Fungal Diversity (2012) 55:155–169
DOI 10.1007/s13225-012-0161-1

Taxonomy of *Pseudolagarobasidium* (Polyporales, Basidiomycota)

Karen K. Nakasone · Daniel L. Lindner

Received: 30 December 2011 / Accepted: 25 February 2012 / Published online: 16 March 2012

Abstract *Pseudolagarobasidium* (Polyporales, Basidiomycota) is a small, monophyletic genus of crustose, wood-inhabiting fungi with spines and a saprobic, endophytic, or parasitic habit. Seven species are accepted in the genus including two new species, *P. belizense* from Belize and *P. pusillum* from Australia. Sequence analysis of the internal transcribed spacer of the ribosomal RNA gene places *P. belizense* in a monophyletic clade with *P. acaciicola* and an undescribed foliar endophyte. New combinations proposed include *P. modestum* for *Irpex modestus* Berk., *P. pronum* for *Hydnum pronum* Berk. & Broome which is an earlier name for *P. calcareum*, and *P. venustum* for *Radulodon venustus* Hjortstam & Ryvarden. *Irpex colliculosum* Berk. & Broome from Sri Lanka is conspecific with *P. subvinosum*. Two species, *Sistotrema ochroleucum* and *Radulum concentricum* are not accepted in *Pseudolagarobasidium*. *Pseudolagarobasidium* is compared with *Radulodon* and similar genera. A key to the species of *Pseudolagarobasidium* is provided.

Keywords *Pirex concentricum* · *Pseudolagarobasidium acaciicola* · *P. leguminicola* · *Hydnum ayresii* · Microbinding hyphae

Introduction

Pseudolagarobasidium J.C. Jang & T. Chen is a small genus of crustose, wood-inhabiting basidiomycetes with spines. It was proposed in 1985 to accommodate the new taxon, *P. leguminicola* J.C. Jang & T. Chen, associated with a stem and root rot of *Leucaena leucocephala* (Lam.) de Wit in Taiwan (Jang and Chen 1985). Wu (1990) synonymized *P. leguminicola* with *Hydnum subvinosum* Berk. & Broome and transferred *H. subvinosum* and *H. calcareum* Cooke & Massee to *Pseudolagarobasidium*. Later, Hjortstam (1995) transferred *Radulum concentricum* Cooke & Ellis to *Pseudolagarobasidium*, and the new species *P. acaciicola* Ginns from South Africa was described (Wood and Ginns 2006). Based on morphological studies, Stalpers (1998) placed *Pseudolagarobasidium* in synonymy under *Radulodon* Ryvarden. Sequence analyses of the nuclear large subunit ribosomal RNA (nLSU) gene, however, showed that *Pseudolagarobasidium* is a well-supported, monophyletic genus distinct from *Radulodon* and *Pirex concentricus* (Ellis & Cooke) Hjortstam (Hallenberg et al. 2008).

An unusual crustose species with small spines was collected from Doyle's Delight in 2004 by the junior author. Doyle's Delight Peak, the highest peak in the Maya Mountains of Belize, is a mycologically productive site that has yielded a number of new taxa (Baroni et al. 2007; Baroni et al. 2008; Ginns et al. 2010; Lindner et al. 2011; Ryvarden et al. 2009). DNA sequence analyses indicated that the crustose species belonged in *Pseudolagarobasidium*, and morphological examination confirmed that it was an undescribed species.

In this paper, we describe and illustrate two new species of *Pseudolagarobasidium* from Belize and Australia and propose the transfer of *Irpex modestus* Berk. and *Radulodon venustus* Hjortstam & Ryvarden to *Pseudolagarobasidium*. Type specimens of *Hydnum pronum* Berk. & Broome and *Irpex colliculosus* Berk. & Broome were examined and found to be congeneric with *Pseudolagarobasidium*. An emended description of *Pseudolagarobasidium* and key to the seven accepted species are presented.

K. K. Nakasone (✉) · D. L. Lindner
Center for Forest Mycology Research, Northern Research Station,
U.S. Forest Service,
One Gifford Pinchot Drive,
Madison, WI 53726-2398, USA
e-mail: knakasone@fs.fed.us

Materials and methods

Morphological methods

Thin, freehand sections from basidiomata were mounted in Melzer's reagent (Kirk et al. 2008) or 1% (weight/volume) aqueous phloxine and 1% (w/v) aqueous potassium hydroxide. Cyanophily of basidiospore and hyphal walls was observed in 0.1% cotton blue in 60% lactic acid (Kotlaba and Pouzar 1964; Singer 1986). Line drawings were made with a camera lucida attachment on an Olympus BH2 compound microscope. Photographs were taken with an Olympus DP12 camera attached to an Olympus SZH stereomicroscope. Q values were obtained from dividing average basidiospore length by width (Kirk et al. 2008). Basidiospores were often scarce in specimens, thus Q values based on less than 30 basidiospores are approximate and indicated with an asterisk (*). Color names are from Kornerup and Wanscher (1978), although capitalized names are from Ridgway (1912). Herbarium designations follow that of Index Herbariorum (Thiers 2012).

DNA sequence methods

DNA sequences of the internal transcribed spacer region (ITS) of the ribosomal RNA were obtained from cultures following methods detailed in Greslebin et al. (2004) and from basidiomata as described in Palmer et al. (2008).

Taxon selection and phylogenetic analyses

Initial BLAST searches placed DCL04-31 near *Pseudolagarobasidium* in the *Polyporales*. Taxa chosen for the phylogenetic analyses were selected after consulting Hallenberg et al. (2008), Lee and Lim (2010), and results from BLAST searches. In addition to newly generated sequences, *Pseudolagarobasidium belizense* (JQ070173, holotype), *Radulodon americanus* Ryvarden (JQ070174, JQ070175), and *R. casearius* (Morgan) Ryvarden (JQ070176), ITS sequences of the following taxa were included in the phylogenetic analyses: *Antrodiella albocinnamonea* Y.C. Dai & Niemelä (FJ613650), *Cerrena aurantipora* J.S. Lee & Y.W. Lim (FJ821532), *C. consors* (Berk.) K.S. Ko & H.S. Jung (FJ821527), *C. unicolor* (Bull.) Murrill (FJ810175, FJ821534, FJ821537), *Pseudolagarobasidium acaciicola* (AM849050, DQ517882, DQ517883), *Spongipellis delectans* (Peck) Murrill (HQ728301), *S. litschaueri* Lohwag (HQ728307), *S. unicolor* (Schwein.) Murrill (HQ728313). Two unnamed taxa were included: 'Fungal sp. ref1' (EU834826) and 'Basidiomycota RCBC XG8D' (HM060641) from leaves of mangrove in Thailand. In addition, outgroup taxa from a related *Polyporales* clade were included: *Aurantiopileus mayaensis* Ginns, D.L. Lindner & T.J. Baroni (HM772140) and *Scopuloides hydnoides* (Cooke & Massee) Hjortstam & Ryvarden (EU118665).

Twenty ITS sequences were aligned with ClustalW in MEGA5 (Tamura et al. 2011) then manually adjusted. In the phylogenetic analyses, maximum likelihood (ML) method based on the Tamura 3-parameter model (Tamura 1992) with gamma distribution was employed, following results from a best-fit substitution model test. As implemented in MEGA5, initial tree(s) for the heuristic search were obtained automatically as follows. When the number of common sites was <100 or less than one fourth of the total number of sites, the maximum parsimony method was used; otherwise BIONJ method (Gascuel 1997) with Markov cluster distance matrix was used. A discrete Gamma distribution modeled evolutionary rate differences among sites in five categories (+*G*, parameter= 0.4593). All positions containing gaps and missing data were eliminated from the analyses. Ten thousand ML bootstrap replicates were conducted with the same parameters. In addition, maximum parsimony (MP) analyses were performed in MEGA5 using close-neighbor interchange algorithm (Nei and Kumar 2000) in which the initial trees were obtained by random addition of sequences (10 replicates). Finally, 10000 MP bootstrap replicates were conducted employing the same parameters. Sequence alignment and ML and MP trees are deposited in TreeBase (accession number 12351).

Results

Phylogenetic analysis

There were 20 nucleotide sequences in the ITS dataset and 657 base pairs in the full alignment with 308 variable and 200 parsimony informative sites. Sequence divergence between sequences was calculated in which ambiguous positions were removed for each sequence pair (data not shown). Within the *Pseudolagarobasidium* clade (Fig. 1), sequence divergence ranged from 0 to 12%. ITS sequence of *P. acaciicola* AM849050, isolated from soil in India, was the most divergent in the clade, differing by 10% from *P. acaciicola* DQ517883 and 9% from DQ517882, both from South Africa, and 12% from *P. belizense* and Basidiomycota RCBC XG8D.

After all positions containing gaps and missing data were eliminated, there remained 498 positions in the final ITS dataset. In both ML and MP analyses, *P. belizense* always clustered with *P. acaciicola* and Basidiomycota RCBC XG8D. The ML tree with the highest log likelihood (−2315.2104) is shown in Fig. 1. With the MP method, 47 most parsimonious trees were recovered with a consistency index of 76.7%, retention index of 84.5%, and composite index of 64.8%. The MP consensus tree is similar to the ML tree except that the *Spongipellis* Pat. and *Radulodon* clades were not joined together. In the ML bootstrap tree, the *Pseudolagarobasidium* clade is supported

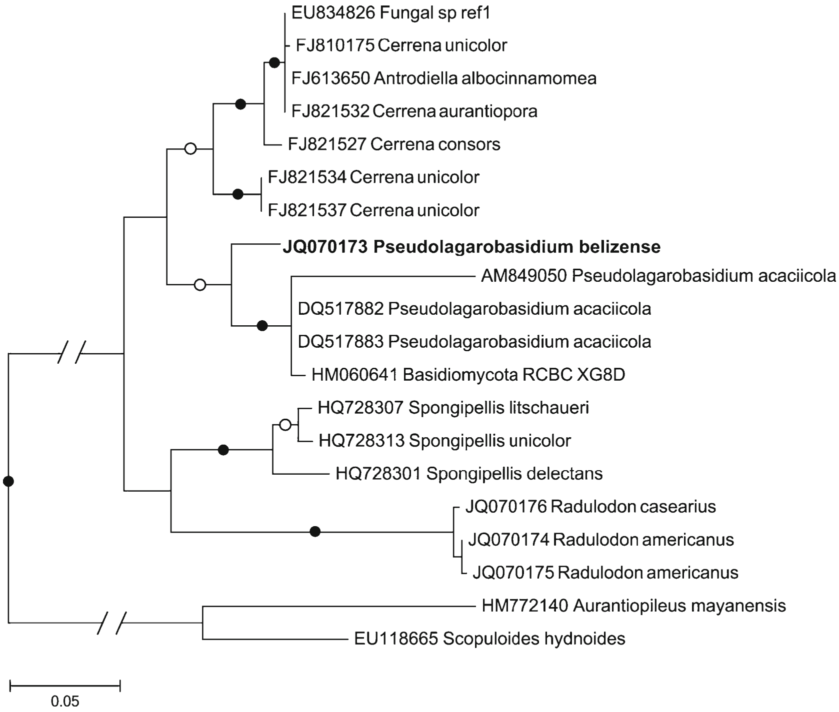


Fig. 1 Maximum likelihood phylogenetic tree based on ITS sequence data of *Pseudolagarobasidium* and allied species. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. Closed circles indicate bootstrap values >90% from ML and MP analyses whereas open circles indicate >80% bootstrap values

at 86% and slightly higher with the MP bootstrap analysis at 92%.

Taxonomy

Pseudolagarobasidium J.C. Jang & T. Chen, Trans. Br. Mycol. Soc. 85(2): 374. 1985, emended

Generic type: *Pseudolagarobasidium leguminicola* J.C. Jang & T. Chen (= *Hydnum subvinosum* Berk. & Broome)

Basidiomata resupinate, effuse, adnate, soft, subceraceous, membranaceous, or cretaceous, context homogeneous, non-agglutinated; hymenial surface spinose, odontioid, or raduloid, occasionally reticulate to subporoid; *aculei* soft, fragile, brittle, terete to conical, single, often fused at base or throughout length to form flattened, truncate aculei or plates. *Hyphal system* monomitic or dimitic, generative hyphae with clamp connections, walls hyaline, yellow to light brown, cyanophilous, often finely encrusted with oil-like particles (observed in water mounts) that readily dissolve in KOH; microbinding hyphae aseptate, frequently branched, nonstaining. *Aculei* a dense fascicle of non-agglutinated tramal hyphae with tramal cystidia embedded or curving into hymenium. *Subiculum* composed of a thin, dense layer of agglutinated hyphae arranged more or less parallel to substrate that ascend to form a non-agglutinated trama, except in one species where the subiculum is partially agglutinated throughout. *Hymenium* composed of cystidia and basidia in a dense palisade. *Cystidia* originating in aculei trama, subiculum, or subhymenium (tramal cystidia) and hymenium (hymenial cystidia), cylindrical, clavate, or subfusiform, clamped at base, contents homogeneous, staining deeply in phloxine and cotton blue, sulfovanillin negative, walls hyaline, thin, often finely encrusted with oil-like particles (observed in water mounts) that readily dissolve in KOH, cyanophilous. *Basidia* clavate to cylindrical, sometimes with a median constriction, contents homogeneous, clamped at base, walls hyaline, thin, often finely encrusted with oil-like particles (observed in water mounts) that readily dissolve in KOH, 4-sterigmate. *Basidiospores* globose to ellipsoid with a small, inconspicuous apiculus, contents homogeneous, walls hyaline, thin to slightly thickened, smooth, not or weakly cyanophilous, not reacting in Melzer's reagent. *Arthroconidia* may be present in basidiomata or cultures. *Incompatibility system* bifactorial. *Inhabiting* wood and bark of angiosperms as saprobes or parasites, possibly as endophytes.

The features that distinguish this genus are the soft-textured basidiomata, non-agglutinated hyphae throughout the aculei and context (except in one species), the distinct, even, clamped hyphae of the aculei trama, the numerous tramal and hymenial cystidia with homogenous contents that stain deeply in phloxine and cotton blue, and the small, globose to ellipsoid basidiospores. Oil-like particles are produced throughout the basidioma but are observed only in water mounts because they readily dissolve in KOH and other mounting media. Because the basidioma context is not agglutinated, hyphae and microscopic elements are readily observed in squash mounts. Microbinding hyphae are easily overlooked but are usually present in the subiculum adjacent to the substrate or in mycelial pockets in the woody substrate beneath the basidiomata. Also noteworthy is the variable hymenophore, ranging from spinose to reticulate. Microscopically, the species included in the genus are remarkably consistent with respect to aculei microstructure and shape and size of hymenial elements but differ in texture, color, and aculei morphology. Bifactorial incompatibility system (tetrapolar mating system) was reported for *P. pronum* (Maekawa and Hasebe 2002) and *P. subvinosum* (Chang and Chen 1984).

Species of *Pseudolagarobasidium* are primarily saprobes although several are endophytes or facultative or opportunistic pathogens. *Pseudolagarobasidium subvinosum* causes a stem canker or root rot (Jang and Chen 1985; Petch 1923; Sankaran and Sharma 1986; Wood and Ginns 2006) whereas *P. acaciicola* and *P. pronum* are associated with a dieback disease (Wood and Ginns 2006). In addition, molecular analyses of the nuclear large subunit ribosomal DNA placed undescribed endophytic fungal isolates from healthy stems of cacao and leaves of mangrove in the monophyletic *Pseudolagarobasidium* clade (Chokpaiboon et al. 2010; Hallenberg et al. 2008).

Key to the species of *Pseudolagarobasidium*

1. Basidioma chalky, dull cream-colored to light brown..*P. pronum*
1. Basidioma subceraceous to submembranous, yellow to dark brown...2
2. Basidiospores 3.4–4.3(−4.7)×2.9–3.2(−3.6) µm..*P. pusillum*
2. Basidiospores larger...3
3. Basidioma yellow to brownish orange.........*P. venustum*
3. Basidioma gray to dark brown...................................4
4. Aculei up to 0.4 mm long, subicular hyphae agglutinated..*P. belizense*
4. Aculei usually≥0.5 mm long, subicular hyphae non-agglutinated...5
5. Basidiospores 5–6(−6.5)×(3–)3.5–4(−4.5) µm...*P. subvinosum*
5. Basidiospores smaller..6
6. Basidiospores 4.2–5(−5.4)×2.9–3.5 µm, from Mauritius..*P. modestum*
6. Basidiospores (4.3–)4.8–5.8(−6.5)×(2.9–)3.2–4(−4.3) µm, from South Africa............................*P. acaciicola*

Pseudolagarobasidium acaciicola Ginns in Wood & Ginns, Can. J. Bot. 84: 752. 2006.

Basidioma resupinate, effuse, adnate, thin, up to 250 µm thick between aculei, soft, membranous; aculei terete or compressed, raduloid, up to 4 aculei per mm, up to 2.5 (−4) mm long, single or fused, often forming a subporoid or reticulate hymenophore, light brown [6D(4–5)], brown [6E5], dark brown [6 F(5–6)], Avellaneous, Wood Brown, Saccardo's Umber, Sepia, or purple. *Hyphal system* dimitic with clamped generative and aseptate microbinding hyphae; microbinding hyphae scarce, observed in substrate or at base of aculei. Subicular and aculei tramal hyphae not agglutinated, even, distinct, walls hyaline to yellow, up to 1.1 µm thick, cyanophilous. *Cystidia* of two types: (a) tramal cystidia numerous, originating in aculei trama and subhymenium then curving into hymenium, obclavate, narrowly clavate, cylindrical, or capitate, 25–72×6–10 µm, clamped at base; (b) hymenial cystidia scarce, originating in hymenium, subfusiform with subacute apex, 10–13×3–6.5 µm, clamped at base. *Basidia* clavate, 18–24×4.5–6 µm, clamped at base. *Basidiospores* ellipsoid, (4.3–)4.8–5.8 (−6.5)×(2.9–)3.2–4(−4.3) µm, averages of three specimens 5–5.6×3.5–3.7 µm, Q=1.4–1.5, walls hyaline, slightly thickened, smooth, weakly cyanophilous, not reacting in Melzer's reagent. Arthroconidia produced in culture, 5–12×2–5 µm (Wood and Ginns 2006).

Habitat and distribution: Saprobic on wood, also pathogenic, attacking root crowns of *Acacia cyclops*; known from South Africa.

Specimens examined: SOUTH AFRICA, Western Cape Province, Stellenbosch, on soil around seedlings, 17 June 2004, A.R. Wood, PREM 58239 and PREM 58240 (PREM); Pietermaritzburg, on Doore stomp, P.A. van der Bijl 602 and 669, as *Irpex modestus* (PREM); Durban, Natal, P.A. van der Bijl 674, as *Irpex modestus* (PREM).

Pseudolagarobasidium acaciicola is characterized by brown basidiomata with flattened, fused aculei, dimitic hyphal system, and ellipsoid basidiospores. It is most similar to *P. modestum* which has slightly smaller basidiospores; see discussion under *P. modestum*. Another morphologically similar species, *P. subvinosum* has slightly larger basidiospores and more prominent hymenial cystidia compared to *P. acaciicola*. Arthroconidia are produced in cultures and basidiomata of *P. subvinosum* and *P. pronum* also. For a complete description with illustrations of basidiomata and cultures see Wood and Ginns (2006). The specimens of van der Bijl cited above were originally identified as *Irpex modestus*; however, the basidiospores were more similar in size to those of *P. acaciicola* than to *P. modestum*. Molecular analyses of the nLSU sequences show that *P. acaciicola* has a basal position in the genus (Hallenberg et al. 2008), although with ITS data (Fig. 1) *P. belizense* is basal to *P. acaciicola*.

Pseudolagarobasidium belizense Nakasone & D.L. Lindner, **sp. nov.** (Figs. 2, 3 and 11)

MycoBank MB 563650

Etymology: from Belize, the type locality.

Differt Pseudolagarobasidio specibus basidiomatibus brunneis pallide, aculeis≤400 µm longis, hyphis subiculi agglutinatis.

Basidioma resupinate, widely effuse, thin, up to 350 µm thick between aculei, subceraceous to subcretaceous, odontioid to raduloid with distinct, smooth, subceraceous or subfelty areas between aculei, Tilleul-Buff, Drab Gray or greyish orange [5B(2–3)], no color change with KOH; cracks scattered, inconspicuous; *hymenial surface* composed of aculei, conical, terete, 3–4 aculei per mm, up to 400×100 µm, smooth, gradually tapering to an acute or rounded, penicillate, sterile apex, apices cream-colored or concolorous with base of aculeus, sometimes fused together at base or along entire length forming flattened raduloid structures with broadly tufted apices; margin gradually thinning out, adnate, irregularly fibrillose, concolorous or paler than mature areas.

Hyphal system dimitic with clamped generative and aseptate microbinding hyphae. *Aculei* composed of a dense core of non-agglutinated tramal hyphae arranged in parallel with a few embedded cystidia that curve into subhymenial and hymenial layers, at apex terminal hyphae undifferentiated, smooth; tramal hyphae 1.5–5 µm diam, clamped, sparingly branched, even, walls hyaline, slightly thickened, coated with a thin layer of oil-like particles that dissolve in KOH, cyanophilous. *Subiculum* up to 300 µm thick, composed of a dense, partially agglutinated trama of distinct, ascending, short-celled hyphae with cystidia and scattered pockets of microbinding hyphae; subicular hyphae 1.5–5 µm diam, clamped, frequently branched, even, walls hyaline to light brown, slightly thickened, rarely thick, coated with a thin layer of oil-like particles that dissolve in KOH, cyanophilous; microbinding hyphae up to 0.5 µm diam, aseptate, branches numerous, short, tapering, arising at right angles, walls hyaline, thickened, smooth. *Subhymenium* up to 70 µm thick with irregular, frequently branched, short-celled hyphae and cystidia in a dense, partially agglutinated tissue; subhymenial hyphae 1.5–3.2 µm diam, clamped, frequently branched, short-celled, walls hyaline, slightly thick, coated with a thin layer of oil-like particles that dissolve in KOH. *Hymenium* up to 30 µm thick, a palisade of basidia and cystidia. *Cystidia* of two types: (a) tramal cystidia numerous, originating in subiculum or aculei trama, fusiform, clavate, or obclavate, sometimes basally lobed, apex obtuse or papillate, embedded or barely protruding, 42–80×6–8 µm, with a basal clamp, contents homogenous, staining dark pink in phloxine and dark blue in cotton blue, sulfovanillin negative, walls hyaline, thin to slightly thickened, coated with a thin layer of oil-like particles that dissolve in KOH, cyanophilous; (b) hymenial cystidia numerous, similar to tramal cystidia except smaller and arising from upper subhymenium and hymenium, broadly fusiform or clavate, sometimes stalked, 9–30×5–9 µm. *Basidia* clavate to cylindrical, occasionally with a slight median constriction, (10–)15–20×4–6 µm, clamped at base, walls distinct, hyaline, slightly thick, coated with a thin layer of oil-like particles, cyanophilous, 4-sterigmate. *Basidiospores* broadly ellipsoid with a small, distinct apiculus, (4.2–)4.4–5.1×3–3.6(−4) µm, average 4.7±0.4×3.4±0.3, Q=1.4, walls hyaline, slightly thickened, smooth, cyanophilous, not reacting in Melzer's reagent.

Habitat and distribution: Saprobic on bark and wood of angiosperms; known only from the type locality, Belize.

Specimen examined: BELIZE, Cayo District, just south-southeast of Doyle's Delight Peak, on bark and wood of angiosperm, 11 August 2004, D. Lindner, DLC 04–31 (BPI, **holotype**; CFMR, **isotype**).

Pseudolagarobasidium belizense is characterized by grayish tan-colored basidiomata, small, subceraceous aculei <500 µm long, and agglutinated subicular hyphae. It is the only species in *Pseudolagarobasidium* in which the ascending subicular hyphae are agglutinated. Microbinding hyphae occur randomly in the subiculum and substrate. Because of its unique color and small aculei, *P. belizense* is readily distinguished from other species in the genus with basidiospores of similar size. *Pseudolagarobasidium venustum*, also known from the Americas, has pale yellow to pale orange basidiomata. ITS sequence analyses place *P. belizense* basally in the monophyletic *Pseudolagarobasidium* clade (Fig. 1).

Pseudolagarobasidium modestum (Berk.) Nakasone & D. Lindner, **comb. nov**. (Figs. 4, 5 and 12)

MycoBank MB 563651

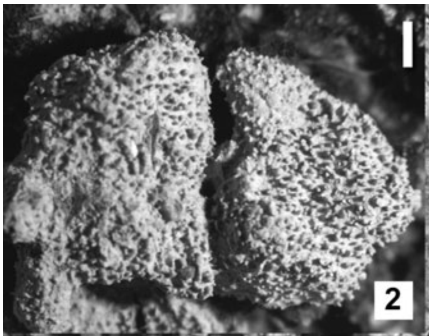
≡ *Irpex modestus* Berk. in Cooke, Grevillea 19(92): 109. 1891.

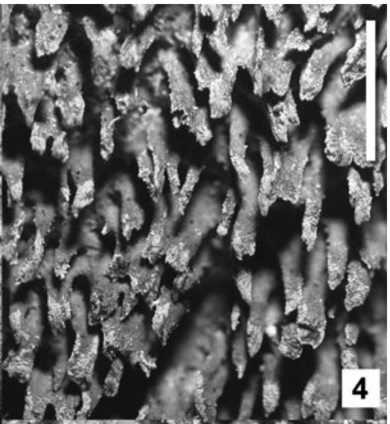
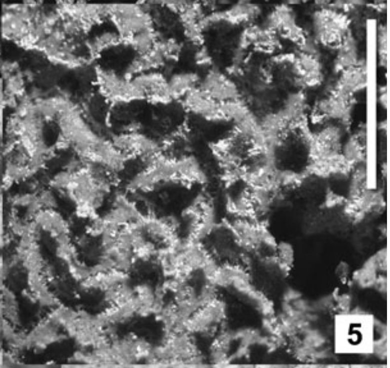
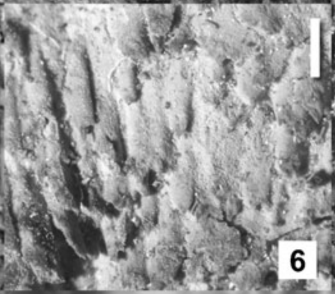
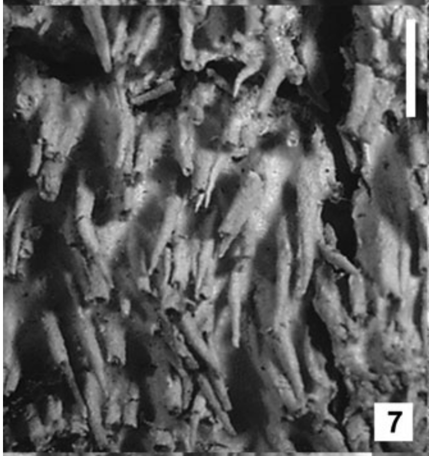
≡ *Xylodon modestus* (Berk.) Kuntze, Rev. Generum Plant. III(2): 541. 1898.

= *Hydnum ayresii* Berk. in Cooke, Grevillea 20(93): 2. 1891.

Basidioma resupinate, widely effuse, thin, up to 300 µm thick excluding aculei, soft, spinose, raduloid, or reticulate, between aculei smooth, felty or porose, sometimes subceraceous with numerous, short, irregular cracks, yellowish brown (5D5), dull brown [6(E–F)(4–5)], or Saccardo's Umber; *hymenial surface* composed of aculei 3–5 per mm, up to 1 mm long, soft, brittle, terete at first then compressed or fusing laterally into plates and reticulated ridges, apices subacute to obtuse, pubescent to hoary; margin gradually thinning out, adnate, indistinct, Tawny Olive.

Hyphal system dimitic with clamped generative and aseptate microbinding hyphae. *Aculei* composed of a central fascicle of non-agglutinated tramal hyphae with tramal cystidia curving into hymenium; tramal hyphae 3.5–5 µm diam, clamped, sparsely branched, walls hyaline to brownish yellow, up to 1.5 µm thick, smooth or near apex encrusted with tiny, black granules (in *I. modestus* holotype), cyanophilous. *Subiculum* a narrow, dense tissue of collapsed, agglutinated, thin-walled hyphae arranged parallel to substrate, then hyphae curving toward hymenium to form a non-agglutinated trama of slightly thick to thick-walled subicular hyphae, microbinding hyphae, and embedded oil-like particles that dissolve in KOH; subicular hyphae 2.5–5 µm diam, clamped, moderately branched, walls hyaline to yellow, thin to 1 µm thick, smooth, cyanophilous; microbinding hyphae scarce, 1–1.5 µm diam, aseptate, frequently branched at



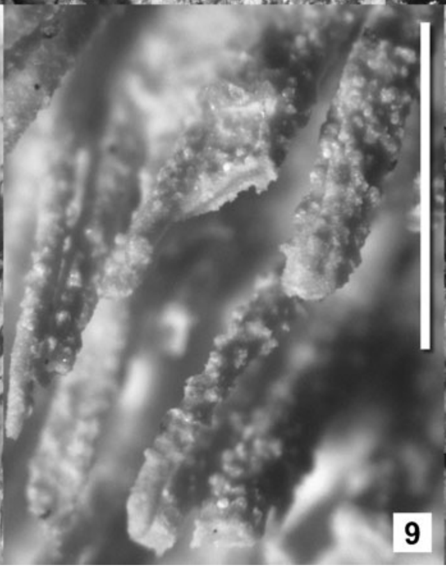



Fig. 2 *Pseudolagarobasidium belizense* (holotype, DLC 04–31) basidioma with odontioid hymenophore

Fig. 3 *P. belizense* (holotype) close-up of aculei and margin

Fig. 4 *Irpex modestus* (holotype, K(M)77598) close-up of mature aculei

Fig. 5 *Irpex modestus* (holotype, K(M)77598) close-up of developing acule

Fig. 6 *Hydnum pronum* (holotype, K(M)167192) aculei prone and fused

Fig. 7 *Hydnum calcareum* (holotype, K(M)56909) aculei with tips broken off

Fig. 8 *Pseudolagarobasidium pusillum* (holotype, PERTH 02340925) close-up of aculei

Fig. 9 *Pseudolagarobasidium venustum* (LR15910) close-up of aculei with knobs

Fig. 10 *Radulodon venustus* (holotype, (KM)77909) aculei smooth or knobby. Scale bars in Figs. 2–10 equals 1 mm

right angles, nonstaining, walls hyaline, thick, smooth. *Subhymenium* up to 20 μm thick, a dense, non-agglutinated tissue of ascending, irregular, short-celled hyphae; subhymenial hyphae 2.2–2.5 μm diam, clamped, frequently branched, walls hyaline, thin, smooth. *Hymenium* a dense palisade of cystidia and basidia. *Cystidia* of two types: (a) tramal cystidia abundant, originating in subiculum or aculei trama, enclosed, obclavate, to subfusiform, 45–165 × 7–13 μm, clamped at

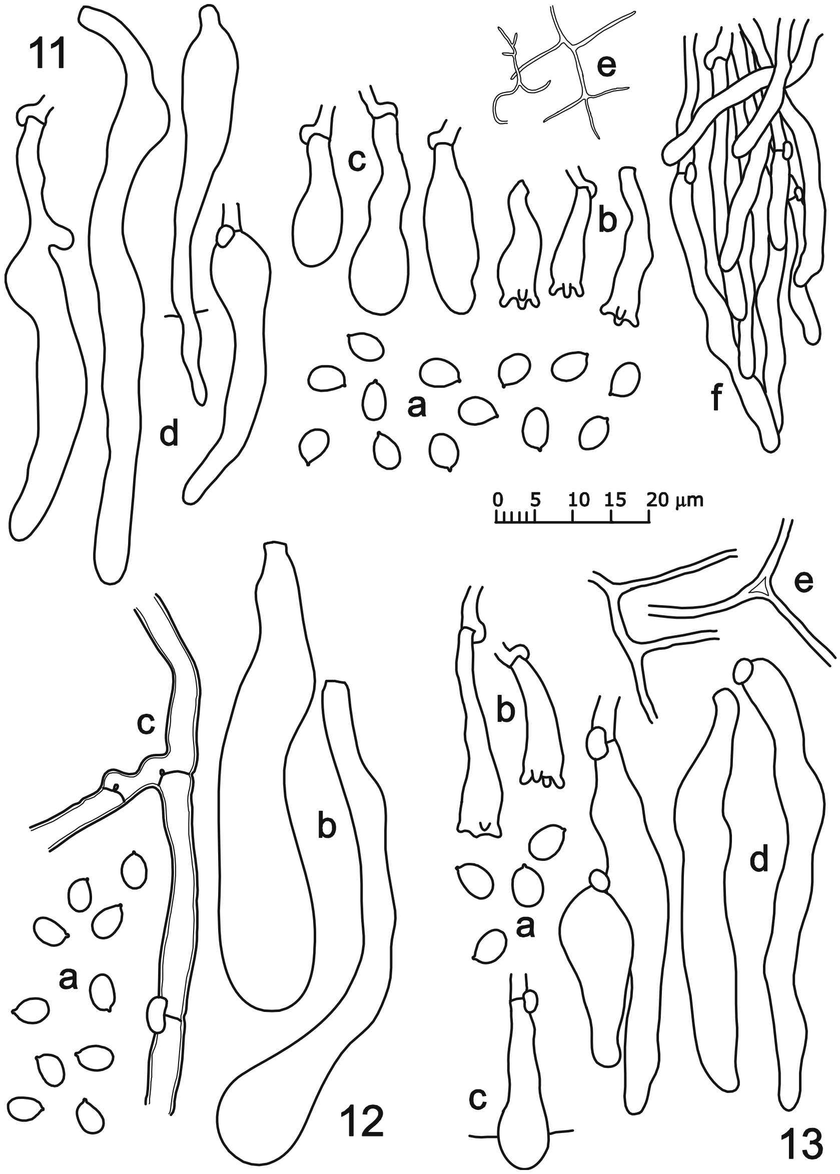


Fig. 11 Microscopic elements of *Pseudolagarobasidium belizense* (holotype, DLC 04–31) **a** Basidiospores; **b** Basidia; **c** Hymenial cystidia; **d** Tramal cystidia; **e** Microbinding hyphae; **f** Apex of aculeus

Fig. 12 Microscopic elements of *Irpex modestus* (isotype, BPI US0263675) **a** Basidiospores; **b** Tramal cystidia; **c** Hyphae from aculeus trama

Fig. 13 Microscopic elements of *Hydnum pronum* (holotype, K(M)167192) **a** Basidiospores; **b** Basidia; **c** Hymenial cystidium; **d** Tramal cystidia; **e** Microbinding hyphae

base, contents homogeneous, walls hyaline, thin, smooth; (b) hymenial cystidia scarce, inconspicuous, enclosed, broadly subfusiform, 15–18×4–5 µm, clamped at base, contents homogeneous, walls hyaline, thin, smooth. *Basidia* rare, clavate, 12–14×4–5 µm, clamped at base, walls hyaline, thin, smooth, 4-sterigmate. *Basidiospores* scarce, often collapsed, ellipsoid, 4.2–5(−5.4)×2.9–3.5 µm, averages of two specimens 4.5–4.6×3.1–3.2 µm, Q=1.4*–1.5*, walls hyaline, thin, smooth, not reacting in Melzer's reagent.

Habitat and distribution: Saprobic on bark and wood of angiosperms; known from Mauritius.

Specimens examined: MAURITIUS, on bark, April 1887, K(M)64594 (K, **holotype** of *H. ayresii*); hills above Port Louis, on bark, April 1857, Ayres, K(M)77598 (K, **holotype** of *I. modestus*; BPI US0263675, **isotype**).

Pseudolagarobasidium modestum is characterized by brown basidiomata with a spinose to reticulate hymenial surface, dimitic hyphal system, brownish yellow, thick-walled tramal hyphae in the aculei, and small ellipsoid basidiospores. Basidiospores were scarce or absent in the specimens examined. *Pseudolagarobasidium modestum* differs from *P. acaciicola* in having slightly smaller basidiospores. In contrast, *P. subvinosum* has slightly larger basidiospores and more prominent hymenial cystidia compared to *P. modestum* and *P. acaciicola*. Moreover, the aculeus tramal hyphae in *P. modestum* are particularly robust with distinctly thickened, brownish yellow walls whereas in *P. subvinosum* they are only slightly thickened and pale yellow. It is possible that *P. modestum* is simply a small-spored variety of *P. acaciicola* or *P. subvinosum*; however, we propose that *P. modestum* be recognized as a distinct species at this time until more specimens from Mauritius are available for study. Genetic and sequence data also may help resolve this issue.

We concur with van der Byl (1934) and Maas Geesteranus (1974) that *Hydnum ayresii* is a later synonym of *P. modestum* whereas Hjortstam and Larsson (1995) and Nakasone (2001) placed *H. ayresii* in synonymy with *P. subvinosum*.

Pseudolagarobasidium pronum (Berk. & Broome) Nakasone & D.L. Lindner, **comb. nov.** (Figs. 6, 7 and 13)

MycoBank MB 563652

≡ *Hydnum pronum* Berk. & Broome, J. Linn. Soc., Bot. 14(2): 59. 1875.

≡ *Odontia prona* (Berk. & Broome) Rick, Egatea 17: 275. 1932.

= *Hydnum calcareum* Cooke & Massee in Cooke, Grevillea 21(98): 38. 1892.

≡ *Irpex calcareus* (Cooke & Massee) Wakef., Bull. Misc. Inf. Kew 8: 367. 1915.

≡ *Odontia calcarea* (Cooke & Massee) G. Cunn., Trans. Royal Soc. N. Z. 86: 70. 1959.

≡ *Radulodon calcareus* (Cooke & Massee) Jülich, Persoonia 9(4): 466. 1978.

≡ *Pseudolagarobasidium calcareum* (Cooke & Massee) Sheng H. Wu, Acta Bot. Fenn. 142: 112. 1990.

Basidioma resupinate, widely effuse, up to 10×4 cm, 0.3–1 mm thick between aculei, soft, submembranous, spinose with areas between aculei distinct, smooth, subceraceous to cretaceous, hymenial layer flaking off readily, yellowish white (4A2), pale yellow (4A3), orange white (5A2), greyish orange (5B4), Light Ochraceous-Buff, Pinkish Buff, Cinnamon Buff, Avellaneous, Wood Brown, or Drab, no color change with KOH; cracks absent or extensive, revealing white, fibrous context; context white, soft, membranous, fibrous; *hymenial surface* composed of fragile, brittle, soft, cretaceous or chalky aculei, 2–5 aculei per mm, up to 4×0.3 mm, terete to conical, single or fused at base or along entire length, sometimes prone, occasionally reticulate, gradually tapering to an acute or rounded, penicillate, sterile apex; apices white or concolorous with base of aculeus; margin abrupt or gradually thinning out, up to 2.5 mm wide, appressed, sterile, slightly raised, velvety, white, yellowish white (4A2) to pale yellow (4A3), with fibrillose or fimbriate edges.

Hyphal system dimitic with clamped generative and aseptate microbinding hyphae. *Aculei* composed of non-agglutinated tramal hyphae arranged in a fascicle with embedded tramal cystidia curving into hymenium, at apex terminal hyphae undifferentiated, smooth; tramal hyphae 2–5 μm diam, clamped, sparingly branched, even, walls hyaline to pale yellow, thin to 1 μm thick, smooth or encrusted with oil-like particles, cyanophilous. *Subiculum* composed of two layers filled with small, yellowish brown, oil-like particles that dissolve in KOH: (a) basal layer next to substrate 100–215 μm thick, dense, composed of subicular hyphae arranged more or less parallel to substrate, often collapsed, compressed, partially agglutinated, intermixed with microbinding hyphae, (b) hyphae curving away from substrate to form an upper, open, loose tissue of non-agglutinated subicular and microbinding hyphae; subicular hyphae 2–5 μm diam, clamped, moderately branched, even, walls hyaline, thin, smooth or encrusted with oil-like particles, cyanophilous; microbinding hyphae observed in subiculum and at the base of aculei, 0.5–2 μm diam, aseptate, sparingly to frequently branched, lumen narrow or lacking, walls hyaline, thick, smooth, nonstaining. *Subhymenium* up to 80 μm thick, composed of irregular, short-celled hyphae in a dense, non-agglutinated tissue; subhymenial hyphae 1.5–3 μm diam, clamped, frequently branched, walls hyaline, thin, smooth. *Hymenium* up to 35 μm thick, a dense palisade of cystidia and basidia. *Cystidia* of two types: (a) tramal cystidia abundant, arising from aculei trama, subiculum, and subhymenium, embedded or slightly protruding, broadly cylindrical, clavate, or obclavate, sometimes strangulated, often with a distinct stalk, apex obtuse, occasionally papillate or branched, 40–70(−105)×5.5–10 μm, tapering to 2–4.5 μm diam at base, with a basal clamp, homogenous contents staining deeply in phloxine and cotton blue, walls hyaline, thin, finely encrusted with oil-like particles, cyanophilous; (b) hymenial cystidia numerous, arising from upper subhymenium, broadly clavate, obclavate or subfusiform, , apex obtuse, 16–30×8–9 μm, with a basal clamp, contents and walls as described for tramal cystidia. *Basidia* clavate, often stalked, 15–28×5–7 μm, clamped at base, walls hyaline, thin, finely encrusted with oil-like particles, 4-sterigmate. *Basidiospores* subglobose to broadly ellipsoid with a small, distinct apiculus, 4–5.5×3–3.7(−4.3) μm, averages of four specimens 4.3–5.1×3.3–3.6 μm, Q=1.3–1.4, walls hyaline, thin, smooth, weakly cyanophilous, not reacting in Melzer's reagent. Arthroconidia 4–20×2–4 μm, present in cultures and sometimes in basidiomata (Maekawa and Hasebe 2002).

Habitat and distribution: Saprophytic, rarely pathogenic, on wood and bark of angiosperms; known from mainland China (Wu 2008), Taiwan, Japan, Sri Lanka, Malaysia, Australia, and Sierra Leone.

Specimens examined (as *H. calcareum* or *P. calcareum* except as noted): AUSTRALIA, New South Wales, Blue Mountains, Katoomba, 1914, W.N. Cheesman, K(M)62576 (K); Victoria, Kangaroo ground, on fallen rotten trunks, 12 July 1953, E.M. Davies 3643, K(M)56910 (K); Victoria, Kurrumburra, Martin 1027, K(M)56909 (K, **holotype** of *H. calcareum*; NY, **isotypes** NY00072514, NY00776159); Western Australia, Kununurra, on *L. leucocephala*, 5 March 1993, R.G. Shivas, PERTH 02340968 and 1986, R.G. Shivas PERTH 00734527 (PERTH) as *Pirex subvinosus*. CEYLON (Sri Lanka), Central Province, December 1868, G.H.K. Thwaites 975, K(M)167192 (K, **holotype** of *H. pronum*). JAPAN, Okinawa Prefecture, Ishigaki City, Nakura, on hardwood (bark), 19 September 1991, T. Hattori, TFM–F–16295 (TFM); Irimote Island, Nakama River, on hardwood (bark), 24 September 1993, T. Hattori, TFM–F–16917 (TFM).

MALAYSIA, Selangor, Kuala Lumpur, Weld Hill, on wood of angiosperm, 16 January 1920, M. Noor 5576, K(M)62577 (K). SIERRA LEONE, Njala, Kori, on dead branch of *Cathormion dinklagei* Hutch. & Dandy, 22 October 1952, F.C. Deighton, M4898, IMI 51684, K(M)62574 (K). TAIWAN. Nantou, Sun-Moon Lake, alt. 800 m, on branch of *Castanopsis kusanoi* Hayata, 26 October 1988, S.-H. Wu 881026–18 (H).

Pseudolagarobasidium pronum is characterized by soft, brittle, cretaceous or chalky aculei, microbinding hyphae, and small basidiospores. It has the softest texture in the genus, and unlike other species, the microbinding hyphae are easily observed. Although Maekawa and Hasebe (2002) reported the presence of arthroconidia in many specimens of *P. pronum* from China and Japan, we observed arthroconidia in only one specimen from Japan, TFM–F–16917. *Pseudolagarobasidium pronum* is mostly likely to be confused with *P. subvinosum* because of an overlap in basidiospore size. However, the lighter colored, softer, chalky basidiomata and microbinding hyphae of *P. pronum* can be used to distinguish it from the darker colored *P. subvinosum*. Sequence analyses of the nLSU show a close relationship between *P. pronum* and *P. subvinosum* (Hallenberg et al. 2008). *Pseudolagarobasidium pusillum*, also from Western Australia, has much smaller basidiospores.

Pseudolagarobasidium pronum is widely distributed across three continents, Africa, Asia, and Australia. For other descriptions and illustrations, see Jülich (1978), Maekawa and Hasebe (2002), Nakasone (2001), Reid (1955), Wakefield (1915), and Wu (1990). Maekawa and Hasebe (2002) also studied cultures and determined that *P. pronum* has a tetrapolar mating system.

The hymenium of the holotype and isotype specimens of *H. calcareum* is poorly preserved; no basidia and few basidiospores were observed. The holotype of *H. pronum* is in better condition with dark-colored areas on the aculei which indicate bruising or improper drying. Maas Geesteranus (1974) provides a brief description of the *H. pronum* holotype, but basidiospores were not observed. Despite the condition of the types, there can be no doubt that *H. pronum* and *H. calcareum* are conspecific.

Shivas and Brown (1989) reported that *Pirex subvinosum* is associated with a dieback of *L. leucocephala* in Western Australia; however, we identified their specimen, PERTH 00734527, as *P. pronum* based on basidioma texture and presence of microbinding hyphae in the subiculum. Although no basidia or basidiospores were observed, another specimen collected in 1993 from the same area and host species, PERTH 02340968, has basidiospores typical for *P. pronum*.

Pseudolagarobasidium pusillum Nakasone & D.L. Lindner, **sp. nov.** (Figs. 8 and 14)

MycoBank MB 563654

Etymology: Refers to the small basidiospores.

Differt Pseudolagarobasidiomate speciebus basidiosporis pusillis (3.4–)3.6–4.3(−4.7)×2.9–3.2(−3.6) μm.

Basidioma resupinate, widely effuse, thin, up to 225 μm thick between aculei, spinose with distinct, smooth areas between aculei, occasionally with large, knobby structures bearing aculei, Buffy Brown, greyish orange (5B4), at first dark brown in KOH or water then fading; cracks scattered; *hymenial surface* composed of fragile, subceraceous to membranous aculei, up to 3 aculei per mm, up to 3 mm long, mostly terete to conical, sometimes compressed or fused laterally, smooth, occasionally with warty outgrowths, gradually tapering to a subacute, sterile apex, apices cream-colored or concolorous with base of aculeus; margin not observed.

Hyphal system dimitic with clamped generative and aseptate microbinding hyphae; microbinding hyphae abundant in mycelial mats embedded in substrate, 0.5–2 μm diam, aseptate, frequently branched at right angles, walls hyaline, thick, smooth. *Aculei* composed of a core of non-agglutinated, distinct tramal hyphae arranged more or less parallel and embedded cystidia that curve into hymenium, at apex terminal hyphae smooth, undifferentiated; tramal hyphae 2.5–5 μm diam, clamped, sparingly branched, even, walls hyaline to yellow, up to 0.5 μm thick, smooth, cyanophilous. *Subiculum* up to 180 μm thick, composed of a dense, agglutinated tissue of distinct hyphae arranged more or less parallel to substrate, then hyphae ascending to form a less dense tissue of intertwining hyphae and cystidia; subicular hyphae 1.5–5 μm diam, nodose septate, moderately branched, even, walls hyaline to light brown, slightly thick, rarely thick, coated with a thin layer of oil-like particles (observed only in water mounts), cyanophilous. *Subhymenium* up to 35 μm thick, a dense, compact tissue of partially agglutinated, often indistinct, sometimes collapsed, short-celled hyphae and cystidia; subhymenial hyphae 2–3.5 μm diam, clamped, frequently branched, short-celled, walls thin, hyaline to pale yellow, smooth. *Hymenium* up to 30 μm thick, composed of cystidia and basidia. *Cystidia* of two types: (1) tramal cystidia originating in subiculum and aculei trama, embedded or barely protruding, clavate to obclavate, apices subacute to obtuse, rounded, 48–95×8.5–10 μm, with a basal clamp, homogenous contents staining dark pink in phloxine and dark blue in cotton blue, sulfovanillin negative, walls hyaline, thin, cyanophilous; (2) hymenial cystidia arising from subhymenium and hymenium, cylindrical, clavate, fusiform to subfusiform, 18–30×6–8 μm, clamped at base, contents and walls as described for tramal cystidia. *Basidia* clavate, 17–23×4.5–5 μm, clamped at base, 4-sterigmate, walls distinct, hyaline, slightly thick, smooth, cyanophilous. *Basidiospores* broadly ellipsoid, with a small, distinct apiculus, (3.4–)3.6–4.3(−4.7)×2.9–3.2(−3.6) μm, average 3.8±0.3×3.1±0.2 μm, Q=1.2, walls hyaline, slightly thickened, smooth, cyanophilous, not reacting in Melzer's reagent.

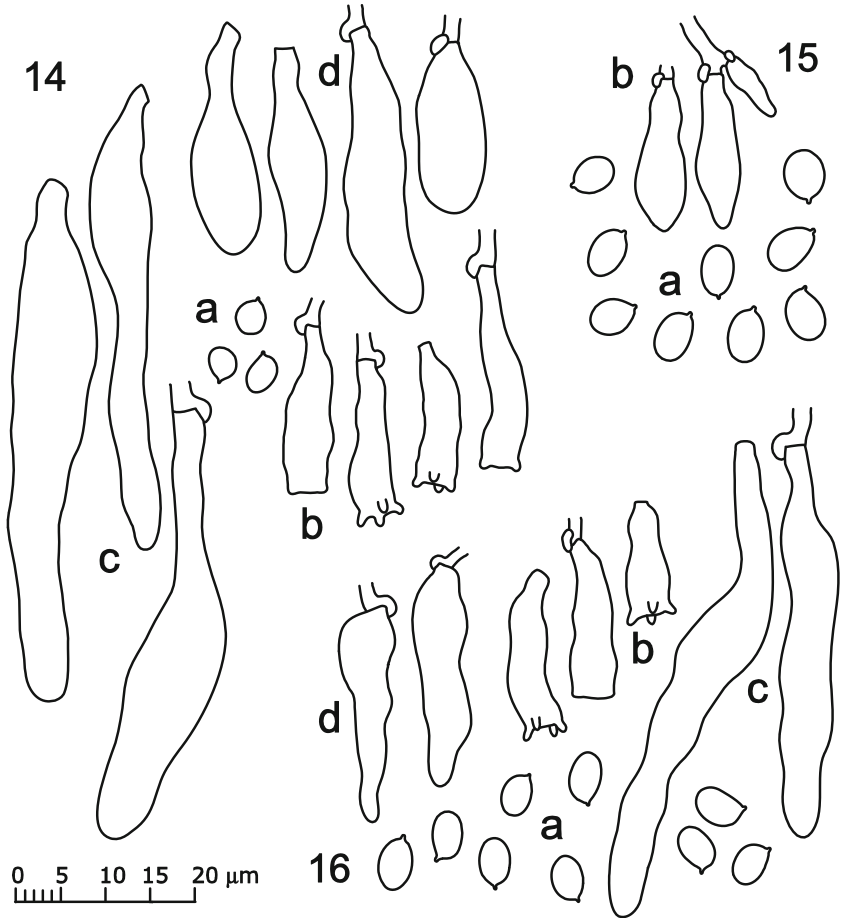


Fig. 14 Microscopic elements of *Pseudolagarobasidium pusillum* (holotype, PERTH 02340925) **a** Basidiospores; **b** Basidia; **c** Tramal cystidium; **d** Hymenial cystidia

Fig. 15 Microscopic elements of *Hydnum subvinosum* (holotype, K(M)56911) **a** Basidiospores; **b** Hymenial cystidia

Fig. 16 Microscopic elements of *Radulodon venustus* (holotype, K(M)77909) **a** Basidiospores; **b** Basidia; **c** Tramal cystidia; **d** Hymenial cystidia

Habitat and distribution: Saprobic on *Acacia* in Western Australia.

Specimen examined: AUSTRALIA, Western Australia, Kununurra, 15°46′S, 128°44′E, on *Acacia trachycarpa* E. Pritz, 5 March 1993, R.G. Shivas s.n., PERTH 02340925 (PERTH, **holotype**).

Pseudolagarobasidium pusillum is characterized by grayish brown basidiomata, long, terete aculei, and the smallest basidiospores in the genus. *Pseudolagarobasidium pronum* is reported from Western Australia also but has chalky basidiomata, larger basidiospores, and arthroconidia.

Pseudolagarobasidium subvinosum (Berk. & Broome) Sheng H. Wu, Acta Bot. Fenn. 142: 113. 1990. (Fig. 15)

≡ *Hydnum subvinosum* Berk. & Broome, J. Linn. Soc., Bot. 14: 60. 1875.

≡ *Irpex subvinosus* (Berk. & Broome) Petch, Dis. Tea Bush p. 173. 1923.

≡ *Pirex subvinosus* (Berk. & Broome) Hjortstam, Windahlia 17: 58. 1987.

≡ *Radulodon subvinosus* (Berk. & Broome) Stalpers, Folia Cryptogam. Estonica 33: 137. 1998.

= *Irpex colliculosus* Berk. & Broome, J. Linn. Soc., Bot. 14: 61. 1875.

≡ *Xylodon colliculosus* (Berk. & Broome) Kuntze, Rev. Generum Plant. (Leipzig) 3(2): 541. 1898.

= *Pseudolagarobasidium leguminicola* J.C. Jang & T. Chen, Trans. Br. Mycol. Soc. 85(2): 374. 1985.

Basidioma resupinate, widely effuse, thin to moderately thick, up to 600 µm thick between aculei, soft, membranous to subceraceous, spinose to raduloid, occasionally reticulate or sparassoid, often with distinct, smooth, felty or subporose areas between aculei, Light Ochraceous Buff, light brown to brown [6(D–F)(4–6)], purple or violet when fresh, no color change with KOH; cracks scattered, inconspicuous; *hymenial surface* composed of soft, brittle, easily detached aculei, up to 3–4 aculei per mm, up to 3.5×1 mm, small, terete to conical at first, often fused at base or along entire length forming flattened raduloid structures, smooth, gradually tapering to a subacute or obtuse, penicillate or broadly tufted, cream-colored, sterile apices; margin gradually thinning out, adnate, smooth, felty, cream-colored, irregularly fibrillose to fimbriate.

Hyphal system monomitic with clamped generative hyphae, possibly dimitic with microbinding hyphae observed in mycelia pockets in substrate in one specimen. *Aculei* composed of a dense fascicle of non-agglutinated tramal hyphae with embedded tramal cystidia curving into hymenium, apex with smooth, undifferentiated terminal hyphae; tramal hyphae 2.7–5(−6) µm diam, clamped, sparingly branched, even, walls hyaline to yellow, thin to slightly thickened, occasionally up to 1 µm thick, coated with a thin layer of oil-like particles that dissolve readily in KOH, cyanophilous. *Subiculum* up to 500 µm thick, a dense tissue of distinct, non-agglutinated hyphae oriented parallel to substrate, then ascending, forming a less dense trama, with small yellowish brown, oil-like particles that dissolve in KOH embedded throughout; subicular hyphae 3–5.5 µm diam, clamped, moderately branched, even, walls hyaline, yellow, or light brown, slightly thick, rarely thick, coated with a thin layer of oil-like particles. *Subhymenium* thickening, up to 50 µm thick, a tissue of vertically arranged, frequently branched, short-celled hyphae and cystidia; subhymenial hyphae 3–3.5 µm diam, clamped, frequently branched, short-celled, walls hyaline, thin, with a fine coating of oil-like particles, weakly cyanophilous. *Hymenium* up to 40 µm thick, a palisade of cystidia and basidia. *Cystidia* of two types: (a) tramal cystidia numerous, originating in subiculum or aculei trama, embedded or barely protruding, cylindrical, obclavate to clavate, apex obtuse, rounded or papillate, with or without a stalk, 47–90×6–10 µm, with a basal clamp connection, homogenous contents staining dark pink in phloxine and dark blue in cotton blue, walls hyaline, thin, with a fine coating of oil-like particles, weakly cyanophilous; (b) hymenial cystidia arising from subhymenium and hymenium, broadly fusiform, obclavate or clavate, apex obtuse to subacute, sometimes stalked, 16–40(−50)×5–11 µm, clamped at base, contents and walls as described for tramal cystidia. *Basidia* clavate, (16–)21–31×(4.5–)5–6.5 µm, clamped at base, 4-sterigmate, walls distinct, hyaline, thin, with a fine coating of oil-like particles, weakly cyanophilous. *Basidiospores* ellipsoid to broadly ellipsoid, with a small, distinct apiculus, 5–6(−6.5)×(3–)3.5–4.5(−5) µm, averages of five collections 5.4–6.1×3.9–4.3 µm, Q=1.3–1.5, walls hyaline, thin to slightly thick, smooth, weakly cyanophilous, not reacting in Melzer's reagent. Arthroconidia produced in basidiomata and cultures, 10–13×4–7 µm (Jang and Chen 1985).

Habitat and distribution: Saprobic or parasitic, on bark and wood of various angiosperms; known from Taiwan, Sri Lanka, India, and Zaire.

Specimens examined: INDIA, Kerala, on corticate hardwood, 9 November 1984, J.K. Sharma no. 52, K(M)56912 (K). CEYLON (Sri Lanka), Peradeniya, November 1867, G. H.K. T(hwaites), K(M)56911 (K, **holotype** of *H. subvinosum*; BPI US0260529, **isotype**); no location, on dead wood, G.H.K. Thwaites 366, K(M)167189 (K, **holotype** of *I. colliculosus*). TAIWAN, Hualien, Hsiulin, Hsiang, on branch of *L. leucocephala*, September 1986, S.-H. Wu 8609 (H). BELGIAN CONGO (Zaire), Kisantu, 23 April 1910, H. Vanderyst, (BPI, US0263676; S, F180882); Belge, 23 April 1910, H. Vanderyst, F180883 (S).

Pseudolagarobasidium subvinosum can be distinguished from other species in the genus by its large, ellipsoid basidiospores. Although microbinding hyphae were found in the substrate, not in the basidioma, of the holotype collection, it is probable that these hyphae occur in other specimens, too. Herbarium specimens are uniformly a shade of brown, but fresh basidiomata were described as deep purple, pale lavender, and blue by Petch (1923) and deep violet or purplish by Jang and Chen (1985). Although *P. subvinosum* is often confused with *P. pronum*, the basidiomata of the former are usually darker brown and lack microbinding hyphae whereas in the latter they are softer, chalky, off-white to light brown, with microbinding hyphae in the subiculum. Basidiospores of *P. subvinosum*, on average, are larger than those of *P. pronum* although there is an overlap in size.

The holotype of *H. subvinosum* at K is in better condition than the isotype at BPI, but basidiospores were abundant in both specimens. Microbinding hyphae were found in pockets of white tissue in the substrate directly beneath the basidioma of the holotype. The holotype of *Irpex colliculosus* is in good condition although few basidiospores were observed. The average size, 6.1×4.2 µm (*n*=14), Q=1.4, is typical for *P. subvinosum*. See Maas Geesteranus (1974) for brief descriptions of holotypes of *H. subvinosum* and *I. colliculosus*.

We follow Wu (1990) who placed *P. leguminicola* in synonymy under *P. subvinosum*. Hjortstam and Larsson (1995) and Nakasone (2001) synonymized *Hydnum ayresii* with *H. subvinosum*; however, we propose that *H. ayresii*, a later synonym of *Irpex modestus*, be recognized as a distinct species. See discussion under *P. modestum*.

See Jang and Chen (1985), Petch (1923), Sankaran and Sharma (1986), and Wu (1990) for additional descriptions and illustrations of *P. subvinosum*. Culture descriptions are provided by Jang and Chen (1985) and Sankaran and Sharma (1986). Chang and Chen (1984) report that *P. subvinosum* has a tetrapolar mating type system. *Pseudolagarobasidium subvinosum* is pathogenic on *L. leucocephala* causing a stem canker in India (Sankaran and Sharma 1986) and a stem and root rot in Taiwan (Jang and Chen 1985). Earlier, Petch (1923) described *P. subvinosum* on diseased roots of *Acacia decurrens* Willd., *Tephrosia candida* DC., and *Camellia sinensis* (L.) Kuntze in Sri Lanka. Although *Pirex subvinosus*, PERTH 734527, was reported from Australia by Shivas and Brown (1989) to cause a stem canker of *L. leucocephala*, we re-identified their specimen as *P. pronum*; for further discussion see *P. pronum*.

Pseudolagarobasidium venustum (Hjortstam & Ryvarden) Nakasone & D.L. Lindner, **comb. nov.** (Figs. 9, 10 and 16)

MycoBank MB 563655

≡ *Radulodon venustus* Hjortstam & Ryvarden, Mycotaxon 74: 250. 2000.

Basidioma resupinate, widely effuse, thin, up to 300 μm thick between aculei, ceraceous, subceraceous, or submembranous, odontioid to raduloid with distinct, smooth or subporose areas between aculei, pale orange (5A3), greyish orange (5B4), Light Buff, Warm Buff, Light Ochraceous Buff, Cream-Buff, or Pinkish Buff, bruised areas light brown; no color change with KOH; cracks numerous, exposing a white, fibrous context; *hymenial surface* composed of aculei, up to 4 aculei per mm, up to 3 mm long, small, terete to conical, smooth, then gradually tapering to a subacute apex, apices white to cream-colored, often fused at base or along entire length to form flattened, raduloid structures, sometimes prone, often developing abundant, tiny warts or knobs along aculei surface; margin adnate, abrupt or rapidly thinning out, short fibrillose, pale yellow (4A3) to orange white (5A2).

Hyphal system monomitic with clamped generative hyphae, possibly dimitic—microbinding hyphae observed in substrate of one specimen. *Aculei* a dense fascicle of non-agglutinated tramal hyphae with tramal cystidia curving into hymenium, at apex terminal hyphae undifferentiated, smooth; tramal hyphae 2–5.5 μm diam, clamped, sparingly branched, even, walls hyaline, slightly thickened, smooth, weakly cyanophilous. *Subiculum* up to 250 μm thick, a dense, partially agglutinated tissue with hyphae oriented parallel to substrate, then ascending to form a less dense tissue of primarily non-agglutinated, vertical hyphae and embedded tramal cystidia; subicular hyphae 3–5.5 μm diam, clamped, moderately branched, walls hyaline, up to 0.7 μm thick, smooth, weakly cyanophilous. *Subhymenium* up to 30 μm thick, a dense tissue of partially agglutinated, indistinct hyphae; subhymenial hyphae 2–4 μm diam, clamped, frequently branched, short-celled, walls hyaline, thin, smooth. *Hymenium* up to 20 μm thick, a dense palisade of cystidia and basidia. *Cystidia* of two types: (a) tramal cystidia numerous, originating in upper subiculum and aculei trama, embedded or slightly protruding, cylindrical, subfusiform, or obclavate, tapering to a subacute or obtuse apex, 40–95×6–9 μm, with a basal clamp connection, contents homogenous, staining dark pink in phloxine and dark blue in cotton blue, walls hyaline, thin to slightly thickened, smooth, weakly cyanophilous; (b) hymenial cystidia arising in subhymenium and hymenium, cylindrical, broadly fusiform, or obclavate, 20–35×4.5–8 μm, clamped at base, contents and walls similar to tramal cystidia. *Basidia* clavate, occasionally slightly constricted, (10–)15–21(−27)×(4–)5–6.3 μm, clamped at base, 4-sterigmate, walls hyaline, thin, smooth. *Basidiospores* broadly ellipsoid, with an inconspicuous apiculus, (3.5–)4–5(−5.5)×(2.8–)3.2–3.7(−4.3) μm, averages of two specimens 4.2–4.9×3.4–3.5 μm, Q=1.2–1.4, walls hyaline, thin, smooth, weakly cyanophilous, not reacting in Melzer's reagent.

Habitat and distribution: Saprobic on bark and wood of palm and angiosperms; known from Brazil and Colombia.

Specimens examined: BRAZIL, São Paulo, Reg. Santos, Cananeia, Ilha do Cardoso, on bark of palm, 2 February 1987, D. Pegler, K. Hjortstam, L. Ryvarden, Hjortstam 16838, K(M)77909 (K, **holotype**); 2–5 February 1987, D. Pegler, K. Hjortstam, L. Ryvarden, LR 24717 (O; K, K(M) 129182). COLOMBIA, Dept. Magdalena, Parque Nacional Natural Tayrona, Estación Cañaveral, 0–30 m, 17–19 June 1978, L. Ryvarden 15910/B (O).

Pseudolagarobasidium venustum is characterized by pale yellow to orange basidiomata, aculei studded with knobs or warts, and lacking oil-like particles in the context. Microbinding hyphae were observed only in the substrate under the basidioma of the holotype specimen. It is probable that microbinding hyphae are present in the substrate and basidioma of other collections. It is most similar microscopically to *P. belizense*, which is distinguished by its drab, brownish gray basidioma, smaller aculei, and abundant oil-like particles found throughout the context. *Pseudolagarobasidium venustum* was transferred from *Radulodon* because of the non-agglutinated tramal hyphae in the aculei, abundant tramal cystidia, and lack of oil-like particles in basidiospores.

Taxa not accepted in *Pseudolagarobasidium*

Pseudolagarobasidium concentricum (Cooke & Ellis) Hjortstam, Mycotaxon 54: 190. 1995.

≡ *Radulum concentricum* Cooke & Ellis in Cooke, Grevillea 14(69): 13. 1885.

≡ ***Pirex concentricus*** (Cooke & Ellis) Hjortstam & Ryvarden, Mycotaxon 24: 289. 1985.

Pirex concentricus is accepted as the correct name for this species. Its narrowly clavate basidia, lack of cystidia, and narrowly ellipsoid basidiospores precludes *P. concentricus* from *Pseudolagarobasidium*. Moreover, in phylogenetic studies, *P. concentricus* is placed with *Terana caerulea* (Schrad. ex Lam.) Kuntze in a clade that is distantly related to *Pseudolagarobasidium* (Hallenberg et al. 2008; Moreno et al. 2011). See Gilbertson (1964), Hallenberg and Hjortstam (1985), and Kropp and Nakasone (1985) for descriptions and illustrations of *P. concentricus*.

Pseudolagarobasidium ochroleucum (Lév.) Hjortstam & K.H. Larss., Windahlia 21: 52. 1995, invalid.

≡ *Sistotrema ochroleucum* Lév., Ann. Sci. Nat., Bot., ser. 3, 5: 145. 1846.

= ***Lenzites acutus*** Berk. in Hooker, London J. Bot. 1: 146. 1842.

Basidioma effuse, 26×5 mm, coriaceous, hydnaceous, light brown [6D(4–6)]; aculei coarse, large, flattened, single or fused, up to 16×6 mm, smooth or studded with a few odontioid structures; context brown; margin not observed. *Hyphal system* trimitic with clamped generative, aseptate skeletal, and aseptate binding hyphae. Generative hyphae indistinct, irregular, clamped, thin-walled, staining in phloxine. Skeletal hyphae present in aculeus trama, terminating in hymenium, 4–5 µm diam, aseptate, unbranched, walls yellow, up to 2.5 µm thick, smooth. Binding hyphae 2–4 µm diam, aseptate, frequently branched, rigid, walls yellow, up to 1.5 µm thick, smooth. No hymenium, basidia, or basidiospores observed.

Specimens examined: (INDIA), Bombay, Polydore Roux (K, K(M)167194; BPI, US0262114, **isotypes** of *S. ochroleucum*).

Because of its coriaceous texture and trimitic hyphal system, *S. ochroleucum* is not congeneric with *Pseudolagarobasidium*. The isotypes examined were fragments, so it was not possible to determine the true form and structure of the basidioma. We follow Ryvarden (1981) who examined the holotype specimen of *S. ochroleucum* at PC and placed it in synonymy with *L. acutus*.

Discussion

Pseudolagarobasidium is established as a monophyletic genus based on morphological and molecular data. The seven accepted species are distributed widely in Africa, Asia, Australia, and Central and South America. Most species are known from fewer than three collections; only *P. pronum* and *P. subvinosum* can be considered not uncommon. The varied nutritional modes associated with species of *Pseudolagarobasidium*, from saprobic, parasitic, and endophytic, are noteworthy. Species of *Pseudolagarobasidium* treated herein are saprobes although some can be described as facultative pathogens. Endophytic taxa are known from DNA sequences obtained from healthy stems of *Theobroma cacao* from Brazil and Cameroon (Crozier et al. 2006; Hallenberg et al. 2008) and leaves of *Xylocarpus granatum* König from Thailand (Chokpaiboon et al. 2010).

The ITS sequence of *P. acaciicola* UDSC-RCK, AM849050, isolated from soil in India, differs significantly from other *P. acaciicola* sequences and may be a different species. Our phylogenetic results also suggest that *Antrodiella albocinnamomea* (FJ613650) and the unidentified taxon 'Fungal sp. ref 1' (EU834826) should be classified in *Cerrena*.

Both nLSU and ITS phylogenetic analyses provide strong evidence that *Pseudolagarobasidium* is a monophyletic genus in a *Polyporales* clade that includes *Radulodon*, *Cerrena* Gray, and *Spongipellis* (Hallenberg et al. 2008; Lee and Lim 2010; Moreno et al. 2011). The four genera are distinct and readily recognizable displaying a wide range in habit (effuse to pileate), hymenophore configuration (odontioid to poroid), and texture (soft and fragile to tough and cartilaginous). They have in common basidia with four sterigmata and hyaline basidiospores that do not react in Melzer's reagent.

Pseudolagarobasidium is most similar to *Radulodon* based on morphology and molecular data. Stalpers (1998) considered *Pseudolagarobasidium* a synonym of *Radulodon* based on overall similarities of the generic types. Later, Nakasone (2001) restricted *Radulodon* to species with a dimitic hyphal system. In this study, we discovered that most species of *Pseudolagarobasidium* are dimitic also, developing microbinding hyphae in addition to clamped generative hyphae. Microbinding hyphae, however, are scarce or apparently absent in most specimens of *P. subvinosum* and *P. venustus*. Although there is some overlap, *Radulodon* basidiomata are ceraceous or cartilaginous with mostly agglutinated, hyaline hyphae whereas in *Pseudolagarobasidium* they are soft to subceraceous and fragile or brittle with mostly non-agglutinated, hyaline to light brown hyphae in the aculeus trama and subiculum. At the microscopic level, *Radulodon* species develop only hymenial cystidia, hyphidia maybe present or absent, and the acyanophilous, slightly thick-walled basidiospores usually contain an oil-like globule. In contrast, *Pseudolagarobasidium* species develop abundant tramal and hymenial cystidia and lack hyphidia. Basidiospores in *Pseudolagarobasidium* lack oil-like particles and may have thin or slightly thickened walls that are acyanophilous or weakly cyanophilous.

As of December 2011, MycoBank (Crous et al. 2004) included 13 species of *Radulodon* of which five are provisionally accepted: *R. americanus* Ryvarden (generic type), *R. casearium* (Cooke & Massee) Jülich, *R. cirrhatinus* Hjortstam & Spooner, *R. erikssonii* Ryvarden, and *R. revolubilis* Hjortstam & Ryvarden. This list differs slightly from Nakasone's (2001) treatment which included the first four taxa and *R. calcareus*. With our current understanding of the generic circumscription of *Radulodon*, we consider *R. americanus*, *R. casearium*, and *R. erikssonii* to comprise *Radulodon* sensu stricto. Preliminary ITS sequence data, however, indicate that *R. americanus* and *R. erikssonii* are conspecific (K.-H. Larsson, pers. comm.). *Radulodon* s. str. species have a ceraceous to subceraceous basidioma, spinose hymenophore, dimitic hyphal system with clamped generative and aseptate microbinding hyphae, simple hyphidia, and slightly thick-walled, acyanophilous basidiospores containing a refractive, oil-like globule.

The placement *R. cirrhatinus* and *R. revolubilis* remain unresolved. *Radulodon cirrhatinus* from Malaysia appears to straddle two genera. It has non-agglutinated tissues, long aculei, and small, subglobose basidiospores with cyanophilous walls, as in *Pseudolagarobasidium*, but oil-like globules in the basidiospores which are characteristic of *Radulodon*. It has a monomitic hyphal system (Hjortstam et al. 1990), for the skeletal hyphae described by Nakasone (2001) are probably better characterized as sclerified generative hyphae. Interestingly, it occurs in southeast Asia where several *Pseudolagarobasidium* species are present. *Radulodon revolubilis* from Venezuela has a resupinate, cartilaginous basidioma with a sublamellate to irpicoid or lacerate hymenophore, monomitic hyphal system, and small, subglobose basidiospores with slightly thickened, cyanophilous walls. This taxon appears to be congeneric with *Spongipellis* but more study is required before a formal transfer is proposed.

Radulomyces M.P. Christ. and *Sarcodontia* Schulzer are similar to *Pseudolagarobasidium* in developing resupinate basidiomata, aculei, clamped hyphae, and globose to ellipsoid basidiospores. *Radulomyces*, however, is distinguished by its ceraceous, hygrophanous basidiomata, large basidia and basidiospores, hyphidia, and lack of cystidia. In addition, its hyphae, basidia and basidiospores are filled with oil-like particles. Molecular analyses of the nLSU sequences show that *Radulomyces* is closely related to *Typhula* (Pers.) Fr. and *Macrotyphula* R.H. Petersen in the *Pterulaceae* Corner (Larsson et al. 2004). The generic type of *Sarcodontia*, *S. crocea* (Schwein.) Kotlaba, has a distinctive, nearly fleshy basidioma bearing ceraceous, slender, yellow to brown aculei 5–15 mm long. At the microscopic level, hyphae in the subiculum are thick-walled and terminally inflated, cystidia are absent, and the slightly thick-walled basidiospores contain oil-like particles. It is associated with cultivated apple trees and other angiosperms. Molecular sequence analyses place it in the *Meruliaceae* Rea (Larsson 2007).

Acknowledgments We thank the curators of BPI, H, K, NY, O, PERTH, PREM, S, and TFM for their assistance in arranging specimen loans. Kyah Norton assisted in obtaining DNA sequences of *P. belizense*. Fieldwork in Belize was made possible by a grant from the National Science Foundation, Biodiversity Surveys and Inventories Program to Dr. T.J. Baroni, the State University of New York, College at Cortland (DEB-0103621), in collaboration with Dr. D.J. Lodge and the Center for Forest Mycology Research, Northern Research Station, U.S. Forest Service. Dr. Lodge helped coordinate logistical support for the field work in Belize, and the British Forces of Belize provided airlift transportation to Doyle's Delight Peak in the Maya Mountains. Alan Whitelaw, the commanding officer of the Belize Forces, and Sharon Matola, Director of the Belize Zoo, were responsible for making the expeditions possible. Several other individuals with government and nongovernmental agencies in Belize are kindly acknowledged for their help and guidance: Hector Mai, John Pinelo, and Natalie Rosado of The Conservation Division, Belize Forestry Department, Belmopan; and Celso Poot, Station Manager of the Tropical Education Center in Belize. Drs. S.P. Gorjón and J. Stalpers reviewed an earlier draft of the manuscript.

References

Baroni TJ, Franco-Molano AE, Lodge DJ, Lindner DL, Horak E, Hofstetter V (2007) *Arthromyces* and *Blastosporella*, two new genera of conidia-producing lyophylloid agarics (*Agaricales*, *Basidiomycota*) from the neotropics. Mycol Res 111:572–580. doi:10.1016/j.mycres.2007.03.007

Baroni TJ, Bocusis N, Lodge DJ, Lindner DL (2008) A new species of *Pleurocollybia* (*Tricholomataceae*: *Agaricales*; Basidiomycetes) from Belize. Mycotaxon 103:353–363

Chang J-C, Chen T (1984) Two kinds of diseases of *Leucaena leucocephala* in eastern Taiwan. Leucaena Res Rep 5:64–65

Chokpaiboon S, Sommit D, Teerawatananond T, Muangsin N, Bunyapaiboonsri T, Pudhom K (2010) Cytotoxic nor-chamigrane and chamigrane endoperoxides from a basidiomycetous fungus. J Nat Prod 73(5):1005–1007. doi:10.1021/np100103j

Crous PW, Gams W, Stalpers JA, Robert V, Stegehuis G (2004) MycoBank: an online initiative to launch mycology into the 21st century. Stud Mycol 50:19–22. http://www.mycobank.org

Crozier J, Thomas SE, Aime MC, Evans HC, Holmes KA (2006) Molecular characterization of fungal endophytic morphospecies isolated from stems and pods of *Theobroma cacao*. Plant Pathol 55(6):783–791. doi:10.1111/j.1365-3059.2006.01446.x

Gascuel O (1997) BIONJ: an improved version of the NJ algorithm based on a simple model of sequence data. Mol Biol Evol 14:685–695

Gilbertson RL (1964) Resupinate hydnaceous fungi of North America. III. Additional type studies. Paper Mich Acad Sci 49:15–25

Ginns J, Lindner DL, Baroni TJ, Ryvarden L (2010) *Aurantiopileus mayanensis* a new genus and species of polypore (*Polyporales*, *Basidiomycota*) from Belize with connections to existing Asian species. N Am Fungi 5(4):1–10. doi:10.2509/naf2010.005.004

Greslebin AG, Nakasone KK, Rajchenberg M (2004) *Rhizochaete*, a new genus of phanerochaetoid fungi. Mycologia 96(2):260–271

Hallenberg N, Hjortstam K (1985) *Pirex* genus nova (Basidiomycetes, *Corticiaceae*). Mycotaxon 24:287–291

Hallenberg N, Ryberg M, Nilsson HR, Wood AR, Wu S-H (2008) *Pseudolargarobasidium* (*Basidiomycota*): on the reinstatement of a genus of parasitic, saprophytic, and endophytic resupinate fungi. Botany 86:1319–1325

Hjortstam K (1995) Two new genera and some new combinations of corticioid fungi (*Basidiomycotina*, *Aphyllophorales*) from tropical and subtropical areas. Mycotaxon 54:183–193

Hjortstam K, Larsson K-H (1995) Annotated check-list to genera and species of corticioid fungi (*Aphyllophorales*, *Basidiomycotina*) with special regards to tropical and subtropical areas. Windahlia 21:1–75

Hjortstam K, Spooner BM, Oldridge SG (1990) Some *Aphyllophorales* and Heterobasidiomycetes from Sabah, Malaysia. Kew Bull 45:303–322

Jang JC, Chen T (1985) *Pseudolagarobasidium leguminicola* gen. et sp. nov. on *Leucaena* in Taiwan. Trans Br Mycol Soc 85(2):374–377

Jülich W (1978) On some *Aphyllophorales* from Australia. Persoonia 9 (4):453–472

Kirk PM, Cannon PF, Minter DW, Stalpers JA (2008) Ainsworth & Bisby's dictionary of the fungi, 10th edn. CAB International, Wallingford

Kornerup A, Wanscher JH (1978) Methuen handbook of colour, 3rd edn. Eyre Methuen, London

Kotlaba F, Pouzar Z (1964) Preliminary results on the staining of spores and other structures of homobasidiomycetes in cotton blue and its importance for taxonomy. Trans Br Mycol Soc 47(4):653–654

Kropp BR, Nakasone KK (1985) Redisposition of *Radulum concentricum* (*Aphyllophorales*, *Corticiaceae*). Mycotaxon 24:423–429

Larsson K-H (2007) Re-thinking the classification of corticioid fungi. Mycol Res 111:1040–1063

Larsson K-H, Larsson E, Kõljalg U (2004) High phylogenetic diversity among corticioid homobasidiomycetes. Mycol Res 108(9):983–1002

Lee JS, Lim YW (2010) *Cerrena aurantiopora* sp. nov. (*Polyporaceae*) from eastern Asia. Mycologia 102(1):211–216. doi:10.3852/09-048

Lindner DL, Ryvarden L, Baroni TJ (2011) A new species of *Daedalea* (*Basidiomycota*) and a synopsis of core species in *Daedalea sensu stricto*. N Am Fungi 6(4):1–12. doi:10.2509/naf2011.006.004

Maas Geesteranus RA (1974) Studies in the genera *Irpex* and *Steccherinum*. Persoonia 7(4):443–581

Maekawa N, Hasebe K (2002) *Pseudolagarobasidium calcareum*: Japanese records and cultural characteristics. Mycoscience 43:271–275

Moreno G, Blanco M-N, Checa J, Platas G, Peláez F (2011) Taxonomic and phylogenetic revision of three rare irpicoid species within the *Meruliaceae*. Mycol Prog 10:481–491. doi:10.1007/s11557-010-0717-y

Nakasone KK (2001) Taxonomy of the genus *Radulodon*. Harvard Pap Bot 6(1):163–177

Nei M, Kumar S (2000) Molecular evolution and phylogenetics. Oxford University Press, New York

Palmer JM, Lindner DL, Volk TJ (2008) Ectomycorrhizal characterization of an American chestnut (*Castanea dentata*) dominated community in western Wisconsin. Mycorrhiza 19:27–36. doi:10.1007/s00572-008-0200-7

Petch T (1923) Diseases of the tea bush. Macmillan and Co., London

Reid DA (1955) New or interesting records of Australasian basidiomycetes. Kew Bull 10:631–648

Ridgway R (1912) Color standards and color nomenclature, 1st edn. Published by the author, Washington

Ryvarden L (1981) Type studies in the *Polyporaceae* 13. Species described by J.H. Léveille. Mycotaxon 13(1):175–186

Ryvarden L, Aime MC, Baroni TJ (2009) Studies in neotropical polypores 26. A new species of Trametes and revisitation of an old. Synop Fungorum 26:27–32

Sankaran KV, Sharma JK (1986) *Hydnum subvinosum*, a rare parasite on *Leucaena leucocephala* in India. Trans Br Mycol Soc 87(3):401–405

Shivas RG, Brown AGP (1989) Die-back of *Leucaena leucocephala* and the first record of *Pirex subvinosus* from Australia. Australas Plant Pathol 18(2):33–34

Singer R (1986) The *Agaricales* in modern taxonomy, 4th edn. Koeltz Scientific Books, Koenigstein

Stalpers JA (1998) On the genera *Sarcodontia, Radulodon* and *Pseudolagarobasidium*. Folia Cryptog Estonica 33:133–138

Tamura K (1992) Estimation of the number of nucleotide substitutions when there are strong transition-transversion and G + C-content biases. Mol Biol Evol 9:678–687

Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S (2011) MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Mol Biol Evol 28:2731–2739. doi:10.1093/molbev/msr121

Thiers B (2012, continuously updated) Index Herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/ih/

van der Byl PA (1934) Die Suid-Afrikaanse Hydnaceae of Stekelswamme. Ann Univ Stellenbosch, Reeks A, Wis-Natuurk 12(A)(1):1–9 + 11 figures

Wakefield EM (1915) On a collection of fungi from Australia and New Zealand. Bull Misc Inform Kew 8:361–376

Wood AR, Ginns J (2006) A new dieback disease of *Acacia cyclops* in South Africa caused by *Pseudolagarobasidium acaciicola* sp. nov. Can J Bot 84:750–758

Wu S-H (1990) The *Corticiaceae* (Basidiomycetes) subfamilies *Phlebioideae*, *Phanerochaetoideae* and *Hyphodermoideae* in Taiwan. Acta Bot Fenn 142:1–123

Wu S-H (2008) Twenty species of corticioid fungi newly recorded from China. Mycotaxon 104:79–88