

New lichenicolous, muscicolous, corticolous and lignicolous taxa of *Burgoa* s. l. and *Marchandiomyces* s. l. (anamorphic Basidiomycota), a new genus for *Omphalina foliacea*, and a catalogue and a key to the non-lichenized, bulbiferous basidiomycetes

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Abstract A catalogue and a key to the non-lichenized, bulbiferous basidiomycetes are given. The new genus *Burgella* is described for the lichenicolous *B. flavoparmeliae*, phylogenetically close to *Sistotrema oblongisporum* and *Multiclavula*. The genera *Pneumatospora* and *Tricellulortus* are placed in synonymy of *Minimedusa*, the new combination *M. obcoronata* is proposed, and the new facultative lichenicolous *M. pubescens* is described. The new facultative lichenicolous *Burgoa angulosa* is phylogenetically close to the generic type *B. verzuoliana*, whilst the new *B. moriformis* and *B. splendens* are provisionally included in the genus *Burgoa*. A *Burgoa*-like species in the Ceratobasidiaceae is left unnamed. Two new species of *March-*

andiomyces, *M. buckii* and *M. nothofagicola*, are described. As *Marchandiomyces aurantiacus* is phylogenetically more close to *Erythricium* than to *Marchandiomyces*, it is proposed to exclude it from that genus and to use the holomorphic generic name *Marchandiobasidium* for both anamorph and teleomorph of this species. The new genus *Marchandiomphalina* is introduced for the lichenized *Omphalina foliacea*, a taxon phylogenetically close to *Marchandiobasidium*.

Keywords Bulbils · Cantharellales · *Minimedusa* · Sclerotia · *Sistotrema*

Taxonomic novelties

Burgella Diederich & Lawrey; *B. flavoparmeliae* Diederich & Lawrey; *Burgoa angulosa* Diederich, Lawrey & Etayo; *B. moriformis* Diederich, Ertz & Coppins; *B. splendens* Diederich & Coppins; *Marchandiomphalina* Diederich, Lawrey & Binder; *Marchandiomphalina foliacea* (P. M. Jørg.) Diederich, Lawrey & Binder; *Marchandiomyces buckii* Diederich & Lawrey; *M. nothofagicola* Diederich & Lawrey; *Minimedusa pubescens* Diederich, Lawrey & Heylen; *M. obcoronata* (B. Sutton, Kuthub. & Muid) Diederich & Lawrey

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Introduction

Most lichenicolous fungi belong to the ascomycetes or heterobasidiomycetes, and only a few lichenicolous homobasidiomycetes are known. These include agarics belonging to the genera *Arrhenia* and *Fayodia*, and sclerotial fungi belonging to *Athelia*, *Leucogyrophana* and *Marchandiomyces* (Lawrey and Diederich 2003). Sclerotia are frequently regarded as being of several types, including true sclerotia, pseudosclerotia and bulbils (Cléménçon et al. 2004). True sclerotia are known from the lichenicolous *Athelia arachnoidea* and *Leucogyrophana lichenicola*, and bulbils from the lichenicolous *Marchandiomyces aurantiacus* and *M. corallinus*.

Hotson (1912, 1917) presented a survey of all known bulbiferous fungi, mainly described in the genus *Papulaspora* (= *Papulospora*), and in his key he grouped those with basidiomycetous affinities, i.e. either presenting clamps or producing basidia in culture. These basidiomy-

cetous, bulbiferous fungi were later accommodated in the new genus *Burgoa* (Goidánich 1938), whilst most other species with ascomycetous affinities were left in *Papulaspora*. Weresub and LeClair (1971) gave a thorough review of the different definitions of bulbils and papulasporae (= papulosporae), and the authors concluded that the term bulbil should be restricted to basidiomycetes, and papulasporae to ascomycetes. They further described the new genus *Minimedusa* for a species with basidiomycetous affinities, in which bulbils develop from a multithyphal base. As *Sistotrema*-like basidia have occasionally been observed in cultures of *Burgoa* species (e.g., Weresub and LeClair 1971), and *Burgoa*-like bulbils were encountered in some *Sistotrema* specimens or cultures (Cléménçon et al. 2004; Eriksson et al. 1984; Hallenberg 1984), it is generally assumed that *Burgoa* is the anamorphic state of *Sistotrema*.

During the past 20 years, we regularly collected or received material of fungi overgrowing corticolous cryptogams (lichens or mosses) or growing directly over bark or lignum, with bulbils resembling *Marchandiomyces* species, but pale colored (whitish to brownish, yellowish or pale orange). Morphological and anatomical studies revealed the existence of at least six apparently undescribed species, amongst which we were able to grow four in pure culture, some of them from up to 5-year-old herbarium specimens. DNA sequences were obtained from these four cultured species, and from one additional species by direct PCR. Phylogenetic analyses suggest that the five species belong to the Cantharellales (Binder et al. 2005, as “cantharelloid clade”), and most of them group with species of *Sistotrema*. We were also able to get DNA sequences of the type cultures of the type species of *Burgoa* and *Minimedusa*, and we found that several of our new species group with them.

Furthermore, we had the opportunity to study, culture and sequence *Marchandiomyces* specimens belonging to undescribed species. Finally, our phylogenetic results suggested that *Omphalina foliacea* is closely related to *Marchandiomyces* s. l.

The phylogenetic results will be published in a separate paper that will include almost all lichenicolous species forming sclerotia or bulbils, a selection of other bulbiferous species, and a selection of lichenized basidiomycetes (Lawrey et al. 2007). A summary tree of these results is given in Fig. 1.

The aim of the present taxonomic paper is to formally describe the new, lichenicolous, muscicolous, corticolous and lignicolous bulbiferous species studied by us, to describe a new genus for *Omphalina foliacea*, to give a catalogue of all known non-lichenized, bulbiferous basidiomycetes, and a key allowing their identification. Although all these new species lack both teleomorphic and anamorphic stages, it is important to formally name them, as they are important in corticolous or lignicolous crypto-

gamie communities, frequently overgrowing or killing other cryptogams, and as they are particularly interesting in phylogenetic and evolutionary studies.

Materials and methods

Specimens from the herbaria BR, E, GMUF, MA, NMW, NY, STU and UPS, and from the private collections of A. Aptroot, M. Cole, P. Diederich, J. Etayo, O. Heylen-Walraevens, B. Schultheis and P. van den Boom, were examined.

Dry herbarium specimens were examined and measured under a binocular microscope Leica MZ 7.5 (magnification up to 50×) and photographed using a Nikon Coolpix 4500. Entire unsectioned bulbils were studied in water, 5% KOH, or lactophenol cotton blue (LCB), either without or with pressure on the coverslip. Microscopic drawings were done using a drawing tube, and photographs of bulbils in LCB were prepared using a Zeiss Photomikroskop III with a Canon PowerShot G5.

Results

New lichenicolous, muscicolous, corticolous and lignicolous taxa of *Burgoa* s. l. and *Marchandiomyces* s. l.

Burgella Diederich & Lawrey, gen. nov.

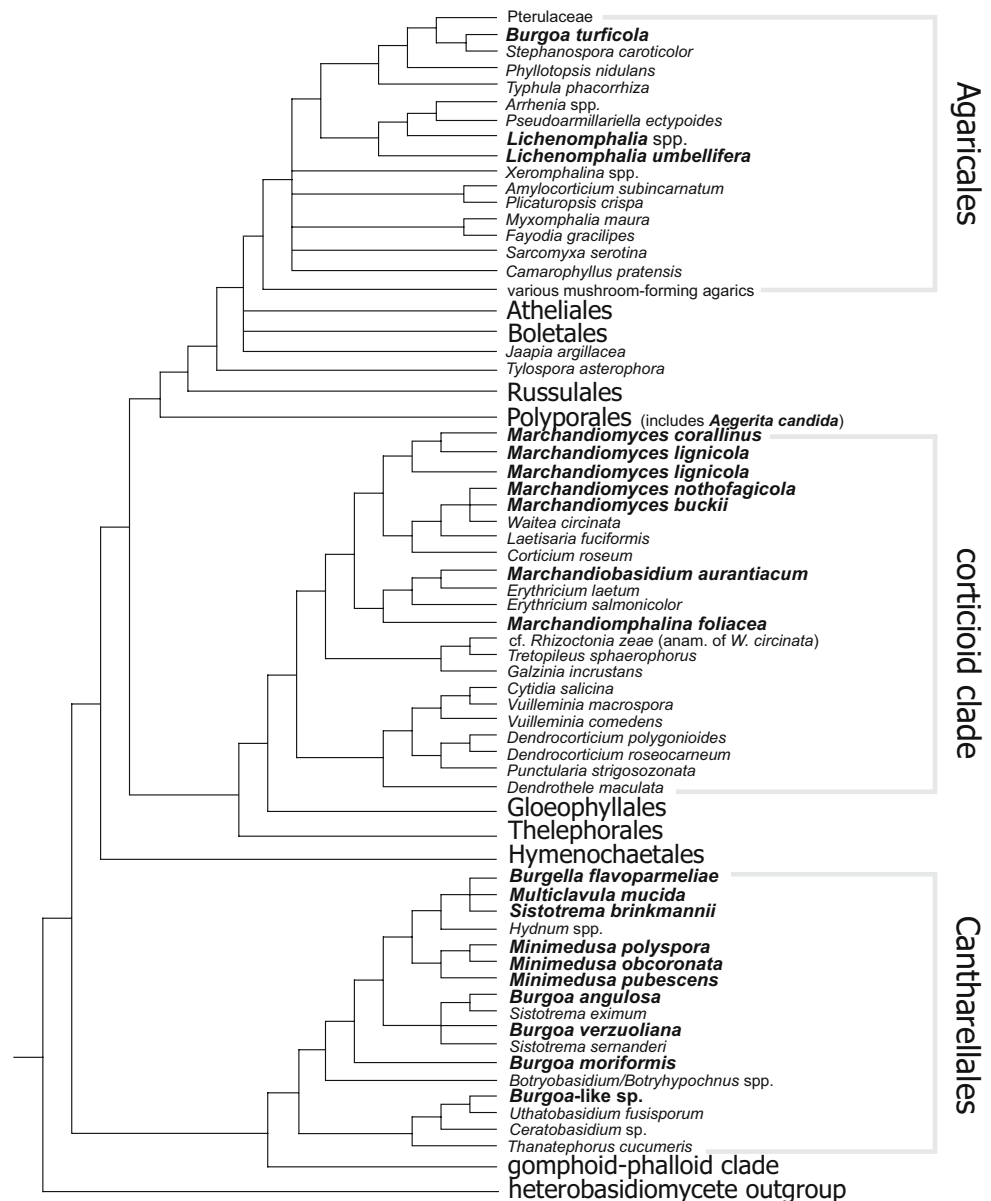
Fungus anamorphicus bulbiferus lichenicola superficialibus vel parve immersis, melleis, subsphaericis ad ellipsoideis vel irregularibus, glabris, cellulis subsphaericis adhaerentibus; in cultura bulbiferus agglomeratis gelatinosis coralloformibus, septis fibulatis.

Type: *Burgella flavoparmeliae* Diederich & Lawrey.

Colonies appearing as dispersed or rarely agglomerate bulbils. *Bulbils* honey-colored, ±shiny, without hairs, roundish to shortly ellipsoid or irregular in form, partly immersed to superficial, externally without specialized cells, cells in surface view polyhedral, internally of strongly adherent, more or less roundish to ellipsoid or polyhedral cells separating only with difficulty; clamps not observed. *Colonies in liquid culture* showing abundant white aerial hyphae, from which orange agglomerations of bulbils arise. *Hyphae* hyaline, septate, straight, rarely branched or anastomosed; *septa* with or without clamp connections. *Agglomerations of bulbils* gelatinous in appearance, almost coralloid, composed of irregularly shaped bulbils; *bulbils* externally and internally composed of irregular, roundish or elongate cells with clamped septa.

Following Lawrey et al. (2007), *Burgella flavoparmeliae* belongs to the subclade of the Cantharellales containing the Clavulinaceae. These results place *B. flavoparmeliae* and

Fig. 1 Phylogenetic relationships of lichenized, lichenicolous, and bulbiferous fungi discussed in the text. A truncated version of a tree from Lawrey et al. (2007) inferred from multi-gene data using Bayesian analyses. Focal species are highlighted in **bold**



Sistotrema oblongisporum as the sister group of the genus *Multiclavula*. *B. flavoparmeliae* is only distantly related to the type of the genus *Burgoa* that appears in a different place in the Cantharellales, close to *Sistotrema eximum* and *S. sernanderi*. This suggests that *B. flavoparmeliae* should not be included in *Burgoa*, and the description of a new genus becomes necessary.

The new genus *Burgella* differs from *Burgoa* and *Minimedusa* by a combination of several minor characters. Bulbils of *B. flavoparmeliae* are clearly lichenicolous, possibly host specific, often slightly immersed in the host thallus, leaving distinct scars when removed. Bulbils of *Burgoa* and *Minimedusa* species are not or facultative lichenicolous, never host specific, and never distinctly immersed in the host thallus. Cultures of *B. flavoparmeliae* produce gelatinous,

almost coralloid agglomerations of irregularly shaped bulbils, which are distinct from the dispersed, more regular, free-living bulbils of *Burgoa* and *Minimedusa* species.

Sistotrema oblongisporum and *S. brinkmannii*, two species closely related to *B. flavoparmeliae* (Lawrey et al. 2007), were reported to produce bulbils (Hallenberg 1984: 404), but the author did not give any description, illustration or reference. Weresub and LeClair (1971) illustrated bulbils of *S. brinkmannii*. However, they considered this name to represent the teleomorph of *Burgoa verzuoliana*, a taxon only distantly related to *S. brinkmannii* (Lawrey et al. 2007), and therefore the genuine identity of their *Sistotrema* species is not certain.

The name *Burgella* represents a contraction of *Burgoa* and the diminutive suffix *-ella*.

Burgella flavoparmeliae Diederich & Lawrey,
sp. nov. Fig. 2a–h

Fungus bulbillis lichenicola superficialibus vel parve immersis, melleis, subsphaericis ad ellipsoideis vel irregularibus, glabris, 60–100 μm diam., cellulis subsphaericis adhaerentibus 6–12 μm diam.; in cultura bulbillis agglomeratis gelatinosis coralliformibus ad 1 cm diam., cellulis subsphaericis ad elongatis 6–17 \times 4–9 μm , septis fibulatis.

Type: U.S.A., Missouri, Wayne Co., Sam A. Bakker State Park, Shut-Ins Trail, 37°15'42"N, 90°30'28"W, T.30N., R.5E., sec. 20, 21, c. 125 m, floodplain forest along Big Creek with dolomite ledges and rhyolite bluffs, on *Flavoparmelia baltimorensis*, 15 Oct. 2003, *W. R. Buck* 45360 (NY–holotype; herb. Diederich–isotype). ATCC MYA-2157.

Basidiomata and *conidiomata* unknown. Colonies appearing as dispersed or rarely agglomerate bulbils overgrowing lichen thalli. Mycelium not observed. Bulbils slightly immersed in the host thallus to superficial, dispersed, yellow to ochraceous or orange (honey-colored), \pm shiny, without hairs, roundish to shortly ellipsoid or rarely irregular in form, 60–110 μm diam.; bulbils externally without specialized cells, cells in surface view polyhedral, smooth 6–12 μm diam.; bulbils internally composed of strongly adherent, more or less roundish to ellipsoid or polyhedral cells separating only with difficulty, 6–12 μm diam., clamps not observed; agglomerations of small crystals visible in polarized light present on the surface of all specimens examined.

Colonies in liquid culture showing abundant white aerial hyphae, from which orange agglomerations of bulbils arise. Hyphae hyaline, septate, straight, rarely branched or anastomosed, 2–3.5 μm thick; septa with or without clamp connections (both situations present on the same hyphae at neighbouring septa); dolipores visible by light microscope. Agglomerations of bulbils up to 1 cm diam., almost as tall as wide, greyish orange (Kornerup and Wanscher 1984: 5B6), gelatinous in appearance, almost coralloid, composed of irregularly shaped bulbils of 150–300 μm ; bulbils externally and internally composed of irregular, roundish or elongate cells with clamped septa, some with a pale orange content, 6–17 \times 4–9 μm .

Distribution and ecology. The species has been collected three times in the U.S.A., where it grows on the thallus of *Flavoparmelia baltimorensis*. Bulbils are frequently slightly immersed in the host thallus, with the host cortex sometimes a little raised around them, and some leave distinct holes in the cortex when removed. The colonies either develop inside the host thallus or over it, with the ability of young bulbils to become slightly immersed. This way of development is reminiscent of that of *Marchandiomyces corallinus* and indicates that the species is

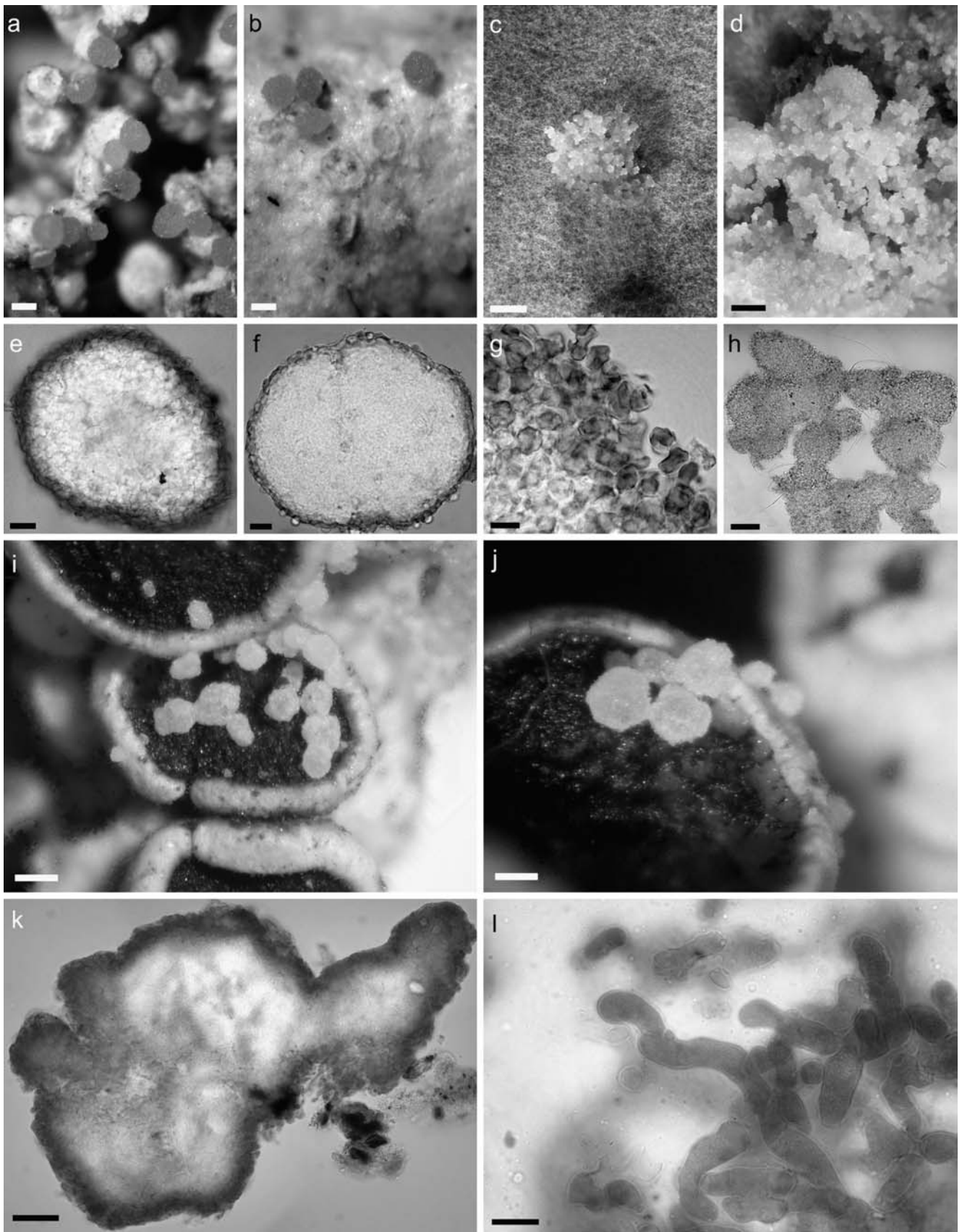
Fig. 2 *Burgella flavoparmeliae*: **a** Bulbils on the thallus of *Flavoparmelia baltimorensis*. **b** Id., bulbils leaving distinct scars on the host thallus when removed. **c** Culture with young agglomeration of bulbils. **d** Culture with mature agglomeration of bulbils. **e** Bulbil in surface view. **f** Bulbil in optical section. **g** Squash preparation of bulbil. **h** Agglomerated bulbils from culture. Scales: 100 μm (a–b, h), 1 mm (c–d), 20 μm (e–f), 10 μm (g). Holotype (a–b); culture ATCC MYA-2157 from *Buck* 38682 (c–d, h), *Buck* 30461 (e, g), *Buck* 38682 (f). – *Burgoa angulosa* (holotype): **i** Bulbils on apothecia of *Physcia aipolia*. **j** Id., bulbils leaving indistinct scars in the host epihymenium when removed. **k** Bulbil in optical section. **l** Squash preparation of bulbil. Scales: 200 μm (i), 100 μm (j), 50 μm (k), 10 μm (l)

probably an obligate lichenicolous fungus, possibly confined to *Flavoparmelia baltimorensis*.

Observations. This is the only species studied by us with yellowish to orange bulbils. When lichenicolous bulbils are examined in lactophenol cotton blue, large orange-colored oil drops emerge from some of them. They are obviously responsible for the yellow orange color of the bulbils, as all cells have a colorless wall. Bulbils of all known specimens are externally covered by dispersed aggregations of small crystals, best visible in polarized light. As such crystals have not been observed inside the bulbils, it is not clear if they are formed by the fungus, or if they originate from the host thallus. Unlike several *Burgoa*-like species studied by us (e.g., *Burgoa angulosa*, *Minimedusa pubescens*), bulbils of *Burgella flavoparmeliae* do not appear to reproduce by budding.

In liquid culture, bulbils do not develop individually, but in large agglomerations. Microscopically, they are not composed of roundish to polyhedral compact structures, but as loosely aggregated roundish to elongate cells separating upon a light pressure. This different morphological and anatomical appearance of bulbils is interpreted here as a response to different nutritional conditions.

Because of the yellowish to orange color of the bulbils, this species has to be compared with *Burgoa aurantiaca*. As that species was described from culture, and as we did not have the opportunity to study any material, we have to compare our *Burgella flavoparmeliae* culture with the description given by Hotson (1917). *Burgoa aurantiaca* often produces agglomerated, but nevertheless distinct bulbils, whilst in cultures of *Burgella flavoparmeliae*, no individual bulbils appear. Bulbils in *Burgoa aurantiaca* develop very slowly, usually taking several months before they mature. Bulbil agglomerates of *Burgella flavoparmeliae* develop more quickly, often in less than one month. Clamp connections are small, more or less inconspicuous in *Burgoa aurantiaca*, whilst they are large and very conspicuous, although not present on all septa, in the mycelium of *Burgella flavoparmeliae*. Finally, *Burgella flavoparmeliae* is known only as lichenicolous, always on the same host, and therefore possibly obligate lichenicolous, whilst *B. aurantiaca* was collected on bark.



Additional specimens examined: **U.S.A.:** North Carolina, Jackson Co., Cedar Cliff Mountain, along NC 281, 3.6 miles E of NC 107 at Tuckasegee, 35°15'N, 83°05' W, 720–1025 m, on *Flavoparmelia baltimorensis*, Sept. 1996, *Buck* 30461 (NY); Oklahoma, Sequoyah Co., Sallisaw-Brushy Lake State Park, c. 6 miles N of Sallisaw, 35° 32'30"N, 94°49'00"W, *Quercus–Juniperus* forest, on *F. baltimorensis*, Nov. 2000, *Buck* 38682 (NY) (culture: ATCC, MYA-2157).

Burgoa angulosa Diederich, Lawrey & Etayo, sp. nov. (Figs. 2i–l and 3a)

Burgoa species insignis bulbillis superficialibus, albis, irregularibus, rotundis ellipsoideis vel elongatis, superficie saepe angulosa, glabris, 100–250×80–160 µm, interne hyphis elongatis, septatis cellulis 5–30×4.5–11 µm, septis fibulatis.

Type: Spain, Huesca, Panticosa, balneario de Panticosa, in garden, on *Acer*, on *Physcia aipolia*, 11 Oct. 1998, *J. Etayo* 16256 (MA–holotypus). ATCC MYA-1121.

Basidiomata and *conidiomata* unknown. Colonies appearing as dispersed or agglomerate bulbils overgrowing lichen thalli. Mycelium absent in most specimens, but abundant in at least one (*Orange* 12865); septa with clamp connections. *Bulbils* occasionally lichenicolous, superficial, dispersed or in short straight or ramified chains of several bulbils, irregular in form, roundish, ellipsoid or elongate, surface uneven, often slightly to distinctly angular, whitish to slightly translucent, mat, without hairs, 100–250×80–160 µm; *bulbils* externally without specialized cells, cells appearing in surface view as roundish, 6–9 µm diam.; *bulbils* internally composed of elongate, straight or curved, rarely ramified, septate hyphae, 4.5–11 µm thick, individual cells 5–30 µm long, cell wall c. 0.5 µm thick, septa with clamps, crystals absent in most specimens (polarized light), rarely abundant on the surface of the bulbils.

Colonies in liquid culture showing white aerial hyphae; bulbils not observed. *Hyphae* hyaline, septate, straight or curved, frequently branched or anastomosed, 3.5–5 µm thick; *septa* with clamp connections.

Distribution and ecology. This species is widespread in central and western Europe and is known from Belgium, France, Great Britain, Hungary, Luxembourg and Spain. It has been collected over macrolichens (*Leptogium lichenoides*, *Lobarina scrobiculata* and *Physcia aipolia*) and in mixed epiphytic vegetations of granulose lichen thalli (e.g., *Bacidina* sp.), mosses or algae. The species is probably not obligate lichenicolous, but frequently collected by lichenologists, and therefore often observed over or between lichen thalli. Sometimes, it grows over dead bryophytes possibly killed by the fungus.

Observations. *Burgoa angulosa* is characterized by whitish bulbils with an irregular shape and an often angular surface, no specialized external cells, and elongate internal hyphae.

Additional specimens examined: **Belgium:** Matagne-la-Grande, ruisseau des Bruyères, on *Salix*, Jan. 2005, *Ertz* 7579 (BR); **France:** Cantal, W of Murat, S of Puy Mary, 0.3 km NE of Col du Pertus, 2°40.7'E, 45°3.6'N, 1350 m, on *Fagus*, on *Lobarina scrobiculata*, July 1998, *van den Boom* 21190 (hb. van den Boom); **Great Britain:** *Wales:* vice-county (VC) 41 (Glamorgan), Cardiff, Lisvane, by Parc Cefn Onn, on dead patches of *Hypnum andoi* and *Metzgeria fruticulosa* (apparently killing these) on shaded stem of *Corylus* in woodland, Nov. 2000, *Orange* 12865 (NMW); VC 48 (Merioneth), Dolgellau, 100 m NE of Parc, on *Hypnum andoi* over *Fraxinus*, Feb. 2002, *Orange* 13451 (NMW); **Hungary:** Zemplén Mountains, Füzér, castle hill, 500 m, on *Fraxinus*, on sterile *Bacidina* sp., Aug. 1995, *Aptroot* 36120 (hb. Aptroot); **Luxembourg:** N of Esch-sur-Alzette, Lankelz, on *Fraxinus*, Feb. 1989, *Diederich* 9002 (herb. Diederich); **Spain:** Aya, Guipuzcoa, on saxicolous *Leptogium lichenoides*, ±1985, *Etayo* (hb. Diederich).

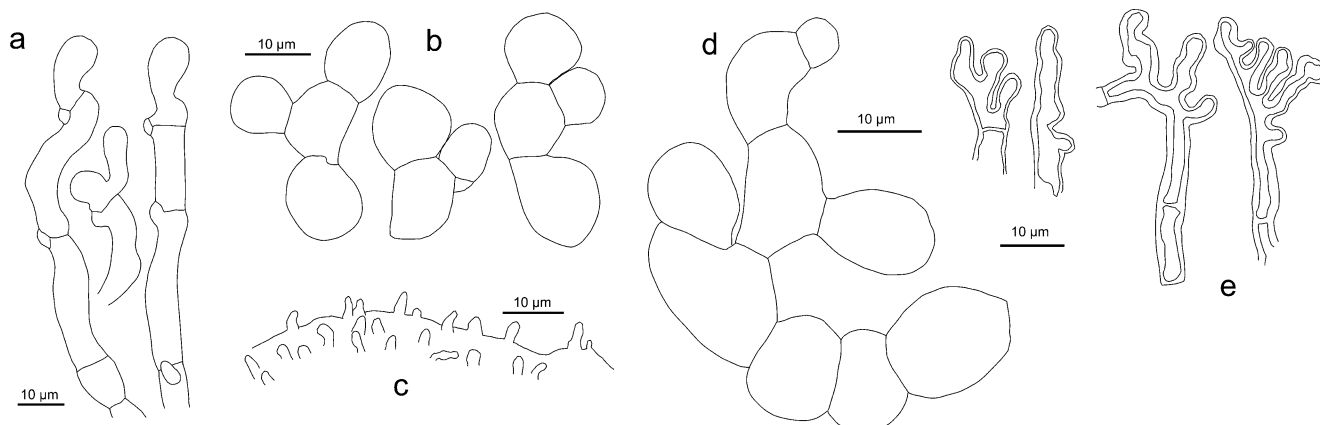


Fig. 3 **a** *Burgoa angulosa* (holotype): internal hyphae of bulbils. **b** *Burgoa moriformis* (holotype): internal hyphae of bulbil. **c** *Burgoa splendens* (holotype): bulbil surface with minuscule hairs. **d** *Burgoa*-

like species of Ceratobasidiaceae (*Diederich* 13475): internal hyphae of bulbil. **e** *Marchandiomyces buckii* (left holotype; right *Buck* 44504): radiating, furcate hyphae inside bulbil

Burgoa moriformis Diederich, Ertz & Coppins,
sp. nov. (Figs. 4a,b and 3b)

Burgoa species insignis bulbillis superficialibus, albis, rotundis ad breviter ellipsoideis, 35–65 µm diam., moriformibus, superficie glabra cellulis inflatis, interne cellulis catenatis subsphaericis ad ellipsoideis 12–18×7–12 µm, septis fibulatis.

Type: Ireland, VC H33 (Fermanagh), Crom, Inisherik, 50 m, over bark between moribund bryophytes and lichens on *Salix*, 12 July 1993, B. J. Coppins 15829 & A. M. O'Dare (E–holotypus; hb. Diederich–isotypus).

Basidiomata and *conidiomata* unknown. *Colonies* developing over bark, several cm diam., appearing as numerous bulbils. *Mycelium* not observed. *Bulbils* superficial, dispersed or indistinctly in short chains or agglomerations of several bulbils, white, with a moriform, slightly shiny surface, without hairs, translucent when dry, roundish to shortly ellipsoid, 35–65 µm diam.; *bulbils externally* moriform, appearing as an agglomeration of hyaline, subspherical, ballooned, smooth cells of 7–12 µm diam.; *bulbils internally* composed of catenate, subspherical to ellipsoid cells of 7–12 µm diam., 12–18 µm long, septa with small, often poorly distinct clamps, crystals absent (polarized light).

Distribution and ecology. The species is known only from the type specimen, collected in Ireland. Bulbils are spread over poorly colonized areas of the bark and are certainly not lichenicolous.

Observations. *Burgoa moriformis* is distinguished from the other species of the genus by the particularly small, white, shiny bulbils composed of ballooned cells, and from *Papulaspora* species by the presence of clamps. No culture was tried as the only specimen is too old and rather small, but a DNA sequence, placing this taxon close to other *Burgoa* species, was obtained by D. Ertz using direct PCR (Lawrey et al. 2007).

Burgoa splendens Diederich & Coppins,
sp. nov. (Figs. 4d–g and 3c)

Burgoa species insignis bulbillis superficialibus, albis, rotundis ad breviter ellipsoideis, 80–140 µm diam., superficie pilis dispersis cylindricis ad conicis aseptatis 1–4×1–2 µm, interne cellulis subsphaericis adhaerentibus 3.5–5.5 µm diam., efibulatis.

Type: Great Britain, Scotland, VC 98 (Argyll Main), 4 km S of Lochgoilhead, Cormonachan Wood, 60 m, on *Quercus*, 11 Sep. 2003, B. J. Coppins & P. Czarnota (E–holotypus; hb. Diederich–isotypus).

Basidiomata and *conidiomata* unknown. *Colonies* developing over poorly colonized areas of the bark, several cm diam., with numerous bulbils. *Mycelium* not observed. *Bulbils* superficial, dispersed or in straight or ramified chains or agglomerations of several bulbils, white or very pale

brownish, with a smooth and shiny surface on which a few minuscule, dispersed hairs are visible at a high magnification, not appearing as translucent (except when very old), roundish to shortly ellipsoid, 80–140 µm diam.; *bulbils externally* with a well-delimited, smooth surface, from which minuscule hair-like cells are protruding, hairs cylindrical to conical, sometimes curved, thin-walled, aseptate, 1–4 µm long, basally 1–2 µm diam.; *bulbils internally* composed of agglomerated, ± roundish, thick-walled cells of 3.5–5.5 µm diam. that do not separate with pressure, septa and clamps not observed, crystals absent (polarized light).

Distribution and ecology. *Burgoa splendens* seems to be widespread in western Scotland and has been collected once in England and in Wales. It is not known from continental Europe and might have an atlantic distribution. In all known collections, the bulbils are developing within mixed epiphytic vegetations of lichens and mosses, but they do not appear to be lichenicolous.

Observations. The species is well characterized by smooth, shiny, whitish, shortly ellipsoid bulbils, covered by minuscule hair-like cells, internally composed of thick-walled cells that do not separate with pressure.

Although fresh material was easily available, we did not succeed in culturing this fungus. Similarly, all attempts to get DNA sequences by direct PCR failed. The inclusion in *Burgoa* is therefore only based on morphological and anatomical similarities with other species. As no clamp connections were observed, the species might even be ascomycetous and should be compared with *Papulaspora* species. Two species with colorless, pale yellow or cream colored papulaspores are keyed out by Hotson (1917): *Papulaspora candida* Sacc. has much smaller papulaspores (30–35 µm diam.); *P. pallidula* Hotson has slightly smaller papulaspores (70–100 µm diam.) devoid of hairs, composed of more loosely aggregated, subspherical cells and thus with a more irregular surface. Superficially, the new species looks similar to *Aegerita candicans*, a species with a very characteristic bulbil anatomy (cells easily separating with pressure; outer cells strongly swollen and pyriform; clamps present). *Burgoa splendens* might well belong to a distinct genus; it is only provisionally described in *Burgoa*, pending further studies.

Additional specimens examined: **Great Britain: England:** VC 4 (North Devon), Arlington, by River Yeo, just S of Tucker's Bridge, 100 m, on *Alnus*, June 1999, Coppins 18780 (E); **Scotland:** VC 97 (Westerness), Glen Beasdale SSSI, WSW of Beasdale Station, 100 m, on *Betula*, May 2003, Coppins 20945 (E); Morvern, Killundine River, on bryophytes on *Quercus*, Feb. 1992, Coppins 14831 & O'Dare (E); N side of Loch Sunart, Camasine Woods, over *Frullania* etc. on *Quercus*, Dec. 1990, Coppins 13830 (E); VC 98 (Argyll Main), Inverary, Glen Shira, Kilblaan Ravine, lower end, 40 m, on mosses on *Fagus*, Mar.

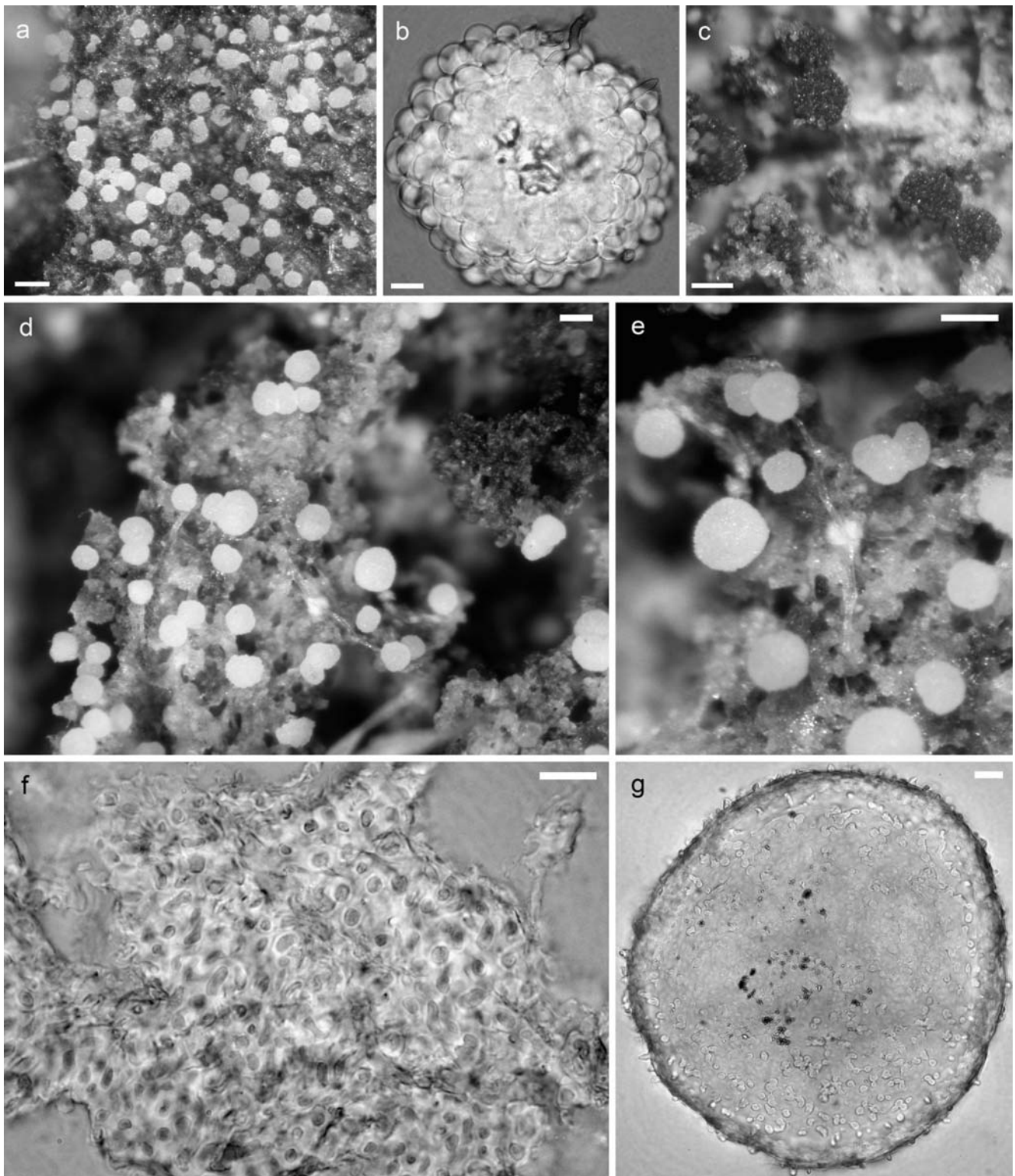


Fig. 4 *Burgoa moriformis* (holotype): **a** Bulbils over bark of *Salix*. **b** Bulbil in optical section. Scales: 100 μm (a), 10 μm (b). – *Burgoa*-like species of Ceratobasidiaceae: **c** Bulbils over bark of *Populus* (Diederich 6561). Scale: 100 μm . – *Burgoa splendens*: **d** Bulbils over bark of *Quercus*. **e** Id., showing rough surface of bulbils at high magnification. **f** Squash preparation of bulbil,

showing the strongly agglutinated, roundish, thick-walled cells. **g** Bulbil, with numerous minuscule hairs (picture obtained from combining a photo in surface view [central part of bulbil] with one in optical section [outer part of bulbil]). Scales: 100 μm (d–e), 10 μm (f–g). Holotype (d–f), *Coppins* 15217 (g)

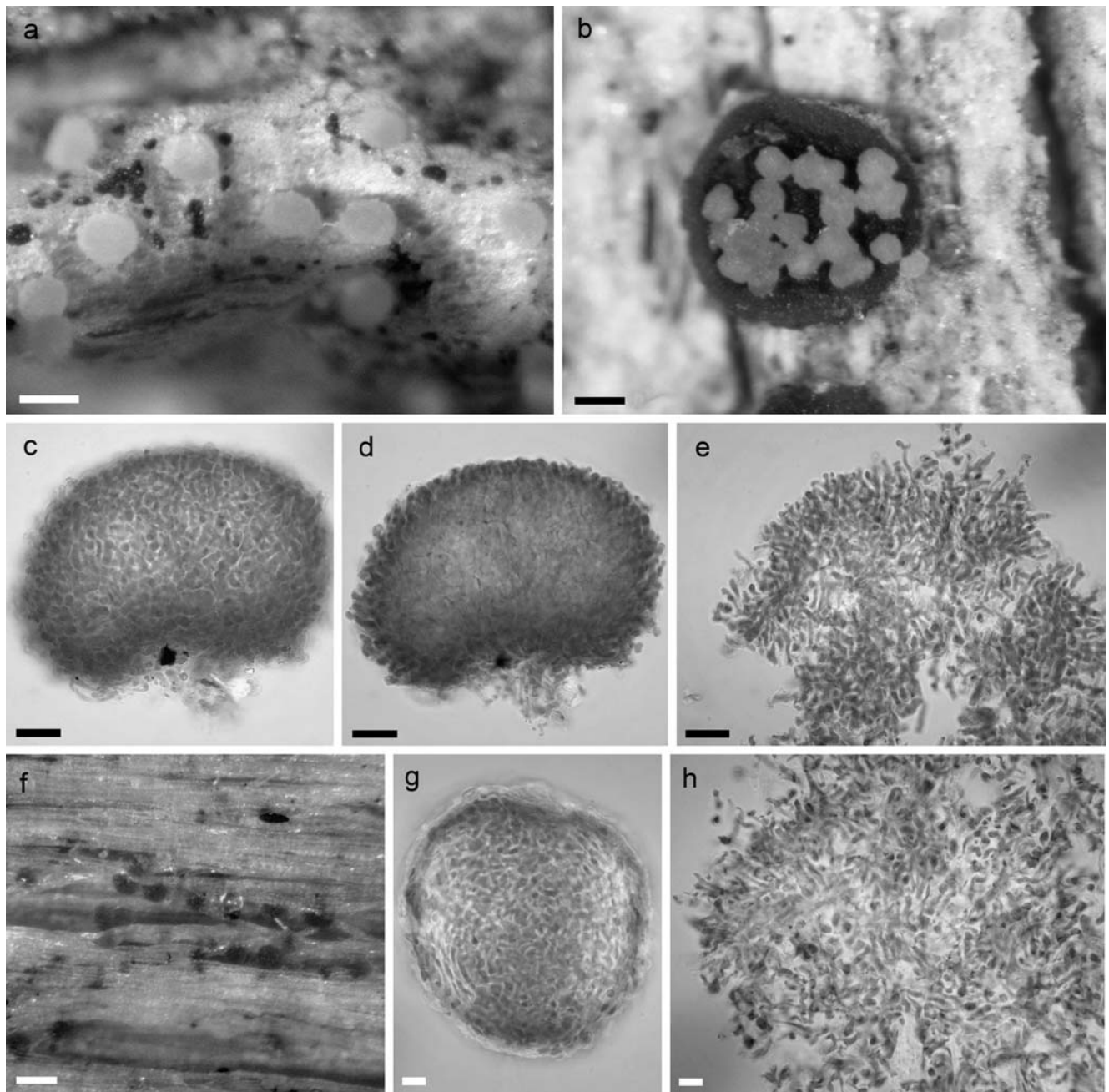


Fig. 5 *Marchandiomyces buckii*: **a** Bulbils developing over a reduced thallus of *Caloplaca pollinii*. **b** Bulbils developing over an apothecium of *Bacidia heterochroa*. **c** Bulbil in surface view. **d** Bulbil in optical section. **e** Squash preparation of bulbil. Scales: 100 μ m (a–b), 20 μ m

(c–e). *Buck* 44601 (a), holotype (b–e). – *Marchandiomyces nothofagicola* (holotype): **f** Bulbils developing on the wood of *Nothofagus*. **g** Bulbil in surface view. **h** Squash preparation of bulbil. Scales: 100 μ m (f), 10 μ m (g–h)

1996, *Coppins* 16847 (E); *ibid.*, SW of Kilblaán, E side of road, 30 m, on *Fraxinus*, Jan. 1996, *Coppins* 16766 (E); VC 101 (Kintyre), 5 km SW of Skipness, Claonaig Wood SSSI (Coille Rubha Dhuibh), over bryophytes on *Sorbus*, June 1994, *Coppins* 16271 & *O'Dare* (E); VC 105 (West Ross), Inverpollly NNR, NW end of Loch Call Uidhean, 90 m, on *Betula*, June 1999, *Coppins* 18684 (E); Coigach, by Abhainn Osgaig, on *Sorbus*, Aug. 1992, *Coppins* 15217 & *O'Dare* (E); *Wales*: VC 48 (Merioneth), 3 km N of Ganllwyd, E side of Afon Gain near Pont Gwyn-fynydd, on *Frullania*

tamarisci on *Quercus petraea* in woodland, Mar. 2002, *Orange* 13657 (NMW).

Burgoa-like species of Ceratobasidiaceae (Figs. 4c and 3d)

Basidiomata and *conidiomata* unknown. Colonies appearing as dispersed bulbils growing over or between corticolous lichen thalli. *Mycelium* not observed. *Bulbils* superficial, dispersed, roundish to shortly ellipsoid, greyish yellow when young (Kornerup and Wanscher 1984: 4B3–

5B4), brown when mature (6D6–7E8), dark brown when old (7F6) (color \pm unchanged in old herbarium specimens), mat, not translucent, without hairs, 100–200 μm diam.; *bulbils externally* without specialized cells; *bulbils internally* composed of branched chains of subspherical to elongate, hyaline cells, 7–23 \times 6–10 μm , septa without clamps, crystals absent (polarized light).

Colonies in liquid culture showing white aerial hyphae; bulbils not observed. *Hyphae* hyaline, septate, straight, rarely branched or anastomosed, 3.5–4.5 μm thick; *septa* without clamp connections. Culture deposited as ATCC 208870.

Distribution and ecology. This species is widespread in Europe and is known from France, Germany, Luxembourg, the Netherlands and Sweden. Bulbils develop over or between lichen thalli or on the naked bark, and normally no damaged lichen thalli are visible; they are most probably not lichenicolous, but often found over lichens, as collected by lichenologists. In almost all collections, the species was found only by chance while examining lichens under the binocular. Owing to the inconspicuous color of the small bulbils, the species is difficult to recognize in the field. Therefore, it is surely much more common than the few specimens examined might suggest.

Observations. Macroscopically, the species is characterized by small, brown, dispersed, corticolous bulbils. It differs from *Burgoa* and *Minimedusa* by bulbils internally composed of branched chains of subspherical to elongate, hyaline cells, and by the absence of clamps. Bulbils of *Burgoa* and *Minimedusa* species are internally composed of polyhedral, subspherical or elongate cells, rarely of branched chains of cells (*Burgoa moriformis*); clamps are always present.

Following Lawrey et al. (2007), the species belongs to the subclade of the Cantharellales containing *Ceratobasidium* and *Thanatephorus* (i.e. the Ceratobasidiaceae). It is only distantly related to *Burgoa*, *Burgella* and *Minimedusa*, precluding an inclusion in one of these genera. As unnamed sclerotia have been reported in many species of Ceratobasidiaceae (Roberts 1999), a study of all these sclerotial or bulbiferous anamorphs should be done prior to formally describing our new species.

Specimens examined: **France:** Pyrénées-Orientales, Targassonne, Chaos de Targassonne, on *Populus*, on *Phaeophyscia orbicularis*, July 1985, Diederich 6561 (hb. Diederich); **Germany:** Baden, Oberrhein, Kleinkems, Gewann Kroatenschanze, on *Sambucus*, on a greenish sterile lichenized crust, Nov. 1998, Wirth 32360 (STU-Wirth; specimen lost?); **Luxembourg:** W of Schengen, Grouf, on *Populus*, over *Candelariella reflexa*, *C. xanthostigma* and *Phaeophyscia orbicularis*, and on bark, Aug. 1987, Diederich 8442 (hb. Diederich); *ibid.*, Dec. 1997, Diederich 13475 (hb. Diederich); **Sweden:** Jämtland, Brunflo par., Torvalla, on *Salix caprea* in a *Populus tremula* grove by a field, Aug. 1948, Santesson 48.502

(d) (UPS); **The Netherlands:** Prov. Friesland, Schiermonnikoog, W side of the village, on *Ulmus*, on an unidentified crustose lichen, Sep. 1996, Aptroot 40082 (hb. Aptroot); prov. Noord-Brabant: SW of Greveschutven, fish-nursery, concrete of diver, on a sterile crust, Oct. 1997, van den Boom 19742 (hb. van den Boom).

Marchandiomyces buckii Diederich & Lawrey, sp. nov. (Figs. 5a–e and 3e)

Marchandiomyces species insignis bulbillis lichenicola, subsphaericis ad ellipsoideis, corallinis, 70–100 μm diam., hyphis radiatis, elongatis, ramosis, interdum septatis, hyalinis, 2–2.5 μm diam., apicaliter 2–6-furcatis.

Type: U.S.A.: North Carolina, Carteret Co., Cape Lookout National Seashore, Shackelford Banks, 34°41'01"N, 76°38'22"W, maritime forest dominated by *Quercus virginiana* and *Juniperus silicicola*, on *Bacidia heterochroa*, 19 Mar. 2003, W. R. Buck 43835 (NY–holotype). ATCC MYA-2992.

Basidiomata and conidiomata unknown. *Colonies* lichenicolous, appearing as numerous bulbils. *Mycelium* not observed. *Bulbils* developing in the host hymenium, soon becoming superficial, densely covering the apothecia and touching each other, or dispersed over the host thallus, subspherical to ellipsoid, 70–100 μm in diam., pale to pastel red [Kornerup and Wanscher 1984: 8A3–4 (3-year-old herbarium specimen)]; bulbils composed of radially oriented, frequently branched and occasionally septate, thick-walled, smooth, hyaline, elongate hyphae, mainly 3–4 μm diam., some of which are apically typically 3–6-furcate, but not distinctly swollen; septa with clamps.

Colonies in liquid culture pinkish, forming smooth spherical masses of 1–2 cm in diam. and rarely erupting to the surface. No growth on maltose, good but very slow growth on various commercial media that contain dextrose (Sabouraud's medium with dextrose is used for routine culture). Bulbils not observed.

Distribution and ecology. Known from the U.S.A. (Missouri and North Carolina), on the apothecia and more rarely the thallus of *Bacidia heterochroa*, on the thallus of *Caloplaca pollinii*, and on the thallus of *Pertusaria hypothamnolica*. Uninfected apothecia of *B. heterochroa* have a dark brown to blackish brown hymenial disk. After infection, apothecia become paler, being finally reddish brown. Bulbils are initially immersed and concolorous to the hymenial disk. They rapidly become erumpent and change to red. When they are removed from the host apothecia, they leave distinct, often decolorized scars.

Observations. Macroscopically, this species looks similar to *Marchandiomyces corallinus*. The bulbils are distinctly smaller, more regularly subspherical to ellipsoid,

and more pale pinkish. Microscopically, both are very distinct: bulbils of *M. corallinus* are composed of large, subspherical to elongate, catenate cells, mainly $5\text{--}12 \times 3.5\text{--}7 \mu\text{m}$, not typically radiating and not furcate. In the phylogenetic tree obtained by Lawrey et al. (2007), *Marchandiomyces buckii* groups with *M. nothofagicola* and *Waitea circinata*, and these species, together with *Laetisaria fuciformis* and *Corticium roseum*, are the sister group of the clade comprising *Marchandiomyces corallinus* and *M. lignicola*.

Additional specimens examined: U.S.A.: Missouri, Christian Co., Mark Twain National Forest, E of Missouri State Highway UU, 3.4 miles S of Merritt Road, $36^{\circ}52'N$, $92^{\circ}56'W$, on *Caloplaca pollinii*, May 2003, Buck 44601 (NY, herb. Diederich); Missouri, Taney Co., Mark Twain National Forest, Hercules Glades Wilderness Road, along trail to Coy Bald, $36^{\circ}41'N$, $92^{\circ}58'W$, 405 m, on *Juniperus* twigs, associated to *Pertusaria hypothamnolica*, May 2003, Buck 44504 (NY).

Marchandiomyces nothofagicola Diederich & Lawrey, sp. nov. (Fig. 5f–h)

Marchandiomyces species insignis bulbillis lignicola, minusculis, subsphaericis ad ellipsoideis, corallinis, $40\text{--}80 \mu\text{m}$ diam., hyphis elongatis, interdum ramosis, raro septatis, $8\text{--}26 \mu\text{m}$ longis, $2\text{--}5.5 \mu\text{m}$ diam., septis fibulatis.

Type: Chile, Prov. Antártica Chilena, Comuna Cabo de Hornos, W coast of Isla Navarino, Puerto Inutil, $54^{\circ}58'32''S$, $68^{\circ}12'49''W$, \pm sea level, wet area in *Nothofagus* forest disturbed by livestock and along small stream through beaver-disturbed area, on decorticated trunk of *Nothofagus*, 21 Jan. 2004, W. R. Buck 45976 (NY–holotype; hb. Diederich–isotype).

Basidiomata and conidiomata unknown. Colonies lignicolous, several cm diam., appearing as numerous bulbils. Mycelium not observed. Bulbils at first partly to almost completely immersed, becoming superficial, sometimes touching each other laterally, subspherical to ellipsoid, $40\text{--}80 \mu\text{m}$ in diam., pastel red [Kornerup and Wanscher 1984: 8A4-5 (2-year-old herbarium specimen)], macroscopically appearing as pale pinkish areas of several cm in length; bulbils externally without specialized cells, composed of a dense agglomeration of thin-walled, smooth, hyaline, irregular, elongate, occasionally branched hyphae, cells mostly $8\text{--}26 \mu\text{m}$ long and $2\text{--}5.5 \mu\text{m}$ diam.; septa rare, with clamps.

Colonies in liquid culture pinkish, forming spherical masses of $1\text{--}2 \text{ cm}$ in diam. and rarely erupting to the surface. No growth on maltose, very slow growth on various commercial media that contain dextrose. Culture lost, not deposited. Bulbils not observed.

Distribution and ecology. Known only from Isla Navarino, southern Chile, on decorticated wood of *Nothofagus*.

Observations. The new species resembles *M. lignicola* in the lignicolous habitat and the very small bulbils. However, *M. lignicola* bulbils are distinctly smaller, $30\text{--}50 \mu\text{m}$ diam., and anatomically different: they are composed of radially oriented, frequently branched and rarely septate, thin-walled, smooth, hyaline hyphae of $2\text{--}2.5 \mu\text{m}$ in diam., which are typically bi- or trifurcate and apically swollen, up to $6 \mu\text{m}$ in diam. Both other known *Marchandiomyces* species have larger bulbils and are lichenicolous.

Minimedusa pubescens Diederich, Lawrey & Heylen, sp. nov. (Fig. 6)

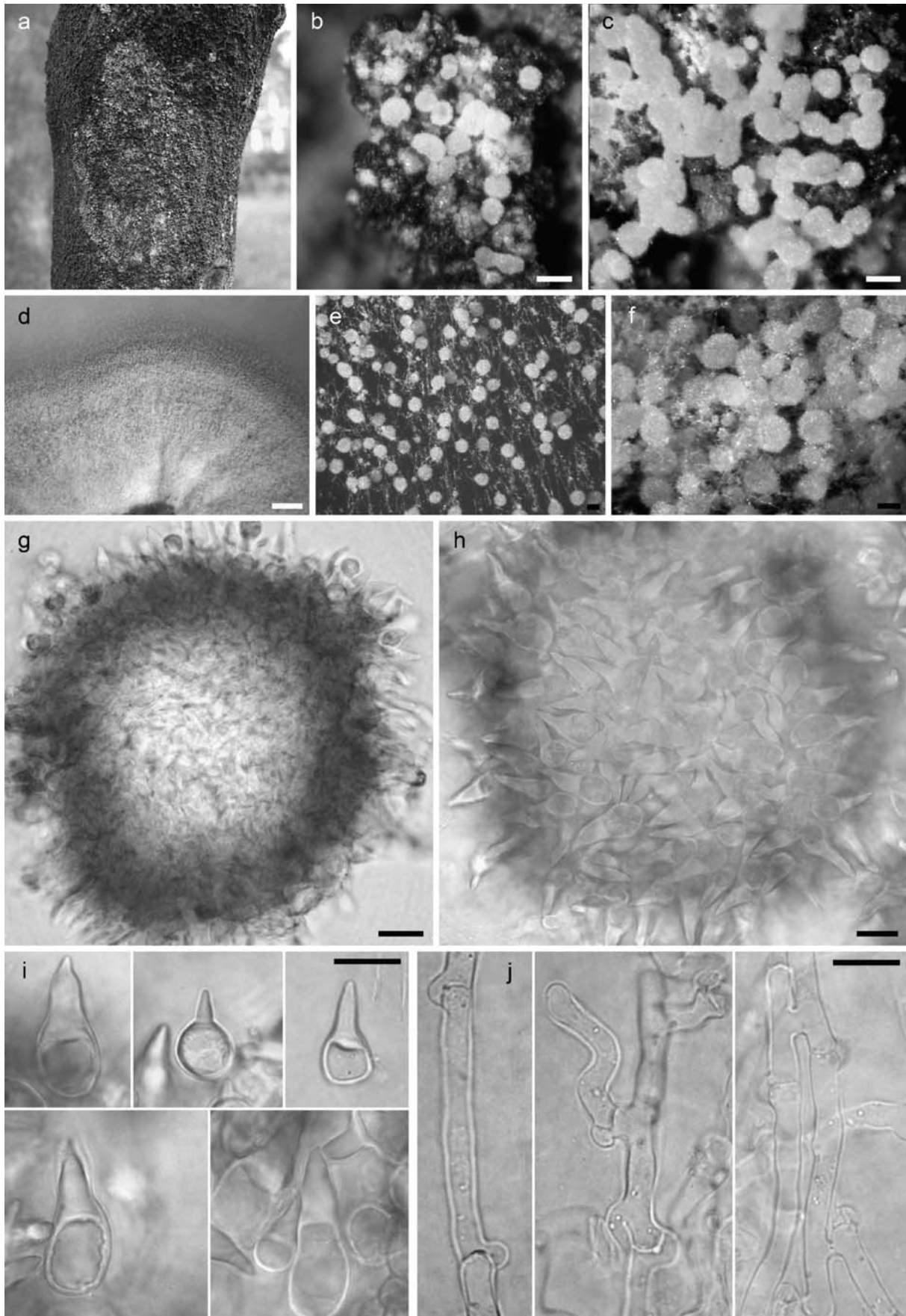
Minimedusa species insignis bulbillis superficialibus, albis ad pallide ochraceis, rotundis ad ellipsoideis, $60\text{--}100 \mu\text{m}$ diam., superficie pubescente, cellulis radiantibus base lata apice acuto $15\text{--}21 \times 3\text{--}8 \mu\text{m}$, interne cellulis subsphaericis $5.5\text{--}12 \mu\text{m}$ diam.

Type: Belgium, prov. Antwerp, Heist-op-den-Berg, comm. Booischot, medieval park “Hof ter Laken”, on *Frangula alnus*, on *Scoliosporium chlorococcum*, 23 May 2003, O. Heylen L03/117 (BR–holotypus; E, LG, NY, UPS, hb. Heylen-Walraevens, hb. Diederich–isotypi). ATCC MYA-2993.

Basidiomata and conidiomata unknown. Colonies appearing as whitish, \pm rounded areas over poorly distinct, corticolous, lichenized crusts, several cm diam., with numerous bulbils covering the inner, necrosed parts of the host, externally with poor or abundant mycelial growth. Mycelium hyaline, \pm straight, $2.5\text{--}3.5 \mu\text{m}$ thick, wall c. $0.5 \mu\text{m}$ thick, septa with clamps. Bulbils superficial, dispersed or in straight or ramified chains of several bulbils, roundish to ellipsoid, pubescent, whitish or pale yellowish to brownish white (but partly reddish in Diederich 8590), mainly due to the whitish ‘hairs’, pale brownish and slightly translucent when ‘hairs’ abraded, $60\text{--}100 \mu\text{m}$ diam.; bulbils externally composed of radially oriented, hyaline ‘hairs’ with a more or less pointed apex and a thin to relatively broad base, sometimes almost ampulliform, $15\text{--}21 \times 3\text{--}8 \mu\text{m}$, thin-walled, except at the apex, where the wall is up to $6 \mu\text{m}$ thick; bulbils internally composed of \pm roundish cells of $5.5\text{--}12 \mu\text{m}$ diam., crystals absent (polarized light).

Colonies in liquid culture showing aerial hyphae from which yellow, dispersed bulbils develop. Hyphae hyaline, septate, straight or curved, frequently branched, sometimes anastomosed, mostly $2\text{--}3 \mu\text{m}$ thick, some c. $1 \mu\text{m}$ thick, others $3\text{--}4.5 \mu\text{m}$; septa with clamp connections. Bulbils subspherical to shortly ellipsoid, yellow (Kornerup and Wanscher 1984: 3A4), pubescent, $100\text{--}170 \mu\text{m}$ diam., externally and internally similar to those developing in nature.

Distribution and ecology. The species is known only from Belgium and Luxembourg, where it appears to be widespread but rare. It is surely overlooked in other



◀ **Fig. 6** *Minimedusa pubescens*: **a** Colony killing *Scoliciosporum chlorococcum* on *Frangula alnus* (photo: Olivier Heylen). **b** Bulbils over *S. chlorococcum*. **c** Catenate bulbils over *Fagus* bark. **d** One-month-old culture. **e** Young bulbils developing in culture. **f** Mature bulbils in culture. **g** Bulbil (free-living, dry herbarium specimen) in optical section. **h** Bulbil (in culture) in surface view. **i** Cells of outer layer with thick-walled hair-like apices and a swollen base (in culture). **j** Hyphae (in culture). Scales: 100 μm (b–c, e–f), 1 mm (d), 10 μm (g–j). Holotype (a–b, g), *Diederich* 8590 (c), culture ATCC MYA-2993 from holotype (d–f, h–j)

European countries. It frequently grows over corticolous lichens (*Bacidina* species, *Physcia tenella*, *Scoliciosporum chlorococcum*), sometimes killing their thalli, but might be only facultative lichenicolous.

Observations. This species is distinguished by pale, roundish to ellipsoid bulbils covered by characteristic aseptate ‘hairs’ with a swollen base, a pointed apex and an apically thickened cell wall. These ‘hairs’ are likely to be homologous structures of the three conical protuberances below bulbils of *Minimedusa obcoronata*. Bulbils in culture differ from those developing in nature by their distinct yellow color.

Phylogenetic results (Lawrey et al. 2007) place this species in a clade with *Minimedusa polyspora*, *M. obcoronata* and *Sistotrema coronilla*.

Additional specimens examined: **Belgium:** Same locality and date as type, on *Acer pseudoplatanus*, *Heylen* L03/118 (BR, hb. Heylen-Walraevens, hb. *Diederich*); **Luxembourg:** SSW of Bascharage, near Moulin de Bascharage, on *Salix*, on sterile *Bacidina*, Aug. 1987, *Diederich* 8356 (hb. *Diederich*); Mamer, vers Dippach, Didenuecht, on *Fagus*, on *Scoliciosporum chlorococcum*, Aug. 1987, *Diederich* 8590 (hb. *Diederich*); SE of Lasauvage, Grand-Bois, on *Acer*, on *Physcia tenella*, Aug. 1987, *Diederich* 8569 (hb. *Diederich*).

A new genus for *Omphalina foliacea*

Marchandiomphalina *Diederich, Binder & Lawrey*, gen. nov.

Basidiolichen insignis thallo foliosa viridi-griseo, in sicco fragili, in humido gelatinoso, subtus sine cortice albido ruguloso goniocystis oblecto, photobionto *Coccomyxa*, basidiomatibus ignotis.

Type: *Marchandiomphalina foliacea* (P. M. Jørg.) *Diederich, Binder & Lawrey*.

Marchandiomphalina foliacea (P. M. Jørg.) *Diederich, Binder & Lawrey*, comb. nov.

Omphalina foliacea P. M. Jørg., *Nord. J. Bot.* 9: 89 (1989); type: Venezuela, Merida, Sierra Nevada de Santo Domingo, towards Laguna Negra in paramo, 9 Jan. 1979, P. M. Jørgensen 7545 (BG–holotype; MERF, US–isotype, non vid.).

For a detailed description and illustrations of the type species, see Jørgensen (1989). The species was originally described as a basidiolichen belonging to the genus *Omphalina*, although no basidiomata have been observed. Palice et al. 2005 used molecular data to confirm that the species belongs to the basidiomycetes. They found that it is not related with *Omphalina* (Agaricales) or other omphalinoid agarics, but probably belongs to the hymenochaetoid clade. New results by Lawrey et al. (2007) place the species in the corticioid clade (Binder et al. 2005) as sister to the clade containing *Marchandiobasidium* and *Erythricium*. As no close relatives are known with a similar biology or morphology, the description of a new genus *Marchandiomphalina* is therefore appropriate.

Catalogue of the named, non-lichenized, bulbilliferous basidiomycetes

Excluded from this catalogue are the basidiomycetes with lichenized bulbils. They belong to *Lichenomphalia* Redhead et al. [c. 5 bulbilliferous species; see Redhead et al. (2002)], *Multiclavula* R. H. Petersen [c. 5 bulbilliferous species; see Fischer et al. (2007), Oberwinkler (1970, 1984), Petersen (1967) and Poelt and Obermayer (1990)] and *Semiomphalina* Redhead [1 species; see Redhead (1984)].

Also excluded are unnamed, bulbilliferous anamorphs of different *Sistotrema* species, of *Peniophora pithya* and *Phellinus nigrolimitatus* (see Cléménçon et al. 2004), most of them known only from culture. The poorly known, basidiomycetous *Glomerulomyces fibulosus* Romero & Lopez (Romero et al. 1989) might represent a further bulbilliferous species.

Aegerita Pers.:Fr.

Syn. meth. fung. (Göttingen): 684 (1801); type: *Aegerita candida* Pers.:Fr.

Teleomorph: *Bulbillomyces* Jülich.

Phylogeny: possibly in the “residual polypore clade” (Binder et al. 2005: 152).

Aegerita candida Pers.:Fr.

Neues Mag. Bot. 1: 120 (1794); type: ?

Teleomorph: *Bulbillomyces farinosus* (Bres.) Jülich.

Widespread in Europe and North America, also known from Japan and New Zealand, on decayed wood in humid conditions. Description and illustrations available in Breitenbach and Kränzlin (1986: 128–129) and Eriksson and Ryvarden (1976).

Specimen examined: **Luxembourg:** Grundhof, Dominiksmillen, 1992, *Schultheis* 18/92 (hb. *Diederich*, hb. *Schultheis*).

Aegeritina Jülich

Int. J. Mycol. Lichenol. 1: 282 (1984); type: *Aegeritina tortuosa* (Bourdot & Galzin) Jülich.

Teleomorph: *Subulicystidium* Parmasto.

Phylogeny: Trechisporoid clade (Binder et al. 2005: 124).

Aegeritina tortuosa (Bourdot & Galzin) Jülich

Int. J. Mycol. Lichenol. 1(3): 282 (1984).—*Aegerita tortuosa* Bourdot & Galzin, *Hyménomycètes de France* (Sceaux): 298 (1928) [1927]; type: ?

Teleomorph: *Subulicystidium longisporum* (Pat.) Parmasto.

Widespread in Europe and America, on decayed wood and plant debris. Descriptions and illustrations available in Abdullah et al. (1997), Eriksson et al. (1984: 1445) and Jülich (1984).

Burgella Diederich & Lawrey

See above; type: *Burgella flavoparmeliae* Diederich & Lawrey.

Teleomorph: unknown.

Phylogeny: Cantharellales, in the subclade comprising *Clavulina*, *Mutliclavula*, *Sistotrema brinkmannii* and *S. oblongisporum* (Lawrey et al. 2007).

Burgella flavoparmeliae Diederich & Lawrey

See above.

Burgoa Goid.

Boll. Sta. Patol. Veg. Roma, N. S. 17: 354 (1938); type: *Burgoa verzuoliana* Goid.

Teleomorph: *Sistotrema* Fr. s. lat.

Phylogeny: Cantharellales (Binder et al. 2005: 124, Lawrey et al. 2007).

A detailed description of the genus *Burgoa*, the delimitation with reference to other genera, and the mode of development of bulbils is given by Weresub and LeClair (1971).

Burgoa angulosa Diederich, Lawrey & Etayo

See above.

Burgoa anomala (Hotson) Goid.

Boll. Sta. Patol. Veg. Roma, N. S. 17: 360 (1938).—*Papulaspora anomala* Hotson, *Proc. Am. Acad. Arts Sci.* 48: 270 (1912); type: ?

Isolated from live oak chips and old paper in the U.S.A. Description and illustrations available in Hotson (1912).

Burgoa aurantiaca (Hotson) Goid.

Boll. Sta. Patol. Veg. Roma, N. S. 17: 355 (1938).—*Papulaspora aurantiaca* Hotson, *Bot. Gazette* 64: 273 (1917); type: ?

Collected on bark in Trinidad (West Indies). Description and illustrations available in Hotson (1917).

Burgoa moriformis Diederich, Ertz & Coppins

See above.

Burgoa nigra (Hotson) Goid.

Boll. Sta. Patol. Veg. Roma, N. S. 17: 355 (1938).—*Papulaspora nigra* Hotson, *Bot. Gazette* 64: 275 (1917); type: ?

Isolated from old cardboard and hardwood chips in the U.S.A. and from sugar cane in Venezuela. Description and illustrations available in Hotson (1917) and Pons and Manzano (1985).

Burgoa pisi S. Q. He & D. Z. Tang

Mycosystema 17: 114 (1998); type: He P-89-5-25 (HMAS 74118—holotype; IPPG—isotype).

Isolated from the diseased root and collar of peas in China. Description and illustrations available in He and Tang (1998).

Burgoa splendens Diederich & Coppins

See above.

Burgoa turficola Schlechte & P. Hoffmann

Gartenbauwissenschaft 65: 144 (2000); type: Germany, Nordrhein-Westfalen, DSM 12882 (DSMZ—holotype).

Teleomorph: *Athelia turficola* Schlechte & Hoffmann. Phylogenetic results (Lawrey et al. 2007) suggest that this species belongs to the Agaricales, as a sister taxon of *Stephanospora caroticolor*. The species must therefore be excluded from *Athelia* (Atheliales), and the anamorph must be excluded from *Burgoa*.

Frequent on peat-based growing media, Germany. Description and illustrations available in Schlechte and Hoffmann (2000).

Burgoa verzuoliana Goid.

Boll. Sta. Patol. Veg. Roma, N. S. 17: 359 (1938); type: ?; type cultures in CBS 131.38, ATCC 24040 (dried culture in hb Diederich), DAOM 129784, MUCL 10055.

Isolated from *Populus* wood, an old door mat, and *Hypocreopsis riccioidea* on stem of *Salix aurita* in Germany,

Italy and the U.K. Description and illustrations available in Goidánich (1938) and Weresub and LeClair (1971).

Marchandiobasidium Diederich & Schultheis

Mycol. Res. 107: 524 (2003); type: *Marchandiobasidium aurantiacum* Diederich & Schultheis.

Phylogenetic results (Lawrey et al. 2007) show that *Marchandiomyces aurantiacum* (teleomorph: *Marchandiobasidium aurantiacum*) groups together with *Erythricium laetum* (a salmon-colored resupinate fungus overgrowing dead stems and branches) and *E. salmonicolor* (a fungus causing pink disease in citrus, coffee and rubber trees), and these species come out as the sister group of the lichenized basidiomycete *Marchandiomphalina* (= *Omphalina*) *foliacea*. This clade is the sister of another clade containing all other *Marchandiomyces* species, but also *Laetisaria fuciformis*, *Waitea circinata* and *Corticium roseum* (the type species of *Corticium*). It is clear from these results, and from similar results obtained in a previous study (DePriest et al. 2005), that the genus *Marchandiomyces* s. l. is polyphyletic, and that *M. aurantiacum* belongs to a distinct genus. However, as the anamorph–teleomorph connection leaves little doubt, the description of a new genus for the anamorph does not seem appropriate to us. Instead, we prefer using the holomorph name *Marchandiobasidium aurantiacum* for both morphs.

Marchandiobasidium differs from *Marchandiomyces* by the color of the bulbils: they are orange (carrot red) in the former, and pastel to coral red in the latter genus. Also the biology and ecology of both genera are distinct. Bulbils of *Marchandiobasidium* are lichenicolous, develop superficially over lichen thalli that they almost entirely degrade, and of which only the cortical layers remain after an invasion by the parasite. Bulbils of *Marchandiomyces* are either lignicolous or lichenicolous, but then they are initially immersed in the host thallus, and they never degrade the host thalli in such a way.

Phylogeny: Corticioid clade (Binder et al. 2005: 127, Lawrey et al. 2007).

Marchandiobasidium aurantiacum Diederich & Schultheis

Mycol. Res. 107: 524 (2003); type: Belgium, Lischert, on *Physcia tenella*, 21 Dec. 2001, Thoen & Diederich 15133 (LG–holotype, hb. Diederich–isotype!).

Anamorph: *Marchandiomyces aurantiacum* (Lasch) Diederich & Etayo, *Mycotaxon* 60: 421 (1996).–*Illosporium aurantiacum* Lasch, in Rabenhorst, *Fungi Eur.*, cent. I, no. 74 (1859); type: Germany, in lichenibus trunci Pyri mali pr. Driesen, Lasch, Rabenhorst *Fungi Eur.*, cent. I, no. 74 (K, M, UPS–isotypes!).

For a description and illustrations of the only species, see DePriest et al. (2005), Diederich et al. 2003 and Etayo and Diederich (1996).

Widespread in Europe, here reported for the first time from North America. Lichenicolous on *Physcia* species (mainly *P. tenella*), rarely overgrowing other corticolous macrolichens.

American specimen examined: U.S.A.: California, San Diego Co., Observatory Trail, end of S6 near entrance to Palomar Observatory parking lot, 33°21'N, 116°51'W, on *Physcia* sp., March 2001, Cole 8457 (hb. Cole).

Marchandiomyces Diederich & D. Hawksw

Mycotaxon 37: 311 (1990); type: *Marchandiomyces corallinus* (Roberge) Diederich & D. Hawksw.

Teleomorph: unknown.

Phylogeny: Corticioid clade (Binder et al. 2005: 127, Lawrey et al. 2007).

Marchandiomyces buckii Diederich & Lawrey

See above.

Marchandiomyces corallinus (Roberge) Diederich & D. Hawksw

Mycotaxon 37: 312 (1990).–*Illosporium corallinum* Roberge, in Demazières, *Pl. crypt. Fr.*, Ed. 1, fasc. 32 no. 1551 (1847); type: France, on *Physcia tenella*, Desmazières *Pl. crypt. Fr.*, Ed. 1, fasc. 32 no. 1551 (K–isotype!).

A relatively frequent lichenicolous fungus, known from Europe and North America, on many different host species. Description, illustrations and discussion available in DePriest et al. (2005), Etayo and Diederich (1996) and Molina et al. (2005).

Marchandiomyces lignicola Lawrey & Diederich

Mycol. Res. 109: 65 (2005); type: USA, Virginia, Rappahannock Co., Aaron Mt, decorticated dead *Quercus* branch on ground, 1999, Lawrey 1716 (NY–holotype; hb. Diederich–isotype); culture: ATCC MYA-835.

Known from the USA (Connecticut, Virginia and West Virginia) on decorticated branches, mainly of *Quercus*. Description and illustrations available in DePriest et al. (2005).

Additional specimens examined: U.S.A.: Connecticut, Litchfield Co., Town of Canaan. North of Falls Village, CT, West of Sand Road, about 0.5 miles N of jct with State Route 126 4, 41°58'N, 73°21'W, on decorticated hardwood branch, July 2002, Lawrey 1784 (GMUF). West Virginia, Grant Co., Wilderrest Inn, 11 miles south of Petersburg, WV on Route 220, 38°50'N, 79°09'W, on decorticated *Quercus* branch, June 2001, Lawrey 1746 (GMUF). Virginia, Prince William Co., Prince William Forest Park, North Valley Trail to Burman Road, east 400 m, 38°36'N, 77°21'W, on

decorticated *Quercus* branch, Nov. 2003, Lawrey 1797 (GMUF).

Marchandiomyces nothofagicola Diederich & Lawrey

See above.

Minimedusa Weresub & P. M. LeClair

Can. J. Bot. 49: 2210 (1971); type: *Minimedusa polyspora* (Hotson) Weresub & P. M. LeClair

= *Pneumatospora* B. Sutton, Kuthub. & Muid, *Trans. Br. mycol. Soc.* 83: 423 (1984); type: *Pneumatospora obcoronata* B. Sutton, Kuthub. & Muid [= *Minimedusa obcoronata*].

= *Tricellulortus* Matsush., *Matsushima Mycological Memoirs* 8: 39 (1995); type: *Tricellulortus peponiformis* Matsush. [= *Minimedusa obcoronata*].

Teleomorph: unknown.

Phylogeny: Cantharellales (Binder et al. 2005: 124, Lawrey et al. 2007).

The genus *Pneumatospora* (= *Tricellulortus*) was distinguished from *Burgoa* and *Minimedusa* by peculiar bulbil-like structures, basally prolonged into three conical protuberances, and acting as diaspores. Like those of *Minimedusa polyspora*, these structures have a multihyphal base. The conical protuberances are likely to be homologous structures to the ‘hairs’ of *Minimedusa pubescens*. Our new phylogenetic results (Lawrey et al. 2007) place *Pneumatospora obcoronata* as the sister taxon of *Minimedusa polyspora*, both being the sister group of *M. pubescens* and *Sistotrema coronilla*. We propose therefore to regard *Pneumatospora* as a synonym of *Minimedusa*.

Minimedusa obcoronata (B. Sutton, Kuthub. & Muid) Diederich & Lawrey, comb. nov.

Basionym: *Pneumatospora obcoronata* B. Sutton, Kuthub. & Muid, *Trans. Br. mycol. Soc.* 83: 423 (1984); type: Kuthubutheen S13 (IMI 267744–holotype).

= *Tricellulortus peponiformis* [as ‘*pepoformis*’] M. Matsush., *Matsushima Mycol. Memoirs* 8: 39 (1995); type: *Matsushima* 2J764 (Matsushima Fungus Collection, Kobe–holotype).

Isolated from leaves and litter in Barbados (West Indies), Japan and Malaysia. Description and illustrations available in Sutton et al. (1984) and Peláez et al. (2001).

Minimedusa polyspora (Hotson) Weresub & P. M. LeClair

Can. J. Bot. 49: 2210 (1971).–*Papulaspora polyspora* Hotson, *Proc. Am. Acad. Arts Sci.* 48: 293 (1912); type: Hotson 23 (DAOM 43326, slide ex G, dried culture–isotype); presumed type cultures in CBS 113.16, ATCC 24041 (dried culture in hb Diederich), DAOM 129790.

Isolated from soil, straw, old paper, oat seed and cotton flowers in Cuba, Denmark, Germany, the Netherlands, the U.K. and the U.S.A (Beale and Pitt 1995). Description and illustrations available in Hotson (1912) and Weresub and LeClair (1971).

Minimedusa pubescens Diederich, Lawrey & Heylen

See above.

Excluded species

Burgoa alutacea Goid.

Boll. Sta. Patol. Veg. Roma, N. S. 17: 355 (1938); nom. inval. (Art. 36).

The material of this species was collected on rotten oak bark in the U.S.A. and incorrectly considered as being the bulbilliferous state of “*Corticium alutaceum* (Schrad.) Bres.” by Hotson (1912, 1917) (Weresub and LeClair 1971).

Burgoa hutsonii Goid.

Boll. Sta. Patol. Veg. Roma, N. S. 17: 355 (1938); nom. inval. (Art. 36).

The material of this species was collected on rotten chips of oak, rotten wood, old canvas, paper, cardboard, rabbit dung, etc. in the U.S.A. and Brazil, and considered as being the bulbilliferous state of “*Grandinia crustosa* (Pers.) Fr.” by Hotson (1912, 1917).

Key to the non-lichenized, bulbilliferous basidiomycetes

Note: unnamed bulbilliferous anamorphs are occasionally found associated with *Sistotrema* basidiomata; they are not included in this key. Bulbilliferous fungi lacking clamps are likely to be ascomycetous anamorphs, which are as well not included here.

- 1 Bulbils orange (carrot red), lichenicolous (mainly on *Physcia tenella*), developing over the host thallus and almost entirely degrading it, with only the host cortex left..... *Marchandiobasidium aurantiacum*
- 1* Bulbils another color, lichenicolous or not, never almost entirely degrading lichen thalli [yellow to orange (honey-colored, never carrot red) bulbils are known from *Burgella flavoparmeliae*, lichenicolous on *Flavoparmelia*, and from the corticolous *Burgoa aurantiaca*] 2
- 2 Bulbils pastel to coral red, immersed to superficial..... 3
- 3 Bulbils small, 30–80 µm diam., lignicolous 4
- 4 Bulbils 30–50 µm diam., composed of radially oriented, frequently branched and rarely septate hyphae, which are typically bi- or trifurcate and apically swollen *Marchandiomyces lignicola*
- 4* Bulbils 40–80 µm diam., composed of irregular, elongate, occasionally branched hyphae that are not radially oriented, and not furcate or apically swollen *Marchandiomyces nothofagicola*
- 3* Bulbils larger, 70–250 µm diam., lichenicolous 5
- 5 Bulbils regularly subspherical to ellipsoid, 70–100 µm diam., composed of radially oriented, frequently branched and occasionally septate, thick-walled, smooth, hyaline, elongate hyphae, mainly 3–4 µm diam., some of which are apically 2–6-furcate..... *Marchandiomyces buckii*
- 5* Bulbils subspherical, ellipsoid or irregular with a slightly or distinctly angular surface, 80–250 µm diam., composed of large, subspherical to elongate, catenate cells, mainly 5–12 × 3.5–7 µm, not visibly radiating and not furcate *Marchandiomyces corallinus*
- 2* Bulbils another color, not or indistinctly immersed 6
- 6 Bulbils pure white, 100–300 µm diam., with long, projecting cystidia encrusted by crystals; composed of intermingled and sinuous hyphae with clamps at all septa *Aegeritina tortuosa*
- 6* Bulbils different, without cystidia (but cylindrical setae present in *Burgoa pisi*, a species with dark brown to black bulbils) 7
- 7 Bulbils white (to yellowish in herbarium), regularly ellipsoid, 100–150(200) µm diam., in section of radiating hyphae with a strongly swollen, ellipsoid or more often pyriform apical cell with a basal clamp, these cells forming a dense layer easily seen when observing an entire bulbil under the microscope..... *Aegeritia candida*
- 7* Bulbils different, without such an external layer of pyriform cells..... 8
- 8 Bulbils lichenicolous, yellow to ochraceous or orange (honey-colored), subspherical to shortly ellipsoid, 60–110 µm diam., sometimes slightly immersed in the thallus of *Flavoparmelia*, leaving distinct scars when removed; cultures with up to 1 cm diam., gelatinous, almost coralloid agglomerations of greyish orange, irregularly shaped bulbils of 150–300 µm, which are distinct from the dispersed, more regular, free-living bulbils *Burgella flavoparmeliae*

- 8* Bulbils lichenicolous or not, but then not tightly attached to the host thallus and not confined to it (see *Burgoa*-like species of Ceratobasidiaceae, and *Minimedusa pubescens*) or more or less angular (see *Burgoa angulosa*), and of a different color (whitish or brown); when known, bulbils in culture distinct, not of coralloid agglomerations..... 9
- 9 Bulbils white or very pale brownish, with a smooth and shiny surface on which minuscule, 1–4 μm long, dispersed hairs are visible at a high magnification, internally composed of agglomerated, \pm roundish, thick-walled cells of 3.5–5.5 μm diam. that do not separate with pressure; septa and clamps not observed *Burgoa splendens*
- 9* Bulbils different, devoid of hairs or entirely pubescent, internally composed of cells usually separating more easily with pressure; clamps present or absent..... 10
- 10 Bulbils brown (pale greyish brown when young, dark brown when old), mat, devoid of hairs, with no cells visible macroscopically, 100–200 μm diam. (not to be confused with sclerotia of *Athelia arachnoidea* that are frequently over 500 μm diam.), internally composed of branched chains of subspherical to elongate, hyaline cells, 7–23 \times 6–10 μm ; clamps absent *Burgoa*-like species of Ceratobasidiaceae
- 10* Bulbils pale colored (even when mature), yellow, orange, brown to almost black, in some species with hairs, internally of polyhedral, subspherical or elongate cells, rarely of branched chains of cells, but then bulbils externally of easily visible, swollen cells (*Burgoa moriformis*); clamps always present..... 11
- 11 Bulbils externally with three basal, or entirely covered by hyaline, smooth, aseptate cells with a swollen base, prolonged into conical protuberances 12
- 12 Bulbils slightly flattened, 16–24 μm diam., 8–13 μm high, of two layers, each consisting of a single central cell, surrounded by 6 peripheral cells; every second peripheral cell of the basal layer producing a conical protuberant cell downwardly directed; bulbils developing over an erect ‘stalk’, 19–29 \times 6.5–8.5 μm , formed by 3 closely appressed, parallel hyphae, later seceding from this stalk and giving rise to a single propagule (‘spore’) *Minimedusa obcoronata*
- 12* Bulbils subspherical, 60–80 μm diam., pubescent, entirely covered by radially oriented ‘hairs’ with a \pm pointed apex and a relatively broad base, internally composed of a larger number of cells, not developing over a conspicuous ‘stalk’, not separating from the basal mycelium..... *Minimedusa pubescens*
- 11* Bulbils externally without such cells 13
- 13 Bulbils whitish..... 14
- 14 Bulbils 35–65 μm diam., subspherical, in surface view with strongly swollen, ballooned cells of 7–12 μm diam. and thus bulbils \pm moriform..... *Burgoa moriformis*

- 14* Bulbils larger, over 80 μm diam., irregular in form, roundish, ellipsoid or elongate, surface uneven, often slightly to distinctly angular; cells in surface view flattened to slightly swollen *Burgoa angulosa* 15
- 13* Bulbils yellow, orange, brown or black 15
- 15 Bulbils yellow, ochraceous to orange; free-living 16
- 16 Bulbils 30–150 μm diam., yellow or reddish to brownish ochraceous; on peat *Burgoa turficola* 16
- 16* Bulbils larger, 100–250 μm diam., pale yellow, becoming orange; corticolous *Burgoa aurantiaca* 17
- 15* Bulbils brown or black; known only from culture 17
- 17 Bulbils medium to dark reddish brown 18
- 18 Bulbils 100–300 μm diam., covered by a thin mucilaginous film and therefore surface shiny, smooth, external cells not visibly swollen or ballooned; internally of textura angularis, with polyhedral cells; juvenile bulbils originating in an areal twist of unexpanded hyphae, becoming apically rounded on multihyphal base *Minimedusa polyspora* 18
- 18* Bulbils 70–170 μm diam., not covered by a mucilaginous film, in surface view with strongly swollen, almost ballooned cells of 12–30 μm diam.; internally of textura globulosa to angularis, with bubble-like cells; juvenile bulbils originating in a reflexively rebranching knot of unexpanded hyphae, becoming globose, more or less sessile or terminal on a single hypha *Burgoa verzuoliana* 19
- 17* Bulbils dark brown to black 19
- 19 Bulbils c. 150–450 x 110–280 μm , with c. 20–170 μm long, cylindrical setae *Burgoa pisi* 20
- 19* Bulbils smaller, 100–180 μm , without setae [two morphologically similar species, differing by their mode of development in culture] 20
- 20 Bulbils arise from slightly swollen, intercalary or lateral cells, from which primordial cell branches develop in different directions, becoming eventually incorporated into bulbils *Burgoa anomala* 20
- 20* Primordial cell branches coil up spirally, from which short branches develop that intertwine, eventually developing into bulbils *Burgoa nigra* 20

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