

**Boletales – Boletaceae s.l.**  
(19 September 2018, © R. E. Halling)

NOTE: genera listed here are conceived in a broad, classical sense (generally the fleshy stipitate mushrooms with pores). Phylogenetic inferences from DNA sequences suggest alignment in suborders: **Boletineae, Suillineae, Sclerodermatineae**. All genera are not well known, equally circumscribed and/or robustly inferred phylogenetically. Mycorrhizal associations may be confirmed, but many are presumed/suspected. Recent phylogenetic inferences based on DNA sequences infer some true gasteroid (truffle-like, sequestrate) taxa (aside from those in Sclerodermatineae) belong here. Some of the diagnoses are from protologues.

***Afroboletus*** Pegler & Young

*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 sterigmal appendage, lacking a plage. *Hymenial cystidia* present. *Clamp connections* absent. Apparently restricted to the African tropics, but one outlier known from peninsular Malaysia based on a single specimen. One sequestrate species known.

Ectomycorrhizae presumed with Caesalpinoid legumes; possibly with Fagaceae or Dipterocarpaceae in Malaysia.

***Afrocastellanoa*** M.E. Smith & Orihara

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 bolete 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 caesalpinoid legumes in sub-Saharan Africa.

***Alpova*** Dodge

*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.

***Aureoboletus*** Pouzar

*Pileus* viscid to dry, rugulose to even. *Context* white, unchanging. *Hymenophore* tubulose, bright yellow at first, unchanging. *Stipe* central, glabrous, sometimes superficially pruinose, viscid to dry. *Spores* olive brown in deposit, smooth, fusoid, inamyloid. *Clamp connections* absent. Mostly north temperate to northern tropics; perhaps southern tropics.

Ectomycorrhizae with Pinaceae, Fagaceae.

***Australopilus*** Halling & Fechner

*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. Australia. Ectomycorrhizae with Myrtaceae, Casuarinaceae.

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

*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 to sinuous pitted, sometimes equatorially verrucose, amygdaliform to elongate-fusoid, inamyloid or dextrinoid. *Hymenial cystidia* usually present. *Clamp connections* absent. KOH & NH<sub>4</sub>OH reactions negative. Mostly E Asia, Australasia, some temperate New World, 3-4(5-6?) in Neotropics. Ectomycorrhizae with Pinaceae, Fagaceae, Myrtaceae, Dipterocarpaceae, Casuarinaceae.

***Baorangia*** G. Wu & Z.L. Yang

*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-yellowish. *Clamp connections* absent. Eastern Asia, eastern North America. Ectomycorrhizae presumed with Pinaceae, Fagaceae.

***Binderoboletus*** T.W. Henkel & M.E. Smith

*Basidiomata* epigeous. *Pileus* olive-yellow to olive-brown, matted fibrillose, trama light yellow, unchanging. *Hymenophore* tubulose, adnate, light yellow, browning with pressure, pores subsodiametric. *Stipe* subequal, concolorous and striate, yellow and reticulate at apex, base yellow tomentose, trama bright yellow. *Basidiospores* olivaceous brown in deposit, smooth, dextrinoid in Melzer's reagent. *Pleurocystidia* present, dextrinoid in Melzer's reagent. *Cheilocystidia* present. *Hymenophoral trama* parallel to slightly divergent (phylloporoid). *Pileipellis* an entangled cutis, terminal cells cylindrical. *Clamp connections* absent. Reminiscent of *Retiboletus* macro- and microscopically. According to the describing authors, it is related to *Retiboletus* in the Leccinoideae of Wu et al (2014), but the ITS sequences are highly unique. Monotypic species from Guyana. Ectomycorrhizae with *Dicymbe*, *Aldina* (Caesalpinoid legumes)

***Boletellus*** Murrill

*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, sometimes lacerate- ridged, dry, 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 & NH<sub>4</sub>OH reactions negative (more species need testing). N Hemisphere, apparently not in 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, with caesalpinoid legumes (e.g., *Dicymbe*).

### ***Boletinellus* Murrill**

*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 sublammellate, 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. There is a well-documented report of its occurrence in Kyushu, Japan. Also, quite possibly in Queensland, Australia.

### ***Boletochaete* Singer**

*Pileus* velutinous, bay-colored. *Tubes* gray. *Stipe* brownish, nearly smooth. *Flesh* white, unchanging. Spore deposit cinnamon brown, *Spores* ovoid, smooth, inamyloid. *Pileipellis* a palisade with conical terminal elements. Seta-like or *pseudocystidia*-like *hymenial cystidia* present. *Clamp connections* absent. Not well studied. Perhaps 3(-4) species known from SE Asia.

Ectomycorrhizae not determined with certainty – probably Fagaceae and/or Dipterocarpaceae.

### ***Boletus* L.**

*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.

Ectomycorrhizae with Pinaceae, Fagaceae, Betulaceae, Dipterocarpaceae (?), Myrtaceae, Casuarinaceae, caesalpinoid legumes(?). Possibly other families less commonly.

**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*).

***Borofutus*** Hosen & Z.-L. Yang

*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. *Stipe* central, glabrous and ribbed above, squamulose below, with whitish basal mycelium. *Spores* purple to purplish red to purplish violet 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 *Ionosporus*.

Ectomycorrhizae with Dipterocarpaceae (*Shorea*).

***Bothia*** Halling, Baroni & Binder

*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 boletoid, 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*).

***Buchwaldoboletus*** Pilát

*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 vouchered reports from southern hemisphere. Mycoparasitic with one species closely associated with *Phaeolus schweinitzii* and rotting Pinaceae wood.

***Butyriboletus*** D. Arora & J.L. Frank

*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 vinaceous-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.

***Caloboletus*** Vizzini

*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.

**Castellanea** T.W. Henkel & M.E. Smith

*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

(=*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. An exotic invasive in Australia.

Putatively mycoparasitic on *Amanita muscaria* (at least *C. piperatus*), but possibly ectomycorrhizal with Pinaceae and Fagaceae for some taxa.

**Chamonixia** Rolland

*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 cyanescent. *Spores* brown, with 8-10 longitudinal ridges. *Clamp connections* absent. Europe and North America. Phylogenetic placement in a leccinoid clade and basal to a western Pacific genus, *Rossbeevera*.

Ectomycorrhizae with Pinaceae.

**Chiua** Yan C. Li & Zhu L. Yang

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 & Z.-L. Yang

*Pileus* convex becoming plane; surface mucilaginous, 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.

Ectomycorrhizae likely with Fagaceae.

***Costatisporus*** T.W. Henkel & M.E. Smith

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 (*Dicycme*, *Aldina*).

***Crocinoletus*** N.K. Zeng, Z.L. Yang & G. Wu

*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* boletocrocins present. Two species known: *C. rufoaureus*, *C. laetissimus*. Eastern Asia, Australia. Ectomycorrhizae presumed with Pinaceae, Fagaceae, Myrtaceae, Casuarinaceae(?).

***Cyanoboletus*** Gelardi, Vizzini & Simonini

*Basidiomata* pileate-stipitate with tubular-poroid hymenophore, epigeal, 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.

***Durianella*** Desjardin, A.W. Wilson, Manfr. Binder

*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, while suggesting placement in the Boletineae, is equivocal in relationships to known taxa. Ectomycorrhizae likely with *Shorea*.

***Exsudoporus*** Vizzini, Simonini & Gelardi

*Basidiomata* stipitate-pileate, epigeal. *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 subtomentose. *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 trichoderm tending to a cutis. *Clamp connections* absent. Known from the Northern Hemisphere.

Ectomycorrhizae presumed with Fagaceae

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

*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, Australia, New Zealand, Japan, Indonesia. Ectomycorrhizae probable for some species with Fagaceae, Nothofagaceae, Leguminosae, Sapotaceae, Myrtaceae; doubtfully present in others.

***Gastroboletus*** Lohwag

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 entities allied to *Heimioporus* in Australia.

Ectomycorrhizae with Fagaceae, Nothofagaceae (?), Pinaceae, legumes (?), Myrtaceae.

***Guyanaporus*** T.W. Henkel & M.E. Smith

*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 RPB1 places the genus on a long unsupported branch near *Tylopilus*, *Xanthoconium* and *Imleria*.

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

### ***Gymnogaster* J.W. Cribb**

*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 not completely clear (poorly supported *Pulveroboletus* group). Probably ectomycorrhizal with Myrtaceae.

### ***Gyrodon* Opatowski**

*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. Widespread, but so far not in Australia. Phylogenetic inference places the genus in the Paxillaceae. Ectomycorrhizae with *Alnus*; sometimes apparently not (at least in *G. exiguus*, perhaps others).

### ***Gyroporus* Quélet**

*Pileus* dry, glabrous to fibrous-subsquamose, microscopically a trichodermium. *Context* white to pale yellow, staining blue or brown in some. *Hymenophore* adnexed, white then pale yellow, with pores staining blue or brown 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 (one species in southern Brazil), but widely distributed and diverse in Australia. Phylogenetic inference places the genus in the Sclerodermatineae. Ectomycorrhizae with Pinaceae, Fagaceae, Myrtaceae, Casuarinaceae(?), possibly Lauraceae.

### ***Harrya* Halling, Nuhn & Osmundson**

*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. Two species: *H. chromapes*, *H. atriceps*. Eastern North America to Central America, China, Japan. Ectomycorrhizae with Pinaceae, Fagaceae, Betulaceae(?).

### ***Heimioporus* E. Horak**

*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, Eastern Asia, SE Asia, Australia, Mexico, Belize, and Costa Rica. Ectomycorrhizae with Fagaceae, Dipterocarpaceae, Myrtaceae, Casuarinaceae.

### ***Heliogaster*** Orihara & Iwase

*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.

### ***Hemileccinum*** Šutara

*Basidiomata* pileate-stipitate, recalling *Leccinum* sect. *Luteoscabrum* (see *Leccinellum* below); *Pileus* dry, subtomentose to glabrous, violet with NH<sub>3</sub>, 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 5 species: *H. impolitum*, *H. depilatum* in Europe & China, *H. subglabripes* from E North America & China, and *H. indecorum*, *H. rugosum* in China. Ectomycorrhizae with Fagaceae, Betulaceae, Ulmaceae.

### ***Hortiboletus*** Simonini, Vizzini & Gelardi

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

### ***Hourangia*** Xue T. Zhu & Zhu L. Yang

*Basidiomata* stipitate-pileate with tubular hymenophore. *Pileus* hemispherical, convex to applanate, sometimes umbonate; 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, brownish yellow, 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*** Yan C. Li & Zhu L. Yang

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 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

*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 incrustated 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.*

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. Pori minuti, primitus lutei vel rubri, tacto caerulescentibus. Caro compacta, odore fortis, flavo-sulphurea, virescens deiunque fracta caerulescens; 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 mono-phyletic 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/>.

***Ionosporus*** Khmelnitsky

*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, 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 granulose with Nomarski DIC optics, irregularly and finely granulose to pitted granulose with SEM, sometimes with a faint germ pore. *Pileipellis* a trichodermium. *Clamp connections* absent. Peninsular Malaysia, E Australia; two species: *I. longipes*, *I. australis* nom prov. Molecular phylogenetics infers placement in Leccinoideae near *Borofutus*, *Rhodactina*, and *Spongiforma*.  
Ectomycorrhizae presumed with Dipterocarpaceae, Myrtaceae, Casuarinaceae.

***Jimtrappea*** T.W. Henkel & M.E. Smith

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

***Lanmaoa*** G. Wu, Z.-L. Yang & Halling

*Basidiomata* stipitate-pileate. *Pileus* hemispherical, convex or applanate, 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.

***Leccinellum*** Bresinsky & Binder

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

***Leccinum*** S. F. Gray

*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 as exotic import associated with horticultural plantings (*Betula*, *Quercus*) fide Watling & Gregory (1988); likewise in New Zealand (McNabb 1968).

Ectomycorrhizae with Pinaceae, Fagaceae, Betulaceae, caesalpinoid legumes.

**Melanogaster** Corda

*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 tramal 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.

**Mycoamaranthus** Castellano, Trappe, & Malajczuk

*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, pedicellate, spinose to minutely verrucose. *Clamp connections* absent. Zimbabwe, Malawi, Congo-Kinshasa, Cambodia, Thailand, Malaysia, Singapore, Australia. Ectomycorrhizae with Dipterocarpaceae, Myrtaceae (*Eucalyptus*, *Syncarpia*), *Allocasuarina*, *Brachystegia*, *Julbarnarida*, *Uapaca*.

**Neoboletus** Gelardi, Simonini & Vizzini

*Basidiomata* stipitate-pileate with tubular hymenophore, epigeal, evelate. *Pileus* convex to appanate, bay-brown, date-brown, olive-brown, reddish-brown to blood red, ochraceous or yellow, opaque, dry, velvety to subtomentose. *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.

**Octaviania** Vittadini

*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. Ectomycorrhizae presumed with Pinaceae, Fagaceae, Betulaceae, Nothofagaceae, Myrtaceae, Casuarinaceae.

**Paragyrodon** (Singer) Singer

*Pileus* viscid, microscopically an ixocutis. *Context* white to yellowish, staining brown. *Hymenophore* adnate to decurrent, bright yellow then brown, staining bright brown. Peronate veil present, forming an annulus. *Stipe* central to eccentric. Spore deposit olive to mustard brown. *Spores* smooth, globose to subglobose. *Hymenial cystidia* present. *Clamp connections* present. Well-known species in north central North America, *P. sphaerosporus*.

Ectomycorrhizae with *Quercus* suspected but not confirmed. Phylogenetic inference places the genus in the Paxillaceae.

### ***Phlebopus*** (Heim) Singer

*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).

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

### ***Phylloboletellus*** Singer

*Pileus* dry, convex, yellow becoming yellowish brown to orangish brown. *Context* yellowish, cyanescent near lamellae. Taste bitter. *Hymenophore* lamellate, adnate to decurrent, sometimes forked, yellowish green becoming olive brown, cyanescent. *Spores* olive brown in deposit, ovoid, longitudinally winged/ridged, inamyloid. *Clamp connections* mostly absent; some aborted. Known from Mexico and Argentina.

Ectomycorrhizae apparently not formed.

### ***Phylloporus*** Quélet

*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). NH<sub>3</sub> 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

This genus used for the typically, somber colored taxa 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 rather a pale greenish yellow to nearly 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), at least a few in Australia and New Zealand; these latter may be generically distinct based on molecular inference. Ectomycorrhizae with Pinaceae, Fagaceae, Myrtaceae, Casuarinaceae, perhaps Dipterocarpaceae, Nothofagaceae, Caesalpinoid legumes.

### ***Pseudoaustroboletus*** Y.C. Li & Z.L. Yang

*Basidiomata* stipitate-pileate with tubular hymenophore. *Pileus* hemispherical to applanate, 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 is most nearly allied to *Tylopilus* (nrLSU) or a Leccinoideae clade (combined 3 gene tree, nrLSU, tef1, mtSSU). Ectomycorrhizae apparently with Fagaceae.

### ***Pseudoboletus* Šutara**

An epigeous bolete with xerocomoid habit that is associated with *Scleroderma* and *Astraeus*. Northern hemisphere. Considered parasitic, but one of the pair is ectomycorrhizal.

### ***Pulveroboletus* Murrill**

*Pileus* dry or barely subviscid, glabrous or sometimes scaly, microscopically a collapsed trichodermium. *Context* white to pale yellow, slowly staining blue. *Hymenophore* adnate to adnexed, yellow, staining blue. Peronate veil present, collapsing to form annular zone or coarse scabers. *Stipe* dry to sticky, apparently glabrous or sometimes scaly. Spore deposit olive brown. *Spores* smooth, fusoid. *Hymenial cystidia* present. *Clamp connections* absent. North America, East Asia, Southeast Asia, Australia, Africa, montane Neotropics.

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

### ***Retiboletus* Binder & Bresinsky**

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.

### ***Rhizopogon* Fries**

*Basidiomata* sequestrate, hypogeous to erumpent. *Peridium* dry, pruinose to subtomentose, 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. *Clamp connections* absent. Northern Hemisphere. Often present where Pinaceae introduced (e.g., Australia, New Zealand, South America).

Ectomycorrhizae with Pinaceae.

### ***Rhodactina* Pegler & T.W.K. Young**

*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 subfam. Leccinoideae near *Ionosporus*, *Borofutus* and *Spongiforma*. Three species known from India and Thailand.

Ectomycorrhizae presumed with Dipterocarpaceae (at least *Shorea robusta*).

**Rosbeevera** T. Lebel & Orihara  
(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. Australia, New Zealand, Singapore, Borneo, China, Japan. Ectomycorrhizae presumed with *Eucalyptus*, *Leptospermum*, *Syncarpia*, *Allocasuarina*, *Acacia*, *Castanopsis*, *Quercus*, *Fagus*, *Nothofagus*.

**Royoungia** Castellano, Trappe & Malajczuk

*Basidiomata* gasteroid (sequestrate), flattened to globose or subglobose, bright golden yellow to dull orange, dry. *Gleba* loculose, 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. *Peridial pellis* compactly interwoven. *Trama* divergent, gelatinous. *Clamp connections* absent. Eastern Australia (Queensland, New South Wales, Tasmania, Victoria). Ectomycorrhizae presumed with Myrtaceae (*Eucalyptus*, *Leptospermum*, *Melaleuca*), Casuarinaceae (*Allocasuarina*).

**Rubroboletus** Zhao & Z.L. Yang

*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 arranged, sometimes gelatinized filamentous hyphae. Hymenophoral trama boletoid. *Basidiospores* smooth, subfusiform to ovoid-ellipsoid, slightly thick-walled. *Hymenial cystidia* present. *Clamp connections* absent. [Adapted from Zhao et al 2014]. China, Europe, North and Central America. Ectomycorrhizae presumed with Pinaceae, Fagaceae.

**Rugiboletus** G. Wu & Z.L. Yang

*Basidiomata* stipitate-pileate. *Pileus* hemispherical, convex or applanate, 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, subfusiform, brownish yellow. *Clamp connections* absent. Eastern Asia (China, Japan, far east Russia, Korea, Nepal, Thailand) and possibly Central America, Colombia. Ectomycorrhizae presumed with Pinaceae, Fagaceae.

**Singerocomus** T.W. Henkel & M.E. Smith

*Basidiomata* epigeous. *Pileus* pinkish red to red, tomentose, trama white to light yellow, unchanging. *Hymenophore* tubulose, depressed at stipe, yellow, unchanging, pores subangular. *Stipe* equal, concolorous or lighter, glabrous or with squamules and scales, base yellow dull yellow tomentose, trama white to light yellow. *Basidiospores* olivaceous brown in deposit, smooth, inamyloid. *Pleurocystidia* present. *Cheilocystidia* present or absent. *Hymenophoral trama* parallel to slightly divergent (phylloporoid). *Pileipellis* a trichodermium, terminal cells cylindrical. *Clamp connections* absent. Inference suggests a long-branch sister relationship with E. Asian *Rugiboletus* based on 28S and RPB1 genes. Two species known from Brazil and Guyana. Ectomycorrhizae with Caesalpinoid legumes (*Aldina*, *Dicymbe*).

**Soliococcus** Trappe, Osmundson, Manfr. Binder, Castellano & Halling

*Basidiomata* gastroid (sequestrate), hypogeous or emergent, subglobose to lobed and irregular in outline, arising from yellow to orange to red rhizomorphs, often wrapped with copious, flattened rhizomorphs, dry, with peridium soon evanescent, exposing loculose gleba, whitish when young, soon yellow to orange to red. 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*).

**Spongiforma** Desjardin, Manfr. Binder, S. Roekring & Flegel

*Basidiomata* epigeous, sessile, cerebriform to sponge-like, rubbery-gelatinous; peridium absent. *Gleba* with locules 2-20 mm broad, irregular in outline. *Columella* poorly developed, pyriform, cream-colored, attached to white rhizomorphs. *Spores* brown to vinaceous brown in mass, amygdaliform, bilaterally symmetrical, rugulose, with an apical pore or depression, reddish brown in water, violet gray in hydroxide, inamyloid, cyanophilic. *Cystidia* common. *Tramal hyphae* gelatinous. *Clamp connections* absent. Molecular phylogenetic inference (*tef1*, *atp6*, *rpb2*) suggests placement in the Boletineae (subfam. Leccinoideae) near *Ionosporus*, *Borofutus* and *Rhodactina*). Two species known from Thailand, Borneo.

Ectomycorrhizae presumed with Dipterocarpaceae (*Shorea*, *Dipterocarpus*)

**Spongispora** G. Wu, S.M.L. Lee, E. Horak, Zhu L. Yang

Description from protologue: Basidiomes stipitate-pileate with tubular hymenophore. *Pileus* convex or plano-convex, surface dry, subtomentose 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, 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 *Hopea odorata* (Dipterocarpaceae).

***Strobilomyces*** Berkeley

*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 subdecurent 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

*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*, *Crocinoletus*, *Exsudoporus*, *Neoboletus*, and *Rubroboletus*.

***Suillus*** Micheli ex S. F. Gray

*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

*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

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* subfusiform-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, subfusiform, 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  
(as *Tubosaeta*)

*Pileus* dry, subvelutinous to tomentose, microscopically a trichodermium or subhymeniform. *Context* white. *Hymenophore* adnate to adnexed, olive yellow, sometimes staining greenish. *Stipe* dry, subvelutinous to glabrous. Spore deposit brownish yellow. *Spores* brownish yellow in deposit, smooth (light microscope) bacillate (SEM), fusoid. *Hymenial cystidia* present as thick-walled, pigmented setae. *Clamp connections* absent. Africa and Madagascar. Ectomycorrhizae with Caesalpinoid legumes.

***Tylocinum*** Yan C. Li & Zhu L. Yang

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, color unchanging 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* (Vadthananarat et al 2018). One species known from SW China. Ectomycorrhizae presumed with Fagaceae.

***Tylopilus*** P. Karsten

*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 (ballouroids) erroneously treated in *Rubinoboletus* (= *Chalciporus*), but molecular inference distinguishes *Tylopilus* from *Porphyrellus*, and embraces the ballouroids in *Tylopilus*. North Temperate, montane Neotropics, northern South America, southern and NE Brazil, E Asia, SE Asia, Australia, New Zealand, Africa. Ectomycorrhizae with Pinaceae, Fagaceae, Betulaceae, Nothofagaceae, Myrtaceae, Casuarinaceae, Caesalpinoid legumes.

***Veloporphyrellus*** Gómez & Singer

*Pileus* dry, tomentose, white to brown, microscopically a trichodermium. *Context* white, pale burgundy red. *Hymenophore* white to pinkish flesh color, unchanging. *Veil* present. *Stipe* white, annulate. *Spores* possibly purplish brown (?) in deposit, smooth, fusoid. *Hymenial cystidia* present. *Clamp connections* absent. Six species known from North America, Central America, E Asia, Africa. Ectomycorrhizae presumed with Caesalpinoid legumes, Dipterocarpaceae, Fagaceae and Pinaceae.

***Xanthoconium*** Singer

*Pileus* dry, subtomentose, often wrinkled, microscopically hymeniform. *Context* white, unchanging. *Hymenophore* adnate or adnexed, white to straw yellow, not staining. *Stipe* dry, glabrous. *Spore deposit* bright rusty brown. *Spores* smooth, fusoid to cylindrical. *Hymenial cystidia* present. *Clamp connections* absent. E North America south to southern Colombia, E Asia, Australia, possibly SE Asia.

Ectomycorrhizae with Fagaceae, possibly Pinaceae in America. Myrtaceae, Casuarinaceae in Queensland.

***Xerocomellus*** Šutara

*Pileus* dry, matte, neither viscid nor sticky when moist, glabrous, velutinous or pruinose, usually without a distinct fibrillose aspect when young, becoming subtomentose with age, often cracking with age and then areolate-rimose. *Pileipellis* a palisadoderm. *Hymenophore* adnate or shallowly depressed or sometimes subdecurrent, yellow to olive brown, cyanescent or not, with angular pores. *Tube trama* intermediate (boletoid-phylloporoid). *Stipe* minutely granulate, sometimes longitudinally striate but mostly non-reticulate. *Lateral stipe stratum* usually absent or quite reduced. *Spores* smooth or longitudinally striate/veined. *Hymenial cystidia* present. *Clamp connections* absent. North Temperate, montane Neotropics, northern South America, East Asia, SE Asia, Australia, New Zealand, Africa.

Ectomycorrhizae with Pinaceae, Fagaceae, Betulaceae, Nothofagaceae, Myrtaceae, Casuarinaceae, Caesalpinoid legumes.

***Xerocomus*** Quélet in A. Mougeot & Ferry

*Pileus* dry, matte, subtomentose, microscopically a trichodermium. *Pileipellis* a trichoderm. *Context* white or yellow, sometimes cyanescent. *Hymenophore* adnate or shallowly depressed or sometimes subdecurrent, yellow to olive brown, cyanescent or not, with angular pores. *Tube trama* 'phylloporoid' not gelatinizing. *Stipe* central rarely eccentric, dry, glabrous to longitudinally ribbed but if reticulate then at apex, sometimes minutely floccose-granulose. *Lateral stipe stratum* thick, never gelatinous. *Spore deposit* olive brown. *Spores* subfusoid to fusoid-elliptical, smooth with light microscopy, 'bacillate' with SEM. *Hymenial cystidia* present. *Clamp connections* absent. North Temperate, montane Neotropics, northern South America, East Asia, Southeast Asia, Australia, New Zealand, Africa. Ectomycorrhizae with Pinaceae, Fagaceae, Betulaceae, Nothofagaceae, Myrtaceae, Casuarinaceae, Caesalpinoid legumes.

***Zangia*** Yan C. Li & Zhu L. Yang

*Pileus* dry, pubescent and rugose, microscopically an ixohyphoepithelium. *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, subfusoid or ellipsoid. *Hymenial cystidia* present. *Clamp connections* absent. So far, known from Southern China. Ectomycorrhizae with Pinaceae, Fagaceae.