**Nuytsia** The journal of the Western Australian Herbarium

https://florabase.dpaw.wa.gov.au/nuytsia/
https://doi.org/10.58828/nuy01046

*Nuytsia* 34: 65–92
Published online 21 March 2023

# Four new species of *Amanita* sect. *Roanokenses* (Basidiomycota) from Western Australia

**Elaine M. Davison[1,2,6], Danielle Giustiniano[3], Matt D. Barrett[4] and Katrina Syme[5]**

[1]School of Molecular and Life Sciences, Curtin University, GPO Box U1987, Perth, Western Australia 6845
[2]Western Australian Herbarium, Biodiversity and Conservation Science,
Department of Biodiversity, Conservation and Attractions,
Locked Bag 104, Bentley Delivery Centre, Western Australia 6983
[3]School of Biomedical Sciences, Curtin University, GPO Box U1987, Perth, Western Australia 6845
[4]Australian Tropical Herbarium, James Cook University, PO Box 6811, Cairns, Queensland 4870
[5]24 Offer Street, Denmark, Western Australia 6333
[6]Corresponding author, email: e.davison@curtin.edu.au

## Abstract

Davison, E.M., Giustiniano, D., Barrett, M.D. & Syme, K. Four new species of *Amanita* sect. *Roanokenses* (Basidiomycota) from Western Australia. *Nuytsia* 34: 65–92 (2021). Four species of *Amanita* Pers. are documented from Western Australia. *Amanita brunneola* E.M.Davison & Giustiniano is described from the Perth region. It is distinguished by its pale brown pileus, white universal veil, globose basal bulb, amyloid, cylindric spores and presence of clamp connections. *Amanita cretaceaverruca* E.M.Davison & Giustiniano is described from the Perth region and the southern jarrah forest. It is distinguished by its brown pileus, with a thick white warty universal veil, globose or ovoid basal bulb, amyloid, elongate spores and absence of clamp connections. *Amanita mallee* E.M.Davison, Giustiniano & M.D.Barrett is described from the Shire of Coolgardie. It is distinguished by its white pileus and universal veil, tapered basal bulb, amyloid, cylindric spores and abundant clamp connections. *Amanita validiuscula* E.M.Davison, Giustiniano & K.Syme is described from the wheatbelt and Yalgoo area. It is distinguished by its white pileus and universal veil, ivory lamellae, fusiform or tapered basal bulb, amyloid, ellipsoid spores and abundant clamp connections. Molecular analysis shows all these species are members of sect. *Roanokenses*. *Amanita brunneola, A. cretaceaverruca* and *A. mallee* form a clade with other species from Australia and New Zealand, which may indicate Gondwanan origin.

## Introduction

Some of the most conspicuous mushrooms in Western Australia are species of *Amanita* Pers. This is a large, cosmopolitan genus of over 1000 described species, although only about 600 are well defined (Yang *et al.* 2018). *Amanita* spp. are important ecologically because most species are mycorrhizal with woody plants; they are important economically because some species are edible whilst others are poisonous (Cui *et al.* 2018).

In Australia the genus has been monographed by Reid (1980) and Wood (1997). Additional species and clarifications have been made by Miller (1991; 1992), Grgurinovic (1997), Davison (2011), Davison and Giustiniano (2020), Davison *et al.* (2013; 2015; 2017a; 2017b; 2020; 2021) and McGurk *et al.* (2016). Currently about 100 named species have been published, but many more await description.


ISSN 2200-2790 (Online)
ISSN 0085-4417 (Print)

*Amanita* is defined by the field character of a membranous or friable universal veil, the microscopic characters of bilateral lamella trama and acrophysalidic stipe trama, and the ontogenetic character of schizohymenial development (Bas 1969). However, molecular analyses are of increasing importance for identifying new species and determining relationships within the genus (Cui *et al.* 2018).

*Amanita* has recently been revised by Cui *et al.* (2018) using concatenated data sets of *nuLSU* (28S nuclear ribosomal large subunit rRNA gene), β-tubulin, *ef1-α* (elongation factor 1-α), and *rpb2* (RNA polymerase II) gene regions. They recognised three subgenera: *Amanita*, *Amanitina* (E.-J.Gilbert) E.-J Gilbert and *Lepidella* Beauseigneur. Most Australian species fall within subgenus *Amanitina* because they have amyloid spores, a bulb at the base of the stipe and are likely to be mycorrhizal. In the same paper six sections were recognised within *Amanitina*: sect. *Amidella* (E.-J.Gilbert) Konrad & Maubl., sect. *Arenariae* Zhu L.Yang, Y.Y.Cui & Q.Cai, sect. *Phalloideae* (Fr.) Quél., sect. *Roanokenses* Singer ex Singer, sect. *Strobiliformes* Singer ex Zhu L.Yang, Y.Y.Cui & Q.Cai, and sect. *Validae* (Fr.) Quél. These sections can be distinguished morphologically by differences in the pileus margin, form of the universal veil, and presence or absence of clamp connections.

Members of *Amanita* sect. *Roanokenses* are agaricoid, the pileus margin is non-striate and usually appendiculate, the universal veil on the pileus is usually fragile, often as pyramids, warts, floccules or patches, the bulb at the base of the stipe is globose to subglobose and not often radicating (Cui *et al*. 2018); however, in northern Australia many members of sect. *Roanokenses* have a radicating bulb. Clamp connections may be present, absent or variable.

In this paper we describe four new species from sect. *Roanokenses* that grow in association with woody native vegetation. All have a non-striate pileus margin, a universal veil on the pileus that breaks into small warts or patches, amyloid spores, two have a globose to subglobose bulb at the base of the stipe, and three of the four have clamp connections. We have used the *nuLSU* gene region to confirm their placement in this section because this is the only gene region available from GenBank for all type species of sections within subgenus *Amanitina*, and other gene regions (β-tubulin, *ef1-α, rpb2*) to look at their relationships with other local species. We have also looked at the variation in the nuclear ribosomal internal transcribed spacer (*ITS*) region, which has been used as a barcode marker for species discrimination within the Basidiomycota (Schoch *et al.* 2012). Hughes *et al.* (2013) found less than 2% base pair divergence between haplotypes within an individual from *Amanita* sect. *Validae*. However, the *ITS* region appears to be less useful in Australian amanitas. Davison *et al.* (2017a) found *ITS* sequences failed to separate three species from sect. *Phalloideae* that differ in spore shape and are geographically separated, whilst the base pair divergence between haplotypes from the same individual is 0.0–8.1% in sect. *Arenariae* (Davison *et al.* 2021).

## Methods

*Taxonomy*. The methodology used for describing the macroscopic and microscopic characters largely follows Tulloss (2000). Colour names, including the colour of spores in deposit and other shades of white to cream (designated by the letters A–G), follow Royal Botanic Garden, Edinburgh (1969) while colour codes are from Kornerup and Wanscher (1983). In the descriptions of basidiospores (and basidia) the notation [x/y/z] denotes x basidiospores measured from y basidiomes from z collections. Biometric variables for spores follow Tulloss (2000), i.e. '**L** = the average spore length computed for one specimen examined and the range of such averages, **L′** = average spore length computed for all spores measured, **W** = the average spore width computed for one specimen examined and the range of such averages, **W′** = average spore width computed for all spores measured, Q = the length/

breadth for a single spore and the range of the ratio of length/breadth for all spores measured, **Q** = the average value of Q computed for one specimen examined and the range of such averages, **Q′** = the average value of Q computed for all spores measured'. Author citations follow Index Fungorum (http://www.indexfungorum.org/Names/Names.asp [accessed 9 Aug. 2022]).

*Phylogenetics*. DNA extraction, amplification and cloning of the *ITS* region, amplification of the *nuLSU*, *ef1-α*, *rpb2* and β-tubulin gene regions follow the methodology in Davison *et al*. (2017b). Sequence data were assembled with Geneious version 10.0.5 (Geneious undated). Additional sequences were accessed from GenBank (http://www.ncbi.nlm.nih.gov/ [accessed 4 July 2022]) (Tables 1 and 2).

Maximum likelihood phylogenetic trees were built using Mega version 5 (Tamura *et al.* 2011). The best model for each dataset was determined using the Model Function in MEGA (version 5, Tamura *et al.* 2011). The general time-reversible model (Travaré 1986) with invariant sites and gamma distribution rates was used to determine the placement of the undescribed species in subgenus *Amanitina* by using the *nuLSU* gene region. The Kimura 2-parameter model (Kimura 1980) with gamma distribution rates was used for the β-tubulin gene region, with invariant sites for the *rpb2* gene region, and with invariant sites and gamma distribution rates for the *ef1-α* gene region. The general time-reversible model (Travaré 1986) with invariant sites and gamma distribution rates was used for concatenated *nuLSU*, *rpb2 ef1-α* and β-tubulin gene regions. Bootstrap consensus trees were inferred from 500 replicates.

## Results

### *Phylogenetics*

The *nuLSU* is the only gene region available from GenBank for all type species of sections within subgenus *Amanitina*. These, together with additional species (Table 1) show *A. brunneola* sp. nov., *A. mallee* sp. nov., *A. cretaceaverruca* sp. nov. and *A. validiuscula* sp. nov. cluster within sect. *Roanokenses*. *Amanita brunneola* clusters with *A. pyramidiferina* D.A.Reid and *A. quenda* E.M.Davison in a well-supported clade (BS 99), *A. cretaceaverruca* clusters with the New Zealand species *A. australis* G.Stev. in a well-supported clade (BS 98), *A. validiuscula* clusters with an undescribed species *A.* sp-AUS20 from New South Wales in a well-supported clade (BS 99), and *A. mallee* clusters with *A. carneiphylla* O.K.Mill. in an unsupported clade (Figure 1).

Additional gene regions (*ef1-α*, *rpb2* and β-tubulin) are available for some collections within sect. *Roanokenses* (Table 2). Phylogenetic analysis of the *ef1-α* (Figure 2A), *rpb2* (Figure 2B) and β-tubulin (Figure 2C) gene regions, have a similar topology, to the phylogeny resulting from the concatenated *nuLSU*, *rpb2, ef1-α* and β-tubulin gene regions (Figure 2D), which shows the Australian and New Zealand species *A. australis, A. brunneola, A. carneiphylla, A. cretaceaverruca, A. mallee* and *A. quenda* form a well-supported clade (Figure 2D). Only the concatenated analysis shows very strong support for this clade (BS 100; Figure 2D). The other Australian and New Zealand species (*A. hiltonii* D.A.Reid, *A. pareparina* G.S.Ridl. *A. preissii* (Fr.) Sacc. and *A. validiuscula*) cluster with species from China (Figures 2A, 2B, 2C, 2D), indicating at least two lineages for these Australian and New Zealand species.

**Table 1.** Voucher information and GenBank accession numbers for *nuLSU* sequences from type of sections and other relevant collections used to place new species in subgenus *Amanitina*. Newly published sequences are shown in bold. *nuLSU*, nuclear ribosomal large-subunit rRNA region; NSW, New South Wales; SA, South Australia; WA, Western Australia.

| Section | *Amanita* spp. | Voucher number | Location | *nuLSU* |
|---|---|---|---|---|
| *Amidella* | *A. volvata* (Peck) Lloyd | KA12-1367 | Gyeongbuk, Korea | KF245907 |
| | *A. brunneomaculata* Zhu L.Yang, Y.Y.Cui & Q.Cai | HKAS 70032 | Yunnan, China | MH486411 |
| | *A. lanigera* Y.Y.Cui, Q.Cai & Zhu L.Yang | HKAS 89030 | Yunnan, China | MH486621 |
| | *A. parvicurta* Y.Y.Cui, Q.Cai & Zhu L.Yang | HKAS 101215 | Yunnan, China | MH486745 |
| *Arenariae* | *A. arenaria* (O.K.Mill. & E.Horak) Justo | PERTH 07586329, VPI679 (type) | City of Albany, WA | GQ925382 |
| | *A. wadulawitu* McGurk, E.M.Davison & E.L.J.Watkin | PERTH 09144390 | Shire of Serpentine-Jarrahdale, WA | MN918098 |
| | *A. peltigera* | AD282185 | Kangaroo Island, SA | MN900628 |
| *Phalloideae* | *A. phalloides* (Vaill. ex Fr.) Link | HKAS75773 | China | JX998060 |
| | *A. djarilmari* E.M.Davison | PERTH 08776067 | Shire of Cuballing, WA | KY977704 |
| | *A. marmorata* (Cleland & E.-J. Gilbert) E.-J.Gilbert | PERTH 08690596 | Shire of Denmark, WA | KY977711 |
| *Roanokenses* | *A. roanokensis* Coker | FLAS-F-60892 | Florida, USA | MH620252 |
| | *A. australis* G.Stev. | JAC12865 | New Zealand | MT862264 |
| | *A. avellaneifolia* Zhu L.Yang, YY.Cui & Q.Cai | HKAS80011 | Yunnan, China | MH486378 |
| | *A. carneiphylla* O.K.Mill. | PERTH 08793530 | City of Melville, WA | MN911351 |
| | *A. carneiphylla* | PERTH 08793565 | Shire of Cuballing, WA | **MN911352** |
| | A. carneiphylla | AD282179 | Kangaroo Island, SA | **MN911353** |
| | *A. elliptica* Q.Cai, Y.Y.Cui & Zhu L.Yang | HKAS96797 | Hainan, China | MH486488 |
| | *A. farinacea* (Sacc.) Cleland & Cheel | AD-C4470 | SA | HQ539692 |
| | *A. gymnopus* Corner & Bas | HKAS89031 | Yunnan, China | MH486583 |
| | *A. hiltonii* D.A.Reid | PERTH 09004564 | Shire of Mundaring, WA | MT364456 |
| | *A. hiltonii* | PERTH 09004580 | Shire of Manjimup, WA | MT364457 |
| | *A. hiltonii* | PERTH 09004599 | Shire of Cuballing, WA | MT364455 |
| | *A. manginiana* Har. & Pat. | HKAS56933 | China | KJ466438 |
| | *A. miculifera* Bas & Hatan. | HKAS101425 | Shenyang, China | MH486643 |
| | *A. modesta* Corner & Bas | HKAS79688 | China | KJ466440 |
| | *A. mumura* G.S.Ridl. | PDD 82690 | New Zealand | MT862255 |
| | *A. neo-ovoidea* Hongo | HKAS89025 | Yunnan, China | MH486656 |
| | *A. ochrophylla* (Cooke & Massee) Cleland | AD-C49440 | SA | HQ539717 |
| | *A. pareparina* G.S. Ridl. | JAC13371 | New Zealand | MT862271 |

| Section | *Amanita* spp. | Voucher number | Location | *nuLSU* |
|---|---|---|---|---|
| | *A. preissii* (Fr.) Sacc. | PERTH 08690766 | Kings Park, WA | KY290654 |
| | *A. preissii* | PERTH 08774765 | Kings Park, WA | KY290655 |
| | *A. preissii* | PERTH 08774803 | City of Melville, WA | KY290656 |
| | *A. pyramidiferina* A.E.Wood | AD-C53054 | SA | HQ539732 |
| | *A. quenda* E.M.Davison | PERTH 08587116 | City of Melville, WA | **OP235471** |
| | *A. quenda* | PERTH 09472754 | City of Melville, WA | **OP235473** |
| | *A. roseolifolia* Y.Y.Cui, Q.Cai & Zhu L.Yang | HKAS101403 | Hainan, China | NG_064593 |
| | *A.* sp-AUS20 | RET 474-3 | City of Lithgow, NSW | ON817223 |
| | *A.* sp-AUS20 | RET 623-3 | City of Lithgow, NSW | ON817224 |
| | *A. virgineoides* Bas | HKAS77278 | Hainan, China | MH486945 |
| | *A. yenii* Zhu L.Yang & C.M.Chen | HKAS89016 | Yunnan, China | MH486952 |
| *Strobiliformes* | *A. strobiliformis* (Paulet ex Vittad.) Bertill. | MB-001177 | Germany | MH486895 |
| | *A. cinereopannosa* Bas | RET 318-8 | Maine, USA | HQ539678 |
| | *A. aspericeps* Y.Y.Cui, Q.Cai & Zhu L.Yang | HKAS 77783 | Guangdong, China | MH486372 |
| | *A. cinereoradicata* Y.Y.Cui, Q.Cai & Zhu L.Yang | HKAS63641 | Yunnan, China | MH486452 |
| *Validae* | *A. excelsa* (Fr.) Bertill. | HKAS96169 | Austria | MH486492 |
| | *A. citrina* Pers. | BW JLR 102106-1 | New Jersey, USA | HQ539679 |
| | *A. flavoconia* G.FAtk. | BW_PH22 | Massachusetts, USA | HQ539693 |
| | *A. karea* G.S. Ridl. | JAC13435 | New Zealand | MT862273 |
| | *A. nothofagi* G. Stev. | CS AK400 | New Zealand | MT862267 |
| *Amanita* | *A. subglobosa* Zhu L.Yang (outgroup) | HKAS58837 | China | JN941152 |
| | *A. brunneola* | PERTH 09472517 | City of Melville, WA | **OP235469** |
| | *A. brunneola* | PERTH 09472614 | City of Cockburn, WA | **OP235474** |
| | *A. cretaceaverruca* | PERTH 09479627 | Shire of Manjimup, WA | **OP235470** |
| | *A. cretaceaverruca* | PERTH 09479716 | City of Melville, WA | **OP235467** |
| | *A. mallee* | PERTH 09472797 | Shire of Coolgardie, WA | **OP235468** |
| | *A. validiuscula* | PERTH 09480056 | Shire of Cuballing, WA | **OP235472** |

**Table 2.** Voucher information and GenBank accession numbers for some species from sect. Roanokenses. Newly published sequences are shown in bold. *ITS,* nuclear ribosomal transcribed-spacer region; *ef1-α*, translation elongation-factor 1-α region; *rpb2*, polymerase-II region; β-tubulin, β-tubulin region; WA, Western Australia; SA, South Australia.

| *Amanita* spp. | Voucher number | Location | *ITS* | *ef1-α* | *rpb2* | β-tubulin |
|---|---|---|---|---|---|---|
| *A. australis* | PDD89861 | New Zealand | GU222314 | | | |
| *A. australis* | JAC12865 | New Zealand | MT863756 | MT977103 | MT993772 | MT993785 |
| *A. avellaneifolia* | HKAS80011 | Yunnan, China | | MH508680 | MH485872 | MH485410 |

| *Amanita* spp. | Voucher number | Location | *ITS* | *ef1-α* | *rpb2* | β-tubulin |
|---|---|---|---|---|---|---|
| *A. brunneola* | PERTH 09472517 | City of Melville, WA | **OP235497–500, OP235506** | **OP272679** | **OP272667** | **OP272663** |
| *A. brunneola* | PERTH 09472614 | City of Cockburn, WA | **OP235501** | **OP272683** | **OP272666** | **OP272671** |
| *A. carneiphylla* | PERTH 08793530 | City of Melville, WA | | MN909832 | MN928556 | MN909829 |
| *A. carneiphylla* | PERTH 08793565 | Shire of Cuballing, WA | | MN909833 | MN928557 | MN909830 |
| *A. carneiphylla* | AD282179 | Kangaroo Island, SA | **MN919212–16** | **MN909834** | **MN928558** | **MN909831** |
| *A. cretaceaverruca* | PERTH 09479627 | Shire of Manjimup, WA | **OP235481–87, OP235507** | **OP272680** | **OP272668** | **OP272674** |
| *A. cretaceaverruca* | PERTH 09479716 | City of Melville, WA | **OP235491–96** | **OP272677** | | **OP272673** |
| *A. elliptica* | HKAS96797 | Hainan, China | | MH508765 | MH485966 | MH485490 |
| *A. gymnopus* | HKAS89031 | Yunnan, China | | MH508852 | MH486045 | MH485563 |
| *A. hiltonii* | PERTH 09004564 | Shire of Mundaring, WA | MT365216–20 | MT370480 | MT370479 | MT370482 |
| *A. kalamundae* | PERTH 08616019 | Shire of Murray, WA | JX398319 | | | |
| *A. kalamundae* | PERTH 08615993 | Shire of Manjimup, WA | KP898376–82 | | | |
| *A. mallee* | PERTH 09472797 | Shire of Coolgardie, WA | **OP235475–80, OP235490** | **OP272678** | **OP272665** | **OP272672** |
| *A. manginiana* | HKAS56933 | China | | KJ481943 | KJ466603 | KJ466515 |
| *A. miculifera* | HKAS101425 | Shenyang, China | | MH508901 | MH486093 | MH485609 |
| *A. modesta* | HKAS79688 | China | | KJ481944 | KJ466604 | KJ466516 |
| *A. neo-ovoidea* | HKAS89025 | Yunnan, China | | MH508913 | MH486106 | MH485621 |
| *A. pareparina* | JAC13371 | New Zealand | | MT977110 | MT993779 | MT993794 |
| *A. preissii* | PERTH 08690766 | Kings Park, WA | | KY273109 | KY288484 | KY273105 |
| *A. quenda* | PERTH 08587116 | City of Melville, WA | NR151652 | **OP272681** | **OP272669** | **OP272663** |
| *A. quenda* | PERTH 09472754 | City of Melville, WA | **KP137058–62** | | **OP272670** | **OP272676** |
| *A. roseolifolia* | HKAS101403 | Hainan, China | | MH509032 | MH486219 | MH485723 |
| *A. validiuscula* | PERTH 09480056 | Shire of Cuballing, WA | **OP235502–05, OP235508** | **OP272682** | | **OP272675** |
| *A. virgineoides* | HKAS77278 | Hainan, China | | MH509166 | MH486340 | MH485846 |
| *A. yenii* | HKAS89016 | Yunnan, China | | MH509172 | MH486345 | MH485851 |
| *A. djarilmari* (outgroup) | PERTH 08776067 | Shire of Cuballing, WA | | MF000750 | MF000755 | MF000742 |

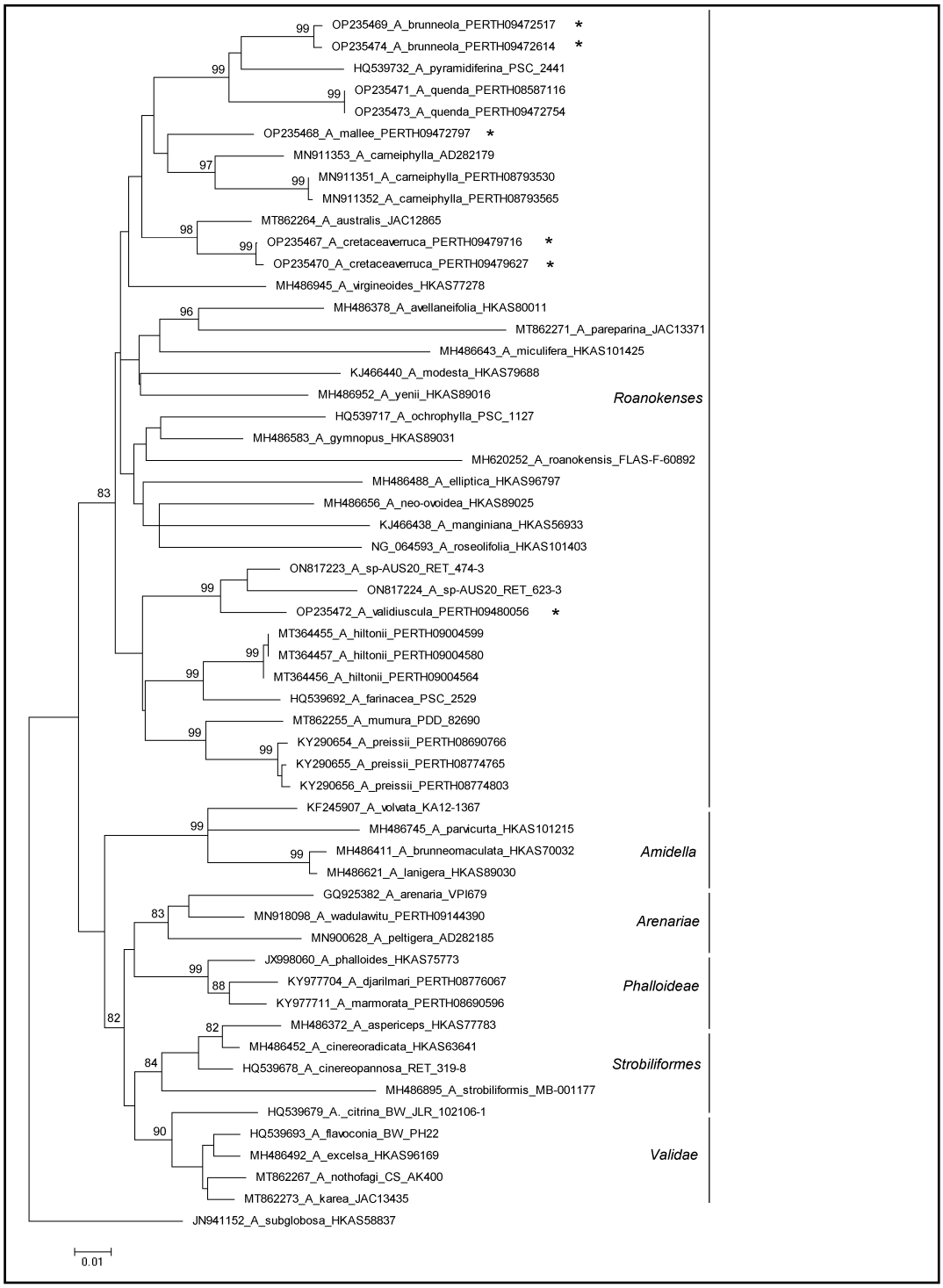


Figure 1. Molecular phylogenetic analysis by the maximum-likelihood method of *nuLSU* (nuclear ribosomal large sub-unit rRNA region) sequences (809 base pair positions), showing the position of *Amanita brunneola, A. cretaceaverruca, A. mallee* and *A. validiuscula* within subgen. *Amanitina*. The tree is rooted with *A. subglobosa* (subgen. *Amanita* sect. *Amanita*). Each section is listed on the right the new species are indicated by *. Maximum-likelihood bootstrap values greater than 80% are shown on the branches.

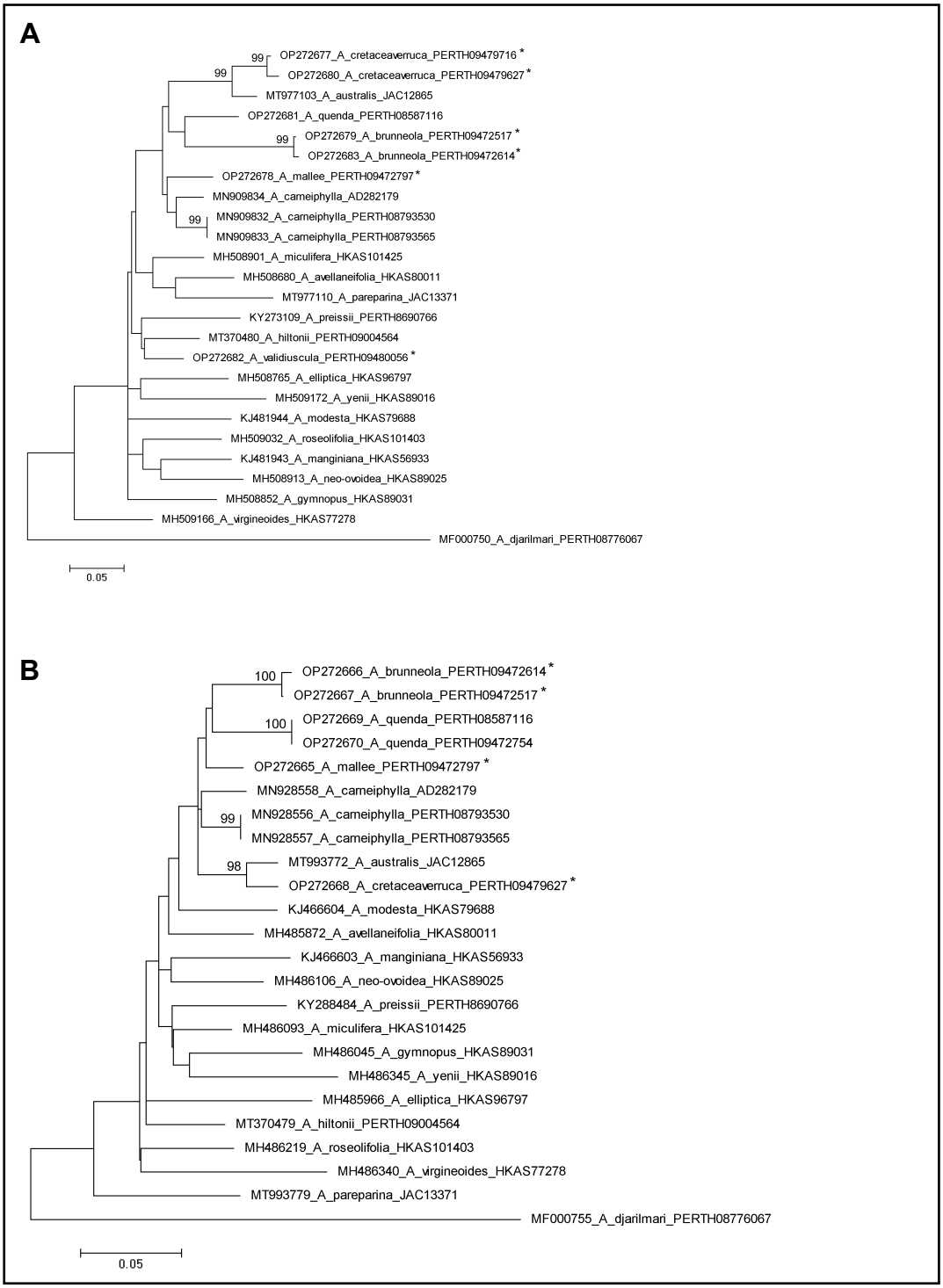


Figure 2. Molecular phylogenetic analysis by the maximum-likelihood method of the sequences 2A. *ef1-α* (translation elongation-factor 1-α (473 base pair positions). 2B. *rpb2* (RNA polymerase-II region) sequences (639 base pair positions). 2C. β-tubulin (β-tubulin region) sequences (218 base pair positions). 2D. Concatenated *nuLSU, rpb2, ef1-α* and β-tubulin sequences (2115 base pair positions) of species in sect. *Roanokenses*. All trees are rooted with *Amanita djarilmari* (sect. *Phalloideae*). The new species are indicated by *. Maximum-likelihood bootstrap values greater than 80% are shown on the branches.

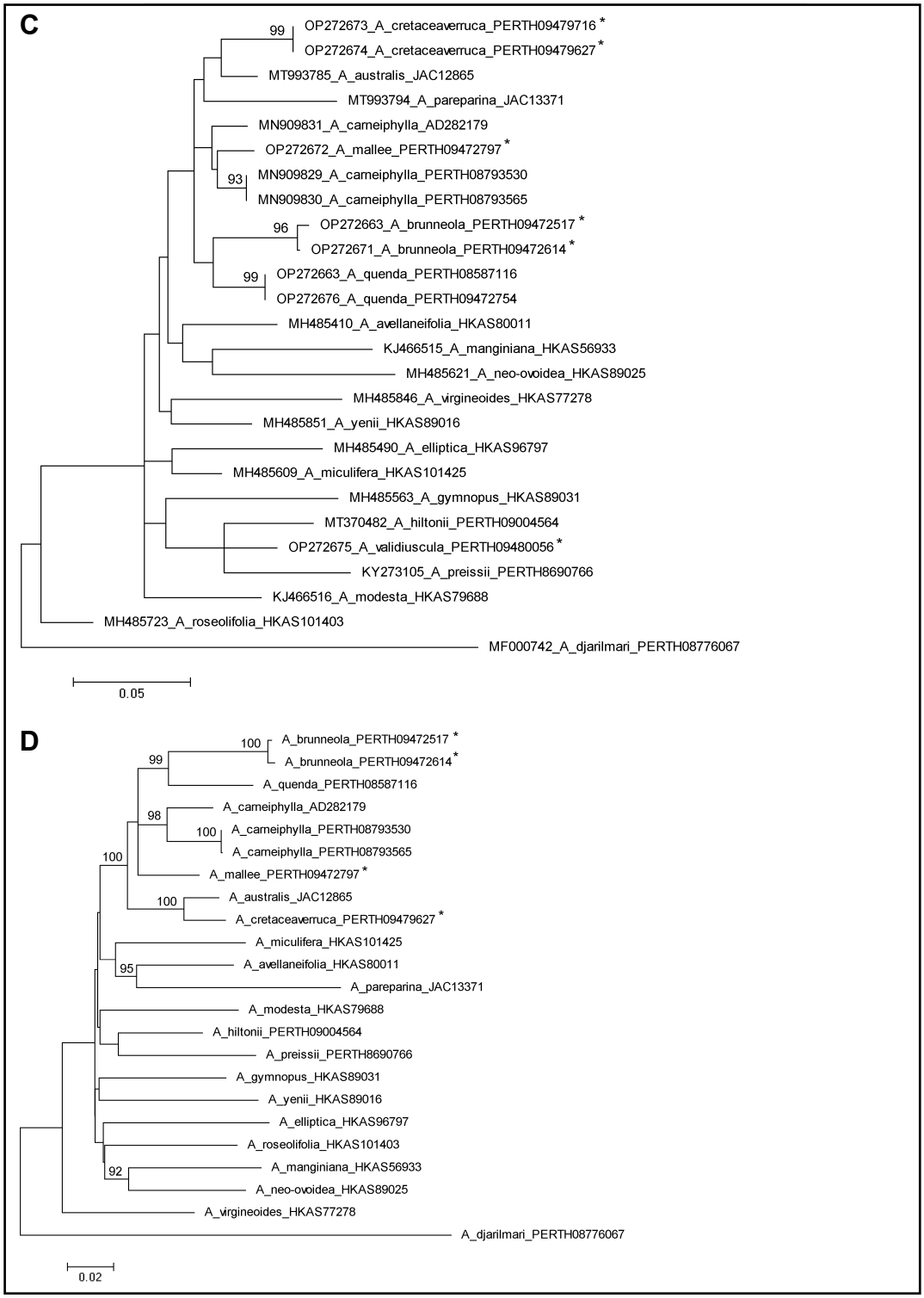


Figure 2. cont.

## Taxonomy

**Amanita brunneola** E.M.Davison & Giustiniano, *sp. nov.*

*Type*: Wireless Hill Park, City of Melville, Western Australia [precise locality withheld for conservation reasons], 14 June 2020, *E.M. & P.J.N. Davison* EMD 22-2020 (*holo*: PERTH 09472517). [MB845575].

*Pileus* 20–64 mm wide, up to 5 mm thick, convex becoming plane with a decurved margin, depressed with age, ivory white (B) cream (D) to buff to clay buff to milky coffee (3A3–4A2–3–5B2–D4) with pale margin, surface tacky when moist, margin non-striate, slightly appendiculate. *Universal veil on pileus* adnate, thin, submembranous, crustose breaking into patches or small floccose warts in centre of disc, white or ivory white (B) or cream (D) or pale vinaceous buff (5B2). *Lamellae* adnate to adnexed, subcrowded to close, white ageing cream (4A2), 3–8 mm broad, margin concolorous, fimbriate; lamellulae scarce to plentiful, in several lengths, truncate or rounded truncate or subattenuate or attenuate. *Stipe* 30–71 × 4–10 mm, cylindric, white, surface smooth. *Partial veil* superior or apical, descendant, flaring, striate above, membranous, persistent, white. *Bulb* 10–17 × 11–20 mm globose or globose with pointed base, white to buff to brown to grey. *Remains of universal veil at top of bulb* not apparent or a rim or small ridges or a free limb up to 2 mm high, white. *Pileus and stipe context* white, unchanging, stipe solid. *Smell* none. *Spore deposit* white. (Figure 3)

*Basidiospores* [280/14/10] (9–)10.5–15(–18) × (4–)4.5–5.5(–6) µm, (**L** = 11.5–15.5 µm; **L'** = 12.5 µm, **W** = 4.5–5.2 µm; **W'** = 5.0 µm; Q = (1.83–)2.10–3.00(–3.40); **Q** = 2.35–2.98; **Q'** = 2.51), hyaline, colourless, thin-walled, smooth, amyloid, cylindric, contents monoguttulate, apiculus sublateral, cylindric or tapered, *c.* 1 × 1.5 µm, truncate or rounded. *Pileipellis* up to 200 µm thick with a colourless gelatinised suprapellis up to 100 µm thick and a colourless or pale brown subpellis, consisting of filamentous hyphae and very infrequent vascular hyphae (inflated cells not observed), filamentous hyphae 3–15 µm wide, radially orientated with some interweaving, thick-walled, colourless, gelatinising; vascular hyphae 2–3 µm wide, colourless; clamp connections not observed. *Pileus context* consisting of filamentous hyphae (dominant or equal), inflated cells and very infrequent vascular hyphae, filamentous hyphae 3–50 µm wide with widest constricted at septa, thin-walled, colourless; inflated cells to 150 × 50 µm, thin-walled, clavate or ellipsoid or ventricose or cylindric, terminal, colourless; vascular hyphae 3–10 µm wide, occasionally branched, pale yellow; clamp connections not observed. *Lamella trama* bilateral, divergent. *Central stratum* up to 40 µm wide, consisting of filamentous hyphae (inflated cells and vascular hyphae not observed), filamentous hyphae 3–18 µm wide with widest constricted at septa, thin walled, colourless, axially orientated; clamp connections very infrequent. *Subhymenial base* with angle of divergence *c.* 15–30° from central stratum, with filamentous hyphae following a smooth curve to subhymenium, consisting of dominant filamentous hyphae, inflated cells and very infrequent to frequent vascular hyphae; filamentous hyphae 3–22 µm wide, widest close to subhymenium and constricted at septa, frequently branched, thin-walled, colourless; inflated cells up to 95 × 35 µm thin-walled, clavate or ventricose or ellipsoid or ovoid or pyriform, colourless; vascular hyphae 2–5 µm wide, occasionally branched, pale yellow; clamp connections frequent. *Subhymenium* initially ramose becoming coralloid to inflated ramose, with basidia arising terminally from narrow hyphae or barely inflated hyphal segments 4–15 µm wide; clamp connections frequent. *Lamella edge tissue* sterile, with inflated cells frequent to abundant, up to 25 × 10 µm when clavate or up to 35 × 20 µm when pyriform or up to 25 × 18 µm when ovoid, colourless, some disarticulating. *Basidia* [200/10/10] (27–)38–54(–58) × (9–)10–13(–14) µm, thin-walled, colourless, *c.* 98% 4-spored, *c.* 0.5% 3-spored, *c.* 1.5% 2-spored, sterigmata to 7 × 2 µm, clamp connections frequent, proliferating. *Universal veil on pileus* not layered, elements with no dominant orientation, consisting of frequent filamentous hyphae, dominant inflated cells and very infrequent vascular hyphae, filamentous hyphae 4–20 µm wide with widest constricted

at septa, colourless, gelatinising; inflated cells up to 90 × 30 µm when pyriform or up to 70 × 70 µm when spherical or up to 100 × 50 µm when ovoid or up to 100 × 35 µm when clavate, terminal or occasionally in chains of up to 3, colourless, gelatinising; vascular hyphae 3–5 µm wide, colourless; clamp connections very infrequent. *Universal veil on stipe base* not layered, elements with somewhat axial orientation, consisting of dominant to frequent filamentous hyphae, frequent to dominant inflated cells and very infrequent to frequent vascular hyphae, filamentous hyphae 2–15 µm wide, colourless or pale yellow, gelatinising; inflated cells up to 60 × 60 µm when spherical or up to 110 × 55 µm when pyriform or up to 50 × 40 µm when ellipsoidal or up to 120 × 60 µm when ovoid or up to 150 × 50 µm when clavate, terminal, colourless or pale yellow, gelatinising; vascular hyphae 3–15 µm wide, occasionally branched, pale yellow or colourless; clamp connections not observed. *Stipe context* longitudinally acrophysalidic, consisting of frequent filamentous hyphae, dominant acrophysalides and frequent to infrequent vascular hyphae, filamentous hyphae 2–10 µm wide, colourless or pale yellow, gelatinising; acrophysalides to 300 × 40 µm, clavate, terminal, colourless or pale yellow, gelatinising; vascular hyphae 3–20 µm wide, occasionally branched, pale yellow or pale yellowish-brown; clamp connections very infrequent. *Partial veil* elements with a radial orientation, consisting of frequent filamentous hyphae, equal to dominant inflated cells and infrequent vascular hyphae, filamentous hyphae 2–8 µm wide, colourless, gelatinising; inflated cells up to 50 × 27 µm when pyriform or up to 60 × 20 µm when clavate or up to 40 × 25 µm when ovoid or up to 25 × 25 µm when spherical, colourless, gelatinising; vascular hyphae 2–8 µm wide, pale yellow or colourless; clamp connections very infrequent. (Figure 4)

*Diagnostic features*. Basidiomata small to medium. Pileus ivory white becoming cream to buff to clay buff to milky coffee, paler at margin., margin appendiculate when young. Universal veil on pileus white, thin, as patch or small slightly floccose warts mainly in centre of disc. Lamellae white. Stipe white. Partial veil superior, white, descendant, flaring, membranous. Universal veil at stipe base a narrow white rim at the top of the globose basal bulb. Spores amyloid, cylindric. Universal veil on pileus of dominant inflated cells and filamentous hyphae. Clamp connections present, most frequent in lamellae.

*Other specimens examined*. WESTERN AUSTRALIA: [localities withheld for conservation reasons] 25 Apr. 1990, *E.M. & P.J.N. Davison* EMD 16/90 (PERTH 03097056); 24 May 1992, *E.M. & P.J.N. Davison* EMD 25/92 (PERTH 03096823); 16 June 1992, *E.M. & P.J.N. Davison* EMD 57-1992 (PERTH 09472355); 11 May 2008, *E.M. & P.J.N. Davison* EMD 4-2008 (PERTH 09472746); 30 May 2010, *E.M. & P.J.N. Davison* EMD 6-2010 (PERTH 09472614); 8 June 2016, *E.M. Davison & P.J.N. Davison* EMD 47-2016 (PERTH 09479678); 14 June 2020, *E.M. & P.J.N. Davison* EMD 20-2020 (PERTH 09472681); 14 June 2020, *E.M. & P.J.N. Davison* EMD 21-2020 (PERTH 09472649); 14 June 2020, *E.M. & P.J.N. Davison* EMD 23-2020 (PERTH 09472606); 16 June 1989, *O.K. Miller Jr & H. Miller* E 661 (PERTH 07547722).

*Phenology*. Fruiting period is April to June.

*Distribution and habitat*. Singly or gregarious in sandy soil. In degraded native vegetation, nearby plants include *Allocasuarina fraseriana, Corymbia calophylla* and *Eucalyptus marginata*. Occurs on the Swan Coastal Plain Perth SWA02 IBRA subregion (Department of the Environment 2013).

*Conservation status*. To be listed as Priority Two (poorly known species) under Conservation Codes for Western Australian Flora (Tanya Llorens pers. comm.).

*Etymology*. The epithet is from the Latin *brunneolus*, referring to the brownish colour of the pileus.


Figure 3. *Amanita brunneola* basidiomes, *E.M. & P.J.N. Davison* EMD 22-2020 (*holo*: PERTH 09472517). Photographs E.M. Davison.

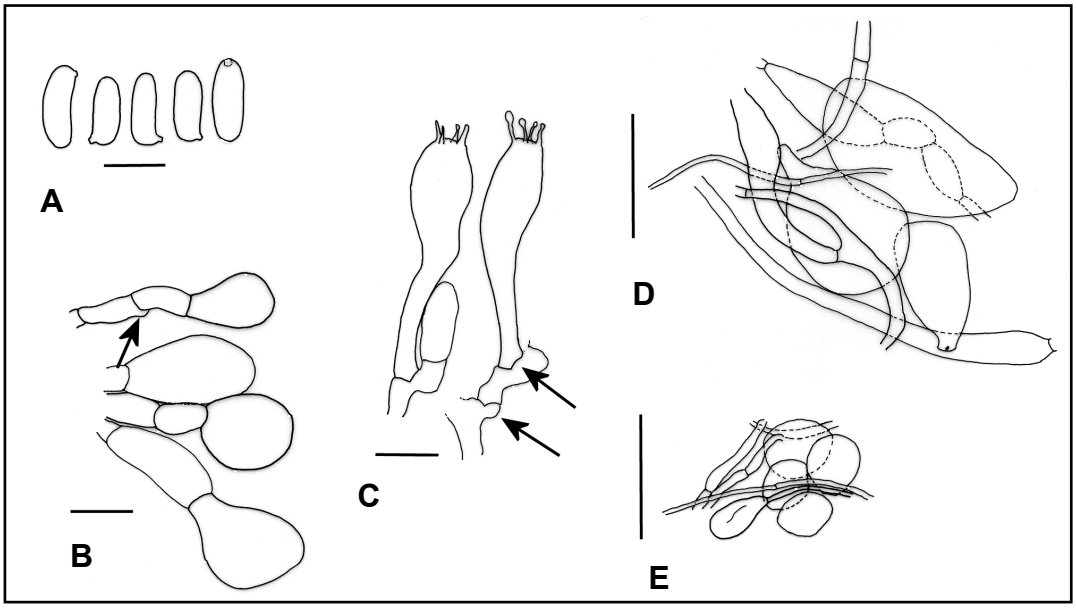


Figure 4. *Amanita brunneola*. A – spores from spore print; B – marginal cells; C – basidia; D – universal veil on pileus, gently squashed; E – universal veil at stipe base, gently squashed. Scale bars = 10 µm (A–C); 50 µm (D, E); clamp connections indicated by arrows. Images from *E.M. & P.N.J. Davison* EMD 22-2020 (*holo*: PERTH 09472517).

*Notes*. *Amanita brunneola* consistently clusters close to *A. pyramidiferina* and *A. quenda* in our molecular analyses (Figures 1, 2). A comparison of cloned haplotypes of the *ITS* region from *A. brunneola* and *A. quenda* (no *ITS* sequences of *A. pyramidiferina* are available) shows there is considerable variation between the clones; they differ by 0.3–3.3% within an individual, and 1.1–2.9% between collections of the same species (Table 3). Clones of these two species differ by 28.4–29.7%, well beyond the observed infraspecific variation.

Several small to medium species with a white or pale brown pileus and cylindrical spores have been described from Australia. *Amanita brunneola* is similar to *A. angustispora* Cleland, a poorly known species from Encounter Bay in South Australia (Cleland 1927). Both species are of similar size and colour, both have a white dependent partial veil, and globose bulb; however, Cleland (1927) mentions that the volva is sheathing, ample and whitish in *A. angustispora*, whilst in *A. brunneola* it is either not apparent, or forms small ridges or a free limb to 2 mm high. This is an important difference. Both species have clamp connections. However, there is considerable confusion about the identity of *A. angustispora* which has been detailed by Reid (1980) and Tulloss (http://www.amanitaceae.org/?Amanita%20angustispora [accessed 7 June 2022]). The uncertainty could be resolved if usable DNA is obtained from the Cleland collections of *A. angustispora.*

*Amanita clelandii* (E.-J.Gilbert) E.-J.Gilbert is another small, white species with cylindric spores collected by Cleland from Encounter Bay and Kinchina in South Australia. Reid (1980) records the spores as being 9.0–16.0 × 4.5–6.0 µm, similar to those of *A. brunneola*, however, clamp connections were not reported in these collections (Reid 1980). This is an important morphological difference (Bas 1969).

On the basis of the absence of a sheathing volva which distinguishes *A. brunneola* from *A. angustispora*, and the presence of clamp connections which distinguishes it from *A. clelandii*, *A. brunneola* is described as a new species.

**Table 3.** Percentage difference between *ITS* clones from *A. brunneola* and *A. quenda.* The *ITS* region is 600–668 base pairs long.

| Name | No. of clones | *A. brunneola* | | *A. quenda* | |
|---|---|---|---|---|---|
| | | PERTH 09472614 | PERTH 09472517 | PERTH 08587116 | PERTH 09472754 |
| *A. brunneola* | | | | | |
| PERTH 09472614, OP235501 | 1 | | | | |
| PERTH 09472517, OP235497–500, OP235506 | 5 | 1.7–2.5 | 0.3–2.2 | | |
| *A. quenda* | | | | | |
| PERTH 08587116, NR_151652 | 1 | 29.0 | 28.6–29.2 | | |
| PERTH 09472754, KP137058–62 | 5 | 28.8–29.5 | 28.4–29.7 | 1.1–2.9 | 0.3–3.3 |

**Amanita cretaceaverruca** E.M.Davison & Giustiniano, *sp. nov.*

*Type*: Perup, Shire of Manjimup, Western Australia [precise locality withheld for conservation reasons], 2 June 2013, *E.M. Davison & P.J.N. Davison* EMD 30-2013 (*holo*: PERTH 09479627). [MB845576].

*Pileus* 26–51 mm wide, up to 5 mm thick, convex becoming plane with a decurved margin, depressed with age, buff to clay buff to fawn (4A3–6C4–E5, pale yellow to brownish orange to brown) with pale margin, surface tacky when moist, margin non-striate, slightly appendiculate. *Universal veil on pileus* easily removed, thick, felted, crustose breaking into patches or straight sided warts in centre of disc, white to ivory white (B) to clay buff to fawn (6C4) with age. *Lamellae* free to adnexed to adnate, subcrowded to close, white ageing ivory white (B) to pale clay buff, 4–5 mm broad, margin concolorous, fimbriate; lamellulae plentiful, in several lengths, shortest truncate longest subattenuate or attenuate. *Stipe* 40–70 × 6–9 mm, cylindric or tapering upwards, white or ivory white, surface floccose below partial veil. *Partial veil* superior, descendant, flaring, striate above, membranous, persistent, white. *Bulb* 12–22 × 15–28 mm globose or ovoid or turbinate, white. *Remains of universal veil at top of bulb* not apparent or small rim, white. *Pileus and stipe context* white or ivory white, unchanging, stipe centre watersoaked. *Smell* none. *Spore deposit* white. (Figure 5)

*Basidiospores* [140/7/2] (8–)9–13(–14) × (5–)6–7.5(–8) µm, (**L** = 9.7–12.2 µm; **L'** = 11.5 µm, **W** = 6.2–7.0 µm; **W'** = 6.6 µm; Q = (1.33–)1.47–2.00(–2.18); **Q** = 1.57–1.84; **Q'** = 1.74), hyaline, colourless, thin-walled, smooth, amyloid, ellipsoid to elongate, contents monoguttulate and granular, apiculus sublateral, tapered or cylindric, *c.* 1 × 1 µm, truncate or rounded. *Pileipellis* up to 150 µm thick with a colourless gelatinised suprapellis up to 100 µm thick and pale yellow or pale brown subpellis, consisting of filamentous hyphae and frequent to very infrequent vascular hyphae (inflated cells not observed), filamentous hyphae 3–7 µm wide, radially orientated with some interweaving, thick-walled, colourless, gelatinising; vascular hyphae 2–10 µm wide, occasionally branched, pale yellow to brownish yellow. *Pileus context* consisting of dominant filamentous hyphae, inflated cells and frequent to infrequent vascular hyphae, filamentous hyphae 3–35 µm wide with widest constricted at septa, thin-walled, colourless; inflated cells to 190 × 50 µm, thin-walled, clavate or ventricose or ellipsoid or ovoid or cylindric, terminal, colourless; vascular hyphae 3–7 µm wide, occasionally branched, very pale yellow or brownish yellow. *Lamella trama* bilateral, divergent. *Central stratum* consisting of filamentous hyphae and infrequent vascular hyphae (inflated cells not observed), filamentous hyphae 2–12 µm wide

with widest constricted at septa, thin walled, colourless, axially orientated; vascular hyphae 3–4 µm wide, pale yellow. *Subhymenial base* with angle of divergence *c.* 10–15° from central stratum, with filamentous hyphae following a smooth curve to subhymenium, consisting of dominant filamentous hyphae, inflated cells and infrequent vascular hyphae; filamentous hyphae 2–20 µm wide, widest close to subhymenium and constricted at septa, frequently branched, thin-walled, colourless; inflated cells up to 50 × 20 µm, thin-walled, clavate, colourless; vascular hyphae 2–6 µm wide, occasionally branched, colourless or pale yellow. *Subhymenium* initially ramose becoming inflated apically, with basidia arising terminally from narrow hyphae or barely inflated hyphal segments 6–23 µm wide. *Lamella edge tissue* sterile, with inflated cells frequent, up to 25 × 20 µm when ovoid or up to 25 × 25 µm when pyriform or up to 18 × 18 µm when spherical, colourless, some disarticulating. *Basidia* [40/2/2] (29–)32–52(–53) × (10–)11–12(–13) µm, thin-walled, colourless, *c.* 85% 4-spored, *c.* 15% 3-spored, sterigmata to 5 × 2 µm. *Universal veil on pileus* not layered, elements with somewhat upright orientation, consisting of frequent filamentous hyphae, dominant inflated cells and very infrequent vascular hyphae, filamentous hyphae 3–10 µm wide, colourless, gelatinising; inflated cells up to 40 × 40 µm when spherical or up to 70 × 55 µm when ovoid or up to 35 × 25 µm when pyriform or up to 80 × 20 µm when clavate or up to 110 × 20 µm when cylindric, terminal or in chains of up to 4, colourless or very pale brown, gelatinising; vascular hyphae 3–5 µm wide, occasionally branched, colourless or pale yellow. *Universal veil on stipe base* not layered, elements with somewhat axial or no dominant orientation, consisting of equal to frequent filamentous hyphae, inflated cells and very infrequent vascular hyphae, filamentous hyphae 3–17 µm wide, colourless, gelatinising; inflated cells up to 80 × 80 µm when spherical or up to 45 × 35 µm when pyriform or up to 50 × 35 µm when ovoid or up to 70 × 55 µm when ellipsoid, terminal, colourless, gelatinising; vascular hyphae 2 µm wide, pale yellow. *Stipe context* longitudinally acrophysalidic, consisting of frequent filamentous hyphae, dominant acrophysalides and frequent to infrequent vascular hyphae, filamentous hyphae 2–10 µm wide, colourless; acrophysalides to 250 × 35 µm, clavate or cylindric, terminal, colourless, gelatinising; vascular hyphae 2–12 µm wide, occasionally branched, pale brownish-yellow. *Partial veil* elements with a radial orientation, consisting of frequent filamentous hyphae, dominant inflated cells and very infrequent vascular hyphae, filamentous hyphae 2–12 µm wide with widest constricted at septa, colourless, gelatinising; inflated cells up to 30 × 20 µm when ovoid or up to 80 × 20 µm when clavate or up to 40 × 20 µm when pyriform or up to 160 × 25 µm when cylindric, colourless, gelatinising; vascular hyphae 3–5 µm wide, occasionally branched, pale yellow. Clamp connections not observed in any tissue. (Figure 6)

*Diagnostic features*. Basidiomata very small to medium. Pileus buff to clay buff to fawn paler at margin, margin appendiculate when young. Universal veil on pileus white, thick, as patch or straight sided warts mainly in centre of disc. Lamellae white. Stipe white. Partial veil superior, white, descendant, flaring, membranous. Universal veil at stipe base not apparent or a narrow white rim at the top of the globose or ovoid basal bulb. Spores amyloid, ellipsoid to elongate. Universal veil on pileus of dominant inflated cells and filamentous hyphae. Clamp connections not seen.

*Other specimens examined*. WESTERN AUSTRALIA: [localities withheld for conservation reasons] 3 June 2011, *E.M. & P.J.N. Davison* EMD 21-2011 (PERTH 09479716).

*Phenology*. Fruiting period is June.

*Distribution and habitat*. Gregarious in sandy clay or peaty soil. In native vegetation, nearby plants include *Gastrolobium biloba, Melaleuca preissii, Eucalyptus grandis* and *E. rudis*. Occurs on the Swan Coastal Plain Perth SWA02 and Southern Jarrah Forest JAF02 IBRA subregions (Department of the Environment 2013).

Figure 5. *Amanita cretaceaverruca* basidiomes, *E.M. Davison & P.J.N. Davison* EMD 30-2013 (*holo*: PERTH 09479627). Photographs E.M. Davison.

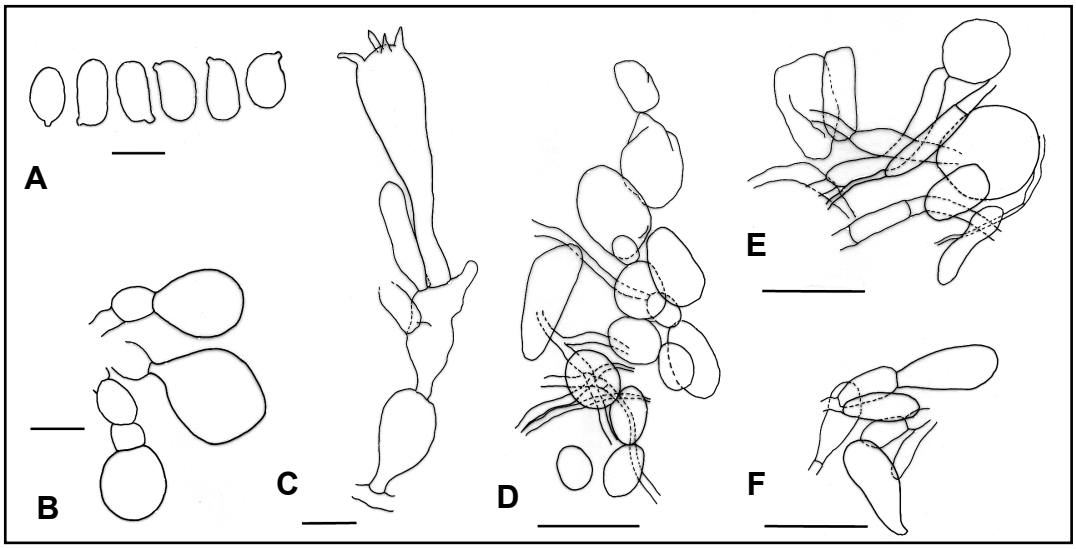


Figure 6. *Amanita cretaceaverruca*. A – spores from spore print; B – marginal cells; C – basidia; D –section through universal veil in centre of pileus; E – universal veil at stipe base, gently squashed; F – partial veil margin, unsquashed. Scale bars = 10 µm (A–C); 50 µm (D–F). Images from *E.M. Davison & P.J.N. Davison* EMD 30-2013 (*holo*: PERTH 09479627).

*Conservation status*. To be listed as Priority Two (poorly known species) under Conservation Codes for Western Australian Flora (Tanya Llorens pers. comm.).

*Etymology*. The epithet is from the Latin *cretaceous* and *verruca* referring to the thick white warts on the pileus.

*Notes*. *Amanita cretaceaverruca* clusters with the New Zealand species *A. australis* (Figures 1, 2). A comparison of cloned haplotypes of the *ITS* region from *A. cretaceaverruca* shows there is considerable variation between these clones; they differ by 0.3–5.6% within an individual, and 1.3–5.9% between collections of the same species (Table 4). The two sequences of *A. australis* differ by 32.1% indicating that one may have been mis-identified. Sequences from *A. cretaceaverruca* differ from MT863756 by 15.1–17.0%, and from GU222314 by 31.2–32.9%, indicating they are not the same.

Published descriptions of Australian amanitas include two small to medium species with a brown pileus, inapparent remains of the universal veil at the top of the globose to ovoid bulb, and elongate amyloid spores. *Amanita subalbida* Cleland has a pallid brownish to nearly white pileus with mealy or thin pulverulent to sub-felted universal veil (Cleland 1931; Bas 1969), not a thick felted, crustose universal veil which breaks into white warts. Also, *A. subalbida* has infrequent clamp connections (Bas 1969, Reid 1980), whilst these have not been seen in *A. cretaceaverruca*.

*Amanita cretaceaverruca* is superficially similar to *A. kalamundae* O.K.Mill. They have similar shaped spores (*A. cretaceaverruca* **Q** = 1.57–1.84, *A. kalamundae* **Q** = 1.44–1.87 (Miller 1991; McGurk *et al.* 2016), however, in *A. kalamundae* the partial veil, warts on the pileus, bulb and context yellow with age or with handling. Also, clamp connections are present, although infrequent in *A. kalamundae*. Cloned haplotypes of the *ITS* region are available for both *A. cretaceaverruca* and *A. kalamundae*. As can be seen from Table 4, there is considerable variation between clones: they differ by 0.3–5.6% within an individual, by up to 7.3% among collections of the same species, but by more than 30% between these two species, well beyond the observed infraspecific variation. On this basis, *A. cretaceaverruca* is described as a new species.

**Table 4.** Percentage difference between *ITS* clones from *A. cretaceaverruca* and *A. kalamundae*, and sequences of *A. australis.* The *ITS* region is 571–608 base pairs long.

| Collection | No. of clones | *A. cretaceaverruca* | | *A. australis* | | *A. kalamundae* | |
|---|---|---|---|---|---|---|---|
| | | **PERTH 09479627** | **PERTH 09479716** | **PDD89861** | **JAC12865** | **PERTH 08616019** | **PERTH 08615993** |
| *A. cretaceaverruca* | | | | | | | |
| PERTH 09479627, OP235481–87, OP235507 | 8 | 0.3–5.6 | | | | | |
| PERTH 09479716, OP235491–96 | 6 | 1.3–5.9 | 0.5–3.3 | | | | |
| *A. australis* | | | | | | | |
| PDD89861, GU222314 | | 31.6–32.9 | 31.2–32.7 | | | | |
| JAC12865, MT863756 | | 15.2–17.0 | 15.1–16.3 | 32.1 | | | |
| *A. kalamundae* | | | | | | | |
| PERTH 08616019, JX398319 | 1 | 35.7–37.4 | 36.0–37.0 | 39.1 | 38.2 | | |
| PERTH 08615993, KP898376–82 | 7 | 34.3–36.7 | 34.4–36.1 | 38.0–38.5 | 36.5–37.5 | 4.4–7.3 | 0.8–4.8 |

**Amanita mallee** E.M.Davison, Giustiniano & M.D.Barrett, *sp. nov.*

*Type*: Shire of Coolgardie, Western Australia [precise locality withheld for conservation reasons], 13 December 2012, *M.D. Barrett* F48/12 (*holo*: PERTH 09472797). [MB845577].

*Pileus* 70–83 mm wide, up to 22 mm thick, plane, margin non-striate, not appendiculate, white. *Universal veil on pileus* adnate, thin patches, white. *Lamellae* adnexed, subcrowded, white with cream tint, margin paler, fimbriate; lamellulae frequent, in several lengths, attenuate. *Stipe* 40–50 mm long, 14–18 mm wide, cylindric or narrowing downwards, white, surface smooth. *Partial veil* central, descendant, membranous, breaking up, striate above, white. *Bulb* 40–55 × 17–20 mm ovoid to carrot shaped, encrusted with sand. *Remains of universal veil at top of bulb* a thin membranous free limb to 5 mm high, white. *Pileus and stipe context* white, unchanging, stipe solid. *Smell* none. (Figure 7)

*Basidiospores* [100/5/1] (10–)10.5–13.5(–14) × (4.5–)5–6(–7) µm, (**L** = 12.0–12.8 µm; **L'** = 12.2 µm, **W** = 5.4–5.9 µm; **W'** = 5.6 µm; Q = (1.83–)2.00–2.60(–3.00); **Q** = 2.09–2.26; **Q'** = 2.19), hyaline, colourless, thin-walled, smooth, amyloid, cylindric, contents monoguttulate, apiculus sublateral, cylindric, *c.* 1 × 1 µm, truncate. *Pileipellis* up to 200 µm thick with colourless gelatinised suprapellis up to 50 µm thick and colourless subpellis, consisting of filamentous hyphae and infrequent vascular hyphae (inflated cells not observed), filamentous hyphae 5–7 µm wide, thick-walled, walls hyaline, gelatinising, contents colourless, radially orientated with some interweaving; vascular hyphae 3–6 µm wide, colourless; clamp connections not observed. *Pileus context* consisting of dominant filamentous hyphae, frequent inflated cells and frequent vascular hyphae, filamentous hyphae 3–50 µm wide with widest constricted at septa, thin-walled, colourless; inflated cells to 350 × 40 µm, thin-walled, ventricose, terminal, colourless; vascular hyphae 10–12 µm wide, occasionally branched, very pale yellow; clamp connections present. *Lamella trama* bilateral, divergent. *Central stratum* consisting of filamentous hyphae (inflated cells and vascular hyphae not observed), filamentous hyphae 2–15 µm

wide with widest constricted at septa, thin walled, colourless, axially orientated; clamp connections present. *Subhymenial base* with angle of divergence *c*. 20° from central stratum, with filamentous hyphae following a smooth curve to subhymenium, consisting of dominant filamentous hyphae, inflated cells and infrequent vascular hyphae; filamentous hyphae 5–30 µm wide, widest close to subhymenium and constricted at septa, frequently branched, thin-walled, colourless; inflated cells up to 150 × 40 µm, thin-walled, cylindric or ventricose or clavate, colourless; vascular hyphae 2–6 µm wide, occasionally branched, very pale yellow; clamp connections frequent. *Subhymenium* ramose, with basidia arising terminally from narrow hyphae or barely inflated hyphal segments 5–10 µm wide; clamp connections present. *Lamella edge tissue* sterile, with inflated cells abundant, up to 45 × 22 µm when pyriform or up to 25 × 25 µm when spherical or up to 30 × 25 µm when ovoid, colourless, some disarticulating. *Basidia* [20/1/1] (41–)43–56 × 10–12 µm, thin-walled, colourless, *c.* 95% 4-spored, *c.* 5% 3-spored, sterigmata to 6 × 2 µm, clamp connections frequent. *Universal veil on pileus* not layered, elements with no dominant orientation, consisting of frequent filamentous hyphae and dominant inflated cells (vascular hyphae not observed), filamentous hyphae 3–12 µm wide, colourless, gelatinising; inflated cells up to 90 × 60 µm when ellipsoid or up to 60 × 60 µm when spherical or up to 85 × 55 µm when ovoid, terminal, colourless, gelatinising; clamp connections frequent. *Universal veil on stipe base* not layered, elements with somewhat axial orientation, consisting of dominant filamentous hyphae, infrequent inflated cells and infrequent vascular hyphae, filamentous hyphae 4–10 µm wide, colourless, many collapsed; inflated cells up to 75 × 20 µm when clavate or up to 175 × 35 µm when ventricose, terminal, colourless; vascular hyphae 5–6 µm wide, pale yellow; clamp connections infrequent. *Stipe context* longitudinally acrophysalidic, consisting of frequent filamentous hyphae, dominant acrophysalides and infrequent vascular hyphae, filamentous hyphae 3–8 µm wide, colourless; acrophysalides to 310 × 30 µm, clavate, terminal, colourless gelatinising; vascular hyphae 10–13 µm wide, occasionally branched, pale yellow; clamp connections infrequent. *Partial veil* elements with a radial orientation, consisting of dominant filamentous hyphae, frequent inflated cells and infrequent vascular hyphae, filamentous hyphae 2–9 µm wide, colourless, collapsing; inflated cells up to 175 × 35 µm when clavate or up to 230 × 30 µm when ventricose, colourless; vascular hyphae 2–8 µm wide, occasionally branched, very pale yellow; clamp connections infrequent. (Figure 8)

*Diagnostic features*. Basidiomata medium. Pileus white with thin, white universal veil. Lamellae white with cream tint. Stipe white. Partial veil median, white, descendant, membranous. Universal veil at stipe base a thin, white membranous free limb at the top of the tapered basal bulb. Spores amyloid, cylindric. Universal veil on pileus with inflated cells dominating, filamentous hyphae also present. Clamp connections present throughout.

*Phenology*. Fruiting period is December or probably after heavy rain.

*Distribution and habitat*. Gregarious in sandy soil in Mallee Woodland and Shrublands. Occurs on the Coolgardie Southern Cross COO02 IBRA subregion (Department of the Environment 2013).

*Conservation status*. To be listed as Priority One (poorly known species) under Conservation Codes for Western Australian Flora (Tanya Llorens pers. comm.).

*Etymology*. Mallee is used as a noun in apposition indicating the Mallee Woodland and Shrubland habitat, where the basidiomes barely emerge above the soil surface.

Figure 7. *Amanita mallee* basidiomes, *M.D. Barrett* F48/12 (*holo*: PERTH 09472797). Photographs M.D. Barrett.

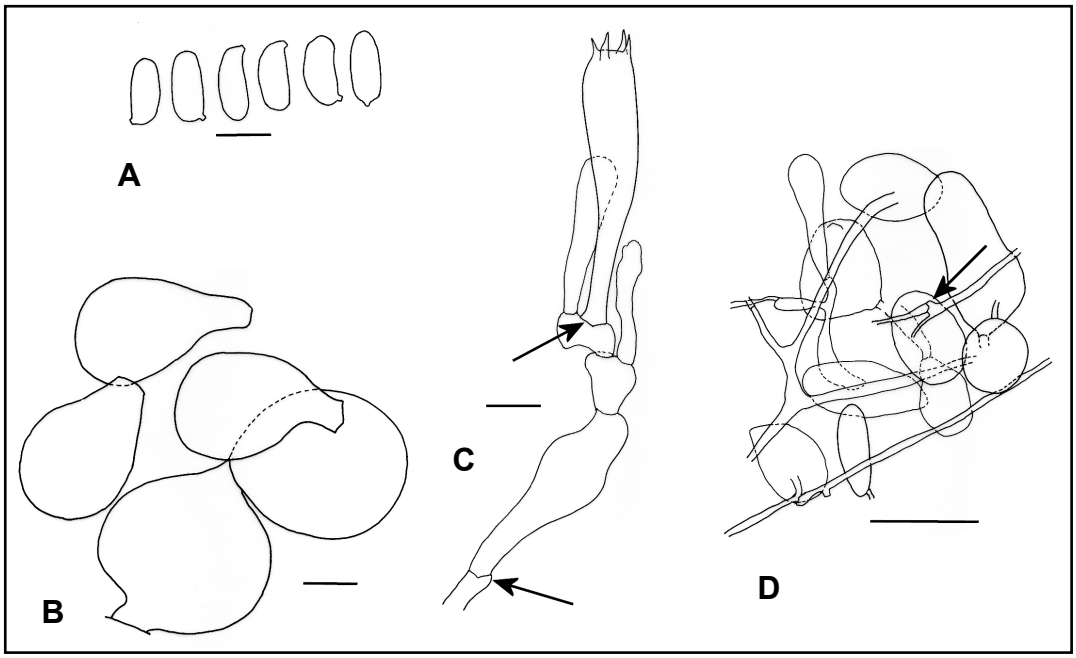


Figure 8. *Amanita mallee*. A – spores from lamella; B – marginal cells; C – basidia; D – universal veil gentle squash. Scale bars = 10 µm (A–C); 50 µm (D); clamp connections indicated by arrows. Images from *M.D. Barrett* F48/12 (*holo*: PERTH 09472797).

**Table 5.** Percentage difference between *ITS* clones from *A. mallee* and *A. carneiphylla* AD282179. The *ITS* region is 571–610 base pairs long.

| Collection | Number of clones | *A. mallee* PERTH 09472797 | *A. carneiphylla* AD282179 |
|---|---|---|---|
| *A. mallee* PERTH 09472797, OP235475–80, OP235490 | 7 | 0.5–8.0 | |
| *A. carneiphylla* AD282179, MN919212–16 | 5 | 22.8–24.4 | 0.4–1.2 |

*Notes*. *Amanta mallee* clusters close to *A. carneiphylla* AD282179 (Figures 1, 2). A comparison of cloned haplotypes of the *ITS* region from *A. mallee* shows there is considerable variation between the clones; they differ by 0.5–8.0% within an individual (Table 5). Sequences from *A. mallee* and *A. carneiphylla* AD282179 differ by 22.8–24.4%, indicating they are not the same.

We are not aware of any species in Australia that are morphologically similar to *A. mallee* and have amyloid spores. *Amanita grossa* Sacc. has large white basidiomes, but ellipsoid not cylindric spores (Bas 1969; Reid 1980; Grgurinovic 1997), whilst *A. conicobulbosa* Cleland has elongate to cylindric spores (*A. mallee* **Q** = 2.09–2.26, *A. conicobulbosa* **Q** = 1.7–2.1 (Bas 1969)). *Amanita lesueurii* E.M.Davison has elongate to cylindric spores, but lacks clamp connections; it is a member of sect. *Arenariae.* Although currently known only from the type collection, *A. mallee* is distinctive both morphologically and molecularly, and on this basis is described as a new species.

**Amanita validiuscula** E.M.Davison, Giustiniano & K.Syme, *sp. nov.*

*Type*: Shire of Cuballing, Western Australia [precise locality withheld for conservation reasons], 13 May 2016, *E.M. Davison & P.J.N Davison* EMD 35-2016 (*holo*: PERTH 09480056). [MB845578].

*Pileus* 54–115 mm wide, up to 14 mm thick, convex becoming plane with slightly depressed centre, margin non-striate, appendiculate, white to ivory white, without surface staining or bruising. *Universal veil on pileus* adnate, floccose, as thick crustose layer or patches to 2 mm thick, white. *Lamellae* adnexed to adnate, close to subcrowded, ivory (4B2), 5–15 mm broad, margin concolorous, fimbriate; lamellulae frequent, in several lengths, truncate or rounded truncate. *Stipe* 70–100 mm long, 30–35 mm wide, cylindric or narrowing upwards, white, surface smooth or fibrillose. *Partial veil* superior to median, descendent, flaring, striate above, thick or thin, white. *Bulb* 50–65 × 40–50 mm, turbinate becoming fusiform or tapered, white. *Remains of universal veil at top of bulb* a short free limb or rings or scales, white. *Pileus and stipe context* white, unchanging, stipe solid. *Odour* none. *Spore deposit* white. (Figure 9)

*Basidiospores* [140/7/2] (8–)8.5–11(–11.5) × 6–7.5(–8) µm, (**L** = 8.9–10.6 µm; **L′** = 9.6 µm; **W** = 6.4–7.3 µm; **W′** = 6.8 µm; Q = (1.23–)1.29–1.58(–1.83); **Q** = 1.39–1.48; **Q′** = 1.42), hyaline, colourless, thin-walled, smooth, amyloid, ellipsoid occasionally broadly ellipsoid or elongate, contents monoguttulate or granular; apiculus sublateral, cylindric or tapered, *c.* 1 × 1 µm, truncate. *Pileipellis* up to 170 µm thick with colourless gelatinised suprapellis up to 120 µm thick and pale yellow subpellis, consisting of filamentous hyphae and frequent to infrequent vascular hyphae (inflated cells not observed), filamentous hyphae 3–10 µm wide, thick-walled, walls hyaline, gelatinising, contents colourless, radially orientated; vascular hyphae 2–11 µm wide, colourless or brownish yellow; clamp connections infrequent. *Pileus context* consisting of dominant filamentous hyphae, frequent inflated cells and frequent to infrequent vascular hyphae, filamentous hyphae 3–25 µm wide with widest constricted at septa, thin-walled, colourless; inflated cells to 235 × 20 µm, thin-walled, cylindrical or clavate or ventricose, terminal, colourless; vascular hyphae 3–8 µm wide, occasionally branched, pale yellow or brownish yellow; clamp connections infrequent to frequent. *Lamella trama* bilateral, divergent. *Central stratum* consisting of filamentous hyphae and infrequent vascular hyphae (inflated cells not observed), filamentous hyphae 3–15 µm wide, thin walled, colourless, axially orientated; vascular hyphae 3–5 µm wide, colourless; clamp connections frequent. *Subhymenial base* with angle of divergence *c.* 30° from central stratum, with filamentous hyphae following a smooth curve to subhymenium, consisting of dominant filamentous hyphae, inflated cells and infrequent vascular hyphae; filamentous hyphae 3–15 µm wide, widest close to subhymenium and constricted at septa, thin-walled, colourless; inflated cells up to 80 × 20 µm, thin-walled, clavate or cylindrical or ventricose, colourless; vascular hyphae 2–6 µm wide, occasionally branched, colourless; clamp connections frequent to abundant. *Subhymenium* ramose, with basidia arising terminally from narrow hyphae or barely inflated hyphal segments 3–12 µm wide; clamp connections frequent to abundant. *Lamella edge tissue* sterile, with inflated cells frequent, to 25–40 × 8–22 µm, clavate, pyriform or cylindrical, colourless, some disarticulating. *Basidia* [40/2/2] (45–)48–66(–71) × 11–15(–16) µm, thin-walled, colourless, *c.* 85% 4-spored, *c.* 15% 3-spored, sterigmata to 7 × 2 µm, clamp connections frequent. *Universal veil on pileus, thin basal layer* (not always present), elements radially orientated, consisting of filamentous hyphae (inflated cells and vascular hyphae not observed), filamentous hyphae 3–5 µm wide, colourless; clamp connections not observed. *Universal veil on pileus, thick distal layer* with elements with somewhat upright orientation, consisting of frequent or dominant filamentous hyphae, dominant or frequent inflated cells and infrequent vascular hyphae, filamentous hyphae 3–20 µm wide, colourless, gelatinising; inflated cells up to 85 × 65 µm when ovoid or up to 120 × 25 µm when clavate or up to 120 × 20 µm when cylindric or up to 70 × 40 µm when ellipsoid or up to 180 × 40 µm when


Figure 9. *Amanita validiuscula* basidiomes, *E.M. Davison & P.J.N. Davison* EMD 35-2016 (*holo*: PERTH 09480056). Photographs E.M. Davison.

ventricose, terminal, or occasionally in chains of up to three cells, colourless, gelatinising; vascular hyphae 4–10 µm wide, colourless or pale yellow; clamp connections infrequent. *Universal veil on stipe base* not layered, elements with somewhat axial orientation, consisting of dominant or frequent filamentous hyphae, frequent or dominant inflated cells and infrequent vascular hyphae, filamentous hyphae 3–12 µm wide, colourless, gelatinising; inflated cells up to 80 × 30 µm when clavate or up to 100 × 55 µm when pyriform or up to 80 × 55 µm when ovoid, terminal, colourless; vascular hyphae 4–10 µm wide, colourless or pale yellow; clamp connections infrequent. *Stipe context* longitudinally acrophysalidic, consisting of frequent filamentous hyphae, dominant acrophysalides and frequent vascular hyphae, filamentous hyphae 2–8 µm wide, colourless; acrophysalides to 420 × 30 µm, clavate or cylindric or ventricose, terminal, colourless, gelatinising; vascular hyphae 3–12 µm wide, occasionally branched, colourless or yellow; clamp connections infrequent. *Partial veil* incoherent; consisting of dominant or equal filamentous hyphae, frequent or equal inflated cells and frequent to infrequent vascular hyphae, filamentous hyphae 3–8 µm wide, colourless, disarticulating; inflated cells up to 50 × 12 µm when clavate or up to 55 × 25 µm when pyriform or up to 50 × 12 µm when ventricose, colourless; vascular hyphae 3–9 µm wide, occasionally branched, pale yellow; clamp connections infrequent. (Figure 10)

*Diagnostic features*. Basidiomata medium to large. Pileus white to ivory with thick, crustose or patchy, white universal veil. Lamellae ivory. Stipe thick, white. Partial veil superior to median, white, descendant, membranous. Universal veil at stipe base as white rings or scale or a short free limb at the top of the fusiform or tapered basal bulb. Spores amyloid, ellipsoid. Universal veil on pileus of dominant inflated cells and filamentous hyphae. Clamp connections present throughout.

*Other specimens examined*. WESTERN AUSTRALIA: [localities withheld for conservation reasons] 11 Sep. 2008, *K. Syme* 2107 (PERTH 08106290).

*Phenology*. Fruiting period is May to September.

*Distribution and habitat*. Gregarious in sandy soil in native vegetation; nearby plants include *Acacia aneura, A. ramulosa, Brachychiton gregoryii, Eucalyptus wandoo.* Occurs in the Avon wheatbelt Katanning AVW02 and Yalgoo Tallering YL02 IBRA subregions (Department of the Environment 2013).

*Conservation status*. To be listed as Priority Two (poorly known species) under Conservation Codes for Western Australian Flora (Tanya Llorens pers. comm.).

*Etymology*. From the Latin *validiusculus* meaning somewhat stout, referring to its stocky appearance.

*Notes*. Depending upon which gene region is analysed, *A. validiuscula* clusters close to an undescribed species from New South Wales, *A.* sp-AUS20 (Figure 1), or to *A. hiltonii* and *A. preissii* (Figures 2A, 2C). A comparison of cloned haplotypes of the *ITS* region from *A. validiuscula* shows there is considerable variation between the clones; they differ by 0.2–3.6% within an individual (Table 6). Sequences from *A. validiuscula* and *A.* sp-AUS20 differ by 9.6–10.1%, indicating they are not the same.

*Amanita validiuscula* is of similar colour and size to *A. grossa* and both have amyloid, ellipsoid spores and clamp connections, however, the universal veil on the pileus of *A. validiuscula* is a thick crustose layer or patches, not thin- crust- to patch-like remnants or of scattered, conical warts, as described for *A. grossa* (Bas 1969; Grgurinovic 1997). Reid (1980) describes the remains of the universal veil on the pileus of *A. grossa* as being composed of abundant oleiferous hyphae (vascular hyphae) whilst in *A. validiuscula* these are infrequent.

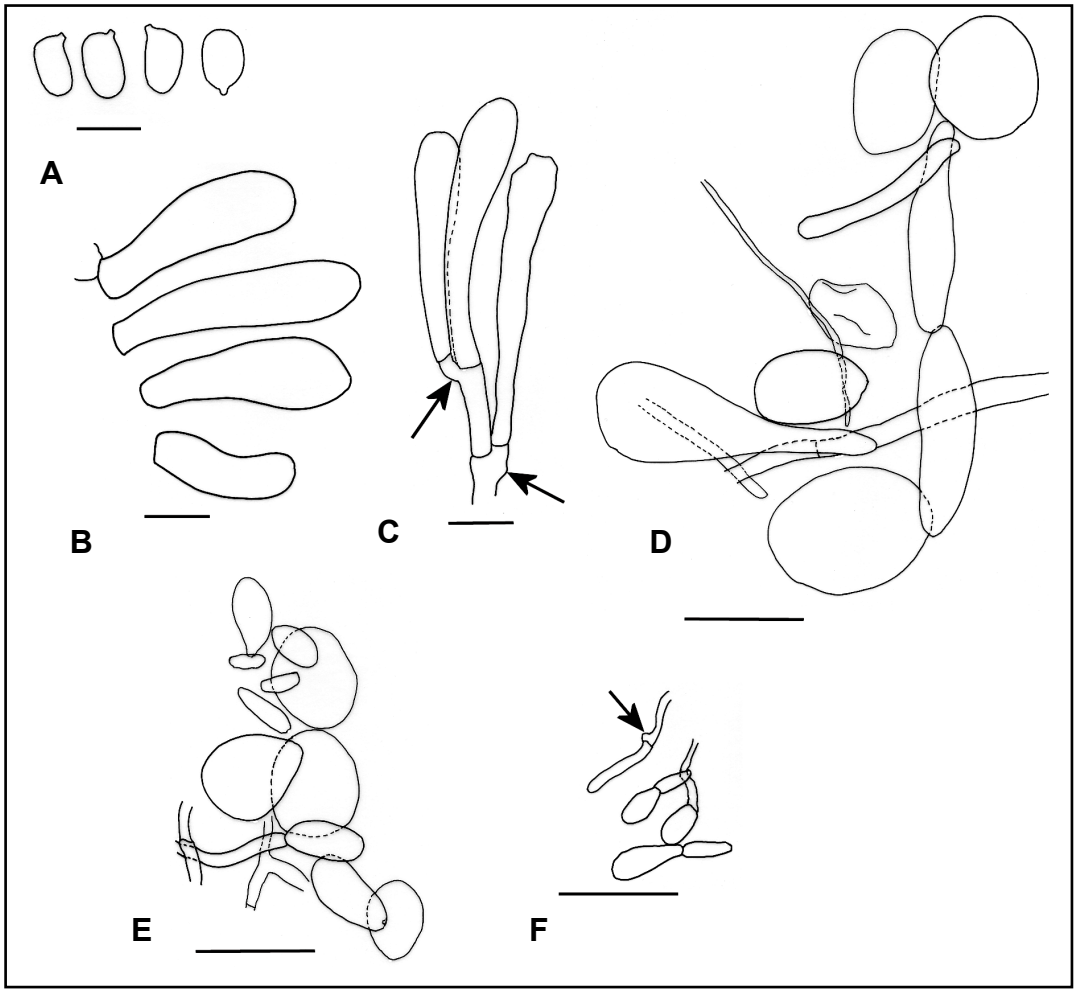


Figure 10. *Amanita validiuscula*. A – spores from print; B – marginal cells; C – basidia; D – universal veil gentle squash; E – universal veil at stipe base unsquashed; F – partial veil gentle squash. Scale bars = 10 µm (A–C); 50 µm (D–F); clamp connections indicated by arrows. Images from *E.M. Davison & P.J.N. Davison* EMD 35-2016 (*holo*: PERTH 09480056).

**Table 6.** Percentage difference between *ITS* clones from *Amanita validiuscula* and sequences of *A.* sp-AUS20. The *ITS* region is 598–613 base pairs long.

| **Collection** | **Number of clones** | ***A. validiuscula* PERTH 09480056** | ***A.* sp-AUS20 ON817223** | **ON817224** |
|---|---|---|---|---|
| *A. validiuscula* PERTH 09480056, OP235502–05, OP235508 | 5 | 0.2–3.6 | | |
| *A.* sp-AUS20 ON817223 | | 9.7–10.1 | | |
| ON817224 | | 9.6–10.0 | 0.3 | |

*Amanita validiuscula* differs from *A. conicobulbosa* because the spores are ellipsoid (**Q** = 1.39–1.48) not elongate to cylindric (**Q** = 1.7–2.1 (Bas 1969)). It differs from *A. hiltonii* because it lacks a conspicuous appendiculate pileus margin (Davison & Giustiniano 2020), and *nuLSU* sequences cluster differently (Figure 1). On this basis, we describe *A. validiuscula* as a new species.

## Discussion

The four new species described in this paper have been confirmed as members of sect. *Roanokenses* (Figure 1). They differ in macroscopic appearance (Figures 3, 5, 7 and 9), microanatomy (Figures 4, 6, 8 and 10), and molecular sequences (Figures 1 and 2). Like other members of sects. *Arenariae* and *Roanokenses* we have studied (Davison & Giustiniano 2020; Davison *et al.* 2017b; 2020; 2021), cloning shows the *ITS* region is much more variable than for clones recorded by Hughes *et al.* (2013).

*Amanita* spp. such as *A. preissii* and *A. xanthocephala* (Berk.) D.A.Reid & R.N.Hilton are amongst the earliest species described from Australia. Their macroscopic descriptions were appropriate at that time, although they would be considered inadequate by today's standards. If the type specimen is well-preserved, it will enable careful description of the microanatomy, as exemplified by Bas (1969). The Cleland collections are extremely important for documenting many species new to science, however, as Reid (1980) pointed out, they pose many difficulties for the taxonomist. Cleland's descriptions were based on a number of collections that have subsequently been found to be of more than one species (Bas 1969; Reid 1980); also, a type collection was not designated because this was not required at the time. This has led to confusion, with some of his names being applied to collections that clearly differ from the original description or nominated lectotype. An example is the uncertainly of the identity of *A. angustispora*; with the misidentification of collections BRIP 23378, BRIP 809253 and UNSW 82/47 by Wood (1997) as *A. angustispora* even though spore shape and presence of clamp connections differ from ADW 9193, the nominated lectotype (E.M. Davison, unpublished observations). The uncertainty over the identity of these Cleland types could be resolved if usable DNA is obtained from these historic collections.

Two of the species we have described (*A. mallee* and *A. validiuscula*) occur in semi-arid shrublands throughout Australia. There are probably many undescribed amanitas in this poorly collected habitat. They are likely to fruit in abundance following heavy rain, however, their low, scarcely emergent stature means they could be easily overlooked (Figure 11).

We have followed Cui *et al*. (2018), in using concatenated datasets of *nuLSU, rpb2*, β-tubulin, *ef1-α* and β-tubulin gene regions where available, to look at deeper relationships between species. Cui *et al*. (2018), have shown that sect. *Arenariae*, within subgenus *Amanitina*, is Gondwanan. The concatenated data (Figure 2D) show a well-supported clade that only includes species from Australia and New Zealand, which may also be of Gondwanan origin. Similarly, we have identified a clade from sect. *Phalloideae* as Gondwanan (Davison *et al*. 2017a). There may be other, unrecognised, Gondwanan clades within *Amanita*.

## Acknowledgements

This work was supported by the Australian Biological Resources Study Grants CN211-40 and CN216-04, by Lotterywest Grant Application 421011392, and the Western Australian Naturalists' Club Gift Fund. We thank N.L. Bougher for his constructive suggestions in a draft of this manuscript, and two anonymous referees for their constructive suggestions that have improved the manuscript.


**Figure 11.** *Amanita validiuscula*, fruiting (A) and drying (B), Sep. 2008, *K. Syme* 2107 (PERTH 08106290). Photographs A: B. Muir, B: K. Syme.

## References


Bas, C. (1969). Morphology and subdivision of *Amanita* and a monograph of its section *Lepidella*. *Persoonia* 5: 285–579.

Cleland, J.B. (1927). Australian fungi: notes and descriptions – No. 6. *Transactions of the Royal Society of South Australia* 51: 298–306.

Cleland, J.B. (1931). Australian fungi: notes and descriptions – No. 8. *Transactions of the Royal Society of South Australia* 55: 152–160.

Cui, Y-Y., Cai, Q., Tang, L.P., Liu, J-W. & Yang, Z.L. (2018). The family Amanitaceae: molecular phylogeny, higher-rank taxonomy and the species in China. *Fungal Diversity* 91: 5–230.

Davison, E.D. (2011). *Amanita ochroterrea* and *Amanita bruneiphylla* (Basidiomycota), one species or two? *Nuytsia* 21: 177–184.

Davison, E.M. & Giustiniano, D. (2020). *Amanita hiltonii* (Amanitaceae), a common but frequently misidentified mushroom in southwestern Australia, and a reconsideration of *A. albifimbriata* and *A. brunneibulbosa*. *Muelleria* 39: 59–73.

Davison, E.M., Giustiniano, D., Bougher, N.L., McGurk, L.E. & Watkin, E.L.J. (2021). Additions to *Amanita* (Amanitaceae, Agaricales) section *Arenaria* from southwestern-Australia. *Australian Systematic Botany* 34: 541–569.

Davison, E.M., Giustiniano, D., Busetti, F., Gates, G.M. & Syme, K. (2017a). Death cap mushrooms from southern Australia: additions to *Amanita* (Amanitaceae, Agaricales) section *Phalloideae* Clade IX. *Australian Systematic Botany* 30: 371–389.

Davison, E.M., Giustiniano, D. & Haska, J.F. (2020). Clarification of the type locality of *Amanita peltigera* (Agaricales, Amanitaceae), phylogenetic placement within subgenus *Amanitina*, and an expanded description. *Swainsona* 33: 51–61.

Davison, E.M., Giustiniano, D., McGurk, L.E., Syme, K. & Robinson, R.M. (2015). *Amanita drummondii* and *A. quenda* (Basidiomycota), two new species from Western Australia, and an expanded description of *A. walpolei*. *Nuytsia* 25: 1–13.

Davison, E.M., Giustiniano, D., McGurk, L.E., Watkin, E.L.J. & Bougher, N.L. (2017b). Neotypification and redescription of *Amanita preissii* (Basidiomycota), and a reconsideration of the status of *A. griseibrunnea*. *Nuytsia* 28: 193–204.

Davison, E.M., McGurk, L.E., Bougher, N.L., Syme, K. & Watkin, E.L.J. (2013). *Amanita lesueurii* and *A. wadjukiorum* (Basidiomycota), two new species from Western Australia, and an expanded description of *A. fibrillopes*. *Nuytsia* 23: 589–606.

Department of the Environment (2013). *Australia's bioregions (IBRA)*. IBRA7, Commonwealth of Australia. https://www.environment.gov.au/land/nrs/science/ibra#ibra [accessed 10 Aug. 2022].

Grgurinovic, C.A. (1997). *Larger Fungi of South Australia.* (The Botanic Gardens of Adelaide and State Herbarium: Adelaide.)

Hughes, K.W., Petersen, R.H., Lodge, D.J., Bergemann, S.E., Baumgartner, K., Tulloss, R.E., Lickey, E. & Cifuentes, J. (2013). Evolutionary consequences of putative intra- and interspecific hybridization in agaric fungi. *Mycologia* 105: 1577–1594.

Kimura, M. (1980). A simple method for estimating evolutionary rates of base substitution through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16: 111–120.

Kornerup, A. & Wanscher, J.H. (1983). *Methuen Handbook of Colour.* 3rd edn. (Methuen: London.)

McGurk, L.E., Giustiniano, D., Davison, E.M. & Watkin, E.J. (2016). *Amanita wadulawitu* (Basidiomycota), a new species from Western Australia, and an expanded description of *A. kalamundae. Nuytsia* 27: 21–30.

Miller, O.K. Jr. (1991). New species of *Amanita* from Western Australia. *Canadian Journal of Botany* 69: 2692–2703.

Miller, O.K. Jr. (1992). Three new species of *Amanita* from Western Australia. *Mycologia* 84: 679–686.

Reid, D.A. (1980). A monograph of the Australian species of *Amanita* Pers. ex Hook. (Fungi). *Australian Journal of Botany; Supplementary Series* No. 8: 1–97.

Royal Botanic Garden, Edinburgh (1969). *Flora of British fungi: colours identification chart*. (Her Majesty's Stationery Office: Edinburgh.)

Schoch, C.L., Seifert, K.A., Huhndorf, S., Robert, V., Spouge, J.L., Levesque, C.A., Chen, W. & Fungal Barcoding Consortium (2012). Nuclear ribosomal internal transcribed spacer (ITS) region, a universal DNA barcode marker for Fungi. *Proceedings of the National Academy of Sciences* 109: 6241–6246.

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011). Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution* 28: 2731–2740.

Travaré, S. (1986). Some probabilistic and statistical problems on the analysis of DNA sequences. *Lectures on Mathematics in the Life Sciences* 17: 57–86.

Tulloss, R.E. (2000). *Notes on methodology for study of Amanita (Agaricales).* http://www.amanitaceae.org/content/uploaded/pdf/methodsb.pdf [accessed 11 Aug 2016**].**

Tulloss, R.E. (2022). *Amanita angustispora* (http://www.amanitaceae.org/?Amanita%20angustispora [accessed 7 June 2022].

Wood, A.E. (1997). Studies in the genus *Amanita* (Agaricales) in Australia. *Australian Systematic Botany* 10: 723–854.

Yang, Z.L., Cai, Q. & Cui, Y-Y. (2018). Phylogeny, diversity and morphological evolution of Amanitaceae. *Biosystematics and Ecology-Series* 34: 359–380.