The genus *Lentinula*  
(Tricholomataceae tribe Collybieae)

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Summary. - The genus *Lentinula* is revised and redefined to include five species with a subtropical – tropical distribution. It includes two edible species, *L. edodes* from eastern Asia, and *L. boryana*, from tropical America. New combinations are proposed for *Lentinula guarapiensis* (Spec.) Pegler, *L. lateritia* (Berk.) Pegler, and *L. novaezelandiae* (Stev.) Pegler.

Introduction

The genus *Lentinula* Earle, originally based on *Lentinus cubensis* Berk. & Curt. (= *Lentinula boryana* (Berk. & Mont.) Pegler), was long thought to be a later synonym of the much larger and more widespread genus, *Lentinus* Fr. Little attention was given to it until Pegler (1975) analysed the hyphal structure and found it to be quite distinct to that found in species of *Lentinus*, and secondly, that the well known Shiitake Japanese Mushroom, widely called *Lentinus edodes* (Berk.) Singer, had a similar structure and would be more appropriately placed in *Lentinula*. Although the type species, *L. boryana*, and *L. edodes* are macroscopically distinctive and widely separated geographically, nevertheless there are a number of common features. Both are known to be edible and have been gathered for consumption over a long period of time, and both are associated with growing on dead *Quercus* – tree hosts. The lamellae darken with brownish or vinaceous patches at maturity, and they conspicuously separate away from the stipe apex at maturity. Although the pileal surface may darken considerably during development, the pileal margin always remains pale.

The genus *Lentinula* is not related to *Lentinus* but is closely allied to *Nothopanus* Singer, and belongs in Tricholomataceae tribe Collybieae Imai. A revised, illustrated account of the five recognized species is presented below.

*Lentinula* Earle  

Pileus convex to applanate, firm-fleshy, initially smooth and glabrous, sometimes becoming squamose or fissured. – Lamellae adnato- or adnexo-sinuate,
sometimes with a decurrent tooth, often soon separating from the stipe and becoming free, whitish, often discoloring brownish or vinaceous at maturity, crowded; edge entire or minutely serrulate. — Stipe central to excentric, rarely lateral, cylindric or compressed, solid. — Veil cortinoid, fugacious, limited to remnants on the pileal margin and sometimes a ring-zone on the stipe. — Context firm-fleshy, pale coloured, not discoloring. — Hyphal system monomitic, with inflated generative hyphae, with sclerified walls, often noticeably constricted at the septa, and conspicuous clamp-connexions. — Spore print white. — Spores small, ovo-ellipsoid to ellipso-cylindric, hyaline, inamyloid, non-dextrinoid, thin-walled. — Lamella-edge fertile or heteromorphic, sometimes with inconstant, inflated cheilocystidia. — Pleurocystidia absent. — Hymenophoral trama regular to subregular, hyaline. — Pileipellis an indefinite cutis of repent hyphae. — Development pseudoangiocarpic. — Tropical-subtropical, growing on dead wood. Family: Tricholomataceae tribe Collybieae IMAI. Type species: Lentinus cubensis BERK. & CURT. [= Lentinula boryana].

EARLE (1909: 416) proposed the genus Lentinula to accommodate Lentinus cubensis BERK. & CURT., stating it to be a small genus distinguished from Lentodium MORGAN, based on a gasteroid form of Lentinus tigrinus (LINN.: FR.) FR., solely by the absence of a veil. On examination of fresh, very young basidiomes of L. cubensis (= Lentinula boryana), the hymenophore is observed to be covered by a very thin, membranous veil, and was first indicated by MURRILL (1939: 31). PEGLER (1975: 18) showed that Lentinula contrasted sharply from Lentinus FR. and Lentodium, in having a monomitic hyphal system with sclerified yet inflated generative hyphae, rather than a dimitic system with skeleto-ligative hyphae.

The hyphal system found in Lentinula species is indicative of the order Agaricales, rather than Aphylllophorales in which Lentinus would be placed. The spore type and the undifferentiated cutis structure are typical of Tricholomataceae tribe Collybieae IMAI, and Lentinula very closely approaches the pleurotoid genus Nothopanus SINGER, by virtue of the sclerified hyphae, the absence of cystidia, the lignicolous habit, and the tendency to develop brownish or vinaceous discolouration of the basidiome surfaces.

One of the more interesting characteristic features of the genus is the pseudoangiocarpic development in which the hymenium in the primordial state is exposed and then subsequently covered by lip-saranchyma tissue which leaves cortinoid fragments on the upper stipe and pileal margin of young, expanded basidiomes.

Lentinula is now seen to be a widespread genus, of subtropical and tropical distribution, although not yet recorded from Africa, containing at least five species.

Key to the Species of Lentinula

1. Stipe central to strongly excentric but never lateral
2. Pileus with dark reddish brown or vinaceous brown pigmentation;
Asia or Australasia

3. Stipe glabrous or with a few appressed squamules towards the base

4. Pileus 5–15 cm diam., tawny to dark vinaceous brown, after much paler at the margin, with fibrillose squamules or areolate cracks; context fleshy, 5–8 mm thick; stipe short, stocky, 8–15 mm diam.; eastern Asia ................. 1. L. edodes

4*. Pileus 2–5(–8) cm diam., uniformly reddish brown, smooth and glabrous; context thin; stipe slender, 3–9 mm diam.; south-east Asia ...... 2. L. lateritia

3*. Stipe covered with minute, erect reddish brown fibrillose squamules; pileus 4–7.5 cm diam., fuscous, rugulose; stipe slender, 4–6 mm diam.; New Zealand .........

3. L. novaezelandiae

2*. Pileus initially ivory-white, later developing brownish patches from the centre, smooth or finely rimulose; context 2–5 mm thick; stipe slender, 2–8 mm diam., central or slightly excentric; tropical America ........ 4. L. boryana

1*. Stipe lateral or nearly so, 3–5 mm diam.; pileus 1–3(–5) cm diam., reddish brown, smooth. Paraguay .... 5. L. guarapiensis

1. Lentinula edodes (BERK.) PEGLER in Kavaka 3: 20 (1975). – Fig. 1, A–E


Collybia shiitake SCHROET. in Gartenfl. 35: 105 (1886).

Armillaria edodes (BERK.) SACC., Syll. Fung. 5: 79 (1887).

Agaricus russaticeps BERK. apud Cooke in Grevillea 16: 106 (1888).


Tricholoma shiitake (SCHROET.) LLOYD, Mycol. Writ. 5, lett. 67: 11 (1918).


Lentinus edodes (BERK.) SINGER in Mycologia 33: 451 (1941).

Pileus 5–15 cm diam., fleshy, convex to applanate, subumbonate or depressed; surface variable in colour ranging from ochraceous-buff (M.9YR/7.0/6.5) to tawny (M. 5YR/5.2/6.5), russet (M.4.5YR/4.0/4.2) to dark vinaceous brown (M.3.OR/3.7/3.0), darker at the centre, often very pale at the margin in young specimens, dry, smooth but soon either disrupting to form innate, appressed trian-
gular squamules or becoming areolately cracked and deeply fissured exposing the white underlying context; margin at first incurved and bearing cortinoid, pale cartridge buff remnants of the veil, soon glabrescent. – Lamellae adnexo-adnate, at times with a decurrent tooth, soon separating from the stipe to become free, whitish, sometimes developing reddish brown spots, 4–7 mm broad, somewhat ventricose towards the stipe, moderately crowded, with lamellulae of two lengths; edge entire or weakly serrulate. – Stipe central to excentric, 3–7 cm × 8–15 mm, cylindric to slightly fusoid, often compressed, rarely with a subbulbous base, solid, surface pale reddish brown or concolorous but paler than the pileus, fibrillose, smooth and glabrous above, with small, darker brown squamules below. – Veil poorly developed, cortinoid, at times forming a ring-zone on the stipe, evanescent. – Context 5–8 mm thick at the disk, white, tough fleshy, of loosely woven hyphae, 3–8 μm diam., inflating to 23 μm diam., with a slightly thickened wall (1–3 μm), frequently branching, with prominent clamp-connexions at the constricted septa.

Spore print pure white. – Spores 5–6.5(–7)×3–3.7 (5.7±0.3×3.2±0.2) μm, Q=1.78, ovoid to ovo-ellipsoid, sometimes oblong ellipsoid, hyaline, inamylloid, non-dextrinoid, thin-walled, smooth, with few contents. – Basidia 17–23×4–5 μm, narrowly clavate, bearing four sterigmata. Lamella-edge fertile or heteromorphous with scattered or clustered small cheilocystidia. – Cheilocystidia 24–32×8–12 μm, inflated clavate, hyaline, thin-walled, with few contents. – Hymenophoral trama regular to subregular, hyaline, inamylloid, of more or less parallel hyphae, 5–6 μm diam., with a slightly thickened wall. Subhymenial layer well developed, 10–15 μm wide, interwoven. – Pileipellis an indefinite cutis of more or less radially parallel or subwoven hyphae, 2.5–7 μm diam., little inflated, with a pale brown wall, and with some surface encrustation on the outermost hyphae.

Specimens examined: Japan: 28 Apr. 1875, Challenger Exped., Herb. BERK. (K, type of A. edodes); 1883, Herb. COOKE (K, type of A. russaticeps); Otsu City, Mudera, 12 Apr. 1952, HONGO, 324. – China: Canton, Poon Ue Distr., purchased from shop, 19 Oct. 1932, McCLURE, 20194. – Vietnam (Tonkin): Mt. Bavi, Dec. 1873, BALANSA, 77 (FH, type of L. tonkinensis); May 1888, BALANSA, 99.

The well known ‘Shiitake Mushroom’ has been widely cultivated throughout Japan and China for many centuries, and is extensively exported throughout the world. The volume of commercial production is exceeded only by the ‘Commercial Mushroom’, Agaricus bisporus (J. Lange) IMBACH. Other common names include the ‘Oakwood Mushroom’, ‘Japanese Forest-Mushroom’, ‘Black Mushroom’ and ‘Pasania’. The original description (BERKELEY, 1877: 230
Fig. 1. A–E. Lentinula edodes (Berk.) Pegler: A. habit and section, × 1. – B. spores, × 1000. – C. basidia, × 1000. – D. cheilocystidia, × 1000. – E. context hyphae, × 500. – F–K. L. lateritia (Berk.) Pegler: F. sketch of type, × 1. – G. spores, × 1000. – H. basidia, × 1000. – J. cheilocystidia, × 1000. – K. context hyphae, × 500.
50, see also Anon., 1877: 105) was based on a very poor specimen purchased from a shop in Japan and brought to England where Berkeley thought it probably represented a species of *Armillaria* (Fr.) Kummer.

It grows on the dead wood of a wide range of tree hosts, especially species of *Quercus*, *Lithocarpus*, *Castanea*, *Castanopsis cuspidata* (Shii-tree) and *Fagus* in the Fagales, and in addition *Carpinus*, *Platycarya*, *Juglans*, *Elaeocarpus*, *Magnolia*, *Pinus* and *Picea* (ITO & IMAI, 1925: 329). Extensive accounts on the methods of cultivation are given by Delmas (1975), Ito (1978), Passecker (1968), and Singer (1961: 138–146). *Lentinula edodes* is to be found growing throughout much of eastern Asia, especially Japan and China, but does not extend to the colder or more tropical zones, preferring an optimal temperature of around 24°C. In recent years this range is seen to extend westwards to Kazakhstan (Samgina, 1981: 87).

Although it is such a well known fungus, the taxonomic position has remained in dispute over the past century, when it has been assigned to nine separate genera. It is most commonly referred to as *Lentinus edodes*, but the ovo-ellipsoid spores, the monomitic hyphal system with much inflated, sclerified generative hyphae, and the fertile lamella-edge preclude the genus *Lentinus* and Lentinaceae Julich. Comparison with other species of *Lentinula*, especially the tropical American species, *L. boryana*, indicate its true position in this small but well defined, inter-tropical genus.

2. *Lentinula lateritia* (Berk.) Pegler, comb. nov. – Fig. 1, F–K


Pileus 2–5(–8) cm diam., plano-convex, subumbonate or slightly depressed at the centre; surface cinnamon-rufous (M.2.5YR/5.2/7.0) to hazel (M.4YR/4.5/5.5), darker to cinnamon brown (M.7YR/4.3/4.0) at the centre, smooth and glabrous, neither squamose nor fissured, margin thin, incurved, sinuous, with pale ochraceous, cortinoid velar remnants in young specimens. – Lamellae adnexo-sinuate, soon separating from the stipe, white to ivory, developing fulvous or purplish brown tints at maturity, narrow, 2–3 mm wide, crowded, with lamellulae of three lengths; edge entire or minutely serrulate. – Stipe 2.5–7 cm × 3–9 mm, central or eccentric, often curved, slender, subcylindric, solid, surface concolorous with the pileus, at times with purplish brown tints, paler above, smooth or with fine, scattered brownish fibrils below. – Veil poorly developed, cortinoid, occasionally leaving traces of a ring-zone on the stipe. – Context thin, up to 6 mm thick at disk, very thin at margin, white, consisting of loosely woven hyphae, 4–8 μm diam.,

232
inflating to 17 µm diam., with a thickened wall (1–3 µm), and clamp-connexion.

Spore print white. – Spores 5.3–6(–6.5)×3–3.7 (5.5±0.3×3.2±0.2) µm, Q=1.72, ovoid to ellipsoid, hyaline, inamyloid, non-dextrinoid, thin-walled, with few contents. – Basidia 15–28×4–5.5 µm, clavate, bearing four sterigmata. Lamella-edge fertile or heteromorphous, with scattered cheilocystidia. – Cheilocystidia at times very sparse, 21–24×7.5–10 µm, pyriform to inflated clavate, hyaline thin-walled, with few contents. – Hymenophoral trama regular, hyaline, of inflated, parallel hyphae, 2–11 µm diam., with a slightly thickened wall. Subhymenial layer well developed, 10–16 µm wide, loosely woven. – Pileipellis an indefinite cutis of repent, more or less radially parallel hyphae, 2.5–6 µm diam., with a pale reddish brown wall.


*Lentinula lateritia* may be no more than a tropical form of *L. edodes*, for it is scarcely separable on the basis of the micro-structure alone. Nevertheless, the overall appearance of the basidiomes found in southeast Asia and Australasia remain distinctive, and the distribution of true *L. edodes* does not extend to the tropics but prefers a subtropical-subtemperate climate. *Lentinula lateritia* generally produces smaller basidiomes with a more slender aspect, having a thinner context and a thin, often more elongated, stipe. The colour of the pileus is constantly and uniformly reddish brown and never forms the squamules and fissures of *L. edodes* nor does it show the range of colour of the latter species.

BERKELEY (1881: 384) based the original description on specimens received from Australia, via Baron F. von MÜLLER, but no other locality or habitat details were provided other than growing on wood. Examination of this type collection shows it to be in good condition, fertile, and agreeing in every aspect with specimens received at Kew from Mt. Kinabalu in Sabah, and with a second Australian collection, from New South Wales. Records of *L. edodes* from Sabah by KOBAYASI (1966: 258), and from Papua New Guinea by KOBAYASI, OTANI & HONGO (1973: 351) are both typical of *L. laterititia*. In all cases the collections were gathered in highland areas. KOBAYASI (1966: pl. X, A–B) has provided excellent colour photographs of *L. laterititia*.
3. **Lentinula novaezelandiae** (Stev.) Pegler, comb. nov. – Fig. 2, A–E

*Crinipellis novaezelandiae* Stev. in Kew Bull. 19: 45, pl. 9/2 (1964).  

Pileus 4–7.5 cm diam., plano-convex, at times subumbonate; surface hazel brown (M.4YR/4.5/5.5), darkening to fuscous (M.3.5YR/3.5/1.0) at the centre, dry, smooth to rugulose; margin incurred, at first coated with pale ochraceous, cortinoid velar fibrils. – Lamellae adnexo-adnate, pale vinaceous fawn, darkening to brown on drying, 4–7 mm wide, ventricose towards the stipe, moderately crowded, with lamellulae of three lengths; edge entire or minutely serrulate. – Stipe 2–4 cm × 4–6 mm, central, cylindric or nearly so, at times with a subbulbous base, solid; surface vinaceous fawn, smooth and glabrous above, covered with minute, reddish fuscous or darker, erect fibrillose squamules below. – Veil very slightly developed, limited to remnants on pileal margin, evanescent. – Context 5–8 mm thick, cream colour to vinaceous fawn, tough, of loosely woven hyphae, 3–7 μm diam., inflated to 22 μm diam., with a thin or thickened wall (–3 μm), bearing conspicuous clamp-connexions at the constricted septa.

Spore print white. – Spores 4.5–6×2.8–3.7 (5.5±0.3×3±0.2) μm, Q = 1.83, ellipsoid to oblong cylindric, hyaline, thin-walled, with few contents. – Basidia 13–20×3.5–4.5 μm, clavate, bearing four sterigmata. Lamella-edge fertile or heteromorphous, with fascicles of inflated cheilocystidia. – Cheilocystidia numerous to sparse, 25–36×8–12 μm, elongated, inflated clavate, hyaline, with few contents. – Hymenophoral trama regular, hyaline, of parallel, inflated hyphae, 2–12 μm diam., mostly thin-walled. Subhymenial layer 6–12 μm wide, interwoven. – Pileipellis a cutis of radially parallel or interwoven hyphae, 3–9 μm diam., with a brown, thin wall, and some encrusting pigment. – Stipitipellis disrupting to form erect of semierect fascicles of brown thick-walled hyphae.

Specimens examined: **New Zealand**: North Island, Otari, Wilton’s Bush, on fallen rotten logs, 18 May 1947, Stevenson, 150 (K, type); Levin, Cockburn’s Bush, on fallen in pukutea and podocarp forest, 22 June 1958, Cone, 1387; Haurangi Mts., Pararaki Riv., on fallen timber, 15 Sep. 1958, Davidson.

A species closely related to *L. edodes* and *L. lateritia*, differing in having a stipe surface covered with erect, reddish brown, fibrillose squamules, and narrower spores. It is known only from New Zealand. Stevenson (1964: 45) described the species within the genus *Crinipellis* Pat., presumably on account of the arachnoid fibrils towards the pileal margin. The robust, fleshy basidiomes are quite atypical of that marasmoid genus, and Horak (1971: 440) transferred...
the species to *Collybia* (Fr.) Kummer although at the same commenting on the uncertainty of the generic position.

4. **Leninula boryana** (Berk. & Mont.) Pegler in Kavaka 3: 19 (1975). – Fig. 2, F–J.

*L. proximus* Berk. & Curt., loc. cit.
*C. boryana* (Berk. & Mont.) Sacc., loc. cit.: 240.
*L. detonsa* (Fr.) Murr. in Mycologia 3: 28 (1911).
*A. raphanica* Murr. in Mycologia 35: 422 (1943).

Pileus 1–5(–8) cm diam., soft fleshy, convex to broadly aplana- nate or slightly depressed, at times umbilicate or umbonate; surface ivory white, discolouring with age, in streaks or patches to yellowish brown (M.8YR/5.9/9.5) or vinaceous rufous (M.10R/4.7/8.5), moist, shining, somewhat translucent, smooth and glabrous or minutely subsquamulose at the disk, non-striate; margin inrolled, entire, remaining white, bearing minute, white, triangular, fibrillose velar squamules near the edge. – Lamellae adnexed to adnate, finally separating from the stipe, cream colour, staining vinaceous brown, narrow, 2–3 mm wide, very crowded, with lamellulae of two lengths; edge entire or nearly so. – Stipe 1–6 cm×2–5(–8) mm, at first central becoming slightly excentric, often curved, solid; surface white above to pale rusty below, with minute fibrillose squamules either extending over the entire length or confined towards the discoid base. – Veil fibrillose, cortinoid, white, leaving one or more fugacious ring-zones on the upper stipe. – Context 2–5 mm thick at centre, whitish, aqueous, at times appearing gelatinized in dried material, consisting of loosely woven hyphae, 3–8 µm diam., inflated to 16 µm diam., with a thickened wall (–4.5 µm), with prominent clamp-connexion at the constricted septa.

Spore print pure white. – Spores 5–6×2–3.5 (5.7±0.3×2.7±0.3) µm, Q = 2.0, oblong ellipsoid, hyaline, inamyloid,
non-dextrinoid, thin-walled, with few contents. – Basidia 15–17×3–4 μm, narrowly clavate, bearing four sterigmata. Lamella-edge fertile. – Hymenophoral trama subregular, hyaline, of more or less parallel hyphae, 5–12 μm diam. Subhymenial layer interwoven. – Pileipellis an indefinite cutis of tightly interwoven, thin-walled hyphae, 4–7 μm diam.


This species may be found, growing in large numbers, throughout tropical America, on decaying branches, logs and stumps of many forest trees. In the Caribbean islands it is particularly associated with species of Sloanea L. (Elaeocarpaceae), although according to Murrill (1939: 31) it frequently occurs on oaks in the Gainesville region of Florida, U.S.A., similar to L. edodes in eastern Asia. For many years the basidiomes have been gathered for eating on the island of Dominica.

Lentinus glabratus Mont. has sometimes been listed as an earlier name for this species but examination of authentic material at Kew shows it to be a true Lentinus species, belonging to the section Tigrini, with an interveined hymenophore, skeleto-ligative hyphae, and elongate cylindric spores.

5. Lentinula guarapiensis (Speg.) Pegler, comb. nov. – Fig. 2, K–N.


Pileus laterally attached, 1–3(–5) cm diam., thin fleshy, apllanate, dimidiate, truncated behind; surface fulvo-ferruginous when dried, smooth and glabrous, slightly tomentose towards stipe.
attachment; margin thin, undulate. — Lamellae adnexo-sinuate with a short decurrent tooth, concolorous with the pileus but paler, narrow, about 1–1.5 mm broad, very crowded, with lamellulae of three lengths; edge finely denticulate. — Stipe lateral or almost so, 1–2.5 cm × 3–5 mm, curved, cylindric or with a subbulbous base, solid; surface concolorous with pileus, more or less white pruinose. — Context 1–2 mm thick at disk, pale coloured, consisting of interwoven, hyaline hyphae, 3–6 μm diam., inflated to 10 μm diam., inflated to 10 μm diam., with a slightly thickened wall (–1.5 μm), and clamp-connexions at the constricted septa.

Spores (?) 4–4.5 × 2.3–3 μm, ovoid to ovo-ellipsoid, hyaline, inamyloid, non-dextrinoid, thin-walled, with few contents. — Basidia 12–14 × 3–3.5 μm, small, cylindric-clavate. Lamella-edge probably fertile. — Hymenophoral trama subregular, hyaline, of more or less paler or slightly woven, inflated hyphae. Subhymenial layer poorly developed, narrow. — Pileipellis an indefinite cutis of closely woven, thin-walled hyphae.

Specimens examined: Paraguay: Guarapi, amongst moss on dead, rotting tree-trunks, Apr. 1879, Balansa, 3373 (K, PC, type).

The above description is based upon the original account given by Spegazzini (1883: 246) and an examination of the type material located in the Kew and Paris herbaria. Unfortunately this description remains incomplete with regard to the colour of the fresh basidiomes and the microstructure. The available basidiomes are heavily mould infected and the hymenophores are covered in glue. There are to be found, amongst the numerous mould spores on the hymenium, a few loose basidiospores which match in size with the basidia present and therefore possibly belong to this species. The sinuate, crowded lamellae and the thickened-walled, inflated hyphae indicate that Lentinula is the more appropriate genus for the species.

References


