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A new species of *Globulisebacina* from Taiwan and new record of *Chaetospermum camelliae* with *Efibulobasidium* teleomorph (Sebacinales) from Panama

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With 3 figures

Abstract: Two specimens of Sebacinales from Panama and Taiwan were identified based on morphology and partial LSU rDNA sequences. A specimen on oak fruits from Panama was identified as *Chaetospermum camelliae*, which contained an *Efibulobasidium* teleomorph. Conidiogenesis in this species is classified as postsomatogamic and sympodial. For a specimen from Taiwan, a new species of *Globulisebacina* is described based on its placement in a molecular phylogeny of partial LSU rDNA sequences, two-celled basidia and lack of a *Chaetospermum* anamorph. Nomenclatural errors of two recently newly combined *Sebacina* species are corrected.

Key words: endophytes, environmental samples, mycorrhiza, *Quercus*, Sebacinaceae.

Introduction

For many decades, *Sebacina*-like fungi were considered a curiosity mainly for experts interested in jelly fungi and evolution of Basidiomycota (Berbee et al. 2016). The lack of clamp connections was perceived as phylogenetic significant characteristic, which lead to erecting the family Sebacinaceae by Wells & Oberwinkler (1982). Before the end of the millennium, a new sebacinoid fungus called *Pirifomispora indica* Sav.Verma et al. was recommended as "super mycorrhiza fungus" with high potential benefit for agriculture (Varma et al. 1999). Following this discovery and by rapidly increasing

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DNA data from environmental samplings, an unprecedented ubiquity and diversity of *Sebacina*-like fungi was revealed from soil and mycorrhizal associations, indicating the ecological importance of these fungi for soil life and vegetation. A similar trend can be observed in the research of *Tulasnella* species (Cruz et al. 2016, Oberwinkler et al. 2013b, Yu et al. 2015). In Sebacinales, sequences spanning the D1/D2 regions of the ribosomal large subunit RNA gene (LSU rDNA) are most prevalently used (Oberwinkler et al. 2014, Weiß et al. 2011). Using these findings on cryptic biodiversity as "treasure chart", Oberwinkler et al. (2013a, 2014) aimed at detecting and bringing to light the "treasures", i.e. the sebacinoid species, by an organismic approach uncovering the species previously merely known as DNA sequence data. A detailed outline of this process and its initial results has been presented in Oberwinkler et al. (2013a, 2014). This process has not yet been finished. Presently, many data about sebacinoid fungi are limited to the biodiversity informatics level, i.e. DNA sequences from environmental samples or sterile cultures, but cannot be connected to species in a strict scientific sense. The knowledge of Warcup & Talbot (1967) how to induce the development of basidia and basidiospores in cultures derived from mycorrhizas has been lost. Even with alpha taxonomy, particularly few species are described from South and Central America (Kisimova-Horovitz et al. 2000, Wartchow et al. 2015)

Among the pioneer studies of sebacinoid classification, Wells (1975) established the genus *Efibulobasidium*, based on *E. rolleyi* (L.S.Olive) K.Wells and the type species *E. albescens* (Sacc. & Malbr.) K.Wells. Wells & Bandoni (2001) found an anamorph-teleomorph connection between the teleomorphic *Efibulobasidium* and the coelomycetous anamorph *Chaetospermum*, which was confirmed by subsequent studies (Kirschner & Oberwinkler 2009, Rungjindamai et al. 2008). Oberwinkler et al. (2014) found that *E. rolleyi* lacks the *Chaetospermum* conidial stage and is phylogenetically not closely related to the *Chaetospermum* clade. For this reason, the new genus and combination *Globulisebacina rolleyi* (L.S.Olive) Oberw., Garnica & K.Riess were proposed.

During collection trips in Panama and Taiwan, we found two species of sebacinoid fungi hitherto not known for these areas and report them here in detail. Two nomenclaturally invalid new combinations of *Sebacina* species proposed in Oberwinkler et al. (2014) are corrected.

Materials and methods

Field collection was done in the mountainous areas of western Panama and northern Taiwan. Samples were investigated morphologically in the fresh stage with a dissecting and a light microscope. Mountings in 5–10% KOH with and without staining with 1% aqueous phloxine or Kongo Red were used at 1000× magnification for measurements and drawings. Sizes given in the descriptions were based on n measurements given as extreme values in brackets and mean values ± standard deviation. In the specimen from Taiwan, basidiomata were fixed beneath a Petri dish lid and allowed to disperse spores onto the below corn meal agar. This culture was used for extracting DNA. The culture died before it could be deposited at a culture collection. The methods for DNA extraction and analysis of the nuclear ribosomal large subunit RNA gene (LSU rDNA) were done as in Yeh & Kirschner (2014), except for DNA extraction for a specimen from Panama, which was performed with Whatman FTA® card technology according to the manufacturer's protocol. Because of high legal restrictions against exporting cultures from Panama and the lack of a national culture collection,

isolation of strains was not attempted in Panama. Following the major contributions about Sebacinales, LSU rDNA sequences were adopted for the present study. For phylogenetic estimates, sequences of Sebacinales, Clade A (Weiß et al. 2011), were selected from matches of BLAST searches at GenBank and recent publications (Crous et al. 2014, Garnica et al. 2013, Oberwinkler et al. 2014, Rungjindamai et al. 2008, Selosse et al. 2009, Tan et al. 2014, Tangthirasunun et al. 2014, Weiß & Oberwinkler 2001, Weiß et al. 2011, Wells et al. 2004). *Paulisebacina allantoidea* (R.Kirschner & Oberw.) Oberw., Garnica K.Riess & R.Kirschner was chosen as outgroup (Oberwinkler et al. 2014). Except for trimming the ends of the alignment block obtained with the default options of MUSCLE in MEGA6, no further manipulation was undertaken. Relationships were estimated with Maximum Likelihood using the Kimura-2 model with gamma distribution as best model and 1000 bootstrap replicates. An unrooted tree with the species names and GenBank accession numbers is shown in Fig. 1. Specimens from Panama and Taiwan were dried on an electrical dryer and deposited at the herbaria of the Autonomous University of Chiriquí, Panama (UCH) and the National Museum of Natural Science, Taichung, Taiwan (TNM), respectively.

Results

The specimen from Panama morphologically identified as *Chaetospermum camelliae* clusters with high support in the clade of *Ch. camelliae* (Fig. 1). BLAST searches revealed matches between the specimen from Panama (GenBank accession KY304487) and sequences of *Ch. camelliae* with similarities of 99–100% with 0–7 deviating positions, whereas there were eight deviating positions (99% similarity) in *Ch. chaetosporum* (Pat.) A.L.Sm. & Ramsb. and more in other species (similarity 98% and lower). *Chaetospermum camelliae* represents a new record for Panama. Some sporomata contained conidiophores and conidia, but others basidia and basidiospores (Fig. 2). A sequence from an *Efibulobasidium*-like specimen from Taiwan (GenBank KY304488) clustered with low support with the monotypic genus *Globulisebacina* (Fig. 1). Since the morphology of this specimen (Fig. 3) conforms to the morphological concept of *Globulisebacina*, it is described as new species in this genus.

Taxonomy

Chaetospermum camelliae Agnihothr., Mycopath. Mycol. appl. 16: 115 (1962) Fig. 2

Fresh CONIDIOMATA AND BASIDIOMATA superficial, pustulate, subglobose, gelatinous, hyaline with opaque white core, easily detachable from the substrate, 0.2–0.6 mm diam., solitary, adjacent pustules forming aggregated pustules up to 1 mm wide, with individual ones still recognizable. HYPHAE gelatinized, efibulate, hyaline, anastomosing, in the outermost part of the sporoma wall up to 3 µm wide, in the inner part hyphidia-like, 1–1.5 µm wide and having irregular nodular outgrowths and branches, basal hyphae parallel, strongly agglutinated without space between, 1–4 µm wide.

ANAMORPH: Basal hyphae giving rise to prostrate and profusely branching hyphae which form conidiophores. CONIDIOPHORES profusely branched, up to ca. 80 µm high, cells 2–3 µm wide. CONIDIOGENOUS CELLS arising in terminal and subterminal whorls of 1–4 on ca. 3–11 µm long and 2–3 µm wide branch cells, almost terminal, exceptionally intercalary, flask-shaped, 8–14 × 2–3 µm, or particularly during maturation of the conidia becoming elongated, slender filaments, ca. 35–45 × 1–2 µm, eventually

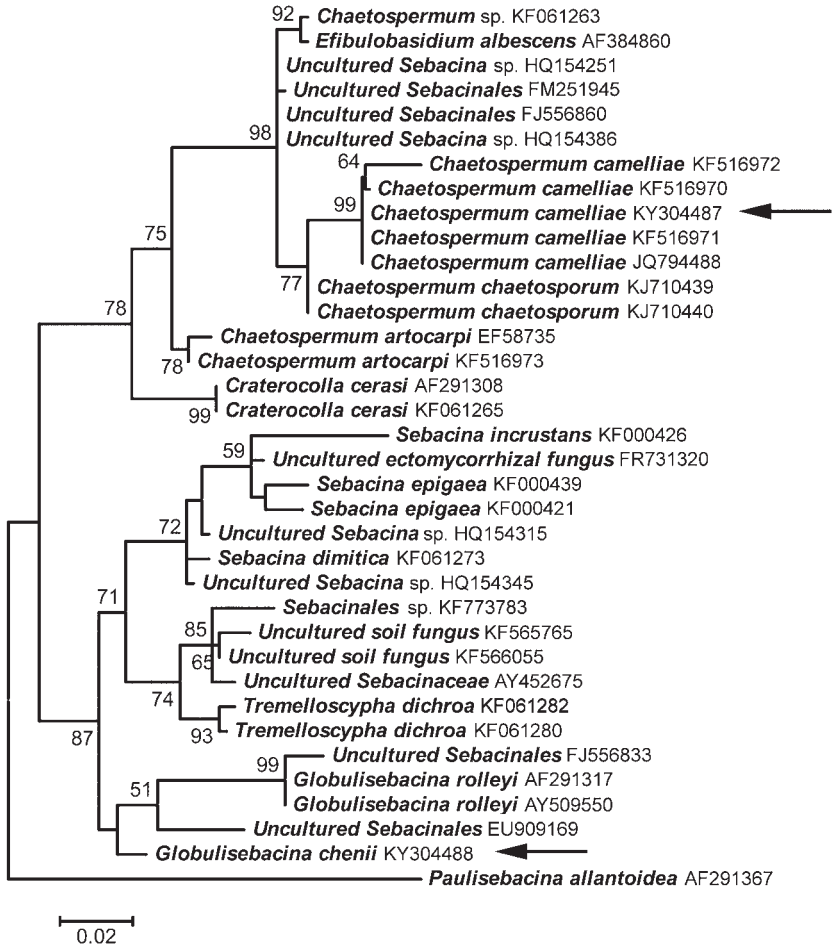
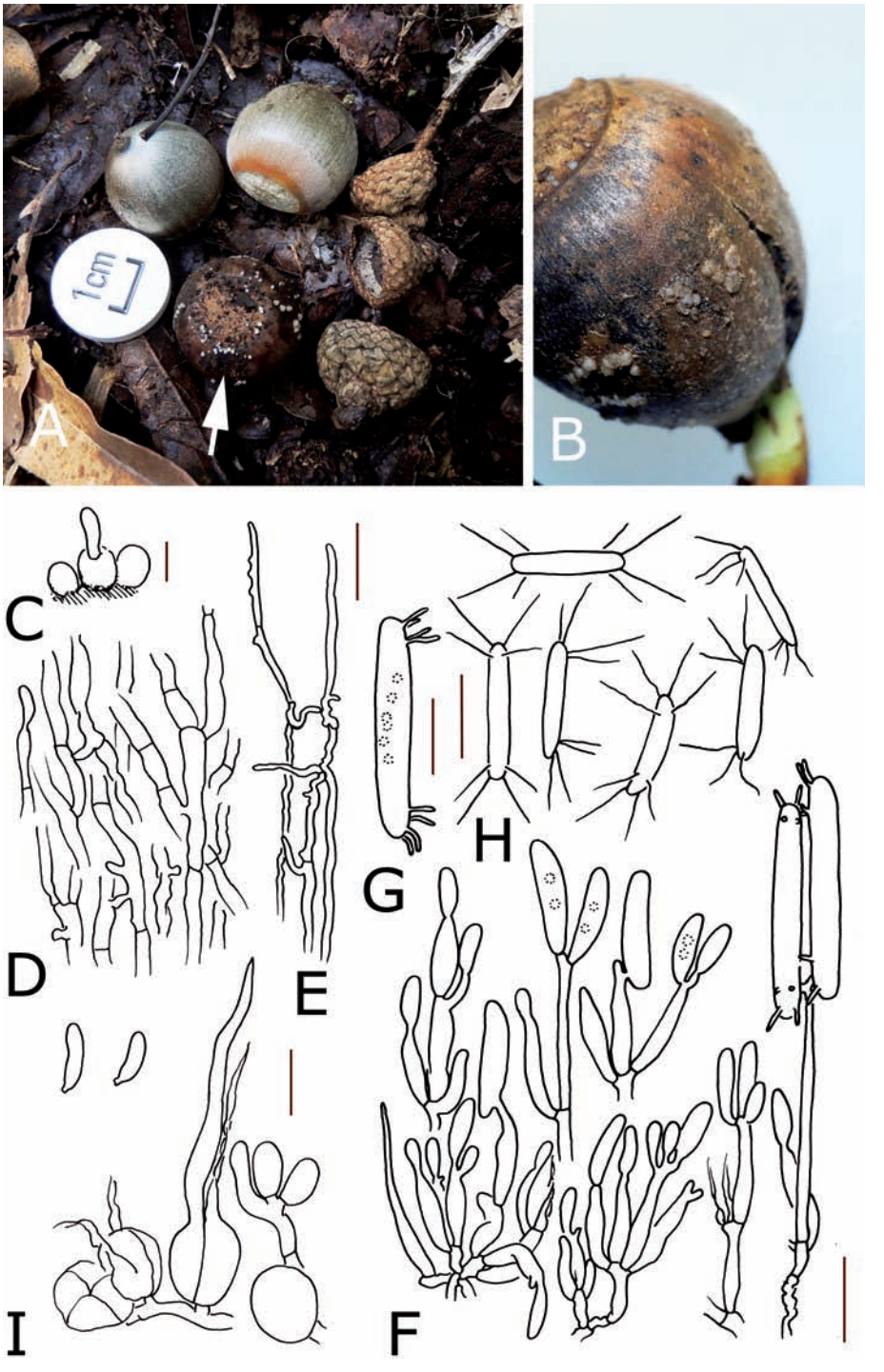


Fig. 1. Phylogenetic hypothesis derived from Maximum Likelihood analysis of partial LSU rDNA sequences of selected Sebacinales with their respective GenBank accession numbers performed with MEGA6. The two new sequences from this study are marked with arrows. Bootstrap values above 50% of 1000 replicates shown at the branches.

Fig. 2. *Chaetospermum camelliae*. A. Photograph from habitat showing nuts and cupules of *Quercus* sp. and white pustules of *Ch. camelliae* (arrow). B. Photo showing germinating nut with *Ch. camelliae* on the pericarp. C. Pycnidia, the middle one with extruded spore mass on the top after squeezing. D–E. Hyphae from outer (D) and inner (E) pycnidial wall. F. Conidiophores and developing conidia. Nuclei in young conidia indicated with dotted lines. G. Conidium with developing appendages. Nuclei or vacuoles indicated with dotted lines. H. Mature conidia. I. Basidia and basidiospores of the *Efibulobasidium* teleomorph. Scale bars: C = 0.5 mm, D–G, I = 10 μm, H = 20 μm.


A
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collapsing and only leaving remnants of cell walls on the conidiophore. Conidia formed directly on the conidiogenous cell when young or sympodially on short, 1–3 × 1 µm denticles during maturation, during which the point of attachment becomes displaced from the future base of the conidium. Young conidia appearing binucleate in Kongo Red and phase contrast, becoming multi-nucleate (or vacuolate?) during maturation when appendages are sprouting out from both ends, but nuclei or vacuoles not distinct anymore in conidia with fully developed appendages. Mature conidia cylindrical, straight or slightly bent, (22–)25–29(–33) × (4–)5(–6) µm (n = 50), appendages developing continuously with the cell lumen of the conidium, with an apical and a subapical pair of filamentous appendages each at each end, i.e. typically with four appendages at each end; some appendages destroyed or not fully developed so that the number is lower, 10–20 × 0.5 µm. Conidia extruding as white cirrhus from the top of the young conidioma when it is laterally squeezed with a pair of tweezers.

Teleomorph: Basidia found in identical pustules on nuts after one week of incubation at ca. 8°C, developing directly from a 1 µm short stalk without clamp connection, subtending hyphae proliferating in order to form further basidia so that 2–3 basidia become clustered, ellipsoidal when young, subglobose to broadly ellipsoidal when mature, longitudinally 2- or 4-septate, but only two sterigmata per basidium found, up to 80 × 3 µm, basidial body 11–13 × 10–11 µm. Basidiospores rare, slightly allantoid, 8–11 × 2.5–3 µm.

Specimen examined: Panama, Prov. Chiriquí, Parque Nacional Volcán Barú, Paso Ancho, trail to summit of volcano, forest, ca. N08°48'53.7"W082°34'47.9" ± 8 m, 1900–2000 m, on pericarp of germinating nuts of *Quercus* sp. on the ground, 1. August 2016, R.Kirschner et al. 4308 (UCH).

Notes: Fonseka (1960) and Nag Raj (1964) also indicated the lateral displacement of the conidium base as well as elongation of conidiogenous cells and successive production of two or more conidia at different conidiogenous loci at the apex of the conidiogenous cell. We conclude that this conidiogenesis can be classified as sympodial. The presence of the dikaryon in the young conidium found in our study indicates that compatible sexual cytoplasmic fusion had taken place prior to conidiogenesis, i.e. conidiophore development is postsomatogamic according to the terminology of Clémençon (1997). The cell components in conidia at later stages of development could be interpreted as several nuclei or vacuoles and could not be resolved anymore in mature conidia with fully developed appendages. The formation of transversal septa prior or during germination shown by Fonseka (1960) indicate that mitotic divisions took place so that conidia could become multinucleate and after that multicellular at a late ontogenetic stage.

The identification of *Chaetospermum* followed the keys given in Nag Raj (1993) and Rajeshkumar et al. (2010). Marincowitz et al. (2010) listed the known substrates and geographic distribution of *Ch. camelliae*, which has additionally been recorded from Thailand (Tangthirasunun et al. 2014). When summarizing the molecular-based distribution of sebacinoid mycorrhiza, Oberwinkler et al. (2013a) concluded that *Efibulobasidium/Chaetospermum* may be saprobic rather than mycorrhizal. Tan et al. (2014) isolated a new *Chaetospermum* species from orchid roots, which may indicate some endophytic or mycorrhizal interaction. Weiß et al. (2011) classified DNA sequences from roots of herbaceous plants as endophytic in a clade of *Chaetospermum*/

Efibulobasidium. The occurrence of sporomata on the pericarp of germinating *Quercus* seeds may facilitate an early interaction between the germinating root and the fungus.

Following Wells (1975), the teleomorph could be identified as *Efibulobasidium*. The sizes of basidia and basidiospores are smaller than in the other three species, *E. albescens* (Sacc. & Malbr.) K.Wells, *E. dimorphobasidii* Maham., Kund. & M.S.Patil, and *E. patiliense* Maham., Kund. & M.S.Patil (Kisimova-Horovitz et al. 2000, Mahamulkar et a. 2002, Wells 1975). The sizes are similar to those of *E. rolleyi*, but the spores are more slender relatively to their width than those of *E. rolleyi*. The teleomorph of *Ch. camelliae* is, therefore, not identical to a previously described species of *Efibulobasidium*.

Globulisebacina chenii R.Kirschner, **sp. nov.** Fig. 3

Index Fungorum IF552811

Fresh BASIDIOMATA superficial, pustulate, subglobose, gelatinous, hyaline, easily detachable from the substrate, less than 1 mm in diam., solitary. Hyphae and hyphidia efibulate, hyaline, irregularly branched, 1.5–2.5 µm wide. BASIDIA sessile or developing directly from a 1 µm short stalk on the subtending hypha without clamp connection, subtending hyphae proliferating in order to form further basidia so that 2–3 basidia become clustered, ellipsoidal to broadly ellipsoidal, longitudinally one-septate, with two sterigmata per basidium, up to 53 × 2–3 µm, basidial body 11–15 × 7–9 µm. BASIDIOSPORES rare, allantoid, 17–24 × 4–5 µm, germinating with secondary spores. No conidiomata in culture.

SPECIMEN EXAMINED: Taiwan, Taipei, Yangmingshan, 200–1120 m, on rotting branch on ground, 6. June 2012, R.Kirschner 3653 (HOLOTYPE, TNM).

ETYMOLOGY: In honor of Chee-Jen Chen, who contributed great progress to the taxonomy and application of jelly fungi in Taiwan. The first and second author would like to thank him for his friendship and help during the last decades.

NOTES: The species differs from *G. rolleyi* by its longer basidiospores and basidia. Although *E. dimorphobasidii* and *E. patiliense* are invalidly published (www.index-fungorum.org) and need recollection and clarification whether they phylogenetically belong to *Efibulobasidium* or to *Globulisebacina*, they are compared here, too. The new species differs from them by its two-celled basidia, whereas basidia are four-celled in the other two species, and by its broader (4–5 µm) basidiospores compared to those from the two species from India (3–4 µm, Mahamulkar et al. 2002).

Validation of *Sebacina* species

Sebacina pseudocandida Oberw., **nom. nov.**

Index Fungorum IF552812

≡ *Sebacina candida* (Schwein.) Oberw., Garnica & K.Riess, in Oberwinkler, Riess, Bauer & Garnica, Mycol. Progr. 13(3): 468 (2014), nom. illegit., because later homonym of *Sebacina candida* L.S.Olive, Bull. Torrey bot. Club 85: 21 (1958) ≡ *Exidiopsis candida* (L.S.Olive) K.Wells, Mycologia 53(4): 334 (1962)

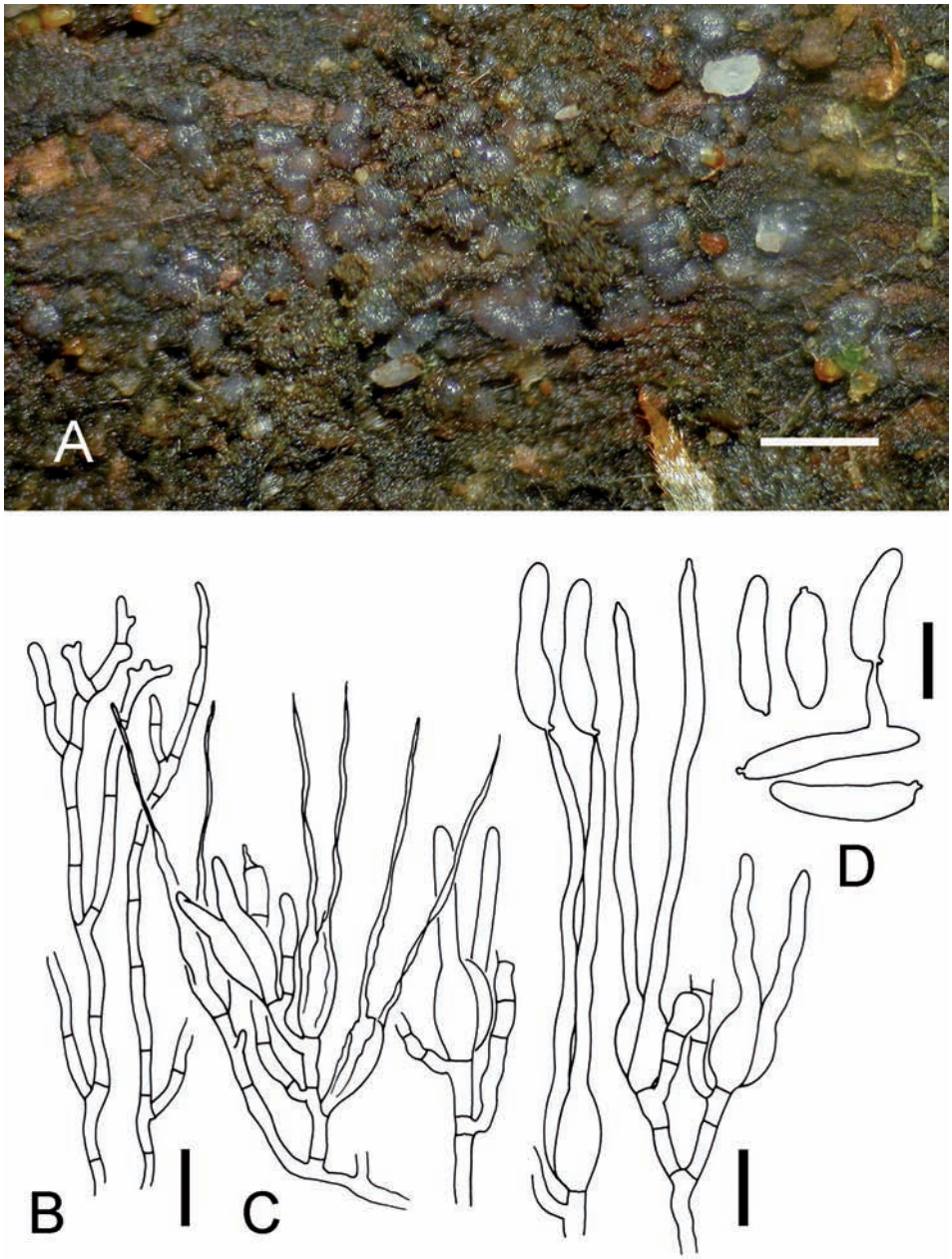

Fig. 3. *Globulisebacina chenii*. A. Photograph showing pustulate basidiomata on the woody substrate. B. Hyphidia. C. Basidia. D. Basidiospores. Scale bars: A = 1 mm, B–D = 10 μm.

Sebacina schweinitzii (Peck) Oberw., **comb. nov.**

Index Fungorum IF552813

Basionym: *Thelephora schweinitzii* Peck, Ann. Rep. N.Y. St. Mus. nat. Hist. 29: 67 (1878) [1876]

≡ *Sebacina pallida* (Schwein.) Oberw., Garnica & K.Riess, in Oberwinkler, Riess, Bauer & Garnica, Mycol. Progr. 13(3): 468 (2014), nom. illegit., based on illegitimate basionym *Thelephora pallida* Schwein., Trans. Am. Phil. Soc., Ser. 2, 4 (2): 186 (1832), later homonym of *Thelephora pallida* (Pers.) Pers. 1800

Discussion

The distinction between *Efibulobasidium* and *Globulisebacina* is based on the absence of conidiomata in *Globulisebacina* and by the positions in different molecularly based phylogenetic clades (Oberwinkler et al. 2014). The weak support of the clade containing the type and the new species may indicate insufficient sampling for this genus. This hypothesis is supported by two sequences from environmental samples classified as root endophytes from *Allium triquetrum* L. and *Papaver rhoeas* L. (GenBank EU909169, Selosse et al. 2009; FJ556833, Weiß et al. 2011) in the same clade. Sequence FJ556833 is closely related to those of *G. rolleyi* (Fig. 1). Presently, data are not sufficient for segregating a new genus so that the new species is tentatively placed in *Globulisebacina*.

Although conidium development in *Chaetospermum* was investigated in previous studies (Fonseka 1960, Nag Raj 1964), it was not yet classified with the standard terminology as sympodial and postsomatogamic. Since conidia are produced in slimy masses, they may serve for passive short-distance dispersal by water, whereas the actively discharged basidiospores may be responsible for the widespread occurrence in different regions and in diverse plant associations (Weiß et al. 2011). Several sequences labeled as "uncultured *Sebacina* sp." or "uncultured Sebacinales" (Garnica et al. 2013, Weiß et al. 2011) represent unidentified *Chaetospermum* species, i.e. undescribed species or described species for which sequence data are lacking. Although there is no doubt that *Chaetospermum* Sacc. 1892 is congeneric with and has precedence against *Efibulobasidium* K.Wells 1975, taxonomic conclusions on the species level are not yet possible due to the lack of robust data (Oberwinkler et al. 2014).

Paulisebacina allantoidea is a good example how biodiversity informatics and traditional approaches complement each other. This fungus was first described as a *Sebacina* species based on traditional field collection and morphology (Kirschner & Oberwinkler 2002), then revealed to be a widespread root endophyte by molecular approaches and to form a separate lineage within the Sebacinales (Weiß et al. 2011); it was eventually transferred to a new genus, *Paulisebacina* Oberw., Garnica & K. Riess (Oberwinkler et al. 2014). The discovery of the teleomorph of *Ch. camelliae* and the new species described in this study illustrate the importance of further field collections and accurate morphological analysis for complementing the information associated with the accumulated sequence data which could not yet be connected to scientific names. By further field collections, also species, hitherto only known by DNA sequences, such as the two sequences of "uncultured *Sebacina*" in Fig. 1, will then be connected to a specific morphology and ecology. The biodiversity informatics

approach based on environmental samples and sterile cultures urgently needs to be complemented by concrete approaches, which include comparison of the unknown with known taxa, also considering those lacking sequence data, and characterization and preservation of physical specimens as a basis for scientific reproducibility.

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