Three *Cercophora* species from Indian elephant dung. An opportunity to establish new combinations and a new taxon

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Abstract: Elephant dung, when compared with other dungs from mammalian herbivores, was regarded as an ideal substrate for cellulolytic fungi. One sample of Indian elephant dung, examined for detecting coprophilous ascomycetes, was found to have developed three different *Cercophora* species. *Cercophora elephantina*, *Cercophora* sp. of the complex-*sordarioides*, and a new species, *C. cephalothecoidea*, were classified based on morphological characteristics. *C. elephantina* was described in detail and compared with species having the so called "pseudobombardioid" peridium. *Cercophora* sp. and *C. cephalothecoidea* were described, compared and placed in keys with species having a membraneous or carbonaceous peridium, respectively. *Bombardia mutabilis* and *B. rostrata* were recombined in *Cercophora*. Following recent phylogenetic analyses, the morphological and physiological features of family *Lasiosphaeriaceae*, *Cercophora* and related genera were re-examined and discussed.
Keywords: cellulases, coprophilous fungi, exoperidium, morphological study, phylogenetic studies, *Sordariales*.

Introduction

Elephant dung is largely composed of cellulose (Farouq *et al*., 2012), the main structural polysaccharide of plant cell walls, whose fibers consist of monosaccharide chains bound together by glycosidic linkages. Man and most mammals do not possess cellulase enzymes hydrolyzing the glycosidic linkages, so they can not make use of cellulose as feed. In several ruminants cellulases are produced by symbiotic bacteria of the digestive tract, whereas in elephants the bacterial cellulolytic activity is poorer and the absorption of nutrients less efficient: only about 44% of the ingested food is digested and absorbed (EREC www.asianelephantresearch.com/about-elephant-anatomy-and-biology-p3.php). It follows that elephant dung is rich in potential nutrients, especially cellulose, for which only cellulolytic bacteria and fungi can benefit. All fungi growing on elephant dung have always been regarded as potentially cellulase producers (Farouq *et al*., 2012) and, concerning *Cercophora* Fuckel, production of cellulase enzymes was proved (Abdel-Raheem & Shearer, 2002) in *C. newfieldiana* (Ellis & Everh.) R. Hilber isolated from submerged wood.

A basic survey on coprophilous Central African fungi (Cailleux, 1971) showed a comparatively low occurrence of ascomycetes on elephant dung but also a good frequency of occurrence of *Cercophora* species (s.n. *Bombardia*), particularly of *C. rostrata* (Cailleux) Doveri. Similar results were obtained by a study on elephant dung decomposition (Masunga *et al*., 2006) in Botswana (Southern Africa) and by two surveys of coprophilous ascomycetes in Thailand (Jeamjitt *et al*., 2007; Mungai *et al*., 2011): *C. coprophila* (Fr.) N. Lundq. frequently occurred on African elephant (Loxodonta africana) dung, whereas *C. silvatica* N. Lundq. and *C. kalimpongensis* Mukerji *et al*. were frequently and exclusively recorded from Asian elephant (*Elephas maximus*) dung.

Many other records of *Cercophora* spp. were from elephant dung (Cailleux, 1971; Lundqvist, 1972; Piasai & Manoch, 2009), as well as the type material of *C. caerulea* (Petch, 1925) N. Lundq., *C. citrina* (Petch, 1922) N. Lundq., *C. elephantina* (Henn., 1895) N. Lundq., and *C. rostrata* (Cailleux) Doveri.

Recently I was lucky enough to study one sample of elephant dung coming from the Indian state of Kerala and, after Cailleux (1971), I was not surprised at all to find on it very few species of ascomycetes. They were *Saccobolus depauperatus* (Berk. & Broome) E.C. Hansen, *Saccobolus succineus* Brumm., and three pyrenomycetes which soon attracted my attention as possessing very similar morphological features. The study that followed allowed me to classify them as *Cercophora elephantina* (Henn.) N. Lundq., *Cercophora* sp. of the complex-*sordarioides*, and the new species *C. cephalothecoidea* Doveri. The aim of this work is to describe the three species in detail, analysing their relationships with similar taxa and also revealing the difficulties encountered in the study of this genus.

Materials and methods

A sample of elephant dung was collected in Kerala and a few days later brought to Italy where, after a first observation, was placed in a non-sterilised damp chamber, following the methods suggested by Richardson & Watling (1997) and Richardson (2001), slightly modified by Doveri (2004). Cultured material, incubated at room temperature (18–25°C) under natural light, but not exposed to direct sunlight, was examined every day under a stereomicroscope. The three *Cercophora* species had already developed in the natural state, therefore they were observed since the first day of damp chamber. No development of new specimens was noticed in the next forty days. Some mature ascomata of each species were extracted from the dung with a sterile needle and streaked on PDA (Potato Dextrose Agar, Difco Lab.), amended by 2 mg L-1 streptomycin and used for single ascospore cultures according to Doveri *et al.* (2012). All the attempts to isolate these fungi in axenic cultures were unsuccessful. Microscopic examinations were carried out on specimens picked up from dung in the damp chambers and mounted in water, Congo red, cotton blue in lactic acid, and methyl blue. Spore size was measured in water. Perithecial height is recorded inclusive of the neck.

Abbreviations: CLSM = author's personal herbarium.

Taxonomy

Cercophora elephantina (Henn.) N. Lundq., *Symb. Bot. Upsal*., 20 (1): 111 (1972). Plates 1–5

≡ *Sordaria elephantina* Henn., *Bot. Jahrb. Syst*., 22: 77 (1895), basionym.

≡ *Lasiosphaeria elephantina* (Henn.) J.C. Krug & R.S. Khan, *in* Khan & Krug, *Proc. Thirteenth Plenary Meeting of AETFAT*, 1: 761 (1994).

= *Sordaria pilosa* Petch, *Ann. R. Bot. Gard. Peradeniya*, 7: 302 (1922), *nom. illegit.*

= *Bombardia coprophila* (Fr.) Kirschst., *s.* Moreau (1947, 1953) (*fide* Lundqvist, 1972).

Perithecia 320–850 × 180–550 µm, obovoidal to ellipsoidal or broadly ellipsoidal, sometimes slightly curved, non-stromatic, coriaceous, pale brown, fully covered, except for the upper third of the neck, with dense, but not fasciculate, rigid hairs. Neck conical, 200–250 × 180–220 µm, or hemispherical-papillate, 80 × 50 µm, black, carbonaceous, sometimes vaguely longitudinally ridged. Perithecial contents whitish. **Peridium** pseudo-bombardioid, four-layered: first layer from outside (exostratum) a *textura angularis* of pale brown,

fairly thin-walled, polygonal cells, 7–17 × 6–15 µm, at the neck formed of blackish, papillate cells; second layer of seemingly gelatinised, thin-walled hyphae; third layer of hyaline (the innermost) to pale brown (the outermost), parallel, cylindric hyphae; fourth layer pseudoparenchymatous, a *textura angularis* of pale, thin-walled, polygonal cells, slightly larger than exoperidial cells. **Neck hairs** and **peridial hairs** very similar to each other, arising from exoperidial cells, 40–60 × 4–5 µm, straight or somewhat curved, rarely branched, greyish brown, hyaline and roundish at the tips, quite thin-walled, 1–poly-septate, enlarged or sometimes bulbous at the base, up to 10 µm diam. **Paraphyses** numerous, exceeding the asci, cylindrical, septate, somewhat or strongly constricted at septa, 4–12 µm diam., tapering upwards, containing many hyaline vacuoles. **Asci** 200–220 × 11–15 µm, unitunicate, non-amyloid, 8-spored, cylindrical, slightly enlarged in the middle, slightly flattened at the apex, without a subapical plasma globulus, with a simple apical ring and a long, lobate stalk. **Ascospores** bi-triseriate inside the ascus, hyaline and cylindrical at first, becoming sigmoidal, with fifteen oil droplets or more at this stage, one-celled, 45–50 × 4.5–5 µm, finally two-celled, with a transverse septum subdividing them into two parts, an upper cell, the so called "spore head", and a lower cell or "pedicel". Spore head remaining hyaline even in late stages, 15–18

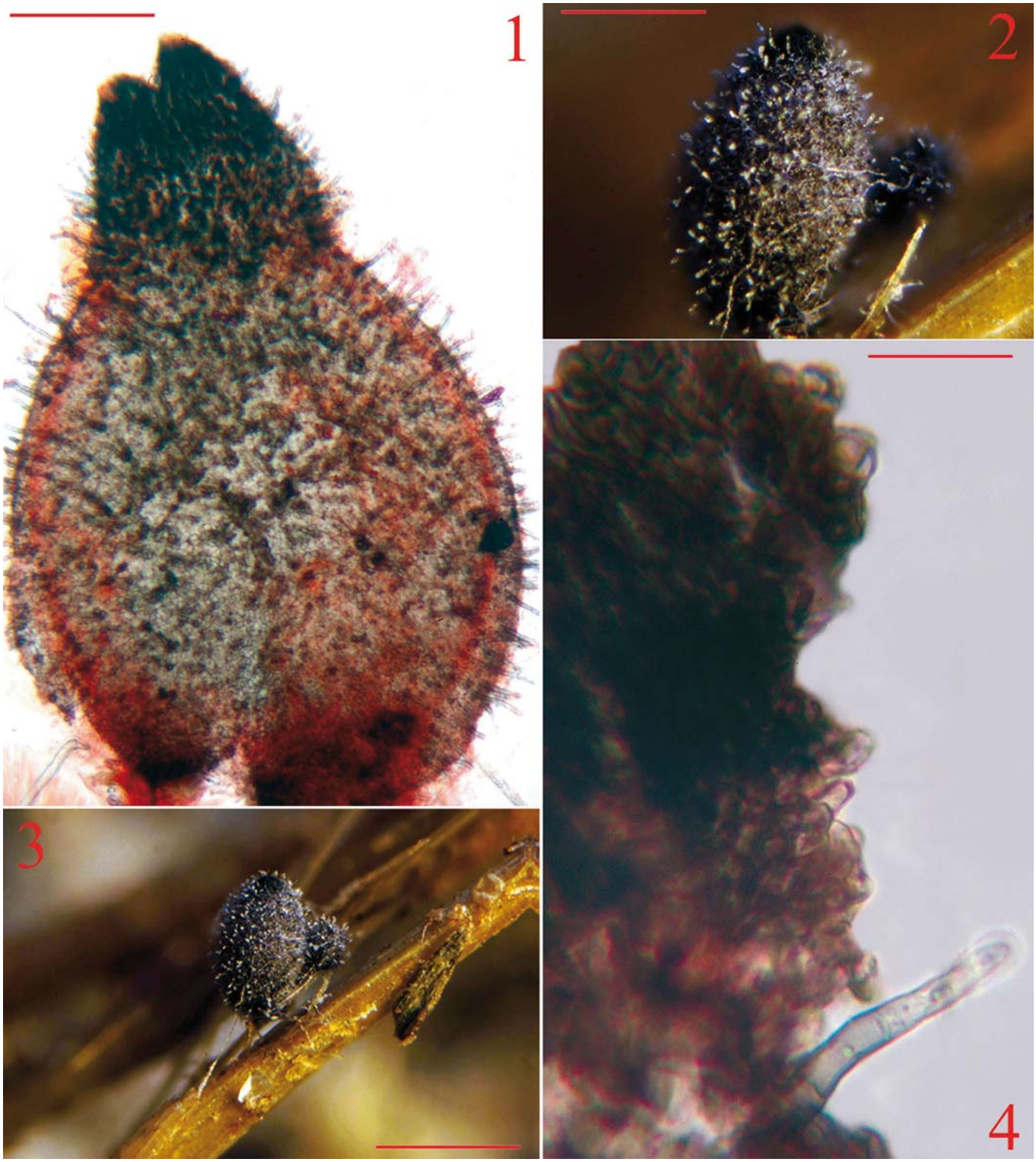

Plate 1 – *Cercophora elephantina*
1–3. Ascomata (1 = Congo red). 4. Detail of perithecial neck. Scale bars: 1 = 100 µm; 2 = 300 µm; 3 = 500 µm; 4 = 20 µm.

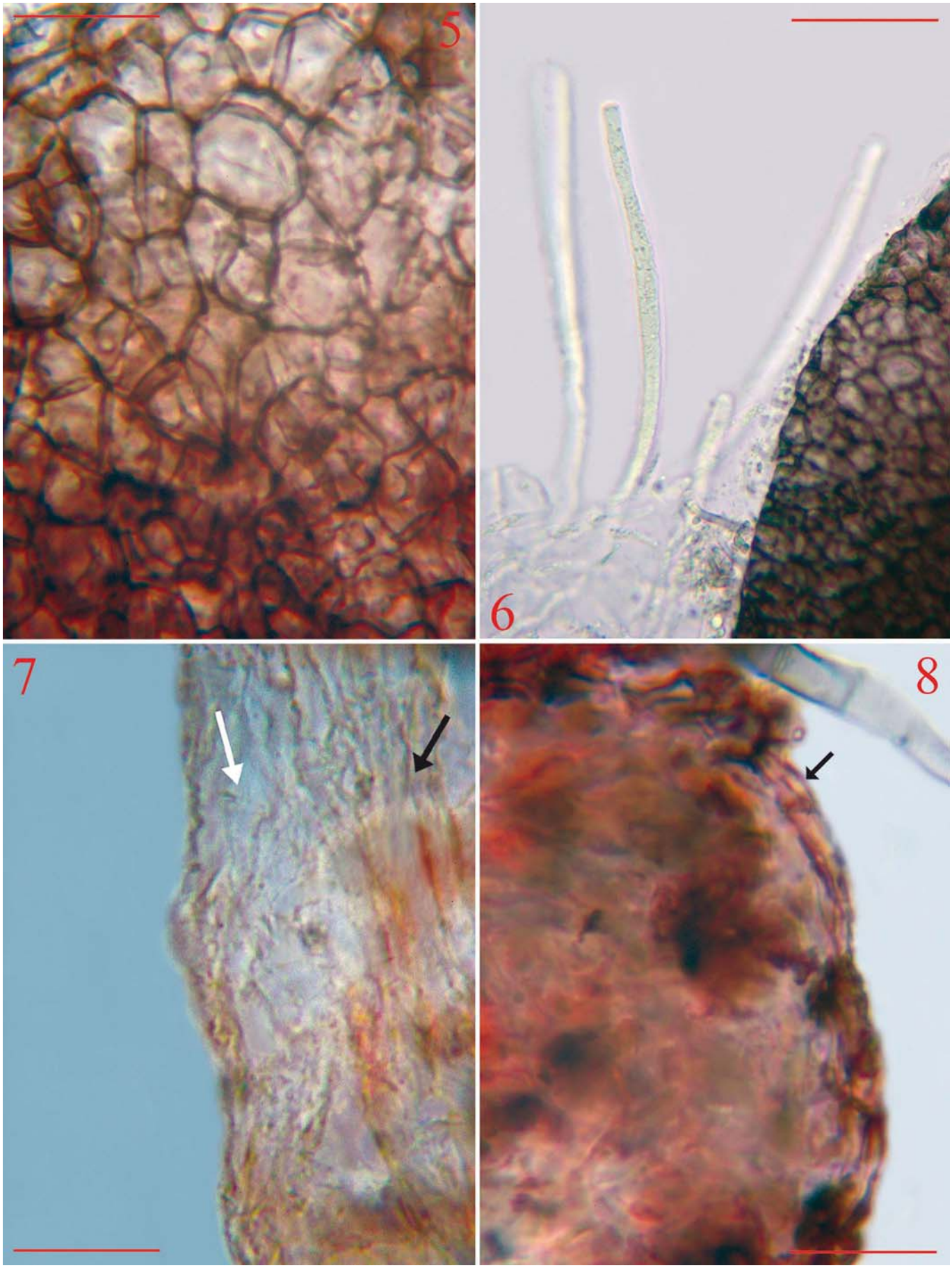

Plate 2 – *Cercophora elephantina*

5. *Textura angularis* of outer peridial layer. 6. Detail of outer peridial layer, and immature asci. 7. Second, gelatinous (white arrow) and third (black arrow) peridial layers. 8. Parallel, flattened cells of the third peridial layer. Scale bars: 5 = 20 µm; 6–8 = 40 µm.

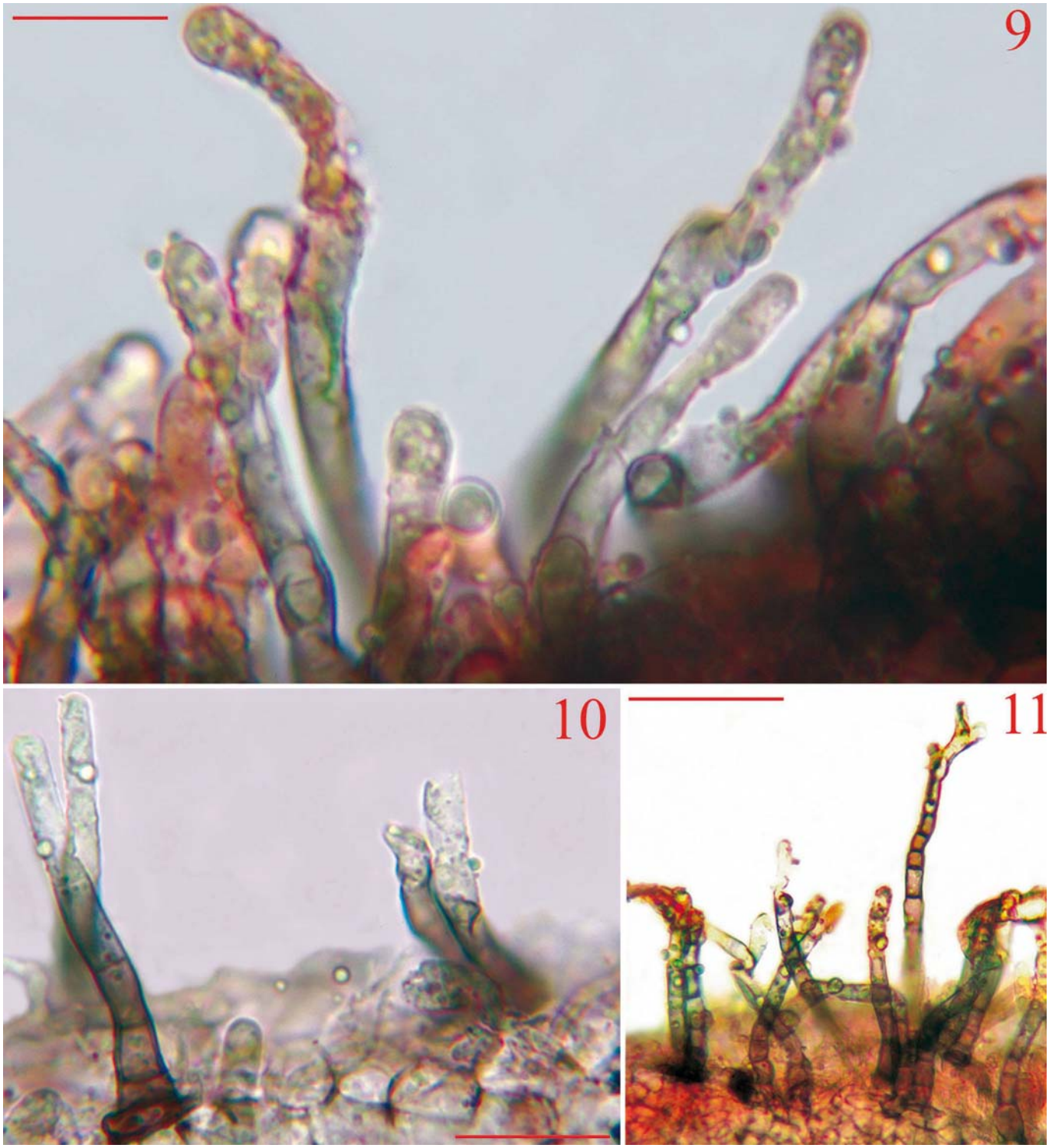

Plate 3 – *Cercophora elephantina*
9–11. Peridial hairs. Scale bars: 9 = 10 µm; 10 = 20 µm; 11 = 30 µm.

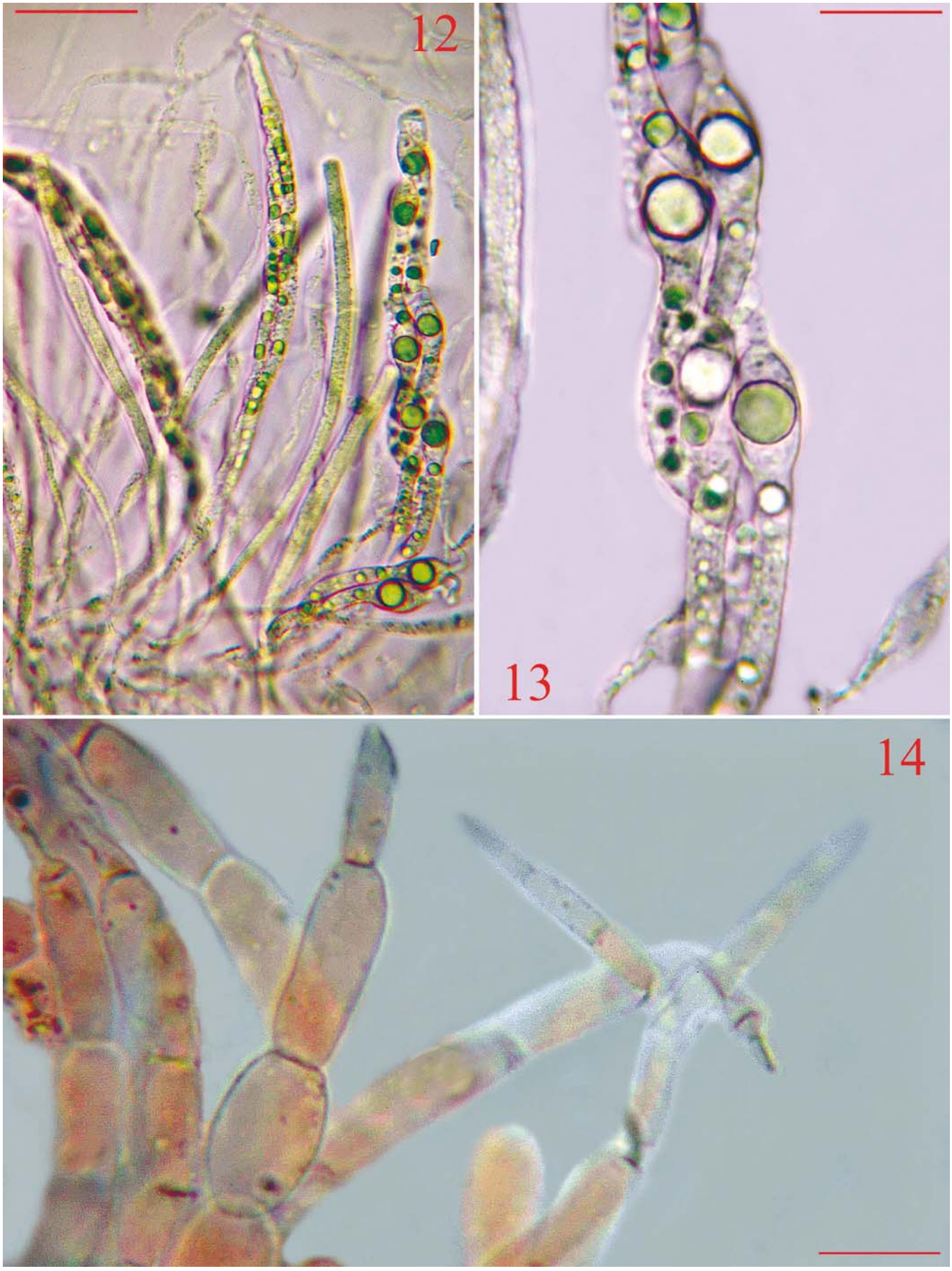

Plate 4 – *Cercophora elephantina*
12. Asci mixed with exceeding paraphyses. 13. Ascospores inside the ascus. 14. Paraphyses. Scale bars: 12 = 25 µm; 13–14 = 15 µm.

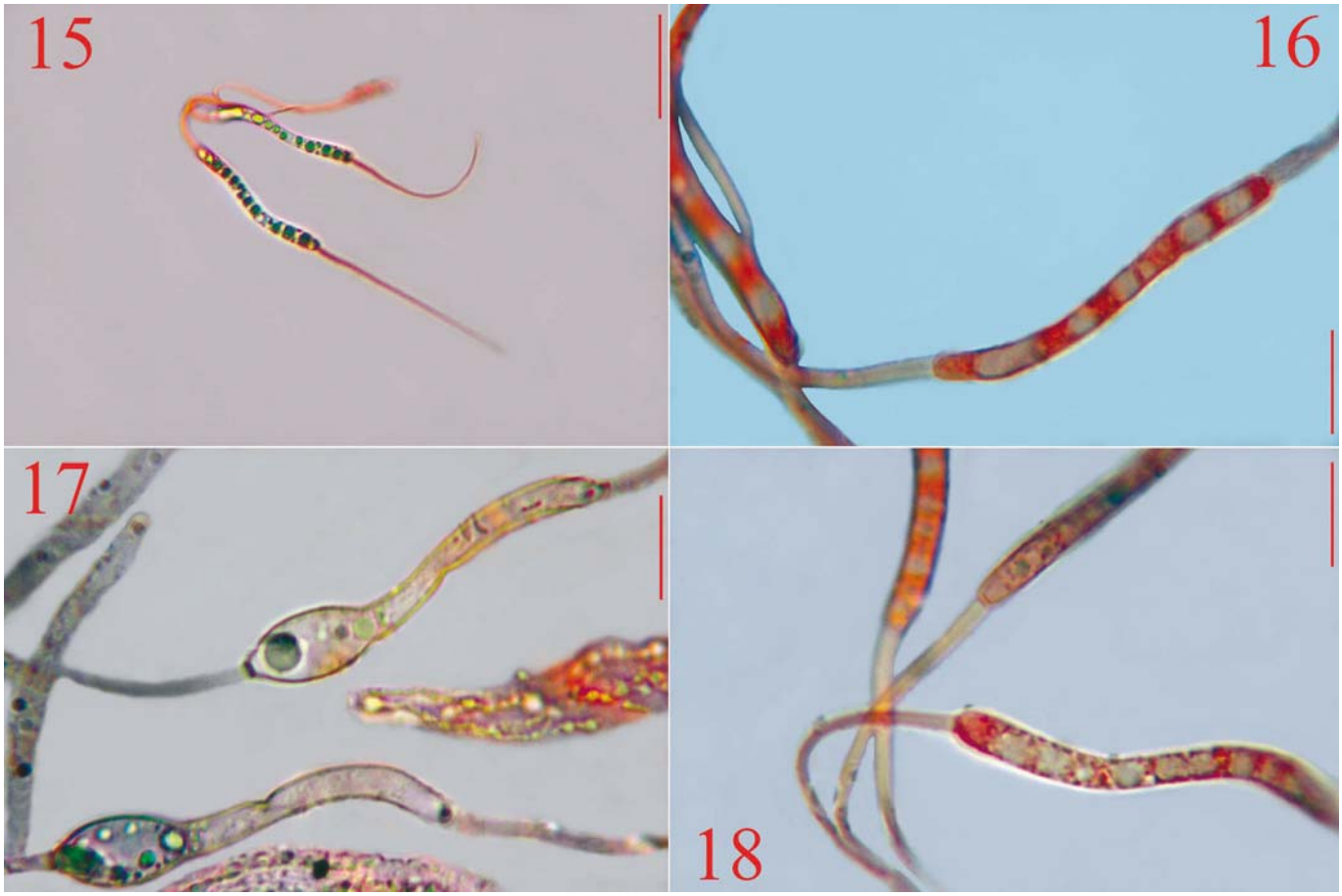

Plate 5 – *Cercophora elephantina*
15–18. Ascospores in different stages (Congo red). Scale bars: 15 = 30 µm; 16–18 = 15 µm.

× 8–9 µm, ellipsoidal, sometimes subumbonate, equilateral, flattened at the base, with a large oil drop. Germ pore not seen. Pedicel 30–35 × 4.5–5 µm, hyaline, sigmoidal or cylindric-geniculate. A central, lash-shaped, solid gelatinous cauda, 35–55 × 2–2.5 µm, is observable at each spore end since the early stages. **Asexual morph** not observed.

Material examined: India, Kerala State, Periyar, Periyar National Park, 9°27′53″S 77°13′58″E, 1400 m a.s.l., about ten scattered, superficial specimens naturally developed on Indian elephant (*Elephas maximus indicus*) dung, *leg*. M.T. Seu, 16.02.2016, CLSM 001.16.

***Cercophora* sp. "complex-*sordarioides*"**. Plates 6–11

Perithecia 500–600 × 320–400 µm, obpyriform, non-stromatic, brownish with reflected light, pale olive-brown with transmitted light, membraneous, semitransparent, sparsely to densely covered with hyphoid hairs. Neck hairy, cylindric or cylindric-conical, 150–250(–330) × 100–170 µm, straight or somewhat curved, blackish, sometimes vaguely longitudinally ridged. Perithecial contents whitish. **Peridium** three-layered. First layer from outside (exostratum) a *textura mixta, angularis* and *epidermoidea*, of very pale brown, fairly thin-walled (somewhat thicker towards the neck), polygonal or irregular cells, 7–12 × 5–10 µm, at the neck formed of black- and thick-walled, short cylindrical cells, 6–7 × 3 µm, more elongated around the ostiole; some carbonaceous sprinkles spread on the upper portion of exoperidium, just below the neck base. Second layer (mesostratum) of pale brown, parallel, cylindric hyphae. Third layer (endostratum) pseudoparenchymatous, a *textura angularis* of pale, thin-walled, polygonal cells, 15–30 × 13–20 µm. **Neck hairs** scarcely observable at low magnification, usually abundant, superficial, often appearing as lengthenings of the cylindrical peridial cells, 70–150 × 3 µm, spread on both sides of the neck base, or fasciculate at one side, straight or slightly curved or even slightly flexuous, dark brown, paler at the apex, thick-walled, septate, with a hidden base and a slightly pointed or roundish or sometimes subcapitate tip. **Hyphoid hairs** sparse in some specimens, numerous in others, spread over the whole peridial surface, hyaline to very pale brown, septate, thin-walled, 3–4 µm diam. **Paraphyses** abundant, exceeding the asci, cylindrical-moniliform, septate, somewhat or strongly constricted at septa, 4–8 µm diam., tapering upwards, containing many hyaline vacuoles. **Asci** 170–180 × 12–20 µm, unitunicate, non-amyloid, 8-spored, cylindrical at first, cylindric-clavate later, then fairly enlarged in the middle, slightly flattened at the apex, without a subapical plasma globulus, with a simple apical ring and a long stalk. **Ascospores** bi-triseriate inside the ascus, one-celled, hyaline, cylindrical or somewhat curved or slightly geniculate at first, containing several oil droplets or 3–5 large drops and some droplets, swelling at one end and becoming clavate-geniculate or clavate-sigmoidal, 35–40 × 3 µm, finally transversely septate and divided into a dark brown head and a lower hyaline pedicel. Spore head 15–18 × 9–11 µm, ellipsoidal to broadly ellipsoidal, often umbonate, equilateral, flattened at the base, with a slightly eccentric germ pore. Pedicel 27–30 × 4–4.5 µm, sigmoidal or cylindric-geniculate. A central, lash-shaped, solid, gelatinous cauda, 40–55 × 2 µm, is observable at each spore end since the early stages. **Asexual morph** phialophora-like.

Material examined: India, Kerala State, Periyar, Periyar National Park, 9°27′53″S 77°13′58″E, 1400 m a.s.l., about ten scattered, superficial specimens naturally developed on Indian elephant dung, *leg*. M.T. Seu, 16.02.2016, CLSM 002.16.

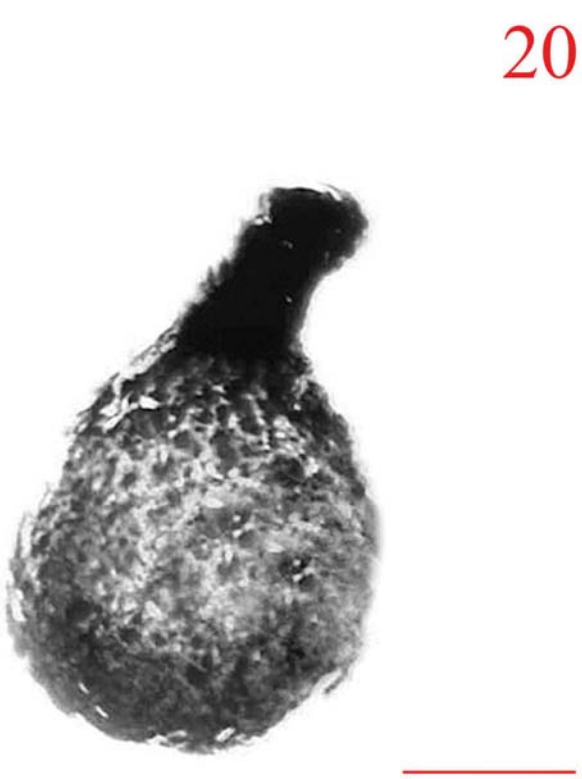

Plate 6 – *Cercophora sp.* complex-*sordarioides*
19–20. Ascomata. Scale bars: 19 = 200 µm; 20 = 150 µm.

Cercophora cephalothecoidea Doveri, *sp. nov.* – Mycobank MB817707. Plates 12–16

Holotype: India, Kerala State, Periyar, Periyar National Park, 9°27′53″ N 77°13′58″ S, 1400 m a.s.l., on Indian elephant dung (*Elephas maximus indicus*), *leg*. M.T. Seu, 16.02.2016, in Herbarium MCVE 29061 (dried specimens).

Etymology: from the Latin (in turn from the Greek) = "similar to *Cephalotheca*", referring to the exoperidial frame close to the genus *Cephalotheca*.

Perithecia 650–800 × 450–500 µm, obpyriform, non-stromatic, blackish, carbonaceous, opaque, densely hairy. Neck hairy, cylindric-conical or cylindric, 150–250 × 120–180 (at the base), usually straight, blackish, carbonaceous, longitudinally but imperceptibly furrowed. Perithecial contents very pale cream. **Peridium** seemingly two-layered (not seen a middle layer usually present in this genus): exostratum a densely areolate *textura cephalothecoidea* with plates of cylindric, straight or slightly flexuous, thick-walled (about 1 µm), very dark brown cells, 2–3 µm diam., in frontal view appearing radiate from a central, blackish, carbonaceous mass, which shows a central translucent hole when the base of a hair is subtended; endostratum pseudoparenchymatous, a *textura angularis* of pale, thin-walled, polygonal cells, 12–22 × 10–15 µm. **Neck hairs** dense, scattered or fasciculate, superficial, arising from the whole surface, 2–3 µm diam., up to 150 µm long, straight or slightly flexuous, occasionally branched, dark greyish brown, paler at the apex, thick-walled, septate, with a slightly enlarged base and a pointed or somewhat roundish tip. **Peridial hairs** abundant, dense, similar to the neck hairs, but more flexuous, dark grey, septate, thick-walled, 3–4 µm diam., up to 550 µm long, with a slightly enlarged or sometimes bulbose base. **Paraphyses** exceeding the asci, cylindrical-moniliform, septate, 7–15 µm diam., tapering upwards, containing many hyaline vacuoles. **Asci** 225–300 × 20–25 µm, unitunicate, non-amyloid, 8-spored, cylindrical at first, cylindric-clavate later, quite enlarged in the middle, slightly flattened at the apex, long-stalked, with a rough, rounded subapical plasma globulus, 4–5 µm diam., and a simple apical ring. **Ascospores** bi-triseriate inside the ascus: at first one-celled, hyaline, sigmoidal, 80–100 µm long, containing fifteen oil droplets or more and with two central, solid, lash-shaped gelatinous caudae, one at each end, equal in size, 50–90 × 2.5–3 µm but stretching up to 200 µm after compression; swelling later at one end and becoming clavate-sigmoidal; finally two-celled as divided by a transverse septum into an upper head and a lower pedicel. Spore head never seen dark pigmented, remaining pale, 24–27 × 11–12 µm, ellipsoidal to narrowly ellipsoidal, usually equilateral, slightly pointed at the apex and flattened at the base, transversely subdivided by a supra-equatorial septum, with a seemingly apical germ pore. Pedicel 47–62 × 5.5–6 µm, hyaline, usually sigmoidal, sometimes transversely septate. **Asexual morph** not seen.

Material examined: India, Kerala State, Periyar, Periyar National Park, 9°27′53″S 77°13′58″E, 1400 m a.s.l., about thirty scattered, superficial specimens naturally developed on Indian elephant dung, *leg.* M.T. Seu, 16.2.16, MCVE 29061.

Discussion

An overview of *Cercophora* and related genera of *Lasiosphaeriaceae*

Since the phylogenetic study based on partial LSU nrDNA sequence analysis by Huhndorf *et al.* (2004), *Sordariales* Chad. ex D. Hawksw. & Erikss. were redefined and restricted to three families, i.e. *Lasiosphaeriaceae* Nannf., *Sordariaceae* G. Winter and *Chaetomiaceae* G. Winter. *Lasiosphaeriaceae* were also proved to be paraphyletic and encompass genera with similar ascospore morphology, which was regarded as phylogenetically highly informative.

The *Lasiosphaeriaceae* genus *Cercophora* along with another thirty widespread genera (Maharachchikumbura *et al.*, 2015) is saprobic on dung, decaying wood, herbaceous debris, and soil (Cannon

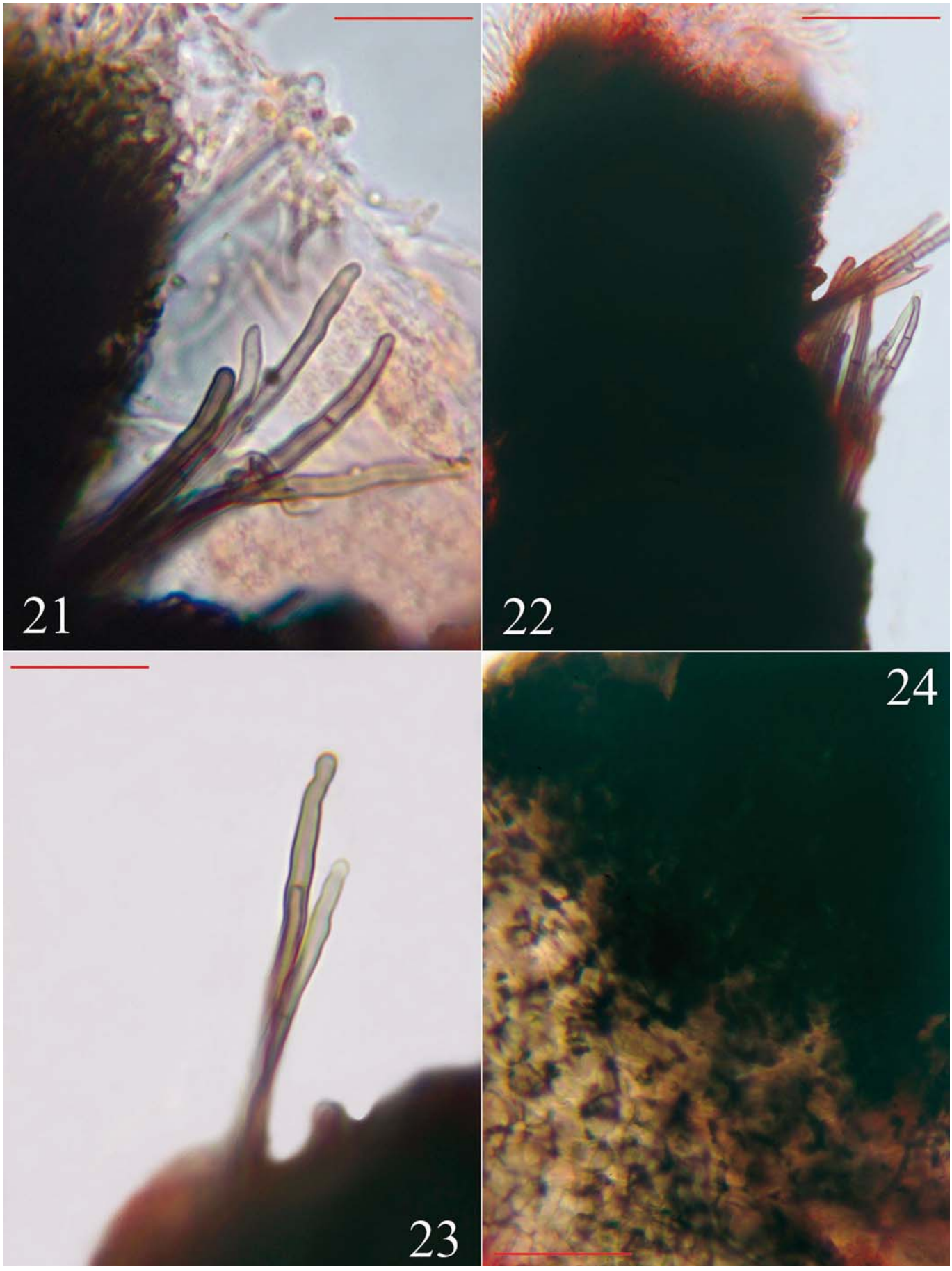

Plate 7 – *Cercophora sp.* complex-*sordarioides*
21–23. Neck hairs (Congo red). 24. Detail of neck base and upper peridial portion (Congo red). Scale bars: 21, 23 = 20 µm; 22, 24 = 40 µm.

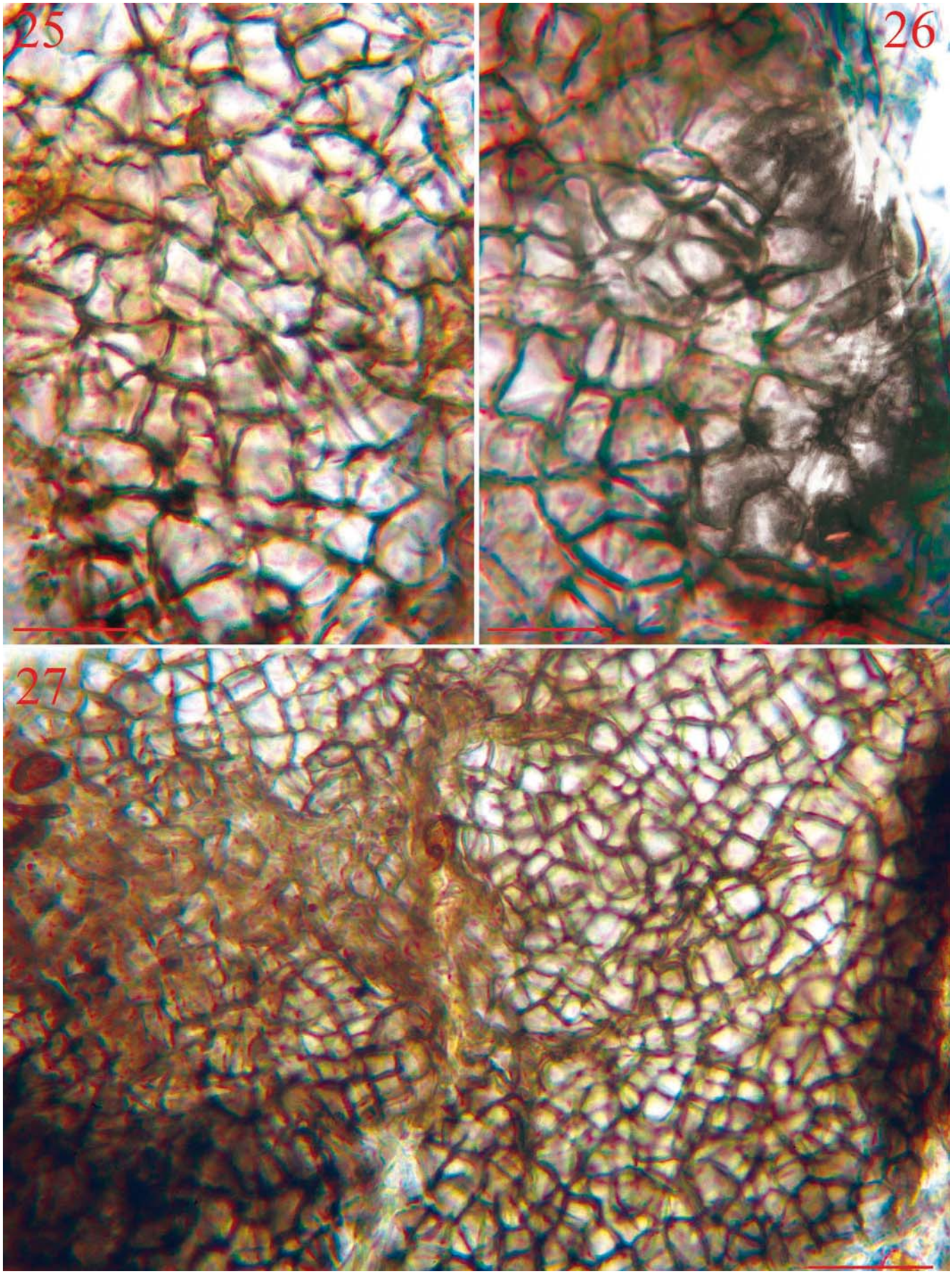

Plate 8 – *Cercophora sp.* complex-*sordarioides*
25–27. Exoperidial areas of predominantly *textura angularis*. Scale bars: 25–26 = 20 µm; 27 = 30 µm.

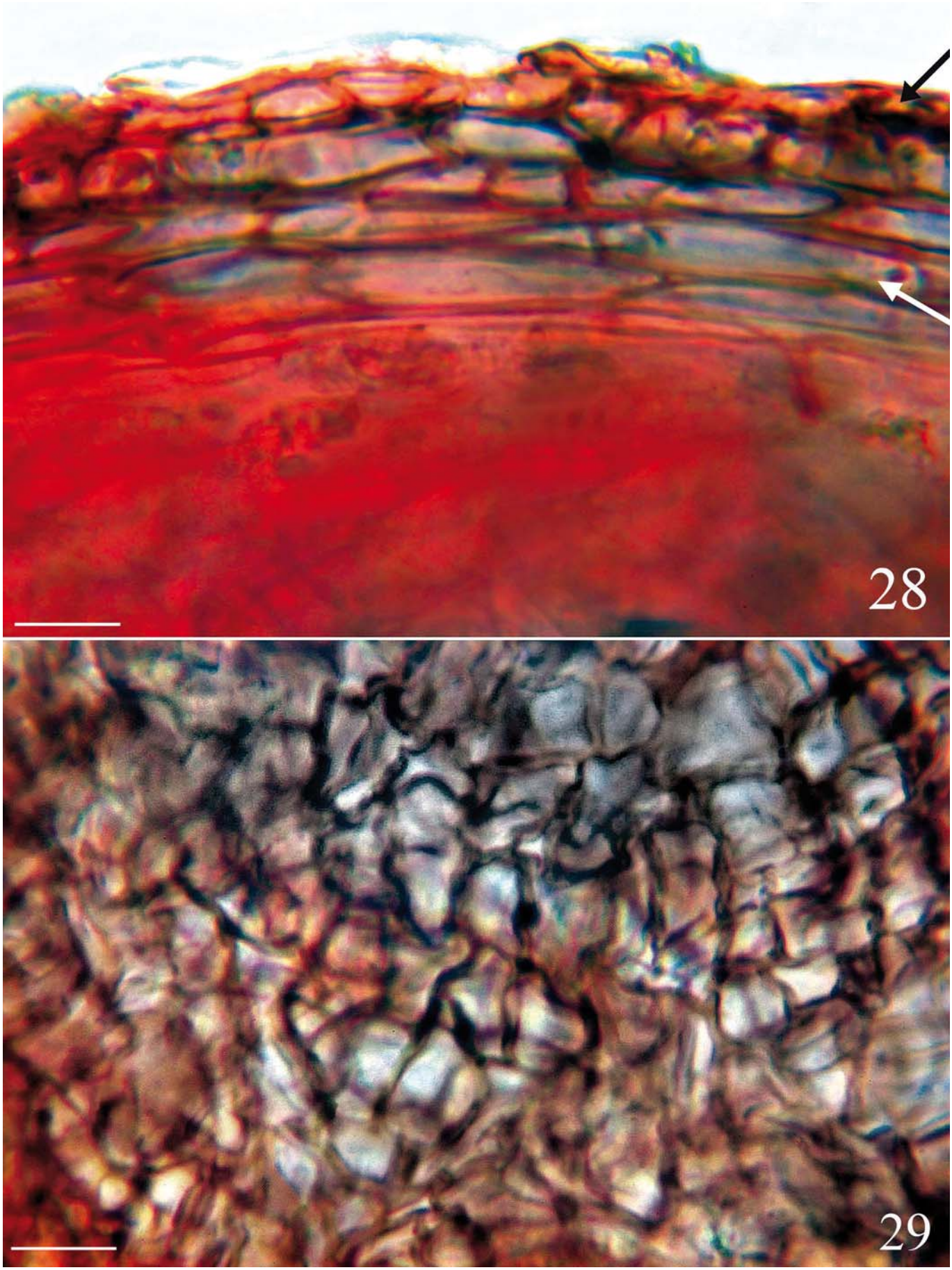

Plate 9 – *Cercophora sp.* complex-*sordarioides*

28. Detail of exostratum (black arrow) and mesostratum (white arrow) in longitudinal section (Congo red). 29. Exoperidial area of *textura epidermoidea* (Congo red). Scale bars: 28–29 = 15 µm.

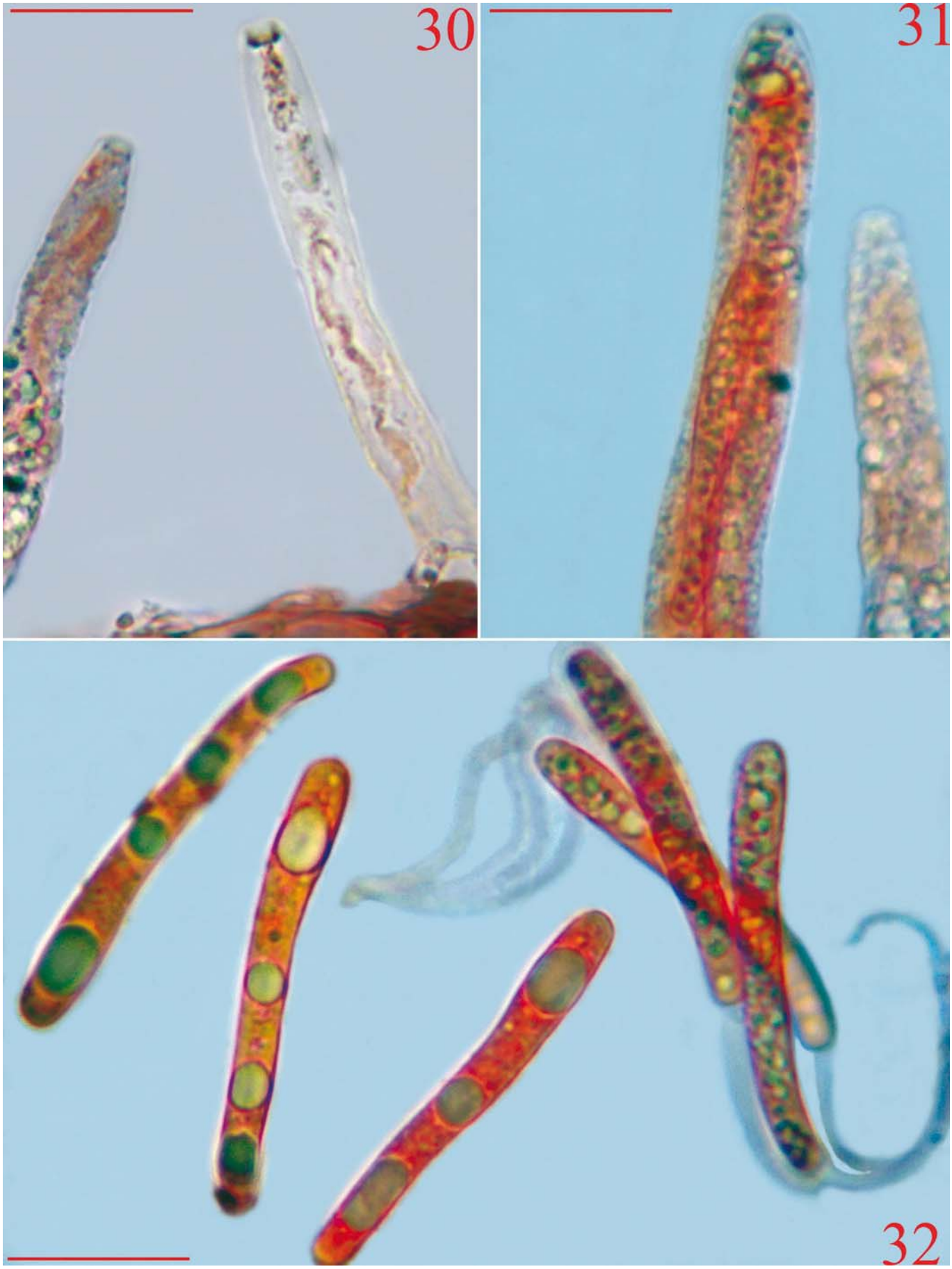

Plate 10 – *Cercophora sp.* complex-*sordarioides*
30–31. Immature asci (Congo red). 32. Free ascospores in an early stage (Congo red). Scale bars: 30–31 = 25 µm; 32 = 15 µm.

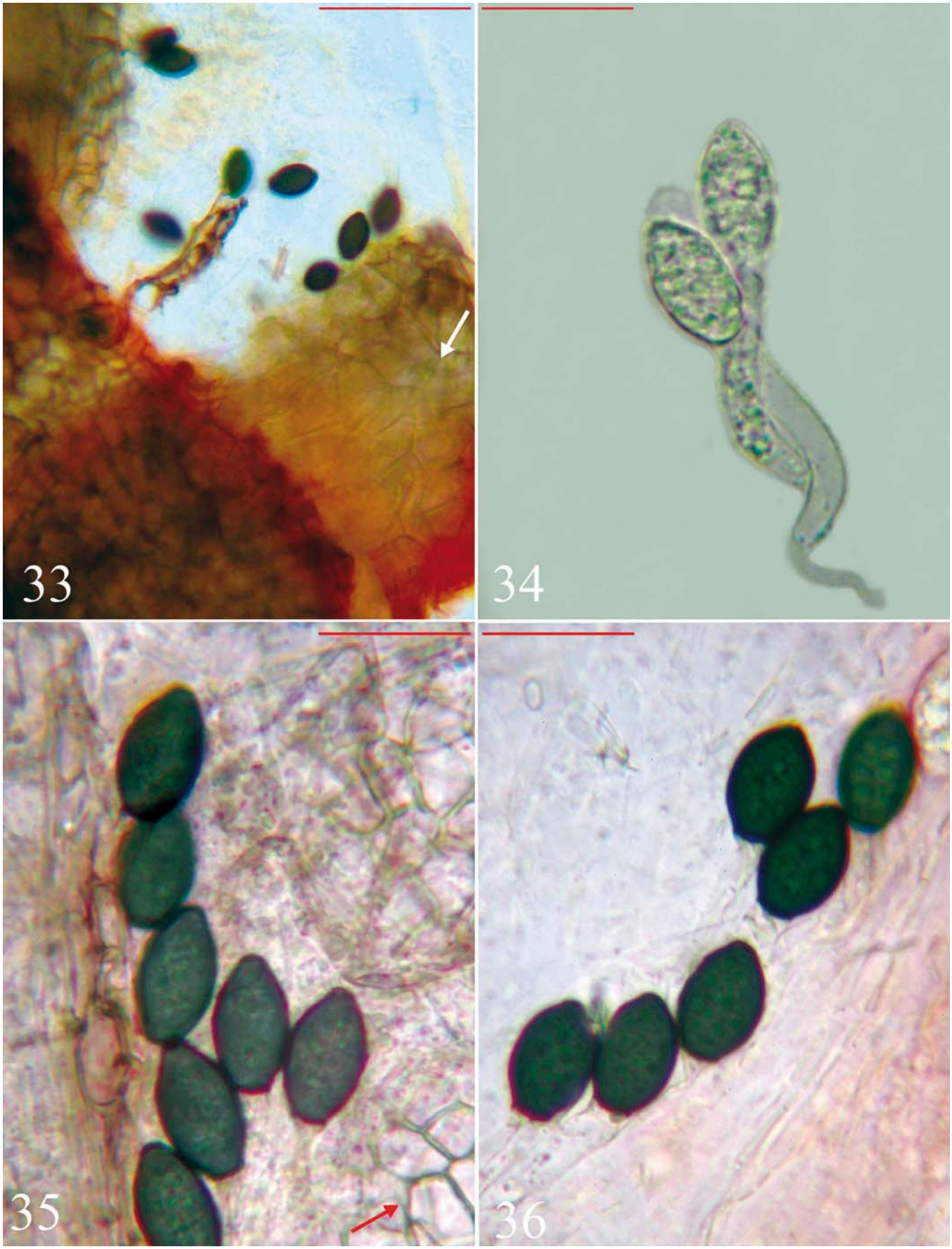

Plate 11 – *Cercophora sp.* complex-*sordarioides*
33–36. Ascospores in late stages and endoperidial cells (arrows). Scale bars: 33 = 50 µm; 34–36 = 20 µm.

& Kirk, 2007). Their usually non-stromatic, immersed to erumpent, dark perithecial or cleistothecial ascomata have a multi-layered, pseudoparenchymatous peridium, and a centrum of well-developed paraphyses and fasciculate, cylindric or claviform to saccate asci, sometimes with an apical ring. The ascospores are hyaline or often dark pigmented, one- or two-celled, rarely poly-celled, often with germ pore(s) and gelatinous caudae and/or sheaths. The asexual state, when present, is hyphomycetous (Cannon & Kirk, 2007).

In *Cercophora* the non-stromatic, membraneous, coriaceous or even carbonaceous perithecial ascomata have a pseudoparenchymatous, sometimes cephalothecoid peridium, often clothed with different types of vestiture, such as hairs, setae, and tomenta. The cylindric-clavate asci show a thickened apical ring and often a subapical plasma globulus. The young ascospores are hyaline, one-celled, cylindrical, filled with several oil droplets and usually provided with two lash-like gelatinous caudae, one at each end. They become cylindric-sigmoidal or geniculate and sometimes transversely one- to poly-septate, swelling at last and taking an ellipsoidal shape at their apical part (or "head"), which is usually separated from the lower part (or "pedicel") by a transverse septum. Their maturation is slow and does not necessarily coincide with a dark pigmentation of the head. In some species, indeed, or in the same species but under individual conditions, the ascospores remain at the hyaline state but are equally capable of germination (Lundqvist, 1972; Guarro *et al*., 2012). Most *Cercophora* have a cladorrhinum- (intercalary phialides predominant) or phialophora-like (lateral phialides predominant, also arising from ascospores) asexual morph (Hilber & Hilber, 1979; Udagawa & Muroi, 1979; Mouchacca & Gams, 1993; Miller & Huhndorf, 2001; Cai *et al*., 2006).

Podospora Ces., a genus closely related to *Cercophora*, has a phialophora-like asexual morph, but *P. fimiseda* (Ces. & De Not.) Niessl a cladorrhinum-like (Bell & Mahoney, 1997; Lundqvist *et al*., 1999). *Podospora* also differs from *Cercophora* in that it has polymorphous but not cylindric-vermiform immature ascospores, and clavate to saccate asci, usually lacking a plasma globulus and often an apical ring. The mature ascospores usually have a much more complex gelatinous equipment, a dark pigmented apical cell and an easily collapsing, hyaline pedicel. With few exceptions, only at this pigmented stage are the ascospores extruded from asci and able to germinate (Lundqvist, 1972).

Phylogenetic studies based on multiple gene sequence analyses proved that *Podospora* and *Cercophora* are polyphyletic (Cai *et al*., 2005, 2006; Miller & Huhndorf, 2005; Chang *et al*., 2010). It was also suggested that the peridial frame is more phylogenetically informative than ascospore morphology and substrate association in the *Sordariales* (Miller & Huhndorf, 2005; Kruys *et al*., 2015). This suggestion provided proof for groups of both *Podospora* and *Cercophora* species with similar four-layered, pseudobombardioid (with a non-stromatic, gelatinous layer) peridia being nested together in two well supported clades.

Lasiosphaeria, another genus closely related to *Cercophora*, was accepted by Lundqvist (1972), but regarded as hardly separable from the latter based on morphological characteristics. He assigned to *Lasiosphaeria* only lignicolous or herbicolous species with pale, cylindric-sigmoidal or cylindric-geniculate ascospores, rarely swelling at the apical part and not developing a dark pigmented head.

For many subsequent years *Lasiosphaeria* was conceived in a broad sense as a heterogeneous genus including species with immersed to superficial ascomata, glabrous to tomentose, hairy or setose perithecia, cylindrical but also allantoid, reniform or filiform ascospores with or without gelatinous appendages (Hilber & Hilber, 1979, 2002; Réblová, 1999; Candoussau *et al*., 2001). As in some *Cercophora* species, a phialophora-like asexual morph was also observed in *Lasiosphaeria* (Gams, 1973, 2000; Gams & Holubová-Jechová, 1976; Miller & Huhndorf, 2001, 2004b; Miller *et al*., 2007).

Combined morphological and phylogenetic studies (Miller & Huhndorf, 2004a,b) resulted in a more natural circumscription of *Lasiosphaeria*, which was restricted to accommodate the sole species with tomentose peridial walls and yellow or rarely pinkish orange perithecial contents (Miller & Huhndorf, 2004a). This also led them to accept in *Lasiosphaeria* some fimicolous or lignicolous *Cercophora* species with similar peridial characteristics and contents (Miller & Huhndorf, 2004b). The same studies (Miller & Huhndorf, 2004a, 2004b) excluded some species from *Lasiosphaeria* and transferred them to new or reintroduced genera in the *Lasiosphaeriaceae* or even outside the order *Sordariales*.

Bombardia (Fr.) P. Karst. was related to *Cercophora* by Lundqvist (1972) and conceived almost in the original sense of Fries (1849), i.e. restricted to stromatic lignicolous species with centrum characteristics practically indistinguishable from *Cercophora*. The main differential feature of *Bombardia* was the so-called "bombardioid" peridium, consisting of at least two outer stromatic layers, one of which being gelatinous. The usually coriaceous, multi-layered "pseudo-bombardioid" peridium of other *Lasiosphaeriaceae*, including some *Cercophora* species, has a gelatinous, but non-stromatic second layer (Lundqvist, 1972).

Following the results of some phylogenetic analyses (Miller & Huhndorf, 2005; Kruys *et al*., 2015), I started with a detailed exami-

Key to *Cercophora* species of the complex-*sordarioides*

1) Asci without a subapical plasma globulus. Perithecia less than 600 µm high **2**
1*) Asci with a globulus **3**
2) Perithecial neck with scattered or fasciculate rigid hairs. Exoperidium of a *textura angularis* and *epidermoidea*. Spore head 15–18 × 9–11 µm. Pedicel sigmoidal or bent below, 27–30 × 4–4.5 µm ..... ***Cercophora* sp.**
2*) Neck glabrous. Exoperidium of a *textura angularis*. Spore head 26–32 × 15–18 µm. Pedicel straight-cylindrical, 43–58 × 6–7 µm ..... ***C. recta***
3) Neck hairy or setose **4**
3*) Neck glabrous **5**
4) Perithecia 650–850 × 450–750 µm. Neck 200–220 µm high, with tufts of rigid, fasciculate hairs. Spore head 20–22.5 × 12.5–15 µm. Pedicel 35–37.5 × 6.5 µm ..... ***C. kalimpongensis***
4*) Perithecia 560–625 × 335–480 µm. Neck 190 µm high, with thick-walled rooting setae. Spore head 17–19 × 7–9 µm. Pedicel 24–30 × 4–4.5 µm ..... ***C. muskokensis***
5) Perithecia 500–650 × 335–410 µm. Neck up to 140 × 120 µm. Spore head with a late septum below the middle, 15–22 × 6–10 µm. Pedicel 37–38 × 4–5 µm ..... ***C. sordarioides***
5*) Perithecia larger, up to 950 µm high. Spore head not transversely septate **6**
6) Perithecia long-necked, up to 450 µm. Spore head 22.5–25 × 15–17 µm. Pedicel 25–30 × 4–4.5 µm. Upper cauda shorter than the lower ..... ***C. aligarhiensis***
6*) Neck up to 150 µm high, with basal tubercles. Spore head 17.5–20 × 7.5–8.5 µm. Pedicel 25–30 × 4–5 µm. Caudae equal in size ..... ***C. tuberculata***

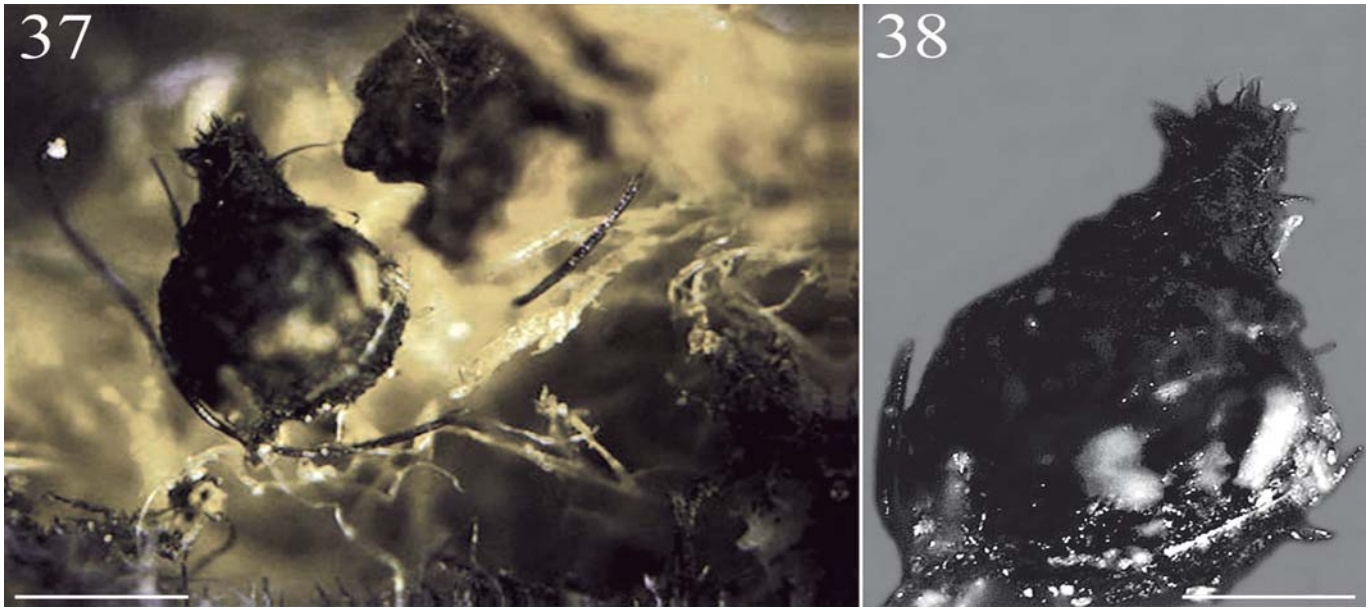

Plate 12 – *Cercophora cephalothecoidea*
37–38. Ascomata. Scale bars: 37 = 300 µm; 38 = 200 µm.

nation of the peridial morphology to define the three *Cercophora* species described in this paper and to compare them with similar taxa both in the same and related genera. My approach was somewhat different from that adopted by others, who subdivided and primarily classified *Cercophora* spp. according to their fimicolous (Lundqvist, 1972) or lignicolous (Hilber & Hilber, 1979) habitat. After Moreau (1947) I found, in fact, that the elephant dung, in comparison with other dungs from herbivores, is poorly homogeneous and abounds in virtually undigested, woody or herbaceous material, on which *Cercophora* species grow immersed or erumpent. Also for this reason I thought it was irrational not to compare my collections of fimicolous *Cercophora* species with lignicolous species even belonging to other genera of the *Lasiosphaeriaceae* with a similar peridial structure. I also remembered that, besides on dung and wood, a few *Cercophora* spp. grow on less common substrates, and that terricolous (Ueda, 1994) and aquatic (Spegazzini, 1880; Kirschstein, 1911; Chaudhary *et al.*, 2007; Crous *et al.*, 2016) species were described, for a total of over eighty taxa (Guarro *et al.*, 2012).

About *Cercophora elephantina* and other species with a pseudo-bombardioid peridium

Cercophora elephantina is characterised by coriaceous perithecia covered with scattered, brownish but hyaline-tipped hairs, a "pseudo-bombardioid" peridium (Lundqvist, 1972) with a gelatinous, non-stromatic layer, asci lacking a subapical plasma globulus, and growth on elephant dung in tropical climates.

Lundqvist (1972) interpreted the gelatinous layer of the pseudo-bombardioid peridium as a pseudoparenchyma of thick-walled cells and described it in seven species of *Lasiosphaeriacae*: three *Cercophora* spp., i.e. *C. albicollis* N. Lundq., *C. elephantina*, *C. scortea* (Cain) N. Lundq.; three *Podospora* spp. all belonging to the type section *Podospora*, i.e. *P. appendiculata* (Auersw. ex Niessl) Niessl, *P. fimiseda*, *P. perplexens* (Cain) Cain; and *Arnium ontariense* (Cain) J.C. Krug & Cain.

The pseudo-bombardioid peridium of *Podospora* spp. with coriaceous perithecia (sect. *Podospora*) was also described in detail by Bell & Mahoney (1997) and interpreted, like Lundqvist (1972), as formed of gelatinised, thick-walled, angular cells.

Miller (2003) reinterpreted and emended the concept of pseudo-bombardioid peridia in the *Lasiosphaeriaceae*. After studying longitudinal sections of perithecia obtained with a freezing microtome, he proved that the gelatinous layer is formed of interwoven, thin-walled hyphae, instead of thick-walled, angular cells, in all the seven species stated to possess a pseudo-bombardioid peridium (Lundqvist, 1972). He also observed a hyphal gelatinous layer in peridia of *C. costaricensis* (G.C. Carroll & Munk) O. Hilber & R. Hilber and in *C. palmicola* Hanlin & Tort., both previously described as pseudo-bombardioid but with a gelatinous layer of thick-walled cells (Hilber & Hilber, 1979; Hanlin & Tortolero, 1987; Hanlin, 1999).

Cercophora costaricensis was also later recorded from Argentina (Del Valle Catania *et al.*, 2011) and the middle layer of its pseudo-bombardioid peridium was described and illustrated as composed of gelatinised hyphae.

Doveri (2015) described some *Podospora* species of sect. *Podospora* from Italy and also accomodated in this section *Podospora lindquistii* García-Zorrón, *P. minipistillata* R.S. Khan & J.C. Krug, *P. minor* Ellis & Everh. and *P. pistillata* Mirza & Cain on the basis of morphological characteristics described in the original diagnoses (Ellis & Everhart, 1897; Mirza & Cain, 1969; García-Zorrón, 1977; Krug & Khan, 1989). He called pseudo-bombardioid the peridium of section *Podospora*, but simply mentioned or misinterpreted the gelatinous layer as shapeless or formed of thick-walled cells. Since then no other new species of *Lasiosphaeriacae* with a pseudo-bombardioid peridium were described (http://www.indexfungorum.org/names/Names.asp, consulted 30.5.2016).

Cercophora elephantina differs from the lignicolous *C. costaricensis* and *C. palmicola* in that it develops scattered or loosely gregarious perithecia on dung, whereas the latter grow densely gregarious or often crowded and tend to form crusts (Carroll & Munk, 1964; Hanlin & Tortolero, 1987). In addition, *C. palmicola* has turbinate (Hanlin & Tortolero, 1987) rather than obovoid or ellipsoid ascomata and *C. costaricensis* has glabrous perithecia and an outer peridial layer with a petaloid (radiating) arrangement of angular cells around dark centres (Hilber *et al.*, 1987; Del Valle Catania *et al.*, 2011).

As for the other two fimicolous *Cercophora* spp. with a pseudo-bombardioid peridium, *C. scortea* is distinguishable from *C. elephantina* by having the outer peridial layer with a *textura epidermoidea*, asci with a subapical globulus, and growth on different types of herbivore dung in nordic or north-temperate areas (Lundqvist, 1972; Moyne & Petit, 2006) while *C. albicollis* differs from *C. elephantina* in that it has glabrous ascomata, a perithecial neck covered with an amorphous whitish material, asci with a plasma globulus, and growth on cattle dung (exceptionally on soil) preferably in temperate climates (Lundqvist, 1972).

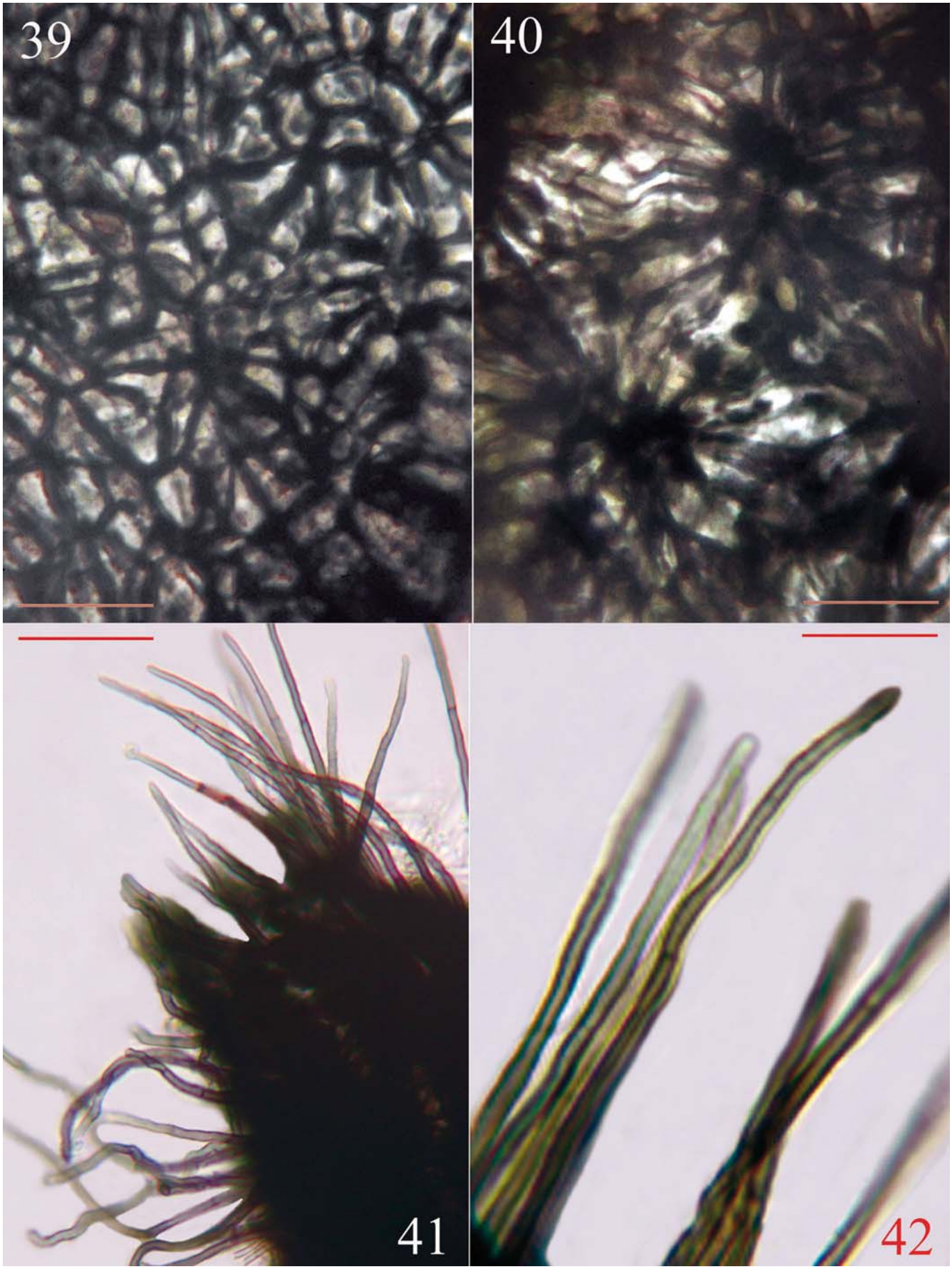

Plate 13 – *Cercophora cephalothecoidea*
39–40. Details of cephalothecoid peridium. 41–42. Neck hairs. Scale bars: 39–40, 42 = 20 µm; 41 = 50 µm.

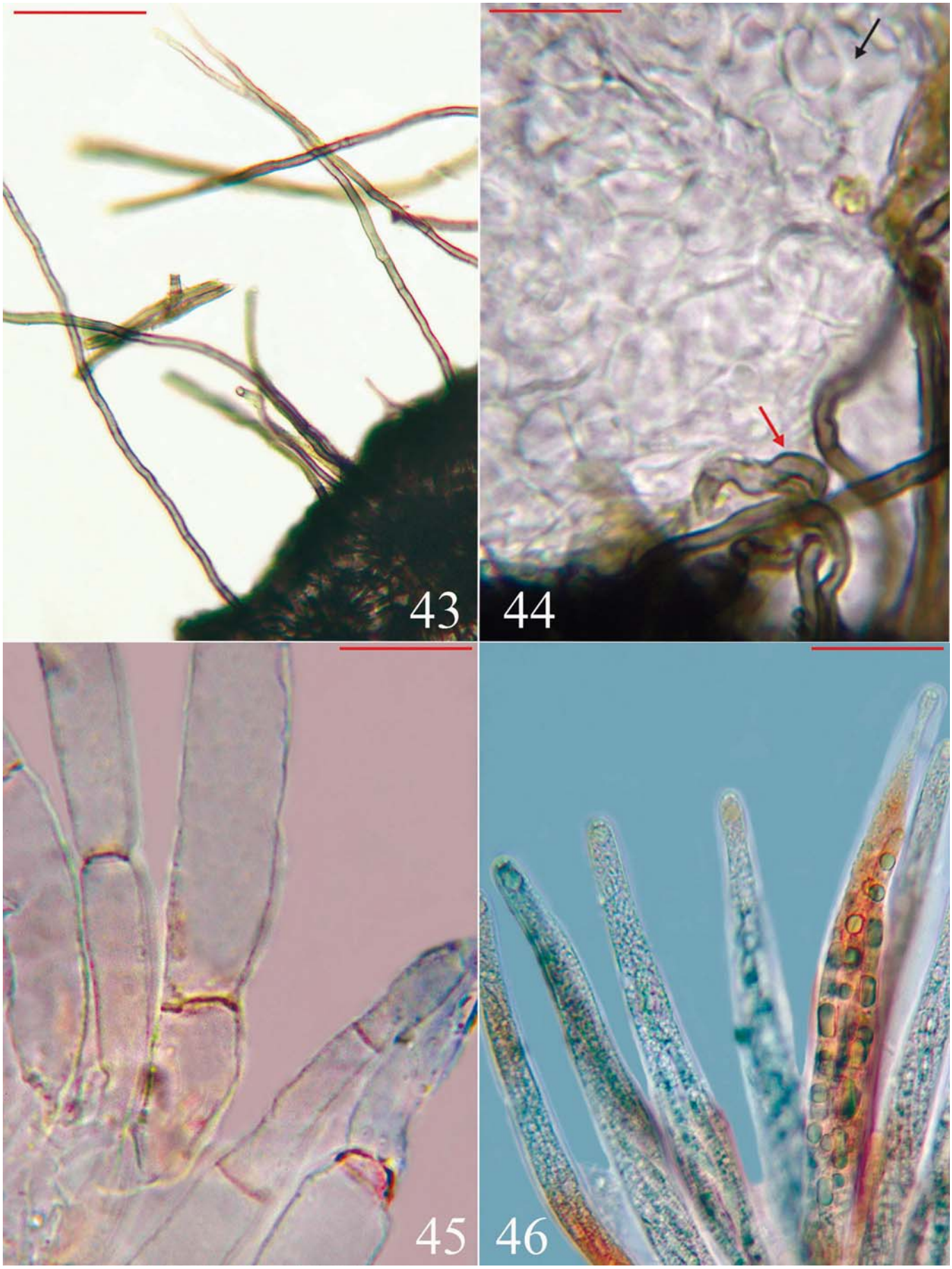

Plate 14 – *Cercophora cephalothecoidea*

43. Peridial hairs. 44. Peridial hairs (red arrow) and endoperidial cells (black arrow). 45. Paraphyses. 46. Immature asci. Scale bars: 43 = 80 µm; 44–45 = 20 µm; 46 = 40 µm.

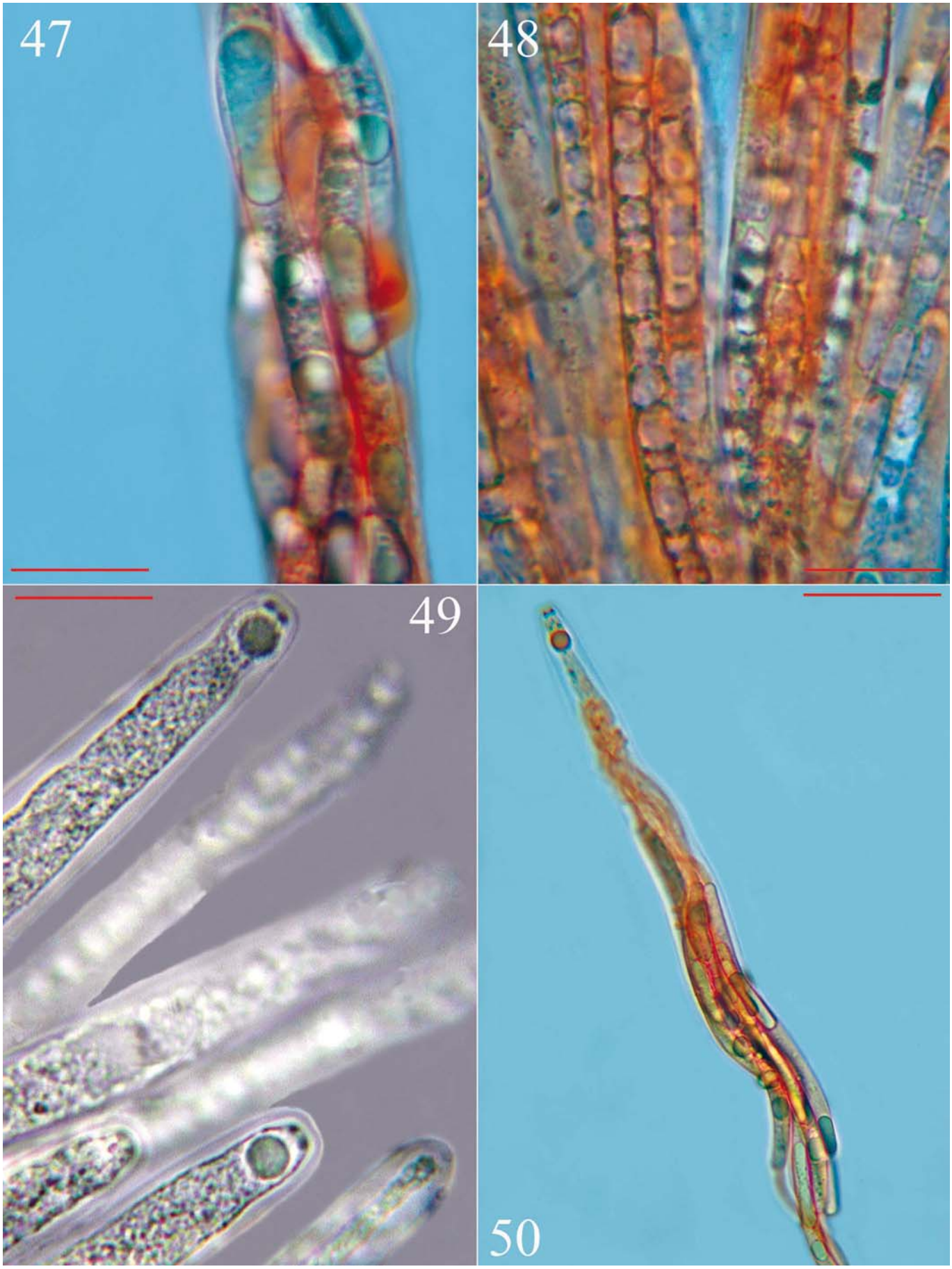

Plate 15 – *Cercophora cephalothecoidea*

47–48. Ascospores inside the asci (Congo red). 49. Apices of asci. 50. Ascus with ascospores (Congo red). Scale bars: 47–49 = 20 µm; 50 = 50 µm.

Plate 16 – *Cercophora cephalothecoidea*
51–52. Ascospores in different stages (Congo red). Scale bars: 51 = 50 µm; 52 = 20 µm.

Key to *Cercophora* species with a carbonaceous peridium

1) Perithecia partly carbonaceous. Outer peridial layer vaguely and/or partly areolate **2**
1*) Perithecia wholly carbonaceous, with an usually striate, furrowed or ridged neck and a distinctly areolate outer peridial layer **9**
2) Perithecia with a white to greyish tomentum disappearing with age. Perithecial neck bare, not longitudinally cracking. Peridium with some carbonaceous splashes, vaguely areolate. Asci with a double apical ring, without a subapical globulus. Spore head 17–25 × 8.5–13 µm. Pedicel 30–50 × 4–5 µm. Mostly on cattle dung ..... ***C. coprophila***
2*) Perithecia not tomentose or with a differently coloured tomentum. Perithecial neck slightly to deeply furrowed or ridged and longitudinally cracking. Peridium partly with larger carbonaceous deposits and usually more distinctly areolate **3**
3) Perithecia brown-tomentose, sometimes covered with a pallid, amorphous substance. Asci with a simple ring, without a globulus. Spore head 17–21 × 8.5–11 µm. Pedicel 35–45 × 3.5–5 µm. On horse dung ..... ***C. aggregata***
3*) Perithecia not tomentose **4**
4) Perithecia glabrous. Asci with a double ring and a plasma globulus. Spore head 22–24 × 9–10 µm, pedicel 24–27 × 5 µm, gelatinous caudae absent. On wood in fresh water Lundqvist's (1972) ..... ***Cercophora* sp. 2**
4*) Perithecia with straight or flexuous brownish hairs. Asci lacking a globulus. Spore gelatinous caudae present **5**
5) Perithecia with violet or bluish tinges. Perithecial neck glabrous. Asci with a double ring **6**
5*) Perithecia without such tinges. Neck sometimes with short, straight, brown hairs. Asci with a simple ring **7**
6) Perithecia sometimes immersed in a dense blue weft. Spore head 14–16 × 7–9 µm. Pedicel 30 × 4 µm. On elephant, horse, cattle, rabbit dung in tropical climates ..... ***C. caerulea***
6*) Perithecia not immersed in a weft. Spore head 14–18 × 7–8.5 µm. Pedicel 24–25.5 × 3.5–4 µm. On horse dung in boreal and temperate areas ..... ***C. septentrionalis***
7) Perithecia 625–960 × 300–580 µm. Spore head 14–18 × 7–9 µm. Pedicel 27–36 × 3 µm. Usually on cervine dung ..... ***C. silvatica***
7*) Perithecia somewhat smaller. Spore head larger. On soil **8**
8) Spore head tuberculate, 21.5–25 × 9–10 µm. Pedicel 22.5–27.5 × 4.5–5 µm ..... ***C. himalayensis***
8*) Spore head smooth, 20–24 × 8–10 µm. Pedicel 22–25 × 5–6 µm ..... ***C. terricola***
9) Perithecia glabrous. Asci lacking a subapical globulus **10**
9*) Perithecia glabrous or variously hairy. Asci with a globulus **14**
10) Perithecia dark purple, on the upper part with a fugacious outer layer of polygonal cells containing a purple substance. Asci with a double apical ring, without a plasma globulus. Spore head 15.5–19 × 8–9 µm. Pedicel 41–50 × 4–5 µm. On partially or entirely submerged wood ..... ***C. vinosa***
10*) Perithecia without such tinges **11**
11) Outer peridial layer indistinctly fuliginous. Spore head 25–28 × 14–15 µm. Pedicel 50 × 5–6 µm. On herbivore dung ..... ***C. crustosa***
11*) Outer peridial layer distinctly areolate. Spore head and pedicel smaller. On wood **12**
12) Asci with a double apical ring. Spore head 15–18.5 × 7–12 µm. Pedicel 23–34 × 4–6 µm. On partially submerged wood ..... ***C. aquatica***
12*) Asci with a simple apical ring **13**
13) Perithecia upon drying with granules or flakes below the neck. Ascospores sigmoidal or bent below, with gelatinous caudae. Spore head 17.5–21.5 × 8.5–13.5 µm. Pedicel 29.5–41 × 4–6 µm ..... ***C. striata***
13*) Perithecia without such features. Ascospores comma-shaped, without gelatinous caudae or sometimes with a faint basal cauda. Spore head 10–14 × 7 µm. Pedicel 8–13 × 3–7 µm ..... ***C. solaris***
14) Perithecial neck glabrous, venter glabrous or with brown hairs. Asci with a double apical ring and an indistinct, sometimes missing subapical globulus. Spore head 14–18 × 6–10 µm, sometimes with a subequatorial septum. Pedicel 25–32 × 3–5 µm. On horse dung ..... ***C. areolata***
14*) Asci with a simple ring and a distinct globulus. Spore head larger **15**
15) Perithecia 650–800 × 450–500 µm, with a distinctly dark-hairy neck and venter. Spore head 24–27 × 11–12 µm, with a supra-equatorial septum. Pedicel 47–62 × 5.5–6 µm. On elephant dung ..... ***C. cephalothecoidea***
15*) Perithecia larger, 850–1000 × 600–900 µm, glabrous or with a different hairy vestiture **16**
16) Perithecia with a glabrous neck. Perithecial venter glabrous or with brown hairs. Spore head (25–) 30–35 × (11–) 14–16 µm. Pedicel 60–70 × 6–10 µm. On cow dung ..... ***C. californica***
16*) Perithecia glabrous all over. Spore head 20–25 × 8–11 µm. Pedicel 18–36 × 3.5–4.5 µm. On wood ..... ***C. macrocarpa***

Three species, at least, of *Podospora* sect. *Podospora*, the extensively studied *P. appendiculata*, *P. fimiseda* and *P. perplexens* (Lundqvist, 1972; Bell & Mahoney, 1997; Doveri, 2015), share most morphological and physiological characteristics with *C. elephantina*, i.e. a pseudobombardioid peridium, ellipsoid or ovoid perithecia (only in *P. appendiculata*), hyaline-tipped peridial hairs, asci with an apical ring, ascospores able to germinate when still at the hyaline stage, and growth on dung. The differences, however, are manifest since the hyaline young ascospores are clavate in section *Podospora*, the spore head is much larger and consistently dark pigmented at maturity, and the spore gelatinous caudae have a much more complex structure.

Arnium ontariense is macroscopically very similar to *C. elephantina* in that it has ovate-conical, coriaceous perithecia (Cain, 1934; Krug & Cain, 1972) with hyaline-tipped hairs and growth on dung (Lundqvist, 1974), but it is distinguishable by having fusiform, 500/600-spored asci, and dark brown, ellipsoidal ascospores lacking a pedicel and with two long polar gelatinous caudae.

Cercophora elephantina was always recorded from elephant dung, the original description (Hennings, 1895) from Cameroon (West Central Africa), and subsequent African collections from Cameroon (Moreau, 1947, 1953, as *Bombardia coprophila*) and Tanzania (Khan & Krug, 1994). Petch (1922) described *Sordaria pilosa* on Indian elephant dung from Ceylon (today's Sri Lanka) a taxon regarded by Lundqvist (1972) as conspecific to *C. elephantina*. I do not know further records worldwide except for mine on elephant dung from Kerala, an Indian state very close to Sri Lanka. I had studied before (1996, unpublished data) another collection from Sri Lanka, which Lundqvist (pers. comm.) compared with the type material (Hennings, 1895) deposited in the Swedish Museum of Natural History, and confirmed as *C. elephantina*. Petch's (1922) Asian collection and part of mine have somewhat smaller perithecia (500 × 300 µm or less)

than the African collections, and also the spore heads of mine are somewhat smaller on average and remain unpigmented, but these must be considered mere ecological variants.

About *Cercophora* sp. of the "complex *sordarioides*"

The species I describe as *Cercophora* sp., in what I call "complex *sordarioides*", is characterised by a hairy, quite long neck, a membraneous, semitransparent peridium with an outer layer of angular or irregular cells (*textura mixta, angularis* and *epidermoidea*), asci lacking a subapical globulus and growth on elephant dung in a tropical climate. The study of this taxon, like that of *C. elephantina*, started from a detailed examination of the peridial morphology, moving later to the ascal characteristics and habitat. My comparative analysis was based on Hilber & Hilber (1979) for lignicolous *Cercophora* species and Lundqvist (1972) and Doveri (2004) for fimicolous species, taking also into account all new taxa published after these works. The survey allowed me to circumscribe a group of fimicolous *Cercophora* species that I have chosen to call "complex *sordarioides*", characterised by obpyriform perithecia with a well differentiated conical to cylindrical neck, a membranous, often semitransparent peridium with an outer layer of thin-walled angular cells, covered with pale hyphoid hairs or glabrous, and growth on dung. The other features, such as glabrous or hairy or even setose perithecial necks, presence or absence of an ascal plasma globulus, and size of ascospores, are quite variable from species to species and sometimes in the same species. In this group are included, in my opinion, *C. sordarioides* (Speg.) N. Lundq., the oldest taxon, which several authors of subsequent new species referred to, *C. aligarhiensis* Mukerji, R.N. Kumar & N. Singh, *C. kalimpongensis* Mukerji, R.N. Kumar & N. Singh, *C. muskokensis* (Cain) N. Lundq., *C. recta* A. Bell & D.P. Mahoney, and *C. tuberculata* Mukerji, R.N. Kumar & N. Singh.

My *Cercophora* sp. and *C. recta* are the only two species of the group without a subapical globulus and *C. recta* is also distinguished from all the others in that it has straight-cylindrical ascospores clustered in the middle portion of the ascus, and significantly larger spore heads and pedicels. *C. recta* was originally described (Bell, 2005) with an exoperidial *textura prismatica*, possibly due to a misprint, as the annexed drawing shows a *textura angularis*.

Cercophora aligarhiensis, *C. kalimpongensis* and *C. tuberculata* have the largest perithecia (more than 600 µm high) and *C. aligarhiensis* also differs from *Cercophora* sp. in its longer perithecial neck (up to 450 µm), larger spore heads, and upper gelatinous caudae shorter than the lower; *C. tuberculata* differs in having bare necks with basal tubercles, and *C. kalimpongensis*, which shares tufts of rigid, dark, agglutinated neck hairs with my *Cercophora* sp., but is distinguished by its larger ascospores (Mukerji *et al*., 1995).

Cercophora muskokensis is easily identifiable for having aseptate, thick-walled, rooting setae on the neck (Cain, 1934; Lundqvist, 1972; Chang & Wang, 2005), whereas *C. sordarioides* differs from *Cercophora* sp. in that it has almost glabrous necks and spore heads developing a late subequatorial septum (Lundqvist, 1972; Mukerji *et al*., 1995).

Despite my *Cercophora* sp. having a unique combination of characters, I have not established a new taxon since this group is quite confused in my opinion. Several species were not extensively described, so a combined morphological and molecular revision of the complex is required, based on type materials when available. Furthermore the description of my *Cercophora* sp., as that of most species in the group, is solely based on morphological characteristics of naturally developed specimens. It is very difficult, in fact, to develop *Cercophora* spp. in damp chamber cultures because of their slow growth on dung, where the fast-growing species excel in a ruthless competition. It is also difficult to isolate fimicolous *Cercophora* spp. in pure culture, due to the almost inevitable sampling contamination and exploitation of the culture medium by faster growing species. All my attempts to isolate collections of new or rare *Cercophora* spp. in axenic culture were unsuccessful, as were those of Del Valle Catania *et al.* (2011). Difficulties were also encountered by Candoussau *et al*. (2001) when they attempted to isolate species of *Lasiosphaeria*, since the ascospores of that genus, like those of *Cercophora*, "germinate slowly and, before this happens, the culture is already contaminated" (Réblová, in litt.).

About *Cercophora cephalothecoidea* and related species with a carbonaceous peridium

Cercophora cephalothecoidea is characterised by entirely dark-hairy, carbonaceous perithecia, an areolate, cephalothecoid peridium, asci with a subapical globulus, fairly large ascospores with a transversely septate, unpigmented head, and growth on dung.

Several stages of carbonisation are known in *Cercophora* and related genera (Lundqvist, 1972), ranging from sparse splashes, as in *C. coprophila* (Fr.) N. Lundq., or larger but partial amounts [*C. aggregata* N. Lundq., *C. caerulea* (Petch) N. Lundq., *C. himalayensis* Udagawa & Y. Sugiy., *C. septentrionalis* N. Lundq., *C. silvatica* N. Lundq., *C. terricola* S. Ueda, and Lundqvist's (1972) *Cercophora* sp. 2], to massive deposits [*C. aquatica* P. Chaudhary, J. Fourn. & A.N. Mill., *C. areolata* N. Lundq., *C. californica* (Plow.) N. Lundq., *C. cephalothecoidea*, *C. crustosa* (Massee) P. Chaudhary, J. Fourn. & A.N. Mill., *C. macrocarpa* (G.C. Carroll & Munk) O. Hilber & R. Hilber, *C. solaris* (Cooke & Ellis) R. Hilber & O. Hilber, *C. striata* (Ellis & Everh.) N. Lundq., *C. vinosa* A.N. Mill. & J. Fourn.], affecting the consistency of perithecia. The carbonisation is usually associated with a particular morphology of exoperidium commonly known as "areolate". In scarcely or partially carbonaceous peridia, the areolas are sometimes indistinct and formed of usually polygonal cells, radiating from a dark centre. In coarsely, entirely carbonaceous peridia, the areolas are usually distinct and often appear as plates of radiating, very thick-walled, short-cylindrical cells, which form a scleroplectenchymatous *textura prismatica* (Chaudhary *et al*., 2007, Del Valle Catania *et al*., 2011). A so structured peridium is not uncommon in *Lasiosphaeriaceae*, particularly occurring in the cleistocarpic genera *Chaetomidium* (Zopf) Sacc. (Doveri *et al.*, 1998) and *Zopfiella* G. Winter (Guarro *et al*., 1996), and outside *Sordariales* in *Cephalotheca* Fuckel, hence the alternative name *textura cephalothecoidea* given to this type of tissue. According to Lundqvist (1972) the occurrence of a cephalothecoid peridium in perithecial ascomata represents an advanced evolutionary stage resulting in the cleistocarpy. Cleistothecia with a cephalothecoid peridium dehisce, in fact, by detachment of the plates along certain lines of suture.

Five out of the nine *Cercophora* species with a completely carbonaceous and usually distinctly areolate peridium are lignicolous (*C. aquatica*, *C. macrocarpa*, *C. solaris*, *C. striata*, *C. vinosa*), more precisely *C. aquatica* and *C. vinosa* were isolated from wood partially or entirely submerged in fresh water (Chaudhary *et al*., 2007; Crous *et al*., 2016). All those stand quite distant from *C. cephalothecoidea* as they have a glabrous peridial venter, asci lacking a subapical globulus (except for *C. macrocarpa*), and smaller spore heads and pedicels. *C. aquatica* also differs from *C. cephalothecoidea* in that it has a subiculum, a scleroplectenchyma of polygonal rather than short-cylindrical cells, and asci with a double apical ring (Chaudhary *et al*., 2007), whereas *C. solaris* is further distinguishable by having a subiculum and comma-shaped ascospores (Del Valle Catania *et al*., 2011), and *C. striata* perithecia covered with white granules or flakes below the neck (Miller & Huhndorf, 2001). *C. macrocarpa* has larger perithecia with a deeply furrowed neck and a star-like ostiole (Carroll & Munk, 1964; Hilber & Hilber, 1979). *C. vinosa* has purple perithecia and asci with a double apical ring (Crous *et al.*, 2016).

The remaining three species with entirely carbonaceous perithecia are fimicolous. All those differ from *C. cephalothecoidea* in that they possess glabrous perithecial necks. *C. crustosa* further differs in having a glabrous venter, an indistinctly fuliginous peridial textura, and asci without a plasma globulus (Massee, 1910; Chaudhary *et al.*, 2007) and *C. areolata* in having an almost glabrous perithecial venter, asci with a double apical ring and an indistinct plasma globulus, smaller ascospores, and typically grows on horse dung in nordic areas (Lundqvist, 1972; Udagawa & Muroi, 1979). *C. californica* [= *C. coprogena* (Speg.) N. Lundq.] stands very close to *C. cephalo-*

thecoidea, with which it shares a perithecial venter with brown hairs (Bell, 2005) and asci with a globulus, but is distinguished by a glabrous neck, its somewhat larger ascomata, asci and ascospores, and its growth on cattle dung in temperate climates (Plowright, 1878; Del Valle Catania *et al*., 2011).

I was not able to develop *C. cephalothecoidea* in a damp chamber nor to isolate it in axenic cultures. I can state, however, that the whole of its macro- and microscopic features is so different from the other *Cercophora* spp. with a cephalothecoid peridium that I have decided to establish *C. cephalothecoidea* as a new species, based only on its morphology.

New combinations

Cercophora mutabilis (Cailleux) Doveri, *comb. nov.* – MB817708
Basionym: *Bombardia mutabilis* Cailleux, *Bull. Soc. mycol. Fr.*, 87: 623 (1971).

Cercophora rostrata (Cailleux) Doveri, *comb. nov.* – MB817709
Basionym: *Bombardia rostrata* Cailleux, *Bull. Soc. mycol. Fr.*, 87: 623 (1971).

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