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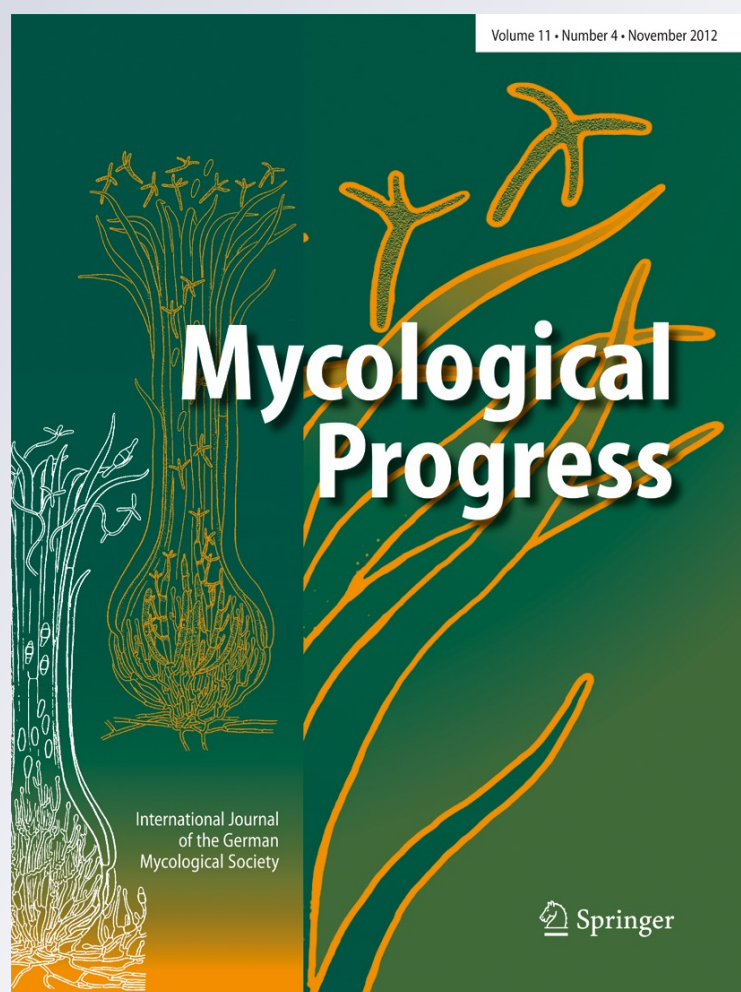
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Two new species of *Pluteus* (*Pluteaceae*, *Agaricales*) from India and additional observations on *Pluteus chrysaegis*

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Abstract Two new species of *Pluteus* collected in Kerala State (India) are described based on morphological and molecular (nrITS) characters. *Pluteus brunneosquamulosus* of sect. *Celluloderma* is characterized by the squamulose, ‘*Lepiota*-like’, pileus, subglobose to broadly ellipsoid spores, cheilocystidia with a long flexuous neck and lageniform or narrowly utriform caulocystidia. *Pluteus velutinus* belongs in sect. *Hispidoderma* and is unique in its shallowly depressed, hygrophanous, orange-brown, \velvety, squamulose pileus, the pleurocystidia very commonly provided with an apical digitate projection up to 10 µm long or tapering towards apex and the pileipellis as a trichoderm or trichohymeniderm. *P. chrysaegis* from India and *P. conizatus* var. *africanus* from Africa are considered synonymous based on morphological and molecular evidence.

Keywords Taxonomy · Kerala · *Hispidoderma* · *Celluloderma* · ITS phylogeny

Introduction

During our continuing study on the agaric family *Pluteaceae* (Basidiomycota, Agaricales) of Kerala State, India, several noteworthy collections belonging to the genus *Pluteus* Fr. were made. It seems that the genus *Pluteus* is particularly diverse in the region as earlier publications

(Pradeep et al. 2002; Pradeep and Vrinda 2005a, b; 2006; 2008) documented 15 species from the State.

Morphological and molecular studies revealed two previously undescribed species: *P. brunneosquamulosus*, belonging to section *Celluloderma* Fayod and *P. velutinus* of section *Hispidoderma* Fayod which also occurs in northern Japan. Molecular data from new collections of *P. chrysaegis* suggest that this rarely recorded species is probably widely distributed in the tropics and it is the same taxon which is also known under the name *Pluteus conizatus* var. *africanus*. Morphological, molecular and phylogenetic details of these three species are discussed in detail in the present article.

Materials and methods

Conventional morphology based taxonomic methods were employed for this study (Pradeep et al. 2002). Colour notations refer to Kornerup & Wanscher (1978). Descriptive terms used in the descriptions follow Vellinga (1988). All Indian holotypes are deposited in the Herbarium of Royal Botanic Gardens, Kew (K) and isotypes at the Mycological Herbarium of Tropical Botanic Garden and Research Institute (TBGT).

Standard procedures for DNA isolation, PCR and sequencing were applied (Justo et al. 2011a, b). The ITS region was amplified using primer pairs ITS1-F and ITS4 (Gardes and Bruns 1993; White et al. 1990). ITS sequences generated by Justo et al. (2011a, b) and additional GenBank sequences were used for the phylogenetic analyses. Sequences were aligned using MAFFT version 6 (<http://mafft.cbrc.jp/alignment/server/>; Katoh and Toh 2008) with the Q-INS-i option. The alignments were then examined and manually corrected using MacClade 4.05 (Maddison and

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Maddison 2002). Alignments have been deposited in TreeBASE (<http://purl.org/phylo/treebase/phyloids/study/TB2:S11974>). A Maximum Likelihood analysis was run using the RAxML servers (<http://phylobench.vital-it.ch/raxml-bb/index.php>; Stamatakis et al. 2008).

Taxonomy

Pluteus brunneosquamulosus Pradeep & Vrinda **sp. nov.**
Figs. 1, 6a–c

Mycobank MB563402

Pileus 8–26 mm latus, convexus vel applanatus, brunneus, squamulosus. Lamellae liberae, confertae, albae ad roseae. Stipes 5–27×1–2.5 mm, albidus, centralis, cylindricus. Sporae 4.5–7×4.5–6 µm, subglobose vel ellipsoideae. Basidia 21–28.5×6–6.5 µm, clavata, 4-sporigera. Cheilocystidia 22.5–57.5×7.5–10 µm, lageniformia. Pleurocystidia 42–73×11.5–16 µm, hyalina. Trama hymenophoralis bilateralis, inversa. Cuticula pilei cellulis, clavatis vel vesiculosus. Caulocystidia 16–73×8–16.5 µm, versiformia. Fibulae absentes.

Basidiomes small to medium-sized, thin. Pileus 8–26 mm in diameter, convex when young becoming plano-convex to applanate with a low umbo or with a low depression at the

centre; surface uniform with predominant brown colours ['brown' (6E4), 'teak brown' (6E5/6 F5)] in buds which are smooth and entire, becoming darker at the disc ['brownish beige' (6E3), 'café-au-lait' (6D3), 'burnt umber' (6 F6), 'dark brown' (6 F7), 'brownish grey' (6 F8)] and paler elsewhere; splits or breaks in concentric fashion in dry weather exposing the underlying white context to appear squamulose except at the disc (appears like a *Lepiota*) or washed off during heavy rain to become pellucid–striate, moist or dry; margin straight to slightly uplifted in old ones, entire to incised. Lamellae free, white, 'orange white' (5A2), 'yellowish orange' (5A3) to pink, up to 5 mm wide, crowded with lamellulae of different lengths, edge concolourous to sides, entire. Stipe 5–27×1–2.5 mm, central, cylindric, curved, equal or narrowly tapering down, hollow; surface silky white, smooth except at extreme base which is greyish and pruinose. Context in pileus and stipe white, thin. Basal mycelium none. Odour mild not distinctive. Spore print pink.

Spores 4.5–7×4.5–6 µm, avL=5.4 µm, avW=4.8 µm, Q=(1) 1.05–1.33, avQ=1.16, subglobose to broadly ellipsoid, a few ellipsoid, thick-walled with a guttule. Basidia 21–28.5×6–6.5 µm, clavate, 4-spored, thin-walled, hyaline. Lamella edge heteromorphous with scattered cheilocystidia. Cheilocystidia 22.5–57.5×7.5–10 µm, lageniform with a stalk and a long (often flexuous) neck with obtuse apices,

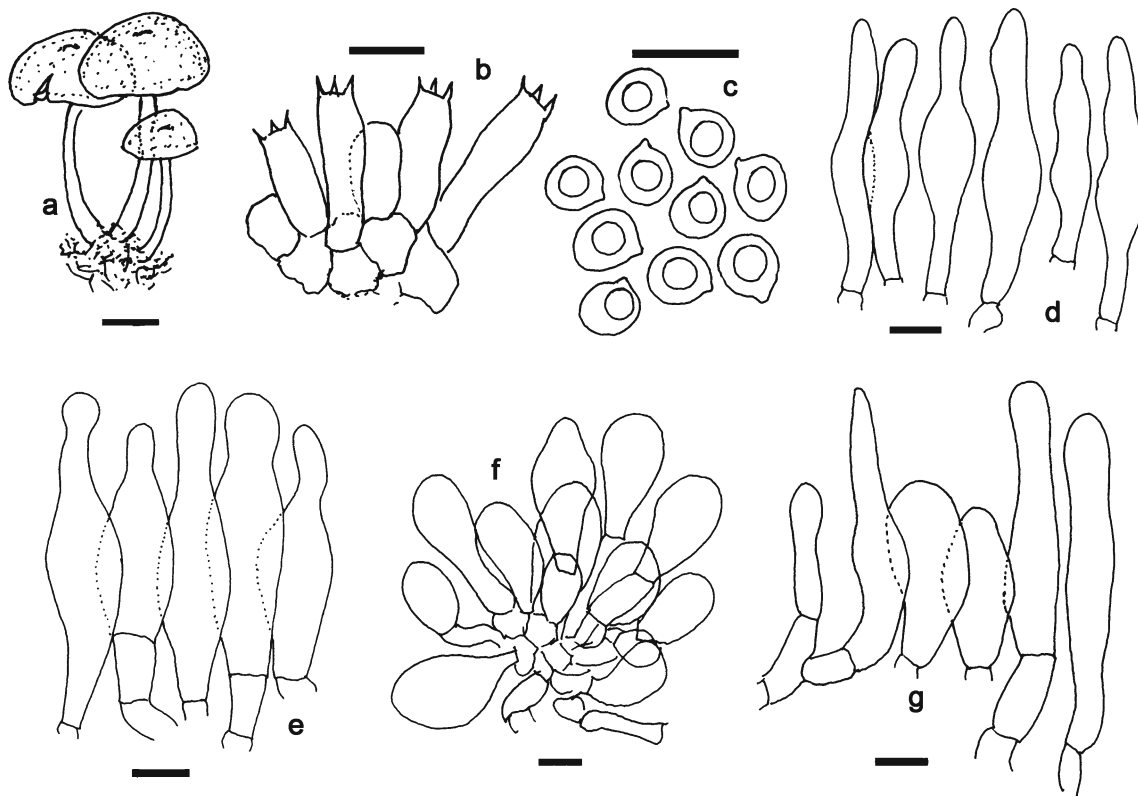


Fig. 1 *Pluteus brunneosquamulosus*. **a** habit, **b** basidia, **c** spores, **d** cheilocystidia, **e** pleurocystidia, **f** terminal pileipellis elements, **g** caulocystidia [K (M) 172152]. Scale bars=10 µm for microstructures and 10 mm for habit

thin-walled, hyaline. Pleurocystidia less frequent, similar to cheilocystidia except for slightly larger size, $42\text{--}73 \times 11.5\text{--}16\text{ }\mu\text{m}$, thin-walled, hyaline. Hymenophoral trama inversely bilateral with convergent hyphae, $4\text{--}11\text{ }\mu\text{m}$ wide, thin-walled, hyaline. Subhymenium well developed, pseudoparenchymatous. Pileal trama composed of interwoven hyphae, $5\text{--}16\text{ }\mu\text{m}$ wide, thin-walled, hyaline. Pileipellis a hymeniderm with transitions towards an epithelium composed of clavate, vesiculose to pyriform elements, $20.7\text{--}70.6 \times 5\text{--}40.8\text{ }\mu\text{m}$, thin-walled with brown intracellular contents. Stipitipellis composed of parallel hyphae, $7\text{--}13.6\text{ }\mu\text{m}$ wide, thin-walled, hyaline. Caulocystidia present on both upper and lower part. Caulocystidia $16\text{--}73 \times 8\text{--}16.5\text{ }\mu\text{m}$, lageniform, narrowly utriform, clavate to cylindro-clavate, thin-walled, hyaline in the upper part, but with greyish contents in the lower part. Oleiferous hyphae present. Clamp-connections absent.

Habit and habitat: In groups or scattered on fallen palm sheath and among exposed dead roots of *Caryota urens* L. or among moss in tropical evergreen forest, India.

Specimens examined: India, Kerala state, Trivandrum district, Palode, TBGRI campus: 27 Jul 2009, TBGT 12794 (**holotype, K (M) 172152**); 10 Aug 2009, TBGT 12839; 20 Aug 2009, TBGT 12875; 21 Aug 2009, TBGT 12878; 26 Aug 2009, TBGT 12886.

Discussion: The epithelial pileipellis, the non-metuloidal hymenial cystidia, together with the molecular data (Fig. 2), place *Pluteus brunneosquamulosus* in section *Celluloderma* Fayod. It is characterized by the (i) medium sized basidiomes with convex to plano-convex brown squamulose pileus; (ii) distinctive concentric cracking of pellicle to appear like a *Lepiota*; (iii) silky white stipe; (iv) subglobose to broadly ellipsoid spores; (v) cheilocystidia with a long flexuous neck; (vi) lageniform to narrowly utriform caulocystidia; (vii) and absence of clamp-connections. A comprehensive literature search was made (Singer 1956, 1958, Smith and Stuntz 1958; Horak 1964; Homola 1972; Pegler 1977, 1983, 1986; Orton 1986; Vellinga 1990; Banerjee and Sundberg 1993; Minnis and Sundberg 2010) which confirmed the uniqueness of this fungus. Morphologically the most similar taxa are those placed by Singer (1986) in stirps *Pulverulentus* (e.g. *P. pulverulentus* Murrill, *P. eliae* Singer), *Jamaicensis* (e.g. *P. fluminensis* Singer, *P. cinereofuscus* J.E. Lange, *P. pallenscens* P.D. Orton, *P. rimosus* Murrill), and *Tucumanus* [e.g. *P. tucumanus* Singer, *P. albolineatus* (Berk & Broome)] Sacc. which are characterized by the predominantly brown colours or olive-brown colours in the basidiocarps, without distinct yellow, orange or red tints. Though some taxa in this group (viz. *P. albolineatus*, *P. rimosus*) may exhibit a radially rimose or cracking pileipellis it does not have the same squamulose *Lepiota*-like aspect of *Pluteus brunneosquamulosus*. Moreover, the shape and size of the spores and cystidia also separate our new species from all the taxa mentioned above.

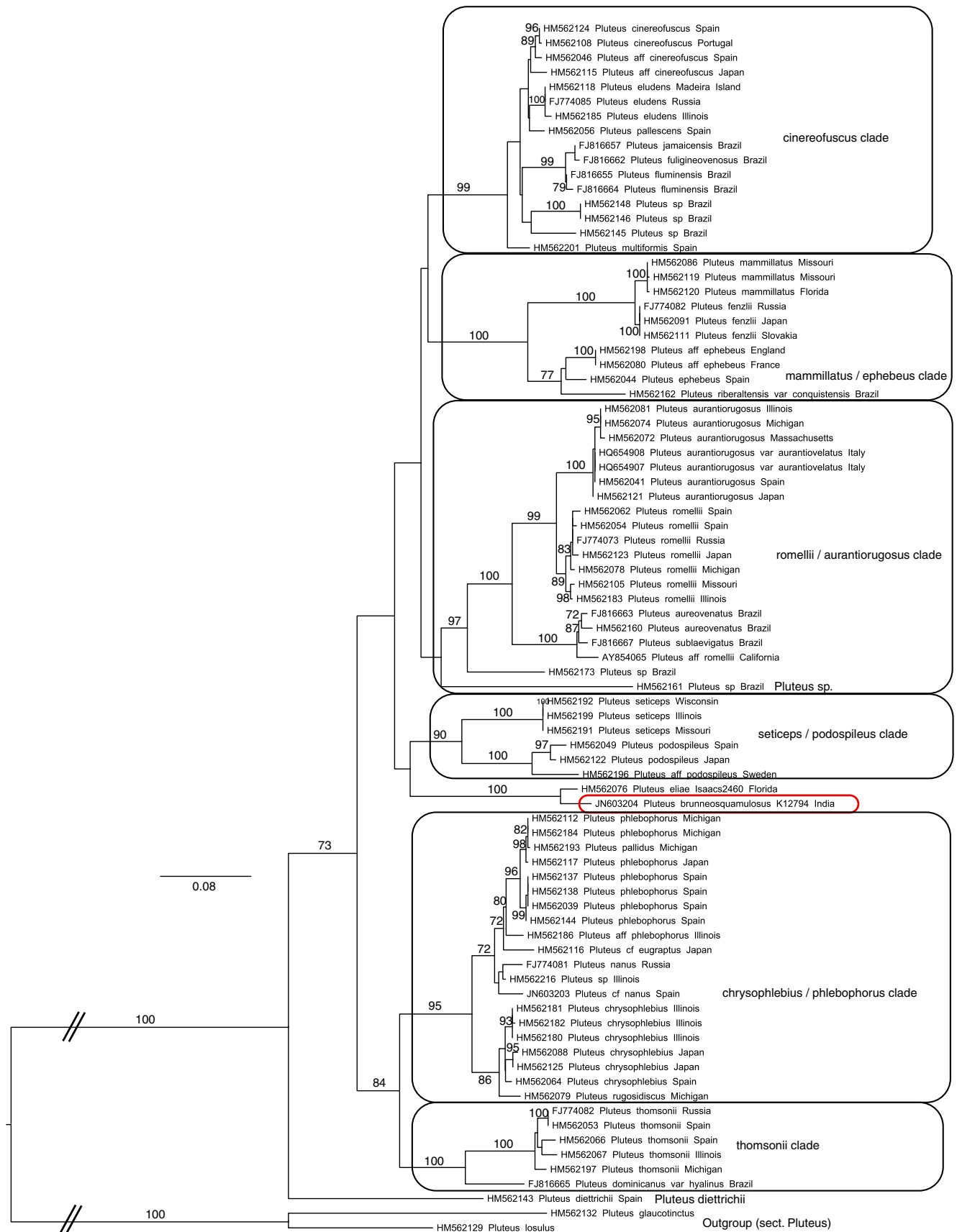
In the phylogenetic analyses (Fig. 2) *P. brunneosquamulosus* is placed as the sister taxon of the North American collection tentatively reported by Homola (1972) as *Pluteus eliae*. Minnis and Sundberg (2010) considered this collection to be *P. jamaicensis* but molecular data showed that it is not that species (Fig. 2). Whether it actually represents the authentic *Pluteus eliae*, a species described from Bolivia (Singer 1958), remains uncertain and additional South American collections will be required to verify this. Among other characters, Homola's *P. eliae* differs from the present taxon by the entire, non-cracked pileipellis, wider and clavate or narrowly clavate cheilocystidia, (up to $24\text{ }\mu\text{m}$ wide) in contrast with the narrowly lageniform (up to $10\text{ }\mu\text{m}$ wide) cheilocystidia of *P. brunneosquamulosus*. The percentage similarity between the ITS sequences of *P. brunneosquamulosus* and *P. eliae* is 95% (31 base pair differences). Both taxa are placed in an unresolved position outside the major lineages recognized in Sect. *Celluloderma* by Justo et al. (2011a, b). Many species of stirps *Jamaicensis* for which molecular data are available (*P. cinereofuscus*, *P. fluminensis*, *P. jamaicensis* and *P. pallenscens*) are placed together in the *cinereofuscus* clade (Fig. 2).

***Pluteus velutinus* Pradeep, Justo & Vrinda sp. nov.**
Figs. 3, 6d-f

Mycobank MB563403

Pileus $9\text{--}42\text{ mm}$ latus, convexus vel applanatus, brunneus, velutinus, pruinosis vel squamulosus. Lamellae liberae, confertae, albae ad roseae. Stipes $25\text{--}75 \times 2\text{--}9\text{ mm}$, centralis, cylindricus. Sporae $5.5\text{--}9.5 \times 5\text{--}7\text{ }\mu\text{m}$, subgloboae vel ellipsoideae. Basidia $18\text{--}32 \times 6.5\text{--}10\text{ }\mu\text{m}$, clavata, 4-sporigera. Cheilocystidia $32\text{--}70 \times (9.5)\text{ }\mu\text{m}$, lageniformia. Pleurocystidia $45\text{--}88 \times 12\text{--}28\text{ }\mu\text{m}$, hyalina. Trama hymenophoralis bilateralis, inversa. Cuticula pilei trichodermialis. Caulocystidia $35\text{--}76 \times 10\text{--}30\text{ }\mu\text{m}$, versiformia, clavata vel vesiculosa. Fibulae absentes.

Pileus $9\text{--}42\text{ mm}$ in diam., convex to applanate with a small shallow depression at centre; surface brown to orange brown ['greyish orange' (5B3), 'brownish orange' (5 C3), 'flesh' (6B3), 'café-au-lait' (6D3), 'brown' (6E3), 'cognac' (6E7)] uniformly or with a slightly darker disc, becoming paler ['brownish grey' (6 C2), 'camel' (6D4)] hygrophanous, velvety in young specimens, pruinose throughout when mature, becoming squamulose around the disc, in some specimens squamulose all over, dry; margin straight, entire to incised, pellucid striate. Lamellae free, 'orange white' (5A2), 'pale orange' (6A3), up to 6 mm , crowded with lamellulae of different lengths; edge concolourous to sides, entire. Stipe $25\text{--}75 \times 2\text{--}9\text{ mm}$, central, cylindric, often compressed in lower half, curved, tapering up from a bulbous base, stuffed becoming hollow, brittle with white mycelium at the base; surface cream to brown ['orange white' (5A2), 'greyish orange' (5B3), 'brownish orange' (5 C3), 'brownish grey' (6 C2)] extreme base with



◀ **Fig. 2** Best Tree from the Maximum Likelihood analysis of sect. *Celluloderma*. Bootstrap values $\geq 70\%$ are shown on the branches. Scale bar indicates nucleotide substitutions per site. Root length has been reduced to facilitate graphical representation. Clade names follow Justo et al. (2011a)

greyish tinge, fibrillose-striate. Context in pileus and stipe white, thin. Odour mild, agreeable, becoming strongly unpleasant when dried. Spore print pink.

Spores $5.5\text{--}9.5 \times 5\text{--}7\text{ }\mu\text{m}$, $\text{avL}=7.7\text{ }\mu\text{m}$, $\text{avW}=6.2\text{ }\mu\text{m}$, $Q=(1)\text{ }1.17\text{--}1.50$, $\text{avQ}=1.29$, broadly ellipsoid to ellipsoid,

very rarely globose or subglobose, thick-walled with a guttule. Basidia $18\text{--}32 \times 6.5\text{--}10\text{ }\mu\text{m}$, clavate, 4-spored, thin-walled, hyaline. Lamella edge sterile with crowded cheilocystidia. Cheilocystidia $32\text{--}70 \times (9.5)\text{ }12\text{--}30\text{ }\mu\text{m}$, lageniform, narrowly utriform or ovoid, more rarely clavate, with obtuse apices, rarely with a small projection up to $9\text{ }\mu\text{m}$ long, thin-walled, hyaline. Pleurocystidia $45\text{--}88 \times 12\text{--}28\text{ }\mu\text{m}$, scattered to abundant, present all over lamellar sides, (broadly) clavate, fusiform, narrowly lageniform or narrowly utriform, very commonly with an apical digitate projection up to $10\text{ }\mu\text{m}$ long or tapering towards apex, thin-walled, hyaline.

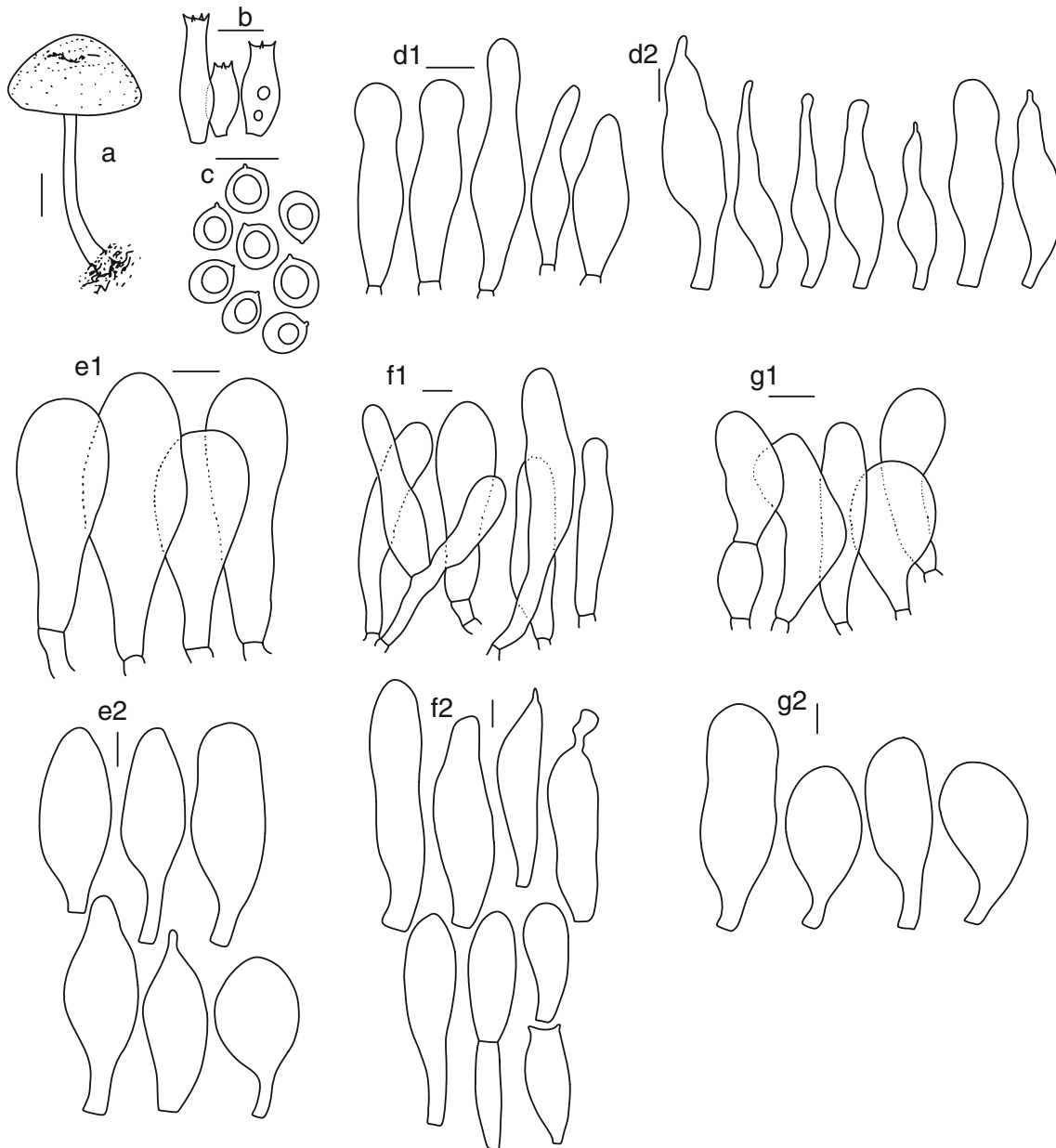


Fig. 3 *Pluteus velutinus*. **a** habit, **b** basidia, **c** spores, **d** cheilocystidia, **e** pleurocystidia, **f** terminal pileipellis elements, **g** caulocystidia; **d1-g1** [K (M) 172153]; **d2-g2** (TNS-F 12365). Scale bars=10 μm for microstructures and 10 mm for habit

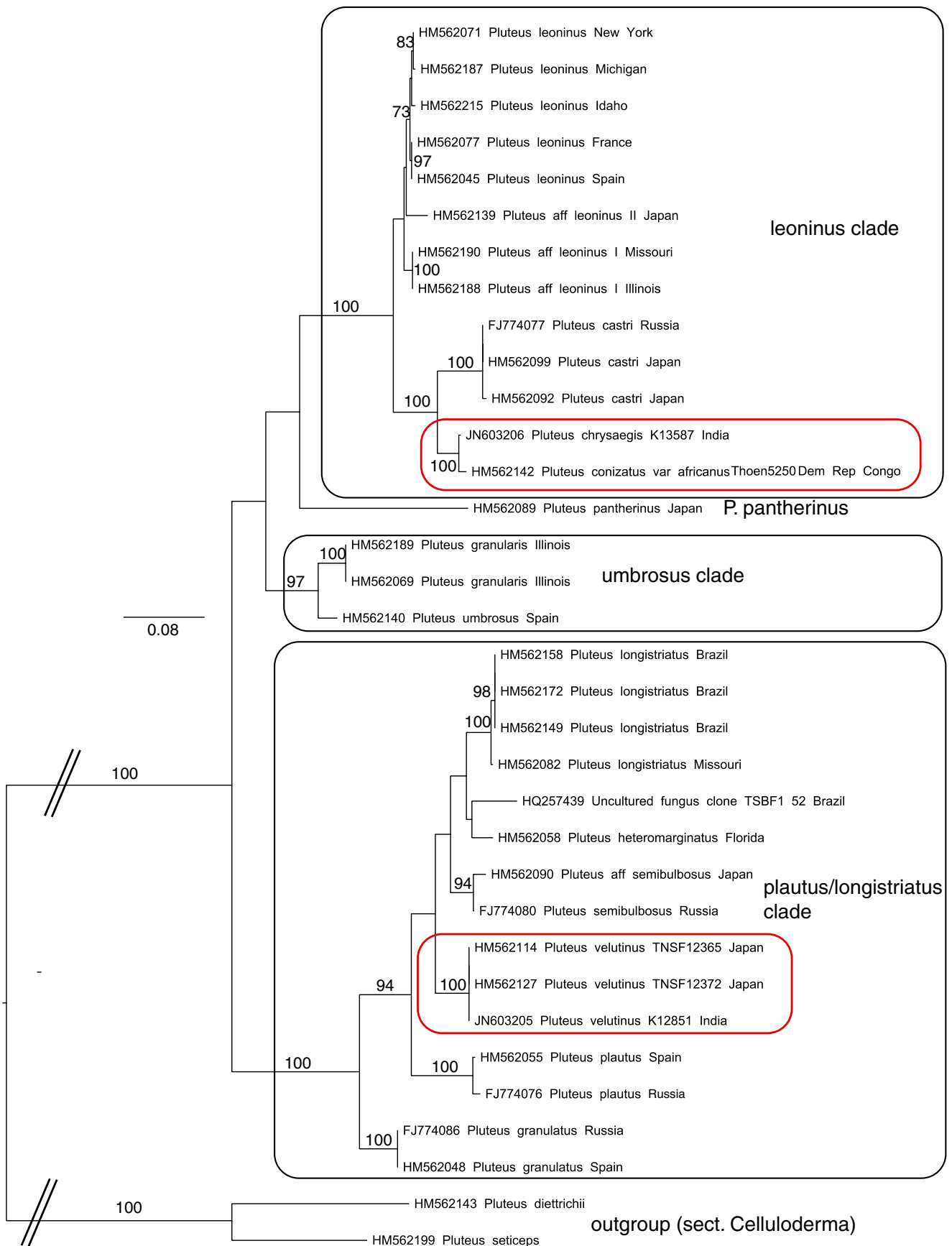


Fig. 4 Best Tree from the Maximum Likelihood analysis of sect. *Hispidoderma*. Bootstrap values $\geq 70\%$ are shown on the branches. Scale bar indicates nucleotide substitutions per site. Root length has been reduced to facilitate graphical representation. Clade names follow Justo et al. (2011a)

Hymenophoral trama inversely bilateral with convergent hyphae, 3–24 μm wide, inflated, thin-walled, hyaline. Subhymenium well developed, pseudoparenchymatous. Pileal trama composed of interwoven hyphae, 4–26.5 μm wide, inflated, thin-walled, hyaline. Pileipellis a trichoderm or trichohymeniderm composed of clavate, cylindro-clavate, cylindrical or fusiform elements, a few with apical projections, (40) 70–140 \times 13–27 μm , thin-walled with brown intracellular contents. Stipitipellis composed of longitudinally parallel hyphae, 4–5.5 μm wide, thin-walled, hyaline or with brown intracellular pigment. Caulocystidia abundant, present all over stipe surface, 35–76 \times 10–30 (40) μm , mostly clavate but also narrowly utriform or ellipsoid, some slightly strangulated, thin-walled, with brown intracellular contents. Oleiferous hyphae present. Clamp-connections absent.

Habit and habitat: Gregarious and scattered on dead leaf sheath of *Elaeis guineensis* Jacq. (Arecaceae) in tropical evergreen forest, India. Gregarious on fallen rotten wood of broad-leaved trees (in deciduous forest) in Japan.

Specimens examined: **India**, Kerala State, Trivandrum district, Palode, TBGRI campus: 14 Aug 2009, TBGT 12851 [**holotype**, **K (M) 172153**]; 17 Aug 2009, TBGT 12855; 19 Aug 2009, TBGT 12869; 7 Sept 2009, TBGT 12902; 8 Sept 2009, TBGT 12904; 14 Sept 2009, TBGT 12911; 18 May 2010, TBGT 13225; 20 May 2010, TBGT 13237; 30 Jun 2010, TBGT 13354; 9 Nov 2011, TBGT 13040. **Japan:** Hokkaido, Iwamizawa-shi, Midorigaoka, Tonebetsu Nature Park, 9 July 2005, coll. S. Takehashi, TNS-F 12365; ibidem, 17, Sept 2005, TNS-F 12372.

Discussion: *Pluteus velutinus* is characterized by the shallowly depressed, hygrophanous, orange-brown, velvety to squamulose pileus; relatively large subglobose to broadly ellipsoid spores; lageniform or clavate pleurocystidia with digitate projections; lageniform or utriform cheilocystidia; clavate caulocystidia and trichodermial pileipellis. The general morphological characters, especially the aspect of the pileus, point to a relationship with the European *Pluteus granulatus* Bres., and the results from the phylogenetic analysis place both taxa in the same clade but they are clearly distinct species and are not sister taxa (Fig. 4). The taxonomy of the species of *P. granulatus* and *P. plautus* Weinm. is not well resolved, with very different taxonomic opinion existing in the literature (Vellinga and Schreurs 1985, Orton 1986). *P. depauperatus* Romagn. and *P. dryophiloides*

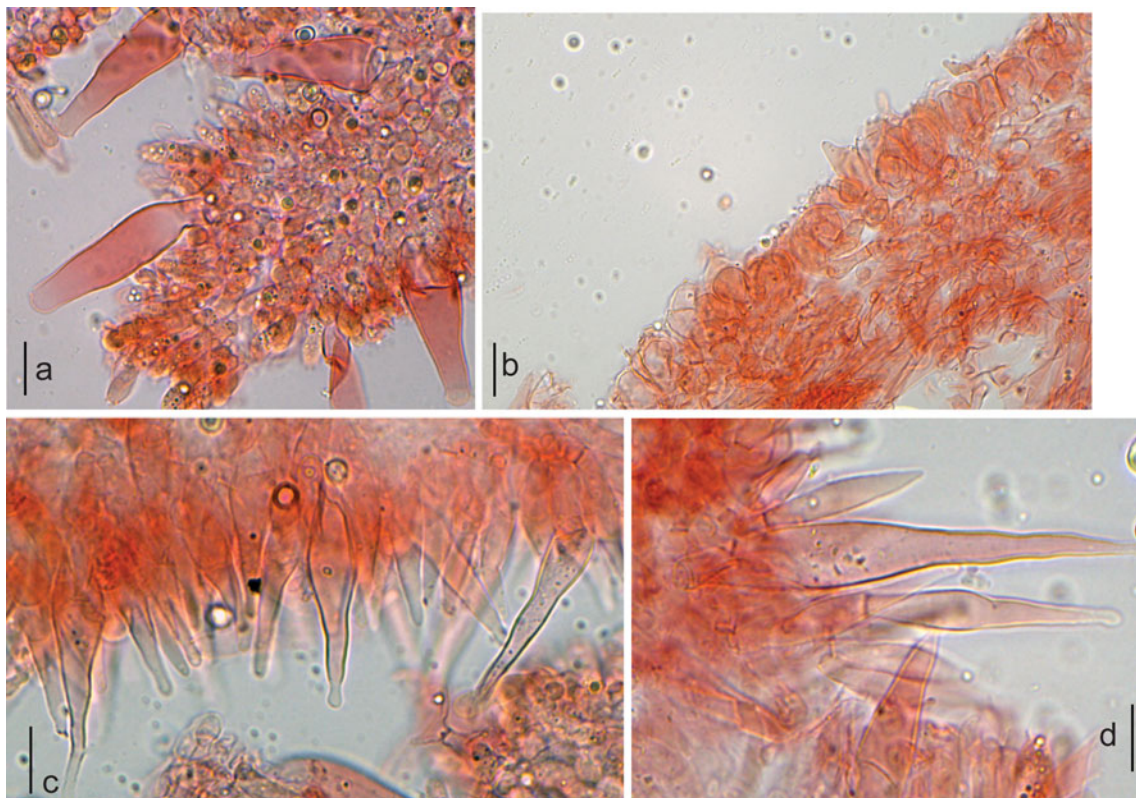


Fig. 5 *Pluteus chrysaegis*. **a.** pleurocystidia, **b.** pileipellis, **c.** **d.** cheilocystidia [K (M) 172154]. All structures mounted in Congo red and KOH. Scale bars=20 μm

P.D. Orton are morphologically similar to *P. velutinus*. *P. depauperatus* differs in its ellipsoid to oblong spores with $avQ=1.65$ and utriform, lageniform pleurocystidia without a narrow apex or digitate projections (Kühner and Romagnesi 1956; Vellinga and Schreurs 1985). *P. dryophiloides* has predominantly utriform and much wider ($60\text{--}94\times 24\text{--}52\text{ }\mu\text{m}$) pleurocystidia, without narrow apex or digitate projections (Orton 1986).

The Japanese collections studied by us were reported by Takehashi et al. (2010) as '*Pluteus cf. exiguus*'. However, *P. exiguus* Pat. has a distinctly squamulose and smaller (up to 20 mm) pileus, pleurocystidia very scarce or absent and clavate cheilocystidia with a distinct narrow apex or apical projections (Kühner and Romagnesi 1956; Vellinga 1990; pers. obs.). *Pluteus exiguus* is a very rarely recorded mushroom in Europe and it is known from Central-Western Europe (Kühner and Romagnesi 1956; Orton 1986; Vellinga 1990) and South into Mediterranean Spain (Justo and Castro 2007).

The ITS sequences from the Japanese collections of *P. velutinus* were reported as '*Pluteus sp. I*' in the molecular phylogenies of Justo et al. (2011a, b) as no satisfactory species level identification was possible. The ITS sequence

of the holotype of *P. velutinus* from India is 99% identical (one single nucleotide difference) with the Japanese sequences, therefore confirming that the same species occurs in two places separated by more than 7000 km under totally different climate conditions and habitat characteristics. Other species of *Pluteus* (e.g. *P. cervinus*, *P. longistriatus*, *P. romellii*) show similarly wide geographic distribution (Justo et al., 2011a) but it is not known what dispersal mechanisms are responsible for these distribution patterns and whether they are natural or anthropogenic.

Pluteus chrysaegis (Berk. & Broome) Petch, *Ann. Royal Bot. Gard. Peradeniya* 5: 271, 1912 Fig. 5, 6g

≡ *Agaricus chrysaegis* Berk. & Broome, *J. Linn. Soc., Bot.* 11: 536, 1871

≡ *Entoloma chrysaegis* (Berk. & Broome) Sacc., *Syll. Fung.* 5: 61, 1887

= *Pluteus conizatus* var. *africanus* Horak, *Bull. Jard. Bot. Nat. Belgique* 47: 89, 1977

P. chrysaegis was originally described from Sri Lanka and known only from the type collection (Pegler 1986) until it was recently found again in Kerala State, India by Pradeep



Fig. 6 Basidiomata in situ. **a–c** *Pluteus brunneosquamulosus*, **d–f** *Pluteus velutinus*, **g** *Pluteus chrysaegis*. Scale bars=10 mm

and Vrinda (2006). An additional collection of this species was recently made at a second locality in Kerala (India: Kerala State, Trivandrum district, Palode, TBGRI campus: 3 May 2011, TBGT 13587 [K (M) 172154] and sampled for molecular analysis. The ITS sequence of *P. chrysaegis* is 98% identical with the sequence of *P. conizatus* var. *africanus* from Central Africa. Morphologically both taxa are almost identical and characterized by the golden-yellow pileus with dark-brown rugulose center and the only difference is in the size of the pileus, up to 55 mm in *P. chrysaegis* (Pegler 1986, Pradeep and Vrinda 2006) and up to 80 mm in *P. conizatus* var. *africanus* (Horak and Heinemann 1978). Microscopically they are also practically identical; however, this is not immediately obvious when comparing the descriptions of *P. conizatus* var. *africanus* by Horak (Horak and Heinemann 1978) and of *P. chrysaegis* by Pegler (1986) or Pradeep and Vrinda (2006) as the different authors emphasizes different aspects of the microanatomy of this species.

Pluteus conizatus var. *africanus* as described by Horak (Horak and Heinemann 1978) is mainly characterized by the (sub-) globose spores $5\text{--}6\times 4\text{--}4.5$ (5) μm ; pleurocystidia $50\text{--}70\times 14\text{--}27$ μm , lageniform to utriform, mostly with thin walls but some with slightly thickened wall, cheilocystidia $25\text{--}60\times 7\text{--}17$ μm , fusiform, with thickened wall; pileipellis a hymeniderm composed of clavate or subfusiform cells $10\text{--}25\times 5\text{--}8$ μm . Our observations on the original collections deposited at BR (Goossens-Fontana 623 (holotype), Goossens-Fontana 950, Thoen 5250) agree well with Horak's description except in the slightly longer pleurocystidia (up to 80 μm) and pileipellis elements (up to 40 μm). Horak emphasized the combination of golden-yellow basidiocarps, thick-walled cystidia and hymenidermal pileipellis as the most defining characters of this variety, which he separated from *P. conizatus* (Berk. & Broome) Sacc. var. *conizatus* by the smaller pileipellis cells and the pleurocystidia mostly with thin walls. Despite the fact that Singer (1956) included *P. conizatus* in sect. *Pluteus*, because of the thick-walled cystidia that he considered metuloids, Horak treats *P. conizatus* var. *africanus* as a member of sect. *Celluloderma* because of the hymenidermal pileipellis.

Pluteus chrysaegis as described by Pegler (1986) and Pradeep and Vrinda (2006) is mainly characterized by the (sub-)globose spores $4.5\text{--}6\times 4\text{--}5.5$ μm ; pleurocystidia $38\text{--}84\times 10\text{--}23$ μm , lageniform more rarely fusoid, with thin walls; cheilocystidia $22.5\text{--}57\times 6\text{--}15$ μm , fusiform, with thin walls; pileipellis composed of clavate cells $19.5\text{--}33$ (40) $\times 9\text{--}18$ μm intermixed with fusiform pileocystidia $31\text{--}60\times 7\text{--}13$ μm . Pradeep & Vrinda also noted the presence of caulocystidia in the upper part of the stipe, $19.5\text{--}33\times 7.5\text{--}10.5$ μm , ventricose, mucronate. Both Pegler (1986) and Pradeep & Vrinda (2006) described the hymenial cystidia as 'thin-walled' but in *Pluteus chrysaegis* the cheilocystidia, and also some pleurocystidia, show slightly thickened 0.5--

1.5 (2) μm wide walls, especially near the apex (Fig 5). These authors considered the more fusiform elements in the pileipellis (Fig. 5) to be dermatocystidia, and consequently placed *P. chrysaegis* in Sect. *Celluloderma* subsect. *Mixtini* Singer, but molecular data places *P. chrysaegis* in sect. *Hispidoderma*, and not related with any of the taxa with *Mixtini*-type pileipellis (e.g. *P. eludens*, *P. multiformis*, *P. podospileus*, *P. seticeps*, *P. thomsonii*) of sect. *Celluloderma* (Fig 4; Justo et al. 2011a).

Given the similarity of the Indian and African collections in morphology and molecular characters both taxa are considered to represent one species for which the name *Pluteus chrysaegis* is more appropriate. Molecular data places *P. chrysaegis* as part of the *P. leoninus* lineage (Fig. 4) and sister to *P. castri* Justo & E.F. Malysheva; another yellow species, known from Russia and Japan and also characterized by the relatively short elements of the pileipellis in comparison with other members of sect. *Hispidoderma* (Justo et al. 2011a). This position of *P. chrysaegis* also indicates that the slightly thick-walled cystidia of this species do not have the same origin as the metuloids found in sect. *Pluteus*.

Pluteus conizatus var. *conizatus* originally described from Sri Lanka, and so far only known from the holotype and an additional collection (Singer 1956; Pegler 1986), apparently differs from *P. chrysaegis* in the 'dull yellowish brown, greyish towards umbo' pileus, and the narrowly fusoid or lageniform pleurocystidia with up to 3 μm thick wall (Pegler 1986). Cheilocystidia are described as 'similar to the pleurocystidia but with thinner walls' and the pileipellis as 'a disrupted trichodermium of narrow, semi-erect to erect septate hyphae, with terminal elements $20\text{--}42\times 4\text{--}7.5$ μm ' (Pegler 1986). Both Pegler and Singer (Singer 1956; Pegler 1986) placed this species in sect. *Pluteus*, but the structure of the pileipellis suggests a closer relationship with *P. chrysaegis* and *P. castri* in sect. *Hispidoderma* despite the thick-walled cystidia. Modern collections of *P. conizatus* are needed to clarify its taxonomic position.

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