



A. Aethalium, habit on leaf (bar = 1 cm). **B.** Aethalium, habit on moss (bar = 1 cm). **C.** Aethalium, habit on bark (bar = 1 cm). **D.** Capillitium and spores (bar = 20 µm). [Photographs: A. Michaud]

Fuligo septica (L.) F.H. Wigg., *Primitiae Florae Holsatiae*: 112 (1780). [*IndexFungorum* 149977; *Physaraceae*, *Stemonitidiida*]

Mucor septicus L., *Species Plantarum* Edn 2, 2: 1656 (1763). [*IndexFungorum* 432977]

Reticularia septica (L.) With., *A Botanical Arrangement of British Plants* Edn 2, 3: 470 (1792). [*IndexFungorum* 192205]

Aethalium septicum (L.) Fr., *Systema Mycologicum* 3(1): 93 (1829). [*IndexFungorum* 171952]

Mucor mucilago Scop., *Flora Carniolica* Edn 2, 2: 492 (1772). [*IndexFungorum* 142877]

Mucor ovatus Schaeff., *Fungorum qui in Bavaria et Palatinatu circa Ratisbonam Nascentur Icones* 4: 132, pl. 192 [vol. 2] (1774). [*IndexFungorum* 433205]

Reticularia ovata (Schaeff.) With., *A Botanical Arrangement of British Plants* Edn 2, 3: 471 (1792). [*IndexFungorum* 183742]

Fuligo ovata (Schaeff.) T. Macbr., *The North American Slime-Moulds* Edn 1: 23 (1899). [*IndexFungorum* 634762]

- Reticularia lutea* Bull., *Herbier de la France* **8**(85-96): pl. 380, fig. 1 (1788). [*IndexFungorum* 189161]
Reticularia hortensis Bull., *Herbier de la France* **9**(97-108): pl. 424, fig. 2 (1789). [*IndexFungorum* 234124]
- Fuligo hortensis* (Bull.) Duby, *Aug. Pyrami de Candolle, Botanicon Gallicum, seu Synopsis Plantarum in Flora Gallica Descriptarum* Edn 2, **2**: 863 (1830). [*IndexFungorum* 241715]
- Fuligo varians* Sommerf., *Supplementum Florae Lapponicae*: 239 (1826). [*IndexFungorum* 140592]
- Fuligo flava* Pers., *Neues Magazin für die Botanik* **1**: 88 (1794). [*IndexFungorum* 241687]
- Aethalium flavum* (Pers.) Link, *Dissertationes Biologicae* **1**: 42 (1795). [*IndexFungorum* 151092]
- Aethalium septicum* var. *flavum* (Pers.) Fr., *Systema Mycologicum* **3**(1): 93 (1829). [*IndexFungorum* 171747]
- Fuligo septica* var. *flava* (Pers.) Morgan, *Journal of the Cincinnati Society of Natural History* **19**: 32 (1895). [*IndexFungorum* 439633]
- Fuligo septica* f. *flava* (Pers.) Y. Yamam., *A Myxomycete Biota of Japan*: 401 (1998). [*IndexFungorum* 450612]
- Fuligo rufa* Pers., *Neues Magazin für die Botanik* **1**: 88 (1794). [*IndexFungorum* 241211]
- Aethalium septicum* var. *rufum* (Pers.) Fr., *Systema Mycologicum* **3**(1): 93 (1829). [*IndexFungorum* 171917]
- Reticularia rufa* (Pers.) Schwein., *Transactions of the American Philosophical Society New Series* **4**(2): 262 (1834) [publ. 1832]. [*IndexFungorum* 192142]
- Aethalium rufum* (Pers.) J. Becker, *Flora der Gegend um Frankfurt am Maine* **2**(1): 345 (1828). [*IndexFungorum* 633954]
- Fuligo septica* var. *rufa* (Pers.) Lázaro Ibiza, *Compendio de la Flora Española* Edn 1: 381 (1896). [*IndexFungorum* 438350]
- Fuligo septica* f. *rufa* (Pers.) Y. Yamam., *A Myxomycete Biota of Japan*: 402 (1998). [*IndexFungorum* 450613]
- Fuligo vaporaria* Pers., *Observationes Mycologicae* **1**: 92 (1796). [*IndexFungorum* 236038]
- Reticularia vaporaria* (Pers.) Chevall., *Flore Générale des Environs de Paris* **1**: 342 (1826). [*IndexFungorum* 180706]
- Aethalium vaporarium* (Pers.) J. Becker, *Flora der Gegend um Frankfurt am Maine* **2**(1): 345 (1828). [*IndexFungorum* 159161]
- Aethalium septicum* var. *vaporarium* (Pers.) Rabenh., *Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz* **1**: 253 (1844). [*IndexFungorum* 159052]
- Fuligo septica* var. *vaporaria* (Pers.) Lázaro Ibiza, *Compendio de la Flora Española* Edn 1: 381 (1896). [*IndexFungorum* 634755]
- Fuligo candida* Pers., *Observationes Mycologicae* **1**: 92 (1796). [*IndexFungorum* 238909]
- Aethalium candidum* (Pers.) Schltl., in K.P.J. SPRENGEL, *Systema Vegetabilium* Edn 16, **4**(1): 533 (1827). [*IndexFungorum* 179133]
- Fuligo septica* var. *candida* (Pers.) R.E. Fr., *Svensk Botanisk Tidskrift* **6**: 744 (1912). [*IndexFungorum* 123714]
- Fuligo septica* f. *candida* (Pers.) Meyl., *Bulletin de la Société Vaudoise de Sciences Naturelles* **55**: 240 (1924). [*IndexFungorum* 407692]
- Fuligo pallida* Pers., *Observationes Mycologicae* **2**: 36 (1799) [publ. 1800]. [*IndexFungorum* 240809]
- Reticularia cerea* Sowerby, *Coloured Figures of English Fungi or Mushrooms* **3**: [84], tab. 399, fig. 4 (1803). [*IndexFungorum* 674756]
- Fuligo carneae* Schumach., *Enumeratio Plantarum in Partibus Sællandiae Septentrionalis et Orientalis* **2**: 194 (1803). [*IndexFungorum* 239632]
- Reticularia carneae* (Schumach.) Fr., *Systema Mycologicum* **3**(1): 91 (1829). [*IndexFungorum* 143924]
- Fuligo flavescens* Schumach., *Enumeratio Plantarum in Partibus Sællandiae Septentrionalis et Orientalis* **2**: 194 (1803). [*IndexFungorum* 241760]
- Fuligo cerebrina* Brond., *Mémoires de la Société Linnéenne de Paris* **3**: 74 (1824). [*IndexFungorum* 248987]
- Aethalium septicum* var. *cinnamomeum* Fr., *Systema Mycologicum* **3**(1): 93 (1829). [*IndexFungorum* 562338]

- Aethalium ferrincola* Schwein., *Transactions of the American Philosophical Society New Series* **4**(2): 261 (1834) [publ. 1832]. [*IndexFungorum* 150727]
- Licea lindheimeri* Berk., *Grevillea* **2**(no. 17): 68 (1873). [*IndexFungorum* 178885]
- Tubulina lindheimeri* (Berk.) Massee, *A Monograph of the Myxogastres*: 42 (1892). [*IndexFungorum* 634756]
- Tubifera lindheimeri* (Berk.) E. Sheld., *Minnesota Botanical Studies* **1**: 465 (1895). [*IndexFungorum* 634757]
- Fuligo varians* f. *ecorticata* Rostaf., *Śluzowce (Mycetozoa) Monografia*: 136 (1874). [*IndexFungorum* 674758]
- Fuligo varians* var. *ecorticata* (Rostaf.) Cooke, *The Myxomycetes of Great Britain Contributions to Mycologia Britannica*: 24 (1877). [*IndexFungorum* 674759]
- Fuligo tetrica* Racib., *Hedwigia* **24**(4): 169 (1885). [*IndexFungorum* 149902]
- Fuligo candida* E. Jahn, in H. RÖNN, *Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein* **15**(1): 56 (1911), nom. illegit., *ICN* Art. 53.1 (non *Fuligo candida* Pers., 1796). [*IndexFungorum* 515964]
- Fuligo septica* var. *cinnamomea* R.E. Fr., *Svensk Botanisk Tidskrift* **6**: 744 (1912) ['irregularly and probably invalidly published' *fide* MARTIN & ALEXOPOULOS (1969): 267]. [*IndexFungorum* identifier not issued]
- Fuligo septica* f. *corticata* Meyl., *Bulletin de la Société Vaudoise de Sciences Naturelles* **55**: 240 (1924). [*IndexFungorum* identifier not issued]
- Fuligo septica* var. *rosea* Nann.-Bremek., *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen Series C, Biological and Medical Sciences* **76**(5): 485 (1973). [*IndexFungorum* 348129]
- Fuligo candida* f. *persicina* Y. Yamam., *Bulletin of the National Science Museum Series B* **26**(3): 110 (2000). [*IndexFungorum* 580573]

Vernacular names. Dutch: *heksenboter*. English: *dog vomit slime mould, flowers of tan, scrambled eggs*. French: *fleurs de la tannée*. German: *Gelbe Lohblüte*.

Diagnostic features. Large conspicuous irregular yellow or white plasmodia and aethalia; spores <10 µm diam.; cortex rough, not persistent; *Mucilago crustaea* P. Micheli ex F.H. Wigg., a common lookalike species found in similar habitats, is sometimes misidentified as *F. septica*, but its thickened cortex has crystalline, not granular, calcium carbonate.

On natural substratum. Amoebal state no information. *Plasmodium* white or yellow, sometimes very large (KELLER *et al.*, 2016). *Hypothallus* white, thin, papery, basal, ± developed. *Sporocarps* each a large pulvinate sessile aethalium formed from a single plasmodium, round, or mound-shaped, rough on the outside and fragile with irregular forms, initially white, later lemon yellow, yellow-green or ochraceous, 2–13 cm diam., 0.5–3(–8) cm thick, maximum size 76 × 56 cm, extending up to a surface of 500–600 cm², exuding reddish brown droplets at maturity. *Cortex* impregnated with lime, densely compacted or fragile, later crumbling away, spongy, foamy, rough, alveolate, rarely absent, the sporocarp then resembling a pseudoaethalium. *Pseudocapillitium* abundant, consisting of fragments of the peridium and containing calcareous granules. *Capillitium* consisting of slender non-calcareous ± reticulate threads connecting larger calcareous nodes, with few or many small spindle-shaped nodules of lime, sometimes scanty or poorly developed, sometimes almost entirely composed of limy elements. *Spores* dark brown or black *en masse*, individually pale, minutely warted, 6–9 µm diam. [Description derived partly from POULAIN *et al.*, 2011].

ASSOCIATED ORGANISMS & SUBSTRATA: *Animalia.* *Agathidium angulare* Mannerheim, 1852, *A. exiguum* Melsheimer, 1844, *A. oniscoides* Beauvois, 1817, *Agathidium* sp.; *Anisotoma basalis* (LeConte, 1853), *A. bifoveata* Wheeler, 1979, *A. discolor* (Melsheimer, 1844), *A. errans* Brown, 1937, *A. geminata* (Horn, 1880), *A. globososa* Hatch, 1929, *A. horni* Wheeler, 1979; *Baeocera* sp.; *Bos taurus* L., 1758 (dung); *Bradysia* sp.; *Diptera* indet.; *Drapetis nigritella* Zetterstedt; *Drosophila repleta* Wollaston, 1858; *Enicmus rugosus* (Herbst, 1793), *Enicmus* sp.; *Equus ferus* subsp. *caballus* L., 1758 [as 'horse'] (dung); *Eucinetus morio* LeConte, 1853; *Eurusphindus comatus* McHugh, 1993; *Formicidae* indet.; *Hylemyia cilicrura* Robineau-Desvoidy; *Latridius hirtus* Gyllenhal, 1827; *Leptocera fontinalis* Fallén, 1826; *Lonchaea vaginalis* Fallén, 1820; *Odontosphindus clavicornis* Casey, 1898; *Perisoreus canadensis* (L., 1766); *Scaphisoma* sp.; *Scatopse fuscipes* Meigen, 1830; *Sphindus americanus* LeConte, 1866, *S. trinifer*

Ornithogalum nutans L.; *Palmae* indet. (bark); *Pandanus tectorius* Parkinson ex Du Roi; *Picea abies* (L.) H. Karst. (branch, litter, log, root, stump, trunk, twig, wood), *P. schrenkiana* Fisch. & C.A. Mey., *P. sitchensis* (Bong.) Carrière (log, root, stump), *Picea* sp. (branch, cone, log, stump, trunk, woodchip); *Pinophyta* indet. (branch, litter, log, stump, wood); *Pinus nigra* J.F. Arnold (litter, stump), *P. ponderosa* Douglas ex C. Lawson (bark), *P. radiata* D. Don, *P. sylvestris* L. (bark, branch, leaf, log, stump, trunk, wood), *Pinus* sp. (branch, cone, litter, log, stump, twig, wood); *Plantae* indet. (bark, debris, leaf, litter, log, root, stem, stump, trunk, wood); *Podocarpus* sp.; *Populus alba* L. (wood), *P. balsamifera* L., *P. ×canescens* (Aiton) Sm. (log), *P. nigra* L. [also as *P. pyramidalis* Rozier] (bark, wood), *P. tremula* L. (wood), *Populus* sp. (leaf, wood); *Prunus lusitanica* L. (stump), *Prunus* sp. (trunk); *Pseudotsuga menziesii* (Mirb.) Franco (stump, wood), *Pseudotsuga* sp.; *Pteridium aquilinum* (L.) Kuhn (frond, litter); *Quercus petraea* (Matt.) Liebl., *Q. robur* L. (bark, branch, fruit, leaf, litter, log, root, stump, trunk, twig, wood), *Q. suber* L. (trunk), *Quercus* sp. (bark, branch, leaf, log, root, stump, wood); *Rhizophoraceae* indet.; *Rhopalostylis sapida* (Sol. ex G. Forst.) H. Wendl. & Drude (frond); *Rosaceae* indet. (branch); *Rubus fruticosus* agg. (leaf, wood); *Saccharum officinarum* L. (culm, leaf); *Salix alba* L. (wood), *Salix* sp. (branch, leaf, log, trunk, wood); *Sequoiadendron giganteum* (Lindl.) J. Buchholz (litter); *Sorbus aucuparia* L. (wood, woodchip); *Sphagnum* sp.; *Spiraeanthus schrenkianus* (Fisch. & C.A. Mey.) Maxim.; *Terminalia catappa* L. (log, wood); *Tilia cordata* Mill. (branch, stump), *Tilia* sp. (branch, wood); *Ulmus glabra* Huds., *Ulmus* sp. (branch, log, trunk); *Weinmannia silvicola* L. f. **Protista**. *Arcyria denudata* (L.) Wettst.; *Lycogala epidendrum* (J.C. Buxb. ex L.) Fr.; *Stemonitis fusca* Roth, *S. flavogenita* E. Jahn; *Trichia scabra* Rostaf., *T. varia* (Pers. ex J.F. Gmel.) Pers. **Substances**. Humus; soil (sandy). **Associated organism of type specimen.** None named. **Comment.** This species occurs on litter, fallen leaves, bark, decorticated branches, rotten stumps, fallen trunks, rotten wood and burnt logs of a very wide range of plants. It also occurs on soils, artefacts (particularly those from plant sources) and, occasionally, on dung. Environmental factors affecting this species on bagasse in Brazil were studied by CHIAPPETA *et al.* (2003).

INTERACTIONS & HABITATS: For a thorough introduction to myxomycete ecology, see MADELIN (1984).

The dead plant material with which myxomycetes are very widely associated, while undoubtedly a platform for their sporocarps, is not necessarily a source of nutrition. Sporocarps are the only stage in myxomycete life cycles where species can be identified by morphology. The other states, as amoebae and plasmodia, have received little attention. SHCHEPIN *et al.* (2019) suggested that populations of myxomycete amoebae may inhabit much wider ecological niches than indicated by records of their sporocarps. There is no specific information about the ecology and nutrition of the amoebal state of *F. septica*. In their amoebal state, myxomycetes are known to feed on small organic particles and micro-organisms (including some fungi). Although the identity of those micro-organisms is rarely recorded, SCHOLES (1962) isolated a species of *Penicillium* Link and two yeasts from plasmodia of *F. septica*, and noted that they, and a commercially produced strain of baker's yeast (*Saccharomyces cerevisiae*), when forming two-member cultures with *F. septica*, resulted in satisfactory growth of the myxomycete. By comparison, two-member cultures involving ten Gram-negative bacteria (not isolated from plasmodia) generally failed, with only *Corynebacterium* sp. and *Escherichia coli* resulting in limited growth for up to two weeks.

Fuligo septica has been observed in the following habitats: amenity & protected areas (cemeteries, national parks, ornamental gardens, parkland, public amenity areas, urban parks); coastal (coastal heaths, dune slacks); cultivated ground (domestic gardens, farmland, herb beds); freshwater (fens, marshes, streams, wetlands); grassland (acidic, calcareous, disturbed grassland, dune grassland, meadows, pasture, modified ['semi-improved'], unmodified ['unimproved']); margins (sides of canals, lakes, rivers, roads, riverside restoration plantings, woodland clearings); marine (mangroves); moorland (heath); ruderal (disused railway lines, industrial areas, industrial tips, urban areas, woodyards); woodland (broadleaf plantations, natural and semi-natural broadleaf woodland, conifer plantations, natural and semi-natural conifer woodland, mixed plantations, natural and semi-natural mixed woodland, scrub). *Fuligo septica* is often observed in gardens on woodchips used for mulching. There is also a record growing on ornamental plants in greenhouses (CARRAI *et al.*, 1987).

The remarkable tolerance by *F. septica* of high levels of toxic metals (see **Economic Impacts** below) means that this species is also found in highly specific environments. During a biological survey of iron ore caves near San Sebastian (Basque Country, Spain) numerous sporocarps were found in limestone cavities, on stalagmites and on plant remnants near cave exits. This humid, dark and toxic environment is not suitable for most organisms because of the high concentrations of toxic metals (Zn, Cu, Pb), iron ore, carbonates, sulphides, sulphates and silicates, but *F. septica* survives and grows there, accompanied by numerous populations of chemolithotrophic bacteria (mainly *Ferrobacteriales*), thought to be a source of nutrition for the myxomycete (GALÁN, 2015).

Several fungi and protists have been observed growing on the same substratum (DUDKA & ROMANENKO, 2006), and some fungi may parasitize the present species (ROGERSON & STEPHENSON, 1993). Many beetles are known to be associated with this species (STEPHENSON *et al.*, 1994) and there is a study of their rôle in spore dispersal (BLACKWELL *et al.*, 1982). Flies are known to be associated with this species (BUXTON, 1954), ants have been observed inhabiting aethalia [*Cybertruffle*, accessed 22 November 2019], and birds have been observed eating colonies (SUTHERLAND & CRAWFORD, 1979). Associations with micro-organisms are known. Recent molecular work, using 16s rDNA genes (commonly used to detect and construct phylogenies of prokaryotes) amplified from plasmodia of *F. septica*, detected 86 different operational taxonomic units (OTUs). Among these there were common OTUs representing groups of bacteria, mostly *Proteobacteria*, with a few *Bacteroidetes* and *Firmicutes* (LI *et al.*, 2018). It is still the case, however, that no observations have been found where the associated organism was identified to genus or species level.

GEOGRAPHICAL DISTRIBUTION: AFRICA: Algeria, Burundi, Democratic Republic of the Congo, Equatorial Guinea, Eritrea, Lesotho, Liberia, Madagascar, Malawi, Mayotte, Morocco, Nigeria, Sierra Leone, South Africa, Tanzania, Tunisia, Uganda, Zimbabwe. NORTH AMERICA: Canada (Alberta, British Columbia, Manitoba, New Brunswick, Newfoundland, Northwest Territories, Nova Scotia, Nunavut, Ontario, Prince Edward Island, Quebec), Mexico, USA (Alabama, Alaska, Arizona, Arkansas, California, Colorado, Connecticut, Delaware, Florida, Georgia, Idaho, Illinois, Indiana, Iowa, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Montana, Nebraska, Nevada, New Hampshire, New Jersey, New Mexico, New York, North Carolina, North Dakota, Ohio, Oklahoma, Oregon, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Texas, Utah, Vermont, Virginia, Washington, West Virginia, Wisconsin, Wyoming), Mexico. CENTRAL AMERICA: Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama. SOUTH AMERICA: Argentina, Bolivia, Brazil (Bahia, Maranhão, Paraíba, Pernambuco, Roraima, Santa Catarina, São Paulo, Sergipe), Chile, Ecuador (including Galapagos), French Guiana, Guyana, Paraguay, Peru, Uruguay, Venezuela. ASIA: Brunei, China (Fujian, Guizhou, Jiangsu, Zhejiang), Georgia, India (Assam, Chandigarh, Himachal Pradesh, Tamil Nadu, Uttar Pradesh, Uttarakhand), Indonesia, Iran, Japan, Jordan, Kazakhstan (Akmola, Aktobe, Almaty, East Kazakhstan, Karaganda, former Kokshetau, Kostanai, North Kazakhstan, Pavlodar, former Tselinograd, West Kazakhstan), Malaysia, Nepal, North Korea, Pakistan, Papua-New Guinea, Philippines, Russia (Altai Krai, Khanty-Mansi Autonomous Okrug, Krasnoyarsk Krai, Magadan Oblast, Novosibirsk Oblast, Tyumen Oblast), Singapore, South Korea, Turkey, Uzbekistan, Vietnam. ATLANTIC OCEAN: Spain (Canary Islands). AUSTRALASIA: Australia (New South Wales, Queensland, South Australia, Tasmania, Victoria, Western Australia), New Zealand. CARIBBEAN: American Virgin Islands, Antigua and Barbuda, Cuba, Dominica, Dominican Republic, Guadeloupe, Jamaica, Martinique, Puerto Rico, Saint Lucia, Trinidad and Tobago. EUROPE: Andorra, Austria, Belarus, Belgium, Croatia, Czech Republic, Denmark, Estonia, Finland, France, Germany, Greece, Hungary, Ireland, Italy, Latvia, Lithuania, Luxembourg, Moldova, Netherlands, Norway, Poland, Portugal, Romania, Russia (Astrakhan Oblast, Chelyabinsk Oblast, Chuvash Republic, Kaliningrad Oblast, Komi Republic, Krasnodar Krai, Kursk Oblast, Leningrad Oblast, Moscow Oblast, Murmansk Oblast, Orenburg Oblast, Pskov Oblast, Republic of Karelia, Stavropol Krai, Tver Oblast, Volgograd Oblast), Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland, Turkey, Ukraine, UK. INDIAN OCEAN: Christmas Island, Mauritius, Réunion, Seychelles. PACIFIC OCEAN: French Polynesia, Marshall Islands, New Caledonia, Solomon Islands, USA (Hawaii).

Elevation (m above sea level). Records up to 3450 (Guatemala); 3440 (Venezuela); 3330 (Mexico); 2250 (Japan); 2200 (Andorra); 2000 (Malawi).

Comment. Recorded from all continents except Antarctica, and from many oceanic islands. Probably native throughout its known distribution.

ECONOMIC IMPACTS: SETÄLÄ & NUORTEVA (1989), STIJVE & ANDREY (1999) and ZHULIDOV *et al.* (2002) showed that *F. septica* tolerates extreme levels of zinc. ZHULIDOV *et al.* (2002), working with many samples from a range of sources, reported (extrapolated) levels of 840–23000 mg/kg aethalium dry weight. In dry museum samples of *F. septica* and *Lycogala epidendrum* collected in Finland from 1860 to 1964, an abnormally high concentration of zinc and significant metal content as a whole were noted in *F. septica*, but no similar trend was observed for *L. epidendrum* (SETÄLÄ & NUORTEVA, 1989). The mechanism of this possibly unique tolerance was explored by LATOWSKI *et al.* (2008). They found that the ability to resist zinc and other heavy metals was due to synthesis of a yellow pigment, fuligorubin A (responsible for the distinctive colour of *F. septica* plasmodia; see also below), which forms chelating complexes with Zn, converting them into an inactive form. Spectrometric analysis revealed correlation between increases in zinc concentration and pigment synthesis. The same mechanism may also operate on other metals, resulting in high tolerance of *F. septica* to toxic elements. Fuligorubin A may also be involved in photoreception and energy conversion in this species. The remarkable tolerance of *F. septica* to toxic metals at dose levels which would be lethal for many other organisms prompted LATOWSKI *et al.* (2008) to suggest that the species has value as a model for exploring interactions between these elements and living cells.

There is further experimental evidence that *F. septica* can accumulate heavy metals (KRYVOMAZ, 2015, 2016; KRYVOMAZ & MAXIMENKO, 2016; KRYVOMAZ *et al.*, 2017c). KRYVOMAZ (2017a) measured metal levels in samples of *F. septica*, and in its substrata and surrounding soil. The levels of different elements were, in descending order, as follows [µg of metal per g of myxomycete tissue]: Ca (82533·33), Zn (10931·35), P (8033·33), Ba (6011·33), K (3133·33), Mn (2383·90), Sr (1239), Mg (886·66), Fe (208·86), Al (79·58), Cu (10·93), Cr (9·05), As (5·98), Ni (4·45), Bi (1·95), Cd (1·69), Sn (0·52), Pb (0·29), Hg (0·01). Analysis of those results showed that Mn and Cd were accumulated much more strongly by this species than by the others included in the study. An accumulation coefficient was used to calculate the concentration ratios between myxomycete and substratum, and between myxomycete and soil. The ratios revealed different accumulation patterns. These were termed by KRYVOMAZ (2017a) as:

- accumulation [concentration in myxomycetes higher than in substrata and soil]: in *F. septica* this pattern was observed for Mg, Ca, Cd, Mn, Zn, Cu, Bi, As;
- soil-dependent accumulation [concentration in myxomycetes less than in soil, but more than in substrata]: in *F. septica* this pattern was observed for Pb, Fe, Cr;
- no accumulation [concentration in myxomycetes lower than in substrata and soil]: in *F. septica* this pattern was observed for Al, Ni.

Heavy metal accumulating properties are likely to have significant positive economic potential (STEPHENSON & MCQUATTIE, 2000). Although nothing has yet been developed for the present species, there is considerable interest in use of fungi with similar abilities for bioremediation and other applications (GADD, 2007).

Some myxomycetes, including *F. septica*, have long been known to produce bioactive compounds. CONSIDINE & MALLETT (1965) cited research by J.C. Sobels in 1950, who found that slime produced by myxomycete plasmodia inhibited growth of certain bacteria and yeasts. LOCQUIN & PREVOT (1948) reported extraction of two pigmented antibiotic materials thought to be anthraquinone acids from *F. septica*. CASSER *et al.* (1987) isolated the tetramic acid derivative fuligorubin A from *F. septica* (see also above), which makes the plasmodium yellow. Tetramic acid derivatives are also found in mycotoxins, antibiotics, and antitumor agents. Extracts from *F. septica* show antibiotic activity against *Bacillus subtilis* (Ehrenberg) Cohn and *Candida albicans* (C.P. Robin) Berkout (CHIAPPETA *et al.*, 1999). Crude extracts from *F. septica* inhibited *Bacillus subtilis* and *Escherichia coli* (inhibition rates of 68.00% and 59.45% respectively), but had only minor effects on *Salmonella typhimurium* [= *S. enterica* subsp.

enterica serovar *Typhimurium*] and *Staphylococcus aureus* Rosenbach, 1884 and no effect on *Pseudomonas pyocyanea* (Zopf, 1884) Migula, 1895 [= *P. aeruginosa* (Schröter, 1872) Migula, 1900] (WANG *et al.*, 2017).

NAKATANI *et al.* (2004) and ISHIBASHI (2005) reported cytotoxic activity by extracts from *F. septica* [as *F. candida*], including cycloanthranilylproline, against murine leukaemia P388 cells. Methanol extracts from the plasmodia and sclerotia of *F. septica* displayed an inhibitory effect on B16 F1 murine melanoma cells (WANG *et al.*, 2017). JIANG *et al.* (2014) studied antibacterial activity of *F. septica* plasmodia and sclerotia, and showed that methanol extracts from the plasmodia and sclerotia all demonstrated good antioxidant activities. There are further reports of other novel compounds from *F. septica* with as yet undetermined biological activities and functions. These include the glycoside derivative of a multibranched polyunsaturated fatty acid ((2E,4E,7S,8E,10E,12E,14S)-7,9,13,17-tetramethyl-7,14-dihydroxy-2,4,8,10,12,16-octadecahexaenoic acid), a surfactant of potential commercial interest particularly in the food and pharmaceutical industries (ŘEZANKA, 2002; DEMBITSKY, 2004), and fuligoic acid from *Fuligo septica* f. *flava* (SHINTANI *et al.*, 2009). No evaluations have been made of any other possible positive economic impact of this organism (e.g. as a recycler, as a source of useful products, as a provider of checks and balances within its ecosystem, etc.).

There are some reports of negative economic impacts. *Fuligo septica* was used in medical studies to investigate the possibility that myxomycete spores can trigger allergic responses (e.g. GIANNINI *et al.*, 1975). SANTILLI *et al.* (1985a) used dialyzed extracts from spores of this species and several fungi for intradermal skin testing of patients with asthma and allergic rhinitis, and made similar tests on highly ragweed-sensitive subjects (SANTILLI *et al.*, 1985b) and on mould-sensitive patients (ROCKWELL *et al.*, 1988). Similar work was reported from Venezuela (BENAÍM PINTO, 1992). In a study of human seasonal allergic rhinitis, LIERL (2013) found that 42% of patients were sensitized to myxomycete spores, including those of the present species.

Fuligo septica has also been reported on plastic and wood from mushroom-growing farms in Taiwan as a weed and potential parasite (CHUNG *et al.*, 1998). There are several reports of *F. septica* causing damage to plant crops (AGRA *et al.*, 2018). It was listed as a disease on seedling leaves of *Elaeis guineensis* in Malaysia (THOMPSON & JOHNSTON, 1953; TURNER, 1971). BERESTETSKAYA (1998) reported a pathogen of strawberries from Omsk, Russia, identifying it as *F. septica*, and briefly reviewed its geographical distribution, harmfulness and control. SILVA & BEZERRA (2005) similarly reported *F. septica* causing serious losses of *Eryngium foetidum* and *Lactuca sativa* in Maranhão, Brazil, providing photographs of symptoms and spores. There are further reports of this species from Korea, infesting *Ipomoea batatas* (KIM *et al.*, 2007), and from Zhejiang province, China, causing economic damage to *Dendrobium candidum*, a plant widely cultivated for traditional herbal medicines (TU *et al.*, 2016). In all of these reports, damage seems to be either mechanical or the result of extensive plasmodial growth smothering plants, rather than genuine parasitism. No other reports of negative economic impacts have been found.

INFRASPECIFIC VARIATION: Several subspecific taxa have been described. *Fuligo septica* var. *laevis* (Pers.) R.E. Fr. is the basionym of *Fuligo laevis* Pers., which is a separate accepted species [<http://eumycetozoa.com>, accessed 14 November 2019]. The others are all listed in the synonymy above. Three of them are in current use. *Fuligo septica* var. *septica*, the typical variety, is distinguished by pale yellow to whitish ochraceous aethalia, a colourless capillitium with few or very small lime nodules, and a yellow plasmodium. *Fuligo septica* var. *candida* has white aethalia, white inner lime, and a white plasmodium. *Fuligo septica* var. *flava* has yellow aethalia, yellow inner lime, and a yellow plasmodium. BERRY & FRANKE (1973) observed that within *Fuligo septica* distinct isozyme patterns could be detected between white and yellow strains.

DISPERSAL & TRANSMISSION: For a general discussion about myxomycete dispersal, see KRYVOMAZ & STEPHENSON (2017). Myxomycete spores are dispersed considerable distances by wind. Field experiments and mathematical modeling have shown that, with winds of 0·1 m/s, spores can travel up to c. 1·8 km, and when wind speed reaches 28 m/s, this rises to over 500 km (TESMER & SCHNITTNER,

2007). Spores and myxamoebae may be dispersed by rainwater and water in soil. Some local dispersal may also occur by movement of myxamoebae and plasmodia. Insects and other invertebrates feed on sporophores, as probably do terrestrial vertebrates including birds, and myxomycete spores have been found in insect faeces, suggesting that animals may play a part in their dispersal. Plant debris floating in seawater may also contribute to dispersal between land masses.

CONSERVATION STATUS: The IUCN's Red Listing Criteria were originally designed for evaluation of vertebrate animals and flowering plants, and present challenges to those trying to apply them to organisms like myxomycetes which are unicellular for a significant part of their life cycle. A discussion of those challenges, particularly in respect of myxomycetes and climate change, is provided by KRYVOMAZ & STEPHENSON (2017). **Previous evaluations.** None, but one of the most common and widely distributed of all myxomycetes. **Information base.** Over 15,000 records (specimens, databases and bibliographic sources combined, excluding duplicates) from at least 1763 to June 2019, with observations in every month of the year, peaking in the northern hemisphere between June and October. **Estimated extent of occurrence** [calculated using <http://geocat.kew.org>]. Well over 180·6 million km² (Africa [sub-Saharan only]: 27·7 million km²; Asia: 61·4 million km²; Australasia: 9·2 million km²; Europe [including north Africa]: 13·0 million km²; North America [including the Caribbean and Central America]: 28·2 million km²; Pacific Ocean: 17·7 million km²; South America: 23·4 million km²). **Estimated area of occupancy** [calculated using <http://geocat.kew.org>]. Well over 6100 km². The method for estimating area of occupancy has produced an artificially low figure. The species is likely to be under-recorded, particularly because of the small number of people with the skills to search for and identify it. Many of the plants with which it is associated are common and widespread species. **Threats.** Insufficient information to enable threats to be identified. In particular, possible vulnerabilities of the amoebal and plasmodial states of this species are currently completely overlooked. **Population trend.** In general, not known. Very common in Mexico (LIZÁRRAGA *et al.*, 1998); occasional and local in northern Thailand (TRAN *et al.*, 2006); very common and increasing in Saxony, Germany (HARDTKE *et al.*, 2015). Of datable records, c. 10% are pre-1961, 40% post-1960 but pre-2001, and 50% post-2000. **Evaluation.** Using IUCN criteria (IUCN SPECIES SURVIVAL COMMISSION. 2006 *IUCN Red List of Threatened Species* [www.iucnredlist.org]). Downloaded on 15 May 2006), the species is assessed globally as Least Concern. **In situ conservation actions.** None noted. **Ex situ conservation actions.** 263 nucleotide sequences, 12 PopSet sequences and 62 protein sequences were found in a search of the NCBI GenBank database [www.ncbi.nlm.nih.gov, accessed 3 October 2018]. No living strains of this species are listed by the ATCC, CABI and Westerdijk Institute [formerly CBS] culture collections. *Fuligo septica* can be grown successfully in culture (LAZO, 1961). A full account of some relevant culturing techniques was provided by SCHOLES (1962).

NOTES: *Fuligo septica* is sufficiently iconic and well known to have a presence on YouTube [e.g. www.youtube.com/watch?v=pTcv_E7LhpM, accessed 20 November 2019]. Being iconic, it was one of the first myxomycetes to be noticed. STEPHENSON (2010) speculated observations could go back as far as the 9th century in China, while ING & STEPHENSON (2017) suggested that in Europe accounts may go back to a description in 1727 by the French author, Jean Marchant, of 'fleurs de la tannée'. In the 19th century, it was one of the first two myxomycetes to be collected from Australia. There are numerous reports in the media of home-owners worried by the unexpected and rapid development of large plasmodia of this species on garden lawns [e.g. www.thewashingtondailynews.com/2019/05/10/what-is-this-alien-growth-on-my-mulch, accessed 21 November 2019].

COWDRY (1918) provided an account of the cytology of this species, with special reference to mitochondria. PARKER (1946) reported that *F. septica* can grow under water. ELLIOTT (1949) provided a general account of myxomycete swarm cells, including the present species. BRAUN (1971) showed that aeration was an important factor in inducing spores of *F. septica* to germinate in water. In a study of spore germination in this species, DAHLBERG & FRANKE (1977) found that the process was complex and controlled, not random, and that logarithmic kinetics were involved. They suggested that germination may be influenced by a soluble, dialyzable, auto-catalytic factor present in the aethalium. Spores may

remain able to germinate after 75 years, although viability decreases with age and the possibility of contamination cannot be ruled out. Freshly collected spores often germinate within 30 minutes, and swarm cells can be seen sometimes within an hour, making *F. septica* useful in teaching (KELLER & EVERHART, 2010). The presence of a cell coat in the amoebal state was demonstrated by DYKSTRA & ALDRICH (1978). NELSON & ORLOWSKI (1981) confirmed that oxygen is needed for spore germination, and provided a detailed account of part of the life cycle of this species, from spores, through germination to morphogenesis of motile flagellated swarm cells, illustrated by scanning electron micrographs.

Scanning electron micrographs of *F. septica* spores were also provided by LIZÁRRAGA *et al.* (1998). Plasmodia of this species were examined using transmission electron microscopy (McMANUS, 1965). Acrylamide disc electrophoresis was used to determine enzyme and general protein profiles for 45 isolates of *F. septica* from different places (BERRY & FRANKE, 1973). Some myxomycetes can, in unfavourable environments, form dormant plasmodia called sclerotia. KRZYWDA *et al.* (2008) made a detailed study of such sclerotia in *F. septica*. Yellow and white plasmodia had different profiles, suggesting that the technique might have useful applications in myxomycete taxonomy. The chemical composition of *F. septica* spore cases was studied by CHAPMAN *et al.* (1983), and of plasmodia by SONG *et al.* (2014). The possibility of using flow cytometry to characterize DNA content of *F. septica* spores was explored by ALLMAN (1992). Acidity electrophoresis was investigated by WANG *et al.* (2007a) as a tool for identifying this and other myxomycetes. The same team (WANG *et al.*, 2007b) provided an ultrastructural level description of nuclei and nucleoli.

Molecular techniques are now being introduced (HAUGEN *et al.*, 2003; MARTÍN *et al.*, 2003; LUNDBLAD *et al.*, 2004), and findings are resulting in changes to understanding of phylogeny (FIORE-DONNO *et al.*, 2005). There is a report on primers design and PCR optimization for amplification of the elongation factor of this species (LIU *et al.*, 2013). Another molecular technique now being developed helps detection of myxomycetes in soil. This may make it possible to identify species in their amoebal state. *Fuligo septica* was included in one such pioneering study (HOPPE & SCHNITTNER, 2015).

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