

## = Russulaceae =

The Russulaceae are a diverse family of fungi in the order Russulales , with roughly 1 @, @ 900 known species and a worldwide distribution . They comprise the brittlegills and the milk @-@ caps , well @-@ known mushroom @-@ forming fungi that include some edible species . These gilled mushrooms are characterised by the brittle flesh of their fruitbodies .

In addition to these typical agaricoid forms , the family contains species with fruitbodies that are laterally stiped ( pleurotoid ) , closed ( secotoid or gasteroid ) , or crust @-@ like ( corticioid ) . Molecular phylogenetics has demonstrated close affinities between species with very different fruitbody types and has discovered new , distinct lineages .

An important group of root @-@ symbiotic ectomycorrhizal fungi in forests and shrublands around the world includes *Lactifluus* , *Multifurca* , *Russula* , and *Lactarius* . The crust @-@ forming genera *Boidinia* , *Gloeopeniophorella* , and *Pseudoxenasma* , all wood @-@ decay fungi , have basal positions in the family .

## = = Systematics and taxonomy = =

The family Russulaceae was first validly named in 1907 by Dutch botanist Johannes Paulus Lotsy , who included three genera : *Russula* , *Lactarius* , and *Russulina* ( now considered a synonym of *Russula* ) . He emphasised features such as the granular flesh , thick gills , spiny spores , and milky hyphae and rounded cells ( sphaerocytes ) . A prior usage of " Russulariées " by French mycologist Ernst Roze in 1876 is not considered a valid publication , since the proper Latin termination for the family rank specified in article 18 @. @ 4 of the nomenclature code was not used .

Synonyms of Russulaceae include : Ernst Albert Gäumann 's *Lactariaceae* ( 1926 ) , Fernand Moreau 's *Asterosporaceae* ( 1953 ) , and David Pegler and Thomas Young 's *Elasmomycetaceae* ( 1979 ) . The latter family was proposed to contain species with statismosporic ( non @-@ forcibly discharged ) and symmetric spores , including the gasteroid genera *Elasmomyces* , *Gymnomycetes* , *Martellia* , and *Zelleromyces* . Calonge and Martín reduced the *Elasmomycetaceae* to synonymy with the Russulaceae when molecular analysis confirmed the close genetic relationship between the gasteroid and agaricoid genera .

## = = = Placement of the family = = =

Historically , the gilled mushrooms of the family Russulaceae were classified with other gilled species in the order Agaricales , but microscopical studies of spore and fruitbody flesh features raised the possibility that they were more closely related with certain " lower fungi " presenting nongilled , crust @-@ like fruitbodies . The use of molecular phylogenetics confirmed that these morphologically diverse fungi form a distinct lineage , first termed the " russuloid clade " and today classified as order Russulales in the class Agaricomycetes . The family 's sister group within the order appears to be the crust @-@ like *Gloeocystidiellaceae* .

## = = = Internal systematics = = =

A 2008 molecular phylogenetic study clarified the relationships among the mushroom @-@ forming species of the family . The authors demonstrated the existence of four distinct lineages of gilled mushrooms , which led to the description of *Multifurca* as a new genus separated from *Russula* and the segregation of *Lactifluus* from *Lactarius* .

Genera with closed fruitbodies within the family are form taxa instead of natural groups : *Arcangeliella* , *Gastrolactarius* , and *Zelleromyces* are phylogenetically part of *Lactarius* , while *Cystangium* , *Elasmomyces* , *Gymnomycetes* , *Macowanites* , and *Martellia* belong to *Russula* . Nevertheless , some of these genus names are still in use , as many of the concerned species have not yet formally been synonymised with *Lactarius* or *Russula* .

The crust @-@ like genera *Boidinia* , *Gloeopeniophorella* , and *Pseudoxenasma* , formerly placed

in the Corticiaceae or Gloeocystidiellaceae , are now classified in the Russulaceae and basal to the clade of mushroom @-@ forming species described above . Studies have so far failed to clearly circumscribe and place these genera within the family . Boidinia in its current extent is polyphyletic , with some species not falling into the Russulaceae .

### = = = Species diversity = = =

Altogether , the Russulaceae comprise around 1 @, @ 900 accepted species . Russula is by far the largest genus with ca . 1100 species , Lactarius has ca . 550 , Lactifluus ca . 120 , Boidinia 13 , Multifurca 6 , Gloeopeniophorella 6 , and Pseudoxenasma 1 species . Closed @-@ fruitbody species not yet synonymised with Lactarius or Russula ( see above ) account for some 150 species .

New species in the Russulaceae continue to be described from various regions , such as the US , Guyana , Brazil , Patagonia , Togo , Sri Lanka , or Thailand . It has been estimated that the real number of Russula species in North America alone ( currently around 400 described ) might be as high as 2000 . Cryptic species may increase true diversity : some morphologically well @-@ defined species , especially in Lactifluus , have been shown to actually encompass several phylogenetic species .

### = = Description = =

#### = = = Macroscopic characteristics = = =

Three major types of fruitbodies occur in the Russulaceae : agaricoid and pleurotoid forms with a cap , gills , and a stipe ; forms with closed ( gasteroid ) or partially closed ( secotioid ) fruitbodies , and corticioid , crust @-@ like forms .

The agaricoid species in Lactarius , Lactifluus , Multifurca , and Russula are readily distinguished from other gilled mushrooms by the consistency of their flesh , which is granular , brittle and breaks easily , somewhat like a piece of chalk . Russulaceae never have a volva , but a partial veil can be found in some tropical species . Gills are adnate to decurrent , and the colour of the spore print ranges from white to ochre or orange ( with the brown @-@ spored Lactarius chromospermus as an exception ) .

Caps can be dull to very colourful , the latter especially in Russula ; their size ranges from 17 mm diameter or less in Russula campinensis to 30 cm ( 12 in ) in Lactifluus vellereus . Concentrically ringed ( zonate ) caps occur in all Multifurca and several Lactarius species . Laterally stiped ( pleurotoid ) fruitbodies exist in some , mainly tropical Lactifluus and Russula species . Taste is a distinguishing characteristic in many species , from mild to very acrid . A conspicuous feature of the " milk @-@ caps " in Lactarius , Lactifluus , and Multifurca furcata is the latex or " milk " their fruitbodies exude when bruised .

The secotioid and gasteroid species in Lactarius and Russula are derived from agaricoid forms . Secotioid species still have a stipe but the cap does not open fully , while in gasteroid species , fruitbodies are completely closed and the stipe is reduced ; in both cases , the spore @-@ bearing structure is made up of convoluted gills that are more or less crowded and anastomosed . These closed @-@ fruitbody species represent a continuum of secotioid to gasteroid , above @-@ ground to below @-@ ground fruitbodies , with spores forcibly discharged or not . Secotioid or gasteroid Lactarius exude latex just like their agaricoid relatives .

The corticioid species of Boidinia , Gloeopeniophorella , and Pseudoxenasma develop crust @-@ like fruitbodies with a smooth , porous , or flaky surface and grow on tree logs or dead branches .

#### = = = Microscopic characteristics = = =

All Russulaceae , including the corticioid species , are characterised by spherical to elliptic

basidiospores with a faint to very distinct ( e.g. warty , spiny , or crested ) ornamentation that stains bluish @-@ black with Melzer 's reagent ( an amyloid stain reaction ) . Basidia ( spore @-@ bearing cells ) are usually club @-@ shaped and four @-@ spored . Russulaceae species do not have clamp connections .

Characteristic cells with an oily content ( gloecystidia ) are found in the hymenium . In Russulaceae , these show a positive colour reaction when treated with sulfoaldehydes ( sulfovanillin is mostly used ) . They are also present in the hyphal sheath of ectomycorrhizal roots colonised by Russulaceae .

The feature responsible for the brittle fruitbody structure in the mushroom @-@ forming species are globular cells , called sphaerocytes or sphaerocysts , that compose the flesh ( trama ) alongside the usual hyphae . Sometimes , these cells are clustered , and the position and arrangement of these clusters differs among genera .

Another particular trama cell type are lactiferous hyphae ( also lactifers ) . These are hyphae carrying the " milk " or " latex " exuded by the milk @-@ caps ; they react positively with sulfoaldehydes , form an abundantly branched system in the trama and end as pseudocystidia in the hymenium . In general , only *Lactarius* , *Lactifluus* and *Multifurca furcata* possess lactifers . In *Russula* , similar hyphae can sometimes be observed in the trama , but these are not as abundantly branched as real lactifers and do not extend into the hymenium as pseudocystidia . This traditional distinction line between the " milk @-@ caps " and *Russula* is however less evident in some tropical species presenting intermediate states .

= = = Genera distinction = = =

Some characteristics of the mushroom @-@ forming genera ( marked with \* below ) can be less obvious or absent in tropical species . Distinguishing between *Lactarius* and *Lactifluus* based on morphology alone is quite difficult , as clear synapomorphies for both genera have yet to be identified . Most field guides treat the two genera together , often because *Lactifluus* is not yet recognised as a separate genus .

*Boidinia* : corticioid ; loose texture ; surface smooth , with pores , or flaky ; spores spherical with spiny to warty ornamentation . Note that the genus is polyphyletic and needs to be redefined .

*Gloeopeniophorella* : corticioid ; surface almost smooth ; hyphae without clamp connections ; thick @-@ walled cystidia ( metuloids ) and gloecystidia present ; spores with wrinkled ( rugose ) ornamentation .

*Lactarius* : agaricoid or gasteroid ; exuding latex \* ; caps sometimes zonate , viscose or glutinate , but never annulate ; rarely thick @-@ walled cells in cuticles of the cap ( pileipellis ) and the stipe ( stipitipellis ) and sphaerocytes in the gills .

*Lactifluus* : agaricoid or pleurotoid ; exuding latex \* ; caps never zonate , viscose or glutinate , but sometimes annulate ; thick @-@ walled cells in cap and stipe cuticles ; often sphaerocytes in the gill trama .

*Multifurca* : agaricoid ; caps zonate ( also visible in cut through trama ) ; gills regularly forked ; only *M. furcata* exuding latex ; spore print orange ; spores very small ; microscopical trama and hymenium features very variable .

*Pseudoxenasma* : corticioid ; wax @-@ like texture ; gloecystidia with spherical apical appendices ; basidia developing laterally on hyphae ( pleurobasidia ) ; spores broadly ellipsoid to roughly spherical , with warty ornamentation .

*Russula* : agaricoid , gasteroid or pleurotoid ; never exuding latex ; caps often brightly coloured with stipe and gills much paler ; caps not zonate \* ; spore print white , cream , ochre , or orange ; no true lactiferous hyphae \* ; sphaerocytes abundant in gill , cap , and stipe trama .

= = Distribution = =

The Russulaceae as a whole have a worldwide distribution , but patterns differ among genera . *Russula* is the most widespread , found in North , Central and South America , Europe , temperate

and tropical Asia , Africa , and Australasia . It is the only Russulaceae genus that occurs in the Nothofagus zone of temperate South America .

Lactarius is mainly known from the north temperate zone , but some species also occur in tropical Asia and Africa . Lactifluus has a more tropical distribution than Lactarius , with most species known from tropical Africa , Asia , South America , and Australasia , but some also occurring in the north temperate zone . Multifurca is the rarest among the four mushroom genera , known only from some punctual records in North and Central America , Asia , and Australasia .

Species of Lactarius , Lactifluus , and Russula have repeatedly been introduced with trees outside their native range : An overview article lists introductions in Chile , Argentina , Uruguay , Brazil , the USA , Great Britain , the Faroe Islands , South Africa , China , Thailand , and New Zealand .

Among the corticioid genera , Pseudoxenasma is only known from Europe . In contrast , Boidinia species have been found in Europe , Taiwan , and Japan , and Gloeopeniophorella species in North America , South America , Europe , West Africa , Taiwan , Australia , and New Zealand .

= = Ecology = =

= = = Ectomycorrhizal symbiosis = = =

The genera Lactarius , Lactifluus , Multifurca and Russula form a mutualistic ectomycorrhizal root symbiosis with trees and shrubs , exchanging mineral nutrients for photosynthetic sugar . They are one of several fungal lineages that have evolved such a lifestyle and are sometimes referred to as the " / russula @-@ lactarius " clade in the scientific literature . Worldwide , they are one of the most frequently encountered lineages on ectomycorrhizal roots . While some tropical species were initially believed to be parasitic , the observation that species fruiting on tree trunks do form ectomycorrhiza in tropical Guyana supports the view of an exclusively symbiotic lineage .

Associations are known with several plant families . In the Northern Hemisphere , these are essentially the well @-@ known ectomycorrhizal trees and shrubs in the Betulaceae , Fagaceae , Pinaceae and Salicaceae , but in arctic and alpine habitats , Russulaceae also associate with Bistorta vivipara ( Polygonaceae ) , Kobresia ( Cyperaceae ) , and Dryas octopetala ( Rosaceae ) , ectomycorrhizal plants untypic in their respective families . In the tropics , known plant partners include Dipterocarpaceae , Fabaceae , Nyctaginaceae , Phyllanthaceae , Polygonaceae ( Coccoloba ) , Sarcolaenaceae , and the gymnosperm Gnetum gnemon , and in the Southern Hemisphere , Nothofagaceae , Myrtaceae ( Eucalyptus and Leptospermum ) , and Rhamnaceae ( Pomaderris ) . Some Russulaceae are quite specialised in their ectomycorrhizal symbiosis , such as Lactarius and Russula species that only grow with Cistus shrubs in the Mediterranean basin .

The different plant partners are reflected in the wide variety of habitats worldwide . Ectomycorrhizal Russulaceae have been observed in arctic and alpine tundra , boreal and alpine forest , north temperate forest , mires , mediterranean forests and scrub ( maquis ) , miombo woodland , tropical lowland rainforest , tropical cloud forest , tropical dry forest , Australian eucalypt woodlands , and south temperate forests . Where they are introduced , they typically grow in plantations of their native host species , e.g. with pine in South Africa , Eucalyptus in Thailand , or birch in New Zealand .

= = = Other types of mycorrhiza = = =

Some of the ectomycorrhizal Russulaceae are also involved in other types of root symbioses with plants .

A mutualistic association similar to ectomycorrhiza but with some hyphae penetrating into the plant root cells , termed arbutoid mycorrhiza , is formed by Russulaceae with shrubs of the genera Arbutus and Arctostaphylos , both in subfamily Arbutoideae of the Ericaceae .

Some Russulaceae are associated with myco @-@ heterotrophic plants of the Ericaceae subfamily Monotropoideae , forming monotropoid mycorrhiza . This is an epiparasitic relationship , where the

heterotrophic plant ultimately derives its carbon from the primary , ectomycorrhizal plant partner of the fungus . The association is often very specific , with the heterotrophic plants only associating with selected fungus partners , including Russulaceae .

Russulaceae are also an important group of orchid mycorrhizal fungi . This symbiosis is mutualistic in the case of green orchids , but a partly or fully epiparasitic relationship in the case of myco @-@ heterotrophic and mixotrophic orchids , respectively . In some cases , the association with Russulaceae is , as in monotropoid mycorrhiza , very specific : the Mediterranean orchid *Limodorum abortivum* predominantly associates with *Russula delica* and closely related species ; in *Corallorhiza maculata* , different genotypes of the same species have distinct *Russula* partners .

= = = Wood decay species = = =

The corticioid species in *Boidinia* , *Gloeopeniophorella* , and *Pseudoxenasma* are saprotrophic , wood @-@ degrading fungi that develop on dead wood . Their early @-@ branching positions in the phylogeny suggests this has been the ancestral trophic mode of the Russulaceae , and that the mycorrhizal lifestyle ( see above ) evolved later . The saprotrophic nature of these species has been questioned , based on the observation that other inconspicuous , crust @-@ forming fungi are ectomycorrhizal ; a subsequent author reaffirms nevertheless that " [ n ] one of the corticioid species in the family shows any sign of mycorrhizal activity . "

= = = Hypogeous fruiting = = =

Hypogeous fruitbodies , or fruitbodies developing below ground , occur in *Lactarius* and *Russula* and have previously been considered as distinct genera ( see Systematics and taxonomy : Internal systematics ) . As such species are especially diverse in some warm and dry regions , e.g. in Spain , California , or Australia , below @-@ ground fruiting has been interpreted as an adaptation to drought . However , hypogeous Russulaceae are also known from cold temperate regions and tropical rainforest . The fact that hypogeous species in the Russulaceae do not form their own lineages but are scattered in *Russula* or *Lactarius* shows that this type of fruiting evolved several times . It is believed that these changes are evolutionarily quite recent .

= = = Parasites = = =

Russulaceae fruitbodies are subject to parasitisation by other fungi . The genus *Asterophora* develops on old fruitbodies of the mushroom species in the family , as does *Dendrocollybia racemosa* on at least *Russula crassotunicata* . Fruitbodies of *Lactifluus* or *Russula* species otherwise hot @-@ tasting and unpalatable are regarded as choice edibles in North America when infected by the " lobster mushroom " *Hypomyces lactifluorum* . Heterotrophic plants , including orchids or monotropoids , also parasitise ectomycorrhizal Russulaceae and their plant partners ? see above , Other types of mycorrhiza .

= = = Threats and conservation = = =

As with most fungi , little information is available on the threat of extinction for Russulaceae species , and they have not been assessed in the International Union for the Conservation of Nature 's Red List . However , national lists contain some species of *Lactarius* , *Lactifluus* and *Russula* , indicating that they have small populations and are endangered , e.g. in Great Britain , Switzerland , the Czech Republic , and New Zealand .

Although data on Russulaceae themselves are scarce , more is known about the habitats they occur in , especially for the ectomycorrhizal species which depend on their host plants : Several of these habitats are affected by loss or degradation , such as peatlands , Mediterranean forests and scrub or tropical African dry woodland . Similarly , dead wood , the habitat of the corticioid Russulaceae , is rare in many exploited forests and needs special management .

Recent studies have found some traditional Russulaceae species to comprise several cryptic species ( see Systematics and taxonomy : Species diversity ) . This may imply that distribution range and population size for each of such distinct species are smaller than previously thought .

#### = = Edibility = =

Several species of *Lactarius* , *Lactifluus* and *Russula* are valued as excellent edible mushrooms . This is the case for example for the north temperate species *Lactarius deliciosus* , *Lactifluus volemus* , or *Russula vesca* , and other species are popular in other parts of the world , e.g. *Lactarius indigo* in Mexico , or *Lactifluus edulis* in tropical Africa . Some species , like *Russula vesca* , can even be eaten raw . The brittle texture of *Russula* fruitbodies makes them different from other mushrooms and is not appreciated by some .

Several species have a hot to very acrid taste and can cause gastrointestinal symptoms . Despite this , such species are eaten in some regions , e.g. *Lactarius torminosus* in Finland or Russia . Often , they are parboiled or pickled to make them palatable , and sometimes , they are used as spice , for example *Russula emetica* in Eastern Europe . Some species are however truly poisonous : the East Asian and North American *Russula subnigricans* causes rhabdomyolysis and is potentially lethal , and *Lactarius turpis* from Eurasia contains a mutagenic substance .

Cultivation of edible Russulaceae , as in other ectomycorrhizal fungi , is challenging , since the presence of host trees is required . In spite of this difficulty , the European *Lactarius deliciosus* has been successfully grown in " mushroom orchards " in New Zealand .

#### = = Chemistry = =

Fruitbodies of Russulaceae have been the subject of natural product research , and different classes of organic compounds have been isolated from them .

Aroma compounds are responsible for the particular odour or taste in some species , e.g. sotolon in the fenugreek @-@ smelling *Lactarius helvus* , or the similar quabalactone III in *Lactarius rubidus* which causes a maple syrup @-@ like odour in dried specimens . Pigments have been isolated from brightly coloured species , e.g. ( 7 @-@ isopropenyl @-@ 4 @-@ methylazulen @-@ 1 @-@ yl ) methyl stearate from the blue *Lactarius indigo* or russulaflavidin and a derivative from the yellow *Russula flava* . Some *Russula* species contain pigmented pteridine derivatives called russuapteridines that are not found in the milk @-@ caps . Sesquiterpenes are characteristic secondary metabolites of many Russulaceae , especially milk @-@ caps which have been quite intensively studied . They are thought to be responsible for the hot taste in many species and may have deterrent , antifeeding functions in nature .

Other metabolites isolated from different species include dibenzonaphthyridinone alkaloids , prenylated phenols , benzofurans , chromenes , natural rubber ( polyisoprene ) , sterols , and the sugar alcohol volemitol . Among toxic substances , *Lactarius turpis* contains the mutagenic alkaloid necatorin , and the small compound cycloprop @-@ 2 @-@ ene carboxylic acid has been identified as the toxic agent in *Russula subnigricans* . Some secondary metabolites showed antibiotic properties in laboratory tests . An ethanolic extract of *Russula delica* was antibacterial , and a lectin from *Russula rosea* showed antitumor activity .