

Coprophilous myxomycetes: updated summary, key to species, and taxonomic observations on *Trichia brunnea*, *Arcyria elaterensis*, and *Arcyria stipata*

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ELIASSON, U. H. & KELLER, H. W. 1999: Coprophilous myxomycetes: updated summary, key to species, and taxonomic observations on *Trichia brunnea*, *Arcyria elaterensis*, and *Arcyria stipata*. – Karstenia 39:1–10. Helsinki. ISSN 0435-3402

An updated summary is provided for myxomycete species occurring on dung of herbivorous animals. At least 99 species representing 23 genera have been reported. Most species normally occur on other substrata and are only occasionally found on dung. A restricted number of species are truly coprophilous in that most or all records are from this substratum. These species are *Arcyria elaterensis*, *Badhamia apiculospora*, *B. rhytidosperma*, *B. spinispora*, *Didymium annulispermum*, *D. nullifilum*, *D. rugulosporum*, *Kelleromyxa fimicola*, *Licea alexopouli*, *Licea pescadorensis*, *Macbrideola coprophila*, *Perichaena corticalis* var. *liceoides*, *P. luteola*, *Trichia brunnea*, and *T. fimicola*. A key is provided for species which are truly coprophilous or often found on dung. All species ever reported on dung are listed. *Hemitrichia stipata* var. *fusca* Z. Moravec is conspecific with *Trichia brunnea* J.J.Cox. Taxonomic comments are given on *Arcyria elaterensis* and *A. stipata*, and the taxonomic importance of dextrorse versus sinistrorse spiral ornamentation on the capillitrial threads is discussed.

Key words: Coprophilous myxomycetes, capillitrial ornamentation, *Arcyria elaterensis*, *Arcyria stipata*, *Trichia brunnea*

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Introduction

Myxomycetes grow on a wide range of substrata and in many different habitats. Although no correlation is absolute, the majority of species show preferences for a special kind of substratum and, to varying degree, a special microhabitat. The largest number of species are found on decaying wood, bark and leaf litter. Other species occupy different, and sometimes rather distinct ecological niches, such as living bryophytes, bark of living trees, living leaves of tropical angiosperms, or various living or dead plant material under or in close contact with melting snow. A relatively large number of species have been recorded on

dung of herbivorous animals. The vast majority are species that normally occur on other substrata and are only occasionally and rarely found on dung. A limited number of species can be regarded as truly coprophilous in the sense that most or all records are from this substratum, namely, *Arcyria elaterensis*, *Badhamia apiculospora*, *B. rhytidosperma*, *B. spinispora*, *Didymium annulispermum*, *D. nullifilum*, *D. rugulosporum*, *Kelleromyxa fimicola*, *Licea alexopouli*, *Licea pescadorensis*, *Macbrideola coprophila*, *Perichaena corticalis* var. *liceoides*, *P. luteola*, *Trichia brunnea*, and *T. fimicola*.

This paper summarizes records of coprophilous myxomycetes based on our observations and available literature. The number of species recorded on dung varies widely among genera. For example, the list comprises 20 species of *Didymium*, whereas *Cibraria*, despite over 35 species in the genus, is represented by a single record of *C. violacea* (Hertel 1962).

There are relatively few papers dealing explicitly with coprophilous myxomycetes. Ecological aspects and descriptions of moist chamber techniques are provided in Eliasson & Lundqvist (1979) and Krug et al. (in press). Other publications centering on coprophilous species are those of Merrill (1969), García-Zorrón (1977), Nannenga-Bremekamp et al. (1979), Cox (1981), and Chung & Liu (1995, 1996).

Key to coprophilous myxomycete species

Only myxomycete species that are exclusively or repeatedly recorded on dung are included in this key. For additional records of species known to occur on dung see the comprehensive list of species.

- 1 Capillitium lacking or consisting only of occasional simple threads attached to the peridium; fructifications sporangiate, never exceeding 0.5 mm in height 2
- Capillitium present; fructifications often larger, variable in size and shape 8
- 2 Sporangia spindle-shaped, erect on a constricted base *Kelleromyxa fimicola*
- Sporangia hemispherical to globose 3
- 3 Sporangia stalked; columella large, globose *Macbrideola coprophila*
- Sporangia sessile; columella never present 4
- 4 Peridium with yellow or whitish scales of calcium carbonate crystals *Didymium nullifilum*
- Peridium without calcareous scales 5
- 5 Spore wall thinner and spores paler on one side; sporangia 0.2–0.4 mm in diam. *Licea tenera*
- Spores with evenly thickened walls 6
- 6 Sporangia 0.06–0.15 mm in diam.; capillitium lacking 7
- Sporangia 0.3–0.5 mm in diam; capillitium, if present, of simple threads attached to peridium *Perichaena corticalis* var. *liceoides*
- 7 Peridium black, smooth, shiny; spores 9.5–11 µm in diam. *Licea alexopouli*
- Peridium reddish brown to black; spores 7–8 µm in diam. when globose, 8–10 x 7–8 µm when ovoid *Licea pescadorensis*
- 8 Calcium carbonate lacking in all parts of the fructification 9
- Calcium carbonate present, as crystals or amorphous granules, in the peridium and/or capillitium 18
- 9 Sporangia minute, globose, 40–50 µm in diam., long-stalked; spore mass whitish or pink *Echinostelium minutum*
- Sporangia or plasmodiocarps variable in size and shape, 0.2 mm or more in diam., sessile or stalked 10
- 10 Peridium disappearing; sporangia elongate or cylindric with spore mass dark brown to blackish; capillitium forming peripheral surface net *Stemonitis fusca*
- Peridium partially persistent in mature fructifications, at least at base of sporangium; spore mass grey, brown, or brightly coloured 11
- 11 Capillitium at least partly of free, unbranched elaters with spiral ornamentation 12
- Capillitium branched, sometimes forming a network; free elaters, if present, without spiral ornamentation 14
- 12 Capillitrial threads with 2 spiral bands *Trichia fimicola*
- Capillitrial threads with 3 or 4 spiral bands 13
- 13 Sporangia dark olivaceous brown; peridium iridescent *Trichia brunnea*
- Sporangia yellowish brown; peridium not iridescent *Arcyria elaterensis*

- 14 Peridium in mature fructifications persistent as shallow cup at base of sporangium;
spores mostly whitish or grey in mass *Arcyria cinerea*
- Peridium persistent above and below, lacking a basal cup 15
- 15 Fructifications predominantly plasmodiocarpous; capillitrial threads spiny *Perichaena chrysosperma*
- Fructifications predominantly sporangioid; capillitrial threads not spiny 16
- 16 Dehiscence circumscissile; peridium not translucent *Perichaena corticalis*
- Dehiscence irregular; peridium translucent 17
- 17 Capillitium well developed, forming a network *Perichaena luteola*
- Capillitium sparse, mostly of simple or sparsely branched threads
attached to the peridium *Perichaena corticalis* var. *liceoides*
- 18 Capillitium calcareous throughout or at nodes 19
- Capillitium not calcareous 26
- 19 Capillitium calcareous throughout or almost so, forming a network or a system
of variously branched tubules 20
- Capillitium calcareous only at nodes 22
- 20 Spores globose, wrinkled-reticulate over about half the surface *Badhamia rhytidosperma*
- Spores oval with ridge along one side, surface not reticulate 21
- 21 Spores spiny, spines up to 1 µm long *Badhamia spinispora*
- Spores smooth or almost so *Badhamia apiculospora*
- 22 Fructifications aethaliod, 1–5 mm in extent when on dung;
spores predominantly elliptic *Fuligo cinerea*
- Fructifications sporangioid or plasmodiocarpous 23
- 23 Fructifications plasmodiocarpous, often closely aggregated and convoluted *Physarum gyrosum*
- Fructifications predominantly sporangioid 24
- 24 Sporangia strongly compressed laterally *Physarum compressum*
- Sporangia rounded to cylindric or ovoid, not laterally compressed 25
- 25 Sporangia sessile, pulvinate *Physarum ovisporum*
- Sporangia cylindric or ovoid, mostly attached to substratum by weak stalk-
like extensions of the hypothallus *Physarum dideroides*
- 26 Calcium crystals on peridium united into a smooth shell-like crust 27
- Calcium crystals powdering peridium or forming aggregated scales 29
- 27 Spores 18–20 µm, coarsely warted *Didymium rugulosporum*
- Spores 9–14 µm 28
- 28 Spores minutely warted or almost smooth, 11–14 µm in diam.,
spore wall normally with a thicker portion on one side *Didymium difforme*
- Spores coarsely and irregularly warted, 9–10 µm in diam. *Didymium trachysporum*
- 29 Fructifications sessile, plasmodiocarpous or sporangioid 30
- Fructifications stalked, sporangioid 32
- 30 Outer peridial wall crustose, distant from membranous inner peridium;
fructifications sporangioid *Didymium karstensii*
- Peridial layers closely associated 31
- 31 Peridium mostly covered with a white floccose crust of calcium crystals;
capillitium abundant, rigid; spores distinctly and closely warted;
fructifications predominantly plasmodiocarpous *Didymium dubium*
- Peridium covered with a layer of calcium scales; capillitium sometimes poorly developed
or lacking; spores with widely scattered spines up to 1 µm long *Didymium nullifilum*
- 32 Stalk calcareous 33
- Stalk not calcareous 34
- 33 Columella small, pulvinate, often spiny; stalk, if present, very short *Didymium karstensii*
- Columella discoid to hemispheric; stalk mostly well developed *Didymium squamulosum*
- 34 Columella dark brown *Didymium nigripes*

- Columella yellow or white 35
- 35 Columella yellow, stalked; capillitrial threads with dark swellings *Didymium ovoideum*
- Columella white, not stalked; capillitrial threads without dark swellings *Didymium iridis*

Comprehensive list of species recorded on dung

Species are listed in alphabetical order. Species included in the key have been marked with an asterisk. The list includes all species that, to our knowledge, have been recorded on dung. For species without references, see Eliasson & Lundqvist (1979). References where species are treated in more detail are given in some cases. Author abbreviations follow Brummitt & Powell (1992).

- Arcyodes incarnata* (Alb. & Schwein.) O.F.Cook
- **Arcyria cinerea* (Bull.) Pers.
- **Arcyria elaterensis* Mulleavy
- Arcyria incarnata* (Pers.) Pers.
- Arcyria leiocarpa* (Cooke) G.W. Martin & Alexop.
- Arcyria pomiformis* (Leers) Rostaf.
- Arcyria stipata* (Schwein.) Lister
- **Badhamia apiculospora* (Härk.) Eliasson & N.Lundq. (*Physarum apiculosporum* Härk., *Badhamia semiannulata* Raub & H.W.Keller)
- Badhamia gracilis* (T.Macbr.) T.Macbr. (Blackwell & Gilbertson 1980)
- Badhamia macrocarpa* (Ces.) Rostaf.
- Badhamia ovispora* Racib. (Merrill 1969). This is a doubtful record probably referring to *Badhamia apiculospora*. Mainly due to Raciborski's partially inaccurate description of *B. ovispora*, two species have been referred here. The true identity of the species was clarified by Keller et al. (1975). It is apparently a rarely encountered species, probably mainly occurring on decaying wood or bark.
- **Badhamia rhytidosperma* H.W.Keller & Schokn. (Keller & Schoknecht 1989c)
- **Badhamia spinispora* (Eliasson & N.Lundq.) H.W.Keller & Schokn. (*Physarum spinisporum* Eliasson & N.Lundq.) (Eliasson & Lundqvist 1979, Keller & Schoknecht 1989b)
- Calomyxa metallica* (Berk.) Nieuwl. (Cox 1981)
- Colloderma oculatum* (C. Lippert) G.Lister (García-Zorrón 1977)
- Comatricha mirabilis* R.K.Benj. & Poitras
- Comatricha nigra* (Pers.) J.Schröt.

- Comatricha pulchella* (C.Bab.) Rostaf.
- Craterium leucocephalum* (Pers.) Ditmar
- Cribaria violacea* Rex
- Diderma appланatum* Fr.
- Diderma effusum* (Schwein.) Morgan
- Diderma globosum* Pers.
- Diderma niveum* (Rostaf.) T.Macbr.
- Diderma radiatum* (L.) Morgan (Singh 1984)
- Diderma simplex* (J.Schröt.) G.Lister
- Diderma testaceum* (Schrad.) Pers.
- Didymium anellus* Morgan
- Didymium annulispermum* H.W.Keller & Schokn. (Keller & Schoknecht 1989a)
- Didymium cf. bahiense* Gottsb. (Gøtzsche 1989)
- Didymium clavus* (Alb. & Schwein.) Rabenh.
- **Didymium difforme* (Pers.) S.F.Gray
- **Didymium dubium* Rostaf.
- **Didymium iridis* (Ditmar) Fr. (Blackwell & Gilbertson 1980)
- **Didymium karstensii* Nann.-Bremek. (Merrill 1969, Cox 1981)
- Didymium megalosporum* Berk. & T.Macbr. (Zeller & Tóth 1977)
- **Didymium nigripes* (Link) Fr. (Zeller & Tóth 1977)
- **Didymium nullifilum* (Kowalski) M.L. Farr (*Squamuloderma nullifila* Kowalski) (Farr 1982)
- Didymium ochroideum* G.Lister
- **Didymium ovoideum* Nann.-Bremek. (Cox 1981)
- Didymium quitense* (Pat.) Torrend (Nannenga-Bremekamp et al. 1979)
- **Didymium rugulosporum* Kowalski
- Didymium saturnus* H.W.Keller (Lakhanpal & Mukerji 1978)
- **Didymium squamulosum* (Alb. & Schwein.) Fr.
- **Didymium trachysporum* G.Lister
- Didymium vaccinum* (Durieu & Mont.) Buchet
- Didymium verrucosporum* A.L. Welden
- **Echinostelium minutum* deBary (Critchfield & Demaree 1991, Blackwell & Gilbertson 1980)
- **Fuligo cinerea* (Schwein.) Morgan (Zeller & Tóth 1977)
- Fuligo septica* (L.) F.H. Wiggers (Blackwell &

- Gilbertson 1980)
- **Kelleromyxa fimicola* (Dearn. & Bisby) Eliasson (*Licea fimicola* Dearn. & Bisby) (Eliasson et al. 1991)
- Lamproderma scintillans* (Berk. & Broome) Morgan
- Leocarpus fragilis* (Dicks.) Rostaf.
- Lepidoderma chailletii* Rostaf. (Zeller & Tóth 1977)
- **Licea alexopoulum* Blackw.
- Licea cf. belmontiana* Nann.-Bremek.
- **Licea pescadorensis* C.-H.Chung & C.-H.Liu
- Licea punctiformis* Martin (García-Zorrón 1977, Lakhanpal & Mukerji 1981)
- Licea pusilla* Schrad.
- **Licea tenera* Jahn (Kowalski & Curtis 1968, Lakhanpal & Mukerji 1975, García-Zorrón 1977, Mitchel & Chapman 1980, Cochet & Bozonnet 1984)
- Licea variabilis* Schrad.
- Lycogala epidendrum* (L.) Fries (Singh 1984)
- **Macbrideola coprophila* Nann.-Bremek., Mukerji & Singh (Nannenga-Bremekamp et al. 1979)
- Macbrideola cornea* (G.Lister & Cran) Alexop.
- **Perichaena chrysosperma* (Currey) Lister
- **Perichaena corticalis* (Batsch) Rostaf. var. *corticalis* (Zeller & Tóth 1977)
- **Perichaena corticalis* var. *liceoides* (Rostaf.) Lister (*Perichaena liceoides* Rostaf.) (Gilert 1990)
- Perichaena depressa* Libert (Zeller & Tóth 1977)
- **Perichaena luteola* (Kowalski) Gilert (*Calonema luteolum* Kowalski, *Arcyodes luteola* (Kowalski) Nann.-Bremek.) (Rammeloo 1978, Gilert 1995)
- Perichaena minor* (G.Lister) Hagelst. (Cox 1981, Critchfield & Demaree 1991)
- Perichaena pedata* (Lister) G.Lister
- Perichaena quadrata* T.Macbr. (Keller & Eliasson 1992)
- Perichaena syncarpon* T.E.Brooks
- Perichaena vermicularis* (Schwein.) Rostaf.
- Physarum cf. bitectum* G.Lister
- Physarum bivalve* Pers. (Ing & Spooner 1994)
- Physarum cf. brunneolum* (W.Phillips) Massee (Stephenson 1989)
- Physarum cinereum* (Batsch) Pers. (Zeller & Tóth 1977, Götzsche 1989)
- **Physarum compressum* Alb. & Schwein.
- Physarum confertum* T.Macbr.
- Physarum contextum* (Pers.) Pers. (incl. *P. mucosum* Nann.-Bremek.)
- Physarum diderma* Rostaf. (Zeller & Tóth 1977)
- **Physarum didermoides* (Pers.) Rostaf. (Zeller & Tóth 1977)
- **Physarum gyrosum* Rostaf. (Cox 1981)
- Physarum cf. leucophaeum* Fr. (Götzsche 1989)
- Physarum leucopus* Link
- Physarum nucleatum* Rex
- Physarum nutans* Pers.
- **Physarum ovisporum* G.Lister (Cox 1981)
- Physarum pusillum* (Berk. & M.A.Curtis) G.Lister (Blackwell & Gilbertson 1980)
- **Stemonitis fusca* Roth
- Stemonitis herbarica* Peck (Chung & Liu 1995)
- Stemonitis pallida* Wingate
- Stemonitis smithii* T.Macbr. (Chung & Liu 1995, as *S. axifera* var. *smithii* (T.Macbr.) Hagelst.)
- Trichia botrytis* (J.F.Gmel.) Pers.
- **Trichia brunnea* J.J.Cox (Cox 1981) (*Hemitrichia stipata* var. *fusca* Z.Moravec)
- Trichia contorta* (Ditmar) Rostaf.
- **Trichia fimicola* (Marchal) Ing (*T. varia* var. *fimicola* Marchal) (Ing 1967)
- Trichia varia* (Pers.) Pers.

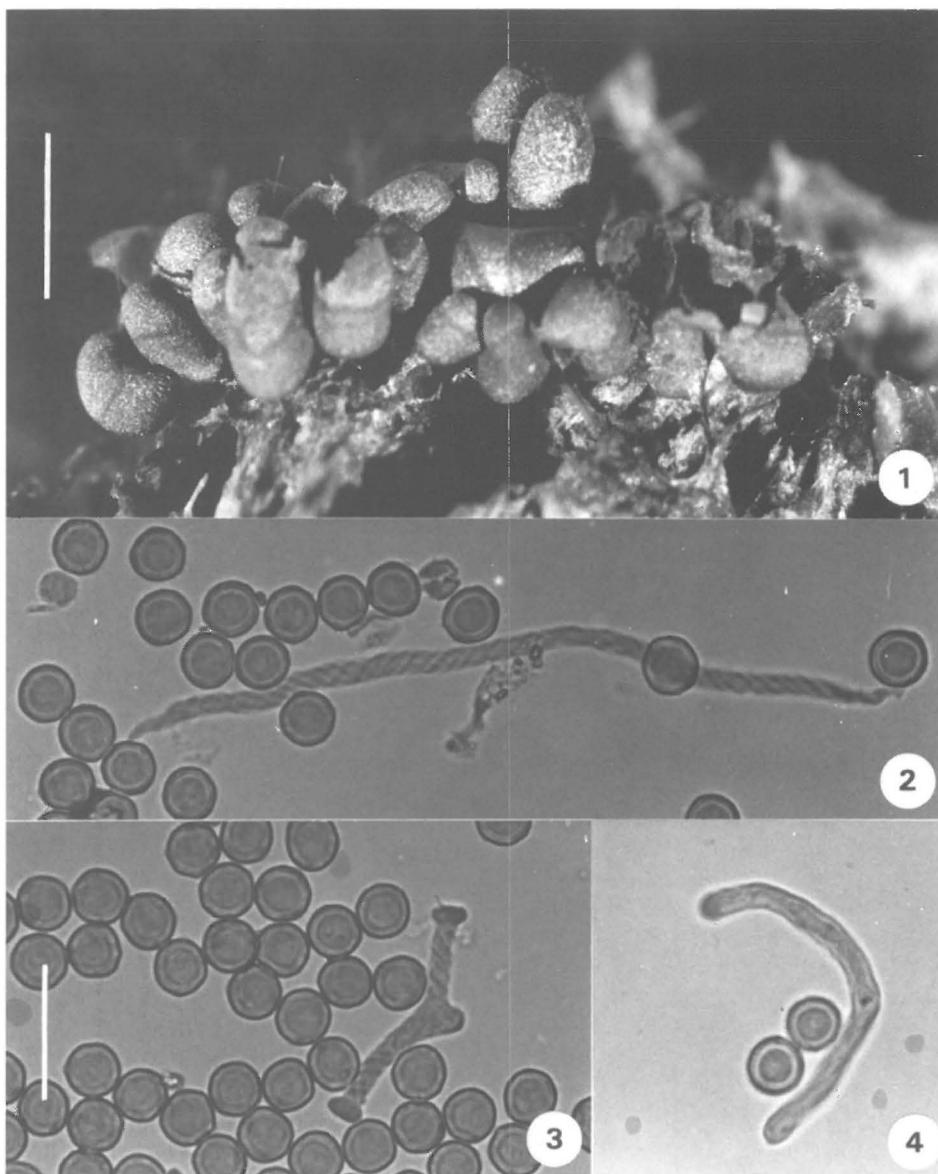
Dubious taxon

Physarum fimetarium Schum. Name rejected by Eliasson & Lundqvist (1979) as a *nomen dubium*.

Taxonomic observations

Spiral ornamentation on capillitrial threads

The direction of spiral ornamentation on the capillitrial threads may be a useful taxonomic character for certain species. Most monographs do not mention this character. One reason may be that the terminology has been confusing; the terms "dextrorse" and "sinistrorse" are mostly used differently today than in older myxomycete literature. We have adopted these terms as defined by Snell & Dick (1971), using "dextrorse" for describing a spiral rising clockwise towards the observer. The direction of the spirals has been constant within the species throughout the material included in this study. Spirals on the capillitium are sinistrorse in *Trichia brunnea* and *Arcyria elaterensis* but dextrorse in *A. stipata*.

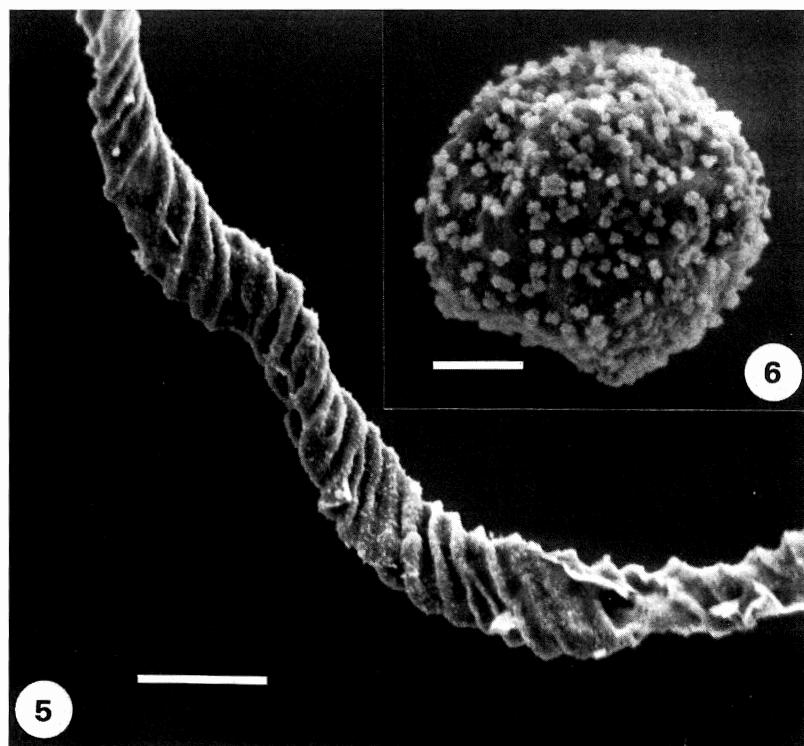


Figs. 1–4. *Trichia brunnea* (Moravec s. num., holotype of *Hemitrichia stipata* var. *fusca*). – 1: Habit, group of sporangia on reindeer dung. 2–4: Spores and capillitium showing variation in ornamentation and tips of free capillitium segments. Spores are thick-walled. – Bars: Fig. 1 = 1 mm, Fig. 3 = 20 µm. Figs. 2–4 are the same magnification.

Trichia brunnea J.J.Cox

Hemitrichia stipata var. *fusca* Z.Moravec was described from a moist chamber culture of reindeer dung collected in Norway (Moravec 1968). The type collection (Moravec s. num., 1965, PRM) consists of small groups of dark sporangia

that blend in with the background (Fig. 1). It has been compared with the type collection (Cox 570, UC) of *Trichia brunnea* J.J.Cox and found to be the same species. The following description is based on the type collection of



Figs. 5, 6. *Trichia brunnea* (Lundqvist 14925-d), SEMs. — 5: Capillitium thread with sinistrorse spiral ornamentation. — 6: Spore. — Bars: Fig. 5 = 5 μm , Fig. 6 = 2 μm .

Hemitrichia stipata var. *fusca*. It broadens and deviates in some respects from the original description of *Trichia brunnea* (Cox 1981).

Sporangia gregarious to densely heaped, subsessile to distinctly stalked, ovoid or pear-shaped to short-cylindric, rounded at apex, total height 0.7–1.0 (–1.2) mm, dark olivaceous brown. Stalks up to 0.4 mm long, filled with rounded cells 8–15 μm in diam. Peridium thin, lustrous and somewhat iridescent with fine undulations 8–10 μm in extension, long-persistent, dehiscing irregularly from above, leaving a deep but sometimes poorly defined and irregular basal cup. Capillitium predominantly of free unbranched elaters, partly of branched threads forming an incomplete network, ornamentation of 3 (–4) distinct, sinistrorse spiral bands (Fig. 5), sometimes poorly defined (Fig. 4) or entirely missing on individual segment or portions of the threads; free elaters (Figs. 2–4) mostly 40–200 μm long, 3.5–4.0 μm wide, pale yellow in transmitted light, with ends rounded, abruptly narrowed, sometimes with the spirals excurrent as one or two points or hooks,

or ending in an abruptly flattened swelling (Fig. 3). Spores dark brown in mass, olivaceous yellow in transmitted light, 8.5–9 μm in diam., almost smooth under the light microscope but with a few large warts giving the spores a slightly angular outline, spore wall 0.8–1.0 μm thick.

The number of spirals on the elaters of *Trichia brunnea* is three (or four), not two as mentioned in previous literature. The elaters are wider and the spores somewhat smaller than in the protologue. Diagnostic characters are the dark sporangia with iridescent peridium, the free elaters bearing three sinistrorse spirals, and the dark, thick-walled spores. In general habit the sporangia resemble *Arcyria*, portions of the capillitium are branched, and the spore ornamentation is reminiscent of that in several species of *Arcyria*.

Trichia brunnea is a true coprophilous species. It is known from three localities. All collections are from moist chamber cultures on herbivore (cow, horse, reindeer) dung. The evenly thickened spore wall may be an adaptation to passage through the intestinal tract of herbiv-

ores, requiring the action of digestive juices on the spore wall before germination can take place (cfr. *Kelleromyxa fimicola*, Eliasson et al. 1991, fig. 13).

Specimens studied: U.S.A. California, Modoc Co., State Hwy. 299, Canby, 1314 m, 1978 Cox 570 (UC, holotype of *Trichia brunnea* J.J.Cox). Norway. Hordaland, alt. 1300 m, 1965 Moravec s. num. (PRM, holotype of *Hemitrichia stipata* var. *fusca* Z.Moravec). Montenegro. Durmitor National Park, Zabljak, 1984 Lundqvist 14925-d (GB, S).

Arcyria elaterensis Mulleavy

In the presence of both free elaters and a branched capillitium, *Trichia brunnea* resembles *Arcyria elaterensis* Mulleavy. Further similarities are the gregarious sporangia, the sinistrorse spiral ornamentation and frequent occurrence of clavate tips on the elaters, the rounded cells filling up the interior of the stalk, and the coprophilous habitat. Differences, based on the type of *A. elaterensis* (U.S.A., California, Contra Costa County, Briones Regional Park, Mulleavy no. 648; UC), are the brighter, yellowish brown sporangia of the latter species, the much more frequent occurrence of branches on the capillitium, the lighter and more thin-walled (ca. 0.4 µm) spores, and the more faintly marked spiral ornamentation on the capillitrial threads, although spirals may be distinct in some portions of the capillitium (Mulleavy 1977, fig. 7). In contrast, the dark iridescent sporangia and dark thick-walled spores separate *Trichia brunnea*.

Differences among genera of Myxomycetes are sometimes vague and there are several examples of transitional species merging into two different genera. *Arcyria elaterensis* appears to be a borderline species between *Arcyria* and *Trichia*. Emphasizing the presence of spiral bands on the capillitrial threads, Lado (in Lado & Pando 1997) transferred *A. elaterensis* to *Trichia*. Although *T. brunnea* and *A. elaterensis* have several features in common, parts of the capillitium of the latter species are branched in an arcyrioid manner, and the spirals on the capillitrial threads are mostly faintly marked and not of the type seen in *Trichia*. Portions of the capillitium may be completely devoid of spiral ornamentation. In our opinion, *Arcyria elaterensis* should be retained in this genus until its true phyloge-

netic relationship can be proven through molecular techniques.

Arcyria stipata (Schwein.) Lister

The presence of free elaters distinguishes *Arcyria elaterensis* from the variable *A. stipata* (Schwein.) Lister, but the two species are similar in habit and colour of the fructifications. The latter species, originally described as *Leangium stipatum* Schwein. (Schweinitz 1832), is one of the transitional species between *Arcyria* and *Hemitrichia*. Schweinitz' original specimen of *Leangium stipatum* (in PENN), referred to as no. 2304-3 in his Synopsis Fungorum and marked with the same number, is a tightly aggregated group of sporangia on bark of decaying wood. The fruiting is about 10 mm across. The sporangia are subsessile or short-stalked; the stalk filled with rounded cells ca 15 µm in diam. The spore mass is yellowish brown or greyish brown. Peridial fragments are transparent, smooth or with faint wrinkled or fan-like markings towards the base of the sporangium. The capillitium is netted and clearly arcyrioid with the threads bearing ornamentation of projections confluent into dense dextrorse spirals. The spores are ca 8 µm, very faintly ornamented, appearing smooth with the light microscope.

Leangium stipatum was transferred to *Hemitrichia* by Rostafinski (1876), to *Arcyria* by Lister (1894), and to *Hemitrichia* by Macbride (1899). Most recent monographs retain it in *Arcyria*. This unstable generic position stems from the variable structure and ornamentation of the capillitrial threads. The most characteristic ornamentation is faintly marked spirals bearing a comb-like or helicoidal crest of processes. Some specimens have capillitrial threads with ornamentation that varies from very faint spirals, sometimes totally lacking, to spirals intermixed with cogs, spines, half-rings, or reticulations. In other specimens, the capillitrial threads may exhibit more prominent spirals. The degree of branching of the capillitium may vary as may frequency of free ends and swellings. In a SEM study (Rammeloo 1986) based on four different specimens of *Arcyria stipata*, none of which was the type, the capillitrial threads had either various processes arranged helicoidally, or faint to distinct uneven ridges bearing various minor processes. Smooth spirals of the *Trichia* or *Hemitrichia* type could

not be demonstrated. The original specimen of *Leangium stipatum* differs from most specimens of *Arcyria stipata* in the dense spirals on the capillitrial threads. Apart from Schweinitz' original specimen, three additional specimens of *A. stipata* have been studied, all from the United States (*Thaxter* 1228, Connecticut; *Picket s. num.*, Massachusetts; *Darker* 546, Massachusetts; all in GB). Although there is some variability in the capillitrial system, none has free elaters and the spiral ornamentation is dextrorse throughout.

Nannenga-Bremekamp (1982) suggested inclusion of *Hemitrichia imperialis* G. Lister in *Arcyria stipata* mainly on grounds of birefringence characteristics in polarized light. The taxonomic delimitation of *Arcyria stipata* requires further study.

Acknowledgements. We thank the curators of herbaria PENN, PRM, and UC for loans of the type specimens used in this study.

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Received on 27 November 1998