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THE GENUS AMANITA IN THE PAKARAIMA MOUNTAINS OF GUYANA

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Six species of *Amanita* (Amanitaceae, Basidiomycota, Fungi), collected in the Pakaraima Mountains of Guyana, are described; four as new and two as new records for Guyana: *A. aurantiobrunnea* spec. nov., *A. calochroa* spec. nov., *A. cyanopus* spec. nov., *A. perphaea* spec. nov., *A. lanivolva* Bas, and *A. xerocybe* Bas. All six species have been collected in forests dominated by *Dicymbe* (Caesalpiniaceae) and are assumed to be ectomycorrhizal. *Amanita perphaea* is commonly eaten by Patamona Indians and is called 'Pulutukwe'.

Ectomycorrhizal fungi, and specifically the genus *Amanita,* were long thought to be well developed in the northern Temperate Zone, but poorly represented in the tropics (Gilbert, 1941b). This viewpoint began to shift with the advent of mycofloristic studies in the paleotropics, where numerous studies have demonstrated an increasingly wide diversity of ectomycorrhizal fungi associated primarily with caesalpinioid legumes in Africa and with Dipterocarpaceae and Fagaceae in Asia (e.g. Heinemann, 1954; Corner & Bas, 1962; Corner, 1972; Watling & Lee, 1995; Buyck et al., 1996). In the lowland forests of the neotropics, however, documentation of ectomycorrhizal associations is limited to the pioneering work of Singer and colleagues in the Central Brazilian Azon and Central America, and Moyersoen in southern Venezuela (Singer & Araujo, 1979; Singer et al., 1983, 1991; Moyersoen, 1993).

Knowledge of *Amanita* in South America is limited. *Amanita* species have been recorded with the vegetation types of the pampas (but a small number of species recorded from the pampas are probably non-ectomycorrhizal), open dry forests and, to a limited extent, lowland rain forests (Bas, 1969). Dennis (1970) described only three species for Venezuela, among which there was only one species (*A. antilliana* Dennis from Trinidad) from tropical lowland forests. Subsequent description of new species from Amazonian Brazil by Bas (1978) and Andean Colombia by Tulloss et al. (1992), among others, did much to reverse this trend of thought, but the number of known *Amanita* species from the continent still remained relatively low.

Recent investigations of the macromycota of Guyana, in northeastern South America, have revealed an extensive assemblage of putatively ectomycorrhizal fungi, including *Amanita*, associated with trees of the legume genus *Dicymbe* Spruce ex Benth. in Benth. Hookf. (Caesalpiniaceae, tribe Amherstieae) (Henkel, 1999; Henkel et al., 2000; Miller & Henkel, 2000). These include, along with *Amanita*, members of the basidiomycete families Boletaceae, Russulaceae, Cortinariaceae, Cantharellaceae, Clavariaceae, and Hygrophoraceae, as well as the hypogeous ascomycete genus *Elaphomyces*. These fungi are tightly

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spatially associated with forest stands dominated by ectomycorrhizal *Dicymbe* species, in particular *D. corymbosa* Spruce ex Benth. and *D. altsonii* Sandwith, which occur in a landscape-scale mosaic interposed with largely anectotrophic mixed forest in the Pakaraima Mountains of west-central Guyana (Fanshawe 1952, 1955; Steege et al., 1993; Henkel, 2000). Discovery of these *Dicymbe*-dominated ectotrophic forests in Guyana has greatly extended the known range of ectomycorrhizal associations in South American rain forests.

Terry Henkel, during the period 1993 to 1998, made 5 collecting expeditions to the Upper Ireng River basin along the western border of Guyana with Brazil. He kindly allowed his Guyanese *Amanita* collections be examined and analysed by the first author, under guidance of the third author. As a preliminary result, four new species and two species previously described from the Brazilian Amazon are recorded and described in the present paper.

The genus *Amanita* consists largely of terrestrial, forest-inhabiting fungi with a rich biogeographic history (Bas, 1969). There are over 600 species known world-wide, with the genus divided into two subgenera based on the amyloidity of the spores and the structure of the margin of the pileus, viz. the subgenera *Lepidella* and *Amanita*, and the macroscopic and microscopic features of the volva being a primary character for dividing the subgenus *Lepidella* into four sections and the subgenus *Amanita* into two sections (Bas, 1969).

COLLECTING SITE DESCRIPTION

The research site was located along the Upper Ireng River which forms the border between Guyana[1] and Brazil in the South Central Pakaraima Mountains (general area: 5°5' N; 59°58'W). This region of western Guyana constitutes the eastern extension of the Guayana[1] Highlands, a distinct phytogeographic province characterized by sedimentary strata overlying the igneous Guiana[1] Shield basement, oligotrophic soils, and a highly autochthonous, endemicized flora (Gansser, 1954; Maguire, 1970; Gibbs & Barron, 1993). Elevations range from 700 m at riverside to 1800 m along the highest ridgelines. The resulting terrain is of high relief and characterized by deeply cut creek and river valleys amidst highly eroded plateaus and pinnacled ridgelines.

Annual rainfall for the remote area can only be inferred from records spanning the years 1935–1947 at a Potaro River site located approximately 100 km to the northeast, at the eastern edge of the Pakaraima escarpment (Fanshawe, 1952). The annual mean for the 12 year period was 3866 mm with a pronounced peak in May and June, a lesser peak in December and January, with relatively drier periods between. Since 1991, the timing of annual wet and drier periods at the Ireng site have, in general, coincided with those indicated by the Potaro data (Henkel, pers. obs.). At the Ireng site, during the onset of the rainy season in May–June 1998, a total precipitation of 585 mm was recorded for a 27 day period, and during May–June 1999 490 mm for a 30 day period, which were in accordance with the mean values of 500–600 mm/month for May and June at the Potaro site. For macromycetes, annual peak production of sporocarps appears to occur during the May–June period (Henkel, unpubl.). Regional temperature records were unavailable, but during the equivalent periods of 1998 and 1999 temperatures were remarkably constant at the Ireng site (daily max.: 25–29°C; min.: 19–21°C). In general, these data correspond to a classification of Submeso-

1) 'Guyana': the country formerly called British Guiana; 'Guayana': the concerning phytogeographical province; 'Guiana': the geological region underlain by the Guiana Shield.

thermic Ombrophilous Climate as indicated by Berry et al. (1995), defined as annual precipitation exceeding 2000 mm with minimal or no dry season (i.e. where monthly precipitation falls below 100 mm), with average annual air temperatures ranging between 18 °C and 24 °C.

Vegetation of the region corresponds to the Dry Evergreen Forest Formation of the Pakaraima Montane Region (Fanshawe, 1952). Fanshawe considered this formation to predominate throughout the entire sandstone belt composing the Pakaraima Mountains, being subdivided into various associations and faciations with attendant dominant tree species according to degree of soil drainage, the series running from sclerophyllous savanna on the most poorly drained sites to well-drained, high canopy mixed forest, and 'clump wallaba' forest dominated by species of *Dicymbe*. *Dicymbe*, in particular *D. corymbosa*, forms extensive mono-specifically dominant stands of five ha and larger on the lower toe slopes of the mountains (Myers, 1936; Fanshawe, 1955; Richards, 1996). These *Dicymbe* stands have, by tropical standards, extremely low woody plant diversity, with roughly 40 species >10 cm dbh per ha, with 80–95% of the basal area of the stand composed of *D. corymbosa* (Henkel, 2000). Mixed forests of the area, generally lacking in *Dicymbe*, have 70–90 woody species per ha, well represented by species of *Eschweilera* Mart. ex DC. (Lecythidaceae), *Ocotea* Aubl. (Lauraceae), *Inga* Mill. (Mimosaceae), and *Eperua* Aubl. (Caesalpiniaceae) (Henkel, unpubl.). Low-lying forests with poor drainage are generally dominated by *Micrandra glabra* (R.E. Schult.) R.E. Schult. (Euphorbiaceae) and *Mora excelsa* Benth. (Caesalpiniaceae).

Soils are poor due to the sandstone nature of the parent materials. Soil impoverishment is further evidenced by the universal presence of tannin-rich 'blackwater' streams throughout the region (Janzen, 1974).

MATERIALS AND METHODS

Fungi were collected from an area of approximately 10 km^2 surrounding a series of previously established base camps (Henkel, 1999). Basidiomata were examined in the field for fresh characteristics. Colour characteristics were coded according to Kornerup & Wanscher (1981) and described subjectively. Spore deposits, when obtained, were examined for fresh colour characteristics. Basidiomata were dried slowly over charcoal and subsequently placed in containers with silica gel to prevent spoilage in the excessively humid conditions.

All anatomical studies were performed on dried specimens. Microscopic examination of tissues were done in 5% and 10% NH_4OH or in 5% KOH. Stains used were Congo red and the spores were observed in Melzer's reagent and measured in 10% NH_4OH and 5% KOH. Bas found that in cases where amyloidity was dubious, soaking overnight in Melzer's reagent and observing in fresh reagent the next morning made amyloidity show more clearly. For spores at least 10 individuals per sample were measured and for basidia at least 6 individuals. Anatomical details were determined with an Olympus CHA microscope containing bright field and phase contrast optics and line drawings were made with the help of a drawing tube.

Because of rather primitive circumstances in the field, the dried specimens were often not in optimal condition. It turned out that even in good looking specimens it sometimes was very difficult or impossible to get the tissues of the trama of the lamellae, the stipe, and the pileus to reinflate.

Herbarium designations: BRG – National Herbarium of Guyana, University of Guyana, Georgetown, Guyana; DUKE – Department of Botany, Duke University, Durham, North Carolina, USA; L – Nationaal Herbarium Nederland, Universiteit Leiden Branch, Leiden

Other abbreviations used were: 'Q' = length/breadth ratio; 'Spores [20/2]' = twenty spores from two specimens measured; 'R' = radius of pileus.

TAXONOMIC PART

Hitherto, not all sections of *Amanita* are represented in the set of collections from the Pakaraima Mountains that has been analysed. The species recognised are treated in taxonomic order. A survey of the subgenera and sections they belong to is given here:

Amanita subgenus *Lepidella*
Section *Phalloideae*: *A. aurantiobrunnea*
Section *Validae*: *A. cyanopus*, *A. perphaea*
Section *Amidella*: not represented
Section *Lepidella*: not represented
Amanita subgenus *Amanita*
Section *Vaginatae*: several specimens collected, but none yet analysed.
Section *Amanita*: *A. calochroa*, *A. lanivolva*[1], *A. xerocybe*

Subgenus **LEPIDELLA**

Section **Phalloideae**

Amanita aurantiobrunnea C. Simmons, T. Henkel & Bas, *spec. nov.* — Fig.1, Plate 2

Pileus 30–70 mm latus, convexus vel applanatus, postea plano-concavus, interdum obtuse umbonatus, margine laevis, aurantio-brunneus vel aurantiacus, viscidus, margine fragmentis volvae minutissimis, albidis vel concoloribus saepe instructus. Lamellae liberae, (sub)confertae, albae; lamellulae attenuatae. Stipes 64–88 × 7–16 mm, basi bulbosus, 22–35 mm latus, annulatus. Volva membranaceo-saccata, alba vel pallide brunneo-salmonea. Annulus apicalis, floccoso-membranaceus, albus, facile diffractus.

Sporae 6.8–9.4 × 5.5–7.5 µm, subglobosae vel late ellipsoideae vel ellipsoideae, amyloideae. Basidia 4-sporigera. Fragmenta volvae supra marginem pilei cellulis turgidis, (sub)globosis vel pyriformibus, 25–95 × 15–50 µm, terminalibus vel catenulatis hyphisque albis vel brunneis composita. Limbus volvae externus hyphis praecipue constructus. Fibulae absentes.

Typus: *T. Henkel 6431*, Guyana, Pakaraima Mountains, Upper Ireng River, 22.V.1998 (BRG holotypus, L isotypus).

Fruit-body terrestrial, solitary, medium-sized and fleshy. Pileus 30–70 mm in diam., convex to applanate, plano-concave with age, sometimes with low broad umbo, viscid when wet, tacky when dry, rich orangish tan (close to K&W 5B8) to light orange at margin (K&W 5A5), with white context and often with inconspicuous, tiny, whitish to concolorous volval fragments on outermost margin. Lamellae free, thin, close to rather close, white, with entire

1) The taxonomic position of *A. lanivolva* is not quite clear. It is placed here in section *Amanita* because it has non-amyloid spores combined with a sulcate-striate pileus margin and a distinctly bulbous base, but it has a saccate volva, which is unique in section *Amanita*.

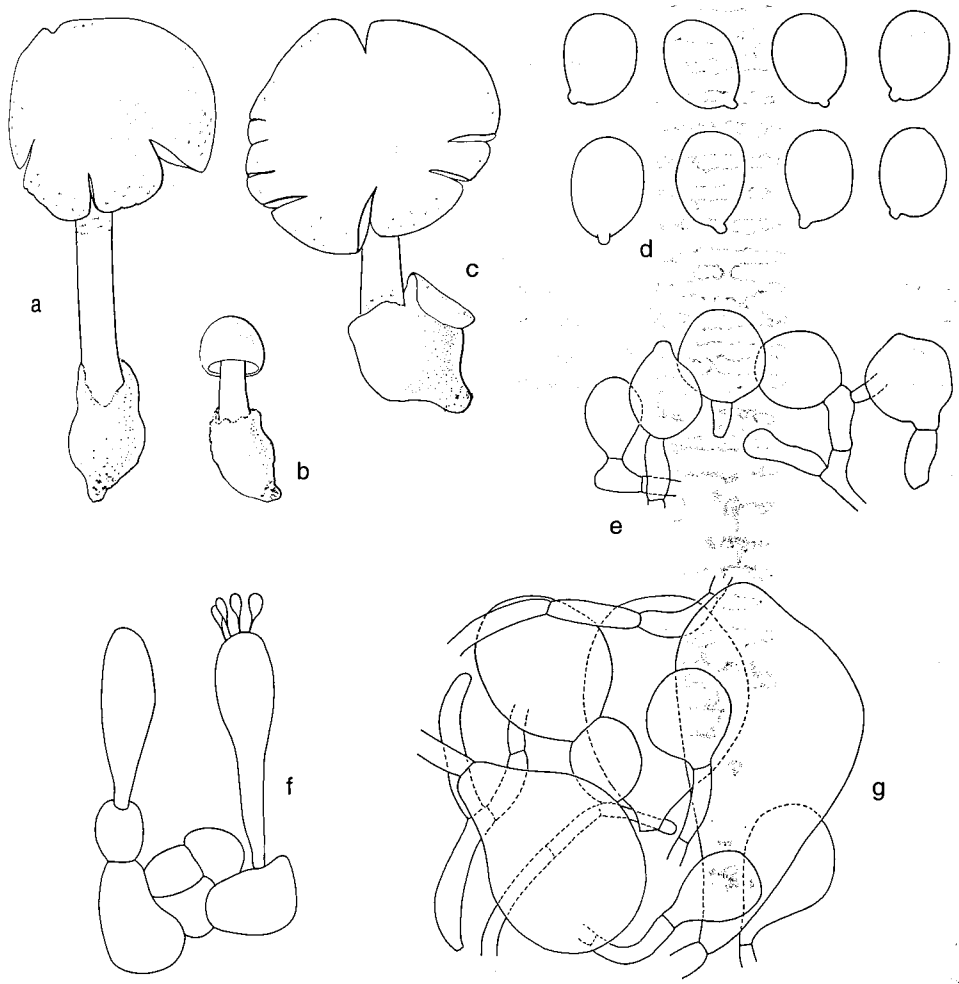

Fig. 1. *Amanita aurantiobrunnea*. a–c. Basidiocarps, × 0.5; d. spores, × 1500; e. elements of marginal tissue of lamella, × 500; f. basidia and subhymenium, × 1000; g. tissue of minute fragment of volva on margin of pileus, × 500 (a, d–f: holotype; b: *TH 6655*; c & g: *TH 6898*).

edge. Lamellulae attenuate. Stipe 64–88 × 7–16 mm, slightly attenuated upwards, white with white floccose squamules when young but glabrescent with age; bulb 22–35 mm in diam., enclosed in a firm, adnate, white to pale brownish salmon, membranous, saccate to limbate volva attached to upper part of bulb with limb free and spreading or more or less appressed against stipe. Annulus apical, white, floccose-membranous, rarely skirt-like, often reduced to small white scales on apex of stipe, rarely forming white appendages at margin of pileus. Spore print not available.

Spores [65/5] (6.2–)6.8–9.4 × (5.0–)5.5–7.5(–7.9) µm, Q = (1.0–)1.1–1.35(–1.45), aver. Q = (1.1–)1.15–1.35, subglobose to broadly ellipsoid to ellipsoid, with thin to very slightly thickened walls, amyloid, with relatively broad and short, rounded hilar appendix. Basidia 27–45 × 7–11 µm, clavate, 4-spored, with up to 5 µm long sterigmata, clampless. Sub-

hymenium pseudoparenchymatic, composed of subglobose to (larger) angular, up to 17 µm wide elements. Marginal tissue an uneven strip of mainly globose to broadly ellipsoid, thin-walled to slightly but distinctly thick-walled, colourless elements 11–28 × 13–25 µm, sometimes in short chains and occasionally with apical papilla, attached to frequently branching, 3–6.5 µm wide hyphae. Hymenophoral trama bilateral. Pileipellis an ixocutis of densely interwoven, 3.8–5.2(–6.6) µm wide, agglutinated, thin-walled, slightly inflated hyphae without clamps; suprapellis colourless in NH_4OH, subpellis pale yellow; superficial hyphae sometimes carrying ovoid, ellipsoid and elongate elements of up to 98 × 25 µm. Tiny volval remnants on margin of pileus consisting of colourless to brownish hyphae carrying terminal, single or more rarely catenulate, globose to pyriform, thin- to slightly thick-walled elements measuring 27–97 × 17–49 µm. Volval limb: outer surface a dense tissue of mainly longitudinal to interwoven, clampless, 1.7–5.5 µm wide hyphae and a few scattered, isolated, subglobose to broadly ovoid and ellipsoid, inflated, thin-walled, colourless elements 25–60 × 21–34 µm; the inner tissue composed of irregularly disposed, branching 2.2–6.2 µm wide hyphae and many subglobose, ellipsoid, ovoid, and elongate, inflated, terminal cells 28–60 × 25–35 µm; inner surface, particularly at outermost limb, with globose to pyriform inflated cells, 28–76 × 25–49 µm, embedded in a tissue of 2.5–5.5 µm wide hyphae, pale yellow in NH_4OH. Trama of stipe composed of longitudinal hyphae carrying acrophysalides up to 308 × 56 µm. No clamp-connections observed.

Habitat & distribution — Slope forest, dominated by *Dicymbe corymbosa* (Paluwayek), on grey sands. Thus far only known from western Guyana.

Collections examined. GUYANA: Pakaraima Mountains, Upper Ireng River: 1 km west of Kurutuik Falls, on adjacent ridges, 6 April 1998, *T. Henkel et al .* (*TH 6852*; BRG); Forest adjacent to Sukabi River, 1–2 km upstream from confluence with Ireng River, 22 May 1998, *T. Henkel et al.* (*TH 6431*; holotype BRG, isotype L); Sakaliu River, 1–2 km upstream from confluence of Ireng River, 25 May 1998, *T. Henkel* (*TH 6445*; BRG); north to south running ridge about 1 km west of confluence of Ireng and Sukabi Rivers, 27 May 1998, *T. Henkel et al.* (*TH 6655*; BRG, L); east bank of Iring River, 1 km downstream from Kurutuik Falls, 6 June 1998, *T. Henkel* (*TH 6898*; BRG).

Amanita aurantiobrunnea clearly belongs to section *Phalloideae* because of the amyloid spores, the saccate to limbate volva attached to the upper part of the bulb and the deeply coloured pileipellis. Within this section very few species have colours that are reminiscent of those in the present one.

Amanita aureomonile Tulloss & Franco-Molano (Tulloss et al., 1992) from Colombia has a bright yellow pileus with a darker disc, a pale yellow stipe and a bright yellow annulus.

Amanita subjunquillea S. Imai from Japan, as illustrated by Imai in Gilbert (1941a), seems close to *A. aurantiobrunnea*, but has a more ochraceous yellow pileus, a more coherent annulus, and more globose spores (7.0–8.0 × 7.0–7.5 µm according to Gilbert (1941a) and (6.0–)6.5–8.5(–9.0) × 6.0–8.5(–9.0) µm, Q = 1.0–1.2, according to Yang, 1997).

It should be mentioned here that the original *A. gayana* (Mont.) Sacc., described by Montagne (1853) from Chile, also has a glabrous red to orange pileus with a non-sulcate margin (specifically mentioned), a white stipe and annulus, and a white saccate volva and thus could represent a species of section *Phalloideae* too, although it seems to have no bulbous base. We prefer to consider the Chilian taxon a dubious one as long as no material has been collected again in Chile and the Melzer's reaction of the spores remains unknown.

Montagne's name has been misapplied by Singer (1969) and Garrido & Bresinsky (1985) to the species now known as *A. aurantiovelata* Schalkw. & G.M. Jansen (1982) which has

non-amyloid spores, a sulcate pileus margin, and orange-yellow volval warts on the pileus and the base of the stipe.

Amanita aurantiobrunnea has a peculiar character, that, as far as we know, has not yet been described in other species of section *Phalloideae*, viz. a thin, white to coloured, friable inner layer at least on the outer limb of the volva that is responsible for the frequent presence of rather inconspicuous, small, thin volval patches on the outermost margin of the pileus.

Because of slight irregularities on the surface of the spores seen in the light microscope, the spores have been scanned with a scanning electron microscope. When enlarged 10.000× they appeared, however, to be perfectly smooth.

Section **Validae**

Amanita cyanopus C. Simmons, Henkel & Bas, *spec. nov.* — Fig. 2, Plate 4

Pileus 65 mm latus, plano-concavus, margine laevis, sordide pallide vel obscure griseo-caeruleus, fragmentis volvae applanatis, coactis, concoloris decoratus praesertim prope margine, minute fibrillosus. Lamellae liberae, confertae, sordide cremeo-alutaceae, margine pallide caeruleae. Stipes 95 × 12 mm, basi bulbosus 18 mm latus, leviter radicans, pallide caeruleus, squamulis flocculosis minutis griseis obsitus, bulbo fragmentis volvae verruciformibus vivide caeruleis obtectis, annulatus. Odor ingratus.

Sporae 7.4–8.7 × 5.6–7.4 µm, late ellipsoideae vel ellipsoideo-elongatae, amyloideae. Basidia 4-sporigera. Fragmenta volvae cellulis turgidis, 9–33 × 7–19.5 µm, terminalibus vel breve catenulatis, olivaceo-brunneis hyphisque rarioris composita. Fibulae absentes.

Holotypus: *T. Henkel 7083*, Guyana, Pakaraima Mts, Upper Ireng River, 30.V.1999 (BRG).

Fruit-body medium-sized, rather slender, solitary. Pileus 65 mm in diam., plano-concave, with smooth margin, rather dull greyish to bluish turquoise (= greyish lavender blue to dark, slightly greyed blue, K&W 23D3 – 24D8), with concolorous, flat, felted volval patches particularly near margin, minutely, rather innately fibrillose. Lamellae free, crowded, thickish, occasionally forking, dull dark greyish tan (according to field notes; in colour slide looking rather pale cream-buff), with finely uneven, light blue edge. Stipe 95 × 12 mm, equal throughout, but with large, slenderly napiform, somewhat rooting bulb, 55 × 18 mm, annulate, light bluish under a coating of minute, grey, floccose scales, but bulb covered with small bright blue, conical volval warts and ridges on a paler blue to whitish background. Annulus present, apical (broken off close to apex of stipe in single specimen available). Smell unpleasant (according to collector distinctly of 'chlorine'). Spore print not available.

Spores [25/1] 7.4–8.7(–9.0) × (5.0–)5.6–7.4 µm, Q = (1.15–)1.25–1.45(–1.6), aver. Q = 1.36, broadly ellipsoid to oblong, with rather small hilar appendix, thin-walled, smooth, colourless, amyloid. Basidia 29–38 × 9.4–10.2 µm, 4-spored, clampless. Subhymenium pseudoparenchymatic, consisting of globose to ellipsoid, ovoid and broadly clavate cells, about 11–18 × 11–18 µm. Marginal tissue a rather broad, (in NH_4OH) colourless strip of thin-walled globose to ellipsoid, ovoid and broadly clavate cells 14–29(–42) × 12.5–20.5 µm, at least partly in chains. Hymenophoral trama: bilateral (very difficult to study in present specimen). Pileipellis (in scalp): suprapellis an ixocutis of 1.4–4.2 µm, interwoven (at centre as well as near margin) hyphae with unevenly distributed, (in NH_4OH) olivaceous brown, intracellular pigment, distant by gelatinification, over a subpellis of (almost) colourless, more radial, 2–7 µm wide hyphae. Volval remnants made up of globose, ellipsoid, ovoid, clavate, and irregularly shaped inflated elements 9–33 × 7–19.5 µm, with (in NH_4OH) dark, slightly olivaceous brown, unevenly distributed intracellular pigment, terminal or in

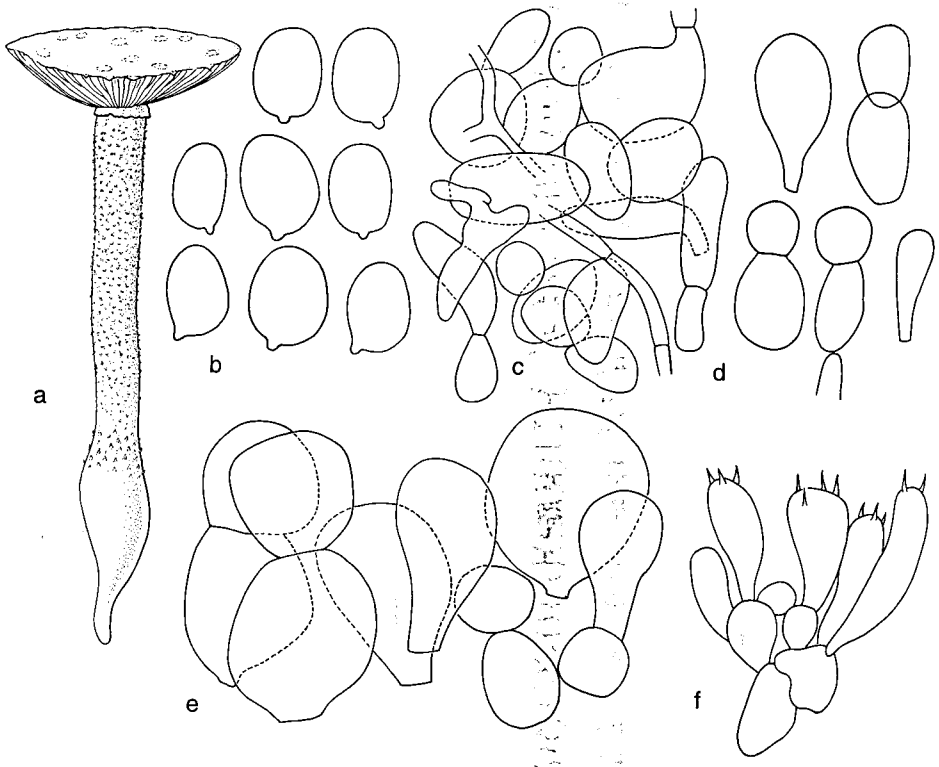

Fig. 2. *Amanita cyanopus*. a. Basidiocarp, × 0.5; b. spores, × 1500; c. slightly crushed scalp of volval patch on pileus, × 500; d. terminal elements from volval patch on pileus, × 500; e. elements of marginal tissue of lamella, × 1000; f. basidia and subhymenium, × 1000 (all from holotype).

terminal chains on relatively scarce 2.8–7.6 µm wide, brown, branching hyphae. Volval remnants on base of stipe not studied. Trama of stipe acrophysalidic, with 3.7–4.3 µm wide, brown, septate hyphae and abundant acrophysalides 83–154 × 10–23 µm. Clamp-connections absent.

Habitat & distribution — On root mat, but rooting into mineral soil, in forest of predominantly *Dicymbe corymbosa* (Paluwayek). Known only from the type locality in western Guyana.

Collection examined. GUYANA: Potaro-Siparuni, Pakaraima Mountains, Upper Ireng River, west bank of Yuarka River, 1 km upstream from juncture with Suruwabaru Creek, 30 May 1999, *T. Henkel et al.* (*TH 7083*; holotypus BRG).[1]

Although only one dried specimen (fortunately with colour slide) was available, we do not hesitate to describe the taxon concerned as a new species in section *Validae*, because of its unique colours, viz. the greyish blue to dark blue pileus with concolorous volval patches, the pale blue stipe with greyish floccose dots and the bright blue volval warts on the pale blue bulb.

1) Recently a second fruit-body has been collected (*T. Henkel s. n.*), but that has not yet been analysed.

The only species bearing a slight resemblance to *A. cyanopus* is *A. odorata* Beeli from the Congo (1931), also illustrated and described by Gilbert (1941a) with a greyish green pileus with brown volval warts. However, that species has been placed in section *Lepidella* by Bas (1969), because of its appendiculate pileus margin and elongate to subcylindrical spores (Q = 1.9–3.0). Moreover it has a smell like bitter almonds.

Amanita perphaea C. Simmons, T. Henkel, & Bas, *spec. nov.* — Fig. 3, Plate 5

Pileus usque ad 150 mm latus, initio convexus, postea plano-convexus vel depressus, obscure griseo-brunneus, nitidus, obscure fibrillosus, verrucis conicis, obscure griseo-brunneis ornatus, margine initio laevus, postea sulcato-striatus. Lamellae liberae, subconfertae, albae vel cremeae. Stipes 60–150 × 10–20 mm, basi bulbosus, obscure griseo-brunneus, fibrillosus, deorsum fragmentis volvae griseo-brunneis inconspicuis instructus. Annulus apicalis (sub)membranaceus, evanescens, pallidus.

Sporae 6.1–7.4 × 4.9–6.9 µm, (sub)globosae, amyloideae. Basidia 4-sporigera. Fragmenta volvae cellulis turgidis, 25–126 × 20–44 µm, subglobosis, ellipsoideis vel clavatis, brunneis, hyphisque copiosis composita. Fibulae absentes.

Holotypus: *T. Henkel 6229*, Guyana Pakaraima Mts, Upper Ireng River, 15.II.1997, (BRG).

Fruit-bodies terrestrial, solitary, large and fleshy. Pileus up to 150 mm in diam., plano-convex, with depressed centre, grey and shiny, darkening towards centre, with sulcate-striate margin, 4–6 grooves per 10 mm, covered with dark grey conical volval warts over entire surface but more concentrated at central region. Lamellae free, slightly crowded and slightly thickened, ventricose, white to cream, with entire edge; lamellulae truncate to subtruncate. Stipe 60–150 × 10–20 mm, central, tapering upwards, with bulbous base, fibrillose, grey and darkening with age; volval remnants forming grey ridge-like fragments at base on upper part of bulb (not visible in dried specimen). Annulus (sub)membranous, in young specimen still attached to lamellae, in matured specimen apical, descending, skirt-like, pallid, easily torn. Spore print not available.

Spores (present only in oldest specimens) [40/5] (5.6–)6.1–7.4 × 4.9–6.9 µm, Q = 1.0–1.1–1.3), aver. Q = 1.05–1.08, globose to subglobose, rarely broadly ellipsoid, with slightly thickened wall, amyloid, with prominent hilar appendix. Basidia 27–34 × 5–11 µm, clavate, 4-spored, clampless. Subhymenium composed of subglobose to ovoid elements, 12–13 × 8–9 µm. Marginal tissue a rather broad strip of 1.7–4.1 µm wide hyphae ± parallel to lamella edge and many, mainly subglobose to ellipsoid and pyriform elements, 15–29 × 14–22 µm. Hymenophoral trama divergent with narrow central stratum of parallel hyphae and diverging zones with subglobose, ovoid and ellipsoid elements single and terminal or in short terminal chains. Pileipellis (at ± 0.25R from centre) consisting of interwoven to subradial, fairly dark, broad, up to 7.5 µm wide hyphae with intracellular and encrusting pigments and scattered long inflated elements of up to 24 µm wide (also with intracellular and encrusting pigments); incrustations very distinct; refractive hyphae also present, on top of a rather thick almost colourless gelatinised layer. Volval remnants on pileus (in wart taken from centre) consisting of very abundantly branched, 4–7 µm wide, irregularly disposed, colourless to pale brown hyphae carrying subglobose, ellipsoid and elongate elements, 25–126 × 20–44 µm, usually in erect position, except just above pileipellis and there often in periclinal position, with brown vacuolar and encrusting pigments, particularly dark just above pileipellis, but paler towards apex (strongly pigmented layer with periclinal inflated elements with hand lens visible as dark line between base of wart and gelatinised pileipellis). Volval remnants on stipe consisting of mass of irregular hyphae with very few longi-

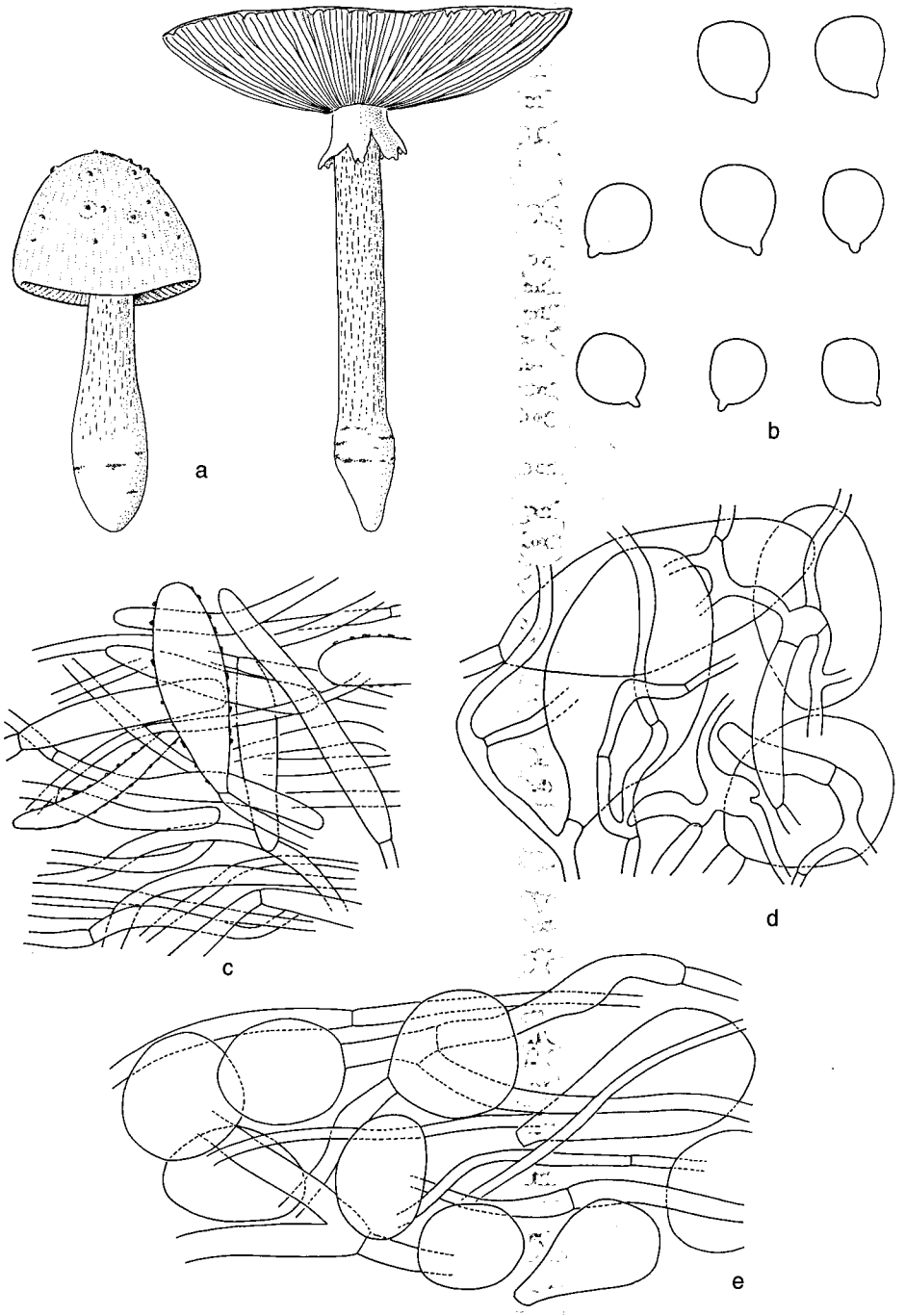

Fig. 3. *Amanita perphaea*. a. Basidocarps, × 0.5; b. spores, × 1500; c. scalp of pileipellis from above, × 500; d. elements of volval remnants on pileus, × 500; e. marginal tissue of lamella, × 1000 (all from holotype).

tudinal inflated cells of up to 43 × 14 µm. Trama of stipe acrophysalidic with elongate cells, 115–355 × 24–41 µm. No clamp-connections observed.

Habitat & distribution — Riverine and adjacent slope forest dominated by *Dicymbe corymbosa* (Paluwayek) with scattered hardwoods including *Caryocar* sp. in wet bottomlands, on sandy soils with thick root mat and organic accumulations So far known only from western Guyana.

Collections examined. GUYANA: Potaro-Siparuni, Pakaraima Mountains, Upper Ireng River: Slopes adjacent to east bank of Sukabi River near mouth of Kukuinang Creek, 1.5 km along south bank of Kukuinang Creek, 16 Feb. 1997, *T. Henkel et al.* (*TH 6255*; BRG, L); 0.2–1 km downstream from Kurutuik Falls, slopes adjacent to west side of river, 15 Feb. 1997, *T. Henkel et al.* (*TH 6229*; BRG holotype, L isotype).

At first it was thought that the collections described above represented *Amanita phaea* Bas nom. prov. (1978) from Brazilian Amazonia, described provisionally because the material available does not have spores. But the pileipellis of *A. phaea* and *A. perphaea* differs considerably. In *A. phaea* the superficial rather dark hyphae only have intracellular pigment, whereas in *A. perphaea* there is an additional encrusting brown pigment. Moreover there are elongate up to 24 µm wide inflated elements, probably all terminal, in the pileipellis of *A. perphaea*, which are lacking in *A. phaea*.

Macroscopically the two taxa differ as well. In *A. perphaea* the volval warts and patches on the pileus are as dark as the pileipellis and have a pallid apex or centre, whereas in *A. phaea* they are uniformly pallid. The aspect of the pileipellis differs also, viz. in *A. perphaea* dark and fibrillose with fibers strongly appressed to a paler background and in *A. phaea* more uniformly greyish brown.

In section *Validae*, where *A. perphaea* clearly belongs, several dark grey-brown species with small spores have been described from different parts of the world.

Amanita fritillaria f. *malayensis* Corner & Bas (1962) resembles *A. perphaea* rather strongly, but has more and smaller volval warts on the pileus, a grey annulus at about the half-way point of the stipe and no elongated inflated elements and apparently no encrusting pigment in the pileipellis. According to Corner & Bas (1962) *Amanita fritillaria* (Berk.) Sacc. f. *fritillaria* has more ellipsoid spores (aver. Q = 1.3–1.35).

Another dark species from south-eastern Asia is *Amanita pilosella* Corner & Bas (1962), which has several characters in common with *A. perphaea*, but has considerably smaller fruit-bodies, more powdery to subvillose volval remnants on the pileus and a grey annulus with blackish edge. It should be mentioned here that *A. pilosella* has the same type of elongate inflated elements in the pileipellis as does *A. perphaea*.

Amanita tristis Corner & Bas (1962) from Singapore has smaller and more ellipsoid spores (4.9–6.1(–7.0) × 4.3–4.6 µm, aver. Q = 1.3–1.35) and the volval warts on the pileus and the base of the stipe are entirely pale greyish to whitish.

Amanita fuscobrunnea A.E. Wood (1997) from Australia has smaller fruit-bodies, a grey pileus with dark pyramidal warts and a stipe entirely decorated with brown powdery granules.

Amanita echinulata Beeli (1927, 1935) from the Congo was placed by Gilbert (1940) in section *Lepidella* (then called *Aspidella*). However, Bas (1969) demonstrated that it belongs to section *Validae* and suggested a position near *A. pilosella*. It has a dark brown pileus with very dark conical warts and a dark brown stipe with a dark grey-brown annulus. Its type has small globose to subglobose spores (5.5–6.5 × 4.5–5.5 µm; pers. obs. C. Bas.).

Amanita morrisii Peck (1910) from North America also has a very dark pileus, at least when young. However, it has no conical volval warts but pallid volval patches on the initially dark grey-brown to blackish brown pileus and, according to Tulloss (1991), larger, more ellipsoid spores (7–9.5 × 5.5–7 µm, Q = 1.28–1.42).

Amanita spissacea S. Imai (1933) from Japan also has crust-like volval patches, in this case very dark grey-brown on a paler background and has brown powdery scales on the stipe. This species has globose to subglobose spores. Yang (1997) suggested that *A. spissacea* is a synonym for *A. fritillaria.*

Since so far pigments in the pileipellis of *Amanita* have always been recorded as a vacuolar, it is remarkable that the very dark superficial hyphae on the pileus of *A. perphaea* have an additional encrusting pigment. This could mean that these hyphae represent a fibrillose, strongly fragmented inner layer of the volva. Encrusting pigments in the volval tissues of *Amanita* have been recorded before.

Amanita perphaea is commonly eaten by Patamona Indians and is called 'Pulutukwe'.

Subgenus **AMANITA**

Section **Amanita**

Amanita calochroa C. Simmons, T. Henkel & Bas, *spec. nov.* — Fig. 4, Plate 6

Pileus 18–30 mm latus, primo hemisphaericus vel convexus margine laevis, postea applanatus margine valde sulcatus, centro applanatus vel depressus, fragmentis volvae pulveraceis rubris vel aurantio-rubris dense obsitus. Lamellae liberae, subdistantes, albae vel cremeae; lamellulae truncatae. Stipes 40–60 × 2.5–5 mm, basi bulbosus, cremeus; pars supera bulbi aurantio-pulveracea, exannulatus.

Sporae 6.3–7.8 × 5.5–7.8 µm, globosae vel late ellipsioideae, inamyloideae. Fragmenta volvae cellulis turgidis, 19–43 × 13–21 µm, subglobosis, ovoideis, ellipsoideis vel elongatis composita. Fibulae absentes.

Typus: Guyana, Pakaraima Mts, Ireng River, 22.V.1998, *T. Henkel et al. (TH 6426*; BRG holotypus, L isotypus).

Fruit-bodies terrestrial, gregarious, small, and fragile. Pileus 18–30 mm in diam., at first hemispherical to convex with smooth margin and flattened centre, later applanate with strongly sulcate-striate (about 0.3 to 0.5R), somewhat crenulate margin and depressed centre, densely covered with a bright red to orange-red (K&W 10A8 to 8A8), pulverulent to minutely subtomentose volval layer with age at margin breaking up into orange-red granules on a yellowish to cream background (in dried state pale yellow and covered with melon-yellow (5A6) powdery substance). Lamellae free, subdistant, thickish, narrow, with even to eroded edges, white to pale cream; lamellulae truncate. Stipe 40–60 × 2.5–5 mm, slightly tapering upwards, with 3–7.5 mm wide, sometimes slightly rooting, bulbous base, white to pale yellow, and lightly covered with orange powdery substance forming a denser pulverulent orange zone on upper part of bulb. Annulus absent. Spore print not available.

Spores [25/2] 6.3–7.8(–8.4) × 5.5–7.8 µm, Q = 1.0–1.2(–1.4), aver. Q = 1.06–1.19, globose to broadly ellipsoid, rarely ellipsoid, with smooth, thin walls, usually with one oil droplet, with rather narrow, but relatively prominent, hilar appendix, colourless, non-amyloid. Basidia 24–38 × 8–11.5 µm, clavate, shorter and broader near edge, 19–21 × 12.5–13.5 µm, 4-spored, clampless. Subhymenium pseudoparenchymatic (reinflating very badly); elements short and broad. Marginal tissue present as small ± conical teeth, pale yellowish in NH_4OH or just a strip of rather amorphous tissue; teeth consisting of subglobose, broadly ellipsoid and pyriform elements, 9–26(–36) × 8.5–18 µm, at least partly attached terminally

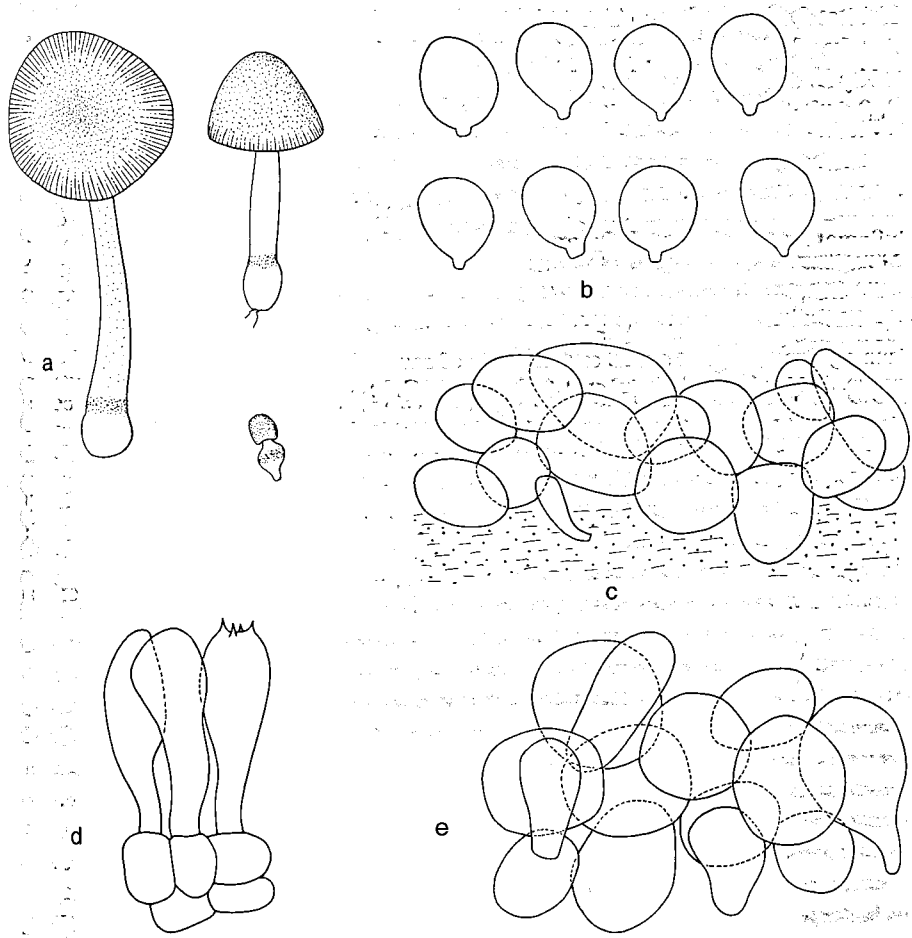

Fig. 4. *Amanita calochroa*. a. Basidiocarps, × 1; b. spores, × 1500; c. velar remnants on gelatinized pileipellis, × 500; d. basidia and subhymenium, × 1000; e. marginal tissue of lamella, × 500 (all from holotype).

to hyphae. Hymenophoral trama bilateral, with a thick subhymenium and rather wide to narrow central stratum. Pileipellis consisting of a strongly gelatinised (in 5% KOH) layer about 70 µm wide, consisting of ± radial, 2–4.5 µm wide hyphae, in upper part disintegrated. Volval remnants on pileus consisting of a mass of broadly ellipsoid to ovoid, rarely subglobose or elongate inflated elements, (14–)19–43 × (14–)13–21(–30) µm, with thin walls, pale yellow in NH_4OH, probably at least partly in short chains, but connection of elements not clearly seen (nearly all elements remaining slightly to strongly collapsed); inflated elements much more abundant than hyphae. Volval remnants on stipe similar to those on pileus, but with an even higher ratio of inflated elements to hyphae. Context of stipe made up of firm, pale, brownish orange tinged 'cortex' and a wide, fluffy, whitish pith, with few, relatively small, up to 175 × 27 µm large acrophysalides; at centre consisting of loose tissue of 3–6 µm wide interwoven to longitudinal hyphae. No clamp-connections observed.

Habitat & distribution — Terrestrial, gregarious in litter mats accumulated in crooks of the trunks of *Dicymbe corymbosa* (Paluyawek) in riverine and adjacent slope forest dominated by *D. corymbosa,* and *D. altsonii* (Edubayek) with *Micrandra glabra* (R.E. Schult.) R.E. Schult. (Euphorbiaceae; Suruwayek), *Moronobea* Aubl. spec. (Guttiferae; Morombayek), and other mixed hardwoods on sand soils with thick organic matter accumulations on grey sands and exposed sandstone boulders and cliff faces. So far known only from the Pakaraima Mountains in western Guyana.

Collections examined. GUYANA: Potaro-Siparuni, Pakaraima Mountains, Upper Ireng River: 0.75–1.5 km downstream from Kurutuik Falls, forest near ridge trail and slopes adjacent river, 14 Feb.1997, *T. Henkel et al.* (field notes only; BRG); Forest adjacent Sukabi River, 1–2 km upstream from confluence with Ireng River, 22 May 1998, *T. Henkel & L. Williams* (*TH 6426*, holotype BRG, isotype L); Mt Kukuinang, fringing forest around southern edge of savannah, about 3 km south-west from peaks of mountain, 25 May 1998, *T. Henkel et al.* (*TH 6589*; BRG, L).

Amanita calochroa is a beautiful species with gregariously growing small fruit-bodies of which the pileus is covered by bright red to orange-red powdery volval remnants. As in addition it has non-amyloid spores, a sulcate-striate pileus margin and a stipe with a bulbous base, it finds its place in section *Amanita*. Within this section several small to medium-sized species with a red or orange pileus and a friable volva are known, but those differ from *A. calochroa* in the following ways:

Amanita aurantiovelata Schalkw. & G.M. Jansen (1982) described from Chile. Originally the collector thought the present taxon to represent *A. aurantiovelata,* but that species has considerably larger spores (8–11.5 × 6.5–8 µm), abundant clamp-connections, and larger fruit-bodies with at least some conical volval warts.

Amanita parcivolvata (Peck, 1900) E.J. Gilbert (1941a) from North America has a glabrous, viscid, yellow-orange to red pileipellis with dirty yellow to cream warts to patches. Moreover its spores are much larger and ellipsoid to nearly cylindrical.

Amanita rubrovolvata S. Imai (1939) described from Japan and occurring widely in Eastern Asia, differs by the presence of an annulus, a volval layer on the pileus that tends to break up into patches and warts, and has larger, more (sub)globose spores.

Amanita armeniaca A.E. Wood (1997) from Australia (Sydney) is a species with a bright orange pileus with membranous, dull cream volval patches near the centre and has an annulus. In addition its spores are larger ((7.4–)8.1–10.2 × 6.9–9.6 µm).

Amanita subfrostiana Z. Yang (1997) described from south-west China and Tibet, has a red to orange pileus, with yellowish to orange, powdery to floccose volval remnants. But it differs by having an annulus, larger spores and clamps.

Amanita bingensis Beeli (1931) described from the Congo region has an orange-yellow powdery volva and lacks an annulus; its spores are much smaller (5–6 × 3–4.5 µm).

Amanita chrysoleuca Pegler (1983), discovered on Martinique and also occurring on the Virgin Islands (Miller et al., 2000), and in Panama and Florida (Tulloss, pers. comm.), resembles the present species in several aspects, such as small size, strongly friable volva, lacking annulus and bright colours, but has a more orange-yellow to yellow pileus and somewhat larger (7–9.5 × 4.5–6 µm), considerably more ellipsoid to oblong spores (aver. Q = 1.56), according to Miller et al. (2000) even still larger (7–10(–10.5) × 5–7 µm, aver. Q = 1.31).

Amanita lanivolva Bas — Fig. 5, Plate 3

Amanita lanivolva Bas, Persoonia 10 (1978) 12.

Fruit-body solitary, medium-sized, slender, terrestrial. Pileus 30–70 mm in diam., first plano-convex, later with wide central depression, with sulcate-striate margin, (original colour not recorded, but in colour-slide from pale brown at margin, K&W about 6C4, to dark brown at centre, about 7E6), glabrous or with a small cluster of grey, conical volval fragments or of small grey volval patches at centre. Lamellae free, crowded, narrow, cream; lamellulae truncate. Stipe 65–88 × 6–8 mm, tapering upwards, exannulate, white, glabrous, at base slightly, but distinctly bulbous with membranous, rather narrowly saccate, grey-brown tomentose to tomentose-squamulose volva enclosing lower 1/4 to 1/3 of stipe like a sock. Spore print not available.

Spores [40/3] 7.4–9.8 × 5.0–6.6(–7.2) µm, Q = 1.3–1.65, aver. Q = 1.4–1.55, broadly ellipsoid to ellipsoid with very slightly thickened wall, non-amyloid, usually with oil droplet, with rather broad hilar appendix. Basidia 24–33 × 8–11 µm, 4-spored, with inconspicuous clamp-connection. Subhymenium made up of subglobose to broadly ellipsoid, 8–25 µm wide elements. Marginal tissue consisting of a broad, sterile, ± amorphous strip of tissue, with outer cells difficult to reinflate, but between amorphous layer and edge of hymenium with quite a few (sub)globose to broadly ellipsoid and broadly clavate elements of up to 20 µm wide and with slightly thickened wall. Hymenophoral trama bilateral. Pileipellis consisting of a gelatinised suprapellis of colourless, thin-walled, 2–3 µm wide, interwoven hyphae, over a subpellis of 4–8 µm wide, interwoven brown hyphae. Volval remnants on pileus consisting of very loosely interwoven brown hyphae carrying (sub)globose, ovoid and broadly ellipsoid brown elements 56–78 × 19–29 µm, with slightly thickened walls. Trama of stipe acrophysalidic with up to 175 × 40 µm large terminal elements. Clamp-connections abundant.

Habitat & distribution — Riverine swamp forest on flat ground dominated by *Dicymbe altsonii* (Edubayek) and *D. corymbosa* (Paluwayek) with scattered associated hardwoods. Known from Brazilian Amazonia and western Guyana.

Collections examined. GUYANA: Pakaraima Mountains, Upper Ireng watershed: Upper Ireng River, forest adjacent Sukabi River, 1–2 km upstream from confluence with Ireng River, 22 May 1998, *T. Henkel & L. Williams* (*TH 6432*; BRG, L); Upper Ireng River, forested slopes adjacent last bank of river, 27 May 1998, *T. Henkel* (*TH 6640*; BRG, L); Mt. Kubinoang, fringing forest around southern edge of savannah, about 3 km south-west from peak of mountain, 25 May 1998, *T. Henkel et al.* (*TH 6593*; BRG, L).

This is the second time that *A. lanivolva* is recorded and the first time from outside Brazilian Amazonia. The present description agrees rather well with the original one, except that in some specimens from Guyana a few small, conical volval warts are present at the centre of the pileus.

There is no longer any doubt about the presence of a small, but distinct basal bulb in this species. Because of this bulb *A. lanivolva* does clearly not belong to section *Vaginatae*, but to section *Amanita*, where, however, it stands well apart from all the other species on account of its saccate volva.

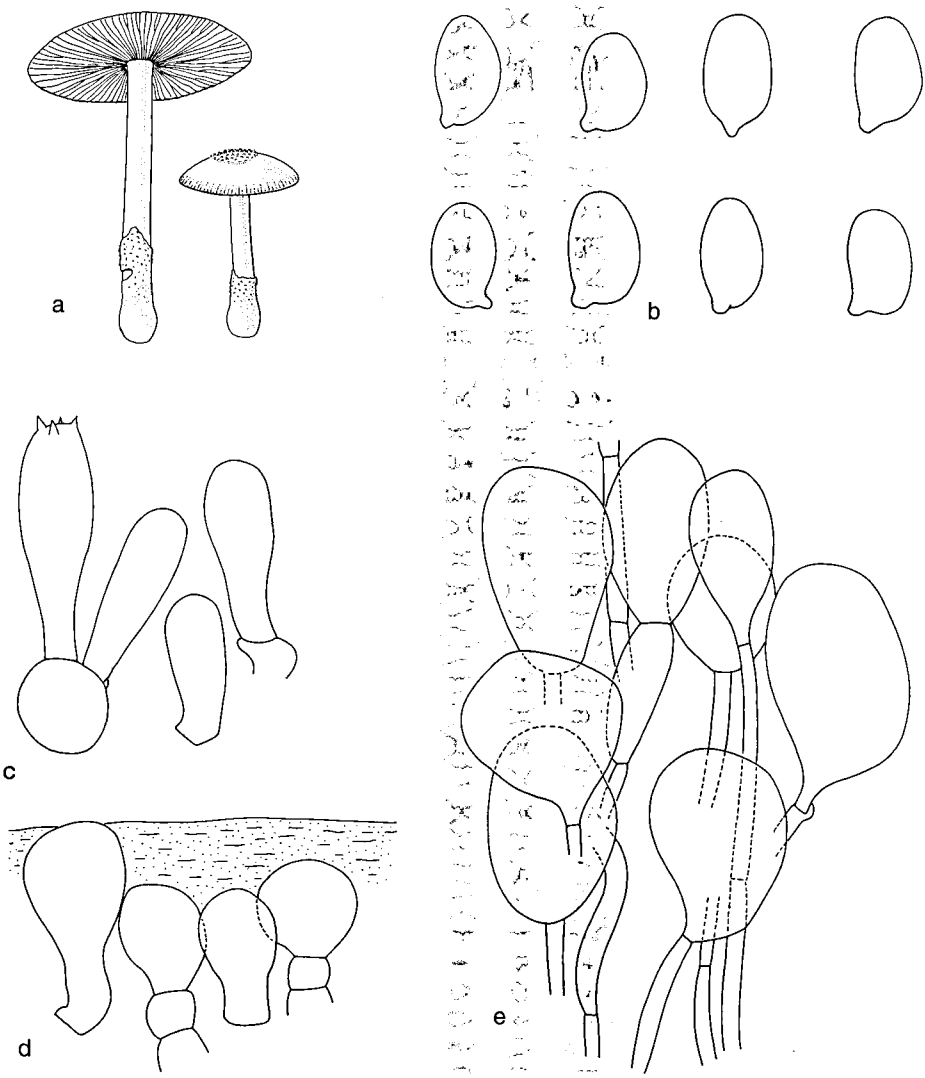

Fig. 5. *Amanita lanivolva*. a. Basidiocarps, × 0.5; b. spores, × 1500; c. young basidia and subhymenium, × 1000; d. elements of marginal tissue of lamella, × 1000; e. slightly crushed longitudinal section of volval wart on centre of pileus, × 500 (a & e: *TH 6432*; b–d: *TH 6640*).

Amanita xerocybe Bas — Fig. 6, Plate 7

Amanita xerocybe Bas, Persoonia 10 (1978) 7.

Fruit-body medium-sized, slender, fragile, solitary to gregarious. Pileus 20–46 mm, young hemispherical to paraboloid, later plano-convex with broadly rounded umbo or with slightly depressed centre, with broad widely sulcate-striate margin (0.25–0.65R), cream (K&W 4A2 – 4A3) with dark red-brown to fairly dark orange-reddish brown (in colour-slides 7E8 to 7D8, later between 7D7 and 7C8) powdery-granular substance over entire

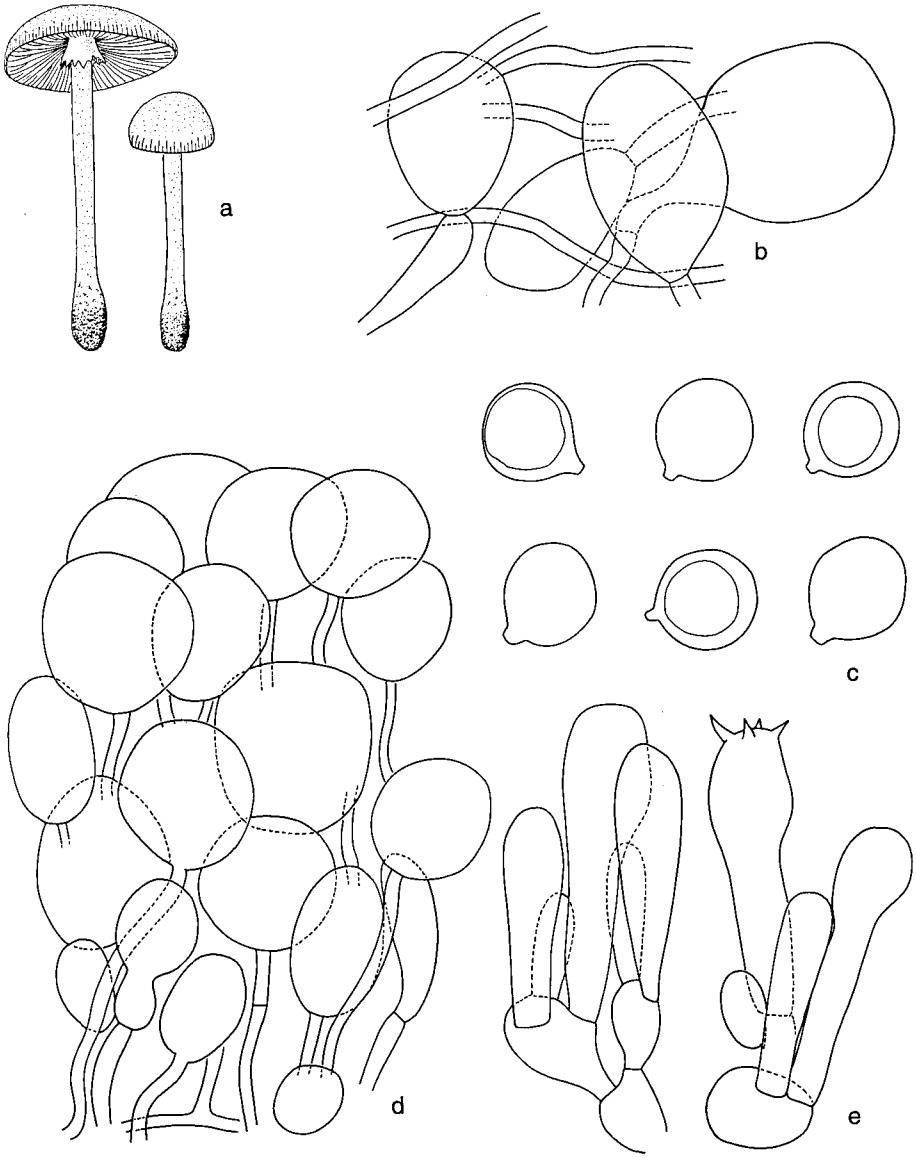

Fig. 6. *Amanita xerocybe*. a. Basidiocarps, × 0.5; b. marginal tissue of lamella, × 1000; c. spores, × 1500; d. velar remnants on pileus, 0.25 R from centre, × 500; e. basidia and subhymenium, × 1000 (a: reconstructed; b & c: *TH 6261*; d & e: *TH 6434*).

surface but more concentrated at central region. Lamella free, distant, narrow, but becoming ventricose, white to cream, with minutely subfloccose-subgranular, concolorous edge; lamellulae not found. Stipe up to 82 × 6 mm, slightly tapering upwards, with up to 9 mm wide, clavate, bulbous base, pallid with minute brown granules all over, at base with scattered, brown, small, irregular, wart-like volval fragments. Annulus submembranous, skirt-

like, but very fragile (lacking in all dried specimen studied, but clearly visible on colour-slide), white and sulcate-striate above and orange-brown with darker brown granules below. No spore print available.

Spores [49/3] 6.0–9.0 × 6.0–8.6(–9.4) µm, Q = 1.0–1.1, aver. Q = 1.03–1.04, globose to subglobose, with normal hilar appendix, with smooth, slightly thickened wall, non-amyloid. Basidia 37–51(–62) × (8.0–)9.0–12.0(–14.0) µm, 4-spored, clampless. Subhymenium consisting of irregularly subglobose and subellipsoid elements, 15–19 × 10–14 µm. Marginal tissue a rather broad strip of amorphous, partly gelatinised tissue with irregularly disposed, globose to broadly ellipsoid, terminal elements, 20–42(–51) × 13.5–25(–32) µm, on 2.5–4 µm wide hyphae. Trama of gills bilateral. Pileipellis consisting of a non-gelatinised layer of 2.5–6 µm wide, colourless, thin-walled hyphae between adnate volval tissue and trama of pileus. Volval remnants on pileus (near centre) pale yellowish brownish in NH_4OH, in scalp seen from above: an irregular arrangement of globose, ellipsoid and ovoid, thin-walled, terminal elements, 22–49(–70) × (12.5–)18–41(–58) µm; in radial section: made up of single, erect, terminal, inflated elements on 3–5.2 µm wide, septate hyphae. Volval remnants on stipe similar to those on pileus, but hyphae more abundant. Trama of stem acrophysalidic; inflated elements up to 325 × 24 µm. Clamp-connections absent.

Habitat & distribution — Riverine swamp forest and adjacent slope forest dominated by *Dicymbe corymbosa* (Paluwayek) and other mixed hardwoods, on sand soils with thick organic accumulations and on exposed sandstone and cliff boulders. Known now from Brazilian Amazonia, and from western Guyana

Collections examined. GUYANA: Potaro-Siparuni, Pakaraima Mountains: Upper Ireng watershed, Suruwaburu Creek, 1–2 km upstream from juncture with Jurka River, immediate riverine environs, 2 March 1997 (*TH 6217*; BRG); Upper Ireng River, forest adjacent Sukabi River, 1–2 km upstream from confluence with Ireng River, 22 May 1998 (*TH 6434*; BRG); Upper Ireng River, Mt. Kukuinang, fringing forest on western side of savannah, ± 3 km WSW from mountain peak, 25 May 1998 (*TH 6614*; BRG, L); Upper Ireng River, 0.2–1 km downstream from Kurutuik Falls, slopes adjacent west side of river, 15 Feb. 1997 (*TH 6261*; BRG, L).

Amanita xerocybe Bas, described in 1978 from Brazilian Amazonia, is recorded for the second time and for the first time from outside Brazil.

The specimens from Guyana usually have a somewhat smaller pileus and a relatively longer marginal striation, whereas the granular-subfloccose volval remnants have a somewhat more reddish brown colour. However, all the other characters being in agreement with the protologue of *A. xerocybe,* we do not hesitate to consider the material from Guyana conspecific with that from Brazilian Amazonia.

Amanita xerocybe is a very characteristic species that belongs to section *Amanita* because of its non-amyloid spores, friable volva, and bulbous base of the stipe.

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