

**Boletales – Boletaceae s.l.**  
(24 September 2024, © R. E. Halling)

**NOTE:** 123 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).

***Abtylophilus*** 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 subfusiform to cylindrical and smooth. *Hymenial cystidia* fusiform to subfusoid-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*, *hymenial 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 sterigmal 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.

***Alessioporos*** 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, *tefl*, *rpb2*) infer placement in the *Suilloleioideae* sister to *Pulveroboletus*. Originally, three species (*A. granulopunctatus*, *A. mcrobbii*, *A. miraculosus*) were described from E Asia, Malaysia, and New Zealand. Based on recent data (Li *et al.*, 2024), *A. phoeniculus*, *A. weberi*, and *A. brachysporus* have been added. 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 becomes 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 *Boletoideae* 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 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, montane and lowland tropics of New World.

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

***Baorangia*** G. Wu & Zhu L. Yang (2015)

*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 (2016)

*Basidiomata* epigeous. *Pileus* olive-yellow to olive-brown, matted fibrillose, trama light yellow, unchanging. *Hymenophore* tubulose, adnate, light yellow, browning with pressure, pores subisodiametric. *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 (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 & NH<sub>4</sub>OH 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)

*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. (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 paleoneotropics. 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 vouchered 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 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.

***Cacaoporus*** Raspé & Vadthananarat (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 *Suilloideae*. 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 *Austroboletoidae*, sister to *Mucilopilus* (sine type) 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 invasives 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 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*. But see *Leccinum* as broadly defined by Kuo & Ortiz-Santana (2020)  
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 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. 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*).

***Crocinoletus*** N.K. Zeng, Zhu L. Yang & G. Wu (2014)

*Basidiomata* epigeous. *Pileus* convex to appanate, 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. Three species known: *C. rufoaureus*, *C. laetissimus*, *C. pinetorum*. Eastern Asia (Japan, China), Papua New Guinea. Non-bluing lookalikes occur in Australia

Ectomycorrhizae presumed with Pinaceae, Fagaceae, possibly Dipterocarpaceae.

***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, 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 (2008)

*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, subtomentose to faintly squamulose or subfloccose 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, 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. The genus was originally phylogenetically inferred for three iconic species (*B. frostii*, *B. floridanus*, *B. permagnificus*). A recent update by Biketova *et al.* (2022) adds *E. ruber* (basionym = *Leccinum rubrum*) and infers cryptic diversity and potentially undescribed entities, for *E. frostii* s.l. in eastern N. America, Mexico and Central America.  
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/re-evaluation 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 ixotrichoderm (*G. salmonicolor*, type species; *G. violaceotinctum*), while *G. viscosum* has a palisadal hymeniderm in a gelatinous matrix. *Spores* are smooth fusoid to subfusoid. Using nrLSU, *rpb2* and *tef1*, 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). **N.B.** Based on the Shenzhen Code of Nomenclature (Turland *et al.* 2018), the genus name was not validly published (Art. 40.1, 40.3, 6.3, 12.1) due to a lack of an identifier prior to publication.

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 *rpb1* 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 *Suilleloideae*.

Probably ectomycorrhizal with Myrtaceae.

**Gyrodon** 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-subsquamose, 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 Sclerodermatineae, 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.

#### ***Hemiaustroboletus*** Ayala-Vásquez, García-Jiménez & Garibay-Orijel (2022)

Based on the protologue, the genus circumscribes at least three taxa (two newly described: *H. vinaceobrunneus*, *H. vinaceus*) that morphologically resemble a molecular phylogenetic clade previously inferred as belonging to *Austroboletus gracilis* s.l. and resides in the *Austroboletoidae*. That inference is based on concatenated LSU and *rpb2* sequences and a separate ITS analysis. In both analyses, *Veloporphyrellus* is inferred as a sister genus, "Even while the phylogenetic relations between both genera are not statistically supported, . . ." However, a BPP = 0.98 supports recognition of a monophyletic group *fide* Ayala-Vásquez *et al.* *MycKeys* 88: 72-73. 2022. Exemplars identified as *Austroboletus gracilis* from North America were included in the concatenated analysis, and additional ITS exemplars from North America and Asia infer the new generic relationship, but *A. gracilis* was not transferred to the new genus. Sequencing of Peck's type specimen was recommended. Global distribution cited as Canada, China, Japan, Mexico, South Korea and USA. *Austroboletus gracilis* s.l. has also been documented from Guanacaste, Costa Rica.

Ectomycorrhizae presumed 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. Basidioma bluing when bruising, pileus subtomentose, 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, subtomentose, dry, margin shortly appendiculate, grayish red to pastel red in 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, *tef1*, *rpb1*, *rpb2*) 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, 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 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. *Stipe* is stout and central nearly glabrous to pruinose. *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  $Q_m < 2.5$ , *stipe context* with small vermilion 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(?).

### ***Hourangia*** Xue T. Zhu & Zhu L. Yang (2015)

*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*** 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 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.* (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. Pori minuti, primitus lutei vel rubri, tacto caerulescentibus. Caro compacta, odore fortis, flavo-sulphurea, virescens deinceps 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 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*** Khmel'nitsky (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 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*. Molecular phylogenetics infers placement in *Leccinoideae* near *Borofutus*, *Rhodactina*, and *Spongiforma*. Ectomycorrhizae presumed with Dipterocarpaceae, Myrtaceae, Casuarinaceae.

***Jimtrappea*** T.W. Henkel, M.E. Smith & Aime (2015)

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 H<sub>2</sub>O and 5% KOH, smooth, elongated to cylindrical, somewhat fusoid. *Cystidia* mostly fusoid. *Pileipellis* an epithelium. *Clamp connections* absent." A four gene (nrLSU, *tefla*, *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).

***Kgaria*** Halling, Fechner & Davoodian (2023)

Based on the protologue: *Basidiomata* epigeous and boletoid. *Pileus* brown to dark brown or nearly black with overtones of lilac to dull violet, even or irregularly bumpy to roughened, sometimes

appressed scaly-areolate with age, viscid or dry. *Context* white, typically oxidizing blue to red then black. *Hymenophore* tubulose, white, then mineral green to dull yellow to olive brown, red to blue then black when bruised. *Stipe* dry, finely scurfy to subpruinose to finely granulose above, fibrillose streaked downward, variously colored with mineral green, lilac to pale violet, and dark brown pigmentation. *Spores* brown in deposit, smooth, subfusoid. *Hymenial cystidia* present, typically with homogenous brown content in alkaline mounts. *Pileipellis* and *stipitipellis* with cyanogranular encrusting pigment. *Clamp connections* absent. Phylogenetically distinct from *Porphyrellus* and *Afrocastellanoa* in subfamily *Boletoideae* based on three gene analyses (28S, *tef1*, *rpb2*). Currently, two species known from Australia (Queensland, New South Wales, Tasmania, Victoria): *K. cyanogranulifera*, *K. similis*. Ectomycorrhizae presumed with Myrtaceae and Casuarinaceae.

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

*Basidiomata* sequestrate, emergent and (sub-)globose, firm, becoming brownish. *Gleba* loculate, with white tramal veins, with brown locules. *Columella* absent. *Spores* asymmetrical, fusoid to allantoid to unevenly ellipsoid, yellow brown, rugulose, dextrinoid. *Hymenial cystidia* and *clamp connections* absent. One ribosomal gene (28S) inferred placement near *Heimioporus* with very low bootstrap support. One species, *K. bakaiana*, from Cameroon. Ectomycorrhizae presumed with *Uapaca*.

***Lanmaoa*** G. Wu, Zhu L. Yang & Halling (2015)

*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 & Manfr. Binder (2003)

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). **NOTE:** see *Leccinum* (below). 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*) *vide* 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. Martín, 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 *tefl* 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 tramal 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 *Zangioideae*. Ectomycorrhizae presumed with Caesalpinoideae, *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 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.

***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 *Veloporphyrillus* (*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, epigeal, evelate. *Pileus* convex to applanate, 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.

***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 *Boletoideae*. 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, ellipsoid 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 *Boletoideae*. Further analyses offered by Halling *et al.* (2023) using *tef1* and LSU infer placement in *Boletoideae* sister to *Anthracoporus*. Ectomycorrhizae presumed with *Coccoloba*, *Guapira* (Brazil) and *Dicymbe corymbosa* (Guyana).

***Nigroboletus*** Gelardi *et al.* (2015)

Original diagnosis: *Basidiome* stipitate–pileate with tubular hymenophore, epigeal, evelate, medium–small sized; *pileus* convex to applanate, subtomentose 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 ellipsoid 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*).

***Niveoboletus*** Yang Wang, G. Wu, B. Zhang & Y. Li (2024)

Based on the original diagnosis and protologue: “Basidioma stipitate–pileate with a tubular hymenophore. Pileus hemispherical or convex, tomentose, usually beaded with amber yellow droplets, margin inrolled. Hymenophore decurrent, surface pure white, staining light brown when injured; tubes concolorous with pores. Stipe central, concolorous with pileus, coarse without reticulations, usually beaded with amber yellow droplets, context at base brown; basal mycelium white. Basidiospores phaseoliform, smooth, thin-walled. Pileipellis an interwoven trichoderm composed of cylindrical hyphae. Clamp connection absent.” The single species from central China, *N. brunneus*, based on four genes (28S, *tef1-α*, *rpb1*, *rpb2*), is allied in an unclear relationship with *Imleria*, *Boletus*, *Tylopilus*, *Porphyrellus*, *Strobilomyces*, *Tengioboletus*, and *Xanthoconium*.

Ectomycorrhizae presumed with *Castanopsis* sp.

***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)

*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. *Spores* olive to mustard brown, smooth, globose to subglobose. *Hymenial cystidia* present. *Clamp connections* present. Well-known species, *P. sphaerosporus*, in north central North America (and southern Rocky Mountains). Ectomycorrhizae with *Quercus* suspected but not confirmed. Phylogenetic inference places the genus in the Paxillaceae.

***Parvixerocomus*** G. Wu & Zhu L. Yang (2015)

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 yellowish. *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 ellipsoid, 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 epigeal, *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, *tefl*, *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* epigeous, 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)

*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. Next gen inference by Tremble *et al.* (2024) places the genus in its own subfamily *Phylloboletelloideae*.

Ectomycorrhizae apparently not formed.

***Phyllobolites*** Singer (1942)

*Pileus* viscid but soon dry, red, glabrous. *Lamellae* deeply decurrent, scattered intervenose, forking once or twice, pallid. *Stipe* dry, central, terete, pallid staining pale brown. *Veil* present, forming a narrow annulus at stipe apex, somewhat fugacious and easily overlooked. *Context* white, unchanging. *Spores* fusoid to fusoid-ovoid, longitudinally rugose with rows of coarse warts and short ridges, inamyloid. *Hymenial cystidia* absent, but *pseudocystidia* present. *Clamp connections* present. In need of recollection and sequencing. Originally described from Amazonas, Brazil under leguminous trees, and placed in the Paxillaceae.

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

From the original diagnosis: *Basidiomata* pileate-stipitate with lamellate to subporoid hymenophore, epigeal, 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, *tefl-α*, and *rpb1* sequences the genus is unrelated to *Phylloporus* and sister to *Bothia* and *Solioccasus* (*Bothia* clade); part of a polytomy in the *Boletoideae*. 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). 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 (1931)

This genus used for the typically, somber colored taxa originally placed in *Tylophilus* 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 porphyrelloid genera/species were described recently from China by Y.-C. Li & Z.L. Yang (2021; *Abtylophilus*, *Anthracoporus*, *Indoporus*). Also, *Brasilioporus* and *Nevesoporus* from Brazil and *Kgaria* from Australia. Ectomycorrhizae presumed with Pinaceae, Fagaceae, Myrtaceae, Casuarinaceae, perhaps Dipterocarpaceae, Nothofagaceae, caesalpinoid legumes.

### ***Pseudoaustroboletus*** Y.C. Li & Zhu L. Yang (2014)

*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 fits in the *Leccinoideae* clade (combined nrLSU, *tef1*, mtSSU).

Ectomycorrhizae apparently with Fagaceae.

### ***Pseudoboletus*** 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 punctuate 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-1a* sequences. Apparently aligned in the *Xerocomoideae* and originally circumscribed just two species, one in Mediterranean Europe and the other in states along the Gulf Coast, USA. A recent study (Ayala-Vásquez *et al* 2023) infers *Boletus neoregius*, found in Mexico and Costa Rica, in the genus.

Ectomycorrhizae presumed with Fagaceae (*Quercus*, *Castanea*), possibly *Cistus*.

### ***Pulveroboletus*** Murrill (1909)

*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 (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.

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

From the original diagnosis: Differs from *Xerocomellus* by the spores smooth in all species, never striate, 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 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, rarely globose and reticulate. *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 (1989)

*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*, *Borofutus* 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*).

***Rosbeevera*** 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* 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. 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 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.

***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.

***Rugiboletus*** G. Wu & Zhu L. Yang (2015)

*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), Mexico, Central America, and Colombia. Ectomycorrhizae presumed with Pinaceae, Fagaceae.

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

*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*) in Guyana and Nyctaginaceae in Brazil.

***Singeromyces*** Moser (1966)

*Basidiomata* hypogeous, lacking a peridium, with percurrent columella. *Gleba* irregularly lacunose, ferruginous. *Spores* honey yellow, ellipsoid-cylindric, punctate-perforate. *Cystidia* absent. *Clamp connections* absent. One species, *S. ferrugineus*, known from Puerto Manzano, Argentina. Ectomycorrhizae presumed with *Nothofagus pumilio*.

***Soliococcus*** 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 rhizomorphs, 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*).

***Spongiforma*** Desjardin, Manfr. Binder, S. Roekring & Flegel (2009)

*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 Boletaceae (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 (2018)

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, 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 *Hopea odorata* (Dipterocarpaceae).

***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*, *Crocinoletus*, *Exsudoporus*, *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 appanate, 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, *tefl*, *rpb1*, *rpb2*); Central China.

Ectomycorrhizae presumed with Fagaceae.

***Tuboseta*** Horak (= *Setogyroporus* fide Singer) (1967) (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.

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

*Basidiomata* sequestrate, hypogeous, subglobose to reniform, rubbery, pink to white of brownish white, often changing to blue when bruised. *Gleba* white, becoming blackish brown, loculate. *Columella* absent, but sterile base sometimes present. *Peridium* thin, composed of filamentous hyphae. *Spores* statismosporic, ovoid to fusoid, inamyloid, red to dark brown with 5–10 longitudinal ridges, often branched. *Clamp connections* absent. Four species known from Japan and China. Allied to *Rossbeevera* in the *Leccinoideae* using molecular inference. But see *Leccinum* as broadly defined by Kuo & Ortiz-Santana (2020).

Ectomycorrhizae presumed with Fagaceae

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

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* (Vadthananarath *et al.* 2018). One species known from SW China. Ectomycorrhizae presumed with Fagaceae.

### ***Tylophilus*** 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 **ballouioids** (see Osmundson *et al.* 2021) erroneously treated in *Rubinoboletus* (= *Chalciporus*), but molecular inference distinguishes *Tylophilus* from *Porphyrellus*, and embraces the ballouioids in *Tylophilus*. 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.

### ***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)

*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.

### ***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, inamyloid. *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 sister 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 subtomentose, 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)

*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, New South Wales.

**Xerocomellus** Šutara (2008)

*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 granulose, sometimes longitudinally striate but mostly non-reticulate. *Lateral stipe stratum* usually absent or quite reduced. *Spores* smooth or longitudinally striate/veined, sometimes truncate. *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 (1887)

*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* often '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** Y.C. Li & Zhu L. Yang (2011)

*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.