



A–C. Sporocarps showing diversity of morphology (bars = 1 mm). D. Capillitium and spores (bar = 10 μ m).
[Photographs: A. Michaud]

- Arcyria cinerea** (Bull.) Pers., *Synopsis Methodica Fungorum* **1**: 184 (1801). [*IndexFungorum* 174952; *Arcyriaceae*, *Trichiida*]
Trichia cinerea Bull., *Herbier de la France* **10**: tab. 477, fig. 3 (1790). [*IndexFungorum* 145193]
Stemonitis cinerea (Bull.) J.F. Gmel., *Systema Naturae* Edn 13, **2**(2): 1467 (1792). [*IndexFungorum* 145971]
Arcyria albida Pers., *Neues Magazin für die Botanik* **1**: 90 (1794). [*IndexFungorum* 170299]
Stemonitis glauca Trentep., in A.W. ROTH, *Catalecta Botanica* **1**: 221 (1797). [*IndexFungorum* 144387]
Stemonitis glauca var. *subglobosa* Trentep., in A.W. ROTH, *Catalecta Botanica* **1**: 221 (1797). [*IndexFungorum* 498970]
Stemonitis digitata Schwein., *Transactions of the American Philosophical Society New Series* **4**(2): 260 (1834) [publ. 1832]. [*IndexFungorum* 150035]
Arcyria digitata (Schwein.) Rostaf., *Śluzowce (Mycetozoa) Monografia*: 274 (1875). [*IndexFungorum* 153611]

- Clathroides digitatum* (Schwein.) E. Sheld., *Minnesota Botanical Studies* **1**: 467 (1895) [as 'Clatrhodes']. [IndexFungorum 634752]
- Arcyria cinerea* var. *digitata* (Schwein.) G. Lister, in A. LISTER, *A Monograph of the Mycetozoa A Descriptive Catalogue of the Species in the Herbarium of the British Museum*, Edn 3: 232 (1925). [IndexFungorum 260819]
- Arcyria trichioides* Corda, *Icones Fungorum hucusque Cognitorum* **2**: 23 (1838). [IndexFungorum 190560]
- Arcyria leprieurii* Mont., *Annales des Sciences Naturelles Botanique*, Série 4, **3**: 141 (1855). [IndexFungorum 235484]
- Stemonitis grisea* Opiz, *Lotos* **5**: 215 (1855). [IndexFungorum 234308]
- Arcyria bicolor* Berk. & M.A. Curtis, in M.J. BERKELEY, *Journal of the Linnean Society Botany* **10**: 349 (1869). [IndexFungorum 169545]
- Arcyria pallida* Berk. & M.A. Curtis, in M.J. BERKELEY, *Grevillea* **2**(no. 17): 67 (1873). [IndexFungorum 242476]
- Arcyria cinerea* subsp. *subleionema* Rostaf., *Śluzowce (Mycetozoa) Monografia*: 274 (1875). [IndexFungorum 634753]
- Arcyria friesii* Berk. & Broome, *Annals and Magazine of Natural History Series* 4, **17**: 140 (1876). [IndexFungorum 168266]
- Arcyria stricta* Rostaf., *Śluzowce (Mycetozoa) Monografia Suppl.*: 36 (1876). [IndexFungorum 190758]
- Lachnobolus arcycella* Rostaf., *Śluzowce (Mycetozoa) Monografia*: 431 (1875). [IndexFungorum 187110]
- Comatricha alba* Schulzer, *Oesterreichische Botanische Zeitschrift* **27**: 167 (1877). [IndexFungorum 183235]
- Arcyria cinerea* var. *cribroides* Raunk., *Botanisk Tidsskrift* **17**: 58 (1888) [publ. 1890]. [IndexFungorum 154049]
- Arcyria cookei* Masee, *A Monograph of the Myxogastres*: 154 (1892). [IndexFungorum 153863]
- Clathroides cookei* (Masee) E. Sheld., *Minnesota Botanical Studies* **1**: 467 (1895) [as 'Clatrhodes'] [IndexFungorum 634754]
- Arcyria tenuis* J. Schröt., in P.C. HENNINGS, *Hedwigia* **35**(4): 207 (1896). [IndexFungorum 190466]
- Arcyria digitata* f. *subglobosa* Meyl., *Annuaire du Conservatoire et du Jardin Botaniques de Genève* **15-16**: 321 (1913). [IndexFungorum 167742]
- Arcyria digitata* f. *globosa* Meyl., *Bulletin de la Société Vaudoise de Sciences Naturelles* **55**: 244 (1924). [IndexFungorum 263201]
- Arcyria cinerea* f. *subglobosa* Meyl., *Bulletin de la Société Vaudoise de Sciences Naturelles* **55**: 244 (1924). [IndexFungorum 260813]
- Arcyria cinerea* f. *rubella* Y. Yamam., *Bulletin of the National Science Museum Series B* **26**(3): 107 (2000). [IndexFungorum 482834]

Vernacular names. Dutch: *asgrauw netwatje*. German: *Grauer Kelchstäubling*.

Diagnostic features. Very variable in form and colour, but never red or pink; on dead wood, often in large groups; microscopically easily distinguished from other *Arcyria* species by its capillitium which is smooth proximally (near the cup) but spinulose distally; similar to *A. pomiformis* (Leers) Rostaf. which differs in having a cup inner surface ornamented with warts or a raised network whereas that of *A. cinerea* is smooth.

On natural substratum. Amoebal state irregular, with no transparent ectoplasm; forming filopodia during locomotion (YANG *et al.*, 2018); swarm cells biflagellate (MIMS, 1971; see also ELLIOTT, 1949). *Plasmodium* white or with a pinkish tinge, sometimes grey or greenish; plasmodial membranes and pseudopods (also called lobopods) are involved in formation of diploid myxamoebae and swarm cells; these occur when a small unit of protoplasm at the leading edge of an advancing plasmodial fan separates from a pseudopod to become a myxamoeba, eventually developing flagella and dispersing; this may also happen along the veinlets (INDIRA, 1964, 1969). *Hypothallus* discoid under isolated sporangia, and extending continuously under groups. *Sporocarps* stalked sporangia, dispersed or in groups which are often large, erect, 0.3–2.5(–4) mm tall; sometimes forming compound structures which are fused or fascicle-stalked, especially in the Tropics. *Stalks* concolorous with the sporothecae or darker, 0.2–2 mm long, filled with

round cells 14–24 µm diam., sometimes clustered, or confluent and fused. *Sporothecae* subcylindrical, rarely almost spherical or ovoid, colours very variable, mostly almost white or pale grey to beige, rarely ochraceous, 0.5–0.8 mm diam. *Peridium* single, membranous, fleeting, with fragments remaining at the base as a calyculus which is small, radially furrowed, smooth, papillate, very minutely punctate or partly reticulate. *Columella* absent. *Capillitium* small-meshed, densely reticulate, expanding slightly, firmly connected to the cup, 2–6 µm diam., in the upper part strongly spinulose with numerous spinules or cogs, the basal threads nearly smooth or with thinner spinules. *Spores* globose, 6–8 µm diam., almost colourless, smooth, with a few larger warts visible under oil immersion; as with some other myxomycetes, larger spores, 10.3–12.5 µm diam., are sometimes encountered when the species is grown in moist chambers.

ASSOCIATED ORGANISMS & SUBSTRATA: **Animalia.** *Anisotoma basalis* (LeConte, 1853), *A. bifoveata* Wheeler, 1979, *A. horni* Wheeler, 1979; *Alces alces* (L., 1758) (dung); *Animalia* indet. (dung); *Baeocera* sp.; *Equus caballus* Boddaert, 1785 (dung); *Lepus timidus* L., 1758 (dung). **Artefacts.** Compost (bagasse); fuel (coal); thatch. **Fungi.** *Aphanocladium album* (Preuss) W. Gams; *Eutypa lata* (Pers.) Tul. & C. Tul.; *Fomes fomentarius* (L.) Fr. (basidioma); *Gliocladium album* (Preuss) Petch; *Heterobasidion annosum* (Fr.) Bref.; *Nectria peziza* (Tode) Fr.; *Nectriopsis candicans* (Plowr.) Maire, *N. exigua* (Pat.) W. Gams [as *Verticillium rexianum* (Sacc.) Sacc.]; *Neonectria coccinea* (Pers.) Rossman & Samuels [as *Nectria coccinea* (Pers.) Fr.]; *Orbilbia coccinella* Fr.; *Polycephalomyces tomentosus* (Schrad.) Seifert [also as *Stilbum tomentosum* Schrad.]; *Stilbum echinatum* Ellis & Everh.; *Trichophaeopsis bicuspis* (Boud.) Korf & Erb. **Plantae.** *Abies borisii-regis* Mattf. (wood), *A. nordmanniana* subsp. *equi-trojani* (Asch. & Sint. ex Boiss.) Coode & Cullen [as *A. nordmanniana* subsp. *bornmuelleriana* (Mattf.) Coode & Cullen] (log), *A. sibirica* Ledeb., *Abies* sp. (wood); *Acer pseudoplatanus* L. (bark, wood), *A. saccharum* Marshall (wood); *Aeonium arboreum* Webb & Berthel. (leaf); *Agathis australis* (D. Don) Lindl.; *Agave lechuguilla* Torr.; *Alnus glutinosa* (L.) Gaertn. (branch), *Alnus* sp. (bark, stump); *Anisotome latifolia* Hook. f.; *Apiaceae* indet. (stem); *Areaceae* gen. indet.; *Artemisia thuscula* Cav. (wood); *Arundo donax* L.; *Asplundia rigida* (Aubl.) Harling (stem); *Bambusa* sp. (stem); *Beilschmiedia pendula* (Sw.) Hemsl.; *Betula pendula* Roth (bark), *Betula* sp. (branch, leaf, wood); *Bromeliaceae* indet.; *Bryophyta* indet. (thallus); *Buchenavia tetraphylla* (Aubl.) R.A. Howard; *Bulbinella rossii* (Hook. f.) Cheeseman; *Bursera graveolens* (Kunth) Triana & Planch. (wood), *Bursera* sp.; *Calophyllum inophyllum* L. (wood); *Calyptronoma plumeriana* (Mart.) Lourteig; *Camellia sinensis* (L.) Kuntze (bark, root); *Carpinus betulus* L. (wood), *Carpinus* sp. (bark); *Castanea sativa* Mill. (bark), *Castanea* sp.; *Catalpa bignonioides* Walter (bark); *Cecropia peltata* L. (bark, liana); *Cirsium arvense* (L.) Scop.; *Cladium mariscus* (L.) Pohl (culm); *Cocos nucifera* L. (stem); *Coniferae* indet. (wood); *Conium maculatum* L. (stem); *Corylus avellana* L. (wood); *Crataegus monogyna* Jacq.; *Cyanus montanus* (L.) Hill [as *Centaurea montana* L.] (wood); *Cyperus papyrus* L.; *Delonix regia* (Hook.) Raf. (bark); *Dracophyllum scoparium* Hook. f.; *Elaeis guineensis* Jacq.; *Epipremnum pinnatum* (L.) Engl. (liana); *Eucalyptus* sp. (bark, wood); *Euphorbia antisiphilitica* Zucc., *E. balsamifera* Aiton, *E. canariensis* L., *E. lamarckii* Sweet, *Euphorbia* sp. (bark); *Fagus orientalis* Lipsky (bark, branch), *F. sylvatica* L. (bark, leaf, trunk, wood), *Fagus* sp.; *Falcataria moluccana* (Miq.) Barneby & J.W. Grimes; *Fraxinus americana* L. (wood), *F. excelsior* L. (bark), *Fraxinus* sp. (bark); *Frullania dilatata* (L.) Dumort. (thallus); *Glyceria maxima* (Hartm.) Holmb. (culm), *Glyceria* sp. (leaf); *Hedychium coronarium* J. Koenig (inflorescence); *Heliconia psittacorum* L. f. (inflorescence); *Hemitelia muricata* (Willd.) Fée [as *Cyathea muricata* Willd.] (frond); *Hepaticae* indet.; *Hoheria populnea* A. Cunn.; *Hypnum cupressiforme* Hedw. (thallus); *Iris pseudacorus* L. (spathe); *Juniperus excelsa* M. Bieb. (bark); *Kleinia neriifolia* Haw.; *Larix decidua* Mill. (stump), *Larix* sp. (bark); *Leptospermum* sp.; *Magnoliopsida* sp. (wood); *Malus domestica* Borkh. (bark), *Malus* sp. (bark); *Metrosideros* sp.; *Mnium hornum* Hedw.; *Muscopsida* indet.; *Myosotis arvensis* (L.) Hill; *Nothofagus fusca* (Hook. f.) Oerst., *N. fusca* var. *colensoi* (Hook. f.) Cheeseman [as *N. truncata* (Colenso) Cockayne], *N. pumilio* (Poepp. & Endl.) Krasser (wood), *Nothofagus* sp. (bark); *Palmae* indet. (log, petiole, stipe, stump, trunk); *Phoenicophorium borsigianum* (K. Koch) Stuntz (leaf); *Phoenix dactylifera* L. (leaf); *Phyllostachys* sp.; *Picea abies* (L.) H. Karst. [also as *P. excelsa* (Lam.) Link] (branch, trunk, wood), *P. sitchensis* (Bong.) Carrière (branch, wood); *Pinus caribaea* Morelet (leaf), *P. heldreichii* Christ [as *P. leucodermis* Antoine] (bark), *P. massoniana* Lamb. (bark), *P. sylvestris* L. (bark, branch, cone), *Pinus* sp. (root, stump, trunk, wood); *Plantae* indet. (bark, branch, debris, litter, log, stick,

stump, trunk, wood); *Platanus orientalis* L. (bark); *Pleurophyllum* sp.; *Poa trivialis* L.; *Podocarpus* sp.; *Populus tremula* L. (twig), *Populus* sp. (branch, wood); *Porella platyphylla* (L.) Pfeiff. (thallus); *Pseudotsuga menziesii* (Mirb.) Franco (bark, stump, wood); *Pyrus communis* L. (bark), *Pyrus* sp. (bark); *Quercus petraea* (Matt.) Liebl. (bark), *Q. pubescens* Willd. (bark, branch, twig), *Q. robur* L. (bark, branch, wood), *Quercus* sp. (bark, wood); *Rhopalostylis sapida* (Sol. ex G. Forst.) H. Wendl. & Drude (frond); *Roystonea regia* (Kunth) O.F. Cook (leaf); *Rubus* sp. (stem); *Rumex lunaria* L., *Rumex* sp. (stem); *Saccharum officinarum* L. (stem); *Salix alba* L. (bark), *S. caprea* L. (wood), *S. cinerea* L. (log), *S. × fragilis* L. (bark), *Salix* sp. (bark, branch); *Sambucus nigra* L. (bark); *Scutia spicata* (Humb. & Bonpl. ex Willd.) Weberb.; *Selaginella* sp. (leaf); *Sorbus torminalis* (L.) Crantz (bark); *Stilbocarpa polaris* (Homb. & Jacq.) A. Gray; *Tamarix chinensis* Lour.; *Taxus baccata* L. (bark); *Terminalia* sp. (bark); *Thuja* sp. (wood); *Thunbergia grandiflora* (Roxb. ex Rottl.) Roxb. (leaf); *Tilia cordata* × *platyphyllos* (bark), *Tilia* sp. (bark); *Ulex europaeus* L. (branch, stem); *Ulmus laevis* Pall. (bark), *Ulmus* sp. (branch); *Urtica dioica* L. (stem); *Yucca elata* (Engelm.) Engelm. **Protista.** *Cribraria tenella* Schrad., *C. violacea* Rex; *Hemitrichia calyculata* (Speg.) M.L. Farr. **Associated organism of type specimen.** Not specified; illustration in protologue shows it on dead wood. **Comment.** This species occurs on fallen branches, dead wood, dead roots, dead stems, dead and living bark, litter, dead leaves, logs and straw of a very wide range of plants, and is also very commonly encountered on bark incubated in moist chambers. It also occurs occasionally on dung, on fungal carpophores, and on artefacts, particularly those derived from plant products. There are several records of other myxomycetes growing on the same substratum, and this species is also seen in association with a range of fungi (DUDKA & ROMANENKO, 2006), and is sometimes parasitized by them (ROGERSON & STEPHENSON, 1993). Several associations between this species and beetles have been observed in North America and Brazil (STEPHENSON *et al.*, 1994; LEMOS *et al.*, 2010). One of the associated organisms, *Phoenicophorium borsigianum*, an endemic of the Seychelles, is ‘the thief palm’. The generic name comes from the Greek words φοῖνιξ (palm) and φῶριος (stolen), and refers to the theft from Kew Gardens of one of the first specimens introduced in Europe. It later ‘appeared’ in the private greenhouse of German industrialist and passionate horticulturist, August Borsig (1804-1854), from whose name the specific epithet is derived.

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. In their amoebal state, myxomycetes are known to feed on small organic particles and micro-organisms (including some fungi), but the identity of those micro-organisms is rarely, if ever, recorded. There is very little specific information about the ecology and nutrition of the amoebal state of *A. cinerea*, but there are published observations of changes in shape and size of *A. cinerea* amoebae during locomotion (YANG *et al.*, 2018). *Arcyria cinerea* has been observed in the following habitats: amenity & protected areas (arboreta, botanic gardens, cemeteries, churchyards, gardens, nature reserves, orchards, parklands); coastal (dunes); cultivated ground; deserts (alpine, subalpine, subantarctic); freshwater (carrs, fens, marshes, ravines, swamps); grassland (meadows, pastures); margins (edges of pools and streams, sides of tracks); montane; ruderal (quarries); and woodlands (conifer forests, conifer plantations, mixed plantations, palm forests, scrub, natural and semi-natural broadleaf woodland). It has also been observed in greenhouses.

Arcyria cinerea is regularly reported from substrata over a wide pH range. It is one of the most consistently abundant and widespread myxomycete species associated with lianas, aerial woody remnants, leaves and inflorescences (all substrata with near-neutral pH values, 5.4–8.5, suitable for many species of myxomycetes) in tropical forests, and in mangrove forests (CAVALCANTI *et al.*, 2015, 2016). These microhabitats were investigated for neotropical forests (LADO *et al.*, 2003; MCHUGH, 2005; SCHNITTLER & STEPHENSON, 2002; WRIGLEY DE BASANTA *et al.*, 2008), forests in northern Queensland in Australia (BLACK *et al.*, 2004) and in southeast Asia (KO KO *et al.*, 2010). In one study in Thailand,

collections of this species were found only during the warm wet season, and not during the cool dry season (KO KO *et al.*, 2011). TAKAHASHI (2004) suggested substratum hardness and state of decay may be significant when this species occurs on wood. The senior authors have observed this species in the Seychelles on fallen wood of *Falcataria moluccana* (with a neutral pH of 7.26), and on *Calophyllum inophyllum* (with an acid pH of 4.61).

GEOGRAPHICAL DISTRIBUTION: AFRICA: Algeria, Angola, Burundi, Cameroon, Democratic Republic of the Congo, Egypt, Equatorial Guinea, Gambia, Kenya, Liberia, Madagascar, Malawi, Mayotte, Morocco, Mozambique, Nigeria, Rwanda, Sierra Leone, Somalia, South Africa, Tanzania, Tunisia, Uganda, Western Sahara, Zambia, Zimbabwe. NORTH AMERICA: Canada (Alberta, British Columbia, Manitoba, New Brunswick, Ontario, Quebec, Saskatchewan), Mexico, USA (Alaska, Arizona, Arkansas, California, Colorado, Connecticut, Delaware, Florida, Georgia, Idaho, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Montana, Nebraska, New Hampshire, New Jersey, New Mexico, New York, North Carolina, North Dakota, Ohio, Oklahoma, Oregon, Pennsylvania, Rhode Island, South Carolina, Tennessee, Texas, Vermont, Virginia, West Virginia). CENTRAL AMERICA: Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama. SOUTH AMERICA: Argentina, Bolivia, Brazil (Alagoas, Amazonas, Bahia, Ceará, Mato Grosso, Minas Gerais, Paraíba, Paraná, Pernambuco, Rio Grande do Norte, Rio Grande do Sul, Rondônia, Roraima, Santa Catarina, São Paulo, Sergipe), Chile, Colombia, Ecuador (including Galapagos), French Guiana, Guyana, Paraguay, Peru, Surinam, Venezuela. ANTARCTICA: Antarctica. ASIA: China (Anhui, Guangdong, Guangxi, Heilongjiang, Hong Kong, Jiangsu, Kwangtung, Yunnan), Christmas Island, Georgia, India (Assam, Chandigarh, Himachal Pradesh, Jammu & Kashmir, Karnataka, Madhya Pradesh, Maharashtra, Orissa, Uttarakhand, Uttar Pradesh, West Bengal), Indonesia, Iran, Japan, Kazakhstan (Aktobe, Atyrau, Pavlodar, West Kazakhstan), Laos, Nepal, Papua-New Guinea, Philippines, Russia (Altai Krai, Altai Republic, Chukotka Autonomous Okrug, Irkutsk Oblast, Khabarovsk Krai, Khanty-Mansi Autonomous Okrug, Krasnoyarsk Krai, Magadan Oblast, Primorsky Krai, Republic of Buryatia, Sakhalin Oblast, Tyumen Oblast, Yamalo-Nenets Autonomous Okrug), Singapore, Sri Lanka, Taiwan, Thailand, Turkey, Uzbekistan, Vietnam. ATLANTIC OCEAN: Ascension Island, Spain (Canary Islands). AUSTRALASIA: Australia (New South Wales, Northern Territory, Queensland, Tasmania, Victoria, Western Australia), New Zealand, Raoul Island. CARIBBEAN: American Virgin Islands, Antigua and Barbuda, Bahamas, Cuba, Dominica, Dominican Republic, Grenada, Guadeloupe, Haiti, Jamaica, Martinique, Puerto Rico, Trinidad & Tobago. EUROPE: Andorra, Austria, Belgium, Czech Republic, Denmark, Estonia, Finland, France, Germany, Greece, Iceland, Ireland, Italy, Lithuania, Luxembourg, Moldova, Netherlands, Norway, Poland, Portugal, Romania, Russia (Astrakhan Oblast, Chelyabinsk Oblast, Kaliningrad Oblast, Komi Republic, Krasnodar Krai, Kursk Oblast, Leningrad Oblast, Moscow Oblast, Murmansk Oblast, Orenburg Oblast, Perm Krai, Republic of Bashkortostan, Republic of Karelia, Rostov Oblast, Smolensk Oblast, Tver Oblast, Voronezh Oblast, Volgograd Oblast, Vologda Oblast), Slovakia, Slovenia, Spain, Sweden, Switzerland, Ukraine, UK. INDIAN OCEAN: Mauritius, Réunion, Seychelles. PACIFIC OCEAN: French Polynesia, New Caledonia, USA (Hawaii).

Elevation (m above sea level). Records up to 4200 (Argentina); 3450 (Guatemala); over 3300 (Mexico); over 3250 (Rwanda); 3000 (China); up to 2050 (New Zealand); up to 2000 (Spain: Canary Islands).

Comment. Recorded from every continent including Antarctica, and from many oceanic islands. Probably native throughout.

ECONOMIC IMPACTS: There is experimental evidence that this species can accumulate heavy metals (KRYVOMAZ, 2015a; KRYVOMAZ *et al.*, 2015, 2016, 2017c). In a study on ultramafic and volcanic soils containing high levels of heavy metals in the Philippines, REA-MAMINTA *et al.* (2015) reported higher Cr and Mn content in myxomycetes, including the present species, than in the leaves on which they were found. KRYVOMAZ (2017a) measured metal levels in samples of *A. cinerea*, 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 (27686.46), Al (11184.5), Fe (2550.26), Mg (1793.48), Si (489.65), Mn (87.99), Zn (34.28), Cu (15.82), Pb (2.6), Ni (2.33), As (0.55), Cd (0.44), Cr (0.3). Analysis of those results showed that Al was 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 much higher than in substrata and soil]: in *A. cinerea* this pattern was observed for Al, Cu, Si;
- substratum-dependent accumulation [concentration in myxomycetes less than in substratum, but higher than in soil]: in *A. cinerea* this pattern was observed for Ca, Cd, Mg, Mn, Pb, Zn, Ni;
- soil-dependent accumulation [concentration in myxomycetes less than in soil, but more than in substrata]: in *A. cinerea* this pattern was observed for Fe, Cr, As.

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).

In a search for novel compounds in the Czech Republic, ŘEZANKA (2002) isolated multibranching polyunsaturated fatty acid ((2E,4E,7S,8E,10E,12E,14S)-7,9,13,17-tetramethyl-7,14-dihydroxy-2,4,8,10,12,16-octadecaheptaenoic acid) and two of its glycoside derivatives from *A. cinerea*. These are surfactants of potential commercial interest particularly in the food and pharmaceutical industries. ISHIBASHI (2005) reported a wide range of bioactive compounds from *A. cinerea*, including some with possible application against human cancers. In another study exploring the cytotoxicity of bisindole alkaloids to cultured human cancer cell lines, *A. cinerea* was shown to produce a range of metabolites, including the previously unknown fatty acid bisindole alkaloids cinereapyrrole A and cinereapyrrole B (KAMATA *et al.*, 2005). SHINTANI *et al.* (2010) isolated a new alkaloid, 6,9'-dihydroxystaurosporinone (4), from *A. cinerea*.

No evaluations have been found for 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.). 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. *Arcyria cinerea* has also been reported on wood from mushroom-growing farms in Taiwan as a weed and potential parasite (CHUNG *et al.*, 1998). No other reports of negative economic impacts have been found.

INFRA-SPECIFIC VARIATION: Several subspecific taxa have been described for *A. cinerea*. All but one are treated by *Nomen.mycetozoa.com* [accessed 27 June 2019] as synonyms of typical *A. cinerea*, and appear in the above synonymy. The other, *Arcyria cinerea* var. *carnea* Lister, is a synonym of *A. minuta* Buchet [*Nomen.mycetozoa.com*, accessed 27 June 2019]. The synonyms *A. cinerea* var. *digitata* and *A. digitata* (the basionym from which it is derived), both included in the above list, have sometimes been used for collections of *A. cinerea*, particularly from the Tropics, with smaller compound and fascicle-stalked sporocarps (ROSTAFIŃSKI, 1875). These infraspecific taxa may represent separate cryptic species, but to date molecular evidence is inconclusive (NOVOZHILOV *et al.*, 2017).

In recent extensive biosystematic studies of *A. cinerea*, most isolates fitted standard species descriptions of the species, but there were often small variations from the norm, for example, in sporotheca shape (CLARK *et al.*, 2004; CLARK & HASKINS, 2010). These authors showed that what is treated in basic monographic works as a species may in certain cases comprise a mixture of nonheterothallic, as well as heterothallic and apomictic strains, which in turn may comprise sexually incompatible biological species.

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 (including, specifically, *A. cinerea*, SCHNITTLER *et al.*, 2006) 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 & SCHNITTLER, 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.** Many authors comment on the frequency with which *A. cinerea* is encountered. It is, for example, common in Mexico (LIZÁRRAGA *et al.*, 1998), the most common species on foliicolous liverworts in Costa Rica, Ecuador and Puerto Rico (SCHNITTLER, 2001), common to abundant in northern Thailand (TRAN *et al.*, 2006), common in the canopies of deciduous trees in Germany (SCHNITTLER *et al.*, 2006), on Mount Makulot, Philippines (CHENG *et al.*, 2013), and in forests of Anhui and Jiangsu provinces, China (DAI *et al.*, 2013); abundant in northeast Brazil Atlantic Forests (COSTA *et al.*, 2014; BARBOSA *et al.*, 2016); and common in southern Vietnam (NOVOZHILOV *et al.*, 2017). **Information base.** Over 10,000 records (specimens, databases and bibliographic sources combined, excluding duplicates) from at least 1790 to August 2019, with observations in every month of the year, peaking in the northern hemisphere from June to September. **Estimated extent of occurrence** [calculated using <http://geocat.kew.org>]. Well over 180.4 million km² (Africa [sub-Saharan only, but including Ascension Island]: 27.6 million km²; Antarctica: insufficient data; Asia [excluding Turkey]: 67.4 million km²; Australasia [including New Caledonia]: 16.2 million km²; Europe [including north Africa, Georgia and Turkey]: 20.6 million km²; North America [including the Caribbean and Central America]: 24.0 million km²; Pacific Ocean: insufficient data; South America: 24.6 million km²). **Estimated area of occupancy** [calculated using <http://geocat.kew.org>]. Well over 4456 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. One of the most widespread and common myxomycete species. 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. *Arcyria cinerea* is tolerant of a wide range of pH in its environment (WRIGLEY DE BASANTA, 2004), suggesting it is less susceptible to acid rain than some other myxomycetes. **Population trend.** In general, not known. Moderately frequent and increasing in Saxony, Germany (HARDTKE *et al.*, 2015). Of datable records, c. 20% are pre-1961, 55% post-1960 but pre-2001, and 25% 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.** 16 nucleotide sequences, 3 PopSet sequences and 5 protein sequences were found in a search of the NCBI GenBank database [www.ncbi.nlm.nih.gov, accessed 11 November 2019]. Although this species can be grown *in vitro*, in moist chamber conditions (HÄRKÖNEN, 1981) and in pure culture on agar (ALEXOPOULOS, 1960), no living strains of this species are listed by the ATCC, CABI and Westerdijk Institute [formerly CBS] culture collections.

NOTES: SHI & LI (2012) provide a description of the life cycle of *A. cinerea* in pure culture. Scanning electron micrographs of spores were provided by LIZÁRRAGA *et al.* (1998). For detailed transmission electron microscope studies of *A. cinerea* – stalk formation (including light microscopy), capillitial formation, precleavage mitosis, meiosis, spore wall formation, spore germination and formation of amoebae – see MIMS & ROGERS (1975), MIMS (1969), MIMS (1972b), ALDRICH & MIMS (1970), MIMS (1972a) and MIMS (1971), respectively. KARPOV *et al.* (2003) made a detailed study of the cytoskeleton of spores of *A. cinerea*. This species is sufficiently well known to have a presence on YouTube [e.g. www.youtube.com/watch?v=J-YtTN2Q2h4, accessed 20 November 2019].

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