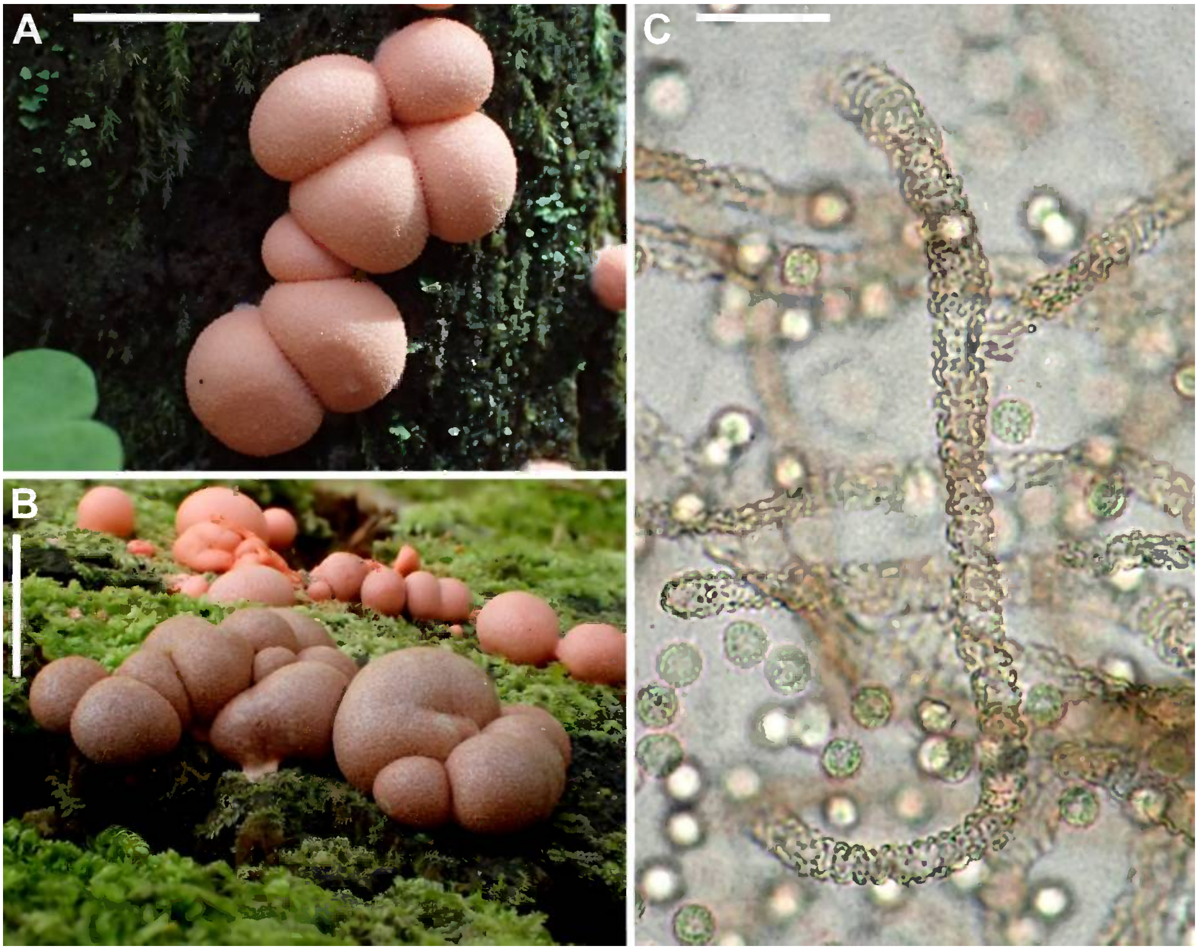
IMI Descriptions of Fungi and Bacteria No. 2219

LYCOGALA EPIDENDRUM



A, **B**. Aethalia, showing colour change during maturation (bars = 10 mm). **C**. Capillitium and spores (bar = 20 µm). [Photographs: A. Michaud]

Lycogala epidendrum (J.C. Buxb. ex L.) Fr., *Systema Mycologicum* **3**(1): 80 (1829). [*IndexFungorum* 205910; *Tubiferaceae*, *Liceida*]

Lycoperdon epidendrum J.C. Buxb. ex L., *Species Plantarum* **2**: 1184 (1753). [*IndexFungorum* 157878]

Galeperdon epidendrum (J.C. Buxb. ex L.) Weber ex F.H. Wigg., *Primitiae Florae Holsaticae*: 108 (1780) [as '*epidendron*']. [*IndexFungorum* 529125]

Lycoperdon sphaericum Gled., *Methodus Fungorum*: 150 (1753), nom. inval., *ICN* Art. 32.1(a). [*IndexFungorum* 153013]

Lycoperdon variolosum L., *Systema Naturae* Edn 12, **3**: 234 (1768). [*IndexFungorum* 444015]

Mucor lycogala Scop., *Flora Carniolica* Edn 2, **2**: 496 (1772). [*IndexFungorum* 148875]

Mucor fragiformis Schaeff., *Fungorum qui in Bavaria et Palatinatu circa Ratisbonam Nascuntur Icones* **2**: tab. 193, **4**: 132 (1774). [*IndexFungorum* 187162]

Lycoperdon pisiforme Jacq., *Miscellanea Austriaca ad Botanicam, Chemiam, et Historiam Naturalem Spectantia* **1**: 137 (1778) [publ. 1779]. [*IndexFungorum* 250402]

Lycoperdon chalybeum Batsch, *Elenchus Fungorum*: 155 (1783). [*IndexFungorum* 208530]

Lycoperdon epidendron Bull., *Histoire des Champignons de la France* **1**: 145, tab. 503 (1791). [*IndexFungorum* 497316]

Lycogala miniatum Pers., *Neues Magazin für die Botanik* **1**: 87 (1794) [as '*miniata*']. [*IndexFungorum* 438636]

Reticularia miniata (Pers.) Poir., in J.B.P.A. DE LAMARCK, *Encyclopédie Methodique* Botanique **6**: 184 (1804). [*IndexFungorum* 318819]

Reticularia rosea DC., *Bulletin de la Société Philomathique de Paris* **1**: 105 (1798). [*IndexFungorum* 183691]

Lycogala ferrugineum Schumach., *Enumeratio Plantarum in Partibus Sællandiae Septentrionalis et Orientalis* **2**: 192 (1803) [as '*ferruginea*']. [*IndexFungorum* 212169]

Reticularia punctata Poir., in J.B.P.A. DE LAMARCK, *Encyclopédie Methodique* Botanique **6**: 184 (1804). [*IndexFungorum* 183581]

Lycogala terrestre Fr. & Lindgr., *Symbolae Gasteromycetum ad Illustrandum Floram Suecicam* **2**: 10 (1817). [*IndexFungorum* 203276]

Lycogala epidendrum var. *terrestre* (Fr. & Lindgr.) Y. Yamam., *The Myxomycete Biota of Japan*: 118 (1998). [*IndexFungorum* 450260]

Lycogala miniatum var. *marginatum* Gray, *A Natural Arrangement of British Plants* **1**: 569 (1821) [as '*marginata*']. [*IndexFungorum* 562324]

Lycogala miniatum var. *fuligineum* Gray, *A Natural Arrangement of British Plants* **1**: 569 (1821). [*IndexFungorum* 562323]

Lycogala affine Berk. & Broome, *Journal of the Linnean Society* Botany **14**: 81 (1873) [publ. 1875]. [*IndexFungorum* 506962]

Lycogala nigricans Lloyd, *Mycological Writings* **7** (Mycological Notes No. 68): 1184 (1923). [*IndexFungorum* 253558]

Vernacular names. Dutch: *gewone boomwrat*. English: *bubblegum slime mould*, *Groening's slime*, *toothpaste slime mould*, *wolf's milk*. Estonian: *limaseen hundipiim*. French: *lait de loup*. German: *Blutmilch-Schleimpilze*. Russian: *волчье молоко*. Ukrainian: *вовче вим'я*.

Diagnostic features. Unmistakable and easily recognized in field to generic level with unaided eye; identification to species level less straightforward: aethalia conspicuous, like small puffballs, usually on dead wood or sawdust, sometimes forming large colonies, gregarious, up to 15 mm diam., pulvinate, wider than high, at first coral red, later brown; scales of cortex not grouped; spores at first pinkish grey *en masse*, rapidly becoming grey or beige.

On natural substratum. *Amoebal state* no information. *Plasmodium* orange to coral red. *Hypothallus* inconspicuous. *Sporocarps* are aethalia, usually scattered or crowded, subglobose or pulvinate, or irregularly angular from mutual pressure, when separate never taller than wide, 3–15 mm diam., carmine pink when young, later beige or dark grey. *Cortex* persistent, consisting of several layers, thin, rough, fragile, the surface covered with irregularly shaped or circular scales and vesicles 0·05–0·3 mm diam., sometimes sunken into the wall; dehiscence starts with an apical pore or crack which later extends by tearing. *Pseudocapillitium* a system of irregular tubes connected to the middle of the cortex layer; tubes branched and anastomosed, 6–25 µm diam., smooth or minutely warted or spinulose, transversally wrinkled, yellowish grey to almost colourless, free ends numerous, club-shaped or rounded. *Spores en masse* pinkish grey when fresh, later fading to grey or beige, individually almost colourless, 6·0–7·5 µm diam., finely banded-reticulate.

ASSOCIATED ORGANISMS & SUBSTRATA: **Animalia**. *Agathidium pulchrum* LeConte, 1853, *Agathidium* sp.; *Animalia* indet. (dung); *Anisotoma bifoveata* Wheeler, 1979, *A. blanchardi* (Horn, 1880), *Anisotoma* sp.; *Baeocera* sp.; *Bradysia* sp.; *Bremia* sp.; *Platurocypta punctum* Stannius, 1831. **Artefacts**. Bagasse; beehive; fence; sawn timber; stave; telegraph pole; woodchips used for mulch. **Fungi**. *Acrogenospora sphaerocephala* (Berk. et Broome) M.B. Ellis; *Aphanocladium album* (Preuss) W. Gams; *Armillaria mellea* (Vahl.) P. Kumm.; *Bisporella citrina* (Batsch) Korf & S.E. Carp.; *Bjerkandera adusta*

(Willd.) P. Karst.; *Brachysporium nigrum* (Link) S. Hughes; *Calocera cornea* (Batsch) Fr.; *Ceriporiopsis mucida* (Pers.) Gilb. & Ryvarden [as *Fibuloporia mucida* (Pers.) Niemelä]; *Clonostachys rosea* (Link) Schroers, Samuels, Seifert & W. Gams [as *Gliocladium roseum* Bainier]; *Coniochaeta ligniaria* (Grev.) Cooke; *Exophiala calicioides* G. Okada & Seifert [as *Graphium calicioides* (Fr.) Cooke et Massee]; *Fomes fomentarius* (L.) Fr.; *Lachnum virgineum* (Batsch) P. Karst. [as *Dasyscyphus virgineus* (Batsch) Gray]; *Lasiosphaeria hirsuta* (Fr.) Ces. & De Not., *L. ovina* (Pers.) Ces. & De Not.; *Lentomitella cirrhosa* (Pers.) Réblová [as *Ceratostomella cirrhosa* (Pers.) Sacc.]; *Lenzites betulinus* (L.) Fr. (basidioma); *Melanomma pulvis-pyrius* (Pers.) Fuckel [also as *Rosellinia conglobata* (Fr.) Sacc.]; *Melomastia mastoidea* (Fr.) J. Schröt.; *Menispora glauca* (Link) Pers. [as *Chaetosphaeria ovoidea* (Fr.) Constant., K. Holm & L. Holm]; *Minimelanolocus subulifer* (Corda) R.F. Castañeda & Heredia [as *Pseudospiropes subuliferus* (Corda) M.B. Ellis]; *Mollisia melaleuca* (Fr.) Sacc.; *Mycetinis alliaceus* (Jacq.) Earle ex A.W. Wilson & Desjardin [as *Marasmius alliaceus* (Jacq.) Fr.]; *Natantiella lignicola* (Berk. & Broome) Réblová [as *Ceratostomella ampullasca* (Cooke) Sacc.]; *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.]; *Orbilia coccinella* Fr.; *Oudemansiella* sp.; *Periconia cambrensis* E.W. Mason & M.B. Ellis; *Phellinus* sp. (basidioma); *Pleurothecium recurvatum* (Morgan) Höhn.; *Pleurotus ostreatus* (Jacq.) P. Kumm.; *Stereum hirsutum* (Willd.) Pers.; *Strickeria kochii* Körb.; *Trichophaeopsis bicuspis* (Boud.) Korf & Erb; *Xylaria longipes* Nitschke, *X. polymorpha* (Pers.) Grev. **Plantae**. *Abies cephalonica* Loudon, *A. grandis* (Douglas ex D. Don) Lindl., *A. lasiocarpa* (Hook.) Nutt., *A. nordmanniana* subsp. *equi-trojani* (Asch. & Sint. ex Boiss.) Coode & Cullen [as *A. nordmanniana* subsp. *bornmuelleriana* (Mattf.) Coode & Cullen], *A. sibirica* Ledeb., *Abies* sp. (stump); *Acer pseudoplatanus* L. (branch, log), *Acer* sp. (stump); *Adenosma glutinosum* (L.) Druce; *Aesculus hippocastanum* L. (branch, log); *Allium ursinum* L.; *Alnus alnobetula* (Ehrh.) K. Koch [as *A. viridis* (Chaix) DC.], *A. glutinosa* (L.) Gaertn. (branch, trunk), *A. rubra* Bong., *Alnus* sp. (log, stump); *Araucaria araucana* (Molina) K. Koch; *Attalea speciosa* Mart.; *Betula pendula* Roth (bark, branch, log, stump, trunk, wood), *B. pubescens* Ehrh. (branch), *Betula* sp. (branch, log, stump, trunk, wood); *Buddleja* sp. (wood); *Bursera* sp.; *Calophyllum inophyllum* L. (wood); *Carica papaya* L.; *Carpinus betulus* L. (trunk, wood); *Carya* sp.; *Castanea dentata* (Marshall) Borkh., *Castanea* sp.; *Cedrus* sp. (stump); *Chamaecyparis lawsoniana* (A. Murray bis) Parl. (trunk), *Chamaecyparis* sp. (stump); *Cibotium glaucum* (Sm.) Hook. & Arn., *Cibotium* sp.; *Cirsium arvense* (L.) Scop.; *Coniferae* fam. indet.; *Cornus sanguinea* L. (leaf); *Corylus avellana* L. (branch, log, stump, trunk, twig, wood), *Corylus* sp. (branch); *Crataegus monogyna* Jacq. (branch); *Cryptomeria japonica* (Thunb. ex L. f.) D. Don; *Epilobium angustifolium* L. [as *Chamerion angustifolium* (L.) Holub] (stem); *Erythrina variegata* L. (bark); *Eucalyptus* sp. (trunk); *Euphorbia kamerunica* Pax (bark, log); *Fagus grandifolia* Ehrh., *F. orientalis* Lipsky (branch), *F. sylvatica* L. (branch, log, sawn timber, trunk, wood), *Fagus* sp. (branch, log, stump, woodchip); *Falcataria moluccana* (Miq.) Barneby & J.W. Grimes (wood); *Fraxinus excelsior* L. (branch, log, trunk), *Fraxinus* sp. (wood); *Hieracium sabaudum* subsp. *vagum* Zahn [as *H. vagum* Jord.]; *Ilex aquifolium* L. (branch); *Juglans cinerea* L., *J. regia* L. [as *J. fallax* Dode]; *Juniperus virginiana* L.; *Laburnum* sp. (stump); *Larix decidua* Mill. [also as *L. europaea* DC.], *L. occidentalis* Nutt., *Larix* sp. (branch, log, wood); *Leiospermum racemosum* (L. f.) D. Don [as *Weinmannia racemosa* L. f.]; *Magnoliophyta* indet. (branch, litter, log, stump, trunk, twig, wood); *Magnoliopsida* indet. (wood); *Malus domestica* Borkh. [as *Pyrus malus* L.]; *Muscopsida* indet. (thallus); *Nothofagus alpina* (Poepp. & Endl.) Oerst. (wood), *N. betuloides* (Mirb.) Oerst. (wood), *N. dombeyi* (Mirb.) Oerst. (wood), *N. menziesii* (Hook. f.) Oerst., *Nothofagus* sp. (wood); *Nyssa sylvatica* Marshall; *Picea abies* (L.) H. Karst. [also as *P. excelsa* (Lam.) Link] (branch, log, stump, trunk, wood), *P. engelmannii* Parry ex Engelm., *P. glauca* (Moench) Voss, *P. schrenkiana* Fisch. & C.A. Mey. [as '*P. schrenkii*'] (stump), *P. sitchensis* (Bong.) Carrière (trunk), *Picea* sp. (log); *Pinophyta* indet. (branch, litter, log, stump, wood); *Pinus contorta* Douglas ex Loudon (branch), *P. densiflora* Siebold & Zucc. (wood), *P. nigra* J.F. Arnold (branch, trunk), *P. pinea* L., *P. ponderosa* Douglas ex C. Lawson (log), *P. radiata* D. Don (branch), *P. rigida* Mill., *P. sibirica* Du Tour, *P. roxburghii* Sarg. (stump), *P. sylvestris* L. (bark, branch, litter, log, stump, trunk, wood), *P. virginiana* Mill., *Pinus* sp. (branch, leaf, litter, log, stump, wood); *Piper auritum* Kunth (stem); *Plantae* indet. (bark, branch, log, stump, trunk, wood); *Poaceae* indet.; *Podocarpus* sp.; *Populus canescens* (Aiton) Sm. (log), *P. deltoides* Marshall, *P. nigra* L. (wood), *P. tremula* L., *P.*

trichocarpa Torr. & A. Gray ex Hook., *Populus* sp. (log); *Pseudotsuga menziesii* (Mirb.) Franco; *Quercus cerris* L., *Q. petraea* (Matt.) Liebl. (branch, log, stump, sawn timber, wood), *Q. robur* L. (wood), *Quercus* sp. (branch, log, stump, wood); *Saccharum officinarum* L. (debris, leaf); *Salix alba* L. (log, stump), *S. caprea* L. (log), *S. cinerea* L. (branch), *S. fragilis* L. (stump), *Salix* sp. (bark, branch, log, trunk, wood, woodchip); *Sambucus nigra* L. (log, trunk); *Silene dioica* (L.) Clairv.; *Sphagnum* sp.; *Tabebuia pallida* (Lindl.) Miers (wood); *Tilia americana* L., *T. cordata* Mill. (branch, trunk), *Tilia ×europaea* L.; *Tsuga canadensis* (L.) Carrière, *T. heterophylla* (Raf.) Sarg. (leaf); *Ulmus glabra* Huds. (wood), *U. minor* Mill. [as *U. procera* Salisb.] (branch), *Ulmus* sp. (branch, log, stump, trunk). **Protista**. *Arcyria denudata* (L.) Wettst.; *Comatricha laxa* Rostaf.; *Fuligo septica* (L.) F.H. Wigg.; *Hemitrichia calyculata* (Speg.) M.L. Farr, *H. clavata* (Pers.) Rost.; *Metatrichia vesparium* (Batsch) Nann.-Bremek.; *Stemonitis fusca* Roth, *S. flavogenita* E. Jahn; *Symphytocarpus amaurochaetoides* Nann.-Bremek.; *Trichia scabra* Rostaf., *T. varia* (Pers. ex J.F. Gmel.) Pers. **Substances**. Soil. **Associated organism of type specimen**. *Plantae* indet. [as '*habitat in lignis*']. **Comment**. This is a largely wood-inhabiting species. It occurs on dead branches, twigs and wood, rotten logs, stumps and trunks, cut logs and other woody debris. There are several records associated with burnt wood and firesides. It is also occasionally observed on dung, on fungal sporocarps, on woody artefacts, and soil.

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 *L. epidendrum*. In their amoebal state, myxomycetes are known to feed on small organic particles, micro-organisms and fungi, but the identity of those organisms is rarely, if ever, recorded. There are, however, observations of *L. epidendrum* parasitic on mycelium (HOWARD & CURRIE, 1932*b*) and basidiomata (HOWARD & CURRIE, 1932*a*) of *Lenzites betulinus*, and of its myxamoebal stage feeding on bacteria (HOPPE & KUTSCHERA, 2015).

This species has been recorded from the following habitats: amenity & protected areas (cemeteries, churchyards, gardens, nature reserves, ornamental gardens, parkland with scattered trees, public amenity areas); coastal (dunes, saltmarshes); cultivated ground (farmland); desert; freshwater (alder & willow carrs, fens, marshes, wetlands); grassland (calcareous, unmodified ['unimproved'], meadows, pasture, upland); margins (canalsides, hedgerows, field margins, lakesides, pathsides, roadside verges, tracksides, woodland clearings); marine (mangroves); moorland (heaths); ruderal (disused railway, disused sand & gravel pits); and woodland (semi-natural broadleaf woodland, semi-natural mixed woodland, conifer plantations, mixed plantations, scrub). Most records come from mixed woodland, mixed plantations and parkland.

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. There are records of a range of fungi and protists growing in association with *L. epidendrum* (DUDKA & ROMANENKO, 2006), some fungi parasitizing its sporocarps (ROGERSON & STEPHENSON, 1993). Associations between this species and various beetles have been observed in Brazil (LEMOS *et al.*, 2010) and North America (STEPHENSON *et al.*, 1994), and flies are known to be associated with this species (BUXTON, 1954). There are also records of *L. epidendrum* on dung as discussed by ELIASSON (2013). Although associations with micro-organisms are known or suspected, no observations were found where the associated organism was identified to genus or species level.

GEOGRAPHICAL DISTRIBUTION: AFRICA: Algeria, Angola, Burundi, Cameroon, Congo, Democratic Republic of the Congo, Egypt, Liberia, Malawi, Morocco, Nigeria, Rwanda, Sierra Leone, South Africa, Tanzania, Uganda, Zambia. NORTH AMERICA: Canada (Alberta, British Columbia, New Brunswick, Newfoundland, Nova Scotia, Ontario, Prince Edward Island, Quebec, Saskatchewan), Mexico, USA (Alaska, Arizona, California, Connecticut, Florida, Georgia, Illinois, Indiana, Iowa, Kansas, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Montana, Nebraska, New Hampshire, New Jersey, New York, North Carolina, Ohio, Oregon, Pennsylvania, Rhode Island, South Carolina, Tennessee, Texas, Vermont, Virginia, Washington, West Virginia). CENTRAL AMERICA: Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama. SOUTH AMERICA: Argentina, Chile, Colombia, Brazil (Acre, Amazonas, Maranhão, Pará, Paraiba, Pernambuco, Piauí, Rio de Janeiro, Rio Grande do Norte, Rio Grande do Sul, Roraima, Santa Catarina, São Paulo, Sergipe), Ecuador (including Galapagos), French Guiana, Guyana, Paraguay, Peru, Suriname, Uruguay, Venezuela. ASIA: China (Fujian, Guangxi, Guizhou, Hainan, Jiangxi, Sichuan, Xinjiang, Yunnan, Zhejiang), Georgia, India (Assam, Chandigarh, Himachal Pradesh, Jammu & Kashmir, Karnataka, Maharashtra, Sikkim, Tamil Nadu, West Bengal), Indonesia, Iran, Japan, Kazakhstan (Almaty, East Kazakhstan, Kostanay, North Kazakhstan, former Kokchetau, former Taldy-Kurgan, former Tselinograd), Kyrgyzstan, Malaysia, Mongolia, Nepal, Papua-New Guinea, Philippines, Russia (Altai, Altai Krai, Chukotka Autonomous Okrug, Kamchatka Krai, Khabarovsk Krai, Khanty-Mansi Autonomous Okrug, Krasnoyarsk Krai, Magadan Oblast, Novosibirsk Oblast, Primorsky Krai, Tomsk Oblast, Yamalo-Nenets Autonomous Okrug), Singapore, South Korea, Sri Lanka, Taiwan, Thailand, Turkey, Uzbekistan, Vietnam. ATLANTIC OCEAN: Bahamas, Spain (Canary Islands). AUSTRALASIA: Australia (New South Wales, Northern Territory, Queensland, South Australia, Tasmania, Victoria, Western Australia), New Zealand. CARIBBEAN: American Virgin Islands, Antigua and Barbuda, Cuba, Dominica, Dominican Republic, Grenada, Guadeloupe, Jamaica, Martinique, Puerto Rico, Saint Lucia, Trinidad and Tobago. EUROPE: Andorra, Austria, Belgium, Bulgaria, Croatia, Czech Republic, Denmark (including Faroe Islands), Estonia, Finland, France, Germany, Greece, Iceland, Ireland, Italy, Kosovo, Latvia, Liechtenstein, Lithuania, Luxembourg, Moldova, Netherlands, Norway, Poland, Portugal, Romania, Russia (Kaliningrad Oblast, Krasnodar Krai, Leningrad Oblast, Moscow Oblast, Rostov Oblast, Vladimir Oblast, Volgograd Oblast), Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland, Ukraine, UK. INDIAN OCEAN: Christmas Island, Mauritius, Réunion, Seychelles. PACIFIC OCEAN: Cook Islands, French Polynesia, New Caledonia, USA (Hawaii).

Elevation (m above sea level). Records up to 3550 (Venezuela); 3260 (USA: Colorado); 2450 (France); 2350 (Rwanda); 2100 (Japan).

Comment. Recorded from every continent except Antarctica, and from many oceanic islands. Probably native throughout its known range.

ECONOMIC IMPACTS: Heavy metal content of *L. epidendrum* in fresh specimens was compared with that of dried museum samples of *L. epidendrum* collected in Finland from 1860 to 1964. Average concentration of Zn and Cu was practically the same, but Cd content of fresh material collected in 1988 was five times higher than in dried preserved nineteenth century specimens, and Al and Fe levels in dried specimens were 10 times larger than in recent field collections (SETÄLÄ & NUORTEVA, 1989). STIJVE & ANDREY (1999), however, noted a tendency by *Lycogala epidendrum* to accumulate copper (52-84 mg/kg) in comparison with the other four species in their study which did not accumulate this metal (3-14 mg/kg).

There is further experimental evidence that this species can accumulate heavy metals (KRYVOMAZ, 2015, 2017*a*, *b*; KRYVOMAZ *et al.*, 2017*c*). KRYVOMAZ (2017*a*) measured metal levels in samples of *L. epidendrum* aethalia, 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 (11739·92), P (5650), Mg (1884·77), K (1500), Si (266·64), Fe (250·03), Zn (108·21), Al (107·41), Sr (39·5), Mn (26·67), Sn (24·5), Ba (16), Cu (15·16), Cr (5·65), Ni (3·29), Cd (1·81), Pb (1·64). Analysis showed that the samples (from dead wood of *Picea abies* in the French Alps and dead wood of *Calophyllum inophyllum* from the Seychelles) did not show great potential to accumulate heavy metals in comparison with the other species studied. 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 (2017*a*) as:

- accumulation [concentration in myxomycetes much higher than in substrata and soil]: in *L. epidendrum* this pattern was observed for Cd, Zn;
- substratum-dependent accumulation [concentration in myxomycetes less than in substratum, but higher than in soil]: in *L. epidendrum* this pattern was observed for Ni;
- soil-dependent accumulation [concentration in myxomycetes less than in soil, but more than in substrata]: in *L. epidendrum* this pattern was observed for Mg, Ca, Mn, Fe, Cr, Si;
- no accumulation [concentration in myxomycetes lower than in substrata and soil]: in *L. epidendrum* this pattern was observed for Al, Pb, 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).

Lycogala epidendrum has been examined in searches for novel compounds. HASHIMOTO *et al.* (1994*a*) found three polyacetylene triglycerides, which they named lycogarides A-C. Tests showed anti-HSV-I [Herpes Simplex Virus] activity. In the Czech Republic, ŘEZANKA (2002) isolated a 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 (DEMBITSKY, 2004), from *L. epidendrum*.

Some of the novel compounds discovered have antibiotic properties. ŘEZANKA & DVOŘÁKOVÁ (2003) isolated two novel polypropionate lactone glycosides, given the names lycogalinosides A and B, from sporocarps of *L. epidendrum*, and these showed growth inhibitory properties against *Bacillus subtilis* (Ehrenberg) Cohn and *Staphylococcus aureus* Rosenbach, 1884. The chemical structure of the two compounds was similar to those usually produced by *Streptomyces* species, and may have been a relict resulting from the food chain of the myxomycete’s amoebal and swarm cell states. The authors further speculated that micro-organisms consumed by those states may even have functioned symbiotically in biosynthesis of these two compounds within the myxomycete.

Other compounds have value in cancer research. ISHIBASHI (2005) reported a wide range of such compounds from *L. epidendrum*; see also KAMATA *et al.* (2005). HOSOYA *et al.* (2005) isolated two novel compounds (6-hydroxystaurosporinone and 5,6-dihydroxyarcyriaflavin A), and six already well-known compounds, all bisindole alkaloids, from carpophores of *L. epidendrum* collected in Japan. The two novel compounds displayed cytotoxicity against HeLa and Jurkat cells (these are immortalized lines of human cells widely used in cancer research), and against vincristine-resistant KB/VJ300 cells (vincristine is a chemotherapy medication used to treat various cancers). One of the two novel compounds (6-hydroxystaurosporinone) was also found to inhibit tyrosine kinase activity (tyrosine kinase is an enzyme which can, under certain circumstances, cause the unregulated cell grown necessary for some cancers to develop). Kinase inhibitors of this sort have potential as effective cancer treatments.

Various other novel compounds have been isolated from *L. epidendrum* (e.g. FRÖDE *et al.*, 1994), including acylglycerols (BUCHANAN *et al.*, 1996). Some of these are summarized by SÁNCHEZ *et al.* (2006), and considered in the review by O’HAGAN (1997). Not all of their functions and/or biological activities are yet fully understood. No evaluation has 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. *Lycogala epidendrum* was used in medical studies to investigate the possibility that myxomycete spores can trigger allergic responses (e.g. GIANNINI *et al.*, 1975). 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. *Lycogala epidendrum* 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.

INFRASPECIFIC VARIATION: Four varieties of this species have been described. *Lycogala epidendrum* var. *terrestre* is included in the synonymy above; *L. epidendrum* var. *cristatum* Flatau & Schimmer is an invalid name [*ICN* Art. 40.1 (Melbourne)]; *L. epidendrum* var. *exiguum* (Morgan) Torrend is an obligate synonym of the accepted species *L. exiguum* Morgan; and *L. epidendrum* var. *tessellatum* (Lister) G. Lister is a facultative synonym of the accepted species *L. confusum* Nann.-Bremek. & Ing.

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 & SCHNITTLER, 2007). Spores and myxamoebae may be dispersed by rainwater and water in soil. This was investigated explicitly for *L. epidendrum* by DIXON (1963), who found that water drops could produce an apical aperture in its carpophores, and could cause them to puff in a similar manner to puffball fungi. 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. **Information base**. Over 18,000 records (specimens, databases and bibliographic sources combined, excluding duplicates) from at least 1753 to August 2019, with observations in every month of the year, with a peak between May and October. **Estimated extent of occurrence** [calculated using *http://geocat.kew.org*]. Well over 179·8 million km^2 (Africa [sub-Saharan only]: 23·4 million km^2; Asia: 67·1 million km^2; Australasia: 11·8 million km^2; Europe [including north Africa]: 17·9 million km^2; North America [including the Caribbean and Central America]: 28·0 million km^2; Pacific Ocean: 11·9 million km^2; South America: 19·7 million km^2). **Estimated area of occupancy** [calculated using *http://geocat.kew.org*]. Well over 4984 km^2. The method for estimating area of occupancy has produced an artificially low figure. The species is likely to be under-recorded 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. Rather common in Hawaii (GILBERTSON & HEMMES, 1997); abundant but local in northern Thailand (TRAN *et al.*, 2006); common in northern Ukraine (DUDKA & KRYVOMAZ, 2008) and Japan (TAKAHASHI & HADA, 2010); abundant in Serbia (KARAMAN *et al.*, 2012); very common and increasing in Saxony, Germany (HARDTKE *et al.*, 2015). Of datable records, *c.* 10% are pre-1961, 35% post-1960 but pre-2001, and 55% 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**. 28 nucleotide sequences, 8 PopSet sequences and 17 protein sequences were found in a search of the NCBI GenBank database [*www.ncbi.nlm.nih.gov*, accessed 11 November 2019]. No living strains of this species are listed by the ATCC, CABI and Westerdijk Institute [formerly CBS] culture collections.

NOTES: As an iconic species, *L. epidendrum* has a long history. A woodcut illustration (reproduced by ING & STEPHENSON, 2017) from a 17th century book mainly about plants (PANCKOW, 1654), together with its very brief accompanying description: '*fungi cito crescentes*' ['fungi which grow rapidly'], probably shows a species of *Lycogala*, quite possibly *L. epidendrum*. It may be the earliest reference to a myxomycete which can be identified with any confidence to species level (ING & STEPHENSON, 2017). The generic name *Lycogala* first appeared in the work of MICHELI (1729), while the specific epithet, one of only four for myxomycetes taken up by LINNAEUS (1753), can be traced back to the work of BUXBAUM (1721). Unabated public interest in *L. epidendrum* is confirmed by its presence on YouTube [e.g. *www.youtube.com/watch?v=iLaLS8w30-w*, accessed 20 November 2019].

COWDRY (1918) provided an account of the cytology of this species, with special reference to mitochondria. ELLIOTT (1949) provided a general account of myxomycete swarm cells, including the present species. Meiosis of *L. epidendrum* was studied by WILSON & ROSS (1955). Sensitivity of *L. epidendrum* to nuclear radiation was studied by HOLT (1973). BUTTERFIELD (1968) examined the effect of dimethylsulphoxide on spore germination of this species. Ultrastructure of its pseudocapillitium and spores was investigated by GAITHER (1976) and ELIASSON (1981). KARPOV *et al.* (2003) made a detailed study of the cytoskeleton of spores of *L. epidendrum*. LIU & LI (2000) made a random amplified polymorphic DNA [RAPD] study of *L. epidendrum* and two other members of the genus in China. FIORE-DONNO *et al.* (2005) and later HOPPE & KUTSCHERA (2010) provided molecular phylogenies of myxomycetes including the present species. Its chromosome number was studied by HOPPE & KUTSCHERA (2014). It was one of the species considered in a discussion about potential molecular barcoding of myxomycetes by SCHNITTLER *et al.* (2017). Using molecular techniques on collections from Germany, FENG & SCHNITTLER (2017) demonstrated that at least three 'ribotypes' of *L. epidendrum* exist, and that this molecular variation can be linked to subtle differences in morphology, including sporocarp colour. This raises the possibility that *L. epidendrum* as currently circumscribed is, in fact, more than one cryptic species.

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Issued by CABI, Bakeham Lane, Egham, Surrey, TW20 9TY, UK