LPAO. – Bar in figs. 1, 9 and 11: 50 µm; 2–10 same magnification.



N. floridana is very common in autumn on mites on beans and hops usually causing epizootics. It was collected between mid-September and end of October. A more detailed description is given by KELLER & WUEST (1983). *N. adjarica*, invalidly described (no type designation), is considered identical with *N. floridana*. Thorough investigations on paratype material and fresh material from North Carolina (USA) revealed no differences with material from Switzerland and Czechoslovakia.

N. tetranychi (WEISER) REMAUDIÈRE & KELLER (1980) is very closely related. Examinations of material kindly provided by J. WEISER gave consistent small differences of the average dimensions of primary and secondary conidia and resting spores.

- Neozygites fresenii (Nowakowski) Remaudière & Keller (1980). Mycotaxon 11: 332. – Pl. 16: figs. 1–11.
 - Bas.: Empusa fresenii Nowakowski (1883). Pamietn. Wydz. Akad. Umiej. W. Krakow 8: 171 – 172.

Hosts. – Homoptera, Aphididae: Aphis fabae Scop., A. rumicis L., Brevicoryne brassicae L., Rhopalosiphum padi L.

Symptoms. – Dead aphids fixed to plants with their proboscis and/or legs, greyish brown to brick or dark brown when conidia are formed, black when resting spores are present.

Rhizoids absent. – Protoplasts elongate, often comma-shaped, 4 nucleate (fig. 1), nuclei measuring 4.2 μ m (3.5 – 5.5 μ m) (1 collection), multiplication by binary fission (fig. 2). – Hyphal bodies spherical, 4 nucleate when forming conidia, 8 nucleate when conjugating to form resting spores (figs. 3–5). Sporogenous hyphal bodies measuring 15.1 – 15.5 x 14.1 – 14.8 μ m (14 – 19 x 13 – 17 μ m) (3 collections); nuclei in 8-nucleate hyphal bodies measuring 2.5 – 2.6 μ m (2.5 – 3.5 μ m) (3 collections). – Conidiophores terminally swollen. – Primary conidia 18.2 – 21.5 x 14.5 – 17.8 μ m (16 – 24 x 12 – 21 μ m) (7 collections), L/D = 1.16 – 1.46, spherical; papilla distinct, cylindrical, blunt to slightly rounded; diameter of nuclei 2.4 μ m (2 – 3 μ m) in histological sections and 2.1 μ m (2 – 2.5 μ m) in FRS-stain (1 collection each). – Secondary conidia like primary on short, thick conidiophore or capilliconidia, almond-shaped 19.7 –

^{Pl. 16. -1-11: Neozygites fresenii. - 1. Protoplasts with 4 nuclei each. - 2. Division of protoplasts. - 3. Protoplasts transforming into hyphal bodies. - 4. - 5. Conjugating protoplasts/hyphal bodies. - 6. Formation of zygospores. - 7. Young zygospore with 2 nuclei and adhering hyphal bodies with remaining nuclei. - 8. Mature zygospores. - 9. Zygospore atypically with 4 nuclei. - 10-11. Germinated resting spores with capillary germ conidium. A second germ tube is visible (fig. 11, arrow). - All LPAO. -}

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 $27.2 \ge 11.2 - 13.7 \ \mu m \ (16 - 33 \ge 9 - 17 \ \mu m) \ (7 \ collections), L/D = 1.55 - 2.43, with disk-, drop- or sucker-like haptor at the apex, on slender capillary 24.0 - 34.5 \ \mu m \ (7 - 54 \ \mu m) \ long \ (2 \ collections). - Resting spores 29.7 - 41.1 \ge 1.45 - 2.32 \ \mu m \ (25 - 48 \ge 17 - 24 \ \mu m) \ (9 \ collections), L/D = 1.45 - 2.10 \ ellipsoid, dark brown to black, binucleate, exceptionally 4-nucleate (figs. 7–9); germinate with slender capillary 135 - 188 \ \mu m \ (73 - 220 \ \mu m) \ long \ (2 \ collections n = 33, 24). - G \ erm \ conidium almond-shaped 22.4 - 22.9 \ge 11.9 \ \mu m \ (18 - 25 \ge 10 - 16 \ \mu m) \ (2 \ collections n = 38, 30) \ L/D = 1.89 - 1.92 \ (figs. 10-11). - Cystidia absent.$

Distribution. – Zürich-Reckenholz ZH, Stammheim ZH, Nussbaumen TG, Eschenz TG, Iselisberg TG, Märstetten TG, Hallau SH, Oberhallau SH, Gächlingen SH.

N. fresenii is very common and widespread, epizootics among *Aphis fabae* on *Beta vulgaris* and *A. rumicis* on *Rumex obtusifolius* were observed. It was collected between end of May and mid-October. LPAO distinctly stained the nuclei in the hyphal bodies. In conidiogenous hyphal bodies, 4 nuclei were consistently present. In sporogenous hyphal bodies the number of nuclei varied from 6 - 10, the majority (82 - 94%) containing 8 nuclei, uneven numbers were rare. The nuclei of germ conidia typically remained unstained, but 4 nuclei were observed in a very few.

Neozygites microlophii Keller sp. nov. – Pl. 17, figs. 1–8; Pl. 18, figs. 1–11.

Corpora hyphalia sphaerica vel subsphaerica, (4–) 5 nucleis in statu conidiali, 4–14 nuclei in statu zgosporali. Conidia primaria (21–) 24–26 (-30) x (15–) 17–19 (-22) µm, sphaerica vel pyriformia, papilla truncata praedita. Conidia secundaria primariis similia, (19–) 23–25 (-29) x (12–) 15–16 (-19) µm aut amygdaliformia, (24–) 30-34 (-40) x (10–) 12–15 (-17) µm, hyphae capillares evolutae, 100–210 µm longae. Sporae perdurantes zgosporae (29–) 35-43 (-50) x (17–) 20–23 (-27) µm, binucleatae, ellipsoideae, fuscae vel nigrae. Conidia ex sporis perdurantibus amygdaliformis, (21–) 29 (-36) x (10–) 12 (-16) µm, hyphae capillares evolutae, (110–) 315 (-430) µm longae. Rhizoidea et cystidia absunt. In Microlophio carnoso Buckton (hospite typico) (Homoptera: Aphididae). Helvetia. Holotypus ZT, cotypi K et BPI.

Host. – Homoptera, Aphididae: *Microlophium carnosum* Buckton (type host).

Pl. 17. – 1–8: Neozygites microlophii. – 1. Conidiogenous hyphal bodies with predominantly 5 nuclei. – 2. Germinating hyphal bodies. – 3. Young conidiophores at different stages of development. – 4–5. Primary conidia. – 6. Formation of secondary conidia of type I. – 7. Formation of capilliconidia. – 8. Capilliconidia. – 1–3: LPAO; 4–8: LPCB. – Bar in figs. 1 and 7: 50 µm; 1–6. 8 same magnification.



Symptoms. – Dead aphids fixed to plants with proboscis and/ or legs; greyish-brownish when fungus forms conidia; black when resting spores present.

Rhizoids absent. - Protoplasts elongate, often comma-shaped, multiplication by binary fission. - Hyphal bodies spherical (4-) 5 nucleate when forming conidia, nuclei measuring $3.4 \ \mu m (2.5 -$ 4.0 μ m) (2 collections) (Pl. 17, figs. 1–2); 10 (4 – 14) nucleate when conjugating to form resting spores (Pl. 18, fig. 1), nuclei measuring $2.4 - 2.8 \ \mu m \ (2.0 - 3.0 \ \mu m)$ (4 collections). Conidiogenous hyphal bodies measuring 20.8 - 22.2 x 19.9 - 21.4 μm (18 - 25 x 18 - 24 μm) (2 collections), the more spherical sporogenous hyphal bodies measuring $17.1 - 17.5 \mu m (15 - 18 \mu m)$ (2 collections). – Conidiophores unbranched, terminally swollen with 5 (4 - 6) nuclei measuring 2.9 µm (2.5 - 4.0 µm) (1 collection) (Pl. 17, fig. 3). - Primary conidia 24.1 - 25.5 x 17.6 - 18.8 μm (21 - 30 x 15 - 22 μm) (6 collections), L/D = 1.33 - 1.38, (4-) 5 nucleate, spherical to pyriform; papilla distinct, truncate (Pl. 17, figs. 4–5). – Secondary conidia like primary on short, thick conidiophore (Pl. 17, figs. 6), 23.8 – 24.4 x $15.3 - 15.5 \,\mu\text{m} (19 - 29 \,\text{x} \, 12 - 19 \,\mu\text{m}) (2 \text{ collections}), L/D = 1.56 - 1.57,$ or almond-shaped $30.1 - 33.6 \ge 12.2 - 14.4 \ \mu m (24 - 40 \ge 10 - 17 \ \mu m)$ (6 collections), L/D = 2.28 - 2.60, with apical disk- or sucker-like haptor, on slender capillary $156 - 168 \mu m (104 - 210 \mu m) \log (3)$ collections) (Pl.17, figs. 7-8). - Resting spores 35.6 - 42.8 x 20.2 -23.3 µm (29 - 50 x 17 - 27 µm) (6 collections), L/D = 1.68 - 1.99, ellipsoidal, dark brown to black, binucleate (Pl. 18, figs. 7-9); nuclei measuring 3.0 μ m (2.5 – 3.5 μ m) (2 collections). Resting spores germinate to form a capillary germ tube with a length of 315(110 - 430) um (1 collection) (Pl. 18, figs. 10-11). - Germ conidia 29.4 x 12.2 µm $(21 - 36 \times 10 - 16 \mu m)$ (1 collection), L/D = 2.40, almond-shaped, similar to capilliconidia produced by primary conidia, with apical disk-like haptor; germinate laterally again with capillary germ tube 152 (36 - 260) um long (1 collection). Secondary germ conidia 21.5 x9.6 μ m (13 – 27 x 6 – 12 μ m) (1 collection), L/D = 2.25, similar to primary germ conidia; germinate again with capillary germ tube 65 $(34 - 110 \,\mu\text{m}) \log (1 \text{ collection}, n = 25)$. Tertiary germ conidia 17.2 x

^{Pl. 18. - 1-11: Neozygites microlophii. - 1-7. Zygospore formation. - 1. Different stages of the conjugation. - 2. Nuclei entering young zygospore. - 3-4. Different stages in the development of the young zygospore. - 5-6. Young zygospores with hyphal bodies adhering and containing remaining nuclei. - 7. Fully grown zygospore; nuclei in adhering hyphal bodies absent. - 8. Zygospores with two nuclei. - 9. Zygospores. - 10. Zygospore with capillary germ conidium (a). - 11. Zygospore with capillary primary (a), secondary (b) and tertiary (c) germ conidia. - All LPAO. - Bar in figs. 1 and 11: 50 µm; 1-9; 10-11 same magnification.}

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 $7.1 \ \mu m (13 - 22 \ge 6 - 8 \ \mu m)$ (1 collection, n = 25), L/D = 2.44, similar to previous germ conidia. A few quaternary germ conidia formed in the same way were observed. No spherical germ conidia resembling the primary conidia occurred. Resting spores as well as germ conidia may produce more than 1 germ tube, but normally only 1 conidium is produced. In a single case two germ conidia per resting spore were observed. – Cystidia absent.

Distribution. – Neunkirch SH (type locality), Hallau SH, Oberhallau SH, Hüttwilen TG, Mauren TG, Rottenschwil AG, Watt ZH.

N. microlophii is common and regularly causes epizootics among dense populations of *M. carnosum*. It was found between mid-June and mid-July. The species was attributed to *N. fresenii* (KELLER & WUEST, 1983), but differs in the size of the hyphal bodies, the primary conidia, the capilliconidia and the resting spores, and by the number of nuclei. 94% of the conidiogenous hyphal bodies were 5-nucleate (2 collections), as well as 70 % of the conidiophores and 86 % of the primary conidia (1 collections each). The sporogenous hyphal bodies contained 4 - 14 nuclei, 64 - 86 % were 10-nucleate (4 collections). 5 nuclei per conidiogenous hyphal body and conidium and 10 per sporogenous hyphal body can be considered typical for *N. microlophii* in contrast to 4 and 8 respectively for *N. fresenii*.

- Neozygites parvispora (Macleod & Karl in Macleod & al., 1976). Remaudière & Keller (1980). – Mycotaxon 11:332. – Pl. 19: figs. 1– 11.
 - Bas.: Entomophthora parvispora MacLeod & Carl in MacLeod & al. (1976).- Entomophaga 21: 307.

Host. – Thysanoptera, Thripidae: *Thrips tabaci* and unidentified species.

Symptoms. – Dead insects attached to plants; light brown when fungus produces conidia, black when resting spores present.

Pl. 19. – 1–11: Neozygites parvispora. – 1. Formation of primary conidia. – 2. Primary conidia and 2 detached capilliconidia. – 3. Mature zygospores. – 4. Hyphal bodies at different stages of development; a: with 4 interphase nuclei; b: nuclear division beginning; c: with 8 nuclei, 4 moving to each polar region; d: with 8 nuclei, 4 in each polar position; e: formation of the cell wall (arrow). – 5. Conjugation of hyphal bodies inducing nuclear division. – 6–8. Zygospore formation: 6. One sickle-like nucleus in each hyphal body at the conjugation site. – 7–8. Entering of the nuclei in adhering hyphal bodies clump together (9), collapse (10) or hypertrophy (11). – 1–3: LPCB; 4–11: LPAO. – Bar in fig. 1: 50 μ m, that in fig. 4 10 μ m; 1–3; 4–11 same magnification.

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Rhizoids absent. – Hyphal bodies rod-shaped (figs. 4–5); those producing conidia measuring $25.7 \ge 6.1 - 7.7 = 100 = 100$ mm (16 - 33 $\ge 5 - 100$ mm (16 - 33 (16 - 100)) $9 \,\mu\text{m}$) (2 collections), L/D = 3.3 - 4.2, multiplication by binary fission (fig. 4), 4-nucleate, nuclei measuring $3.1 - 3.2 \mu m (2 - 4 \mu m) (2$ collections); those forming resting spores $14.4 - 17.0 \ge 6.1 - 8.5 \ \mu m$ $(11-23 \text{ x} 5-10 \mu \text{m})$ (4 collections) L/D = 1.7 - 2.7, 8-nucleate, nuclei measuring $2.3 - 2.8 \ \mu m (2 - 3.5 \ \mu m)$ (3 collections). - Primary conidia $14.5 - 16.0 \ge 12.2 - 13.9 \ \mu m \ (12 - 18 \ge 11 - 16 \ \mu m) \ (3$ collections) L/D = 1.15 - 1.21, spherical, papilla truncate (fig. 2). -Secondary conidia like primary 16.0 x 13.9 µm (15 - 18 x 13 -16 μ m) (1 collection, n = 12) or capilliconidia 17.6 - 19.7 x 9.1 -9.7 μ m (16 – 22 x 7 – 11 μ m) (3 collections), L/D = 1.82 – 2.05, length of capillary 41.4 µm (28 - 63 µm) (1 collection). - Resting spores $16.7 - 18.8 \ \mu m \ (15 - 21 \ \mu m) \ (3 \ collections), zygospores, developing$ after latero-terminal conjugation of two hyphal bodies (figs. 5-11), dark brown to black (fig. 3), ornamented. - Cystidia absent.

Distribution. – Zürich-Reckenholz ZH, Watt ZH, Tägerwilen TG, Tänikon TG, Hüttwilen TG.

N. parvispora was discovered by CARL (1975) at different localities in western Switzerland. We found it between end of August and end of October on *T. tabaci* and on an unidentified species living between the husks of maize ears.

The species has two types of hyphal bodies distinguishable by their length and the L/D-ratio. Those forming conidia and resting spores contained consistently 4 and 8 nuclei respectively. The doubling of the nuclei in the hyphal bodies forming resting spores seems to be induced by the initiation of the conjugation. Some dead thrips contain hyaline resting spores (KELLER & WUEST, 1983).

- Neozygites turbinata (KENNETH) REMAUDIÈRE & KELLER (1980). Mycotaxon 11: 332. – Pl. 20: figs. 1–12.
 - Bas.: Entomophthora turbinata KENNETH (1977). Mycotaxon 6: 388.

Host. – Homoptera, Lachnidae: *Tuberolachnus salignus* GMELIN.

^{Pl. 20. - 1-12: Neozygites turbinata. - 1. Germinating hyphal bodies with nuclei. 2-5. Different stages in the formation of zygospores. - 6. Mature zygospore. 7. Formation of primary conidium. - 8. Primary conidia, some germinating through the papilla. - 9-10. Resting spores with capillary germ conidium. - 11-12. Capillary germ conidia with apical haptor. - All LPAO. - Bar in fig. 1: 50 µm, 1-12 same magnification.}

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Symptoms. - Dead aphids fixed on underside of branches of Salix sp. usually only with their proboscis, black; infected aphids remain in the colonies.

Rhizoids absent. - Protoplasts subspherical or elongate to comma- or drop-shaped with 8(5-11) nuclei (1 collection) (fig. 1). – Hyphal bodies spherical to slightly ellipsoidal or ovoid when forming conidia, $21.1 \ge 17.4 \ \mu m (17 - 24 \ge 15 - 22 \ \mu m)$ (1 collection), L/D = 1.21, containing 8 (4 - 11) nuclei with a diameter of 3.5 μ m $(3.5 - 4 \mu m)$ (1 collection); spherical when resting spores are formed, $17.4 - 17.8 \,\mu\text{m} (13 - 22 \,\mu\text{m}) (3 \text{ collections}) \text{ with } 9 - 10 \,(6 - 16) \text{ nuclei} (3 \,\mu\text{m})$ collections) with a diameter of $3.2 - 3.5 \mu m (3 - 5 \mu m)$ (3 collections) (figs. 2-5). - Primary conidia 21.1 - 22.3 x 16.1 - 17.1 μm (18 - $27 \times 13 - 21 \mu m$) (3 collections), L/D = 1.29 - 1.35, pyriform to obovoid, smoky except papilla; papilla narrow, rounded (fig. 8). -Resting spores $32.0 - 34.6 \ge 20.7 - 22.4 \ \mu m (27 - 44 \ge 18 - 24 \ \mu m)$ (6) collections), L/D = 1.51 - 1.61, ellipsoidal, brown to black, smooth (fig. 6), germinate with slender capillary 51.5 µm (36 - 75µm) long (1 collection, n = 36). – Germ conidia 31.7 x 9.4 µm (22 – 40 x 7 – 12 μ m) (1 collection, n = 23), almond- to banana-shaped (figs. 9–12).

Distribution. – Stammheim ZH, Zürich-Reckenholz ZH, Watt ZH.

N. turbinata was found between end of August and beginning of November, regularly causing epizootics in dense host populations.

The conidia of the Swiss material were slightly larger than those described by KENNETH (1977) whereas the resting spores matched the original description. No secondary conidia were observed. Many primary conidia germinated through the papilla to form an appressorium-like structure though penetration of the host cuticle was not confirmed.

Discussion

The nuclei and their mitotic behaviour in species of this genus differ from the other Entomphthorales. Accordingly BEN-ZE'EV & al. (1987) created the new family Neozygitaceae BEN-ZE'EV & KENNETH to include this genus. It comprises a relatively homogenous group of fungi. *N. turbinata*, however, differs in the shape of the primary conidia and the larger number of nuclei/conidium; further no secondary conidia have been observed. For these reasons BEN-ZE'EV & al. (1987) created a separate genus *Thaxterosporium* for this species. However, this separation now appears doubtful in the light of the recent findings given above (description of *N. microlophii* and addi-

tional data on *N. turbinata*) and can therefore not be adopted. The fact that secondary conidia have not been observed does not necessarily mean that they do not occur. Since we now know that the germ conidium of *N. turbinata* is a capilliconidium as in *N. fresenii* and *N. microlophii* we may assume that capillary secondary conidia also exist. Further, the most important character for erecting a separate genus for *N. turbinata* was the number of nuclei/conidium. Before *N. microlophii* was described, all known species contained 4 nuclei/conidium in contrast to about 8 in *N. turbinata*. *N. microlophii* may be considered as a species intermediate between the 4-nucleate group (particularly *N. fresenii*) and *N. turbinata* since its conidia predominantly contain 5 nuclei and the hyphal bodies from which the resting spores develop contain the same number of nuclei as those in *N. turbinata*.

The taxa described here can be separated into two groups: one comprising the species with rod-shaped hyphal bodies, spherical resting spores with ornamented episporium and, as far as known, spherical primary germ conidia. The other group has spherical hyphal bodies, ellipsoidal resting spores with a smooth surface and capillary germ conidia. A species not found in Switzerland, *N. fumosa*, however, does not fit into either group (REES, 1932).

The genus includes 9 species, the 5 described above and *N. acaridis* (MILNER, 1985), *N. fumosa* (SPEARE, 1922), *N. lageniformis* (THAXTER, 1888), and *N. tetranychi* (WEISER, 1968). An undescribed taxon attacking mites with predominantly 3-nucleate hyphal bodies has been investigated recently by BUTT & HEATH (1988) and BUTT & HUMBER (1989). This may be identical with or is at least closely related to *N. floridana*.

4. Zoophthora

Zoophthora (BATKO) REMAUDIÈRE & HENNEBERT (1980) emend. – Mycotaxon 11: 301.

Bas.: Zoophthora Ватко (1964а). – Bull. Acad. Polon. Sci. Cl. II. Sér. Sci. biol. 12: 323–324.

Hyphal bodies rounded, irregular or hyphae-like. – Conidiophores branched with terminal enlargement. – Nuclei in hyphal bodies, conidiophores and conidia stain distinctly in LPAO. – Primary conidia bitunicate, elongate, cylindrical to slightly fusiform; papilla conical, pointed or sometimes rounded, separated from the conidial body by a raised collar. – Secondary conidia similar to primary, formed on short, thick conidiophore, or falciform to banana-like formed on long, slender capillary. – Resting spores spherical, hyaline, brown or black, smooth or ornamented. Rhizoids monohyphal or pseudorhizomorph, with or without special holdfast, rarely absent. - Cystidia rare or absent.

Most species grow on standard media. Parasites of insects.

Type species: Zoophthora radicans (Brefeld) Ватко (1964a). – l.c. Bas.: Empusa radicans Brefeld (1870). – Bot. Zeitg. 28: 161–166, 177–186.

Key to described species of Zoophthora

1.	Prim	ary conidia smaller than $23 \ge 9 \ \mu m$ 2	
1.*	Prim	ary conidia larger than 23 x 9 μ m	
	2.	Primary conidia $17 - 21 \ge 6 - 7.5 \ \mu m$; capilliconidia $22 - 27 \ge 7$	
		$3.5 - 4.5 \mu m$, ratio length/diameter $5.2 - 6.9$, on Diptera	
		Z. lanceolata (4)	
	2.*	Primary conidia $15-23 \ge 6-8.5 \ \mu m$; capilliconidia $17-22 \ge 3$	
		$4.5 - 6 \ \mu$ m, ratio L/D $3.2 - 4.2$, on insects of several orders	
		Z. radicans (6)	
	2.**	Primary conidia $22 - 26 \ge 8 - 9 \ \mu m$; capilliconidia $26 - 30 \ge 6$	
		$-$ 6.5 $\mu m,$ ratio length/diameter 4.1 $-$ 5.0, on Heteroptera,	
		Miridae Z. viridis (7)	
3.	On a	phids	
3.*	' On other insects		
	4.	Primary conidia 25 – 30 x 10 – 13 μ m, resting spores 34 –	
		47 μ m with loose dark episporium Z. aphidis (1)	
	4.*	Primary conidia $33 - 38 \ge 7 - 9 \ \mu m \dots Z$. phalloides (5)	
5.	On (Coleoptera 6	
5.*	On I	Heteroptera Miridae, primary conidia 22 – 26 x 8 – 9 μm	
		Z. viridis (7)	
	6.	Primary conidia $31-32 \ x \ 10 \ \mu\text{m},$ resting spores $41-45 \ \mu\text{m}$	
		with thick brown episporium, on Cantharidae	
		$\ldots Z. \ crassitunicata \ (2)$	
	6.*	Primary conidia 27 – 32 x 9 – 11 μ m, resting spores 31 –	
		$38 \ \mu m$, hyaline, without distinct episporium, on Elateridae	
		Agriotes Z. elateridiphaga (3)	

Pl. 21. – 1–12: Zoophthora aphidis. – 1. Large numbers of dead aphids in the bud axils of Cornus sanginea. – 2. R. padi containing resting spores with and without rhizoids (ca. 15 x nat size). – 3. Hyphal bodies with nuclei. – 4. Rhizoid emerging from the foot tip. – 5. Monohyphal rhizoids. – 6. Conidiophore on alate aphid. – 7. Conidiophores on sexuales segregating into mononucleate fragments. – 8–9. Primary conidia. – 10. Capilliconidia. – 11. Formation of resting spores with nuclei visible. – 12. Mature resting spores. – 3–5, 7, 11: LPAO, ; 6, 8–10, 12: LPCB. – Bar in figs. 5, 6 and 10: 50 μm; 4–5; 6, 11; 3, 7–10, 12 same magnification.

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- Zoophthora aphidis (HOFFMANN in FRESENIUS) BATKO (1964b). Bull. Acad. Polon. Sci., Sér. Sci. Biol. 12: 405. – Pl.21: figs. 1–12, Pl.22: figs. 1–8.
 - Bas.: Entomophthora aphidis HOFFMANN in FRESENIUS (1858). Abhandl. Senckenb. naturforsch. Ges. 2.: 201–210.

Hosts. – Homoptera, Thelaxidae, Aphididae: Anoecia corni (F.), Rhopalosiphum padi L.

Symptoms. – Dead aphids, larvae and adults, attached to plant, brown when fungus sporulating or black when resting spores are present. Sporulation in apterous aphids limited to dorsal region often restricted to one or several small areas.

Rhizoids monohyphal, with a diameter of $7 - 12 \mu m$ often in parallel threads, endings unspecialised or enlarged (Pl.21: figs. 2,5), rhizoids on legs branched (Pl.21: fig. 4). - Hyphal bodies hyphaelike or irregularly rounded (Pl.21: fig. 3); the rounded ones with 7 (2 – 10) nuclei (1 collection), nuclei measuring $4.6 - 5.5 \mu m (4 - 6.5 \mu m) (4$ collections). - Conidiophores branched, tending to segregate into mononuclear fractions (Pl.21: figs. 6-7). - Primary conidia 24.9 - $30.3 \ge 9.9 - 13.3 \ \mu m \ (21 - 38 \ge 9 - 17 \ \mu m) \ (14 \ collections), \ L/D = 1.99 - 1.99 - 1.99 \ L/D = 1.99 \ L/D =$ 2.72, elongate, slightly fusiform, apex rounded or conically tapering, papilla distinct, conical or rounded, sometimes pointed (Pl.21: figs. 8-9); diameter of nuclei $4.7 - 5.0 \ \mu m (3.5 - 7 \ \mu m)$ (3 collections). -Secondary conidia similar to primary or capilliconidia 21.0 - $27.3 \times 8.5 - 11.3 \mu m (18 - 34 \times 7 - 13 \mu m)$ (13 collections), L/D = $2.22 - 34 \times 10^{-10}$ 3.17, asymmetrically fusoid to falciform (Pl.21: fig. 10); capillary $29.8 - 35.7 \mu m (15 - 82 \mu m) long (3 collections). - Resting spores$ $34.8 - 46.6 \,\mu\text{m}$ (29 - 55 μm) (14 collections). Rough, black episporium, separates easily from hvaline, smooth spore (Pl.21: fig. 12). Spores develop from filamentous hyphal bodies or mycelium (Pl.21: fig. 11). Young resting spores with 14 - 17(7 - 25) nuclei (4 collections), nuclei measuring $6.3 - 7.0 \ge 5.0 - 5.3 \ \mu m \ (5 - 8.5 \ge 3.5 - 6.5 \ \mu m)$ (4 collections). After storage in the dead aphids on the twigs for 1 year at 1C a few resting spores germinated. – Single unbranched germ tube, (Pl.22: fig. 1–2), 11 - 15 (-18) µm thick and 145 - 850 µm long, subdivided by cell walls, with lateral or terminal elongate "buds" Since these "buds" resemble primary conidia, but none was observed to be projected, they are named "sessile germ conidia" (Pl.22: figs. 3, 4, 8). - Capillary germ conidia 24.7 x 11.6 um [7 - 31 x 9 - 13 (-17) um] (1 collection, n = 17), similar to capilliconidia, develop from the sessile germ conidia or directly from the germ tube (Pl.22: figs. 3-7). Length of capillary 67 $(24 - 134) \mu m$ (1 collection, n = 17). A maximum of 3 capillary germ conidia per resting spore was observed (Pl.22: fig. 6). From the primary capillary germ conidia secondary and tertiary ones can develop. – Cystidia absent.

Culture. – Slow growth on SDAEY, EYM and ECM. Primary conidia 32.3 – 38.2 x 11.7 – 13.4 μm (29 – 52 x 10 – 17 μm) (6 collections), L/D = 2.46 – 3.06.

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

Z. aphidis was found between end of September and end of October in populations of alate and sexuales of the two aphid species on their winter host plant. The fungus sometimes caused epizootics in populations of A. corni and high mortalities were also observed among R. padi (Keller, 1987b). Aphids with sporulating fungus are fixed by rhizoids to the underside of leaves. Aphids containing resting spores are mainly found around the buds in the leaf shoulders (Pl. 21, fig. 1), sometimes also along the main nerves of the leaves; rhizoids may be absent (Pl. 21, fig. 2).

 Zoophthora crassitunicata Keller (1980). – Sydowia 33: 170. – Pl. 22: figs. 9–11.

Host. - Coleoptera, Cantharidae: probably Malthodes sp.

Symptoms. – Dead adult insects attached to underside of leaves of *Aegopodium podagraria* L. by rhizoids, wings closed; white mycelial bands along intersegmental membranes and pleura, or no obvious signs of the disease when resting spores are formed.

Rhizoids pseudorhizomorph. – Conidiophores oligonucleate, sparingly branched. – Primary conidia $31.4 - 32.1 \ge 9.8 \ \mu m$ $(25 - 36 \ge 8.5 - 12 \ \mu m)$ (2 collections), L/D = 3.20 - 3.28, subcylindrical to slightly fusiform; papilla distinct, conical (fig. 9); nuclei $8 \ge 8 = 12 \ \mu m$. – Capilliconidia $33 - 39 \ge 8 - 9 \ \mu m$ (n = 4), fusiform-curved to banana-shaped (fig. 10). – Resting spores $41.2 - 44.7 \ \mu m$ (35 – $56 \ \mu m$) (6 collections), spherical, double walled (fig. 11); inner wall hyaline, episporium about as thick as inner spore wall, densely and regularly covered with minute knobs; predominantly binucleate, but up to 8 nuclei observed.

Distribution. - Rickenbach ZH.

Z. crassitunicata seems to be rare. It was found at the beginning of June in one year only. In the original description, the conidio-phores were described as appearing unbranched in histological sections. This impression can be confirmed after reexamining material

prepared in LPCB. Branching was indeed rare, but since young conidiophores contained several nuclei, branching must occur. More data and illustrations are given by KELLER (1980).

- Zoophthora elateridiphaga (TURIAN) BEN-ZE'EV & KENNETH (1980).
 Entomophaga 25: 181. Pl.23: figs. 1–11.
 - Bas.: Entomophthora elateridiphaga Turian (1978). Mitt. Schweiz. Ent. Ges. 51: 398.

Hosts. – Coleoptera, Elateridae: Agriotes sputator L., A. lineatus L.

Symptoms. – Dead click beetles fixed to the top of plants (herbs and grass), head downward (fig. 1). Wings closed or spread revealing the white mycelial bands along intersegmental membranes and pleura.

Rhizoids pseudorhizomorph on ventral side of thorax between the legs, holdfasts disk-like, or unspecialised and sometimes uniting to form a layer. - Hyphal bodies elongate, rounded with 9-12 (5-22) nuclei (4 collections) (fig. 2); nuclei measuring 5.1 - 5.7 (5 -7.5) µm (4 collections). Conidiophores branched, terminally slightly enlarged (fig. 3). - Primary conidia 27.5 - 31.6 x 8.8 -11.4 μ m (24 - 36 x 7 - 13 μ m) (10 collections), L/D = 2.51 - 3.52, cylindrical; papilla distinct, conical (fig. 4), nuclei with a diamter of 5.2 – 5.7 (4.5 – 7) μm (3 collections). – Secondary conidia similar to primary (fig. 7) $25.0 - 25.7 \ge 8.6 - 9.9 \ \mu m (21 - 30 \ge 7 - 12 \ \mu m)$ (2 collections), L/D = 2.50 - 2.99, or capilliconidia $31.4 - 35.5 \ge 6.7 - 2.99$ $7.5 \,\mu\text{m} (27 - 42 \,\mathrm{x} \,6 - 9 \,\mu\text{m}) (10 \,\mathrm{collections}), L/D = 4.53 - 4.86$, fusiform to banana-like (figs. 5–6); length of capillary 86 – 90 µm (67 – 109 µm) (3 collections). – Resting spores $31.2 - 37.7 \ \mu m \ (25 - 46 \ \mu m)$ (10 collections), spherical, hyaline, smooth (fig. 11); azygospores (fig. 8) or zvgospores (fig. 9), young resting spores with 18 - 21 (14 - 29)

Pl. 22. – 1–8: Zoophthora aphidis. 1–2. Resting spores germinated to form a single germ tube and single capillary germ conidium. – 3. Terminal portion of fig. 2 showing capillary germ conidium. – 4. Terminal portion of germ tube, and terminal sessile germ conidium. – 4. Terminal portion of germ tube, and two terminal sessile germ conidiu, one with capillary germ tube. – 5. Capillary germ conidium emerging terminally. – 6. Germ tube with 3 capillary germ conidia, two of them being detached. – 7. Terminal portion of germ tube with two capillary germ conidia and lateral sessile germ conidium. – 8. Germ tube with basal lateral sessile germ conidium. – 11. Resting spores with nuclei. – All LPCB. – 12–15: Zoophthora lanceolata. – 12. Primary conidia. – 13. Capilliconidium. – 14. Detached capilliconidia. – 15. Resting spores. – All

LPCB. – Bar in figs. 1, 3 and 13: 50 um; 1–2; 3–8; 9–15 same magnification.

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nuclei (3 collections) (fig. 10), nuclei measuring $4.9 - 5.0 (5 - 5.5) \mu m$ (2 collections), fully developed but broken resting spores contained 10 (6 - 14) nuclei (1 collections). – Cystidia absent.

Culture. – Slow growth on SDA, good growth on SDAEY, EYM, ECM. Diameter of colony after 15 days at 20C on SDAEY 20 – 50 mm, on EYM 35 – 60 mm. Aerial mycelium on SDAEY white to greyish-greenish, dense, homogenous, velvet-like; colonised medium slightly stained with greenish bands at the growth zones. Aerial mycelium on EYM white to dirty green, colonised medium greenish to brownish with weakly or intensively stained bands at the growth zone. Primary conidia 25.4 – 35.4 x 10.3 – 13.3 µm (21 – 41 x 9 – 18 µm) (16 collections), L/D = 2.12 – 3.16. Capilliconidia 30.8 – 37.9 x 7.0 – 7.6 µm (25 – 48 x 5 – 10 µm) (6 collections), L/D = 4.34 – 5.12. Resting spores 31.5 – 38.9 µm (19 – 48 µm) (13 collections).

Distribution. – Hallau SH, Oberhallau SH, Siblingen SH, Uesslingen TG, Oensingen SO, Romanel s. Lausanne VD.

The fungus is common on *A. sputator*, regularly causing extensive epizootics between end of April and mid-June (Keller, 1976; S. Keller, in prep.). In the area surveyed, it was found only occasionally on *A. lineatus*. It was never found on other Elateridae or on other insects.

Recently BEN-ZE'EV (1986a) synonymized this taxon with Entomophthora anglica PETCH placing it in the genus Erunia. This synonymisation, however, appears doubtful. PETCH (1944) described the primary conidia of E. anglica as "oval, narrow oval or subfusoid, sometimes slightly bent, with a broad, truncate papilla, $22 - 27 \times 11 - 27 \times 11 = 100$ 13 μm", and the secondary conidia "... of the same shape but shorter, $18 - 21 \ge 10 - 11$ µm" While the description of the shape of the conidia may be true for both species, the dimensions of both the primary and secondary conidia and their L/D-ratio differ distinctly. Further the primary conidia of Z. elateridiphaga never have truncate papillae but conical, sometimes slightly rounded and often pointed ones, and the rhizoids were never produced from the sides of the host. The resting spores of Z. elateridiphaga lack the multiple-layered walls as described for *E. anglica*. It is also noteworthy that neither PETCH (1944) nor BEN-ZE'EV (1986a), when reexamining the original material, found capilliconidia although this is the type of secondary

Pl. 23. – 1–11: Zoophthora elateridiphaga. – 1. Agriotes sputator killed by the disease (ca. 8 x nat. size). – 2. Hyphal bodies with nuclei. – 3. Conidiophore. – 4. Primary conidia. – 5. Formation of capilliconidium. – 6. Capilliconidia. – 7. Secondary conidia of type I. – 8. Resting spore formation (azygospore ?). – 9. Zygospore formation. – 10. Young resting spores with nuclei. – 11. Mature resting spores. – 2, 3, 8–10: LPAO; 4–7, 11: LPCB. – Bar in figs. 2 and 4: 50 µm; 2, 3, 10; 4–9, 11 same magnification.

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conidia produced much more abundantly than the secondary conidia resembling the primary ones. For these reasons E. anglica is considered here as distinct.

On the other hand the fungus described by GIARD (1888) as *Entomophthora carpentieri* could be indentical to *Z. elateridiphaga*. Although in GIARD's description no dimensions are given some features were described in detail, especially the rhizoids and their points of emergence from the insect. These correspond to the findings on *Z. elateridiphaga*. TURIAN (1957) observed the same symptoms on the same host and considered the fungus identical with *E. carpentieri*. However, he described the conidia as spherical with a diameter of 32 (29 – 38) μ m and mononucleate; spherical conidia of this type are unknown in this group of fungi.

I examined material identified by TURIAN (1957) as *E. carpentieri*. It consisted of spherical, hyaline resting spores measuring $30.9 (25 - 39) \mu m$. It is striking that these measurements closely match those given by TURIAN for the conidia and it appears likely that Turian took young resting spores for conidia (although the resting spores are not mononucleate).

The sizes of TURIAN'S "conidia" and of the resting spores of *E. carpentieri* correspond to those for the resting spores of *Z. elateridiphaga*. There are therefore good reasons to suspect that *E. carpentieri* is identical with *Z. elateridiphaga*. This conclusion is further supported by the fact that TURIAN subsequently found a fungus discribed as *Z. elateridiphaga* near the site where he had found *E. carpentieri* (TURIAN, 1957; 1978). Because of the lack of type material of *E. carpentieri*, however, the suspected identity of the two fungi can not be confirmed.

 Zoophthora lanceolata KELLER (1980). – Sydowia 33: 167. – Pl.22: fig s. 12–15.

Hosts. – Diptera, unidentified small species.

Symptoms. – Infected insects attached to underside of leaves by rhizoids, partially covered with white to greyish mycelium.

Rhizoids monohyphal, branched or unbranched, endings finger- or root-like or pseudorhizomorph with enlarged sucker-like holdfast. – Hyphal bodies hyphae-like, short, branched or unbranched, multinucleate. – Conidiophores branched. – Primary conidia $17.1 - 20.6 \ge 6.0 - 7.4 \ \mum$ ($15 - 24 \ge 5 - 9 \ \mum$) (9 collections), L/D = 2.44 - 3.38, cylindrical to subcylindrical, oblong ovoid to ellipsoid, symmetrical, largest diameter in apical half; papilla distinct, conical to rounded (fig. 12). – Secondary conidia similar to primary or capilliconidia $22.4 - 26.3 \ge 3.8 - 4.3 \ \mum$ (18 - 30 x 4 – 6 μ m) (5 collections) L/D = 5.28 – 6.90, lancet shaped, slender, symmetrical or slightly curved (fig. 13–14); capillary 53 (40 – 67 μ m) long (1 collection, n = 32). – Resting spores 24.0 (19 – 29) μ m (1 collection), spherical hyaline, smooth (fig. 15). – Cystidia not observed.

Culture. – Good growth on SDA, SDAEY and EYM. Diameter of colonies on SDAEY after 16 days at 20C 70 – 80 mm. Primary conidia $20.2 - 22.4 \ge 7.0 - 8.1 \ \mu m (17 - 28 \ge 6 - 10 \ \mu m)$ (2 collections), L/D = 2.77 - 2.89. Capilliconidia $29.6 - 31.8 \ge 4.4 - 4.8 \ \mu m (23 - 40 \ge 3.5 - 6 \ \mu m)$ (2 collections), L/D = 6.63 - 6.73.

Distribution. - Rickenbach ZH, Eschenz TG, Felben TG.

Z. lanceolata was collected between beginning of June and mid-August. It is very closely related with *Z. radicans* and may be often mistaken for it. It therefore may be more common and widespread than supposed.

5. Zoophthora phalloides Ватко (1966а). – Acta Mycol. 2: 8–13. – Pl.24: figs. 1–5.

Hosts. – Homoptera, Aphididae: *Acyrthosiphon pisum* HARRIS, *Macrosiphum rosae* L. *Metopolophium festucae* THEOBALD, *Rhopalosiphum padi* L.

Symptoms. - Infected aphids attached to plants by rhizoids.

Rhizoids pseudorhizomorph (fig. 1) forming a compact layer or monohyphal with a diameter of $6 - 12 \mu m$, unbranched or branched, endings rounded or enlarged. – Conidiophores branched. – Primary conidia $33.1 - 38.2 \times 6.9 - 8.7 \mu m (27 - 44 \times 6 - 11 \mu m)$ (9 collections), L/D = 3.98 - 5.49, long cylindrical to subfusiform, apically slightly tapering, straight or slightly bent; papilla distinct, conical, often pointed (fig. 3). – Secondary conidia like primary but more rounded (fig. 4), or capilliconidia $24.1 - 25.0 \times 7.7 - 8.9 \mu m$ (19 - $33 \times 7 - 11 \mu m$) (5 collections), L/D = 2.73 - 3.15, elongate falciform (fig. 5). Length of capillary 98 (77 - 116) μm (1 collection). – No resting spores observed. – Cystidia slender with a diameter of $5 - 11 \mu m$ at the level of the conidia, not or only slightly tapering (fig. 2).

Culture. – Slow growth on EYM. Primary conidia $38.3 \times 9.7 \mu m$ $(32 - 53 \times 9 - 13 \mu m)$ (1 collection).

Distribution. – Zürich-Reckenholz ZH, Siblingen SH, Hüttwilen TG, Entlebuch LU. The species was collected between June and October. It was never found on aphids in annual crops, but in meadows and natural habitats. It seems to be widespread but not frequent.

- Zoophthora radicans (BREFELD) BATKO (1964a). Bull. Acad. Polon. Sci.: CI.II, Sér. sci. biol. 12, 323. – Pl.24: figs. 6–16.
 - Bas.: *Empusa radicans* Brefeld (1870). Bot. Zeitg. 28: 161–166, 177–186

Hosts. – Plecoptera, Nemouridae; unidentified species, adults. Heteroptera, Miridae: *Dicyphus pallidus* (H.-S.), larvae and adults. Homoptera, Cicadina: unidentified species. Homoptera, Callaphididae: *Drepanosiphum acerinum* WALKER, adults. Homoptera, Psyllidae: *Trioza urticae* larvae and adults. Hymenoptera: unidentified parasitic wasps, adults. Lepidoptera: unidentified species, adults. Diptera: unidentified small species of Nematocera, adults.

Symptoms. – Infected insects attached to substrate by rhizoids. Mycelial bands white (Diptera, Hymenoptera), white-greenish (*D. pallidus*), white-brownish (*D. acerinum*) or brown (Plecoptera) (figs. 6-7).

Rhizoids abundant, emerging ventrally or latero-ventrally, monohyphal or pseudorhizomorph with disk-like ending. – Conidio phores branched; diameter of nuclei 4.7 (4 – 5.5) µm (1 collection). – Primary conidia 15.5 – 22.5 x 6.3 – 8.4 µm (13 – 28 x 5 – 10 µm), (29 collections), L/D = 2.41 – 2.98, subcylindrical to subfusiform, straight or slightly bent; papilla usually rounded (figs. 11–13); diameter of nuclei 4.0 – 4.6 (3 – 5.5) µm (3 collections). – Secondary conidia similar to primary, 11.9 – 13.2 x 6.9 – 7.1 µm (10 – 16 x 6 – 9 µm) (3 collections), L/D = 1.67 – 1.88, or capilliconidia 17.3 – 21.8 x 4.6 – 5.9 µm (15 – 24 x 4 – 7.5 µm) (15 collections), L/D = 3.23 – 4.18, fusiform, slightly bent or straight, apically rounded (figs. 14–15); length of capillary tube 42.5 – 58.8 µm (30 – 81 µm) (9 collections). – Resting spores 24.5 – 27.2 µm (20 – 33 µm) (9 collections), spherical, hyaline, smooth (fig. 16). – Cystidia not observed.

Culture. – Good growth on SDAEY and EYM. Diameter of colonies after 16 days at 20C 50 - 70 mm. Aerial mycelium white to

<sup>Pl. 24. – 1–5: Zoophthora phalloides. – 1. Pseudorhizomorph rhizoids (phase contrast).
-2. Cystidia. – 3. Primary conidia. – 4. Secondary conidia of type I. – 5. Capilliconidia.
-6–16: Zoophthora radicans. – 6. Sporulating fungus on Dicyphus pallidus (Miridae) (ca. 6 x nat size). – 7. Sporulating fungus on Trioza urticae (Psyllidae) (ca. 6 x nat size).
-8–9: Rhizoids on Plecoptera (ca. 15 x nat. size). – 10. Pseudorhizomorph rhizoid with holdfast on Diptera. – 11–13. Primary conidia produced on Diptera (11), Trioza (12) and Dicyphus (13). – 14. Detached capilliconidia (Dicyphus). – 15. Primary conidium and capilliconidia (Lepidoptera). – 16. Resting spores. – All LPCB. – Bar in figs. 1, 2 and 3: 50 μm; 1, 10; 3–5, 11–16 same magnification.</sup>



slightly greyish-brownish. Colonised medium not or only slightly stained. Primary conidia $17.4 - 20.7 \ge 6.2 - 9.2 \ \mu\text{m}$ ($15 - 24 \ge 6 - 11 \ \mu\text{m}$) (12 collections), L/D = 1.98 - 2.95. Capilliconidia $18.6 - 19.8 \ge 5.5 - 5.8 \ \mu\text{m}$ ($16 - 24 \ge 5 - 7 \ \mu\text{m}$) (2 collections), L/D = 3.4. Resting spores $27.1 - 29.5 \ \mu\text{m}$ ($21 - 34 \ \mu\text{m}$) (4 collections).

Distribution. – Plecoptera: Eschenz TG, Tägerwilen TG. Miridae: Hausener Seen ZH. Callaphididae: Zürich-Reckenholz ZH. Psyllidae: Watt ZH, Neunkirch SH. Parasitic wasps: Watt ZH, Neunkirch SH. Lepidoptera: Zürich-Reckenholz, Siblingen SH. Diptera: Hausener Seen ZH, Rickenbach ZH, Katzensee ZH, Klettgau SH.

Z. radicans is a very common and widespread species with a wide host range unique for members of the Entomophthoraceae. Slight morphological differences between strains of different origin were observed. Strains originating from Lepidoptera tended to have the largest conidia, whereas those from parasitic Hymenoptera had the longest and narrowest capilliconidia closely resembling Z. lanceolata. However, the latter observation needs confirmation with more material. Similar findings were made by BALAZY (1986). Although it seems impossible to subdivide this species by morphological characters there are good reasons to assume that a given strain is more virulent for its original host than for other insects (MIET-KIEWSKI & al., 1986; DUMAS & PAPIEROK, 1989). Without knowledge of this adaptation to a host species or group of host species, TURIAN (1957) proposed that subspecies be designated according to their original host. Such an approach would provide a more specific identification than currently applied.

7. Zoophthora viridis Keller sp. nov. – Pl.25: figs. 1–11.

Conidia primaria 18 – 30 x 7 – 11 µm, subcylindrica vel ellipsoidea, papilla globosa praedita, uninucleata. Conidia secundaria 23 – 35 x 6 – 7 µm, fusiformia, hyphis capillaribus evoluta. Sporae 22 – 35 µm, globosae, flavidae, leves. Conidio-phora ramosa, rhizoma et cystidia praesent. Ad Notostiram elongatam (Heteroptera: Miridae). Helvetia. Typus ZT, Cotypi K et BPI.

Host. – Heteroptera, Miridae: *Notostira elongata* Geoffr. (type host).

11: LPAO. – Bar in figs. 3, 7 and 11: 50 µm; 3–4; 5–9 same magnification.

^{Pl. 25. - 1-11: Zoophthora viridis. - 1. Host with typical symptoms (ca. 7 x nat. size). 2. Rhizoids with disk-like (arrowhead) or unspecialised endings (ca. 30 x nat. size). 3. Cystidium. - 4. Conidiophores. - 5. Primary conidia. - 6. Primary conidium and detached capilliconidia. - 7. Formation of capilliconidium. - 8. Formation of zygo-spore with nuclei. - 9. Mature resting spore - 10. Surface of resting spore (SEM, x 2100). - 11. Pseudorhizomorph rhizoid with unspecialised ending. - 2-7, 9: LPCB; 8,}



Symptoms. — Infected insects fixed with rhizoids near the top of grass leaves, head downwards, wings closed or, when the fungus has started to sporulate, spread (fig. 1). Mycelial layer light to dark green, covering mainly the abdominal parts of adults (fig. 1) or more or less the whole body of nymphs.

Rhizoids pseudorhizomorph; on the ventral surface of thorax and abdomen, holdfast disk-like or unspecialised (fig. 2, 11). – Hyphal bodies filamentous, unbranched or sparsely branched (fig. 4). – Conidiophores branched. – Primary conidia 22.1 – 26.0 x 8.0 – 8.9 µm (18 – 30 x 6 – 11 µm) (12 collections), L/D = 2.55 – 3.25, cylindrical to subfusiform, papilla rounded or conical (fig. 5). – Secondary conidia like primary, 17.6 – 17.7 x 9.2 – 9.5 µm (13 – 20 x 8 – 11 µm) (2 collections), L/D = 1.9, or capilliconidia 26.2 – 30.1 x 5.9 – 6.5 µm (22 – 35 x 5 – 7 µm) (12 collections), L/D = 4.15 – 4.97, fusiform, slightly bent so that one side appears straight (fig. 6–7). Length of capillary tube 52 – 70 µm (40 – 119 µm) (3 collections). – Resting spores 26.6 – 28.6 µm (22 – 36 µm) in diameter (12 collections), spherical, hyaline, smooth (fig. 9–10; zygospores, young spores with 9 – 21 nuclei (fig. 8), diameter of nuclei 4.6 µm (4 – 5.5 µm) (1 collection). – Cystidia few, tapering (fig. 3).

Culture. – Grows easily on SDA, SDAEY, EYM and ECM. Diameter of colonies after 14 days at 21C 15 – 32 mm on SDA, 36 – 50 mm on SDAEY and 34 – 42 mm on EYM. Aerial mycelium on SDA white, on SDAEY and EYM white to greenish. Colonised SDAEY and EYM colorised deeply green to dirty green. Looking from the back side of culture tube, usually sharply delimited green to brown-green transverse bands at the level of the growth zone, sometimes also at the inoculation spot. Primary conidia $27.5 - 32.7 \times 8.0 - 10.9 \,\mu\text{m} (22 - 45 \times 7 - 15 \,\mu\text{m}) (14 collection), L/D = 2.52 - 3.63. Capilliconidia 34.9 - 41.0 \times 6.9 - 7.1 \,\mu\text{m} (29 - 48 \times 6 - 9 \,\mu\text{m}) (2 collections), L/D = 4.9 - 5.9. Resting spores 28.8 - 31.5 \,\mu\text{m} (19 - 42 \,\mu\text{m}) (3 collections).$

Distribution. – Watt ZH (type locality), Zürich-Reckenholz ZH, Siblingen SH.

Z. viridis was originally considered identical with Z. elateridiphaga because of the shape and dimensions of the conidia (Keller,

Pl. 26. -1-9: Tarichium rhagonycharum. -1. Host with typical symptoms (ca. 6 x nat. size). -2. Rhizoids (ca. 25 x nat. size). -3. Histological section through rhizoid attached to a grass leaf (right) (HE). -4. Multiplying hyphal bodies. -5. Hyphal bodies. -6. Hyphal bodies (conjugating or separating ?). -7. Young resting spores with nuclei. (4–7: Material taken from living hosts). -8. Mature resting spores. -9. Minute knobs on the surface of mature resting spores. -4-7: LPAO; 8-9: LPCB. -Ba in figs. 3, 4 and 8:50 um; 4-7; 8-9 same magnification.

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1982). Further criteria like the presence of cystidia, different hosts, the green mycelial layer on infected host, cultural aspects together with the consistent small differences in the dimensions of conidia and resting spores from insects as well as from cultures justify its separation from Z. *elateridiphaga* and the description of a new species. The name refers to the green mycelium on the host insect as well as on slant culture.

The species was collected in the first half of September on both summer and autumn morphs of its host and predominantly on adults.

Discussion

The genus Zoophthora and its 4 subgenera were erected by BATKO (1964a, 1966b) and revised by REMAUDIÈRE & HENNEBERT (1980). The genus as defined by the latter authors consists of 16 species, the 7 described in this paper and Z. anglica (PETCH) HUMBER (1989), Z. anhuiensis (LI) HUMBER (1989), Z. canadensis (MACLEOD, & al.) REMAU-DIÈRE & HENNEBERT (1980), Z. forficulae (GIARD) BATKO (1964b), Z. geometralis (THAXTER) BATKO (1964b), Z. occidentalis (THAXTER) BATKO (1964b), Z. orientalis BEN-ZE'EV & KENNETH (1981a), Z. petchi BEN-ZE'EV & KENNETH (1981b) and Z. phytonomi (ARTHUR) BATKO (1964b).

A further species, Z. jaczewski (ZAPROMETOV in JACZEWSKI) BATKO (1964b) either belongs to the genus *Tarichium* or, when its conspecificity with *Entomophthora zabrii* ROZSYPAL (1951) can be proved, to *Erynia*, since *E. zabrii* is a typical member of the genus *Erynia*. The taxonomic position of *Entomophthora coleopterorum* PETCH (1932), or at least that of the conidial form subsequently attributed to this fungus (PETCH, 1944), and of *Entomophthora nebriae* RAUNKIAER (1892) is uncertain. They probably belong in Zoophthora, especially the conidial form of *E. coleopterorum* (BEN-ZE'EV, 1986). However, the question whether the resting spores of *E. coleopterorum* and the conidia attributed to this fungus represent the same species remains open. Consequently they should be considered two distinct species.

Z. forficulae could be included in the Z. radicans complex. BALAZY (1986) however, having investigated this fungus in detail, proposed that it should be considered as a distinct species.

5. Tarichium

Tarichium COHN (1870). - Beitr. Biol. Pflanzen 1, 58-86.

This genus was erected to include species known only by their resting spores. Such species can not be assigned to any of the previously described genera and must therefore be allocated to a provisional taxon or considered a collection of species with uncertain taxonomic status (*species incertae sedis*: REMAUDIÈRE & KELLER, 1980).

Type species: Tarichium megaspermum COHN (l.c.).

Tarichium rhagonycharum BALAZY (1981). – Bull. Acad. Polon. Sci, Sér. sci. biol. Cl. II, 29, 223. – Pl.26: figs. 1–9.

Host. – Coleoptera, Cantharidae: *Rhagonycha fulva* Scop. Symptoms. – Infected adult beetles attached to plants, usually to the top of grass, head downwards, wings closed (fig. 1).

Rhizoids pseudorhizomorph, numerous, mainly emerging from the ventral side of the abdomen, endings unspecialised or with disk-like holdfast, (figs. 2–3). – Hyphal bodies in living hosts filamentous, usually unbranched, with 7–16 nuclei (figs. 5–6); at an early developing stage (fig. 4) nuclei jammed between oil droplets; diameter of nuclei 7.6 (6–9.5) μ m (1 collection). – Resting spores 45.4 – 48.8 μ m (33–62 μ m) (6 collections), spherical, double-layered wall, inner layer more or less hyaline, outer layer brown with minute knobs at the surface (fig. 8–9). Young resting spores contain 8 – 24 nuclei with a diameter of 5.4 (5 – 6) μ m (1 collection) (fig. 7).

Culture. – Isolation experiments with tissues taken aseptically from infected, freshly killed beetles resulted in no growth, but in the formation of resting spores on the inoculated tissue.

Distribution. - Boppelsen ZH.

T. ragonycharum was collected in different years in the first half of August in the same small meadow surrounded by a forest and a hedge. According to BALAZY (1981) the species probably belongs to the genus *Zoophthora*, where similar rhizoid structures are common. The resting spores closely resemble those of *Z. crassitunicata* and *Entomophthora coleopterorum* PETCH (1932), although their dimensions differ slightly. The resting spores of *T. rhagonycharum* have a rougher surface and contain more nuclei than those of *Z. crassitunicata*.

Discussion

Tarichium was treated monographically by MacLEOD & MÜLLER-Kögler (1970) who recognised 25 species. In the meantime the conidial form of three of them (*T. bullata*, *T. gammae* and *T. hylemiae*) was identified and these three were transferred to the genus *Erynia*. *T.* *hylemiae* was found to be identical with *E. castrans* whereas the two other species retained their specific name.

BALAZY (1981) described two more species (*T. rhagonycharum* and *T. subpunctulatum*). BALAZY & WISNIEWSKI (1978, 1984) added a further 10 species attacking mites, so that the genus now comprises 34 named species. Yet more species described by THOR (1930) in the Protozoa probably exist, but all will probably be transferred eventually to other genera as soon as their conidial state is determined.

Conclusions

The revision of the systematics of the arthropod-pathogenic Entomophthorales by REMAUDIÈRE & HENNEBERT (1980) and REMAU-DIÈRE & KELLER (1980) initiated a competition between other insect mycologists for the creation of more "frames" (BEN-ZE'EV & KENNETH, 1982a), subgenera and new genera and for shuffling species from one genus to another. Species of the genus *Zoophthora* are a sad example of these practices. However, althoug the past decade has seen an excess of new combinations and confusions within this group of fungi, it has also witnessed a substantial improvement in our knowlegde of the morphology, cytology and biology of the species involved.

A sound classification should be based on unequivocal, more or less constant characters allowing the identification of a species through successive systematic levels. The following sets of characters for three different systematic levels are proposed:

- 1. At the generic level:
 - nuclear characters (important also at the familial level)
 - mode of discharge of primary conidia
 - number of nuclei per conidium
 - shape of primary and secondary conidia and mode of formation of secondary conidia
- 2. At a group level:
 - protoplasts: presence/absence and mode of multiplication
 - shape of hyphal bodies
 - morphology of conidiophores
 - rhizoids: presence/absence and morphology including holdfasts
 - cystidia: presence/absence and morphology
 - mode of resting spore formation and germination
 - shape of secondary conidia
- 3. At the species level:
 - conidia and resting spores: dimensions, shape and special aspects
 - nuclei: size and number
 - host range

The criteria listed for separation at the generic level are widely accepted and have been used as the basis for the classification in this paper. Together with criteria given for species separation, these will not be considered here. The significance of the remaining criteria, however, needs discussion with respect to possible use at the generic, subgeneric or simply at a group specific level. These characters have also been discussed by HUMBER (1981b) and by BEN-ZE'EV & KENNETH (1982a).

Although the early developmental stages of certain species of Entomopthorales have been described, it is not known whether such observations are representative of related species. The only well documented exception is the genus *Neozygites*, in which species with spherical hyphal bodies and ellipsoidal resting spores are known to form protoplasts in contrast to the species with rod-shaped hyphal bodies and spherical resting spores which do not. This is also an example of group characterisation by means of hyphal body morphology. Both findings are at variance with the proposal of BEN-ZE'EV & *al.* (1987) to create a separate genus for *N. turbinata*, a species which from these characters appears to be common member of the *N. fresenii*-group. More details about this are given in the discussion on the genus *Neozygites*.

Differences in the hyphal body morphology are reported also in the genus *Erynia*: those of *E. conica* and *E. variabilis* are more or less spherical, while those of *E. athaliae*, *E. dipterigena*, *E. gammae* and *E. myrmecophaga* are more or less rod-shaped and in *E. neoaphidis* they are irregular. The early developmental stages seem to multiply normally by growth and fission but in some cases (e.g. *Entomophthora culicis*, *E. trinucleata*) they multiply by budding. Thus, the early developmental stages provide characters of value for specifying groups within genera, but are not consistent for a genus.

In most genera the conidiophores represent a genus specific character. They are unbranched in *Conidiobolus, Entomophaga, Entomophthora* and *Neozygites* and branched in *Zoophthora*. In *Eryniopsis* they are partly branched, partly unbranched, and in *Erynia* there are two species with unbranched conidiophores: *E. castrans* and *E. magna*. Apart from these exceptions the morphology of the conidiophores appear to be useful criteria at the generic level. Other aspects of the conidiophores (diameter, relation between the number of nuclei/hyphal body and the intensity of branching) are discussed at the end of the section on the genus *Erynia*.

In all genera there are species with rhizoids. In *Neozygites* they are the exception, in *Erynia* and *Zoophthora* they are the rule. Only a few exceptions exist: *E. castrans* and *E. magna; Z. aphidis* may be free of rhizoids when resting spores are formed. In the genus *Conidiobolus, Entomophaga* and *Entomophthora* there are species with and species without rhizoids, in some species the situation appears unclear or variable (e.g. *C. obscurus, E. muscae, E. schizophorae*). Nevertheless presence or absence of rhizoids in these three genera is a group specific character. Two types of rhizoids, monohyphal and pseudorhizomorph, can be distinguished. The latter seems to be limited to the genus *Zoophthora* (*Entomophthora planchoniana* is an exception), while they are monohyphal in *Erynia* and provide a criterion, therefore, for the separation of these two genera with mononucleate conidia. However, there are exceptions (e.g. *Z. aphidis*) and further information is needed to support this statement.

The endings of the rhizoids on an individual host or between hosts may differ. Their structur is influenced by their stage of development and probably also by the substrate. This may lead to misinterpretations. In principle, only those endings which have a function. i.e. which attach the cadaver to the substrate (the so-called holdfasts), should be considered. Very often, however, these fully developed holdfasts are broken during collection and others without function or immature ones may be considered typical. In "aquatic" species of Erynia (e.g. E. conica) the majority of the rhizoids are not involved in attaching the host to the substrate, their endings are therefore unspecialised. Those rhizoids which fix the cadaver to the substrate, however, all have specialised, distinct holdfasts. The statement of HUMBER (1989) that these species have indistinct holdfasts must therefore be revised. Within the genus Erynia rhizoids must be considered a character with limited importance for taxonomic and systematic purposes. Further investigations may reveal their value at the group level.

Investigations of the rhizoids, mainly of *E. conica*, suggest that two fundamentally different types may exist: one is very frequent and consists of relatively fine, filamentous, branched and unbranched rhizoids with rounded, unspecialised endings (Plate 6, fig. 1). They seem to have no function in the attachment of the cadaver to the substrate. The other rarer type is thicker, unbranched and with specialised holdfasts (Plate 6, figs. 2–4). This type is considered to be responsible for the attachment of the cadaver to the substrate. The question arises whether these two types correspond, ontogenetically, to the conidiophores and the cystidia respectively. This hypothesis was supported by observation of a single conidium produced on a thinner rhizoid.

Apart from some rare exceptions in the genus *Conidiobolus* cystidia are restricted to species in the genera *Erynia* and *Zoophthora*. However, only in *Erynia* can the presence of cystidia be considered as a consistent character, unknown or absent only in a few species which include *E. castrans* and *E. magna*. Cystidia vary greatly in number and shape; species can be roughly classified into a group with powerful, thick cystidia (like most of the "aquatic" species) and those with slender ones. Further details are given in the discussion at the end of the genus *Erynia*.

Little is known about the mode of resting spore formation and germination. In addition to sexual and asexual resting spore formation HUMBER (1989) distinguishes between the formation in the axis of the mother cell and the formation by budding from the mother cell. The first type is found in the genus *Conidiobolus* and the second type in all other genera discussed here. The sexual/asexual nature of resting spore formation seems to be constant only in the genus *Neozygites* where all species form zygospores. In all other genera zygospore and azygospore formation occurs, in many species the mode of formation is unknown while in other species both zygospore and azygospore formation is reported. In many cases it is difficult to understand and interprete the process of resting spore formation.

Resting spore germination is described only from a few species. Two types are known: germination directly to form one or more conidia, or by the formation of a limited mycelium (one or more branched or unbranched germ tubes) from which one or more conidia are formed. The first type is represented by the genus *Neozygites* and both types are reported in Conidiobolus (LATGÉ & al., 1978; SOPER & al., 1975). Probably all other genera belong to the second type. Besides Neozygites resting spore germination is best documented in Zoophthora. In all known cases a single (exceptionally two) germ tube is formed. Whereas Z. radicans and Z. canadensis form projectable primary germ conidia (PERRY & al., 1982; TYRRELL & MACLEOD, 1975) Z. aphidis forms capilliconidia directly from the germ tube or from sessile germ conidia resembling primary conidia (S. KELLER, this paper). Resting spore germination in *Erunia* may be similar to that in Zoophthora (PERRY, 1988). Our knowledge in this respect. however, is too limited to draw generalised conclusions.

BEN-ZE'EV & KENNETH (1982a) distinguish 5 types of secondary conidia, 3 of which are important with respect to the genera included in this paper. Secondary conidia of type V (tetraradiate or stellate conidia of some "aquatic" species) should be considered as habitatinduced. It is unknown whether their formation is restricted to species and in the light of current knowledge the value of this character for systematic purposes is very doubtful. The production of capilliconidia (type II), on the other hand, is one of the criteria used to separate genera with mononucleate conidia (REMAUDIÈRE & HENNE-BERT, 1980; REMAUDIÈRE & KELLER, 1980; HUMBER, 1989). The projected secondary conidia within the genus *Erynia* either resemble the primary conidia (type Ia) or are more or less spherical usually with pointed apex (type Ib). The difference between these two types is very conspicuous in species with elongate primary conidia, represented mainly by the "aquatic" ones, but they are not, as HUMBER (1989) stated, limited to these; they are also known at least from *E. athaliae, E. dipterigena* and *E. neoaphidis*, and probably occur in additional species of the genus.

Proposal for a classification of the discussed genera

Based on the foregoing discussion we believe that *Conidiobolus*, *Entomophaga*, *Entomophthora*, *Erynia*, *Eryniopsis*, *Neozygites*, *Strongwellsea*, *Zoophthora* and *Tarichium*, or species with unknown systematic position can be characterised unequivocally.

The genus *Strongwellsea* is now recognised as a genus separate from *Erynia* in contrast to previous statements (REMAUDIÈRE & KEL-LER, 1980; KELLER, 1987a). Its existence is justified by a set of consistent, minor but group-specific characters (unbranched conidiophores, absence of rhizoids and cystidia).

The subdivision of the genus *Entomophaga* into *Entomophaga* and *Batkoa* and of the genus *Erynia* into *Erynia*, *Furia* and *Pandora* as proposed by HUMBER (1989) is perhaps premature, being based on minor, inconstant and insufficiently researched criteria and is rejected in the current monograph.

Summary

Part I (KELLER, 1987a) and part II (this paper) of this monograph list and describe a total of 51 arthropod pathogenic species of Entomophthorales from Switzerland. 50 species are classified in the 7 genera Conidiobolus, Entomophaga, Entomophthora, Erynia, Eryniopsis, Neozygites and Zoophthora. An additional species of unknown taxonomic status is uncluded in Tarichium. These 50 species represent 41% of those recorded globally in the corresponding genera. The complete world list of species, however, is much longer and comprise at least 33 species of Tarichium and some further unclassified ones. During these investigations 13 new species were described, 8 of them in this monograph and numerous new hosts of known species were recorded. This list of the Entomophthorales of Switzerland is certainly not complete and many more previously described and undescribed species will be discovered in the future.

The Swiss records are listed in Tab. 1 together with their corresponding host taxa. The Diptera are attacked by the largest number of species, (23), followed by the Homoptera with 10 species. It is interesting to note that 24 species were found on pest insects and mites, often causing epizootics. This demonstrates the potential of these fungi in the natural regulation of pest populations as well as in their possible use in microbial control. Also, perhaps, it emphasises that more species remain to be discovered on less intensively studied invertebrates.

Host taxa	Species of Entomophthorales
Arachnida	
Opiliones	Entomophaga batkoi
Acari	Neozygites floridana
Insecta	
Plecoptera	Zoophthora radicans
Saltatoria	Entomophaga grylli
Dermaptera	Erynia ellisiana
Thysanoptera	Neozygites parvispora
Heteroptera	Entomophthora helvetica
	Erynia minutospora
	Zoophthora radicans
	Z. viridis
Homoptera	
Cicadina	Conidiobolus major
	Zoophthora radicans
Psyllina	Zoophthora radicans
Aphidina	Conidiobolus obscurus
	Entomophthora planchoniana
	Erynia neoaphidis
	Neozygites fresenii
	N. microlophii
	N. turbinata
	Zoophthora aphidis
	Z. phalloides
	Z. radicans
Hymenoptera	Entomophaga tenthredinis
	Erynia athaliae
	E. myrmecophaga
	Zoophthora radicans
	*

Tab. 1. – Taxa of hosts attacked by the species of Entomopthorales recorded from Switzerland

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Host taxa	Species of Entomophthorales
Coleoptera	Conidiobolus coronatus Entomophaga domestica Zoophthora crassitunicata Z. elateridiphaga Tarichium rhagonycharum
Trichoptera	Erynia rhizospora
Lepidoptera	Entomophaga aulicae Erynia blunckii E. gammae E. virescens Zoophthora radicans
Diptera Nematocera	Entomophaga conglomerata E. domestica E. gigantea E. limoniae E. papillata Entomophthora brevinucleata E. culicis E. trinucleata Erynia aquatica E. conica E. conica E. curvispora E. dipterigena E. variabilis Eryniopsis caroliniana Zoophthora lanceolata Z. radicans
Brachycera	Conidiobolus apiculatus Entomophaga domestica Entomophthora muscae E. schizophorae Erynia bullata E. castrans E. dipterigena

Additions to part I

In part I of this series (Keller, 1987a), *Conidiobolus apiculatus* (Thaxter) Remaudière & Keller and *C. major* (Thaxter) Remaudière & Keller were included in the genus *Conidiobolus*. Two fungi with very similar conidia but different nuclear characteristics were described

as new species of the genus *Entomophaga: E. domestica* Keller and *E. limoniae* Keller. In a recent paper Humber (1989) gave evidence that THAXTER'S type material was of the *Entomophaga* type and consequently synonymized *C. apiculatus* with *E. domestica* and *C. major* with *E. limoniae*. This situation makes it necessary to describe the two species of *Conidiobolus* as new ones and to transfer *Empusa apiculata* THAXTER and *E. apiculata* var. *major* THAXTER to *Entomophaga*.

Entomophaga apiculata (THAXTER) KELLER comb. nov.

- Bas.: Empusa apiculata THAXTER (1888). Mem. Boston Soc. Nat. Hist. 4:163
- Syn.: Batkoa apiculata (THAXTER) HUMBER (1989). Mycotaxon 34:446.

Entomophaga major (THAXTER) KELLER comb. nov.

- Bas.: Empusa apiculata var. major THAXTER (1888). Mem. Boston Soc. Nat. Hist. 4:164.
- Syn.: Entomophthora major (THAXTER) GUSTAFSSON (1965). Lantbrukshögskolans Ann. 31: 133.
- Syn.: Batkoa major (Thaxter) Humber (1989). Mycotaxon 34:446.

E. domestica indeed matches the description of *E.* apiculata THAXTER and the synonymisation appears justified. *E.* limoniae, however, differs from THAXTER's description of *E.* apiculatus var. major mainly by the shape of the conidia and papilla but also by the host. It must therefore be considered as a distinct species.

Conidiobolus cercopidis Keller sp. nov.

- Misid.: Conidiobolus major (THAXTER) REMAUDIÈRE & KELLER ex KELLER (1987a). – Sydowia 40: 132, Pl. 3: figs. 1–10.
- [=non Batkoa major (THAXTER) HUMBER (1989). Mycotaxon 34: 446].

Conidia primaria (34-) 40 – 45 (-56) x (28-) 33 – 39 (-51) μ m, sphaerica, papilla conspicua aut inconspicua, rotundata. Conidia secundaria (29-) 40 – 45 (-55) x (25-) 34 – 40 (-48) μ m habitu primariis similia. Sporae perdurantes (32-) 38 – 44 (-50) μ m, globosae, hyalinae, leves. Conidiophora simplicia, nucleis diametro 2.6 – 2.7 μ m per aceto-orcein. Rhizoidea presentia, cystidia absunt. In *Neophilaenus lineatus*L. (hospes typicus) (Homoptera: Cercopidae). Helvetia. Holotypus ZT, Cotypi K et BPI. Typus differt a *Batkoa majore* (THAXTER) HUMBER conidiis primariis nucleis magnis et valde numerosis.

For further information compare Sydowia 40: 132; Pl. 3: figs. 1–10, 1987.

Conidiobolus pseudapiculatus Keller sp.nov.

- Misid.: Conidiobolus apiculatus (THAXTER) REMAUDIÈRE & KELLER ex Keller (1987a). – Sydowia 40: 128, 130, pl. 1: figs. 1–7.
 - [=non *Batkoa apiculata* (THAXTER) HUMBER (1989). Mycotaxon 34: 446].

Conidia primaria (28-) 35 – 39 (-47) x (23-) 29 – 32 (-41) µm, sphaerica, distincta papilla rotundata vel acuminata praedita. Conidia secundaria habitu primariis similia. Sporae perdurantes (30-) 35 – 38 (-41) µm, globosae, hyalinae, leves. Conidiophora simplicia, nucleis diametro 2.6 – 2.7 µm per aceto-orcein. Rhizoidea mononemata, cystidia absunt. In Dipteris (hospitibus typici) et Hymenopteris Tenthredinis. Holotypus ZT, cotypi K et PBI. Typus differt a *Batkoa apiculata* (THAXTER) HUMBER conidiis primariis nucleis magnis et valde numerosis.

For further information compare Sydowia 40: 128–130; Pl. 1: figs. 1–7, 1987.

Acknowledgments

For the enormous help on both parts of this monograph, the author is greatly indebted to Dr. N. WILDING for critically reviewing the manuscripts and correcting the English phraseology. The author further expresses sincere thanks to Dr. E. HORAK for advising in nomenclatural questions and helping with the latin diagnosis, to Drs. G. BACHLI, D. CHERIX, M. DETHIER, C. DUFOUR, J. EILENBERG, J. FREULER, W. GEIGER, P. GÖLDLIN, H. GÜNTHART, C. LIENHARD, C. MADDALENA, H.R. MAURER, W. MEER, B. PAPIEROK, G. RABOUD, W. SAUTER, E. STADLER, K. THALER and G. ZIMMERMANN and Mr. H. HÖHN and C. SCHWEIZER for identifying hosts and/or providing material, to Dr. J. WEISER for permitting the use of parts of his collection, to Dr. J. WUEST for preparing the electron micrographs and to Mrs. B. BRUDERER for technical assistance and to Mrs. E. WEIBEL for typing the manuscript.

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Digitale Literatur/Digital Literature

Zeitschrift/Journal: Sydowia

Jahr/Year: 1991

Band/Volume: 43

Autor(en)/Author(s): Keller Siegfried

Artikel/Article: Arthropod-pathogenic Entomophthorales of Switzerland. II. Erynia, Eryniopsis, Neozygites, Zoophthora and Tarichium. 39-122