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The new genus *Auritella* from Africa and Australia (Inocybaceae, Agaricales): molecular systematics, taxonomy and historical biogeography

Abstract Recent phylogenetic evidence strongly supports a monophyletic group of Afro-Australian mushroom species with phenotypic affinities to the genus *Inocybe* (Agaricales, Basidiomycota). In this study, this clade is proposed as the new genus *Auritella*. Seven species are fully documented with taxonomic descriptions and illustrations, four of which are described as new, including one sequestrate or truffle-like species. A key to genera and major clades of the Inocybaceae and a key to species of *Auritella* are provided. A maximum likelihood tree using *rpb2* and nLSU-rDNA nucleotide sequences depicts the phylogenetic relationships of five of the seven species of the genus, of which the Australian taxa form a monophyletic group. An ancient split between Australian and African lineages is hypothesized using a molecular clock that dates back at least to the late Cretaceous (about 86 Ma). *Taxonomic novelties*: *Auritella* Matheny and Bougher; *Auritella arenacolens* (Cleland) Matheny and Bougher; *Auritella aureoplumosa* (Watling) Matheny; *Auritella chamaecephala* Matheny, O. K. Miller and Bougher; *Auritella dolichocystis* Matheny, Trappe and Bougher; *Auritella erythroxa* (De Seynes) Matheny; *Auritella geoaustralis* Matheny and Bougher; *Auritella serpentinocystis* Matheny, Trappe and Bougher.

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Introduction

Progress towards generating a phylogenetic-based classification of *Inocybe* and allies in the Agaricales or euagarics clade has been accelerated recently by several molecular systematic studies of the group (Kropp and Matheny 2004; Matheny et al. 2002; Matheny 2005; Matheny and Ammirati 2003; Matheny and Watling 2004). In particular, Matheny (2005) demonstrated the monophyly of five major lineages within *Inocybe* and provided strong evidence for a sister relationship between the Inocybaceae, a monophyletic family of ectomycorrhizal species, and the Crepidotaceae, a family of saprophytic species. A summary cladogram depicts these relationships in Fig. 1. Because the Cortinariaceae does not appear monophyletic based on nLSU-rDNA (nLSU) sequence data (Moncalvo et al. 2000; Moncalvo et al. 2002), Matheny (2005) recommended the recognition of *Inocybe* at the family rank, the Inocybaceae, as was done previously by Jülich (1981). In this paper, we propose a new genus, *Auritella*, to encompass one of the major lineages uncovered in the multigene phylogenetic analysis of this family.

Auritella represents a small but heterogeneous group of African and Australian species with tough agaricoid or sequestrate basidiomata, smooth brownish basidiospores, cheilocystidia often longer than 50 μm (if present), absence of pleurocystidia, and possession of necropigmented basidia. The Mallocybe clade (subg. *Mallocybe* Kuyp.) appears to be the sister group to *Auritella* but differs by the combination of geographic distribution and cheilocystidia usually less than 50 μm long. This study presents a taxonomy of seven species of *Auritella* and explores its diversification using nucleotide sequences of a protein-coding gene, *rpb2* (Liu et al. 1999; Matheny 2005; Matheny and Ammirati 2003; Matheny and Watling 2004), and nLSU. Several additional studies have also demonstrated the utility of *rpb2* at relatively low taxonomic levels in the Basidiomycota and Ascomycota (Chaverri et al. 2003; Desjardin et al. 2004; Miller and Huhndorf 2004; Wang et al. 2004).
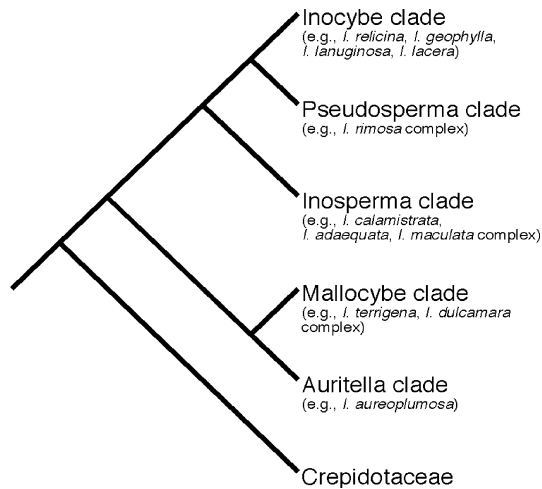
Fig. 1 Summary cladogram of the five major clades of *Inocybaceae* identified in Matheny (2005). Exemplar species of each major clade are provided. The *Crepidotaceae* is the sister group to the *Inocybaceae*

All members of the Auritella clade sampled to date originate from Africa and Australia and thus have a disjunct distribution. Indeed, biotas with a southern distribution that originated before or during the break-up of the major modern southern hemisphere landmasses are described as Gondwanan in distribution (Horak 1983; McLoughlin 2001). These landmasses now include Africa, Antarctica, Australia, Madagascar, New Zealand, and South America. However, long-distance dispersal (LDD) has been shown to satisfactorily explain some animal, fungal, and plant distributions in the southern hemisphere (Hibbett 2001; Hugall and Lee 2004; Knapp et al. 2005; Sanmartín and Ronquist 2004; Tremetserberger et al. 2005; Winkworth et al. 2002). Yet, there are few biogeographic studies of ectomycorrhizal fungi that employ phylogenetic markers (Martin et al. 2002), or such studies have been restricted to groups with a northern hemisphere distribution (Wu et al. 2000; Mueller et al. 2001).

Due to the taxon–area relationship between tropical Africa and temperate Australia in *Auritella*, we evaluated divergence times to test phylogeographic patterns in the group. Essentially, we wished to know if these patterns were consistent with predictions derived from dates based on continental drift or recent long-distance dispersal. Explicitly, we wished to test the following phylogeographic hypotheses using a molecular clock of combined *rpb2* and nLSU nucleotide sequences: (1) can the divergence between African and Australian species be explained by recent long-distance disperal? or (2) was the Afro-Australian split an ancient vicariant event?

Materials and methods

Herbarium materials

Herbarium collections were borrowed from Jim Trappe at Corvallis, OR (OSC), Roy Watling at Edinburgh (E), and Graham Bell from Adelaide, South Australia (AD). Additional material was also available for study at Perth, Western Australia (PERTH). All material is curated at the following herbaria: AD, E, OSC, PERTH, and WTU with herbarium abbreviations following Holmgren et al. (1990). Other materials cited here were, at the time of this study, curated at CSIRO Forestry and Forest Products, Private Bag Post Office, Wembley, Western Australia 6014, Australia but have been recently transferred to PERTH.

Gross morphological features were drawn generally from field notes made by collectors and from personal observations of dried basidiomata. Colors were approximated without the use of color field guides in many cases. However, collections made firsthand by the authors were compared with color field guides such as that of Ridgway (1912), Munsell Soil Color Charts (1954) and Kornerup and Wanscher (1967). Sections of basidiomata were made when fresh or reconstituted in weak alkali solutions of 10% NH_4OH or 3% KOH and examined under a light microscope. Illustrations were drawn with the aid of a drawing tube. Basidiospores are illustrated at ×2,000 and other cells at ×800. All microscopic descriptions were made from personal observation unless where noted. Measurements and descriptive statistics of basidiospores, basidia, and cystidia follow Matheny et al. (2003) and Kropp and Matheny (2004).

DNA extraction and sequencing

Protocols for DNA extraction, PCR amplification, and DNA sequencing follow Matheny et al. (2002), Matheny (2005), and Matheny and Watling (2004). In Table 1 is a list of taxa from which sequences were generated for this study, including those previously published. PCR primers include 5.8SR and LR7 (Vilgalys and Hester 1990) for the nLSU locus and b6F and b7.1R (Matheny 2005; http://faculty.washington.edu/benhall/) for the *rpb2* locus. Sequencing primers include LR0R, LR5, LR3R, and LR16, sequences of which are available at http://www.biology.duke.edu/fungi/mycolab/. nLSU and *rpb2* sequences generated for this study have been deposited at GenBank (Table 1).

Phylogenetic analyses

Matheny (2005) and Matheny and Watling (2004) demonstrated the monophyly of the Auritella clade with strong measures of bootstrap support and/or Bayesian posterior probabilities (PP). Sequences of the Auritella clade and outgroups, including eight new sequences generated for this study, were realigned in Clustal X (Thompson et al. 1997) to facilitate alignment between these taxa and preclude the exclusion of sites that aligned ambiguously in larger data sets. Two different outgroups were considered: (1) two members of the Mallocybe clade, *I. terrigena* and *I. unicolor*, because the Mallocybe clade is sister to the Auritella clade with a PP >0.95 (Matheny 2005); and (2)

Table 1 Materials and sequences used for phylogenetic analyses

Taxon	Voucher	Herbarium	Acc. no. *rpb2*	Acc. no nLSU
Auritella aureoplumosa (Watling) Matheny	Wat 23132 (holotype)	E	not sequenced	AY635766
Auritella chamaecephala Matheny, O. K. Miller & Bougher	PBM 2212 (E7060)	CSIRO	AY635781	AY635765
Auritella dolichocy stis Matheny, Trappe & Bougher	T24838 (holotype)	PERTH	AY635767	AY635763
Auritella dolichocystis	T24843	MEL	AY635780	AY635764
Auritella dolichocystis	T24844	MEL	AY337371[a]	AY380371[a]
Auritella geoaustralis Matheny & Bougher	H7344 (holotype)	PERTH	AY333774[b]	AY380395[a]
Auritella serpentinocystis Matheny, Trappe & Bougher	T25080 (holotype)	PERTH	AY333773[b]	AY038325[c]
Crepidotus cf. *applanatus* (Pers.) Kumm.	PBM 1717	WTU	AY333311[d]	AY380406[a]
Crepidotus versutus (Peck) Sacc.	PBM 856	WTU	AY333312–AY333313[d]	AY820890
Inocybe terrigena (Fr.) Kuyper	JV 16431	WTU	AY333309[d]	AY380401[a]
Inocybe unicolor Peck	PBM 1481	WTU	AY337409[a]	AY380403[a]

Acc. no. GenBank accession number
[a] Matheny 2005
[b] Matheny and Watling 2004
[c] Matheny et al. 2002
[d] Matheny and Ammirati 2003

Crepidotus cf. *applanatus* and *C. versutus* based on Matheny (2005), which showed strong bootstrap support for a sister relationship between the Crepidotaceae and Inocybaceae.

All taxa, except for *A. aureoplumosa* (nLSU only), were sequenced for both genes. The alignment of both *rpb2* and nLSU has been deposited at TreeBASE (http://www.treebase.org) as matrix accession M2410 (S1360). Gene sequences were combined as no topological conflicts were observed when the loci were analyzed separately. Modeltest 3.06 (Posada and Crandall 1998) was used to determine models best fit to the combined *rpb2* and nLSU data under the hierarchical likelihood ratio test (hLRT) criterion. PAUP* 4.0 beta 10 (Swofford 2003) was used to run maximum likelihood (ML) analyses. ML heuristic tree searches were done with five random addition sequence replicates, TBR branch-swapping, and steepest descent option not in effect. A total of 100 bootstrap replicates (Felsenstein 1985) was performed to gauge support for branches in the ML tree also using heuristic searches, TBR, and five random addition sequence replicates per bootstrap.

Phylogeographic analyses

A molecular clock was enforced on the combined data set under the ML criterion. A likelihood ratio test was done to determine if the ML clock tree was significantly worse than the unconstrained ML tree. To test the hypothesis that the combined sequences evolve in a clock-like fashion in *Auritella*, twice the difference in likelihood scores was compared to a chi-square distribution with $n-2$ degrees of freedom, where n equals the number of taxa in the data set (Baldwin and Sanderson 1998; Muse and Weir 1992; Wang et al. 2000).

Confidence intervals of divergence times were estimated by bootstrapping the combined data set for 100 replicates in PHYLIP 3.57 (Felsenstein 1993) using the PHYLIP program SEQBOOT (Baldwin and Sanderson 1998; Donoghue et al. 2001; Sanderson 1998). The resulting outfile was parsed into 100 separate text files. Each bootstrapped data set was uploaded into MacClade 4.0 (Madisson and Madisson 2000) and then analyzed separately under ML in PAUP*. Model parameters were estimated for each data set, and a molecular clock was enforced. Branch lengths and divergence times were then estimated as described above. Standard errors were also determined (Heckman et al. 2001; Hibbett 2001).

Two data sets were evaluated. One included the two *Crepidotus* taxa, and the second excluded them. Outgroups were pruned from the data set before estimation of divergence dates as suggested by Sanderson (2003). Branch lengths with a molecular clock enforced were output using the "trees/describe trees" functions in PAUP*. The branch length of the node shared by *A. serpentinocystis* and *A. geoaustralis* was divided by twice the calibration point in millions of years to get a nucleotide substitution rate, k(the number of substitutions per site per year). Subsequent nodes were dated by taking the branch length and dividing it by twice the rate.

The ML clock tree was calibrated at 15 million years ago (Ma) at the *A. serpentinocystis–A. geoaustralis* node (a soutwest/southeast disjunct species pair) to provide minimum age estimates. This calibration point was chosen because the Nullarbor plain formed over a large part of southern Australia approximately 15 million years ago effectively serving as an edaphic barrier between the western and eastern parts of Australia (Charles-Nelson 1981; Nelson 1974; Specht 1981).

Synoptic key to clades and genera of the Inocybaceae

1 Pleurocystidia present or, if absent, then basidiospores nodulose

*Inocybe*s. s. (containing the type *I. relicina*)

1* Pleurocystidia absent and basidiospores with even outline (smooth)

2 Lamellae subdecurrent to deeply decurrent, habit omphalinoid or tubarioid, amorphous deposits present on cheilocystidia and terminal cells of the pileipellis, known from Spain in xerophytic habitat under *Tuberaria* (Cistaceae) in *Quercus* woodland

Inocybe inexpectata

2* Lamellae adnate or adnexed, exceptionally free or subdecurrent; habit generally not as small as above; amorphous deposits on cheilocystidia and pileipellis hyphae absent; widespread but not recorded from the *Nothofagus* zone of South America

3 Pileus rimose (sect. *Rimosae* s. l.)

4 *rpb2* intron 4 with GC- 5′ splice site

Inosperma clade (containing sect. *Rimosae* p. p.)

4* *rpb2* intron 4 with GT- 5′ splice site

Pseudosperma clade (containing sect. *Rimosae* s. s.)

3* Pileus scaly, matted-fibrillose or tomentose

5 Context often reddening where bruised; odor like fish, bruised geranium leaves, wine barrels, or fruity or sweet; cheilocystidia with cyanophilic contents; *rpb2* intron 4 with GC- 5′ splice site. Some species with necrobasidia

Inosperma clade (containing sect. *Cervicolores*)

5* Context not reddening; odor not fishy, fruity, or sweet as above; cheilocystidia without cyanophilic contents; *rpb2* intron 4 with GT- 5′ splice site. All species with necrobasidia

6 Known only from Australia and Africa; cheilocystidia usually >50-μm long, cylindric, elongate clavate, or skittle-shaped; if basidiomata sequestrate, then cheilocystidia not observed

Auritella gen. nov.

6* Occurring in the northern hemisphere and Australia; if from Australia, then cheilocystidia <50 μm long, short clavate to short cylindric; sequestrate taxa not yet recorded

Mallocybe clade (containing subg. *Mallocybe*)

Artificial key to species of *Auritella* gen. nov.

1 Occurring in paleotropical Africa, known from Cameroon and Gabon

2 Stipe girdled with bands of rich tawny orange scales; basidiospores subglobose, 6.5–8.0×5.5–6.5 μm

A. aureoplumosa

2* Stipe smooth; basidiospores elliptic, 7.0×3.0–4.0 μm

A. erythroxa

1* Occurring in temperate Australia

3 Basidiomata sequestrate (secotioid)

A. geoaustralis

3* Basidiomata agaricoid

4 Basidiospores elongate-cylindric, >10-μm long, pale; cheilocystidia elongate-cylindric to narrowly oblong-clavate

A. arenacolens

4* Basidiospores elliptic, subamygdaliform to subphaseoliform, mostly <10-μm long, ochraceous-buff or tawny; cheilocystidia elongate clavate, skittle-shaped, or with serpentine on sinuous outline

5 Pileus light orange brown to orange brown; stipe length longer or as long as pileus diameter; cheilocystidia narrow, 6–9 μm diameter, often with flexuous outline; tissues exuding yellow pigment in alkali

A. serpentinocystis

5* Pileus light brown, light yellowish brown to brown; stipe length less than pileus diameter; cheilocystidia more broad, 7–16 μm diameter, outline oblong-clavate or skittle-shaped; tissues not exuding yellow pigment in alkali

6 Basidiospores ochraceous-tawny under the light microscope; New South Wales, Australia

A. dolichocystis

6* Basidiospores not as richly pigmented as above, more ochraceous-buff; Western Australia

A. chamaecephala

Taxonomy

Auritella Matheny and Bougher, gen. nov.

Basidiomata carnosa, 'agaricoid' vel 'sequestrate', frequentissime dura, non rubescentia; pileus squarrosus, squamulosus vel tomentosus; cortina praedita vel nulla; cheilocystidia plerumque >50 μm, membrana tenui praedita typice; basidia plena necropigmentata; basidiosporae laeves, pallidae vel 'ochraceous tawny', apiculus plerumque indistinctus; habitat in sylvis tropicis vel temperatis praecipue Fabacearum vel Myrtacearum.

Typus: *Auritella dolichocystis* Matheny, Trappe and Bougher

Basidiomata agaricoid or sequestrate; usually tough; pileus squarrose, squamulose or tomentose; cortina present or absent; context not reddening; cheilocystidia elongated, usually thin-walled, often >50-μm long, when present; basidia necropigmented; basidiospores smooth, very pale brown, ochraceous-buff, or ochraceous tawny in water and weak akaline mounts; apiculus indistinct, rarely distinct. Associated with Myrtaceae and Fabaceae. Holotype: *A. dolichocystis* Matheny, Trappe and Bougher.

Etymology: golden tissue or golden web, in reference to the ochraceous hymenium

Distribution: temperate Australia and tropical Africa

Auritella aureoplumosa (Watling) Matheny comb. nov. Fig. 2a–c

Inocybe aureoplumosa Watling, *Czech Mycology* 52: 331. 2001 (basionym). Pileus 1.5–5.5(8.0) cm diameter, broadly convex to plano-convex with a small, flat, central umbo; margin fluted, ridged, and puckered, upturned in age; surface distinctly punctate-squamulose from fibrils joined at the apex that form distinct tufts against a background of more regularly smaller brown fibrils that are radially fibrillose towards the margin; rich tawny orange becoming

6

Fig. 2 Microscopic characters of *A. aureoplumosa* (type), *A. geoaustralis* (type), *A. arenacolens* (type and PERTH 05429692), and *A. serpentinocystis* (type). **a** Spores of *A. aureoplumosa*. **b** Basidia of *A. aureoplumosa*. **c** Cheilocystidia of *A. aureoplumosa*. **d** Spores of *A. geoaustralis*. **e** Basidia of *A. geoaustralis*. **f** Spores of *A. arenacolens* (four on right from the type). **g** Basidia of *A. arenacolens*. **h** Cheilocystidia of *A. arenacolens* (three on right from the type). **i** Spores of *A. serpentinocystis*. **j** Basidia of *A. serpentinocystis*. **k** Cheilocystidia of *A. serpentinocystis*. The *bar* is equal to 10 μm for spores and 25 μm for basidia and cheilocystidia
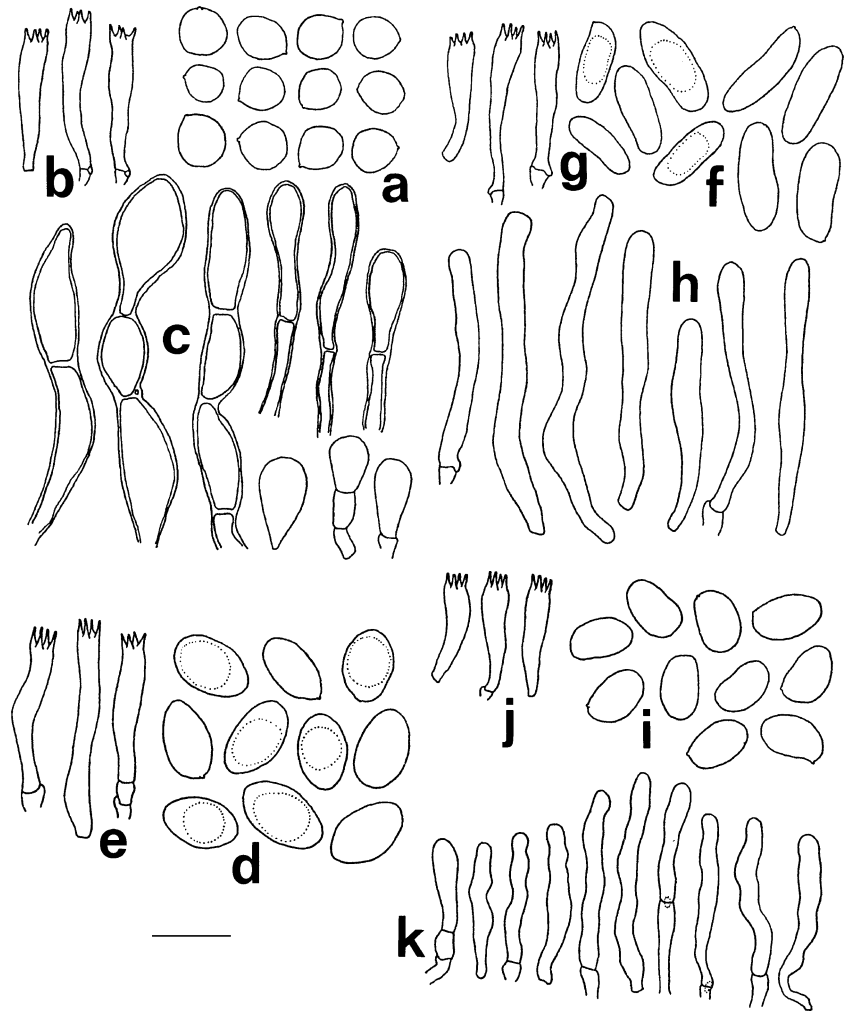
rust brown with reddish ochre, darker at the center; context tough, whitish or honey-colored; odor not described. Lamellae free, clay brown to cigar brown when young becoming tinged hazel or hazel throughout in age, mottled with conspicuous paler floccules on the edge, on dried basidiomata the edges darker than the faces. Stipe 3.1–9.0 cm×5–10 mm, slender with a poorly developed marginate bulb, surface roughened with girdles of rich tawny orange scales resembling a *Leccinum* sp., upper girdle forming a poor ring-like zone, punctate and less fibrillose-scurfy towards the apex, colored like the lamellae but pale towards the apex; context tinged dirty ochraceous downwards, faintly brunnescent downwards on exposure to air or even slightly pinkish brown at the apex.

Basidiospores (6.0) 6.5–7.2 to 8.0 (9.5)×(5.0) 5.5–6.0 to 6.5 (7.0) μm; Q=(1.0)1.1–1.2 to 1.5(1.6) (n=80/4), smooth, mostly subglobose, occasionally broadly elliptic but often elliptic in Watling 26726, "Ochraceous-Tawny" or bright ochre brown in H_2O and alkali mounts, unreactive in Melzer's, walls thickened to thick-walled, at times up to 0.5-μm thick; apiculus usually small and indistinct but occasionally distinct (Fig. 2a). Basidia 32–45×7–11 μm, 4-sterigmate, subclavate to cylindric, hyaline to ochraceous when revived, necropigmented (Fig. 2b). Pleurocystidia absent. Cheilocystidia mostly composed of elongated chains of hyphae that extend 200–400 μm, subtending cells usually cylindric; terminal cells variable—cylindric, fusiform, inflated, globose, pyriform—28–90×7–16 μm, yellowish on young material, "Burnt Sienna" to "Orange Rufous" in age, becoming secondarily thickened, walls accumulating plaques of incrustations, at times coarsely so (Fig. 2c). Caulocystidia absent, superficial hyphae on stipe similar to the pileipellis, bright ferruginous or "Orange Rufous" in mass, thick-walled, cylindric, 6–15 μm diameter; tramal hyphae thin-walled, hyaline to yellowish, 3–7 μm diameter, refractive hyphae present. Lamellar trama parallel, hyphae 5–15 μm diam, cylindric, dull yellowish brown in mass, rusty colored refractive hyphae present; subhymenium of cylindric hyphae. Pileipellis a prominent trichoderm, "Ferruginous" to "Orange Rufous" in mass, rather brightly colored; hyphae 6–10 μm diameter, cylindric to subfusiform, incrusted, walls slightly thickened

to thick-walled, up to 1.0 (1.5)-μm thick; tramal hyphae thin-walled, cylindric, pale yellow to hyaline, up to 10 μm diameter. Clamps present.

Gregarious in troops on soil in lowland rainforest, probably associated with caesalpinioid legumes of tribe Amherstieae in the Fabaceae, west Cameroon, Africa, March to June.

Material examined Cameroon, SW province near Mundemba, Korup Forest Reserve, before North/South line, lowland rainforest, in a troop on trackside, leg. R. Watling, 22. 3. 1991. Watling 23132, Holotype (E). Same locality and date as above but between P1 and North/South line, leg. R. Watling. Watling 23,086 (E). Same locality as above, transect P21–22, east bank of River Ndian, leg. J. Rother, 19. 6. 89. Watling 26,726 (E). Same locality as above, on trail to research area, leg I. Alexander, no date. Watling 26,727 (E).

Commentary The gross morphological description is taken from Watling (2001) and modified to fit the format of this paper. The microscopic data are presented from our personal observations. Tropical taxa of the Inocybaceae are poorly known and not richly represented as in temperate regions (Kuyper 1986; Matheny et al. 2003; Watling 2001). However, several species are now known from paleotropical ectotrophic regions such as Zambia (Buyck and Eysartier 1999; Matheny and Watling 2004) and India (Vrinda et al. 1997; Natarajan et al. 2005).

A. aureoplumosa is a very unusual species in several regards, its gross morphological characters notwithstanding. The basidiospores are mostly subglobose and more richly pigmented (tawny) than other species of *Auritella*. The gill edges are composed of long filamentous chains of pigmented hyphae that may extend several hundreds of microns beyond the hymenium. The terminal cells are usually cylindric, fusiform, clavate, or sphaeropedunculate. On immature specimens, the cheilocystidia are thin-walled and hyaline to yellowish. However, they become secondarily thickened and layered with plaques of incrustations and develop rich tawny pigment apparently as basidiomata mature. The species appears to associate with caesalpinoid legumes of tribe Amherstiae in the paleotropics of west Cameroon (Alexander 1989).

Auritella erythroxa (De Seynes) Matheny (see below) is quite similar to *A. aureoplumosa*. However, according to the protologue, the former can be distinguished by the smooth stipe and elliptic spores. Both share the same type of trichoderm pileipellis and free lamellar attachment that are illustrated by De Seynes (1897).

A. erythroxa (De Seynes) Matheny comb. nov. Fig. 4a

Inocybe erythroxa De Seynes, *Rech. Champ. Congo Fr.* 1:2.1897 (basionym). Pileus 1.5–2 cm diameter, plane, fleshy, center slightly raised, margin at length uplifted irregularly, surface ornamented with red pyramidal scales, ferruginous; context yellowish to yellow, tough. Lamellae free, remote, or barely adnate, unequal in length, ventricose, dirty yellowish brown, edges discolored. Stipe 1.5-cm long, smooth, hollow in age, ferruginous below, paler above [colors per icon].

Basidia 25-μm long, 4-sterigmate, rarely 2-sterigmate, clavate, exserted; parabasidia (sic) upright and straight. Basidiospores 7.0×3.0–4.0 μm, smooth, ovate, ferruginous, numerous. Cystidia [metuloids] not observed. Gabon, Talagouga, on soil, April.

Commentary The above description is a translation of the original Latin diagnosis published by De Seynes (1897). It is not known if the type or authentic material exists. Nevertheless, De Seynes' protologue and colored icons of *A. erythroxa* (Fig. 4a) leave no doubt that it is phenotypically very similar to *A. aureoplumosa* from nearby Cameroon. Based on current knowledge, two characters suggest that *A. erythroxa* represents an autonomous species: (1) the stipe is described as smooth and not girdled with scales and (2) the spores are elliptic, not globose to subglobose. De Seynes comments that the tissue in the pileus ("sous-épidermique") exhibits a large amount of calcium-oxalate crystals. We failed to see a similar observation in reconstituted dried sections in water mounts of *A. aureoplumosa*.

Auritella geoaustralis Matheny and Bougher nom. prov. Figs. 2d,e and 4b

Basidiomata columella-stipitata, pulvinata vel subelliptica, cremea, sicca, odorifera. Gleba brunnea, loculata. Basidia plena necropigmenti. Sporae laeves, ellipticae, non amyloideae et non dextrinoideae, "Ochraceous-Buff" vel "Ochraceous-Tawny", 9–10.5×5.5–6 μm, apiculus non distinctus. Habitat in sylvis eucalyptinis. Holotypus hic designatus in PERTH (H7344), isotypus in WTU.

Basidiomata sequestrate (secotioid like *Thaxterogaster*) up to 2.0×1.2 cm, pulvinate or roughly elliptic, cream, not bruising (Fig. 4b). Peridium thin, <1-mm diameter, cream in section, dry, minutely silky-fibrillose; odor unpleasant. Gleba composed of irregularly empty locules, some radial pattern evident; dark brown (near 7E7); truncate columella cream in section, other minor sterile intrusions present in other parts of the basidiome, emerging from basidiomata only as a bump; no basal mycelium visible.

Basidiospores (8.5)9.0–9.7 to 10.5 (11.0)×5.5–5.9 to 6.0 (6.5) μm; Q=(1.42) 1.50–1.63 to 1.75 (1.83) (n=20/1), smooth, ovate-elliptic; wall slightly thickened, pigmentation normal-"Ochraceous-Buff" to "Ochraceous-Tawny", unreactive in Melzer's, apiculus indistinct (Fig. 2d). Basidia 40–60×8–10 μm, 4-sterigmate, irregularly cylindric to subclavate, at times widest just below the apex, necropigmented, sterigmata often up to 6-μm long, appearing statismosporic and forming a hymenium (Fig. 2e). Cystidia not observed. Peridial hyphae cylindric to somewhat inflated, at times femur-shaped, thin-walled, bands of

possibly incrusting pigment or wrinkles present, at times some hyphae decorated with sparse exterior incrusting granules, these unreactive in Melzer's. Clamps present.

Scattered, emerging from soil under *Eucalyptus wandoo* and *Gastrolobium parviflorum* (Fabaceae), 30 km N of Kellerberrin, Wheat Belt region, Western Australia, July.

Material examined Australia, Western Australia, Wheat Belt region, 30 km N of Kellerberrin (plot 17B S), emerging from soil under under *E. wandoo* and *G. parviflorum*, leg. S. Bolsenbroek, 7. 31. 1996. H7344, Holotype (PERTH), Isotype (WTU).

Commentary A. geoaustralis is currently known only from the type collection. However, multiple genes—*rpb1, rpb2,* and nLSU—strongly support the placement of this sequestrate species in the Auritella clade (Matheny 2005; Matheny and Watling 2004). In addition, *A. geoaustralis* is the sister species to the agaricoid *A. serpentinocystis* (described below). Previously, Francis and Bougher (2003) listed a provisional genus, "*Geoinocybe*", in a table of cortinarioid sequestrate fungi. "*Geoinocybe*", if published, would make *Auritella* a paraphyletic genus. Hence, it is not prudent to recognize such a taxon exclusively for sequestrate taxa of the Inocybaceae.

Despite the secotioid appearance of the holotype, this species exhibits characters shared with other species of *Auritella*, namely, the smooth spores, necropigmented basidia, absence of pleurocystidia, and association with Myrtaceae and Fabaceae. *A. geoaustralis* is the first sequestrate species described in the Inocybaceae.

Auritella arenacolens (Cleland) Matheny and Bougher comb. nov. Figs. 2f–h and 4c

Naucoria arenacolens Clel., *Trans. R. Soc. S. Australia* 57:193. 1933 (basionym). *Inocybe arenacolens* (Cleland) Horak, *Persoonia* 11: 6. 1980. Fig. 2. *BIBL.*Grgurinovic, *Larger Fungi of S. Australia*: 187. 1997. Fig. 114.

Pileus 1.0–5.6 cm in diameter, subovate, convex becoming plane, incurved to decurved, lightly uplifted and undulating with age; surface dry, velvety-tomentose to appressed matted-fibrillose, somewhat coarsely so near the margin, margin entire; pale beige (near 6C4), cinnamon, to dark brown (Fig. 4c); context pale rusty ochraceous, hard or tough and breaking cleanly, odor and taste not remarkable. Lamellae adnate or broadly adnexed, close, with several tiers of lamellulae, thin or thickened, dark beige to dark yellowish brown (6E8) or dark brown (6F7) with age, edges conspicuously pallid-fimbriate, subventricose, 3–8 mm diameter. Stipe 1.0–4.0 cm×5–17 mm at the apex, often short and squat, equal or tapered towards the 6–8-mm-diameter base, central, terete; cortina evanescent if present at all, finely fibrillose or longitudinally striate with fibrils breaking up into fibrillose scales at times; paler than pileus, pale brown to light yellowish brown; context solid or hollow, colored like pileus, fleshy fibrous, usually tough or firm.

Basidiospores (9.5) 10.0–11.7 to 14.0×4.0–4.7 to 5.5 (6.0) μm, *Q*=(1.73) 2.00–2.53 to 3.11 (3.13) (*n*=51/4), smooth, oblong-cylindric, or at times with a ventral depression appearing elongated-subreniform, apices often obtuse; very pale brown or "Warm Buff" to "Light Ochraceous-Buff", walls slightly thickened; apiculus small and indistinct (Fig. 2f). Basidia 37–63×7–11 μm, necropigmented basidia often elongated, 4-sterigmate, slenderly clavate to subcylindric, hyaline or ochraceous (Fig. 2g). Pleurocystidia absent. Cheilocystidia (29) 49–92×6–13 μm, elongated and cylindric, less often slenderly clavate or at times somewhat flexuous, hyaline or ochraceous, thin-walled, apices obtuse; edges of lamellae sterile (Fig. 2h). Apex of stipe with clustered caulocystidia similar to cheilocystidia; tramal hyphae with scattered refractive interhyphal deposits. Pileipellis with a suprapellis of interwoven cylindric hyphae, up to 10 μm diameter, thin-walled; yellowish brown in mass, smooth in appearance; subpellis interwoven, distinctly ochraceous-brown in mass, hyphae 5–10 μm; incrusting pigments not observed or very weak; ochraceous refractive hyphae present in trama. Clamps present.

On sandy soil under *Corymbia calophylla*, *Eucalyptus marginata*, *Melaleuca thymoides*, *Spyridium globulosum* (Rhamnaceae), *Acacia* (Fabaceae), and *Hakea* spp. (Proteaceae), Western Australia and South Australia, May to June.

Material examined Australia, South Australia, Encounter Bay, Waitpinga Rd, emerging from sandy soil, leg. J. B. Cleland, 27. 5. 1932. AD 12222, Lectotype (AD). Australia, South Australia, Encounter Bay, in sand, leg. J. B. Cleland 27. 5. 1933. AD 12261 (AD). Australia, South Australia, Encounter Bay, in sand, leg. J. B. Cleland, 22. 5. 1930. AD 12262 (AD). Australia, Western Australia, Denmark, 34°57'24" S, 117°21'246" E, Haigh's Lot 536, Scotsdale Rd, in litter near boundary firebreak under *C. calophylla*, *E. marginata*, *Hakea* spp., and associated understorey, leg. E. Syme, 25. 5. 1991. PERTH 04988728 (=KS 21/91). Australia, Western Australia, Rocky Point Track, 34°59'12" S, 118°07'06" E, gregarious in sandy soil under *S. globulosum* and *M. thymoides*, leg. K. Syme, 28. 5. 1992. PERTH 05429692 (=KS 540/92). Australia, Western Australia, Wheat Belt region near site 17, along Higginson Rd, 20 km N of Kellerberrin, partially submerged or pileus even with surface, under *Allocasuarina* and *Acacia*, leg. I. Tommerup, W. Dunstan and N. Bougher. 15. 6. 1995. E5465 (CISRO; WTU).

Commentary This species is recorded for the first time since it was originally described from South Australia in the 1930s (Cleland 1933). *A. arenacolens* is believed to be known from three additional sites in Western Australia including the Wheat Belt region under *Allocasuarina* and *Acacia* and the southern coastal region near Denmark where it associates with the myrtaceous genera *Melaleuca*, *Corymbia*, and *Eucalyptus* as well as *Spyridium* (Rhamnaceae). The long cylindric cheilocystidia and pale oblong-cylindric to oblong-subreniform basidiospores are

diagnostic characters for the species. The basidiospores of the Wheat Belt collection (E5465) are more broad than others (their mean Q is 2.17 compared to 2.85 for the type and 2.69 for the Denmark, Australia material). Nevertheless, other critical characters are in agreement including the pale oblong spores, long basidia, and long narrow cheilocystidia.

Grgurinovic (1997) considered this species a member of section *Rimosae* (Fr.) Sacc., a paraphyletic group distributed in two clades, Inosperma and Pseudosperma (Matheny 2005; Matheny and Watling 2004). Although phylogenetic evidence is currently lacking, we believe *N. arenacolens* is better placed in *Auritella* because of the lack of reddening context, tough basidiomata, absence of distinctive odor, lack of a rimose or squamulose pileus, and a gross overall morphology most similar to other species of *Auritella* from Australia.

Auritella serpentinocystis Matheny, Trappe and Bougher nom. prov. Fig. 2i–k

Cheilocystidia serpentina, 35–72×5–10 µm. Basidia plena necropigmenti. Pileus 1.3–3.0 cm latus, aurantiobrunneus vel corylinus, velutinus, interdum areolatus, odor non distinctus. Lamellae adnatae, pallidobrunnae vel umbrinae, manifeste fimbriatae. Stipes 1.3–3.3 cm×2–7 mm, non brevis, fibrillosus, cortina nulla. Basidiosporae laeves, 8–9.5×5–5.5 µm, apiculus non distinctus, "Ochraceous-Buff". Habitat in sylvis eucalypti et acaciae. Holotypus hic designatus in PERTH (Trappe 25,080), isotypus in WTU.

Pileus 1.3–3.0 cm, convex, light orange brown to orange brown, fulvous to hazel, when dry "Amber Brown", "Sudan Brown", to "Antique Brown", minutely velvety, dry, at times cracking circumscissily; context brownish white or pale brown, odor musty or indistinctive. Lamellae adnate, seceding, at first pale brown, later dull brown to dark brown, coarsely fimbriate. Stipe 1.3–3.3 cm×2–7 mm, often longer than pileus diameter, habit not squat, pale brown to brownish white, longitudinally fibrillose, pruinose only at the extreme apex; veil not observed at any stage; context solid. Tissues exuding yellow pigment in alkali solutions.

Basidiospores 8.0–8.6 to 9.5×5.0 to 5.4–5.5 µm; Q=1.45–1.59 to 1.73 (n=10/1), smooth, subphaseoliform, subamygdaliform to elliptic, apices obtuse, apiculus not distinct; brownish yellow or "Ochraceous-Buff" (Fig. 2i). Basidia 28–39×8–9 µm, 4-sterigmate, occasionally 1-, 2-sterigmate, clavate to slenderly so, necropigmented, ochraceous brown to hyaline (Fig. 2j). Pleurocystidia absent. Cheilocystidia (25) 35–72 (82)×5–10 µm, narrowly cylindric to slenderly subclavate, serpentine to flexuous, thin-walled or rarely secondarily thickened, hyaline or less often ochraceous, apices obtuse to swollen, not capitate, at times subtended by concatenated cells and these arising from incrusted lamellar tramal hyphae, occasionally mixed with few clavate cells; entire edge sterile (Fig. 2k). Caulocystidia 25–43×9–15 µm, in dense clusters, restricted

to the extreme apex, dissimilar from cheilocystidia, (sub) clavate to cylindric but not long and serpentine, thin-walled, hyaline, caulobasidia at times scattered at the apex. Lamellar trama parallel, at times incrusted. Pileipellis a cutis composed of (sub)parallel to somewhat upturned cylindric hyphae, 5–11 µm diameter, incrusted, ochraceous to tawny in mass; tramal hyphae pale yellow to subhyaline, up to 13 µm diameter, frequently septate. Mounts of context tissue dissolve pale yellow pigment in alkali. Clamps present.

Scattered in woodlands under *Eucalyptus*, *Acacia*, and *Micromyrtus*, 260–270 m elev, New South Wales, Australia, April.

Material examined Australia, New South Wales, Parkes Shire, Genaren, inside Genaren Hill Sanctuary near south central gate, Easting 579,400/Northing 6,393,750, elevation 260 m, flat area at top of W slope with deep soil, ungrazed woodland of *Eucalyptus sideroxylon* (Large Mugga Ironbark), *E. dealbata* (Tumbledown Gum) and *E. microcarpa* (Grey Box), leg. J. Trappe. 21. 4. 2000. Trappe 25,066 (PERTH; MEL). Same locality as above, Easting 580,100/Northing 6,396,150, elevation 270 m, just E of ridgetop with skeletal rocky soil, under same *Eucalyptus* spp. as above and *Acacia doratoxylon* (Currawang) with *Micromyrtus ciliata* (Fringed Heath Myrtle), leg. J. Trappe, 22. 4. 2000. Trappe 25,080, Holotype (PERTH), Isotype (WTU).

Commentary *A. serpentinocystis* is distinguished by the snake-like, long, narrow cheilocystidia, orange brown velvety pileus and occurrence under *Eucalyptus* in southeast Australia. The species also appears to lack a veil. Rehydrated context tissue exudes a yellow pigment in alkali solution, similar to the genus *Pleuroflammula* Sing. (Singer 1986). *A. arenacolens* has similar cheilocystidia but differs by its much longer spores and russet to cinnamon brown pileal color. *A. dolichocystis* (see below), also described from New South Wales, is light yellowish brown and has elongated clavate cheilocystidia with subcapitate apices. A collection made by Dr. O. K. Miller, Jr. from Western Australia under *C. calophylla* and *Chamelaucium uncinatum* (OKM 23824/E587 CSIRO) may represent an autonomous taxon by virtue of the pileus with a well-developed velipellis and longer basidiospores (9.0–11.0×4.5–5.5 µm). Matheny et al. (2002) informally referred to *A. serpentinocystis* as *Inocybe serpitocystis*.

A. dolichocystis Matheny, Trappe and Bougher nom. prov. Fig. 3a–c

Cheilocystidia longissima, 45–75×9–14 µm. Basidia plena necropigmenti. Pileus 1.2–4.0 cm latus, alutaceus vel subbrunneus, glaber vel fibrillosus, odor typice non distinctus. Lamellae adnexae, adnatae vel subdecurrentae, pallidobrunnae vel umbrinae, fimbriatae. Stipe 0.7–2.7 cm×4–10 mm, ad apicem leviter pruinosus, fibrillosus, cortina nulla. Basidiosporae laeves, 7.5–10.5×4–5.5 µm,

Fig. 3 Microscopic characters of *A. dolichocystis* (type) and *A. chamaecephala* (type). **a** Spores of *A. dolichocystis*. **b** Basidia of *A. dolichocystis*. **c** Cheilocystidia of *A. dolichocystis*. **d** Spores of *A. chamaecephala*. **e** Basidia of *A. chamaecephela*. **f** Cheilocystidia of *A. chamaecephala*. The *scale bar* is equal to 10 μm for spores and 25 μm for basidia and cheilocystidia
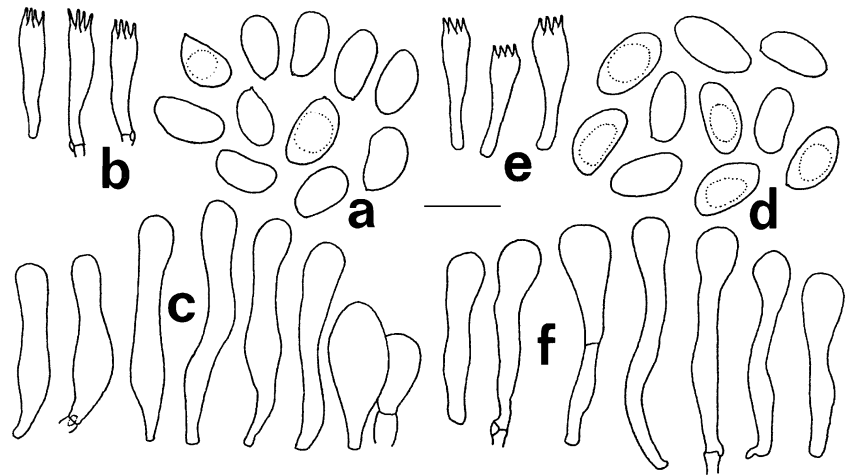
apiculus non distinctus, "Ochraceous-Tawny" vel "Ochraceous-Buff". Habitat in sylvis eucalyptinis, callitrinis et acacinis. Holotypus hic designatus in PERTH (Trappe 24,838), isotypus in WTU.

Pileus 1.2–4.0 cm diameter, convex to plane, surface dry, disc glabrous to obscurely fibrillose, towards margin finely fibrillose to fibrillose, at times slightly sulcate but not striate, edge of pileus appressed against the stipe when young; light yellowish brown to light brown; context brownish white or pale brown, up to 5 mm thick, odor not distinctive or faintly sweetly pungent. Lamellae adnexed, becoming adnate to adnate-subdecurrent; lamellulae infrequent, brownish gray to light grayish brown when young, dull brown with age; edges pallid fimbriate. Stipe 0.7–2.7 cm×4–10 mm, cortina absent even on young basidiomes, longitudinally fibrillose, subsquamulose when young, the upper half or apical 1–2 mm sparsely pruinose, white at apex, brownish white to pale brown below, or concolorous with pileus.

Basidiospores (7.0) 7.5–8.6 to 10.5×4.0–4.8 to 5.5 μm; $Q =$ (1.40) 1.50–1.81 to 2.25 (2.63) (n=57/5), smooth, elliptic, less frequently (sub)amygdaliform to phaseoliform; "Ochraceous-Tawny" to "Ochraceous-Buff", with slightly thickened walls; apiculus indistinct but at times distinct (Fig. 3a). Basidia 30–45×7–10 μm, 4-sterigmate, (narrowly) clavate, ochraceous to hyaline (Fig. 3b). Pleurocystidia none. Cheilocystidia (42) 45–75 (82)×9–14 (16) μm, subfusiform, sublageniform to slenderly clavate with median to basal subventricose swelling, apices swollen to subcapitate; thin-walled, hyaline to ochraceous (Fig. 3c). Caulocystidia present and frequent at apex of stipe, usually similar to cheilocystidia, at times lacking subcapitate apices or shorter, in clusters, irregularly cylindric, fusiform to clavate; stipe hyphae brownish yellow to hyaline, 3–10 μm diameter; refractive hyphae frequent. Lamellar trama parallel. Pileipellis a cutis of incrusted, cylindric hyphae, 4–13 μm diam, ochraceous-tawny in mass; tramal hyphae brownish yellow in mass, cylindric. Clamps present.

On ground under *Eucalyptus* and also occurring with *Callitris* (Cupressaceae) and *Acacia* and *Dillwynia* (Fabaceae), 260–400 m elevation, New South Wales, Australia, April and October to November.

Material examined Australia, New South Wales, Parkes Shire, Bumberry Lake, Easting 629,200/Northing 6,333,300, elevation 400 m, on flat with ungrazed *Eucalyptus*. *sideroxylon* (Large Mugga Ironbark) and a few *E. microcarpa* (Grey Box) with a grass ground cover and a few *Callitris endlicheri*, *Acacia parvifolia*, *Dillwynia juniperina* and several other shrubs, leg. J. Trappe, 11. 11. 1999. Trappe 24,893 (MEL). Australia, New South Wales, Parkes Shire, Genaren inside of Genaren Hill Sanctuary near south central gate, Easting 579,400/Northing 6,393,750, elevation 260 m, flat area in ungrazed woodland of *E. sideroxylon*, *E. microcarpa*, and *E. dealbata*, leg. J. Trappe, 21. 4. 2000. Trappe 25,067 (MEL). Australia, New South Wales, Weddin Shire, Holy Camp Road, Glenrock; Easting 596,500/Northing 6,248,300, elevation 395, sheep-grazed regrowth *E. albens* (White Box) with bare soil and some grass, flat on ridgetop, E aspect, 1% slope, leg. J. Trappe. 25. 10. 1999. Trappe 24,838, Holotype (PERTH), Isotype WTU). Australia, New South Wales, same locality as above, leg. J. Trappe, 24. 10. 1999. Trappe 24,843 (MEL; WTU). Australia, New South Wales, same locality as above, leg. J. Trappe, 24. 10. 1999. Trappe 24,844 (MEL; WTU).

Commentary A. dolichocystis is distinguished by the yellowish brown to light brown, fibrillose basidiomata; long, narrow cheilocystidia with swollen to subcapitate apices and relatively small spores. The elongated narrow cheilocystidia are suggestive of *A. arenacolens* except the latter lacks subcapitate apices and exhibits longer spores that are much paler in pigment. *A. serpentinocystis* occurs in the same region (New South Wales) but differs by the undulating or serpentine narrow cheilocystidia. *Auritella chamaecephala* (described below) is most similar to *A. dolichocystis*, but differs by the spores that are paler in color, distribution in Western Australia and *rpb2* and nLSU nucleotide sequences (see "Phylogenetic results" below).

A. chamaecephala Matheny, O. K. Mill. and Bougher nom. prov. Figs. 3d–f and 4d

Auritella dolichocyste sequentiis "nLSU-rDNA" et "*rpb2*" differt. Basidiosporae "Ochraceous-Buff" to "Light Ochraceous-Buff". Habitat in sylvis eucalypti et allocasuarinae. Holotypus hic designatus in VPI (OKM 23,901), isotypus in WTU.

Pileus 2.0–3.5 cm, ovate or convex becoming broadly convex, incurved to decurved and undulating with age at the margin; surface dull, dry, indistinctly tomentose with smooth appearance or with dense tufts of fibrils, light brown (5C4) with a darker center (5C6) to brown (6D6-D7) (Fig. 4d), brown with 3% KOH, dark green with FeS0$_4$; context firm, beige (near 5B5-A4), 3.5–6 mm diam under the center; odor indistinct. Lamellae adnate to narrowly adnate, close to subdistant, with several tiers of lamellulae, light brown (near 5C5) maturing to brown (5E7-6D5) or dark brown (6F5-F6), 2–5 mm broad; edges pallid and fimbriate. Stipe 1.5–3.0 cm×4–8 mm, terete, equal or only slightly enlarged at the base, cortina not observed, fibrillose, in places minutely punctate, floccose near the base, or with tufts of fibrils, light brown (little paler than 5B3) to brown (6D5); context fleshy fibrous, solid, colored like pileal context.

Basidiospores (7.0) 7.5 to 8.3–9.5×4.0–4.7 to 5.5 μm; Q=1.60–1.77 to 2.00 (2.11) (n=42/3), smooth, mostly elliptic or at times subamygdaliform to subphaseoliform, pale brownish yellow or "Ochraceous-Buff" to "Light Ochraceous-Buff" (10YR 6/6), only slightly thick-walled; apiculus small and indistinct (Fig. 3d). Basidia 30–45×7–9 μm, 4-sterigmate, slenderly clavate, clavate, or cylindrico-clavate, hyaline to ochraceous (Fig. 3e). Pleurocystidia absent. Cheilocystidia 39–88×7–14 μm, often elongated into slenderly clavate outline, or skittle-shaped to irregularly cylindric, at times slightly flexuous but not serpentine, often with subcapitate or swollen apices, thin-walled, hyaline to ochraceous; lamellar edges sterile (Fig. 3f). Caulocystidia 20–55×7–10 μm, numerous at apex of stipe, clavate to cylindric or subutriform, rather similar to cheilocystidia but apices often obtuse. Lamellar trama regular, hyphae often inflated, 6–20 μm diam, pale yellowish brown in mass, smooth, frequently septate. Pileipellis an irregular cutis of cylindric hyphae, 5–11 μm diameter, thin-walled, "Ochraceous-Tawny" in mass, incrusted, many cells also with rusty-ochraceous refractive content; terminal cells undifferentiated; tramal hyphae more pale in mass, smooth, cylindric, refractive hyphae present. All tissues unreactive in Melzer's. Clamps present.

Gregarious on ground under *Eucalyptus diversicolor*, *E. jacksonii*, *C. calophylla*, *Allocasuarina decussata* (Casuarinaceae) and *Agonis flexuosa*, also *E. wandoo* and *E. marginata*; Denmark to Walpole and about 100 km east of Perth, Western Australia, May to June and September.

Material examined Australia, Western Australia, near Walpole and Normalup, middle of Gully Road under *Eucalyptus jacksonii* (Tingle), leg. O. K. and H. Miller, 10. 6. 1989. OKM 23,901, Holotype (VPI), Isotype (WTU). Australia, Western Australia, Denmark, lot 406, SE corner, 34°59'14" S, 117°18'48" E), in old pasture and moss above granite outcrop under *A. decussata*, *C. calophylla*, *A. flexuosa* and *E. diversicolor*, leg. K. Syme, 20. 5. 1993. PERTH 05439353 (=KS 645/93) (PERTH; WTU). Australia, Western Australia, east of Perth, John Forrest National Park, near trail to the lake, solitary on soil under *E. wandoo*, *E. marginata* and *C. calophylla*, leg. P. B.

Fig. 4 Illustrations and photos of *Auritella*. **a** Basidiomata, pileipellis, and spores of *A. erythroxa* reproduced from De Seynes (1897). **b** Sequestrate basidiomata of *A. geoaustralis* (type). **c** Basidiomata of *A. arenacolens* (E5465). **d** Basidiomata of *A. chamaecephala* (E7060). *Scale bars* are equal to 1 cm
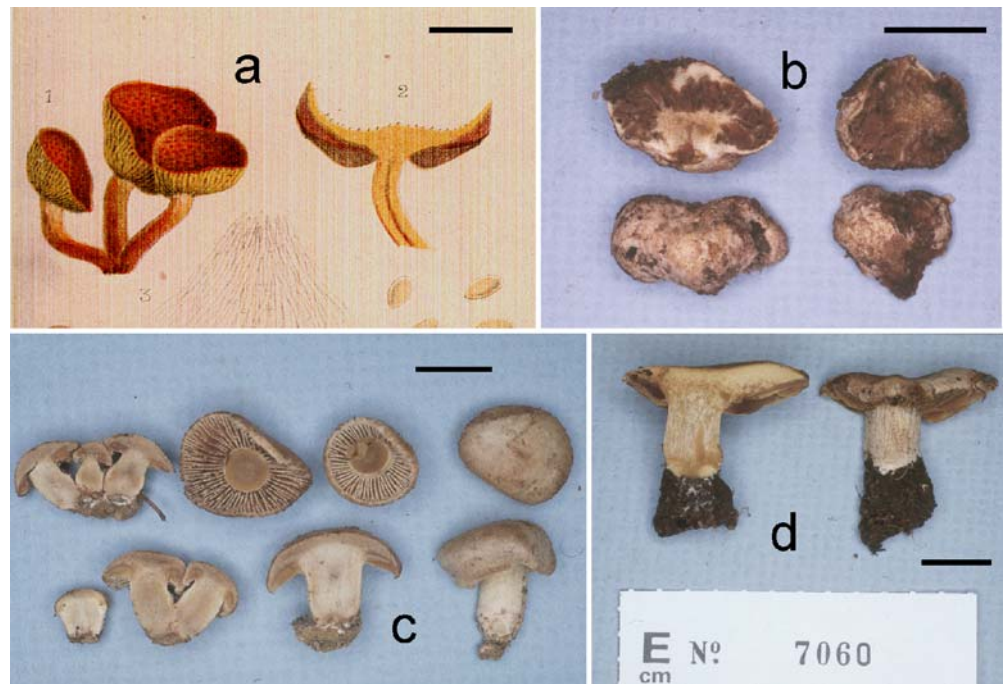
Matheny, 8. 9. 2001. PBM 2212 (=E7060) (WTU; CSIRO).

Commentary A. chamaecephala and *A. dolichocystis* are very similar species. They both share the same gross morphology (light brown to yellowish brown pileus, squat habit), spore size and cheilocystidia characters. However, the basidiospores of *A. chamaecephala* are noticeably paler than the ochraceous tawny spores of *A. dolichocystis* when spores of the two species are compared under the microscope. Eight to 11 nucleotide differences at the *rpb2* and nLSU loci support the distinction between both taxa. So far, *A. chamaecephala* is known from Tingle forests (*E. jacksonii*) and nearby surroundings of Denmark, Western Australia, a region of the state that receives the high end of a steep rainfall gradient across the southwest botanical province (Yates et al. 1999). The collection E7060 (CSIRO) was found in a drier habitat in association with *E. wandoo*, *E. marginata* (Jarrah), and *C. calophylla* (Marri) and exhibited somewhat thickened, narrow lamellae. However, it otherwise appears conspecific with the material cited here.

Phylogenetic results

rpb2 and nLSU sequences

The data set included 11 taxa, seven of which belong to *Auritella*. Nucleotide sequences between conserved domains 6 and 7 of *rpb2*, the most variable region of this gene (Liu et al. 1999; Matheny 2005), were obtained for all samples used in the nLSU analysis with the exception of *A. aureoplumosa*. Both *rpb2* amino acids and nucleotides were easily aligned. One amino acid insertion was shared by both *Crepidotus* taxa. Several insertions and deletions occurred in the sequence of intron 4, but this intron was not completely sequenced for all samples and was thus excluded from the final data set.

The *rpb2* nucleotide partition is composed of 643 sites, and the nLSU partition is composed of 1,287 sites. The combined data set comprises 1,930 sites. No characters were excluded due to ambiguities from either gene. Using the hierarchical likelihood ratio test of Modeltest, the best-fit model to the combined sequences was Tamura–Nei (Felsenstein 2004) with unequal base frequencies (A=0.2714; C=0.1868; G=0.2840; T=0.2577) and a gamma (Γ) distribution shape parameter of 0.1541. The rate of CT transitions was highest among all transformations at 11.9. AG transitions exhibited a rate of 5.7. All transversions were normalized to a rate of 1.0.

ML phylogeographic analyses and hypothesis testing

Initially, a molecular clock was rejected ($p<0.05$). However, after pruning the outgroup *Crepidotus* taxa, a molecular clock could not be rejected ($p=0.10$). For outgroup purposes, we then used two *Inocybe* taxa of the Mallocybe
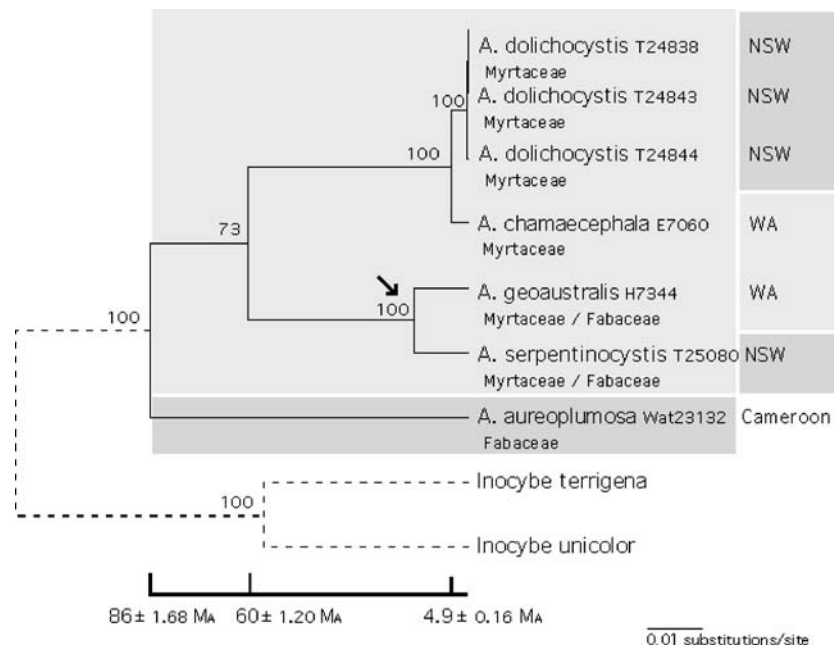

Fig. 5 ML clock phylogeny of *Auritella*. *Numbers* above branches represent bootstrap values. Australian taxa are monophyletic and *highlighted* in the large *light grey box*. The African branch is *boxed* in *dark grey*. Geographic origin of each terminal branch is indicated on the *far right* (NSW, New South Wales; WA, Western Australia). Plant family associates are also indicated *under* each taxon name in *Auritella* for the accession sequenced. The *arrow* refers to the node that was calibrated at 15 Ma. A divergence *time-line* is shown with divergence dates and their associated standard errors. The outgroups *Inocybe terrigena* and *I. unicolor* were used to estimate the two branches that stem from the node between *A. aureoplumosa* and the remainder of *Auritella*. The outgroups were pruned (*dashed lines*) before divergence dates were estimated

clade, which was shown previously to be the sister group to *Auritella* with a significant Bayesian posterior probability (>0.95 PP) (Matheny 2005). The clock-like ML tree is shown in Fig. 5. Bootstrap values are derived from the inclusive analysis.

Australian taxa (branches highlighted in the large light gray box) are monophyletic with 73% bootstrap support. Sister to the Australian clade is the Cameroon species, *A. aureoplumosa* (branch highlighted in dark gray box). Within the Australian clade, two nested clades are strongly supported (100% bootstrap) and composed of east–west disjunct taxa. One of these clades contains a sequestrate species, *A. geoaustralis*, from Western Australia, and an agaricoid species, *A. serpentinocystis*, from New South Wales. The other nested clade contains two very closely related species, *A. chamaecephala* from Western Australia and *A. dolichocystis* from New South Wales. Separate analyses of *rpb2* and nLSU (data not shown) support the three *A. dolichocystis* accessions as a monophyletic group. Following Sanderson (2003), the outgroups (branches shown as dashed lines) were pruned from the tree before divergence time estimation.

Specht (1981) estimated the formation of the Nullarbor plain about 15 Ma. We therefore calibrated the earlier of the two disjunct east–west nodes in Fig. 5 (see arrow) at 15 Ma under the assumption that the Nullarbor plain contributed to the allopatric speciation of both disjunct species pairs. From this calibration, k, the rate of nucleotide substitutions per site per year, was determined at $3.38 \pm 0.6 \times 10^{-10}$. This calibration suggests the Australian clade diverged from the African clade 86 ± 1.68 Ma. The first split among the Australian taxa occurred 60 ± 1.20 Ma. The recent divergence between the western *A. chamaecephala* and the eastern *A. dolichocystis* is dated at 4.9 Ma ± 0.16 Ma.

The molecular clock analysis suggests the divergence between the African and Australian lineages occurred at least no later than the late Cretaceous and thus rejects the hypothesis that a recent long-distance dispersal event accounts for the current distribution pattern of the two lineages. Indeed, the timing of the split is more consistent with a vicariance event between the two southern hemisphere land masses. All taxa that associate with the Myrtaceae, though potentially not exclusively, are monophyletic (large light grey box, Fig. 5). Currently, no species of *Auritella* are known from the *Nothofagus* zones of the South Pacific.

Discussion

The new Afro-Australian genus *Auritella*

Two African and five Australian species of *Auritella* are reported, four of which are described as new. To date, these taxa appear endemic to Africa and Australia although our knowledge in general of southern hemisphere fungi is still rather poor (Bougher and Syme 1998; Grgurinovic 1997; Matheny and Bougher 2005; Watling 2001). Despite this limitation, we used both morphological and/or molecular sequence data of two unlinked nuclear genes to characterize seven species in the genus.

Morphological characters that unite *Auritella* include the combination of elongated cheilocystidia (when present), possession of necropigmented basidia (Kuyper 1986; Matheny and Watling 2004), tough basidiomata, absence of pleurocystidia, smooth basidiospores with an even outline, the restricted geographic distribution to temperate Australia and tropical Africa and putative ectomycorrhizal association with most likely Myrtaceae, Fabaceae, and possibly Casuarinaceae.

All species of *Auritella* share cheilocystidia that often exceed 50 μm in length, with the exception of the sequestrate or truffle-like *A. geoaustralis*. Those of *A. aureoplumosa*, however, are distinctive by virtue of the floccose appearance on the gill edges, their extreme length, rich pigmentation, and secondarily thickened walls. This type of cystidium, however, is not homologous with the metuloid-type or lamprocystidium (Clémençon 2004) that characterizes *Inocybe* sensu stricto or the Inocybe clade (Matheny et al. 2002; Matheny 2005). *Inocybe unicolor* of the Mallocybe clade and *I. inexpectata* (Villarreal et al. 1998) exhibit elongated cheilocystidia (>50 μm); however these two species are endemic to eastern North America and Spain, respectively. An unpublished nLSU sequence of the type of *I. inexpectata* places it in a weakly supported position in relation to the other major depauperate (viz, lacking pleurocystidia) clades of the Inocybaceae, hence, its inclusion in our key as a sixth major lineage of the family. The Australian taxa of the Mallocybe clade can be distinguished by their stipe length that is often equal to or greater than the pileus diameter and their short clavate cheilocystidia less than 50 μm in length. The shape of cheilocystidia is also an important species-level character in *Auritella* ranging in outline from serpentine, cylindric to narrowly elongated clavate, or skittle-shaped. Some species, notably *A. dolichocystis* and *A. chamaecephala*, exhibit similar cheilocystidia to those of many *Simocybe* species of the Crepidotaceae (Singer 1973; Horak 1979a,b, 1980).

Homoplastic characters include presence or absence of a veil, pigmentation of basidiospores and gross morphological habit. To date, *Auritella* represents the only lineage of the Inocybaceae in which a sequestrate species, *A. geoaustralis* (see above), has been formally described. However, the first author has examined sequestrate material with metuloids from Australia with phylogenetic affinities to the Inocybe clade (Matheny and Trappe, unpublished). In any event, sequestrate taxa are very rare in the Inocybaceae in contrast to other dark-spored lineages of ectomycorrhizal euagarics (e.g., *Cortinarius*) (Peintner et al. 2001).

Putative ectomycorrhizal associates of *Auritella*

Field observations indicate all taxa occur on soil near woody angiosperms. Thus, it is not unreasonable to assume *Auritella* is ectomycorrhizal. In Cameroon, *A. aureoplumosa*

most likely associates with legumes of tribe Amherstiae (Fabaceae), which contain taxa that are known to be ectomycorrhizal (Alexander 1989; Matheny et al. 2003). In Australia, *Auritella* is probably mycorrhizal with species of *Eucalyptus* and *Corymbia* (Myrtaceae). Numerous studies have demonstated that *Eucalyptus* sensu lato forms ectomycorrhizas and that natural and plantation eucalypt ecosystems are ectotrophic (Bougher et al. 1990; Brundrett et al. 1996; Castellano and Bougher 1994; Glen et al. 2001). However, other plant associates of the Casuarinaceae (*Allocasuarina*) and Fabaceae (*Acacia*, *Dillwynia* and *Gastrolobium*) remain possible symbionts as well (Warcup 1980; Tommerup and Bougher 1999).

Auritella is composed of disjunct taxa at various geographic scales

The disjunct geographic structure in *Auritella* led us to predict several biogeographic patterns for the group. For instance, given the relatively long branch length of the African *A. aureoplumosa* (Fig. 5), one might predict it has been isolated for a great length of time. This divergence is noteworthy considering how conserved nLSU is generally among closely related species of fungi compared to internal transcribed spacer regions (Bruns et al. 1991; Takamatsu and Matsuda 2004) and among ectomycorrhizal dark-spored genera, e.g., *Cortinarius* (Høiland and Holst-Jensen 2000) and *Hebeloma* (Thomas et al. 2002). Thus, a relatively high divergence at the nLSU locus between Australian and African taxa appears highly inconsistent for a relationship to have been established by a recent long-distance dispersal event (Pirozynski 1983; Vilgalys and Sun 1994; Hibbett 2001).

Two cases of recent vicariance are inferred from the combined phylogeny (Fig. 5). Both events are consistent with an east/west vicariant pattern in Australia also observed for many plant species and possibly some mushroom taxa such as *Descolea* (Green 1964; Nelson 1974; Bougher et al. 1994). Green (1964) recognized about 50 pairs of presumed vicarious angiosperm species in southern Australia. However, discontinuous species, which have remained morphologically identical on either side of the Nullarbor plain, are also recognized. *A. dolichocystis* (from southeast Australia) and *A. chamaecephala* (from southwest Australia) are morphologically very similar but can be distinguished by *rpb2* and nLSU nucleotide sequences.

A molecular clock supports the divergence of African and Australian species of *Auritella* during the late Cretaceous

Our study represents one of few to hypothesize divergence times of low-level taxonomic groups of euagarics based on a molecular clock in a historical biogeographic context (Geml et al. 2004; Hibbett 2001). The paucity of such studies is likely attributed to complex taxon sampling, lack of robust phylogenetic estimates, theoretical concerns over use of molecular clocks, the poor fungal fossil record, and contentious calibration points. Nevertheless, we have demonstrated that ectomycorrhizal fungi can serve as useful biogeographic markers as predicted by Pirozynski (1983) and recently supported in a study on *Pisolithus* (Martin et al. 2002). A late Cretaceous diversification has also been reported in lichens (Printzen and Lumbsch 2000). Similarly, it is possible that ectomycorrhizal taxa may be of ancient descent (Halling 2001). For example, Ducousso et al. (2004) suggest the Dipterocarpaceae, an ectomycorrhizal angiosperm lineage, shares an ectomycorrhizal common ancestor with the endemic Sarcolaenaceae of Madagascar, a relationship that at the minimum dates back roughly 90 million years.

Pirozynski (1983) cited the major obstacle to fungal biogeography was the lack of understanding of evolutionary relationships. In this paper, we are able to present a well-supported and clock-like phylogeny of a small clade of southern hemisphere agarics and allied fungi. The ML-clock estimate of *Auritella* phylogeny (Fig. 5) suggests that the first split in the clade occurred between African and Australian lineages during the late Cretaceous, which corresponds well to several aspects of southern hemisphere plant biogeography. It coincides with the putative arrival of angiosperms to Australia (Raven 1979; Specht 1981), is consistent with the divergence of the Myrtales about 100 Ma and the Fabales about 75 Ma (Ladiges et al. 2003; Wikström et al. 2001), with which *Auritella* is likely mycorrhizal, and is congruent with a Gondwanan distribution that posits a low probability of dispersal between Africa and Australasia after roughly 70 Ma (Raven and Axelrod 1974; Raven 1979). During the late Cretaceous, India was not yet isolated (Briggs 2003) and may have served as a migratory go-between for biotic exchanges between Africa, Madagascar, and Australia up to 75–70 Ma. Thus, the initial divergence in *Auritella* appears more consistent with a late Cretaceous split and hypothesis of Gondwanan vicariance rather than due to a recent LDD event. We recognize that the interpretation of these patterns of relatedness is challenging and cannot rule out an ancient LDD event when oceanic barriers were not as distant as today (McLoughlin 2001).

Several caveats could temper our results. Taxon sampling of species of *Auritella* is not yet exhaustive. For instance, we were unable to generate sequence data for accessions of *A. arenacolens*, and we were unable to generate an *rpb2* sequence for *A. aureoplumosa*. Also, our calibration point may prove questionable (Graur and Martin 2004). We discuss this issue in more detail below.

The choice of 15 Ma as our calibration appears justified because it ties in well with our estimated times of major, and what are likely vicariance, events. In addition, the combined *rpb2* and nLSU substitution rate ($3.38\pm0.06\times10^{-10}$) given a 15 Ma calibration point is not at all grossly dissimilar to the nLSU substitution rate reported, for example, in the Erysiphales (Takamatsu and Matsuda 2004). However, there may have been a barrier to plant migration between eastern and western regions since about

50 Ma when a major marine incursion into southern Australia occurred (Charles-Nelson 1981). From the late Eocene to the mid Miocene, there was a more or less continuous period of marine incursion into southern central Australia. The sediments deposited during these periods constitute the Nullarbor karst region, which emerged in the mid Miocene and has remained as dry land since its emergence (Charles-Nelson 1981). Therefore, the Miocene marked the beginning of the partial isolation of the southwest botanical province from the rest of southern Australia (Marchant 1973). However, this estimate is not agreed upon by all authors. Burbridge (1960), for example, suggests the time of separation between east and west might be as recent as the late Pleistocene, on the basis of discontinuities between the two areas at the plant floral specific level. If gene flow between *A. geoaustralis* and *A. serpentinocystis* ceased later than dictated by our assumptions above, for example, around 10 Ma, then the Afro-Australian and internal Australian splits would have occurred at about 58 and 40 Ma, respectively. Even using this more conservative assumption, we are still able to reject a recent LDD hypothesis concerning the Afro-Australian divergence.

Conclusions

This study demonstrates several significant issues concerning molecular fungal systematics: (1) the taxonomy (morphological characterization and systematic position) of many widespread ectomycorrhizal taxa remains poorly known; (2) DNA-based phylogenetic analyses are necessary to untangle convergent gross and anatomical morphologies; (3) current taxonomic systems are inadequate to reflect information gained from diversity and phylogeographic studies; (4) vicariance-based phylogeographic hypotheses appear suitable to explain the distribution of lineages in *Auritella*; and (5) ectomycorrhizal fungi such as *Auritella* may represent ancient lines of descent dating back at least to the late Cretaceous. Thus, ectomycorrhizal fungi can serve as useful biogeographic markers.

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