Mycological Progress (2022) 21: 85
https://doi.org/10.1007/s11557-022-01836-7

ORIGINAL ARTICLE

Four new genera and six new species of lyophylloid agarics (*Agaricales*, *Basidiomycota*) from three different continents

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Received: 2 May 2022 / Revised: 17 August 2022 / Accepted: 19 August 2022

Abstract
Four new genera encompassing six new species are described in the *Lyophyllaceae* (*Agaricales*): the monotypic *Australocybe* from Australia; the monotypic *Phaeotephrocybe* from Belize; the monotypic *Nigrocarnea* from Laos containing the novel conidia-producing species *N. radicata* and *Praearthromyces* containing two Asian taxa, the conidia-producing *P. corneri* known from Malaysia and Singapore and *P. griseus* from Thailand, which lacks conidial production. In addition, we describe *Arthromyces glabriceps*, which is the first species in the genus *Arthromyces* that lacks conidial production on the basidiome. Alternative options for a classification of these lyophylloid taxa are discussed and based on morphological, ecological and biogeographical considerations rejected.

Keywords *Lyophyllaceae* · *Arthromyces* · *Blastosporella* · *Australocybe* · *Tephrocybe* · *Praearthromyces* · *Termitomyces* · Arthrospores · Phylogeny · Taxonomy

Introduction

The genus *Tephrocybe* as introduced by Donk (1962), as a segregate from the genus *Lyophyllum* P. Karst., contains a number of small collybioid mushrooms, often with a hygrophanous pileus and grey colours (Donk 1962). Various molecular studies have shown the genus to be paraphyletic, which is consistent with the lack of diagnostic features (Hofstetter et al. 2002; Hofstetter et al. 2014; Bellanger et al. 2015). The most recent study which included several members of *Tephrocybe* found eight distinct evolutionary origins within the *Lyophyllaceae* (Bellanger et al. 2015). Several *Tephrocybe* species have been transferred back to *Lyophyllum*, or have been placed in new genera such as *Myochromella*, *Sagaranella* and *Sphagnurus* (Hofstetter et al. 2014). A previous study showed that the type of the genus, *Tephrocybe rancida*, is part of a termitomycetoid clade which, next to the termite-associated genus *Termitomyces*, also contains the insect-faecal associated genera *Arthromyces* and *Blastosporella* (van de Peppel et al. 2021). The study by van de Peppel et al. also showed that five different species, which were provisionally identified as *Tephrocybe* sp. (s.l.), are also part of this termitomycetoid clade. In the present study, we examined these five unnamed

Section Editor: Zhu-Liang Yang

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species and an additional specimen of an unnamed species of the genus *Arthromyces*. In order to test whether any of the currently accepted members of the genus *Tephrocybe* are part of the termitomycetoid clade, several additional fungarium specimens of known species were included in the analysis.

A specimen from Australia (*Tephrocybe* sp. 1) is macroscopically similar to *T. rancida* but phylogenetically distinct, occupying an isolated branch in the termitomycetoid clade. Because of the strong phylogenetic evidence and to conserve monophyletic genera, we propose to place this species in the monotypic genus *Australocybe*. The sole member of this genus, *A. olivacea*, is described below.

The study by van de Peppel et al. (2021) recovered a subclade within the termitomycetoid clade containing *T. rancida*, *Blastosporella zonata* and *Tephrocybe* sp. 2 and 3. Fieldwork in Laos in connection with the production of the first booklet on edible, poisonous and medicinal fungi from this country (Læssøe et al. 2019) led to the recognition of *Tephrocybe* sp. 3, a species with internal conidia in the pileus context. *Tephrocybe* sp. 2 is a species from Belize, similar to *T. rancida*, which lacks the production of conidia on the basidiome. Due to the lack of shared characters among these two species and the genus *Blastosporella*, we propose to erect two monotypic genera; *Phaeotephrocybe* and *Nigrocarnea*. *Tephrocybe* sp. 3 is described below as *Nigrocarnea radicata* and *Tephrocybe* sp. 2 is described below as *Phaeotephrocybe leucophylla*.

Baroni et al. (2007) reported a close morphological similarity of the palaeotropical/Asian *Tricholoma furcatifolium* to the Neotropical/American genus *Arthromyces.* Examination of *Tephrocybe* sp. 5 from the study by van de Peppel et al. (2021) showed this species to be very similar to *T. furcatifolium*. This species together with *Tephrocybe* sp. 4 make up a small clade sister to the *Arthromyces*-*Termitomyces* clade, and these two species thus are not related to the ectomycorrhizal genus *Tricholoma*. In addition, we examined the type collection of *T. furcatifolium*. A DNA sequence generated from one of the paratypes of *T. furcatifolium* shared 99% identity with *Tephrocybe* sp. 5, confirming that this species belongs to the *Lyophyllaceae*. The holotype of *T. furcatifolium* does not produce arthroconidia on the basidiome and therefore the holotype and paratype may represent different species. Therefore, we described *Tephrocybe* sp. 5 as a new species; *Praearthromyces corneri*. As both this species and *Tephrocybe* sp. 4 do not nest phylogenetically with any of the described genera within the termitomycetoid clade, we propose to place them in the new genus *Praearthromyces* and describe *Tephrocybe* sp. 4 as *Praearthromyces griseus*.

The genus *Arthromyces* currently encompasses two species. *A. matolae* was reported from Belize and *A. claviformis* was originally reported from Puerto Rico and the Dominican Republic (Baroni et al. 2007). Recently, *A. claviformis* has also been observed in Colombia near Cali (mushroomobserver.org, observations: 275090, 348275, 367362) and Cogua (observation 363150). A recent soil metabarcoding study identified OTU's as *Arthromyces* sp. from the Andean Yungas forest of Argentina (Eduardo et al. 2018). This indicates that the genus *Arthromyces* has a distribution range spanning the entire continent of South America and extending to the Caribbean islands and Central America. Furthermore, *A. matolae* has been collected as far north as Gainesville, Florida (van de Peppel et al. 2021). Although the production of dark arthroconidia on both the stipe and pileus of the basidiome is one of the key features of *Arthromyces*, we examined several specimens identified as *Arthromyces* sp., which lack conidia on the basidiome. Our molecular phylogenetic analysis shows that these specimens nest within the genus *Arthromyces* and is sister to *A. matolae*. These specimens are described as *Arthromyces glabriceps* below.

Material and methods

Morphological analysis

Colour codes used in species descriptions refer to Kornerup and Wanscher (1978). Presence of hymenial cystidia is examined in longitudinal sections of lamellae and additionally for cheilocystidia in whole mounts of lamellar edges of at least 1 mm in length. All measurements of microscopic structures were made under 1000× magnifications.

DNA extraction and PCR

For DNA extraction, small fragments of dried fungarium specimens were used. DNA was extracted following a modified cetyltrimethylammonium bromide (CTAB) protocol (Nieuwenhuis et al. 2019). For known members of the genus *Tephrocybe*, the nuclear ribosomal region containing the internal transcribed spacer 1 (ITS1), 5.8S and the internal transcribed spacer 2 (ITS2) was amplified using a conventional polymerase chain reaction (PCR). For the five unnamed species of *Tephrocybe* and the unnamed species of *Arthromyces*, a partial sequence of the nuclear ribosomal large subunit (LSU, 28S) and the sequence encoding for elongation factor 1-alpha (*EF1α*) were also amplified using PCR. The following primer pairs were used: the fungal-specific forward primer ITS1f and the universal reverse primer ITS4 for the ITS marker (White et al. 1990; Gardes and Bruns 1993), LROR and LR5 for the LSU (Vilgalys and Hester 1990) and EF595F and EF1160R for *EF1α* (Kauserud and Schumacher 2001). After initial amplification of the holotype of *T. furcatifolium* failed, a PCR was conducted targeting ITS1 and ITS2 separately using the primer pairs ITS1f/ITS2 and ITS3/ITS4 (White et al. 1990; Gardes and Bruns 1993).

All PCR programs were conducted as described previously (van de Peppel et al. 2018). Sequencing was performed by Eurofins genomics (Ebersberg, Germany) using both the forward and reverse primer. For LSU only, the forward primer (LROR) was used as the forward read was of sufficient quality for subsequent analysis. Inspection of the chromatograms and assembly of the forward and reverse sequences was performed using the CLC Genomics Workbench 8. All new sequences were deposited in Genbank (Supplementary Table 1).

Phylogenetic analysis

To test whether any of the current members of the genus *Tephrocybe* are part of the termitomycetoid clade, ITS sequences obtained from various species of *Tephrocybe* (Supplementary Table 1) were compared using NCBI BLAST, to a dataset consisting of all currently known members of the termitomycetoid clade and a representative number of species from the *Lyophyllaceae*. Since the phylogenetic relationships within the termitomycetoid clade already have been estimated and are well supported, based on a phylogenetic reconstruction on a dataset of 1131 orthologous genes (van de Peppel et al. 2021), a three-gene phylogeny would not add any additional phylogenetic resolution. We therefore limited our phylogenetic reconstruction of the termitomycetoid clade to specimens of the genus *Arthromyces*, since *A. glabriceps* was not included in the study by van de Peppel et al. Sequences for each individual marker (ITS, LSU and *EF1α*) were aligned using MAFFT v7.409 online alignment software, using default settings (Katoh et al. 2019). The three resulting alignments were trimmed and concatenated in Geneious 10.0.9 (Kearse et al. 2012). A maximum-likelihood tree was reconstructed using the webserver of IQ-tree with default settings and 1000 ultrafast bootstrap replicates (Trifinopoulos et al. 2016).

Results

Morphology

All taxa described here share the following microscopic features: basidiospore walls are inamyloid but evenly cyanophilic, basidia and basidioles possess siderophilic and cyanophilic bodies (Baroni 1981) typical of all members of the *Lyophyllaceae*.

Phylogenetic analysis

The only known species of *Tephrocybe* which had a close match to a member of the termitomycetoid clade was *T. oldae*. The ITS sequence of this species was very similar (99.72%) to that of our *T. rancida* specimens (OM905964 and OM905967). The study by van de Peppel et al. (2021) found significant support for all branches within the termitomycetoid clade, resulting in a fully resolved tree (Fig. 1A). Our phylogenetic reconstruction on *Arthromyces* specimens shows significant bootstrap support for *A. glabriceps* being sister to a clade containing *A. matolae* and *A. claviformis* (Fig. 1B).

Taxonomy

Australocybe olivacea T.J. Baroni, N. Fechner & L.J.J. van de Peppel, gen. et sp. nov. Fig. 2

Mycobank: MB 843078 (genus), MB 843079 (species)

Etymology: Australocybe—named after the continent of origin. Olivacea—named after the olive-grey colour of the lamellae.

Holotypus: Australia, Queensland State, Great Sandy National Park, Cooloola Sand-Mass, Rainbow Beach area, Freshwater Track, in sandy soil, under *Allocasuarina*, *Eucalyptus pilularis* and other *Eucalyptus* species, and *Leptospermum*, 25°56′46.6″S 153°07′42.6″E, 144 m elevation, 25 May 2011, T.J. Baroni 10521 (BRI1030081; ISOTYPE CORT014480) Genbank: OM905944 (ITS), OM905996 (LSU), OM974129 (*EF1α*), GCA_018221635.1 (Genome).

Diagnosis: Tephrocyboid in stature with the habit of *T. rancida* but differing significantly by the dark fuscous brown colour of the pileus, olive-grey lamellae, pale golden-olive coloured pseudorhiza, presence of cheilocystidia and pleurocystidia with dark golden-brown resinous pigments inside of and also extruded from these cystidia and distinct molecular profile of its combined ITS, LSU and *EF1a* sequences.

Basidiomata dark fuscous overall except for olive-grey lamellae. Pileus 7–20 mm, broadly conical-convex becoming plane with a low rounded umbo, faintly translucently striate near margin when moist, mostly opaque and densely matted fibrillose textured when young, somewhat granular over the disc, becoming glabrous, dark fuscous brown (6-8F3, Negro), fading to greyish brown (6D-E3, Café-au-Lait) or brownish grey (6D2), hygrophanous and becoming a paler brownish grey (5D2, Dust) from disc out radially to margin. Lamellae olive to yellowish grey (3D2–3, Yellowish Grey) or olive brown (4C-D3–4, Flaxen, Sallow; 4E3), adnexed, crowded, rarely forked, broad (2.5–5 mm), edge even, concolorous. Stipe concolorous with pileus, strongly tapered into a long pseudorhiza, which is a pale greenish golden-olive or greyish yellow (4B-C4, Champagne to Blonde), 1–2 × 15–45 mm, some reaching 60 mm in length, with golden olive pruina from apex to mid stipe, glabrous below, hollow and white stuffed in medulla.

Basidiospores 6.0–7.0 (–8) × 3.0–4.0 µm, elliptical in profile and face views, round in polar view, smooth, with slightly congophilous walls. Basidia (15–) 20–25 × (5–) 6–7 µm, narrowly clavate, 4-sterigmate, with large cyanophilic bodies.

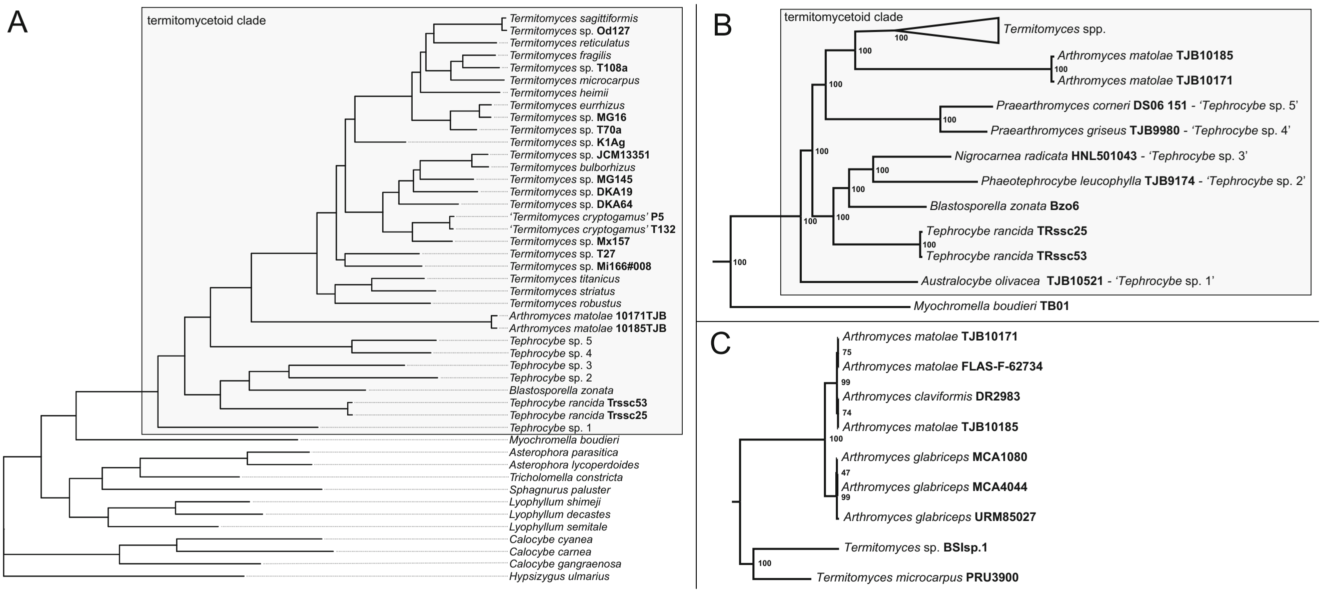

Fig. 1 **A** Phylogenetic tree of the *Lyophyllaceae*, based on 1131 core nuclear genes. The termitomycetoid is highlighted in grey. **B** Subsection of the tree showing the phylogenetic placement of the five unidentified species of *Tephrocybe* in the termitomycetoid clade (Both **A** and **B** are adapted from van de Peppel et al. 2021). Support values at the nodes indicate bootstrap replicates. **C** Maximum-likelihood tree, based on *EF1α*, ITS, and LSU sequences, showing the novel species *Arthromyces glabriceps* nests with other species of *Arthromyces*. Support values at the nodes indicate ultrafast-bootstrap replicates

Cheilocystidia abundant (lamella edge sterile), lageniform, ventricose-rostrate, rostrum sometimes capitate, also some subglobose to ovate and pedicellate, 30–45 × 10–16 μm, mostly with dark golden brown resinous coagulated pigments in the apical regions of the cystidia, sometimes completely filled with resinous pigments (somewhat like chrysocystidia); this golden resinous pigment can be extruded and coating the apex of the cystidia. Pleurocystidia scattered but fairly common, as cheilocystidia in shapes and frequently filled with golden brown resinous pigment. Lamella trama pale to moderately brown from parietal pigments in the hyphal walls, many hyphae also finely to moderately encrusted with brown pigments, hyphae parallel, cylindrical or inflated, 2.5–10 μm in diam. with abundant internal cyanophilic bodies. Pileipellis a cutis of repent dark brown strongly encrusted hyphae, hyphae 3–9 μm in diam, producing scattered or clustered short

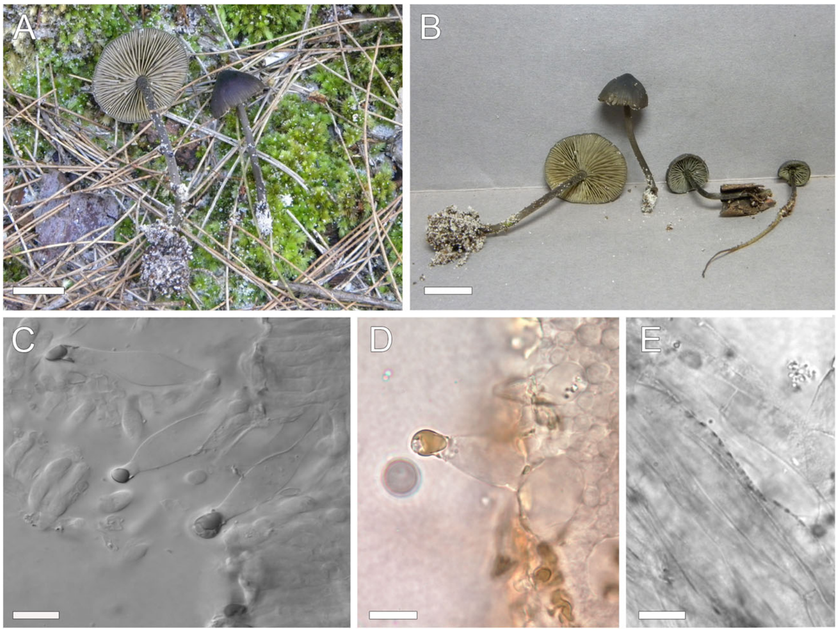

Fig. 2 *Australocybe olivacea* T. J. Baroni 10521 Holotype. **A** and **B** Basidiomata. **C** and **D** cheilocystidia. **E** Pigment encrustations on hyphae of lamella trama. Scale bars, 10 mm for **A** and **B**, 10 μm for **C**–**E**

inflated pilocystidia, 20–30 × 4–7 µm, which also mostly have cylindrical projecting undulating apices on top of the inflated cell, cylindrical projections 2–3 µm in diam. Clamp connections present in all tissues.

Additional material examined: Australia, Queensland State, Great Sandy National Park, Cooloola Sector, Freshwater Track, in sandy soil along the road side, in the same general area as CORT014480, rooting in soil under *Allocasuarina*, *Eucalyptus pilularis* and other *Eucalyptus* species, and *Leptospermum*, 2 basidiomata, 25°56′46.6″S 153°07′42.6″E, 144 m elevation, 25 May 2011, T.J. Baroni 10527 (BRI1030082 and CORT014479).

Discussion: *Australocybe* is the earliest diverging lineage of the termitomycetoid clade and the only taxon with clamp connections in combination with cheilo- and pleurocystidia with resinous contents. *Tephrocybe* and *Blastosporella* also produce clamp connections (Table 1), while all the other taxa in this clade leading up to *Termitomyces*, lack clamp connections on their hyphae. The presence of resin producing hymenophoral cystidia are also distinctive for *Australocybe*, and found in species of *Arthromyces* so far, although refractive resinous particles can be found on basidia and basidioles in *Nigrocarnea radicata* as well. Presumably these resin encrustations would be a deterrent to hymenophore grazing fungivores, thus allowing for prolonged basidiospore production.

It is not clear at the present time if this old world taxon is associated with insects, but the presence of a well-developed pseudorhiza suggests this possibility since other members of the clade, i.e. *Blastosporella*, *Arthromyces* and *Termitomyces*, have evolved this symbiotic (or distinctive) relationship. Future investigations are needed to determine if *Australocybe*, *Nigrocarnea*, *Praearthromyces*, and *Phaeotephrocybe* all share some type of insect association.

Nigrocarnea radicata Sparre P. & Læssøe, gen. et sp. nov. Fig. 3

Mycobank: MB 843080 (genus), MB 843081 (species)

Etymology: Nigrocarnea—referring to the black flesh in the pileus. Radicata—referring to the long pseudorhiza

Holotypus: Laos, Man Xom Village, Pek District, Xieng Khouang Province, Lao PDR, subtropical *Fagaceae* rich forest with *Quercus* and *Castanopsis* 19°32′55.9″N 103°16′50.7′′E, elevation 1230 m asl, 21 August 2015, T. Læssøe & O.S. Pedersen (HNL501043) Genbank: OM905946 (ITS), OM905998 (LSU), OM974131 (*EF1*α), GCA_018855915.1 (Genome).

Diagnosis: Tephrocyboid in stature and because of the long pseudorhiza similar to the habit of *T. rancida*, differing however by the striking black, pulverulent pileus flesh consisting of chains of smooth, dark-coloured arthroconidia and the absence of clamp connections in all tissues, and by the distinct molecular profile of its combined ITS, LSU and *EF1a* sequences.

Basidiomata rooting singly or in pairs in soil under *Fagaceae* in rich broadleaved forest. Pileus 16–25 mm, convex with discrete broad umbo to sub-conical, becoming plano-convex, some with shallowly depressed disc with age, dark brownish grey (near 7F2), minutely pruinose, margin pale grey, inrolled, dry. Lamellae crowded, adnexed, lead grey (ca 14B1), edge slightly paler, eroded, full length lamellae (L) reaching stipe 55+, lamellulae (l) 1–3 tiers, forking quite common, 1.5 mm broad. Pileus 3–4-mm-thick, context deep black. Stipe 16–30 × 2–4 mm, excluding pseudorhiza, central or eccentric, solitary or joined in pairs with very long, very thin pseudorhiza, pruinose and fibrillose, grey, much paler than pileus. Smell and taste somewhat rancid but not very strong. Spore deposit not obtained.

Basidiospores 4.5–8 × 3.0–5.0 µm, av. 5.4 × 3.7 µm, Qav. 1.48 (*N* = 50), not abundant and difficult to find in mounts, ellipsoid, smooth. Basidia 15–23 × 6–9 µm (*N* = 16), clavate, 4-sterigmate. Basidia and basidioles moderate to densely

Table 1 Overview of morphological characters represented by the new species and their close relatives

Species	Characters conidia on/in basidiome	Clamp connections	Cheilocystidia	Pleurocystidia	Insect-faecal association	Continent
Australocybe olivacea	**o**	**x**	**x**	**x**	**?**	Australia
Tephrocybe rancida	**o**	**x**	**o**	**o**	**o**	North America, Europe
Blastosporella zonata	**x**	**x**	**x**	**o**	**x**	South America
Nigrocarnea radicata	**x**	**o**	**o**	**o**	**?**	Asia
Phaeotephrocybe leucophylla	**o**	**o**	**x**	**x**	**?**	South America
Praearthromyces corneri	**x**	**o**	**x**	**o**	**?**	Asia
Praearthromyces griseus	**o**	**o**	**x**	**o**	**?**	South America
Arthromyces glabriceps	**o**	**o**	**x**	**o**	**?**	South America
Arthromyces matolae	**x**	**o**	**x**	**o**	**x**	South America
Termitomyces spp.	**o**	**o**	**o/x**	**o/x**	**x**	Africa

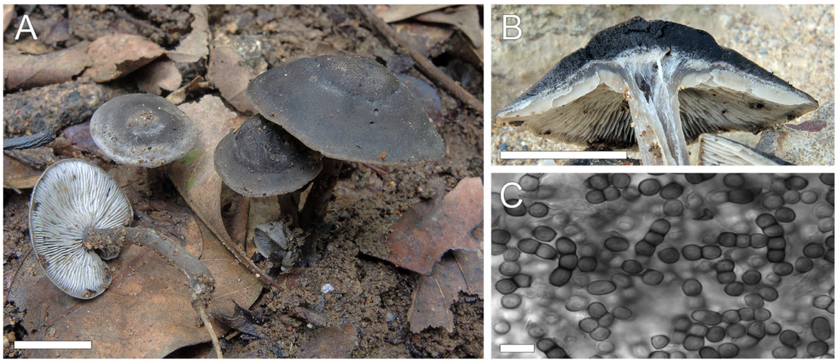

Fig. 3 *Nigrocarnea radicata* HNL501043 Holotype. **A** Basidiomata in situ. **B** Cross section of pileus showing mass of dark arthroconidia. **C** Arthroconidia. Scale bars, 10 mm for **A** and **B**, 10 μm for **C**

covered with hyaline, refractive or golden tinted resinous particles. Hymenial cystidia absent. Lamella trama regular with parallel hyphae, 3–12 (− 18) μm broad, hyaline, thin- to slightly thick-walled. Pileipellis a cutis of repent, brown, cylindrical and inflated hyphae, 5–20 μm in diam, pigments parietal and some weakly encrusting, pileocystidia absent. Context mostly filled with dark brown arthroconidia. Stipitipellis a cutis of smooth hyphae, 5–9 μm broad; without caulocystidia. Clamp connections absent at all septa. Arthroconidia round to squarish, smooth, thick walled (1.5–2.5 μm), pale-brown to grey-brown, 6–10 (–14) × (5–) 6.0–8.0 μm, av. 8.3 × 6.7 μm ($N = 30$), single or in chains with maximum of four conidia per chain.

Additional material examined: Laos, Van Village, Pek District, Xieng Khouang Province, Lao PDR, subtropical *Fagaceae* rich forest with *Quercus* and *Castanopsis* 19°34′4.4″N103°10′31.8″E, elevation 1281 m, 20 August 2017, O. S. Pedersen and W. Sibounheuang (UDB034575/HNL501934).

Discussion: Molecular data shows that *N. radicata* is closely related to *Blastosporella zonata* (Fig. 1). Morphologically, they look somewhat similar as they both produce conidia in/on the pileus and have a rooting stipe. However, they can be distinguished by the type and position of conidia as *N. radicata* produces chains of arthroconidia in the pileus context and *B. zonata* produces ornamented blastoconidia in small spore heads on the surface of the pileipellis. These two species have no overlap in distribution as *N. radicata* occurs in the paleotropics while *B. zonata* occurs in the neotropics. An ITS sequence generated from an additional collection UDB034575/HNL501934 confirms that this collection belongs to the same species. These collections were made some 10 km apart in the same area, forest type and altitude and with similar macroscopic and microscopic features.

Because of the reported insect-faecal association in the closely related *B. zonata* (van de Peppel et al. 2021), we attempted to dig down to find the nutrient substrate to which the pseudorhiza was attached, but it was not possible to follow the very thin strand deeper than about 10 cm in hard soil. The type locality was very rich in ectomycorrhizal fungi and also in species of *Termitomyces*.

Phaeotephrocybe leucophylla T.J. Baroni, T.W. Kuyper & L.J.J. van de Peppel, gen. et sp. nov. Fig. 4

Mycobank: MB 843082 (genus), MB 843083 (species)

Etymology: Phaeo - Tephrocybe—referring to the brown colour of the pileus and stipe and the similarity to the genus *Tephrocybe*. Leucophylla—referring to the white lamellae.

Holotypus: Belize, Orange Walk District, La Milpa Station, Chicle Trail, on soil, scattered, 17°50′31.1″N 89°01′09.4″W, elevation 142 m, 13 August 2001, T.J. Baroni 9174 (CORT014602) Genbank: OM905945 (ITS), M905997 (LSU), OM974130 (*EF1α*), GCA_018850275.1 (Genome).

Diagnosis: Tephrocyboid in stature and somewhat similar in appearance to *Tephrocybe rancida* but distinguished from this grey coloured species by the brown colours of the pileus and stipe and the white gills. It also differs from *Blastosporella zonata*, *Nigrocarnea radicata* and species of *Arthromyces* by the absence of dark blasto- or arthroconidia in/on the pileus and from species of *Praearthromyces*, and all species and genera discussed here, by its distinct molecular profile of combined ITS, LSU, and *EF1a* sequences.

Pileus 10–25 mm, convex or broadly campanulate, some broadly truncate umbonate, dry, hygrophanous, subzonate on some, pale olive yellowish brown at first (4B4 Greyish Yellow, Champagne), becoming dark grey brown (5D-E4 Dark Blonde, Hair Brown), strongly hygrophanous then shiny and paler. Lamellae extremely crowded, adnate, white or some becoming greyish tan (5C3 brownish orange) with age, 1 mm broad, dichotomously forked 2–3 times, mainly when close to stipe. Stipe 30–50 × 1–2.5 mm, equal, terete, mostly tapering at base to a bent short pseudorhiza, rather tough and pliant, concolorous with pileus, densely white floccose over base and especially over the bent pseudorhiza, fine, white, appressed fibrillose over the above ground portions, but especially noticeable over the upper ½ of the stipe, hollow. Odour rancid farinaceous when crushed. Taste farinaceous fabaceous.

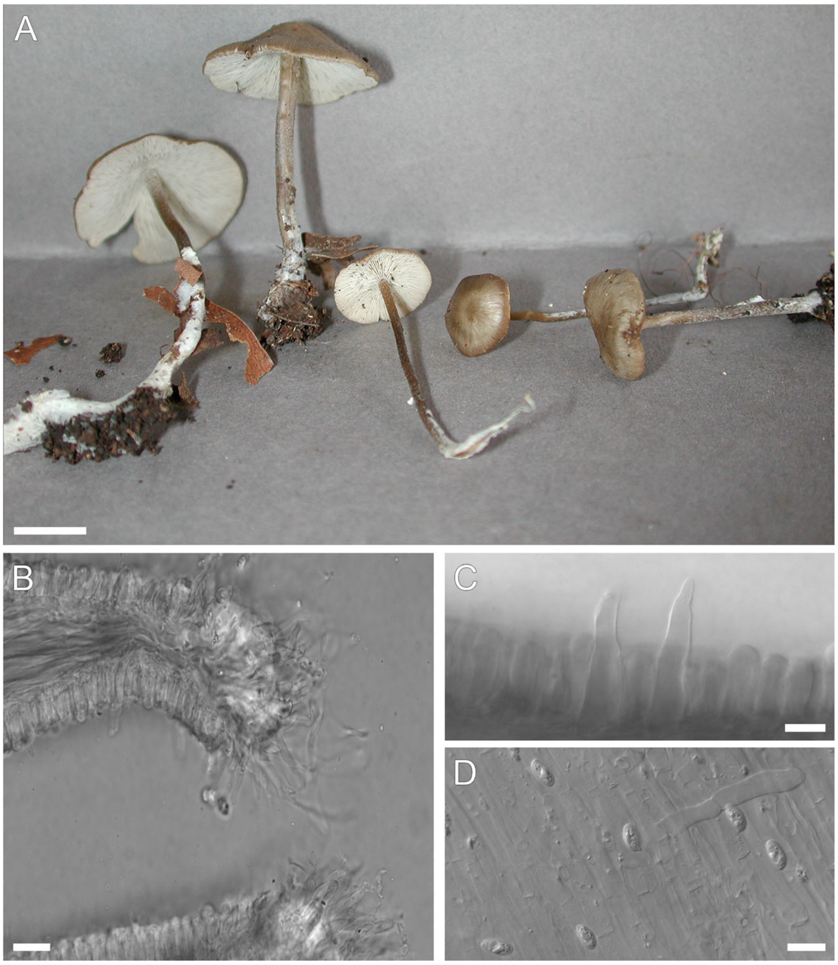

Fig. 4 *Phaeotephrocybe leucophylla* T.J. Baroni 9174 Holotype. **A** Basidiomata. **B** Cheilocystidia. **C** Pleurocystidia. **D** Basidiospores. Scale bars, **A** 10 mm, **B** 5 μm, **C**, D 10 μm

Basidiospores 6.0–8.0 (–10) × 3.5–4 (–5) μm, elliptical or narrowly elliptical or somewhat elliptical-cylindrical in profile and face views, round in polar view, smooth, with slightly thickened, with congophilous walls. Basidia very short, (12–) 15–20 × 5–7 μm, 2 and 4-sterigmate, clavate. Cheilocystidia densely crowded (lamella edge sterile) hyaline, versiform end cells projecting and proliferating from the trama, 20–60 × 3–7 μm, with mixtures of cylindrical, cylindrical-contorted, lageniform with long rostrum, some septate with straight or flexuose narrow apex, some with capitate apices, walls thin to slightly thickened. Pleurocystidia scattered, hyaline, fusiform or lageniform or ventricose-rostrate, some broadly lanceolate, 20–36 × (4–) 6–8 μm. Lamella trama regular, consisting of parallel, cylindrical or slightly inflated hyphae, 3–10 μm in diam, with thin to slightly thickened walls. Pileus context composed of radially arranged, hyaline, mostly inflated hyphae, 8–20 μm in diam. Pileipellis a cutis of brown or pale yellow-brown, repent, cylindrical or slightly inflated hyphae, 3–6 (–8) μm in diam, pale brown pigment mainly parietal, but occasionally minutely encrusting. Stipitipellis a cutis of repent, parallel, colourless hyphae, 2.5–5 μm in diam, producing scattered clusters of cylindrial, erect and interwoven or single caulocystidia, 15–55 × 3–5 μm. Clamp connections absent in all tissues. Arthroconidia absent from all tissues.

Discussion: *Phaeotephrocybe leucophylla* is a neotropical species that is similar in general appearance compared to the European/North American *Tephrocybe rancida* but differs most notably in colour of the pileus, stipe and lamellae. *Phaeotephrocybe leucophylla*, does not produce conidia on its basidiomata, but is phylogenetically related to the arthroconidia producing *Nigrocarnea* from the paleotropics and the blastospore conidium producing genus *Blastosporella* from the neotropics (Fig. 1A). *Phaeotephrocybe leucophylla* has no clamp connections, a feature shared with its phylogenetic sister taxon *Nigrocarnea radicata*, and all taxa (*Praearthromyces*, *Arthromyces*, *Termitomyces*) in the evolutionary lineage leading to the termite farmed agarics. Clamp connections are found in the three early branching genera in the termitomycetoid clade, *Australocybe, Tephrocybe* and *Blastosporella.*

Praearthromyces T.J. Baroni, T.W. Kuyper & L.J.J. van de Peppel, gen. nov.

Mycobank: MB 843084

Etymology: Prae *Arthromyces*—before *Arthromyces.*

Holotypus: *Praearthromyces corneri* D. Stubbe, T.J. Baroni, T.W. Kuyper & L.J.J. van de Peppel

Diagnosis: Species with tephrocyboid or collybioid or mycenoid habit with narrow, densely crowded lamellae, with thin, deeply rooting pseudorhiza, no clamp connections, cheilocystidia variously shaped and mostly lacking internal pigments or resinous materials, and phylogenetically distinct by molecular profile of its combined ITS, LSU and *EF1a* sequences.

Praearthromyces corneri D. Stubbe, T.J. Baroni, T.W. Kuyper & L.J.J. van de Peppel, sp. nov. Fig. 5

Mycobank: MB 843085

Etymology: In honour of Edred John Henry Corner for his great contributions to the field of mycology.

Holotypus: Malaysia, Negeri Sembilan, Pasoh National Forest Reserve, approx. 2°58′54.8″N 102°18′47″E along trail towards plot 3, attached onto a dead and fallen trunk, dead branches and at the base of a living tree trunk, 9 October 2006, Dirk Stubbe, DS06 151 (GENT T00078; ISOTYPUS CORT014856) Genbank: OM905948 (ITS), OM906000 (LSU), OM974133 (*EF1α*), GCA_018854895.1 (Genome).

Diagnosis: Distinguished by densely caespitose collybioid basidiomata with long connate pseudorhizae, densely crowded, narrow and frequently forked lamellae, and concentrically white and grey zonate pileus with darker zones producing profuse dry arthroconidia, and by the distinct molecular profile of combined ITS, LSU, and *EF1a* sequences.

Pileus 10–25 mm wide, applanate to concave or slightly infundibuliform, disc depressed or subumbilicate, margin undulate, smooth, surface strongly velutinous but densely pruinose when older and staining fingers when handled with olive grey dusty conidia, concentrically zoned in white, dark and light grey, the darker zones covered with chains of arthroconidia. Context dull white or pale grey, soft. Lamellae densely crowded, narrow (less than 1 mm), often forked near attachment but also in the middle or near the pileus edge, pale grey or grey, edges white and fimbriate, finely eroded. Stipe 5–13 × 1–3 mm, cylindrical or compressed and twisted, gradually tapering to a long pseudorhiza, pale to dark grey, pale greyish over the pseudorhiza, surface strongly pruinose on above ground parts.

Basidiospores 5–6 (–7) × (3–) 4–4.5 μm, elliptical in profile and face views, round in polar view, smooth, hyaline, wall slightly congophilous. Basidia (12–) 15–20 × 5–6 μm, clavate or narrowly clavate, (1–) 2 and 4-sterigmate basidia present, sterigmata short, conical, 1–2 μm, often inconspicuous. Cheilocystidia 18–40 × 2.5–5.5 μm, cylindrical-contorted, often branched and knobby, also some subclavate, irregularly septate, producing a thick layer of interwoven, often collapsed end cells. Pleurocystidia absent. Lamella trama composed of olive brown inflated hyphae, similar in shapes and size to

Fig. 5 *Praearthromyces corneri* D. Stubbe 06 151 Holotype. **A** Basidiomata in situ showing dense dark powdery arthroconidia on pileus surface. **B** Basidiomata showing caespitose habit. **C** Arthroconidia showing ornamentations. **D** Chain of arthroconidia from pileus surface. **E** Cheilocystidia. Scale bars, **A** and **B** 10 mm, **C**–**E** 10 μm

those of the pileus context. Pileus context pale olivaceous brown, radially arranged, mostly inflated hyphae, (6–) 10–24 µm in diam, also with scattered narrowly cylindrical, dark brown, encrusted hyphae mixed in. Pileipellis a pale or dark brown layer of repent cylindrical hyphae producing a cutis of hyphal cells, 2.5–5.5 µm in diam, with brown parietal pigments and distinctly darker coloured septa; producing erect end cells with straight or often curved hyaline hyphae that eventually form septa and chains of thick-walled, brown, ornamented arthroconidia, up to 10 cells in length but frequently 5–7 cells remain connected, individual conidia ranging from subglobose to broadly ellipsoid, 7–9 × 5.5–7 µm, some conidia becoming elongate ellipsoid or phaseoliform and these up to 10–13 µm in length, thick-walled, dark yellowish brown, with obvious verrucose ornamentation. Clamp connections absent in all tissues.

Discussion: Species in *Praearthromyces* closely resemble *Arthromyces* by having a pseudorhiza and in the case of *P. corneri* by producing chains of dark arthroconidia on the basidiome. However, phylogenetic reconstruction shows a sister relationship of *Praearthromyces* to the *Arthromyces-Termitomyces* clade (Fig. 1) (van de Peppel et al. 2021). Placing *P. corneri* in the genus *Arthromyces* would make the latter genus paraphyletic or would require *Arthromyces* to be synonymized with *Termitomyces*, which is not warranted because of the lack of a termite association (see also discussion at the end). The genus can be distinguished from *Australocybe*, *Blastosporella* and *Tephrocybe* by the lack of clamp connections, a feature that is shared with *Arthromyces*, *Phaeotephrocybe*, *Nigrocarnea* and *Termitomyces*. *Praearthromyces* and *Arthromyces* can be distinguished by their geographic origin, *Arthromyces* from the new world and *Praearthromyces* from the old world, or by DNA sequence data.

The study by van de Peppel et al. (2021) showed that this taxon is part of a two species clade, sister to the *Arthromyces-Termitomyces* clade (Fig. 1). Corner (1994) described *Tricholoma furcatifolium* as being characterised by very crowded, narrow, regularly furcate lamellae (Corner 1994). The description does not refer to the production of dark arthroconidia on the basidiome. Unfortunately, we were unable to obtain a sequence from the holotype. However, another collection of *T. furcatifolium*, a paratype (Singapore, Gardens Jungle, 22 November 1940 made by Corner and illustrated by a painting in the original description) has abundant arthroconidia on the pileus surface and we managed to obtain an ITS sequence from this collection; this sequence was 99% identical to the sequence we obtained from a more recent collection by Dirk Stubbe, DS06 151, made in the Pasoh National Forest Reserve in Malaysia. We are unable to resolve whether the collection designated as the holotype in the protologue by Corner, Singapore, Corner s.n., 30 August 1939, and this second collection, a paratype with arthroconidium producing basidiomata, made by Corner, represent different species or morphological variation within this species. Stubbe's image below and the hand painted icons of Corner's arthroconidium producing paratype look very much alike. All the microscopic features of the basidiomata are also alike in Corner's arthroconidium producing paratype from Singapore and Stubbe's collection from the Pasoh National Forest in Malaysia. As we could not determine whether Corner's holotype and paratype collections represent the same or different species, we chose to describe our collection as the new species *P. corneri*.

Praearthromyces griseus T.J. Baroni & L.J.J. van de Peppel, sp. nov. Fig. 6

Mycobank: MB 843283

Etymology: Griseus—referring to the grey colour of the pileus.

Holotypus: Thailand, Chiang Mai Province, near Mae Sae, KM 55 on Highway 1095, soil, under *Castanopsis armata*, 3 June 2006, Ruilin Zhao (documented by T.J. Baroni 9980) (CORT014481) Genbank OM905947 (ITS), OM905999 (LSU), OM974132 (*EF1α*), GCA_018220975.1 (Genome).

Diagnosis: With a mycenoid or somewhat tephrocyboid habit similar to *Tephrocybe rancida* but differing by having cheilocystidia and no clamp connections, and is phylogenetically distinct from *Tephrocybe* and other morphologically similar taxa by the molecular profile of its combined ITS, LSU and *EF1a* sequences.

Pileus 8–14 mm broad, conical with broad conical umbo or narrowly campanulate, margin incurved, dry, with radiate, innate fibrillose surface, deep greyish with brown hues (5F3–4 Nutria, Sepia, Beaver; to 5E3 Drab or Mouse Grey). Context pale greyish, thin (less than 0.5 mm). Lamellae deeply adnexed, crowded, edges eroded and fimbriate, 1 mm broad, pale greyish or brownish grey (5C-D2 Birch Gray, Nougat). Stipe 8–9.5 × 1–1.5 mm, equal, but strongly tapered into a long sometimes curving pseudorhiza, terete, white pruinose over apex, fine, silvery white, appressed fibrillose below, concolorous with pileus (5E3 Drab or Mouse Grey), except for white, contrasting, subterranean pseudorhiza, narrowly hollow and greyish in context. Odour faintly farinaceous when cut.

Basidiospores 6–9 (–10) × 3–4.5 µm, elliptical or elliptical elongate in profile and face views, round in polar view, walls congophilous. Basidia (17–) 20–30 × (5–) 6–8 µm, 4-sterigmate, with small and sometimes sparse cyanophilic bodies. Cheilocystidia densely crowded, hyaline, cylindrical or sublageniform, frequently undulate over upper ½ of cylindrical neck, 18–32 (–55) × 3–6 µm. Pleurocystidia absent. Lamella trama pale brown from parietal pigment, composed of parallel cylindrical or inflated hyphae, 4–15 µm in diam. Pileus context similar in colour and hyphal make-up to lamella trama, pale brown from parietal pigment, radially arranged,

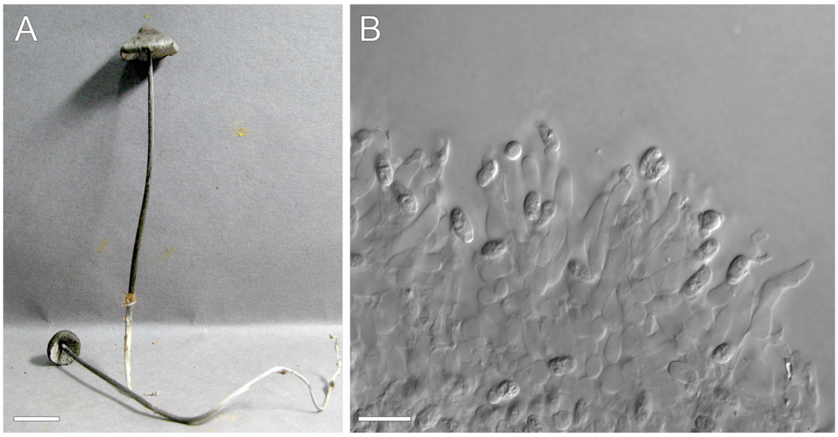

Fig. 6 *Praearthromyces griseus* T.J. Baroni 9980 Holotype. **A** Basidiomata. **B** Cheilocystidia and basidiospores. Scale bars, **A** 10 mm, **B** 10 μm

inflated hyphae mixed with cylindrical hyphae, 5–20 μm in diam. Pileipellis two-layered, with a thin hyaline layer of a few cylindrical hyphae, 2–4 μm diam, overlying a dark brown layer of hyphae that have parietal and clearly encrusting pigments on many of these gradually larger hyphae, 4–13 μm in diam, as one progresses into the context. Stipitipellis similar to the pileipellis, with a thin hyaline layer of cylindrical hyphae, 2–4 μm in diam, overlying a pale brown layer of progressively broader cylindrical or slightly inflated hyphae, 5–15 μm in diam, with parietal pigments. Clamp connections absent in all tissues. Arthroconidia not present.

Discussion: *Praearthromyces griseus* is distinguished from *P. corneri* by its more delicate mycenoid habit, lack of zonate pileus surface, the lack of arthroconidia, by the unforked lamellae, and by not being caespitose. *Praearthromyce griseus* is currently only known from a single collection made in Thailand.

Arthromyces glabriceps M.C. Aime & V. Coimbra, sp. nov. Fig. 7

Mycobank: MB 843284

Holotypus: Guyana, Upper Potaro River, Pakaraima Mountains, two basidiomata on the forest floor under *Dicymbe*, in "Plot P2", 27 May 2010, *M.C. Aime* 4044 (PUL F29136) Genbank OM905939 (ITS), OM905991 (LSU), OM974123 (*EF1α*).

Etymology: glabri-ceps Latin, for the glabrous pileus.

Diagnosis: Similar in morphology to *Arthromyces matolae*, but differing mainly by the lack of arthroconidia production on the pileus surface.

Pileus up to 40 mm in diameter, glabrous, hygrophanous, concentrically grooved, plane with broad, flat or conical to papillate umbo, brown (6F5 Teak to 5E5 Bronze), margin paler than the rest of the pileus, occasionally uplifted, translucent-striate; shallowly corrugated under hand lens. Lamellae narrow, crowded, pallid yellowish (3A2 Yellowish White to 5A2 Orange White) then mottled. Stipe 79–180 × 3 mm, equal with short, narrow tapered pseudorhiza, hollow, taupe to greyish (3D2 Yellowish Grey), surface white fibrillose or densely tomentose under hand lens.

Basidiospores (5–) 6–7 (–7.5) × 3–4 μm, ellipsoid, smooth, often bi-guttulate. Basidia 2-sterigmate, 15–20 × 5–8 μm, clavate. Cheilocystidia mixed with basidia, 29–52 × 2–4 μm, hyaline, cylindrical, in fasciculate clusters along the edge, and covered by deep golden or golden brown, encrusting, resinous pigments often making the individual cystidia difficult to discern. Pleurocystidia absent. Lamella trama hyaline, composed of parallel cylindrical or inflated hyphae, 5–22 m in diam. Pileus context hyaline or pale brown, composed of radially arranged, mostly inflated hyphae, 10–30 μm in diam, with many short barrel-shaped cells. Pileipellis a deep (80–100 μm), hyaline layer, composed of a cutis of repent cylindrical, loosely interwoven hyphae, 2–4 μm in diam. Stipitipellis a hyaline, repent layer, hyphae cylindrical, 2–5 (–7) μm in diam. Clamp connections absent in all tissues. Arthroconidia absent in all tissues.

Discussion: *Arthromyces glabriceps* differs from *A. matolae* and *A. claviformis* in lacking the production of conidia on the pileus, and in its known distribution; *A. glabriceps* is apparently restricted to the Guiana Shield, known only from the western Pakaraima Mountains of Guyana, and from Brazil. Van de Peppel et al. (2021) reported the presence of conidiophores in laboratory cultures of *A. matolae*. Since a culture for *A. glabriceps* was not available, we could not determine the presence of conidiophores in *A. glabriceps*. We have no reports for *A. glabriceps* growing on insect-faecal pellets in the same fashion as has been reported for *A. matolae* and *A. claviformis* (van de Peppel et al. 2021). However, a collection from Pará, Brazil, was found to be growing on faecal pellets. This collection could not be unambiguously identified as *A. glabriceps* and DNA sequence data is also lacking.

Distribution and habitat: In *Dicymbe corymbosa* monodominant forest or adjacent mixed forest; despite

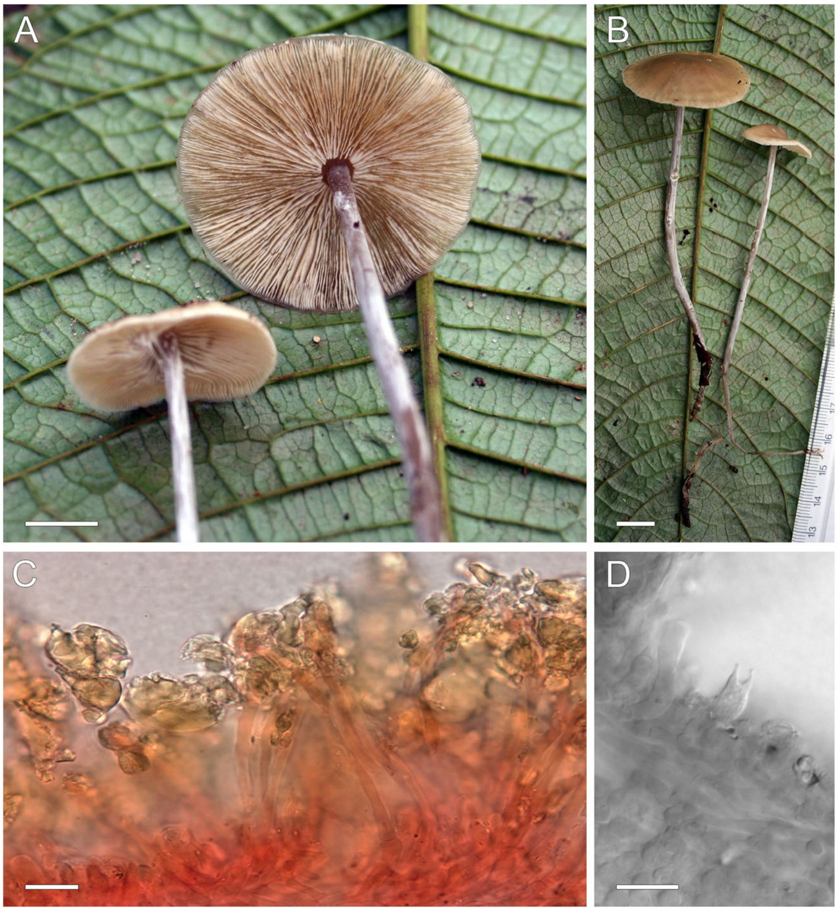

Fig. 7 *Arthromyces glabriceps* M. C. Aime 4044 Holotype. **A**, **B** Basidiomata showing crowded lamellae and short pseudorhiza. **C** Cheilocystidia with golden, resin encrusted apices. **D** Basidium with 2 sterigma. Scale bars, **A** and **B** 10 mm, **C** and **D** 10 µm

multiple years of collecting effort in this region, known only from the Upper Potaro River Basin of Guyana and Rondônia, Brazil.

Additional material examined: Brazil: Rondônia, Floresta Nacional do Jamari, Itapuã do Oeste, 9°11′68″S 63°52′05″W, 25 April 2012, *Victor R. M. Coimbra* 22 with *N. C. Lima-Junior* and *A.C. Gomes-Silva* (URM85027; CORT014857); Rondônia, Porto Velho, Parque Ecológico Municipal, 22 Apr 2013, VRM Coimbra 13 with *N.C. Lima-Junior* and *A.C. Gomes-Silva* (URM85026). Guyana: Region 8 Potaro-Siparuni, Pakaraima Mountains, Upper Potaro River Basin, approximately 15 km east of Mt. Ayanganna, vicinity of Potaro base camp, elev. 710–750 m, 5°18′04″N 59°54′40″ W, *M.C. Aime* 1080 (BRG; PUL F29131); *M.C. Aime* 1170, Black Water Creek, 9 June 2000 (BRG; PUL F29132); *M.C. Aime* 1297 (BRG; PUL F29133); 3 July 2002, *M.C. Aime* 2194A(BRG; PUL F29134 pt. 1); 3 July 2002, *M.C. Aime* 2194B (BRG; PUL F29134 pt. 2); *M.C. Aime* 3988, Upper Potaro River, 20 May 2010 (BRG; PUL F29135); 27 May 2010 *M.C. Aime* 4044 (BRG; PUL F29136); *M.C. Aime* 4318 (BRG; PUL F29137); 31 May 2012 *M.C. Aime* 4784 (BRG; PUL F29138); 18 June 2016, *M.C. Aime* 6216 (BRG; PUL F29139).

Discussion

A recent phylogenomic study, based on 1131 core nuclear genes, included five of the six newly described species (as *Tephrocybe* sp1–5.) (van de Peppel et al. 2021), while the sister group relation between *Arthromyces matolae* and *A. glabriceps* was based on *EF1α* and the ITS and LSU of the rDNA produced in this study. The study by van de Peppel et al. already showed that geography and morphological features such as conidial production, clamp connections and insect-faecal associations are not consistent with the clades recovered from their phylogeny (see also Table 1). The use of these characters as sole foundation for a generic classification that is consistent with the phylogeny is therefore hardly possible. Translating the phylogeny into a new generic classification, primarily based on the genetic data with morphological and biogeographical criteria as additional data, allows a number of possibilities, ranging from one genus for the complete clade to five genera. In order to evaluate these various options, we used the six criteria proposed by Vellinga et al. (2015). These six criteria are (1) monophyly, (2) sufficient phylogenetic coverage, (3) sufficient branch support, (4) discussion of alternative options, (5) no single marker phylogeny and (6) include all supporting evidence and background information. To those criteria we add one additional consideration, viz., the desirability that the approach taken for this clade within the *Lyophyllaceae* is consistent with earlier treatments of that family (Bellanger et al. 2015; Hofstetter et al. 2014).

Criteria (1), (2), (3), (5) and (6) have been amply discussed in Van de Peppel et al. (2021) and all background information on molecular data is available in the public domain. We refer to that study for the information and concentrate on criterion (4), the evaluation of alternative classifications.

Three main taxonomic proposals are consistent with the phylogeny: (A) put all species in one genus, which should be called *Termitomyces*; (B) recognise eight genera, four of which are newly described, as proposed in our paper; (C) recognise three genera, viz., *Australocybe* (for *A. olivacea*, as this species cannot be placed in another genus without making that genus paraphyletic, except when placed in *Termitomyces*, our option (A)), *Tephrocybe* (including *Blastosporella*, *Phaeotephrocybe* and *Nigrocarnea*—as the group is monophyletic), and *Termitomyces* (including *Arthromyces* and *Praearthromyces*). Further options, e.g., combining *Termitomyces* and *Arthromyces*, while recognising *Praearthromyces* as a separate genus; or combining *Phaeotephrocybe* and *Nigrocarnea*, while treating *Tephrocybe* and *Blastosporella* as autonomous species would also be consistent with the phylogeny but would result in the description of three new genera, hardly different from our proposal for four new genera.

The most radical proposal would be to recognise one genus that is then called *Termitomyces*. For mycologists from the temperate region, it would certainly be curious that a species that is never associated with termites (and its distribution area largely excludes the distribution area of termites) has to be placed in *Termitomyces*. Further disadvantages of that proposal would be that the genus has no unique morphological characters (the rooting stipe equally occurs in some more distantly related *Lyophyllaceae*), and, more importantly, is extremely heterogeneous in its ecological lifestyles. Lifestyles and lifestyle transitions have been considered as major arguments for a taxonomy of the early-branching *Lyophyllaceae*, as proposed by Hofstetter et al. (2014) and Bellanger et al. (2015), and where generic distinctions like *Sphagnurus* (parasitic on *Sphagnum*) and *Sagaranella* (nitrophilic, known as ammonia fungi) are partly justified by the ecological transition. It is also noteworthy that many genera in these early-branching *Lyophyllaceae* are very species-poor, often containing one to three species. Previous studies have found *Tephrocybe* (a species-rich genus in the pre-molecular era) to be paraphyletic with up to eight independent origins within the *Lyophyllaceae*, with one species (*T. rancida*) in the termitomycetoid clade (Hofstetter et al. 2014; Bellanger et al. 2015) and both studies have contributed to the dismemberment of this paraphyletic taxon by describing new species rather than by including members of other genera in a very largely circumscribed *Tephrocybe*. Recognising one very broadly circumscribed *Termitomyces* next to a large number of species-poor genera in the early-branching *Lyophyllaceae* would therefore create an unbalanced familial taxonomy. We consider these arguments sufficient to reject that first, radical alternative. Rejecting this option would automatically imply the recognition of a new genus *Australocybe*. While *A. olivacea*, is macro-morphologically similar to *T. rancida*, phylogenetic analysis shows that it does not nest in the same clade as *T. rancida* but occupies an isolated branch (van de Peppel et al. 2021).

The third option, which would necessitate the erection of one new genus only (*Australocybe*) as the other new species are accommodated in the existing genera *Tephrocybe* and *Termitomyces*, would run into similar problems as our radical alternative. Putting the species of *Arthromyces* and *Praearthromyces* in *Termitomyces* would imply recognition of a genus *Termitomyce*s with non-termite associated species that occur in biogeographical regions where the fungus-growing termites do not occur (both species of *Arthromyces* occur in the Neotropics). Although *Arthromyces* species are known to grow on insect faeces and so may be insect-associated, it is highly unlikely that these insects are termites (van de Peppel et al. 2021). As mentioned previously, we consider that the (unique) termite association of *Termitomyces* necessitates maintaining the current definition of the genus. As noted above, only transferring the palaeotropical *Arthromyces* to *Termitomyces* would still necessitate the erection of the genus *Praearthromyces*. Combining *Arthromyces* and *Praearthromyces* in one genus, which could be justified based on morphology, would not be allowed because of paraphyly.

Putting *Phaeotephrocybe*, *Blastosporella* and *Nigrocarnea* in *Tephrocybe* seems at odds with the earlier attempts by Hofstetter et al. (2014) and Bellanger et al. (2015) to create a monophyletic genus that is morphologically recognisable and that is characterised by a saprotrophic lifestyle. Both *N. radicata* and *Ph. leucophylla* share the tephrocyboid habit with *T. rancida* and *Ph. leucophylla* also shares the feature of not producing conidia on the fruitbodies with *T. rancida*. Both *N. radicata* and *B. zonata* produce conidia, while only the latter produces ornamented blastoconidia and all other conidia producing taxa in this clade, including *Nigrocarnea* and *Arthromyces*, form chains of arthroconidia. The genera *Phaeotephrocybe* and *Nigrocarnea* can be separated from the genera *Blastosporella* and *Tephrocybe* by the lack of clamp connections. *Nigrocarnea* can be distinguished from all other conidia-producing genera as it is the only species to produce the conidia inside the pileus trama. We consider this solution as a possible retrograde step as the variation in traits (both absence and presence of conidia on fruitbodies, clamp connections, insect-association) within *Tephrocybe* would leave no synapomorphies to separate *Tephrocybe* from the other related genera. Placing *N. radicata* and *Ph. leucophylla* into a single genus does unlikely seem a useful option as these species do not share many morphological characters (Table 1). Biogeographical considerations equally argue against combining both into one genus, as *Nigrocarnea* is only known from the paleotropics in Southeast Asia, while *Phaeotephrocybe* is only known from the neotropics in Central America. Furthermore, branch lengths suggest significant genetic divergence between the two. The lack of clamp connections in these genera sets them apart from *Blastosporella* and *Tephrocybe*, both of which have clamp connections, a feature that is shared with the genus *Australocybe*. The genus *Phaeotephrocybe* does not produce any type of conidia and is therefore easily distinguished from *Nigrocarnea* which produces dark-pigmented arthroconidia in the pileus context of the basidiomata. This trait of conidial production in the pileus trama morphologically distinguishes *Nigrocarnea* from *Phaeotephrocybe* and all other taxa in this clade.

With the disadvantages associated with the radical option (one genus *Termitomyces*) and the option to recognise three genera (*Australocybe*, *Tephrocybe*, and *Termitomyces*), it seems unavoidable to describe new, currently monophyletic genera that are now morphologically, biogeographically and ecologically, in terms of life style, rather well separated. While it could be stated that erection of these small new genera is an expression of what has been called the excessive multiplication of genera (Romagnesi 1977), we think that the specific evolutionary history of the *Lyophyllaceae* makes such action inevitable.

The addition of four new genera to the *Lyophyllaceae* and especially the termitomycetoid clade shows that even more ecological transitions may have occurred within this group than previously thought (Hofstetter et al. 2014). Insect associations have only been demonstrated in the genera *Arthromyces*, *Blastosporella* and *Termitomyces*; however, the presence of a pseudorhiza and other shared characters with *Termitomyces* suggest that other species also could be insect-associated. The diversity and widespread geographic distribution of these genera suggests that more species await discovery.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11557-022-01836-7.

Acknowledgements Kasem Soytong, King Monkut's Institute of Technology, Bangkok, Thailand, arranged the Material Transfer Agreement initiated by Dennis Desjardin for field work in Thailand. Nigel Fechner of the Queensland Herbarium (BRI) provided necessary field and logistical support for field studies in Queensland. The Queensland Parks and Wildlife Service arranged accommodation and orientation on Fraser Island and access to field sites in the Great Sandy National Park. Logistics for field work in Thailand by TJB and collaborators was supported by the Mushroom Research Center in Chiang Mai. The loan of Corner's Indonesian specimens from the Royal Botanic Garden Edinburgh to TJB (CORT) was kindly arranged by Heleen Plaisier and Rebecca Yahr. We thank Angela Bond and the Royal Botanical Gardens KEW herbarium for letting us use their facilities and providing specimens. We thank the fungarium at Plantentuin Meise for providing specimens and Ann Bogaerts for her assistance in sampling. We thank Ben Auxier for his advice and for proofreading the manuscript.

Author contribution All authors contributed to the study conception and design as well as the collection of fungal specimens. Molecular lab work was performed by L.J.J. van de Peppel. The first draft of the manuscript was written by L.J.J. van de Peppel. All authors commented on the manuscript and approved the final version.

Funding LJJvdP and DKA were supported by the Netherlands Organization for Scientific Research (NWO 86514007; ALWGR.2017.010). Field research in Australia and Thailand by T.J. Baroni was made possible by financial grant support to R.E. Halling from the National Science Foundation (USA) DEB #0414665 and DEB #1020421, and the National Geographic Society Committee for Research and Exploration grant #8457–08 for biodiversity research work by Halling and collaborators in Australia. Field work in Laos was partly GEF-financed under the UNDP-FAO Agrobiodiversity Project (UNTS/LAO/015/GEF) and partly by private means. Field work in Belize by TJB and collaborators was funded by the National Science Foundation Biodiversity Surveys and Inventories Program to the State University of New York College at Cortland (DEB-9525902 and DEB-0103621) and by the National Geographic Society for Research and Exploration, grant #8240-07. Field work and logistical support in Colombia was arranged and in part financially supported by Ana Esperanza Franco-Molano, the Foundation for the Conservation of Colombian Wild Life (FCV) and the University of Antioquia in Medellin. Field work in Brazil by VRM Coimbra was logistically supported by Allyne C. Gomes-Silva and financially supported by CNPq - Conselho Nacional de Desenvolvimento Científico e Tecnológico (GM 130914/2011-8, PROTAX 562106/2010-3, SISBIOTA 563342/2010-2) and FACEPE - Fundação de Amparo à Ciência de Pernambuco (IBPG-0827-2.03/12).

Data availability The DNA sequences generated during the current study are available in NCBI Genbank.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

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