NOTE: 120 genera listed here are conceived in a broad, classical sense (generally the fleshy stipitate mushrooms with pores) including sequestrate morphologies. Phylogenetic inferences from DNA sequences suggest alignment in suborders: Boletineae, Suillineae, Sclerodermatineae, or in the Paxillaceae. Not all genera are well known, equally circumscribed or robustly inferred phylogenetically. Mycorrhizal associations may be confirmed, but many are presumed or suspected. Recent phylogenetic analyses based on DNA sequences infer some true gasteroid (truffle-like, sequestrate) taxa (aside from those in Sclerodermatineae, Suillineae) belong here. Subfamilies named and inferred by Wu et al. (2014) have been corroborated and updated by Tremble et al. (2024). Some of the diagnoses are from protologues. Year of publication follows authority (-ies).

Abtylopilus Yan C. Li & Zhu L. Yang (2021)

From the protologue (diagnosis): This genus differs from other Boletaceae in a nearly glabrous pileus, white to cream or grayish, then grayish pink hymenophore, with fine pores (0.3–1 mm broad), initially red then black discoloration of the context when exposed, and a pileipellis with a palisadoderm of broad, vertically arranged hyphae. Basidiospores are subsfusiform to cylindrical and smooth. Hymenial cystidia fusiform to subfuscoid-ventricose. Clamp connections absent. Phylogenetic inference places the genus in the Boletoideae near Strobilomyces and Porphyrellus. Currently, two species only known from China. Ectomycorrhizae presumed with Fagaceae.

Acyanoboletus G. Wu & Zhu L. Yang (2023)

Based on the protologue: The genus is distinguished from other Boletaceae by possessing a strongly incurved pileus margin when young, pale yellow hymenophore and context that do not change color when bruised or exposed, a smooth stipe, a strong unpleasant odor, a pileipellis with entangled hyphae forming an intricate trichodermium, smooth basidiospores, hynenial cystidia present, and clamp connections are absent. Phylogenetic inference of four genes (ITS, LSU, tef1, rpb1, rpb2) places the genus with two species on a long branch with less than 50% bootstrap support and less than 0.90 Bayesian posterior probability as a sister clade to Cyanoboletus in the Suillelloideae. Distribution of A. controversus and A. dissimilis currently known from SW China and Malaysia. Ectomycorrhizae presumed with Fagaceae and possibly Pinaceae.

Afroboletus Pegler & Young (1981)

Pileus dry, coarsely fibrillose to squamose, black, often with appendiculate veil remnants, microscopically a trichodermium. Context white, staining red then black. Hymenophore adnexed, white then black, staining red then black. Peronate veil present. Stipe dry, squamose, sometimes annulate, white to gray to black. Spores black, short ellipsoid, longitudinally ridged or winged, sometimes with intercostal veins; a basal thickened rim around sterigmial appendage, lacking a plage. Hymenial cystidia present. Clamp connections absent. Apparently restricted to the African tropics. One sequestrate species known. Ectomycorrhizae presumed with caesalpinoid legumes.

Afrocastellanoa M.E. Smith & Orihara (2017)

From the protologue: Basidiomata sequestrate, gasteroid, firm, rubbery, with one or a few rhizomorphs at the base. Similar to Octaviania in the morphology of the basidiome and basidiospores, but different from Octaviania in the multilayered peridium and in basidia that are irregularly distributed within the solid gleba, resulting in the absence of a distinct hymenium and subhymenium. Phylogenetically related to the epigeous genus Porphyrellus, but distantly related to the genus Octaviania s.s. One sequestrate species known, A. ivoryana. Ectomycorrhizal with Anthonotha (Fabaceae), Uapaca (Uapacaceae), and probably with other legumes in
sub-Saharan Africa.

**Alessioporus** Gelardi, Vizzini, & Simonini (2014)

Originally described as a monotypic genus for *Xerocomus ichnusanus*, a thermo-xerophilic taxon in Mediterranean Europe. The taxon, based on a summary of features in the protologue indicate it is a medium-small species, exhibiting an ochraceous-brown to dark olivaceous brown fibrillose pileus, sometimes with copper red hues and a wavy margin at least in young specimens, a yellow to olive colored hymenophore and a stout, deeply rooting stipe covered with a rough and darker net that is rarely absent, bright yellow at the apex, dark red-brown to blackish brown elsewhere and with a whitish gray basal mycelium. The context is whitish in the pileus, yellowish in the stipe with reddish shades, purplish red to brownish black at the base, turns uniformly blue on exposure, as do the external surfaces after injury or bruising. The most important morphological character is the narrow, granular ring-like zone in the middle or lower half of the stipe, formed by the remnants of the connection between the pileus margin and the stipe cortex during the primordial stage. A 3-gene analysis infers a relationship with *Pulchroboletus* near *Hemileccinum* in the Xerocomoideae. A second species, *A. rubriflavus*, was inferred using ITS sequences by Frank et al. (2017) from E USA. Ectomycorrhizae presumed with Fagaceae, possibly Pinaceae (USA).

**Alpova** Dodge (1931)

*Sequestrate*, globose to irregular in shape. *Peridium* well developed, variable in thickness, usually dry, whitish but usually discoloring with age and handling. *Gleba* sticky and gelatinous, with gel-filled chambers, not forming a true hymenium, separated by pale colored veins, pale colored at first, but darkening with age. *Spores* hyaline, ellipsoid to oblong, smooth, inamyloid, strongly cyanophilic when young. *Clamp connections* usually present. At present confined to Northern Hemisphere. Ectomycorrhizae with Betulaceae, possibly Pinaceae or Fagaceae.

**Amoenoboletus** Wu et al. (2021)

*Diagnosis* (from protologue): Distinguished by the combination of unchanging context and hymenophore on bruising, the reddish to red pores and yellowish tubes, furfuraceous squamules on the pileus and stipe, a subcutis in the pileipellis, and ovoid to ellipsoid or sometimes nearly subfusiform, smooth inamyloid spores lacking a suprahilar depression. Phylogenetic inference based on four genes (ITS, 28S, *tef1*, *rpb2*) infer placement in the Suillelloidae sister to *Pulveroboletus*. Three species (*A. granulopunctatus*, *A. microbii*, *A. miraculosus*) are currently described from E Asia, Malaysia, and New Zealand. Based on unpublished data, further distribution and additional taxa are apparent in Australia. Ectomycorrhizae presumed with Nothofagaceae (New Zealand), Fagaceae and Pinaceae (Japan, China), Fagaceae and Myrtaceae (Sabah, Malaysia). Unpublished entities from Australia appear in bushland with Myrtaceae and Casuarinaceae.

**Anthracoporus** Yan C. Li & Zhu L. Yang (2021)

From the protologue (diagnosis): This genus differs from others in the Boletaceae due to its tomentose or rugose pileus, black to grayish black hymenophore when young which changes to grayish pink when mature, with fine pores (0.3–2 mm broad), with context that stains red at first then black when exposed, and a pileipellis with a trichodermium, palisadoderm or epithelium. *Basidiospores* smooth, elongated to cylindrical or subfusiform. *Hymenial cystidia* fusiform to subfusoid-ventricose. *Clamp connections* absent. Phylogenetic inference places the genus in the Boletoidae near *Strobilomyces* and *Porphyrellus*. Currently, three species (*A. cystidiatus*, *A. holophaeus*, *A. nigropurpureus*) known from China, Japan and Singapore. Ectomycorrhizae presumed with Fagaceae.

**Aureoboletus** Pouzar (1957)

*Pileus* viscid to dry, rugulose to even. *Context* white, unchanging. *Hymenophore* tubulose, bright yellow at first, greenish yellow with age in some, not oxidizing. *Stipe* central, glabrous, sometimes
superficially pruinose or lacerate ridged, viscid or dry, rarely with a veil. Spores olive brown in deposit, smooth or rarely with conspicuous longitudinal ridges, fusoid to ovoid, inamyloid. Clamp connections absent. Mostly north temperate to pantropical. Ectomycorrhizae with Pinaceae, Fagaceae.

**Australopilus** Halling & Fechner (2012)

*Basidiomata* epigeous. *Pileus* gray to dark gray, sometimes pink to deep pink pigments present. Context white, unchanging. *Hymenophore* tubulose, white then vinaceous pink. *Stipe* white above, chrome yellow at base, beset with either fine isolated pink scabers or these often arranged in a well-defined or ill-defined raised reticulum, sometimes scattered on low longitudinal ridges. Spores pinkish to reddish brown in deposit, smooth, fusoid. *Pileipellis* a trichodermium. Hymenial cystidia present. *Pseudocystidia* absent. Clamp connections absent. Without explanation, Wu et al. (2016) considered the genus a synonym of *Royoungia* based on analysis incorporating four epigeous entities from China. So far, known only from Australia. Ectomycorrhizae with Myrtaceae, Casuarinaceae.

**Austroboletus** (Corner) C.B. Wolfe (1980)

*Pileus* viscid or dry, tomentose to subtomentose, microscopically a trichodermium or ixotrichodermium, sometimes with appendiculate remnants at margin. Context white or yellow, unchanging. *Hymenophore* tubulose, adnexed, white at first, pinkish flesh colored to brownish pink with maturity (rarely yellow), sometimes staining light brownish to pinkish brown. *Stipe* central, pruinose to alveolate-reticulate, dry or sometimes glutinous-viscid, not staining or developing stains in situ from aging; basal mycelium white. Spores vinaceous pink in deposit, obscurely pitted to pitted, sometimes equatorially verrucose, amygdaliform to elongate-fusoid, inamyloid or dextrinoid. *Hymenial cystidia* usually present. Clamp connections absent. KOH & NH₄OH reactions negative. Mostly E Asia, Australasia; some temperate, montane and lowland tropics of New World. Ectomycorrhizae with Pinaceae, Fagaceae, Myrtaceae, Dipterocarpaceae, Casuarinaceae.


*Basidiomata* stipitate-pileate. *Pileus* hemispherical, convex or applanate, subtomentose, dry, usually incurved at the margin when young. Context pale yellow to yellow, slowly staining pale blue when cut. *Hymenophore* relatively thin (1/3–1/5 of pileal context midway from disc to margin), usually decurrent, yellow, immediately staining light blue to greenish blue when injured; pores angular, or sometimes nearly round; tubes short. *Stipe* smooth or occasionally with reticulations at the upper part; context pale yellow to yellow, basal mycelia white to pale yellow. *Pileipellis* a trichodermium to an interwoven trichodermium. *Hymenial cystidia* present. *Basidiospores* smooth, subfusiform to elongated subfusiform, light yellow to brownish-yellow. Clamp connections absent. Eastern Asia, eastern North America. Ectomycorrhizae presumed with Pinaceae, Fagaceae, Myrtaceae, Dipterocarpaceae, Casuarinaceae.

**Binderoboletus** T.W. Henkel & M.E. Smith (2016)

Boletellus Murrill (1909)

Pileus typically dry, rarely subviscid, scaly or tomentose, microscopically a trichodermium, sometimes with appendiculate remnants at margin. Context white or yellow, often changing to blue. Hymenophore tubulose, adnexed, white at first, soon yellow, often staining blue. Stipe central, usually pruinose, rarely with an apical reticulum, dry, rarely subviscid and annulate, sometimes staining blue; basal mycelium white, very rarely yellow or olive colored. Spores olive brown in deposit, longitudinally ridged/winged or slightly veined, cleft, dimpled or entire at apex, inamyloid or rarely dextrinoid. Hymenial cystidia usually present. Clamp connections usually absent, rarely present (one sp., B. fibuliger). KOH & NH4OH reactions negative (more species need testing). N Hemisphere, temperate South America, Mesoamerica, Andean and Amazonian Colombia, one sp. in Venezuela (B. fibuliger), four spp. in Guyana, Amazonian and NE Brazil, central Africa, Australia, E Asia, SE Asia. Ectomycorrhizae with Pinaceae, Fagaceae, Myrtaceae, Dipterocarpaceae, Casuarinaceae, caesalpinoid legumes (e.g., Dicymbe), possibly Euphorbiaceae.

Boletinellus Murrill (1909)

Pileus dry, usually glabrous but sometimes finely tomentose to matted tomentose, soft textured, microscopically a repent entangled interwoven layer. Context pale yellowish, rarely cyanescent. Hymenophore tubulose, quite decurrent and with a radial boletinoid orientation, occasionally sublamellate, dull yellow, slowly cyanescent then brownish. Stipe lateral or eccentric, very rarely nearly central, dry, mostly glabrous. Sclerotia present. Spores olive brown in deposit, ovoid to nearly globose, smooth. Hymenial cystidia inconspicuous, often absent on the pores. Clamp connections present. Not ectomycorrhizal. The type of the genus, B. merulioides is widespread in eastern North America where it is associated with Fraxinus, but is not mycorrhizal. Rather it is associated with a parasitic aphid restricted to Fraxinus roots. Other species, erroneously placed in Gyrodon occur in the Neotropics. There is a well-documented report of its occurrence in Kyushu, Japan. Also, quite possibly in Queensland, Australia.

Boletochaete Singer (1944)


Boletus L. (1753)

Pileus dry to subviscid, glabrous to tomentose to fibrillose, microscopically a trichodermium or ixotrichodermium. Context white, not changing. Hymenophore adnexed to adnate, white to yellow to greenish yellow, not changing with pores occluded ("stuffed") when young, concolorous or sometimes red to brownish red in aged specimens. Stipe dry, glabrous to subpruinose to reticulate or sometimes nearly alveolate, with basal mycelium white. Spore deposit olive brown. Spores smooth, fusoid. Hymenial cystidia present. Clamp connections absent. Mostly temperate northern hemisphere, a few in paleo-neotropics. In southern hemisphere, one sequestrate in New Zealand (B. semigastroideus), one in northern Queensland (B. austroedulis). Boletus edulis sometimes appearing with exotic Pinaceae planted outside native range.

Note: This genus remains after all others have been separated based on molecular phylogenetic analyses or other idiosyncratic features. Monophyly inferred from molecular phylogenetics suggests restriction to the 'porcini' clade (i.e., Boletus edulis etc.). Also included here are some sequestrate species (B. subalpinus, B. semigastroideus). Ectomycorrhizae with Pinaceae, Fagaceae, Betulaceae, Dipterocarpaceae (?), Myrtaceae, Casuarinaceae, caesalpinoid legumes(?). Possibly other families less commonly.
**Borofutus** Hosen & Zhu L. Yang (2012)

Pileus squamulose, microscopically a trichodermium. Context usually unchanging, but slowly pale reddish to pale reddish purple. Hymenophore subdecurrent, with broad pores, pallid to cream colored at first, then yellowish to golden brown, staining brownish red. Stipe central, glabrous and ribbed above, squamulose below, with whitish basal mycelium. Spores purple to purplish red to purplish violet in KOH with light microscope optics, boletoid to subamygdaliform, with shallow pits (regular to irregular). Hymenial cystidia present, lageniform, thick-walled. Clamp connections absent. Tropical Asia (Bangladesh, Thailand). Apparently phylogenetically allied to the sequestrate Rhodactina, Spongiforma, and epigeous Ionosporus.

Ectomycorrhizae with Dipterocarpaceae (Shorea).

**Bothia** Halling, Baroni & Binder (2007)

Pileus dry, coarsely tomentose to subtomentose to aggregated fibrillose or appressed fibrillose, microscopically a trichodermium. Context soft textured, whitish, not cyanescent. Hymenophore decurrent, shallow, conspicuously boletinoid, often with compound pores, pale brown, staining darker brown. Stipe dry, central or eccentric, pale brown, staining darker brown, frequently reticulate at least at the apex, with white basal mycelium. Spores yellow brown in deposit, ellipsoid to long ovoid, smooth, inamyloid. Hymenial cystidia present and conspicuous. Clamp connections absent. Eastern North America, China. Ectomycorrhizae with Fagaceae (Quercus).

**Brasilioporus** A.C. Magnago, Alves-Silva, T.W. Henkel (2022)

Based on the protologue: Basidiomata are epigeous and stipitate, a dry pileus ranging in color from light olivaceous to nearly black; hymenophore is tubulose, off-white at first [pale bluish green in one species apparently not mentioned in the protologue of *B. simoniarum*], changing to red then black with bruising; stipe subglabrous to reticulate, grayish brown to black, bruising [apparently black in published habit images], with context staining red then black on exposure. Spores smooth, fusoid, inamyloid, pinkish brown in deposit. Hymenophoral cystidia present. Pileipellis a palisadal trichodermium, with encrusting pigment. Caulocystidia present. Clamp connections absent. Overall morphology is reminiscent of Porphyrellus-like taxa (see Abtylopilus, Anthracoporus) and dark-colored Tylopilus species. Phylogenetic inference infers relationships with these porphyrelloid taxa as well. Three species known from Guyana and eastern Brazil. Ectomycorrhizae presumed with *Dicymbe corymbosa* (Guyana), and *Coccoloba, Guapira, Pisonia* (Brazil).

**Buchwaldoboletus** Pilát (1969)

Pileus dry, unpolished, sometimes subtomentose, microscopically a collapsed trichoderm or cutis. Context pale colored, usually unchanging but sometimes with a cyanescence just above hymenophore. Hymenophore adnexed, adnate to decurrent, yellow to olivaceous, rarely bruising brownish or cyanescent. Stipe central to sometimes eccentric, dry, smooth and lacking ornamentation. Spores ellipsoid to short-subfusoid, smooth, inamyloid. Hymenial cystidia present, variously shaped. Clamp connections absent. North temperate zone, some tropical, and vouched reports from southern hemisphere. Mycoparasitic with one species closely associated with Phaeolus schweinitzii and rotting Pinaceae wood.

**Butyriboletus** D. Arora & J.L. Frank (2014)

Basidiomata epigeous and stipitate. Pileus mostly brown to reddish. Hymenophore with tube layer yellow, often turning blue when bruised. Stipe yellow or reddish tinged and reticulate over the upper portion. Context of pileus pale yellow, turning blue erratically if at all when cut; context of stipe often vinaceos-tinged at the base. Spores fusoid, smooth, brown (olive brown in mass); pileipellis a trichodermium. Clamp connections absent. North temperate zone and possibly montane neotropics. Ectomycorrhizae with Pinaceae and Fagaceae.
**Cacaoporus** Raspé & Vadthanarat (2019)

From the protologue: *Basidiomata* similar to *Sutorius* but differs in that this genus is a chocolate brown to blackish-brown overall, without any violet tinges; the *hymenophore* is not separable from the pileus context; basal mycelium of the stipe is white and rubescent; *context* is rubescent. *Spores* in deposit dark brown, smooth, amygdaliform to ovoid, sometimes with acute apex. Phylogenetic inference based on four genes (*atp6, rpb2, tef1, cox3*) places the genus near *Cupreoboletus* and *Cyanoboletus* in the *Suillelloidae*. Two species known from Thailand and so far, known from mid- to high elevation forests. Ectomycorrhizae presumed with Dipterocarpaceae, Fagaceae.

**Caloboletus** Vizzini (2014)

*Basidiomata* stipitate-pileate with tubular hymenophore. *Pileus* usually pale, whitish to smoke-grey, clay-buff, often with ochraceous/olivaceous tinges, rarely with red tinges, gradually darkening, not turning blue when bruised. *Context* whitish to pale lemon-yellow, sometimes with red tinges at stipe base, gradually changing to blue when cut. *Tubes and pores* at first lemon-yellow to sulphur-yellow (but pores are orange to red in *Caloboletus firmus*), then olivaceous, blue when injured. *Hymenophoral trama* bilateral-divergent of the *Boletus*-subtype. *Stipe* central, pale yellow to yellow, with or without red tinges, usually reticulated, reticulum sometimes reduced or even absent. *Taste* bitter (presence of cyclocalopins), fading with age. *Spores* boletoid, smooth. *Clamp connections* absent. Northern Hemisphere. Ectomycorrhizae with Pinaceae, Fagaceae.

**Carolinigaster** M.E. Smith & S. Cruz (2018)

From the protologue: *Basidiomata* hypogeous to partially emergent, sequestrate, globose to subglobose. *Peridium* not changing color when handled. *Gleba* loculate. *Stipe* or *columella* lacking. *Basidiospores* statismosporic, globose to subglobose, ornamented with short irregular warts at maturity, pink in water and inamyloid but strongly dextrinoid, bleaching to almost hyaline in KOH. *Clamp connections* and *hymenial cystidia* absent. The type species, *C. bonitoi*, described from North Carolina, USA, is inferred to belong in the subfamily *Austroboletoideae*, sister to *Mucilopilus* (since typ) without support, based on ITS, LSU and tef1 sequences. Ectomycorrhizae presumed with Fagaceae and Pinaceae.

**Castellanea** T.W. Henkel & M.E. Smith (2015)

*Basidiomata* sequestrate, with a short stipe, orange brown peridium, brown, loculate gleba, with a short columella arising from a sterile pad, with smooth subfusoid basidiospores that are frequently dextrinoid, lacking clamp connections and hymenial cystidia. Molecular inference places the taxon within a clade containing several species of *Tylopilus* without bootstrap support. Monotypic species in Guyana. Ectomycorrhizae with Dipterocarpaceae (*Pakaraimaea*), Caesalpinoid legumes (*Dicymbe*).

**Chalciporus** Bataille (1908) (=*Rubinoboletus*)

*Pileus* dry or subviscid, glabrous, microscopically a trichodermium. *Context* pale yellow or white or rarely pale pinkish, staining blue in some. *Hymenophore* adnate to subdecurrent, dull red, cinnamon brown, carmine to salmon pink, not staining or rarely staining blue. *Stipe* dry, pruinose to glabrous, with bright yellow basal mycelium. *Spores* brown in deposit, fusoid or short ellipsoid, smooth. *Hymenial cystidia* present. *Clamp connections* absent. North Temperate and Pantropical. Some dubious reports from southern Hemisphere; possibly native in New Zealand, but also exotic. *Chalciporus piperatus* and *C. piperatoides* are exotic invaders in Australia brought in on roots of *Pinus*. Possible Australian natives found in NSW in 2017 (Prichard, unpublished). Putatively mycoparasitic on *Amanita muscaria* (at least *C. piperatus*), but possibly ectomycorrhizal with Pinaceae, Fagaceae and Myrtaceae for some taxa.

**Chamonixia** Rolland (1899)

*Basidiomata* sequestrate, globose to subglobose, dry, white at first, soon staining blue, with basal rhizomorphs. *Gleba* whitish when young, brown when mature, with peridial trama and columella soon

Ectomycorrhizae with Pinaceae.

**Chiua** Y.C. Li & Zhu L. Yang (2016)

From the protologue: *Basidiomata* stipitate-pileate with tubular hymenophore. *Pileus* hemispherical to subhemispherical or convex; surface subtomentose, dry, slightly extended at the margin when young; context yellow to bright yellow, unchanging in color when injured. *Hymenophore* depressed around apex of stipe; hymenophoral surface white when young, and becomes pinkish or pink to purplish when mature; *pores* angular or roundish; *tubes* concolorous with hymenophoral surface, unchanging in color when injured. *Stipe* central, yellow to lemon yellow at upper part, bright yellow to chrome yellow at the base; *basal mycelium* chrome yellow. *Basidiospores* smooth, subfusiform.

*Pleuro- and cheilocystidia* subfusiform to ventricose or clavate. *Pileipellis* subcutis or trichodermium composed of filamentous interwoven hyphae, or hypoepithelium composed of filamentous hyphae and concatenated subglobose cells. *Clamp connections* absent. Gene inference indicates the genus is distinct in the *Zangioideae*. Four species known from southern China, Thailand. Ectomycorrhizae presumed with Fagaceae, Pinaceae.

**Corneroboletus** N.K. Zeng & Zhu L. Yang (2012)

*Pileus* convex becoming plane; surface mucilaginosus, covered with conical to subconical to irregularly shaped squamules, microscopically an ixohyphoepithelium. *Hymenophore* yellow to olivaceous yellow, turning reddish brown slowly when injured. *Stipe* central, cylindrical; surface covered with conical to subconical to irregularly shaped squamules, but apical part nearly smooth. *Spores* subfusiform to ellipsoid, smooth under light microscopy but irregularly warted to irregularly bacillate with SEM. *Hymenial cystidia* present. *Clamp connections* absent. One species, *C. indecorus*, known from Singapore, Malaysia, tropical China. In Wu et al. (2016), the genus was reduced to synonymy with *Hemileccinum*, so *C. indecorus* was transferred to *Hemileccinum*. Ectomycorrhizae likely with Fagaceae.

**Costatisporus** T.W. Henkel & M.E. Smith (2015)

From the protologue: *Basidiomata* hypogeous to partially emergent, sequestrate. *Peridium* greyish yellow, staining dark blue, glabrous to subtomentose, thin. *Gleba* brown, unchanging, loculate, sterile veins absent. *Basidiospores* statismosporic, subglobose to oblong, light brown, inamyloid, with costate ornamentation of longitudinal ridges pole to pole; these entire or discontinuous; pedicel infrequent. *Basidia* clavate. *Cystidia* and *clamp connections* absent. A relationship within Boletaceae is inferred from molecular analysis which infers *Costatisporus* is a sister taxon to *Sutorius*. Monotypic with one species, *C. cyanescens*, from Guyana.

Ectomycorrhizae with Caesalpinoid legumes (*Dicymbe, Aldina*).

**Crocinoboletus** N.K. Zeng, Zhu L. Yang & G. Wu (2104)

*Basidiomata* epigeous. *Pileus* convex to applanate, surface yellowish orange, bright orange to reddish orange, covered with minute, reddish brown squamules, turning bluish olivaceous quickly, then blackening when bruised. *Context* vivid golden yellow, turning bluish olivaceous quickly when bruised. *Hymenophore* poroid, adnate or slightly depressed around apex of stipe; *tubes* orange, turning bluish olivaceous quickly, then blackening when bruised. *Stipe* centrally attached, subcylindric, concolorous with the pileus, sometimes with reddish orange squamules, turning bluish olivaceous quickly, then blackening when bruised. *Spores* subfusiform to ellipsoid, smooth. *Pleuro- and cheilocystidia* present. *Pileipellis* an interwoven trichoderm at the middle part of the pileus but a cutis at the margin of the pileus. *Clamp connections* absent. Polyene pigments boletocrocs present. Three species known: *C. rufaureus, C. laetissimus, C. pinetorum*. Eastern Asia (Japan, China), Papua New Guinea. Non-bluing lookalikes
Cupreoboletus Simonini, Gelardi & Vizzini (2015)

A former member of Boletus sect. Luridi, with reticulate stipe, the taxon produces peculiar protruding crystals on the hymenophore along with pseudocystidia. Odor is described as intense and sweet, recalling propolis, cinnamon or poplar flower buds. Four-gene molecular phylogenetics infer placement as a sister genus to Cyanoboletus on a well-supported polytomic clade. Monospecific, C. poikilochromus, in thermophilic southern Europe.

Ectomycorrhizae assumed with Quercus.

Cyanoboletus Gelardi, Vizzini & Simonini (2014)

Basidiomata pileate-stipitate with tubular-poroid hymenophore, epigean, small to medium- small, evelate. Pileus tomentose to glabrous, dry to slightly tacky. Context yellowish, often reddish- tinged at the base of stipe, instantly discoloring dark indigo blue to blue-blackish when handled or injured, inamyloid. Taste mild. Tubes adnate to depressed around the stipe, yellow to olive-green. Stipe surface smooth to pruinose, transversely streaked-scissurate or occasionally reticulate. Spores olive-brown in deposit, smooth, ellipsoidal to ellipsoidal-fusoid. Hymenial cystidia present. Pileipellis a trichodermium. Hymenophoral trama bilateral-divergent of the 'Boletus-type'. Lateral stipe stratum of the 'boletoid type'. Clamp connections absent. Northern Hemisphere.

Ectomycorrhizae with Pinaceae, Fagaceae.


Basidiomata sequestrate, globose to somewhat flattened, dry, covered with yellow brown, short, conical warts. Gleba with dark, gelatinized locules, deep indigo blue to black with exposure, with white sterile trama, also deep blue-black on exposure. Spores globose to subglobose, with straight to curved conical spines. Clamp connections absent. One species, D. echinulata, known from Malaysia and Borneo. Molecular phylogenetic inference indicates placement in the Leccinoideae.

Ectomycorrhizae likely with Shorea.

Erythrophylloporus Ming Zhang & T.H. Li (2018)

From the protologue: Basidiomata epigeous, small to medium-sized, stipitate-pileate with lamellate hymenophore. Pileus convex to applanate, dry, pruinose or velutinous, submentose to faintly squamulose or subflocose towards the center, orange, deep orange, yellowish red to reddish orange. Context vivid yellow to orange yellow, gradually changing dark violet, blackish blue to dark blue when exposed. Hymenophore decurrent, lamellate, yellowish orange, orange, deep orange, reddish orange to orange red changing grayish blue, grayish turquoise to grayish green when bruised. Stipe central, solid, subcylindrical or clavate, orange, yellow, reddish orange to yellowish red, with orange, reddish orange to orange red pruinose scales on surface, basal mycelium vivid yellow. Basidiospores broadly ellipsoid, ellipsoid to nearly ovoid, smooth, thin-walled. Pleuro- and cheilocystidia present, usually containing yellowish brown pigment, slowly dissolving in KOH. Pileipellis a subcutis to trichoderm, becoming a subcutis when mature. Clamp connections absent. Five species, known from southern China (1), Thailand (2), Mexico (1) and Costa Rica (1). Two separate four gene (nrLSU, tef1, rpb1, rpb2; atp6, tef1, rpb2, cox3) phylogenetic inferences place the genus ambiguously in the Suillelloideae near Lanmaoa and Rugiboletus (first inference) and Singerocomus and Rugiboletus (second inference).

Ectomycorrhizae presumed with Fagaceae.

Exsudoporus Vizzini, Simonini & Gelardi (2014)

Basidiomata stipitate-pileate, epigean. Pileus convex to applanate, bright blood red, crimson- red, purplish-red, reddish-pink or reddish-brown, opaque to shiny, dry to subviscid with moist weather, glabrous to subpruinose or submentose. Context pale yellow to bright yellow, quickly turning dark blue
when injured or exposed, then fading blackish *Hymenophore* tubulose, adnate or slightly depressed around stipe apex; *tubes* yellow to olivaceous-brown; *pores* pinkish-red, reddish-orange, blood red to dark red, rarely yellowish-orange or yellow, often beaded with golden yellow or amber yellow droplets when young and fresh. *Stipe* central, solid, yellowish to concolorous with the pileus, conspicuously reticulate with elongated, red meshes or deeply reticulate-alveolate. *Spores* olive-brown in deposit, smooth, subfusiform to ellipsoidal to ellipsoidal-fusoid. *Cystidia* present. *Pileipellis* an interwoven trichodermum tending to a cutis. *Clamp connections* absent. Known from the Northern Hemisphere. Genus phylogenetically inferred for three iconic species (*B. frostii*, *B. floridanus*, *B. permagnificus*). Ectomycorrhizae presumed with Fagaceae

**Fistulinella** Henn. (= *Mucilopilus*) (1901)

*Pileus* dry or viscid, glabrous, fibrillose or tomentose, often scrobiculate, microscopically a trichodermium, cutis, ixotrichodermium, or ixocutis. *Context* white, unchanging, soft-textured. *Stipe* dry or viscid, glabrous or pruinose. *Spores* brownish pink in deposit, smooth, fusoid. *Clamp connections* absent. Mexico, Caribbean, Brazil, Africa, Asia, Australia, New Zealand, Japan, Indonesia. The type species, *F. staudtii*, needs recollection for phylogenetic inference so that the genus can be interpreted in a modern sense. Compare *Mucilopilus* (below).

Ectomycorrhizae probable for some species with Fagaceae, Nothofagaceae, Leguminosae, Sapotaceae, Myrtaceae; doubtfully present in others.

**Garcileccinum** Ayala-Vásquez & Pérez-Moreno (2023)

Based on the protologue, the *pileus* can be pinkish salmon to mustard brown and sometimes has a sterile margin. *Hymenophore* is tubulose, cream-colored to grayish orange; *context* is white and oxidizes to pale gray, vinaceous to dark violet, pale blue green to deep blue, sometimes developing orange pink to coral pink colors. *Stipe* is finely floccose to scabrous, white to pale apricot colored at first, becoming pale caramel to grayish orange. *Pileipellis* is variable in that two of the species have an ixotrichodermum (*G. salmonicolor*, type species; *G. violaceotinctum*), while *G. viscosum* has a palisadal hymenidermum in a gelatinous matrix. *Spores* are smooth fusoid to subfusoid. Using nrLSU, *rpb*2 and *tef*1, the genus is phylogenetically inferred to belong in subfamily *Leccinoideae* as a distinct clade sister to *Rossbeevera pachydermis* and *Leccinellum s.s.* There appear to be three species known at present from Latin America (Mexico, Belize).

Ectomycorrhizae probable with *Pinus* and *Quercus*.

**Gastroboletus** Lohwag (1926)

The genus appears polyphyletic and circumscribes taxa that have lost the ability to forcibly discharge spores (they are truffle-like, sequestrate). Further, the macromorphology is “reduced” in that the hymenophore is rarely exposed because the pileus does not expand and the stipe does not elongate. These taxa are typically hypogeous to suberumpent. Based on phylogenetic inferences from DNA sequences, this is a polyphyletic genus with alignments in clades of epigeous genera such as *Boletus*, *Xerocomus*, *Leccinum*, and *Suillus*. The majority have been described from North America, one from Africa, one from Chile, and two from China. There appear to be undescribed entities allied to *Heimioporus* in Australia. Ectomycorrhizae with Fagaceae, Nothofagaceae(?), Pinaceae, legumes(?), Myrtaceae.

**Guyanaporus** T.W. Henkel & M.E. Smith (2016)

*Basidiomata* epigeous. *Pileus* grayish brown, dry, tomentulose, trama white to pale yellow, bluing slowly on exposure. *Hymenophore* tubulose, shallowly depressed at stipe, grayish yellow, bluing slowly with pressure, immature pores nearly stuffed, eventually ovate and angular. *Stipe* equal, grayish brown, pale yellow at extreme apex, longitudinally striate to reticulate at apex, base densely white tomentose, trama white, unchanging. *Basidiospores* brownish olive in deposit, smooth, inamyloid. *Pleurocystidia* present. *Cheilocystidia* absent. *Hymenophoral trama* parallel to slightly diverging (phylloporoid), mediostratum barely distinct, concolorous. *Pileipellis* a trichodermium with variously-
shaped terminal elements. *Stipitipellis* hymenidermous at apex. *Clamp connections* absent. One species, *G. albipodus*, from Guyana. True relationships for this genus in the Boletaceae are not apparent. A phylogenetic analysis of the nrLSU and *rpb*1 places the genus on a long unsupported branch near *Tylopilus*, *Xanthoconium* and *Imleria*.

Ectomycorrhizae with *Dicymbe* (caesalpinoid legume), *Pakaraimaea* (Cistaceae, formerly in Dipterocarpaceae).

**Gymnogaster** J.W. Cribb (1956)

_Basidiomata_ sequestrate, but stipitate with fertile portion exposed and surrounding percurrent stipe-columella, with pileal disc depressed, dry, dark brown to reddish brown to orangish brown, finely subtomentose. _Context_ yellow, immediately cyanescent. _Hymenophore_ loculose to irregularly poroid, slightly subdecurrent, whitish with some brownish red stains at first, then grayish yellow to olive, immediately cyanescent. _Stipe_ central, tapering downward to a point, dry, deep yellow to orange yellow at apex, red to deep red downward, short sulcate at apex, subpruinose, immediately cyanescent, with interior yellow, immediately cyanescent, becoming hollow. _Spores_ smooth, citriform to amygdaliform, with a germ pore, rarely dextrinoid, rarely cyanophilic. One species known: *G. boletoides* from SE Queensland, N New South Wales, Australia. Phylogenetic relationships to ballistosporic taxa infer placement in the _Suillelloideae_.

Probably ectomycorrhizal with Myrtaceae.

**Gyrodont** Opatowski (1836)

_Pileus_ glabrous or rarely subsquamose, dry, microscopically a trichodermium. _Context_ pale yellow to whitish. _Hymenophore_ decurrent, with _tubes_ and pores radially elongated, staining blue. _Stipe_ central to eccentric, often curved and short. _Spores_ olive to olive brown in deposit, smooth, short-ellipsoid to phaseoliform. _Hymenial cystidia_ present to rarely present. _Clamp connections_ present. Known from Europe, western USA, and Andean Neotropics; so far not in Australia. Phylogenetic inference places the genus in the Paxillaceae.

Ectomycorrhizae with *Alnus*.

**Gyroporus** Quélet (1886)

_Pileus_ dry, glabrous to fibrous-subsquamous, microscopically a trichodermium. _Context_ white to pale yellow, staining blue or brown in some. _Hymenophore_ adnexed, white then pale yellow, with pores staining brown or blue in some. _Stipe_ dry, glabrous or fibrous-subfurfuraceous, hollow or solid, composed of circumferentially arranged hyphae (not longitudinal). _Spores_ yellow in deposit, smooth, ellipsoid. _Hymenial cystidia_ present. _Clamp connections_ present. North Temperate and Pantropical; less common in the southern hemisphere, but widely distributed and diverse in Australia. Phylogenetic placement inferred in Sclerodermatinaceae, family _Gyroporaceae_.

Ectomycorrhizae with Pinaceae, Fagaceae, Betulaceae, Myrtaceae, Casuarinaceae(?), possibly Lauraceae.

**Harrya** Halling, Nuhn & Osmundson (2012)

_Pileus_ rose pink to brownish pink to pinkish gray. _Context_ white, not staining. _Hymenophore_ tubulose, adnexed, white then vinaceous pink. _Stipe_ white above, chrome yellow at base, beset with fine pink scabers either isolated or rarely arranged on a raised reticulum. _Spores_ pinkish to reddish brown in deposit, smooth, fusoid, dextrinoid in Melzer’s reagent. _Hymenial cystidia_ present. _Pseudocystidia_ absent. _Pileipellis_ a trichodermium. _Clamp connections_ absent. Six species: *H. chromapes*, *H. atriceps* plus four others from China (*H. alpina*, _atrogrisea_, _moniliformis_, _subalpina*). Eastern North America to Central America, China, Japan.

Ectomycorrhizae with Pinaceae, Fagaceae, Betulaceae(?)

**Heimioporus** E. Horak (2004)

_Pileus_ dry, rarely subviscid, subtomentose to subvelutinous, even or rarely shallowly alveolate or
rarely cerebriform, microscopically a palisadic trichodermium or approaching a hymeniform epithelium. Context white to yellow, not staining or erratically cyanescent near Tubes. Hymenophore adnexed, yellow, sometimes staining blue. Stipe dry, pruinose to reticulate or rarely with sublacerate ridges, with white basal mycelium. Spores olive brown in deposit, alveolate- reticulate to reticulate or with irregular, pit-like perforations, extremely rarely rugulose and with crater-like pits, elongate-ellipsoid to short ellipsoid, lacking a suprahilar plage. Hymenial cystidia present. Clamp connections absent. A sequestrate entity allied to H. cooloolae known from SE Australia. Asia, SE Asia, Australia, Eastern USA, Mexico, Belize, and Costa Rica.
Ectomycorrhizae with Fagaceae, Dipterocarpaceae, Myrtaceae, Casuarinaceae.

**Heliogaster** Orihara & K. Iwase (2010)
Basidiomata sequestrate (secotioid to gasteroid), hypogeous to nearly epigeous, soft-textured, primarily pale yellow then ochre to light brown. Stipe-columella usually present, forming dendritic sterile tissue. Gleba dry, loculose with empty locules, whitish to grayish white, soon bluish to purplish when cut and exposed. Basidiospores hyaline to pale ochraceous, with pyramidal conical spines, dextrinoid. Hymenial cystidia absent. Peridial surface formed from filamentous interwoven hyphae. Clamp connections absent. Allied to Xerocomellus chrysenteron complex of epigeous boletes according to describing authors (Orihara et al. 2010). Morphologically reminiscent of *Octaviania*. Apparently only in Japan.
Ectomycorrhizae expected with Pinaceae and Fagaceae.

**Hemilanmaoa** Yang Wang, Bo Zhang, Y. Li (2023)
From the protologue: “This genus is similar to *Lanmaoa* but differs from the latter by pores red at the mature, stipe covered with distinctly[sic] reticulations and hyphae dextrinoid. Basidiomata bluing when bruising, pileus submentosetos, hymenophore decurrent with surface red, stipe covered with reticulations and red dots, and hyphae of context dextrinoid. Basidioma stipitate-pileate with tubular hymenophore. Pileus hemispherical and depression at the center, pale yellow toward margin; context whitish to pale yellow, discoloring to blue when injured. Hymenophore decurrent, surface orange-red, turning to blue when bruised; pores compound, angular to round, tubes light yellow, changing to blue when cut. Stipe central, yellow at the upper partition, brownish red downwards base, surface reticulate, especially on the upper partition, and erratically covered with brownish red dotted elements, staining blue when touched. Context of stipe brownish red at the base, changing to blue when injured. Basidiospores smooth, ellipsoid, yellowish brown, Pileipellis an interwoven trichodermium. Stipitipellis fertile, caulobasidia scattered. Hyphae of context dextrinoid. Clamp connections absent. Odor mild.” The genus was placed in the *Suillelloideae* based on phylogenetic inference using four nuclear genes (28S, *tef*1, *rpb*1, *rpb*2) immediately sister to *Suillellus*. However, macroscopic comparison of the one species (the type and one other collected the same day in China, Guizhou Prov.) is made to *Lanmaoa* and *Cyanoboletus*. Ectomycorrhizae presumed with *Cyclobalanopsis* sp. and Lauraceae.

**Hemileccinum** Šutara (2008)
Basidiomata pileate-stipitate, recalling *Leccinum* sect. *Luteoscabrum* (see *Leccinellum* below); Pileus dry, submentosetos to glabrous, violet with NH3, with pileipellis a trichodermium or hymeniform. Context yellow or white, unchanging. Hymenophore adnexed, light yellow to deep yellow, unchanging when bruised, with fine pores. Stipe dry, scabrous, with scabers light colored, and barely darkening with age. Spores olive brown in deposit, smooth, fusoid. Hymenial cystidia present. Clamp connections absent. Molecular inferences indicate distinction from *Leccinum*, *Boletus*, *Xerocomus*. Includes 15 species: eight from China, Singapore and Thailand, two from Europe, and five from the Americas. At least one undescribed from Australia.
Ectomycorrhizae with Fagaceae, Betulaceae, Ulmaceae and possibly Myrtaceae in Australia.
**Hongoboletus** G. Wu & Zhu L. Yang (2023)

Based on the protologue: *Basidiomata* are pileate-stipitate with a tubular hymenophore. All parts of the basidiomata quickly change to a dark blue when bruised or exposed. **Of note**: the yellow hymenophore is very thin compared to the thick, yellow context. Spores are smooth, subfusoid; *hymenial cystidia* are present; *pileipellis* is an interwoven, tangled trichoderm; *stipitipellis* is hymeniform; **clamp connections** absent. The type species, *Boletus ventricosus* Taneyama & Har. Takah. (2013), was described from Japan and also occurs in China, based on molecular phylogenetics of ITS, LSU, *tef1*, *rpb1*, *rpb2* from five exemplars (plus one indet. from Thailand), and is inferred to belong to the *Suillelloideae*. The genus appears slightly supported (56% ML) sister to *Neoboletus*. Named in honor of Tsuguo Hongo. Ectomycorrhizae presumed with Pinaceae and Fagaceae.

**Hortiboletus** Simonini, Vizzini & Gelardi (2015)

*Basidiomata* pileate-stipitate, recalling *Xerocomellus*. Spores smooth, not ornamented, with Qm < 2.5, *stipe context* with small vermillion red dots in the base. **Clamp connections** absent. Molecular inferences indicate distinction in *Boletoideae*. Northern Hemisphere. Apparently two species from Europe: *H. bubalinus*, *H. rubellus* (this latter also N. America). Ectomycorrhizae with Fagaceae(?).


*Basidiomata* stipitate-pileate with tubular hymenophore. *Pileus* hemispherical, convex to applanate, sometimes umbонate; surface densely covered with granular squamules when young, becoming rimose-diffract to small tufted squamulose with age, dry. **Context** whitish, cream-colored to yellowish, first bluish or indistinctly bluish, then reddish to brownish red, finally brownish to blackish when injured. *Hymenophore* adnate, sinuate or slightly decurrent; thickness of hymenophore 3–5 (7) times that of pileal context at the position halfway to the pileus center, *flesh* yellow to dull yellow, staining blue when injured; *pores* compound, angular; *tubes* concolorous with hymenophoral surface, staining blue when injured. **Stipe** central, pale yellow-brown, pale red-brown to dirty pale brown, nearly smooth, sometimes finely fibrillose; context dirty white to yellowish, first typically becoming bluish, then reddish to brownish red, and finally brownish to blackish when exposed; *basal mycelia* whitish. *Pileipellis* a trichoderm composed of cylindrical or tumid cells. *Hymenial cystidia* present. Spores subfusiform, yellowish, with bacillate ornamentation (under SEM), rarely only partially ornamented. **Clamp connections** absent. Known from China, Japan, Indonesia, Malaysia. Phylogenetic inference indicates the genus is sister to *Phylloporus* with 4–5 species. Ectomycorrhizae presumed with Pinaceae, Fagaceae, Dipterocarpaceae.

**Hymenoboletus** Y.C. Li & Zhu L. Yang (2016)

From the protologue: *Basidiomata* stipitate-pileate with tubular hymenophore. *Pileus* hemispherical or convex, subtomentose, dry; **context** white to cream, without discoloration when injured. *Hymenophore* depressed around apex of stipe; hymenophoral surface white when young, and becoming pinkish or pink when mature; *pores* angular or roundish; *tubes* concolorous with hymenophoral surface, unchanging in color when injured. **Stipe** central, pink to purplish pink, but yellow to yellowish at apex and bright yellow to chrome yellow at base; basal mycelium chrome yellow. **Basidiospores** smooth, subfusiform. *Pleuro- and cheilocystidia* subfusiform to subfusiform-ventricose or clavate. *Pileipellis* hymeniform. **Clamp connections** absent. One species (*H. luteo-purpureus*) phylogenetically inferred in the *Zangioideae*, between *Royoungia-Australopilus* and *Harrya*, but lacks any further phylogenetic support. The single species appears clearly distinct based on microscopic features. Ectomycorrhizae presumed with Fagaceae.

**Imleria** Vizzini (2014)

*Basidiomata* epigeous. *Pileus* reddish brown, chestnut brown to dark brick brown, sometimes
pallid, minutely to distinctly tomentose when young and dry, soon becoming smooth and polished, viscid in wet weather. **Contexts** of pileus and stipe whitish to lemon-yellow, becoming blue particularly around the tubes and at the stipe apex when handled. **Tubes** cream to lemon-yellow, becoming dull yellow with age, bluing on cutting. **Pores** compound, angular, quite large at maturity, concolorous with tube, bluing when handled. **Stipe** central, concolorous with pileus or slightly paler, minutely flocculose or fibrillose-striate. **Spores** boletoid, smooth. **Pileipellis** an ixotrichoderm, consisting of long, slender and cylindrical interwoven hyphae, smooth to slightly incrusted by a minutely granular, yellowish pigment and embedded in a gelatinous matrix. **Clamp connections** absent. Northern Hemisphere. One well-known species in N. Hemisphere, *I. badia*, is inferred from molecular phylogenetics. Three others described from E. Asia; another European one placed here without justification. Ectomycorrhizae presumed with Pinaceae, Fagaceae.

**Imperator** Koller, Assyov, Bellanger et al. (2015)

From the protologue in Index Fungorum 243: Habitus robustissimarum Boletacearum typicus. A gen. *Rubroboletus* differt pileo tacto caeruleo- dein nigro maculoso, contextum in stipites basi rubropurpureo. Stipes robustum, totaliter reticulato atque flavo-purpurascens. Porii minuti, primitus lutei vel rubri, tacto caerulecentibus. Caro compacta, odore foris, flavo-sulphurea, virescens deintunque fracta caerulecentibus; stipite basi. Holotype: *Boletus torosus* Fr. 1835. Phylogenetic results based on ITS and 28S rDNA sequences reveal that the three species cited above (*I. luteocupreus*, *I. rhodopurpureus*, *I. torosus*) belong to a monophyletic lineage, not characterized in earlier works (Nuhn et al. 2013, Fungal Biology 117: 479-511; Arora & Frank 2014, Mycologia 106(3): 464-480; Gelardi et al. 2014, Mycologia 106 (6): 1168-1187; Simonini & Vizzini 2014, Mycol. Progress 13(1): 95-109; Wu et al. 2014, Fungal Diversity on line, DOI: http://dx.doi.org/10.1007/s13225-014-0283-8; Wu et al 2015, Fungal Diversity on line, DOI: 10.1007/s13225-015-0322-0). The three species identified in this clade are all European, known from broadleaved forests on calcareous soils. This group is characterized by a unique combination of features: yellow to reddish-orange reticulate stipe, staining dark purplish red from base with age, a typical blue to blackish staining on pileus surface when touched, and an intense bluing reaction of the context when cut. Pores are either yellow, red or purplish with a high chromatic variability of all parts of basidiome in *I. rhodopurpureus*. Phylogenetic results supporting this publication (ITS and 28S ML phylogenetic trees) are accessible online at http://boletales.com/phylogenetics/.

**Indoporus** Parihar, Das, Hembrom & Vizzini (2018)

Based on the protologue: *Basidiomata* epigeous; pileus gray with black squamules, dry, with yellowish white context, quickly dull red to grayish red then eventually black when exposed. **Hymenophore** tubulose, depressed around stipe, reddish gray or brownish orange when bruised, eventually black, with simple angular pores. **Stipe** smooth, grayish violet above, gray to blackish brown below, with context grayish violet to dark violet above, dark blackish brown below becoming black when exposed. **Spores** grayish brown in deposit, smooth, inamyloid. **Pleurocystidia** hyaline and rare; **cheilocystidia** hyaline and common. **Pileipellis** a trichoderm, with hyphae containing blackish brown pigment, sometimes with zebroid incrustations. **Clamp connections**? The type species *I. shoreae* was described from Jharkhand, India based on several specimens. Molecular phylogenetic analyses based on nrLSU, ITS, and rpb2 infer an independent clade sister to *Afroboletus* and *Imleria pallida* (LSU, rpb2 with no support) and *Chalciporus* and *Buchwaldoboletus* (ITS with less than 70% support). Ectomycorrhizae with Dipterocarpaceae (*Shorea robusta*) probable.

**Ionosporus** Khmelnitsky (2019)

*Basidiomata* epigeous, dry, dark gray to sooty gray brown on pileus and stipe; **hymenophore** tubulose with angular pores, whitish to grayish yellow to pale greenish yellow, staining red when bruised; **stipe** usually central, finely but conspicuously reticulate and densely finely subpruinose, concolorous with pileus, conspicuously white at the base; **context** white or very pale yellow, unchanging when exposed. **Spores** pale violet to reddish brown in deposit, deeply purple-violet in dilute KOH solutions, dextrinoid in Melzer’s Reagent, fusoid to elongate, appearing smooth with bright field light microscopy, barely

Distinguished by morphological features (and sequestrate habit), including molecular inference, allied to *Tylopilus*. See latter for morphological features. One species from Guyana. Ectomycorrhizae with caesalpinoid legumes (*Dicymbe*, *Aldina*).

**Kaziboletus** Iqbal Hosen & Zhu L. Yang (2021)
Based on the protologue: “*Pileus* glabrous to rimose, red to dark reddish brown when young, becoming off white to cream-white or gray to grayish white with age. *Hymenophore* tubular, free, depressed around the stipe, white to cream white. *Stipe* central, cylindrical, covered with reddish brown scabrous squamules when young, becoming grayish brown at maturity, longitudinal striations with fine cross lines present from the apex almost to the base, the ridges somewhat anastomosing but not reticulate; basal mycelium whitish. *Context* white, turning pale red to pale reddish orange in some patches when exposed. *Basidiospores* light yellow to deep yellow in H2O and 5% KOH, smooth, elongated to cylindrical, somewhat fusoid. *Cystidia* mostly fusoid. *Pileipellis* an epithelium. *Clamp connections* absent.” A four gene (nrLSU, tef1α, rpb1, rpb2) phylogenetic inference supports placement in subfamily *Leccinoideae* always basal to *Chamonixia*, *Octaviania*, *Leccinum*, *Leccinellum*, *Turmalinea*, and *Rossbeevera* on a long branch. One species, *K. rufescens*, from three specimens in Bangladesh and possibly Malaysia (nrLSU root tip sequences). Ectomycorrhizae presumed with *Shorea robusta* (Dipterocarpaceae).

**Kombocles** Castellano, T.W. Henkel, & Dentinger (2016)

**Lanmaoa** G. Wu, Zhu L. Yang & Halling (2015)
*Basidiomata* stipitate-pileate. *Pileus* hemispherical, convex or planate, subtomentose, dry, slightly incurved at the margin when young. *Context* off-white to cream yellow, slowly staining pale blue to light blue when injured. *Hymenophore* adnexed or sinuate, thin (1/3–1/5 thickness of context midway from disc to margin), cream yellow to lemon yellow, staining dull blue when injured with *tubes* concolorous with hymenophoral surface or light red, staining dark blue when injured with *pores* angular or nearly round. *Stipe* central, cream yellow, light yellow to lemon yellow at the apex and light to dark purple red towards the base with basal mycelia yellowish white to white. *Pileipellis* often an interwoven trichodermium to subcutis, rarely ixosubcutis. *Hymenial cystidia* present. *Spores* smooth, narrowly suboblong to subfusoid, light yellow to brownish yellow. *Clamp connections* absent. Eastern Asia, eastern North America, Central America. Ectomycorrhizae presumed with Pinaceae, Fagaceae.

Accommodates most of the taxa with yellow *hymenophore* formerly placed in *Leccinum* sect. *Luteosacbrum* (but see *Hemileccinum* above). This includes several European taxa (e.g., *L. nigrescens*, *carpini*, *corsicum*, *crocipodium*, *griseum*, *lepidum*, & *luteosacbrum*, and *L. quercophilum* from E N America). Apparently restricted to the Northern Hemisphere (Europe, E North America, E...
Ectomycorrhizae with Fagaceae, Betulaceae.

**Leccinum** S. F. Gray (1821)

_Pileus_ viscid or dry, glabrous to subtomentose, microscopically a trichodermium or hymeniform. _Context_ white or pale yellow, unchanging or staining red, pink, gray, or blue to blue-green. _Hymenophore_ adnexed, white to tan to yellow, often staining pale brown. _Stipe_ dry, scabrous, with scales whitish at first becoming brown to black. _Spores_ brown (olive brown?) in deposit, smooth, fusoid. _Hymenial cystidia_ present. _Clamp connections_ absent. North Temperate, montane Neotropics, Asian and African tropics. In Australia, it is considered an exotic import associated with horticultural plantings (Betula, Quercus) fide Watling & Gregory (1988); likewise in New Zealand (McNabb 1968). **NOTE**: A paper by Kuo & Ortiz-Santana (2020) recently reviewed the genus based largely on material from North America. They adopted a very broad concept of the genus to incorporate _Leccinellum_, _Chamonixia_, _Octaviania_, _Rossbeevera_, and _Turmalinea_. Ectomycorrhizae with Pinaceae, Fagaceae, Betulaceae, caesalpinoid legumes.

**Longistriata** Sulzbacher, Orihara, Grebenc, M.P. Martin, Baseia (2020)

_Basidiomata_ sequestrate, hypogeous to subhypogeous, subglobose with short stipe. _Peridium_ bright yellow, smooth with an interwoven cutis and inflated gelatinous hyphae. _Gleba_ is loculate, white to yellowish brown staining dark green to black with age, lacking a columella. _Basidiospores_ broadly ellipsoid, hyaline in alkali, dextrinoid, with thin, irregular longitudinal ridges, sometimes anastomosed. _Cystidia_ lageniform. _Clamp connections_ absent. One species known from northeastern Brazil. nrLSU and tef1 inferences indicate alliance with _Mackintoshia_. Ectomycorrhizae presumed with _Coccoloba_, and _Guapira_.

**Mackintoshia** Pacioni & Sharp (2000)

_Basidiomata_ sequestrate, hypogeous, subglobose to pyriform. _Peridium_ well developed, pale yellow to orange yellow with rusty colored cracks. _Gleba_ white to ochraceous to olivaceous, soft and rubbery with gelatinous trama plates, gel-filled at maturity. _Spores_ smooth, elliptical, slightly thick-walled, sometimes reported with a germ pore. _Hymenial cystidia_ with dense, yellow, cyanophilous content, thin-walled. _Clamp connections_ absent. Odor fruity. So far, only one species, _M. persica_, reported from Zimbabwe. 28s and ITS infer placement in the Zangioidae. Ectomycorrhizae presumed with Caesalpinioideae, _Brachystegia_ and _Burkea_.

**Melanogaster** Corda (1831)

_Basidiomata_ sequestrate, usually hypogeous. _Peridium_ well developed, dry, slightly pruinose, ochre to ochraceous yellow to reddish brown, sometimes with adherent rhizomorphs. _Gleba_ gel-filled at maturity, whitish at first then dark brown to black at maturity, lacking well-developed hymenium, with whitish to yellowish trama plates, lacking a sterile base and columella. _Spores_ smooth, dark brown, orthotropic, with well-developed sterigmal appendage, ovoid to ellipsoid, fusoid to limoniform. _Clamp connections_ present. Northern Hemisphere, Central America. Phylogenetic inference places the genus in the Paxillaceae. Ectomycorrhizae presumed with Pinaceae, Fagaceae, Betulaceae.

**Mucilopilus** Wolfe (1979)

The genus is based on _Porphyrellus viscidus_, described by McNabb from New Zealand. Five other species were placed here by Wolfe. Some, including the type species, were incorporated earlier in _Fistulinella_ (see above) by Singer, and another was moved to _Veloporphyrrellus_ (_V_. conicus) based on molecular phylogenetic analyses. Only _M. castaneiceps_ and _M. mexicanus_ have not been transferred. If the type species is truly a _Fistulinella_, then the genus becomes a synonym of that genus and some other generic name is needed for _castaneiceps_ and _mexicanus_. Refer to _Fistulinella_ for features.
Mycoamaranthus Castellano, Trappe, & Malajczuk (1992)
Basidiomata sequestrate, bright chrome yellow to orange yellow, dry, glabrous to squamulose, globose to subglobose, with numerous rhizomorphs. Gleba viscid to spongy-gelatinous to rubbery, variously colored at first, but darker (grayish-brownish) at maturity. Spores ovoid to obpyriform, with apparent germ pore at apex, pedicillate, spinose to minutely verrucose. Clamp connections absent. Zimbabwe, Malawi, Congo-Kinshasa, Cambodia, Thailand, Malaysia, Singapore, Australia. Ectomycorrhizae with Dipterocarpaceae, Myrtaceae (Eucalyptus, Syncarpia), Allocasuarina, Brachystegia, Julbernarda, Uapaca.

Neoboletus Gelardi, Simonini & Vizzini (2014)
Basidiomata stipitate-pileate with tubular hymenophore, epigeral, evelate. Pileus convex to planate, bay-brown, date-brown, olive-brown, reddish-brown to blood red, ochraceous or yellow, opaque, dry, velvety to submentose. Context firm, pale yellow to bright yellow, quickly turning dark blue when injured or exposed. Hymenophore tubulose, adnate or slightly depressed, with tubes yellow to olivaceous-brown, with pores reddish-orange, blood red to reddish-brown, yellowish-orange or yellow. Stipe central, solid, yellowish, ornamented by conspicuous reddish to reddish-brown or yellow punctuations throughout or at least in the upper part, sometimes reticulate, with or without strigose base. Spores olive-brown in deposit, smooth, subfusiform to ellipsoidal to ellipsoidal-fusoid. Cystidia present. Pileipellis a subparallel or interwoven trichoderm tending to a cutis. Clamp connections absent. North Temperate. Ectomycorrhizae presumed with Pinaceae, Fagaceae.

Neotropicomus A.C. Magnago, Alves-Silva, T.W. Henkel (2022)
Based on the protologue: Basidiomata are epigeous, xerocomoid in habit, with a dry, smooth to rugulose pileus, unchanging context, olivaceous yellow hymenophore with isodiametric to subangular pores; spores olivaceous in deposit, fusoid and smooth; hymenophoral trama phylloporoid; pileipellis is a trichoderm of subglobose cells in an apparent hymeniderm configuration; hymenial cystidia and caulocystidia present; clamp connections absent. Two species described from Guyana and eastern Brazil. Phylogenetic inference indicates relationship with Tengioboletus in the Boletoidae. Ectomycorrhizae presumed with Guapira, Pisonia (Brazil) and Dicymbe (Guyana).

Nevesoporus A.C. Magnago & T.W. Henkel (2022)
Based on the protologue: Basidiomata small, epigeous, with pinkish brown to nearly black, dry pileus; white unchanging context; hymenophore tubulose, off white to pale pink, oxidizing to black or not; stipe narrow and slender, dark gray to black, subvelutinous to subglabrous; spores dark reddish brown in deposit, ellipsoidal to subfusoid, smooth, inamyloid to weakly dextrinoid; hymenial cystidia present; pileipellis a trichoderm or palisade; caulocystidia infrequent; clamp connections absent. Two species described: one from Guyana and one from southeastern Brazil. Published phylogenetic inference by Magnago et al. (2022) curiously shows placement in Chalciporoideae, yet BLAST searches of the GenBank unverified tef1 locus indicates placement with taxa in Boletoidae. Further analyses offered by Halling et al. (2023) using tef1 and LSU infer placement in Boletoidae sister to Anthracopus. Ectomycorrhizae presumed with Coccoloba, Guapira (Brazil) and Dicymbe corymbosa (Guyana).

Nigroboletus Gelardi et al. (2015)
Original diagnosis: Basidiome stipitate–pileate with tubular hymenophore, epigeral, evelate, medium–small sized; pileus convex to planate, submentose to glabrous; hymenophore very thin, poroid, adnate to subdecurrent, yellow to olive–yellow; stipe solid, dry, smooth to minutely pruinose–punctate, reticulation absent; context firm, yellowish; tissues turning dull grayish to blackish throughout when injured or exposed; taste mild; spore print olive–brown; spores smooth, broadly ellipsoidal to subovoid; pleuro–, cheilo–, and caulocystidia present; pileipellis consisting of subparallel to loosely interwoven erect hyphae; hymenophoral trama bilateral–divergent of the Boletus–type or intermediate
between the *Boletus*–type and the *Phylloporus*–type; lateral stipe stratum of the boletoid type; *clamp connections* absent; ontogenetic development gymnocarpic. Molecular phylogenetic inference places the single known species, *N. roseonigrescens*, in the *Boletoideae* near *Xerocomellus*. Currently only known from tropical SE China. Ectomycorrhizae presumed with *Fagaceae* (*Castanopsis*, *Castanea*, *Lithocarpus*).

**Octaviania** Vittadini (1831)

*Basidiomata* sequestrate, frequently hypogeous, or more rarely emergent. *Peridium* persistent, glabrous to floccose or warty to scaly, often discoloring when bruised. *Gleba* whitish at first, marbled, becoming brown to black at maturity, dry to gelatinized. *Spores* globose to ellipsoid, beset with thick, conspicuous, pyramidal to conical projections (warts?) sometimes fused to form irregular ridges, dextrinoid. *Sterile base* absent or present. *Clamp connections* absent. North America, Europe, Asia, Australasia. But see *Leccinum* as broadly defined by Kuo & Ortiz-Santana (2020). Ectomycorrhizae presumed with *Pinaceae*, *Fagaceae*, *Betulaceae*, *Nothofagaceae*, *Myrtaceae*, *Casuarinaceae*.

**Paragyrodon** (Singer) Singer (1942)


Based on the protologue: *Basidioma* stipitate-pileate with tubular hymenophore, small. *Pileus* convex to applanate, subtomentose, dry; *context* yellowish to yellow, staining blue immediately when injured. *Hymenophore* subdecurrent, often with teeth on the apex of stipe; hymenophoral surface yellowish to yellow, staining blue immediately when injured; *pores* irregular, angular to nearly round, often compound; tubes concolorous with hymenophoral surface, staining blue immediately when injured. *Stipe* central, light brown, brownish red to reddish brown, surface often pruinose; basal mycelia cream to grayish yellow. *Pileipellis* an epithelium composed of submoniliform to moniliform hyphae with cystidioid terminal cells. *Pleuro- and cheilocystidia* subfusiform-ventricose or clavate, with subacute apex or with long beak. *Basidiospores* smooth, ovoid to fusiform, yellowish to brownish yellow. *Clamp connections* absent. Phylogenetic inference places the genus in the *Boletoideae* near *Xerocomellus*. Two species known from China and Japan. Ectomycorrhizae presumed with *Fagaceae* and possibly *Pinaceae*.

**Paxilloboletus** Furneaux, De Kesel, & F.K. Khan (2022)

Based on the protologue: The genus is epigal, *pileate-stipitate*, with lamellate decurrent *hymenophore* that is regularly bifurcate and anastomosed. *Context* is white, unchanging when exposed, amyloid in the lamellae. *Basidiospores* are smooth, ellipsoid-fusiform. *Cystidia* present, with *pleurocystidia* more abundant. *Lamellar trama* divergent near pileus context, subregular to regular toward the lamellar edge, gelatinized. *Clamp connections* absent. According to the authors, the genus is macroscopically most reminiscent of *Paxillus*, but the phylogenetic inference based on LSU, *tef1*, *rpb1*, *rpb2*, supports placement in the *Boletoideae*. So far, two species known from tropical Africa. Ectomycorrhizae with *Uapaca*; but also occurring in woodlands in Africa containing *Anthonotha*, *Berlinia*, *Brachystegia*, *Julbernardia*, *Isoberlinia*, *Marquesia*, *Monotes*.

**Paxillogaster** Horak (1966)

*Basidiome* epigal, pyriform to lycoperdon-like, dry, not expanded, with interwoven hyphae in
the epicutis. *Gleba* loculose to sublamelliform, typically enclosed, rarely exposed. *Stipe* well developed, with fragmented veil absent. *Spores* bilaterally symmetric, fusoid to inequilaterally ellipsoid, smooth but with exosporium indistinctly perforate, yellow. *Cystidia* claviform, *Clamp connections* absent. One species known, *P. luteum*, from Antarctic beech forests in Argentina.

Ectomycorrhizae presumed with *Nothofagus dombeyi, pumilio, antarctica*.

**Phlebopus** (Heim) Singer (1936)

*Pileus* dry to subviscid, glabrous, microscopically a trichodermium. *Context* white or pale yellow, unchanging or staining blue. *Hymenophore* adnate, tubulose, staining blue or not. *Stipe* dry, glabrous. *Spores* olive brown in deposit, smooth, short-ellipsoid. *Hymenial cystidia* sometimes present. *Clamp connections* present. Pantropical and subtropical to south temperate (Australia, Brazil, central Africa. SE Asia).

Ectomycorrhizae absent or possibly facultative with legumes. Some associated with insects (aphids).

**Phylloboletellus** Singer (1952)


Ectomycorrhizae apparently not formed.

**Phyllobolites** Singer (1942)


**Phylloporopsis** Angelini et al. (in Farid et al. 2018)

From the original diagnosis: *Basidiomata* pileate-stipitate with lamellate to subporoid hymenophore, epigean, evelate, medium-small sized; pileus convex to applanate, velvety-tomentose to fibrillose; *hymenophore* lamellate to subporoid with anastomosing and intervenose gills, strongly decurrent, beige to olive-cream or olive buff; *stipe* solid to sometimes hollow at maturity, dry, pruinose to longitudinally fibrillose, reticulation absent; basal mycelium whitish to yellowish, context firm, whitish but cream-yellowish in the stipe; *tissues* unchangeable or turning light blue especially on hymenophore and pileus context when injured or exposed; taste mild to slightly bitter; olive-brown spore print; purplish-pink or reddish reaction with ammonia on pileus cuticle; *basidiospores* smooth, ellipsoid-fusiform, spore wall cyanophilic; pleuro-, cheilo and caulocystidia present; *pileipellis* a trichodermium; *hymenophoral trama* bilateral-divergent of the “Phylloporus-type”; lateral stipe stratum absent; *clamp connections* absent; ontogenetic development gymnocarpic. According to the phylogenetic analysis of the combined ITS, 28S, *tef1*-α, and *rpb1* sequences the genus is unrelated to *Phylloporus* and sister to *Bothia* and *Solioccasus* (*Bothia* clade); part of a polytomy in the *Boletoidae*. One species, *P. boletinoides*, found in Central America, Caribbean, and eastern-southeastern USA. Ectomycorrhizae presumed with Pinaceae and Fagaceae.

**Phylloporus** Quélet (1888)

*Pileus* dry, tomentose to subtomentose, microscopically a trichodermium or a modified hymeniform layer. *Context* usually white, sometimes yellow, sometimes changing to blue when exposed.
*Hymenophore* lamellate to subtubulose to radically boletinoid, sometimes changing to blue when bruised. *Stipe* central, rarely slightly eccentric, usually pruinose; basal mycelium white or yellow (IMPORTANT!). *Spores* olive brown in deposit, smooth, fusoid or ovoid, dextrinoid. *Hymenial cystidia* present. *Clamp connections* absent (present in 1 or 2 species). NH₃ reactions negative or positive (blue or blue green, sometimes pinkish lilac or rarely other colors – IMPORTANT!). Mostly tropical, but some temperate (north and south) taxa. Ectomycorrhizae with Pinaceae, Fagaceae, Myrtaceae, Dipterocarpaceae, Casuarinaceae.

**Porphyrellus** E.-J. Gilbert (1931)

This genus used for the typically, somber colored taxa originally placed in *Tylopilus* with very dark brown to dark pinkish brown colored spore print. They are often cyanescent and/or rufescent and then nigrescent. The *hymenophore* is usually not pinkish vinaceous with maturity, but might be a pale greenish yellow becoming black. Based on the European *P. pseudoscaber* nom. inval. (= *P. porphyrosporus*). A distinct genus inferred from DNA sequences. Further taxon discovery and phylogenetic inference should help clarify generic boundary. Many north temperate (one in Europe, several in North America, E Asia), and possibly in Australia, New Zealand; these latter may be generically distinct based on molecular inference (see *Kgaria* from Australia). Also, a few porphyrellloid genera/species were described recently from China by Y.-C. Li & Z.L. Yang (2021; *Abtylopilus*, *Anthracoporus*, *Indoporus*). Also, *Brasilioporus* and *Nevesoporus* from Brazil and *Kgaria* from Australia. Ectomycorrhizae presumed with Pinaceae, Fagaceae, Myrtaceae, Casuarinaceae, perhaps Dipterocarpaceae, Nothofagaceae, caesalpinoid legumes.


*Basidiomata* stipitate-pileate with tubular hymenophore. *Pileus* hemispherical to planate, not viscid when wet, with radially arranged filamentous squamules. *Context* white to pallid, unchanged in color when injured, but occasionally with yellowish discoloration on the base of the stipe. *Hymenophore* adnate to depressed around apex of stipe, white to pallid when young, and becoming pale pinkish or pinkish to pink when mature, unchanged in color when injured. *Stipe* pallid to white, reticulate with elongate meshes. *Basal mycelia* white. *Pileipellis* an interwoven trichoderm. *Hymenial cystidia* with brown to dark brown vacuolar pigment. *Spores* pinkish to pink in deposit, smooth, pinkish to light olivaceous to nearly colorless. *Clamp connections* absent. Currently known from Japan, China, Malaysia, Singapore. One species, with two varieties. 

**NOTE**: Despite the generic name, the genus is not close to *Austroboletus*; rather based on the molecular inference, it fits in the *Leccinoideae* clade (combined nrLSU, tef1, mtSSU).

Ectomycorrhizae apparently with Fagaceae.

**Pseudooboletus** Šutara (1991)

An epigeous bolete with xerocomoid habit that is associated with *Scleroderma* and *Astraeus*. Based on recent next gen inference, it is allied with *Phylloboletus*. Northern hemisphere. Considered parasitic, but one of the pair is ectomycorrhizal.

**Pulchroboletus** Gelardi, Vizzini & Simonini (2014)

*Original diagnosis*: Differing from *Alessioporus* by the pastel pink, cream-pinkish to whitish pink or rarely blood red pileus surface, the smooth to densely punctate stipe surface, rarely with a coarse reticulum, the pseudo-annulus usually located in the upper or middle part of the stipe, the pinkish lilac context of the pileus and unique ITS, LSU and tef-1α sequences. Apparently aligned in the *Xerocomoideae* and circumscribes just two species, one in Mediterranean Europe and the other in states along the Gulf Coast, USA. Ectomycorrhizae presumed with Fagaceae (*Quercus, Castanea*), possibly *Cistus*.

**Pulveroboletus** Murrill (1909)

Retiboletus Binder & Bresinsky (2002)
Recognized as distinct from Boletus. In research published by V. Hellwig, the genus produces a unique group of butenolide compounds called retipolides (rarely without) that are responsible for the bitter taste and the intense yellow color of the context. Spores olive brown in deposit, fusoid, smooth. Hymenial cystidia present. Clamp connections absent. Circumscribes 12 northern hemisphere species with conspicuously reticulate stipes. Temperate New World (Japan?) to montane Neotropics. Ectomycorrhizae with Fagaceae.

Rheubarbariboletus Vizzini, Simonini & Gelardi (2015)
From the original diagnosis: Differs from Xerocomellus by the spores smooth in all species, never striae, never truncate, elements of the pileipellis smooth or only with finely incrusting pigment, the presence of congophilous plaques on hyphal surface, the tapered and rooting stipe base, the bright yellow-ochraceous to orange-rhubarb and unchangeable context in the stipe base, and the dark blue-green to blackish reaction with iron sulphate on pileus surface and in the stipe base context. Apparently restricted to Europe. Ectomycorrhizae presumed with Fagaceae, Pinaceae.

Rhizopogon Fries (1817)
Basidiomata sequestrate, hypogeous to erumpent. Peridium dry, pruinose to submentose, sometimes with overlaying rhizomorphs, sometimes bruising, white to yellow to brown to reddish brown. Gleba dry, minutely loculose, whitish at first, eventually brownish, lacking a columella. Spores smooth, ellipsoid to fusoid, hyaline to pale yellowish, rarely globose and reticulate. Clamp connections absent. Northern Hemisphere. Often present where Pinaceae introduced (e.g., Australia, New Zealand, South America). Ectomycorrhizae with Pinaceae.

Basidiomata sequestrate, globose to pyriform, white with a silky sheen and drab gray tinges, bruising brownish gray to dark brown. Gleba enclosed, loculose, vinaceous at first, then soon pale cinnamon to avellaneous, with empty locules. Stipe absent but with a sterile basal pad. Spores reddish purple, broadly ellipsoid to subfusoid, longitudinally costate, with 6-10 ribs, dextrinoid. Peridial pellis repent, with fine to coarse encrustations. Clamp connections absent. Phylogenetic relationships inferred from atp6, tef1, and rpb2 sequences indicate placement in Leccinoideae near Ionosporus, Borofitus and Spongiforma. Three species known from India and Thailand. NOTE: there appear to be epigeous entities in SE Asia (Viet Nam, Thailand, Malaysia) with similar spore morphology. One epigeous species is well-described as Afroboletus vietnamensis by T.H.G. Pham et al. (2018). Ectomycorrhizae presumed with Dipterocarpaceae (at least Shorea robusta).

Rossbeevera T. Lebel & Orihara (2012) (originally Rosbeeva)
Basidiomata sequestrate, flattened to globose or subglobose, sometimes slightly cerebriform, white or rarely pink developing greenish blue colors in situ, sometimes slowly staining bluish or greenish blue when handled or on exposure. Gleba finely loculose, without gel-filled chambers, white at first,
becoming cinnamon to dark brown with maturity. *Rhizomorphs* present at a sterile base. *Spores* pale brown to dark brown, ellipsoid to broadly fusoid, smooth but with 3–5 longitudinal ridges, angular to stellate in polar view. *Clamp connections* absent. A sequestrate genus described by Lebel et al. (2011) allied to *Leccinum*, it is a western Pacific entity with species formerly placed in the north temperate *Chamonixia*. Distinction is primarily supported by molecular inferences and spore morphology. But see *Leccinum* as broadly defined by Kuo & Ortiz-Santana (2020). Australia, New Zealand, Singapore, Borneo, China, Japan.

Ectomycorrhizae presumed with *Eucalyptus, Leptospermum, Syncarpia, Allocasuarina, Acacia, Castanopsis, Quercus, Fagus, Nothofagus*.

**Rostrupomyces** Vadthanarat & Raspé (2024)

Based on the protologue: *Basidiomata* stipitate-pileate, with *pileus* rugulose to subrugulose; *hymenophore* tubulose, with white pores at first, becoming pale yellow to grayish yellow, unchanging when bruised; *context* white to off white then yellowish to pale and dull orange, unchanging when exposed; *stipe* is central, subscabrous with scattered granulose squamules, with white basal mycelium; *spores* yellowish brown in deposit, ellipsoid to broadly ellipsoid, smooth, thin-walled; *cystidia* present in hymenium and on stipe surface; *pileipellis* an intricate trichodermium; *clamp connections* absent.

Molecular phylogenetic analyses based on 4-gene loci (*atp6, cox3, rpb2, tef1*) infer placement of the single species, *R. sisongkhramensis*, in the *Xerocomoideae* near *Rubinosporus* and *Amylotrama*, sister to *Hemileccinum*. Currently only known from northern, northeastern Thailand. Named in honor of F.G.E. Rostrup.

Ectomycorrhizae presumed with Dipterocarpaceae (*Anthoshorea, Dipterocarpus, Pentacme, Shorea*), perhaps Fagaceae at low elevation.

**Royoungia** Castellano, Trappe & Malajczuk (1992)

*Basidiomata* gastricoid (sequestrate), flattened to globose or subglobose, bright golden yellow to dull orange, dry. *Gleba* loculate, somewhat cartilaginous, chocolate brown or a sordid yellow in color when mature, with empty locules. *Rhizomorphs* numerous, concolorous with peridium. *Columella* absent or sometimes present as a basal pad, white, or nearly concolorous with peridium, erroneously described as staining bright red (in the type species). *Spores* subfusoid, smooth. *Peridal pellis* compactly interwoven. *Trama* divergent, gelatinous. *Clamp connections* absent. Curiously, without explanation, Wu et al. (2016) infer a broader concept to include epigeous elements from China and consider *Australopilus* as synonymous. Eastern Australia (Queensland, New South Wales, Tasmania, Victoria).

Ectomycorrhizae presumed with Myrtaceae (*Eucalyptus, Leptospermum, Melaleuca*), Casuarinaceae (*Allocasuarina*).

**Rubinosporus** Vadthanarat, Raspé & Lumyong (2022)

*Basidiomata* stipitate-pileate; *pileus* even, with matted tomentum that becomes areolate; *stipe* surface is even with scattered minute squamules; *hymenophore* is tubulose, thin when young, golden yellow in color; not changing colors when bruised or when context exposed; *basidiospores* dark ruby colored in deposit, smooth and broadly ellipsoid. *Clamp connections* not seen. Phylogenetic inference from three exemplars based on *atp6, cox3, rpb2, tef1* supports placement on a long branch in the *Xerocomoideae* sister to *Hemileccinum* (robust support lacking at *Hemileccinum/Rubinosporus* node). One species known, *R. auriporus*, from northern Thailand.

Ectomycorrhizae presumed with Dipterocarpaceae (*Dipterocarpus, Shorea, Hopea*), Fagaceae.

**Rubroboletus** Zhao & Zhu L. Yang (2014)

*Basidiomata* stipitate-pileate. *Pileus* hemispherical, convex or applanate, grayish, pinkish to red. *Context* white, yellowish to lemon-yellow, cyanescent. *Hymenophore* surface orange red to blood red, sometimes orange-yellow when mature, rapidly bluing when bruised. *Tubes* yellow to olivaceous green, cyanescent when injured, then back to the original color slowly. *Stipe* central, covered with pinkish, red to brownish red reticula or spots. *Pileipellis* an interwoven trichoderm composed of more or less vertically

**Rufoboletus** N.K. Zeng & Zhi Q. Liang (2024)

Originally described as *Butyriboletus hainanensis* in Liang et al (Phytotaxa 2016), 3–4 gene molecular phylogenetic analyses (ITS, 28S, tef1, rpb2) infer a novel genus basal and sister to *Exsudoporus* and *Butyriboletus*. According to the generic protologue, *Rufoboletus* is characterized by large basidiomata with thick pileus, thin hymenophore, smooth (faintly reticulate?) stipe and smooth spores. Also, the oxidation reaction of the context and hymenophore progresses from blue to red then black as opposed to blue only in *Butyriboletus*. So far, known only from tropical forest in Hainan, China. Ectomycorrhizae presumed with Fagaceae.


*Basidiomata* stipitate-pileate. *Pileus* hemispherical, convex or planate, subtomentose, dry, strongly wrinkled (especially when young), usually with incurved or extended margin. *Context* cream, light yellow to yellow, unchanging or staining light blue slowly when bruised. *Hymenophore* adnexed to adnate, light yellow, yellow, or brown, reddish brown to yellowish brown, unchanging or staining blue to dark blue quickly when bruised, with *tubes* grayish-yellowish, brownish yellow, unchanging or staining blue, dark blue to greenish blue quickly when bruised, with *pores* nearly round to round. *Stipe* central, light yellow to yellow, covered by minute squamules, with *basal mycelia* off-white to light yellow. *Pileipellis* an ixotrichodermium to an interwoven ixotrichodermium. *Hymenial cystidia* present. *Basidiospores* smooth, subfusciform, brownish yellow. *Clamp connections* absent. Eastern Asia (China, Japan, far east Russia, Korea, Nepal, Thailand), Mexico, Central America, and Colombia. Ectomycorrhizae presumed with Pinaceae, Fagaceae.

**Singerocomus** T.W. Henkel & M.E. Smith (2016)


**Singeromyces** Moser (1966)


**Solioccasus** Trappe, Osmundson, Manfr. Binder, Castellano & Halling (2013)

*Basidiomata* gastroid (sequestrate), hypogeous or emergent, subglobose to lobed and irregular in outline, arising from yellow to orange to red rhizomorph, whitish when young, soon yellow to orange to red often wrapped with copious, flattened rhizomorphs, dry, with peridium soon evanescent, exposing loculose gleba. *Gleba* loculose, developing yellow to orange to red colors, with a prominent to inconspicuous, dendroid, cartilaginous *columella*. *Spores* pale yellow, smooth (light microscope), faintly and irregularly roughened (Nomarski DIC, SEM), ellipsoid or rarely subangular to subfusoid, inamyloid.
Clamp connections absent. Papua New Guinea, Australia (Queensland, Northern Territory). Ectomycorrhizae with Myrtaceae (Corymbia, Eucalyptus, Leptospermum, Lophostemon, Melaleuca), Casuarinaceae (Allocasuarina).


Description from protologue: Basidiomes stipitate-pileate with tubular hymenophore. *Pileus* convex or plano-convex, surface dry, submentose to squamulose, in age often cracked into isolated squamules; *context* whitish to cream, very slowly staining pale brown after exposure. *Tubes* adnexed, concolorous with pores when young, becoming yellowish brown to light brown with age, not narrow. *Pores* roundish to irregular-angular, cream colored when young, becoming apricot yellow to grayish orange with age, staining brownish to brown where bruised. *Stipe* central, coarsely reticulate to reticulate; context whitish to cream in the upper part, pale yellow in lower half, slowly staining pale brown to light brown on exposure. *Basidiospores* nearly elliptical to ovoid, with surface irregularly warty under light microscopy but with sponge-like perforated exospore under SEM. *Pleurocystidia* and *cheilocystidia* subfusiform-ventricose, sometimes with apical beak. *Pileipellis* an interwoven trichodermium. Clamp connections absent. One species known from the Singapore Botanic Garden (*S. temasekensis*). Robust molecular phylogenetic signal places this genus in the Leccinoideae on a long branch basal to Leccinum, Leccinellum, Octaviania, Turmalinea, and Rossbeevera.

Ectomycorrhizae with Pinaceae, Fagaceae, Myrtaceae, Casuarinaceae(?), Dipterocarpaceae, Caesalpinoid legumes.

Strobilomyces Berkeley (1851)

*Pileus* dry, coarsely fibrillose to squamulose, black, infrequently dark brown, very rarely pale yellow, often with appendiculate veil remnants, microscopically a trichodermium. *Context* white, staining reddish orange to dull reddish then black, or sometimes slowly blackening straightaway with only a hint of the reddish tints. *Hymenophore* adnexed to adnate, sometimes with subdecurrent lines, white then black, staining red then black or sometimes slowly black straightaway. Peronate veil present or sometimes absent and then remains hanging from *Pileus* margin. *Stipe* dry, squamose, sometimes annulate, white to gray to black. *Spores* black in deposit, globose, reticulate to irregularly echinate or sparrasoid to cristate. *Hymenial cystidia* present. Clamp connections absent. North Temperate Zone, montane Neotropics, Southeast Asia, Australia. Some African representatives have been transferred to Afroboletus.

Ectomycorrhizae with Pinaceae, Fagaceae, Myrtaceae, Casuarinaceae(?), Dipterocarpaceae, Caesalpinoid legumes.

Suillellus Murrill (1909)

*Pileus* surface glabrous or nearly so, dry or slightly viscid. *Context* white or yellow, fleshy, very firm, cyanescent. *Tubes* usually free, small, yellowish within, their mouths closed when young, and red or orange from the first, not covered with a veil, cyanescent. *Stipe* solid, usually reticulated or dotted. *Spores* oblong-ellipsoid, smooth, yellowish-brown, sometimes with greenish tints. Clamp connections absent. North Temperate.

Ectomycorrhizae assumed with Pinaceae, Fagaceae.

**NOTE:** This genus circumscribes a portion of the original *Boletus* subsect. *Luridi* (those with red pores). See also Caloboletus, Crocinoboletus, Exsudopus, Neoboletus, and Rubroboletus.
**Suillus** S.F. Gray (1821)

*Pileus* viscid and glabrous or dry and squamulose, sometimes with appendiculate remnants, microscopically an ixotrichodermium or a trichodermium. *Context* white or pale yellow, unchanging or sometime staining a pale reddish. *Hymenophore* adnate to adnexed, yellow or pale cinnamon brown. *Stipe* dry, annulate or not, typically with glandular dots or smears. Spore deposit pale cinnamon brown. *Spores* smooth, short fusoid. *Hymenial cystidia* usually clustered, with amorphous brown pigmentation at the base. *Clamp connections* absent. North Temperate and southward into the tropics to the southern limit of Pinaceae (*S. subaureus* with *Betula*). Absent in Africa. Frequently occurring with exotic Pinaceae transplanted beyond natural range.

Obligate ectomycorrhizae with Pinaceae but one known with *Betula* in NE USA.

**Sutorius** Halling, Nuhn & Fechner (2012)

*Pileus* dry, rarely viscid (wet weather), very finely matted, brown to chocolate brown to violet brown. *Context* white and mottled brownish lilac, unchanging. *Hymenophore* adnexed, lilac to pale brown to violet brown. *Stipe* dry, with scissurate fine scales, lilac brown to violet brown. Spore deposit reddish brown. *Spores* ellipsoid to subfusoid, smooth. *Hymenial cystidia* present, scattered. *Pileipellis* a trichoderm. *Clamp connections* absent. Africa; E & SE Asia; Indomalaya; North & Central America; northern South America; Australia.

Ectomycorrhizae with Myrtaceae, Casuarinaceae, Fagaceae, Dipterocarpaceae, Pinaceae, Caesalpinoid legumes.

**Tengioboletus** G. Wu & Zhu L. Yang (2016)

From the protologue: *Basidiomata* stipitate-pileate with tubular hymenophore. *Pileus* convex or applanate, glabrous to subtomentose, dry, sometimes viscid when wet; *context* yellowish to yellow, color unchanging when cut. *Hymenophore* adnate to sinuate; hymenophoral surface white when young, yellowish to yellow when mature, color unchanging when injured; *pores* roundish; *tubes* concolorous with hymenophoral surface, color unchanging when injured. *Stipe* central, yellow-orange-yellow to brownish yellow, glabrous or reticulate; basal mycelium light yellow. *Pleuro- and cheilocystidia* subfusciform-ventricose or clavate, with subacute apex or long beak. *Pileipellis* an epithelium to an ixotrichodermium composed of distinctly inflated or cystidioid terminal cells. *Basidiospores* smooth, subfusciform, brownish yellow. *Clamp connections* absent. 2–3 species sister to *Porphyrellus* but lack deep node support with four genes (28S, *tef1*, *rpb1*, *rpb2*); Central China.

Ectomycorrhizae presumed with Fagaceae.

**Tuboseta** Horak (= *Setogyroporus* fide Singer) (1967) (as *Tubosaeta*)


Ectomycorrhizae with caesalpinoid legumes.

**Turmalinea** Orihara & N. Maek. (2015)


Ectomycorrhizae presumed with Fagaceae.

From the protologue: Basidiomata stipitate-pileate with tubular hymenophore. Pileus hemispherical or applanate; surface densely covered with granular or tomentose squamules, dry; context soft when mature, white to pallid, without discoloration when injured. Hymenophore depressed around apex of stipe; hymenophoral surface white to pallid or pinkish when young, and becoming pink to grayish pink when mature; pores relatively wide up to 1.5 mm, angular; tubes concolorous with hymenophoral surface, colorunchanging when injured. Stipe central, concolorous with pileus or much deeper in color than the pileus; surface with concolorous verrucose or granular like squamules; basal mycelium pallid. Basidiospores subfusiform, smooth (under SEM). Pileipellis a trichodermium, composed of hyphae with 3–5 concatenated cells. Pleuro- and cheilocystidia fusiform to subfusiform, often with a sharp apex and a long pedicel. Clamp connections absent. Gene inference places genus in leccinoid clade sister to Retiboletus (Vadthanarat et al. 2018). One species known from SW China. Ectomycorrhizae presumed with Fagaceae.

Tylopilus P. Karsten (1881)

Pileus dry, glabrous to subtomentose, microscopically a trichodermium or subhymeniform. Context white, unchanging or staining pale brown, red then black, or rarely blue, with mild or bitter taste. Hymenophore adnexed, white then pinkish flesh colored to purplish brown to rusty brown, staining brown. Stipe dry, pruinose to glabrous to reticulate, to finely scabrous. Spores pinkish flesh colored to purplish brown, to rusty brown in deposit, smooth, fusoid to ovoid-phaseoliform. Hymenial cystidia present as pseudocystidia. Clamp connections absent. Some concepts include Porphyrellus; some ballouoioids (see Osmundson et al. 2021) erroneously treated in Rubinoboletus (=Chalciporus), but molecular inference distinguishes Tylopilus from Porphyrellus, and embraces the ballouoioids in Tylopilus. North Temperate, montane Neotropics, southern South America, southern and NE Brazil, E Asia, SE Asia, Australia, New Zealand, Africa. Ectomycorrhizae with Pinaceae, Fagaceae, Betulaceae, Nothofagaceae, Myrtaceae, Casuarinaceae, Caesalpinoid legumes.

Veloboletus Fechner & Halling (2020)

Diagnosis: Distinguished from other Xerocomoideae (Boletaceae) by virtue of a universal, dry, squamulose veil rupturing to form a limbate bulbous stipe base, a cyanescent oxidation reaction and smooth spores. Phylogenetic analyses with six genes infer placement on a long branch in subfamily Xerocomoideae but without a clear sister group. As far as we know, there are no other members of the Boletaceae with a distinctive and conspicuous squamulose, universal veil rupturing to form an obvious limbate rim. That and the conspicuous cyanescence are diagnostic. Currently known from Queensland, Western Australia, New South Wales in Australia. Ectomycorrhizae presumed with Myrtaceae, Casuarinaceae.

Veloporphyrellus Gómez & Singer (1984)


Villoboletus L. Fan & N. Mao (2023)

Based on the protologue, the genus is distinguished by copious flocculent hairs on the stipe surface. Pileus dry, pink, finely pubescent. Context is white to a pale yellowish white, and lightly and slowly cyanescent. Hymenophore is tubulose, bright yellow, then orange to pale reddish, and cyanescent. Stipe dry, yellowish white to pale pink to pinkish red downward, covered with dense covering of flocculent hairs. Spores smooth, fusoid, inamylloid. Hymenial cystidia present. Pileipellis an intricate
trichodermium. *Stipitipellis* a tangled mass of densely interwoven, cylindrical hyphae. *Clamp connections* absent. Currently known only from Shanxi Province, China, SW of Beijing. Based on four nuclear gene fragments (28S, *tef1*, *rpb1*, *rpb2*), the genus with one species, *V. persicinus*, is inferred as an isolated, basal taxon to *Leccinoideae*. However, morphological distinction is made in comparison to *Baorangia*, *Lanmaoa*, *Butyriboletus*, and *Caloboletus* in the *Suillelloideae*.

Ectomycorrhizae inferred with *Quercus* sp.

**Wakefieldia** Corner & Hawker (1953)

*Basidiomata* globose-depressed, minutely submentose, white then yellow, subcartilaginous, lacking a columella, with a sterile, golden yellow, sterile base. *Gleba* white then vinaceous pink, with gyrose lacunae, not becoming rubbery or gelatinous. *Spores* globose, sculpted with irregular curved plaques, sectors or wedges, thick-walled, cyanophilic. Type species: *W. striaespora* from Singapore. Molecular inference (*Tremble et al.* 2024) of the type species is in subfamily *Zangioideae*.

Ectomycorrhizae not noted, but presumed with *Dipterocarpaceae* and/or *Fagaceae* in Thailand based on specimens NY1193852, NY1193884 collected in 2006.

**Xanthoconium** Singer (1944)


**Xerocomellus** Šutara (2008)


**Xerocomus** Quélet (1887)


**Zangia** Y.C. Li & Zhu L. Yang (2011)
Pileus dry, pubescent and rugose, microscopically an ixohyphoeithelium. Context white, unchanging. Hymenophore adnexed, white then pinkish to pink or purplish when mature, unchanging. Stipe central, dry, whitish to yellowish or reddish, with red to purplish red scabrous squamules, chrome yellow at base, with context slowly cyanescent in some. Spores pinkish to pink to pale purple in deposit, smooth, subfuscoid or ellipsoid. Hymenial cystidia present. Clamp connections absent. So far, known from Southern China. Ectomycorrhizae with Pinaceae, Fagaceae.