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Gloiocephala pilosella Corriol & Jargeat, sp. nov., a new foliicolous marasmioid Basidiomycota from the French Pyrenees and position of the neotropical *Gloiocephala spathularia* Singer

Gilles CORRIOL & Patricia JARGEAT

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Gloiocephala pilosella Corriol & Jargeat, sp. nov., a new foliicolous marasmioid Basidiomycota from the French Pyrenees and position of the neotropical *Gloiocephala spathularia* Singer

Gilles CORRIOL
Conservatoire botanique national des Pyrénées et de Midi-Pyrénées
Vallon de Salut. B.P. 315, 65203 Bagnères-de-Bigorre Cedex (France)
gilles.corriol@cbnpmp.fr (corresponding author)

Patricia JARGEAT
Université de Toulouse, Centre national de la Recherche scientifique (CNRS),
Institut de recherche pour le développement (IRD), Institut national polytechnique (INP),
Centre de Recherche sur la Biodiversité et l'Environnement (CRBE)
118 route de Narbonne, 31062 Toulouse Cedex (France)

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ABSTRACT
Gloiocephala pilosella Corriol & Jargeat, sp. nov., a new marasmioid species within the Physalacriaceae Corner, is described based on anatomical and molecular analyses. Morphologically similar marasmioid species of the families Physalacriaceae and Marasmiaceae Roze ex Kühner are compared. Within the polyphyletic genus *Gloiocephala* Massee, none of the documented or molecularly related species express close morphological similarity to *Gloiocephala pilosella*. This new species is distinguished by its pileipellis and stipitipellis featuring long sclerified hairs, comparatively smaller spores, and capitate hymenial cystidia. Additionally, *Gloiocephala spathularia* Singer is briefly described and illustrated with a colour photograph based on an Amazonian collection. The LSU sequence of this collection suggests its exclusion from the genus *Gloiocephala*. The boundaries between *Gloiocephala* and related genera are discussed, and the new combination of the last into the genus *Physalacria* Peck is introduced.

KEY WORDS
France,
molecular phylogeny,
Physalacriaceae,
new species.

RÉSUMÉ
Gloiocephala pilosella *Corriol & Jargeat, sp. nov., un nouveau basidiomycète marasmioïde foliicole des Pyrénées françaises et position du néotropical* Gloiocephala spathularia *Singer.*
Gloiocephala pilosella Corriol & Jargeat, sp. nov., une nouvelle espèce de Physalacriaceae marasmioïde est décrite sur des bases anatomiques et moléculaires. Les espèces marasmioïdes de Physalacriaceae et Marasmiaceae morphologiquement similaires sont comparées. Au sein du genre polyphylétique *Gloiocephala* Massee, aucune des espèces documentées ou moléculairement apparentées ne sont morphologiquement comparable à celle que nous présentons. Elle se distingue notamment par ses revêtements piléiques et caulinaires pourvus de longs poils sclérifiés, ses spores relativement petites, ses cystides hyméniales capitées. *Gloiocephala spathularia* Singer est brièvement décrit et illustré d'une photographie en couleur sur la base d'une récolte amazonienne. La séquence LSU de cette récolte suggère son exclusion du genre *Gloiocephala*. Les limites entre les deux genres sont discutées et une nouvelle combinaison dans le genre *Physalacria* Peck est proposée.

MOTS CLÉS
France,
phylogénie moléculaire,
Physalacriaceae,
espèce nouvelle.

INTRODUCTION

The inventory of the agaricoid fungal flora of the Pyrenees is far from complete and still has plenty of surprises in store. Indeed, several new species were described, some highly taxonomically original (Corriol & Moreau 2007; Corriol & Jargeat 2018), and others related to genera found typically in the tropics such as *Pyrrhoglossum* Singer (Corriol 2009), *Cyptotrama* Singer (Moreau *et al.* 2015), *Dennisiomyces* Singer (Corriol & Jargeat 2019), and a *Leucoagaricus* Locquin ex Singer with a blue-green pigment reaction (Corriol & Chalange 2020). A new marasmioid species related to the genus *Gloiocephala* Massee, which also has an essentially tropical distribution (Singer 1976; Antonín 2007), was found, in the Pyrenees, in France.

The genus *Gloiocephala* Massee, was introduced by Massee (1892) for a tropical foliicolous species collected in Jamaica, resembling a miniature Agaricales, with a smooth hymenium and a pseudoparenchymatous pileipellis bearing numerous large, projecting cystidia embedded in a mucus. The type species, *G. epiphylla* Massee, has been reported from Argentina, Ecuador, Venezuela (Singer 1976), Brazil (Pegler 1997), New Caledonia (Horak & Desjardin 1994), Taiwan (Chang & Ju 2017) and seems to have a pantropical distribution. Subsequently, several dozen species were described around the world, mainly in intertropical area: South America (Singer 1960), Sri Lanka (Pegler 1986), Australasia (Horak & Desjardin 1994), India (Manimohan & Thomas 1998), Africa (Antonín 2003, 2007), South China (Adamčík *et al.* 2015). In Europe, only five species are recognized by Antonín & Noordeloos (2010), all of them rare or overlooked.

Singer (1976) defined the genus *Gloiocephala* within the tribe Marasmieae Fayod as producing sessile or stipitate fruiting bodies with lateral, eccentric, or central stipes. The hymenophore is undifferentiated and can be vein-like, merulioid, or lamellate. The pileipellis is hymenodermic, and both hymenial and pileal cystidia are present. Spores are inamyloid, though rarely partially dextrinoid. Antonín & Noordeloos (1993) and Bon (1999) considered this genus to be part of *Marasmius* within the family Marasmiaceae. Later, Antonín & Noordeloos (2010) recognized *Gloiocephala* as a distinct genus in the Physalacriaceae, following the molecular results of Wilson & Desjardin (2005) and Binder *et al.* (2006). Their circumscription of the genus remained largely consistent with that proposed by Singer, although they included a recently described centrally stipitate species, *Gloiocephala cerkezii* Tkalčec & Mešić.

Moreau *et al.* (2015) provided a phylogenetic reconstruction of Physalacriaceae, incorporating the marasmioid genera *Gloiocephala*, *Cryptomarasmius* T.S.Jenkinson & Desjardin, and *Rhizomarasmius* R.H.Petersen into an updated concept that also included the typical marasmioid species *Marasmius setosus* (Sowerby) Noordel. They emphasized the difficulty of circumscribing such a monophyletic genus, molecularly closely related to *Gloiocephala*, and the need to improve molecular sampling, particularly for tropical species of *Gloiocephala*. Molecular analyses indicate that the delimitation of *Gloiocephala* and *Physalacria* within the Physalacriaceae is not straightforward since a sequence attributed to *Gloiocephala spathularia* Singer is close to *Physalacria* (Binder *et al.* 2006).

Berthier (1985), after Corner (1950), characterized the genus *Physalacria* as producing small, erect or pendulous, whitish basidiomata with diminutive capitula. These structures feature either an amphigenous hymenium or a peltate hymenium restricted to the upper surface, along with emerging hymenial cystidia, a caulocystidiate stipe, and smooth, hyaline, inamyloid spores. Singer (1986) further described the genus as having a lacunose pileus and a pseudostipe that is not negatively geotropic. Although this last characteristic is relevant, it does not appear to be exclusive, as De la Peña-Lastra *et al.* (2022) described a species exhibiting negative geotropism that was molecularly confirmed to belong in *Physalacria*. Notably, Corner (1950) had already emphasized the lacunose structure of the fertile head in *Physalacria*.

In line with its traditional range, this predominantly tropical and southern-hemisphere genus now comprises around forty species (Corner 1950; Berthier 1985; Antonín 2007; Qin & Yang 2016). In Europe, only three species of *Physalacria* are known to date, including two naturalised species (Laessøe & Spooner 1993; Reid 1997; Cochard & Réaudin 2019; De la Peña-Lastra *et al.* 2022).

Gloiocephala spathularia, which is molecularly closer to *Physalacria*, possesses an inferior hymenium and a hymenodermal pileipellis – features that likely influenced Singer's decision to assign it to *Gloiocephala*. At present, anatomical distinctions between the two genera remain challenging, due to the limited sequence data available for several species traditionally placed in *Gloiocephala*.

Based on an Amazonian collection we morphologically identified as "*Gloiocephala*" *spathularia* and included in our phylogenetic analysis, we re-examine the circumscription of the genera *Gloiocephala* and *Physalacria*, seeking diagnostic features that could justify the placement of this species in *Physalacria,* and we propose a new combination accordingly.

MATERIAL AND METHODS

Morphological description

Basidiomata were described on the fresh specimens and photographed *in situ* and under binocular lens. Colours were coded based on Munsell Soil Color Charts (2000). Microscopy observations were performed on fresh material in distilled water and in Congo red (Clemençon's formula), Melzer's reagent. Spore measurements, made on N spores observed on spore print in distilled water, are presented according to the D1,9 format: [N] (mini) d1-*median*-d9 (maxi), where d1 and d9 are the 1st et 9th deciles (Fannechère 2006). The length/width rate (Q) was recorded following the same rules. As for the other elements, only minimum and maximum dimensions were indicated. Microscopic images were taken using an Amscope MU500 camera mounted on the trinocular tube of a Zeiss Axiostar plus microscope equipped with Zeiss 40× planachromatic and 100× planapochromatic lens. Unless

otherwise indicated the scale bars on the microscopy picture chart represent ten micrometers.

Studied material

The speciemens GC19112202 and GC23110104 collected in Fance (Hautes Pyrénées) in 2019 and 2023 and one specimen collected in Guyana (GC19062402) in 2019, were described and submitted to molecular analysis.

Molecular analysis

Total DNA was extracted from the three specimens using the Wizard Genomic DNA kit (Promega). The ITS1-5.8S-ITS2 region (ITS, Internal Transcribed Spacer) was amplified by PCR (Polymerase Chain Reaction) for GC19112202 and GC23110104 samples, using the primer pair ITS1-F / ITS4-B (Gardes & Bruns 1993). Part of the DNA coding for 28S ribosomal RNA was amplified for GC19112202 and GC19062402 specimens, using LR0R/LR7 primers (Vilgalys & Hester 1990). PCR conditions were as in Jargeat *et al.* (2010). Sequencing was performed by Eurofins Genomics (Ebersberg, Germany).

Sequences were edited and corrected manually using the BioEdit software (Hall 1999). LSU sequences (780 positions) and combined ITS and LSU sequences (1640 positions), along with a set of GenBank sequences from specimens belonging to Physalacriaceae were aligned with MAFFT v6.814b (Katoh *et al.* 2002), without filter, using Geneious® 9.0.5. PhyML method (Guindon & Gascuel 2003) was used via the Geneious® plateform to generate maxim likelihood phylogenetic tree with the following settings: GTR substitution model, 100 bootstraps, estimated transition/transversion ratio, estimated proportion of invariable sites, estimated gamma distribution, branch length and substitution rate optimized. Phylogenetic trees were visualized and edited with MegaX (Kumar *et al.* 2018). Sequences are available under accession number PQ785771 to PQ785773 (*Gloiocephala*) and PV389261 (*Physalacria*).

RESULTS

Phylogenetic analyses

A preliminary phylogenetic analysis was conducted with LSU sequences from all the genera belonging to Physalacriaceae (data not shown). This allowed us to select sequences to generate a more readable tree (Fig. 1). Although the bootstraps values were weak for several branches, this analysis revealed that the sequence of the French specimen GC19112202 was clustered to the *Gloiocephala* genus while the sequence from the Guyana specimen GC19062402, morphologically identified as *Gloiocephala spathularia* was included in the *Physalacria* genus, close to *Physalacria inflata* (Fr.) Peck BD347 (DQ284915) from Minnesota (USA) and *G. spathularia* JMCR.15 (AF261349, Moncalvo *et al.* 2002).

The *Rhizomarasmius*-clade encompassed *Gloiocephala*, including *Cyptotrama*, *Rhizomarasmius*, *Laccariopsis* Vizzini and *Cibaomyces* Zhu L.Yang, Y.J.Hao & J.Qin. It was noteworthy that *Rhizomarasmius cunninghamietorum* Chun Y.Deng, J.P.Li & Gafforov is not included in the genus *Rhizomarasmius.*

Phylogenetic analysis of combined ITS and LSU (1640 positions), focusing on *Rhizomarasmius*-clade, including *Cyptotrama*, revealed that this genus was in basal position and was excluded from the *Rhizomarasmius*-clade (Fig. 2). This analysis clearly placed the two Pyrenean specimens into a monophyletic clade, encompassing several *Gloiocephala* species and other unnamed sequences belonging to Physalacriaceae. The closest ITS sequences available in GenBank were that of the holotype collection of *G. resinopunctata* Manimohan & K.A. Thomas (88% identity on 764 positions), described from tropical India and JN225055, and an ITS sequence of a Physalacriaceae from New-Zealand lacking a description (90% identity on 741 positions).

If we exclude *R. cunninghamietorum,* as suggested by the LSU-analysis, the *Gloiocephala* clade is sister to the genus *Rhizomaramius* (Physalacriaceae). This analysis also revealed that *Gloiocephala phormiorum* E. Horak & Desjardin is not included in the *Gloiocephala*-clade.

Taxonomy

Family Physalacriaceae Corner
Genus *Gloiocephala* Massee

Gloiocephala pilosella Corriol & Jargeat, sp. nov.
(Fig. 3)

Diagnosis. — *Basidiomata marasmioidea, hymenium paucis lamellis pliciformibus instructum,* Marasmium favrei *Antonín referens; pileipellis et stipitipellis pilosa cum numerosis sclerocystidiis subulatis, pileipellis hymenodermica, cystidiis hymenialibus lagenicapitatis, sporis fusiformibus mediocribus 9.4 × 3.6 µm (Q = 2.7), tramate non-dextrinoidea, fibulis praesentibus, foliicola*.

Type material. — **France** • Hautes-Pyrénées, Castet of Gerde; 620 m alt.; 22.XI.2019; *leg. G. Corriol*; BBF[GC19112202]; GenBank: PQ785771 (ITS), PQ785773 (LSU).

Additional material examined. — **France** • Hautes-Pyrénées, Castet of Gerde; 620 m alt.; 1.XI.2023; *leg. G. Corriol*; BBF[GC23110104]; GenBank: PQ785772 (ITS); holotype: GC19112202 *in herbario* BBF.

Etymology. — Refers to the pilose pileus and stem due to abundant pileocystidia and setiform caulocystidia.

Mycobank. — MB861261; GenBank: PQ785771 (ITS), PQ785773 (LSU).

Habitat. — Both collections were found in deep wet litter under tussocks of the fern *Asplenium scolopendrium* L. in a young broadleaf forest on freshly exposed (north-east) slope at collinean level, under Atlantic humid umbroclimate, on dead leaves of broadleaf trees: *Acer platanoides* L. (holotype) and *Betula pendula* Roth (GC23110104).

Locality. — France, Hautes-Pyrénées, Castet of Gerde.

Description

Pileus 1.5-3 mm in diameter, irregularly convex, with slight central depression and inflexed sinuate margin; surface pure white, mate, densely minutely hairy under length.

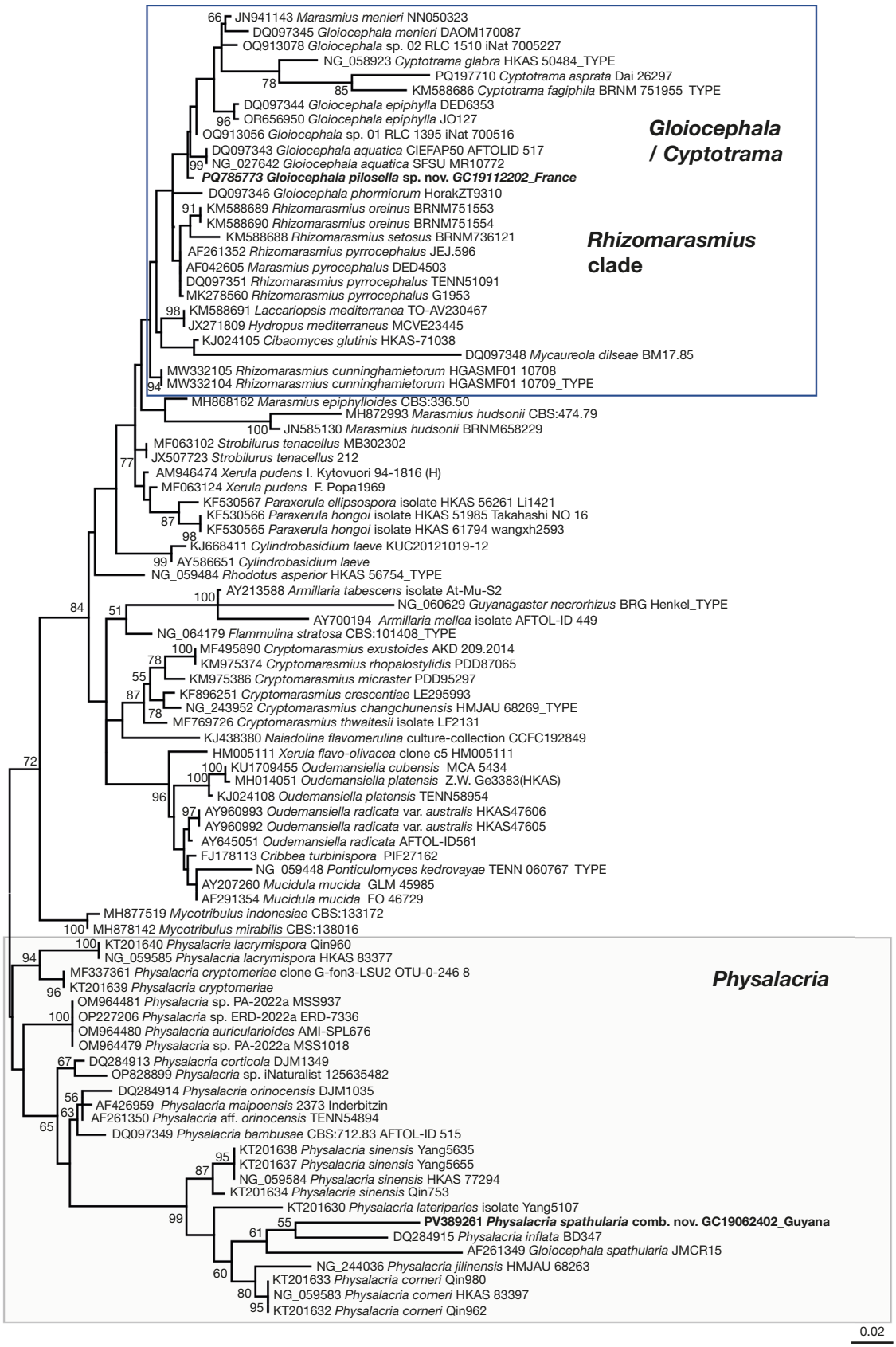

FIG. 1. – Maximum-likelihood phylogenetic analysis based on LSU sequences from our samples (in **bold**) and from selected GenBank sequences. The tree was obtained by using PhyML on the Geneious® plateform. Bootstrap values above 50% are indicated on branches.

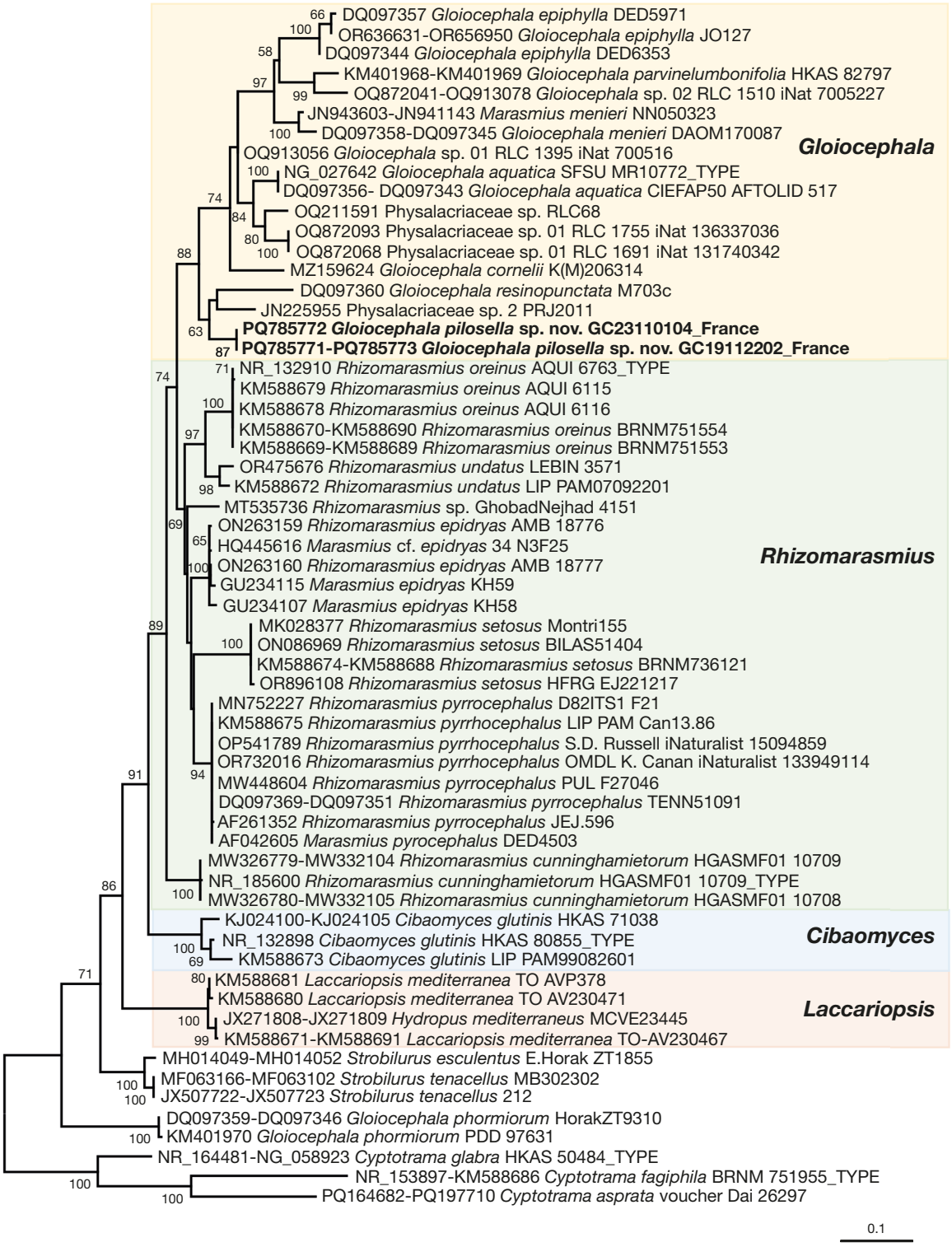

Fig. 2. – Maximum-likelihood phylogenetic analysis based on combined ITS and LSU sequences from our samples (in **bold**) and from a selected GenBank dataset. The tree was obtained by using PhyML on the Geneious® plateform. Bootstrap values above 50% are indicated on branches.

Hymenium pliciform to venose, with 3-6 incomplete folds adnate on stem, not reaching margin, to almost smooth, white concolour.

Stem 8-15 × 0.1 mm, insititious, flexuose-sinuose, surface reddish brown, blackish brown at base and whitish at apex, shiny, initially entirely hairy under lens, more densely near base.

Fig. 3. — Basidiomata from holotypus *in situ* on dead leaf of *Acer platanoides* L.: **A**, **B**, overview of basidiomata *in situ*; **C**, **D**, show detail of pliciform rudimentary hymenium; **F**, **G**, show hairy insititious stems; **H**, shows hairy (pileocystidious) cap. Scale bars: A, B, C, 5 mm; C, G, 3 mm; D, F, H, 2 mm. Photo credits: Gilles Corriol.

Flesh pellicular. odour not perceived.

Microscopy

Spores [N=25] (8.2)8.3-*9.4*-10.8(11.3) × (3.1)3.2-*3.6*-4.1(4.2) µm, Q= (1.94)2.22-*2.68*-2.96(3.00), fusiform or lacrymoid with thick apiculus, thin-walled, smooth, hyaline, inamyloid (Fig. 5A, B).

Basidia 14-22 × 5-6 µm, four-spored, slightly clavate, clamped.

Hymenial cystidia 25-49 × 5-10 µm, scattered, cheilocystidia (Fig. 5C-E) and pleurocystidia (Fig. 5F-I) similar, lageniform-subcapitate, sublecithiform, cylindrical-ventricose with capitate apex (× 2.7-5.8 µm) (Fig. 5), lamella edge fertile.

Pileipellis hymenodermioid, made of 16-32 × 7-13.5 µm lageniform, fusiform, ventricose to ampullate-appendiculate, occasionally forked, more or less thicken-walled elements (Fig. 4E, F), mixed with numerous protruding lageniform pileocystidia with long subulate neck, 18-70 × 5.5-12 × 1.5-2.5 µm, often with snake-headed apex (× 3-4 µm), distinctly thick-walled (wall × 0.5-1 µm), often rough, encrusted and occasionally brown-pigmented, containing small oily droplets (Fig. 4B-D, G-J).

Stipitipellis made of parallel, hyphae (60-80 × 2-3 µm, wall 0.7 µm thick), with brick red smooth intraparietal pigment (Fig. 5J); hairs 30-90 × 3.5-6 × 1.5-2 µm, abundant, more densely and longer towards the base subulate-sinuous, setiform, inflated at base, thick-walled with smooth brown intraparietal pigment.

No part of basidiome reactive to Melzer reagent (neither amyloid nor dextrinoid). No gelatinized tissue noticed. Clamps abundant in all parts of basidiome.

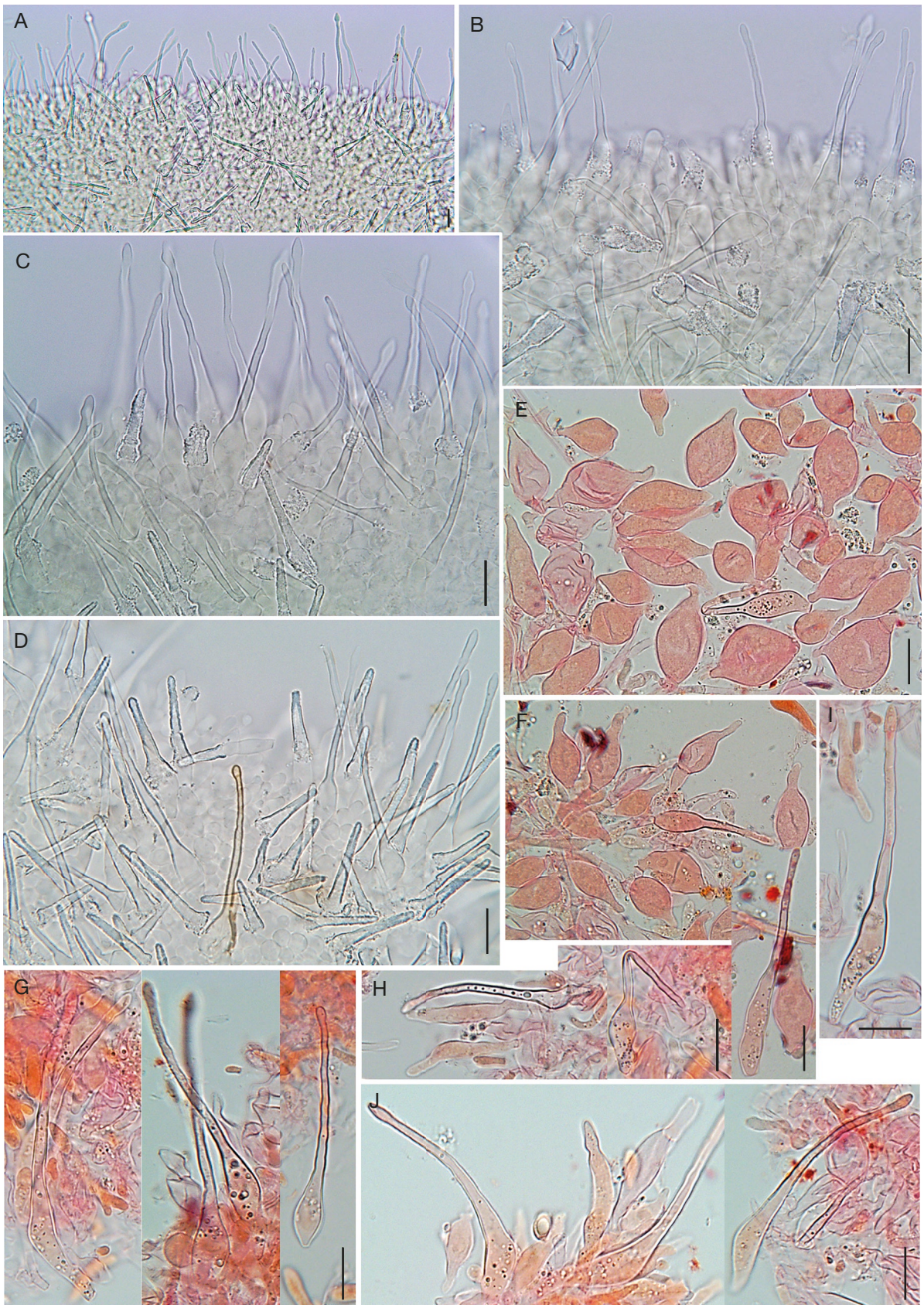

FIG. 4. – *Gloiocephala pilosella* Corriol & Jargeat, sp. nov. – microanatomical structures of the pileipellis: **A**-**C**, pileipellis showing numerous projecting pileocystidia; **B**, **C**, showing their long, thick-walled neck, swollen apex, and cristaliferous wide basis, from holotypus, in water; **D**, pileipellis in water showing rugulose-cristalliferous thickened neck and one brown pigmented thick walled pileocystidia, from GC23110104; **E**, **F**, ampullate-fusiform cells of pileipellis mixed with pileocystidia, from holotypus in Congo red; **G**-**J**, thick walled pileocystidia in Congo red. Scale bar: 10 µm. Photo credits: Gilles Corriol.

Macroscopical description based on a fresh specimen collected in Guyana

The specimen GC19062402, identified by us as *Gloiocephala spathularia*, is characterized by basidiomata with a spathulate pileus measuring up to 8 × 10 mm, lobate-cordiform (or heart-shaped) at stipe insertion (pseudostipe, see below in discussion), displayed a rough, whitish to creamy, slightly translucent irregular surface. The stipe was laterally fused to the upper part of the pileus, giving the appearance that the hymenium was suspended beneath the apex of the stipe, which was itself integrated into the pileus. The stipe reached dimensions of 10 × 0.7 mm and was entirely covered with pubescence, white at the top and yellowish at the base. Basidiomata were fasciculate, arising from a white mycelial subiculum. The hymenium was rugose to distinctly merulioid, whitish. The context was soft, membranous, and elastic (see Fig. 6).

Microscopical description based on exsiccatum collected in Guyana

Spores measured 3.5-4.5 × 2.3-2.5 µm, were ellipsoid, smooth, hyaline, and non-amyloid. Basidia are either tetrasporic and bisporic, cylindrical-fusiform, measuring 12.5-17 × 2.7-4 µm, with long (4 µm) and thin sterigmata. Hymenial cystidia were abundant, utriform in shape, with slightly thickened wall and crowned by crystalliferous deposits. Trama was aeriferous-lacunose, consisting of thick-walled, inamyloid, entangled hyphae. Pileipellis was an hymeniderm consisting of a palisade of terminal ampullate elements measuring 12-18 × 5.8-7.8 µm. Stipitipellis was covered by multiseptate hairs embedded in a yellowish resinous substance. Clamp connections were abundant in all parts of the basidiome.

Gloiocephala spathularia Singer

Material examined. — **France** • Guyana, Saül; 220 m alt.; 24.VI.2019; *leg. & det. G. Corriol*; BBF[GC19062402]; GenBank: PV389261 (LSU).

DISCUSSION

Based on phylogenetic analyses, we could conclude that our specimens from French Pyrenees and from Guyana, morphologically identified as *Gloiocephala*, actually belong to *Gloiocephala* and *Physalacria*, respectively. This study highlights the difficulty to define species belonging to the Physalacriaceae on the basis of morphology only.

The small pellicular pileus, insititious stipe, hymenodermioid pileipellis and hymenial cystidia of the specimen GC23110104 and GC19112202 suggest a placement to marasmioid genera of Agaricomycetideae Parmasto previously grouped in the genus *Marasmius* (Singer 1986; Antonín & Noordeloos 1993; Bon 1999). The combination of very small size, white pileus, vein-like reduced hymenium, foliicolous habitat, exclusively non-dextrinoid hyphae (even in stipititrama), smooth cells of hymeniderm, and presence of conspicuous pileocystidia, potentially matches with several groups in the traditional systematics of Marasmiaceae (Singer 1986). However, these characters have now been shown to be also present in various genera within the family Physalacriaceae (see for example Moreau *et al.* 2015; Voitk *et al.* 2022). The better morphological and ecological match for GC23110104 and GC19112202 seemed to be *Marasmius* sect. *Epiphylli* Kühner, which has been split into the genera *Rhizomarasmius* (Moreau *et al.* 2015) and *Owingsia* I. Saar, Voitk & Thorn (Voitk *et al.* 2022). However, several anatomical features of *Gloiocephala pilosella*, such as the concomitant presence of long, thick-walled and pigmented setiform caulocystidia, together with numerous sclerified pileocystidia bearing crystalline deposits, some of which are also pigmented, clearly distinguishes it from the species traditionally within the *Marasmius epiphyllus* (Pers.) Fr. clade. The morphological characters shared by *Gloiocephala* species and marasmioid genera phylogenetically related to the Physalacriaceae but traditionally treated within *Marasmius* sect. *Epiphylli* are a hymenodermoid epicutis with differentiated and sclerified and/or heterogeneous terminal cells (pileocystidia); a setulose or caulocystidiate stipitipellis (differentiated and often sclerified terminal cells); and a homomorphous hymenium with a fertile lamellar edge and scattered, morphologically similar cheilocystidia and pleurocystidia. *G. pilosella* could be confused in the field with *Marasmius favrei* Antonín. This taxon (and its variety *sorbi* Antonín) is traditionally treated in section *Epiphylli* of the genus *Marasmius*, and it shares some morphological similarities with *G. pilosella*. However, Antonín *et al.* (2010) demonstrated the phylogenetic affinity between *M. favrei* and "*Marasmius*" *epiphyllus* and not with the clade containing *Gloiocephala pilosella*.

Marasmius epiphylloides (Rea) Sacc. & Trotter, which shares the presence of sclero- pileo and caulocystidia with *G. pilosella*, likewise falls outside the *Gloiocephala* clade (Fig. 1). The remaining species, *M. saccharinus* (Batsch) Fr. and *M. helleboricorsici* Romagn., which both lack sclerocystidia, are currently not represented by molecular data.

Concerning *Owingsia*, it is worth noting that Voitk *et al.* (2022) did not attempt to circumscribe this new genus from *Gloiocephala* but a phylogenetic analysis including sequences from *Owingsia umbellifera* (L.) Voitk, I. Saar & Thorn indicates that this species is not related to the *Rhizomarasmius-Gloiocephala* clade (data not shown)

The genus *Rhizomarasmius* could also be mentioned, because *Marasmius setosus* (Sowerby) Noordel. was transferred there by Moreau *et al.* (2015), alongside several species presenting pigmented thicker pileus and densely brown tomentose thick stem, as well as a habitat on necrotic parts of vascular plants. *Marasmius setosus* with its white pileus and insititious pilose stem actually looks like our fungi in the field and it is likely that it has been previously mistaken with it in the past. But one can notice that its morphology is far from being homogenous with other species classified by Moreau *et al.* (2015) in the genus *Rhizomarasmius* making the definition of this genus, amended in this way, confusing.

It is noteworthy that *Gloiocephala*, *Owingsia* and *Rhizomarasmius* belong in Physalacriaceae, not in Marasmiaceae

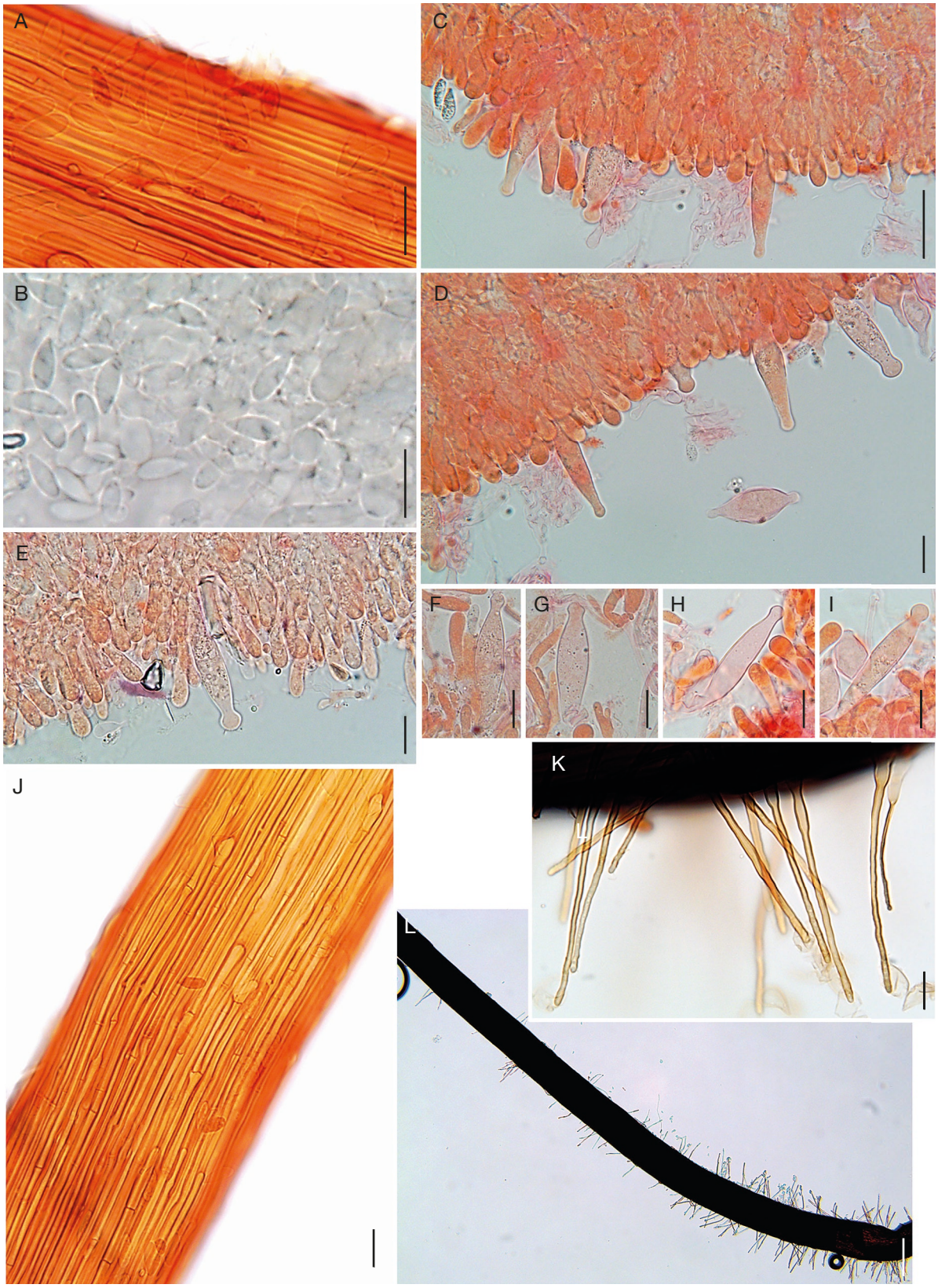

FIG. 5. – **A**, Spores (natural spore-print on stipitipellis), from holotypus, in water; **B**, spores on hymenium, from holotypus, in water; **C**, **D**, heterogenous lamella edge with scattered cheilocystidia, from holotypus, in Congo red; **E**, basidia and a cystidia, from holotypus, in Congo red; **F-I**, pleurocystidia, from holotypus, in Congo red; **J**, bottom of stipitipellis, scalp view, from holotypus, in water; **K**, stipitipellis setae, from GC23110104, in water; **L**, stipe with dense setae at base, from GC23110104, in water. Scale bars: A-J, 10 µm; L, 100 µm. Photo credits: Gilles Corriol.

Fig. 6. – *Physalacria spathularia* (Singer) Corriol & Jargeat, *in situ*, on old perithecium stroma on rotten wood; Saül, French Guiana; 24.VI.2019; *leg. & det. G. Corriol*; herb. GC19062402. Photo credits: Gilles Corriol.

(Binder *et al.* 2006; Antonín *et al.* 2010; Jenkinson *et al.* 2014; Voitk *et al.* 2022).

In the genus *Gloiocephala*, no species described in Europe has the remarkable set of microscopic characters observed in our collections (Antonín & Noordeloos 2010). The pileipellis and stipitipellis of *G. cornelii* (Lassøe & Noordel.) E. Horak bear some resemblance to those of our fungus, but the hymenial cystidia, spores, basidiomes and ecology are in no way comparable. *Gloiocephala cerkezii* Tkalčec & Mešić (Tkalčec & Mešić 2008), the only European *Gloiocephala* species with a centrally well-developed stem described so far, is a rusty brown-capped species, devoid of long sclerocystidia on stem and cap. *Gloiocephala menieri* (Boudier) Singer, has a *Campanella*-like brown crepidotoid basidomata growing on leaf-sheaths of *Typha* L., 15-22 µm long fusiform spores (average Q = 3.5) and lacks long sclerocaulocystidia. The two remaining European *Gloiocephala*, *G. caricis* (P. Karst.) Bas and *G. pseudocaricis* (Noordel.) Tkalčec & Mešić, are caricicolous species with reduced stem. They lack the typical long sclero-, pileo- and caulo-cystidia of *G. pilosella* and their spores are also much larger. Among these European species, only *G. cornelii* and *G. menieri* are molecularly documented so far and are included in our phylogeny.

In the Neotropics, following Singer's monograph (1976), *G. pilosella* would key out in subsection *Confusae* Singer and may be compared to *G. confusa* Singer and *G. epiphylla* Massee (the type of the genus). The first has almost acicular spores measuring 8-12 × 2.5-3.3 µm and a pileipellis lacking subulate pileocystidia, while the second has a smooth hymenium lacking cystidia (Singer 1960, 1976). In tropical Africa *G. albocapitata* (Petch) Singer shares with our fungus scleropileo- and caulo-cystidia, but they are much longer than those of *G. pilosella*, and lagenicapitate hymenial cystidia, but those are embedded in brown resinous matter (Pegler 1977; Antonín 2007). *G. albocapitata* is also found in Sri Lanka (Pegler 1986). *Gloiocephala mucrocystidiata* Antonín, another tropical African species, lacks subulate pileosclerocystidia and has a dextrinoid stipe medulla (Antonín 2003, 2007). Following Antonín's monograph of tropical African *Gloiocephala*, none of the seven species described (including the apparently pantropical *G. epiphylla*) matches our species (Antonín 2007).

In New Zealand, *Gloiocephala phormiorum* Horak & Desjardin produces centrally stipitate, lamellate basidiomata and a hymenodermic pileipellis with numerous fusiform pileocystidia bearing long, gradually tapering necks. However, these are thin-walled and lack crystalline deposits, and its spores are considerably larger than those of *G. pilosella* (Horak & Desjardin 1994). Moreover, our phylogenetic data clearly indicates that this species should be placed outside the genus *Gloiocephala*.

Although relatively few species described in *Gloiocephala* are documented by DNA sequences so far, it is likely that they constitute a polyphyletic group, as already noted by Moncalvo *et al.* (2002), Binder *et al.* (2006) and Antonín & Noordeloos (2010). One of the closest ITS sequences available in GenBank is that of the holotype collection of *G. resinopunctata* Manimohan & K.A.Thomas, described from tropical India (Manimohan & Thomas 1998). This pleurotoid stipitate species with interveined hymenium, reddish gloeocystidia on hymenium, pileipellis and stipitipellis and large spores (11-13 × 7.5-9 µm), is anatomically very different from our species and the percentage of ITS identity is low (88%). Thus, our collections should be considered as a new species, *Gloiocephala pilosella*, in reference to the pilose pileus and stem. The *G. pilosella* – *G. resinopunctata* group seems to constitute an independent lineage with regard to a monophyletic genus *Gloiocephala*. As we are unable to find discriminating characters for this clade in the current state of knowledge, we refrain from defining a new genus and adopt for our species the genus *Gloiocephala* in its current broad sense.

We had the opportunity to collect in Amazonia a species identified morphologically as *Gloiocephala spathularia,* originally described from the rainforests of Argentina and Ecuador by Singer (1960, 1976), and subsequently reported from the tropical zone in southern Mexico (Valenzuelo *et al.* 1981). It forms singular spathular basidiomes, with a pileus attached laterally to a slender foot, and a merulioid hymenium (Fig. 6; see also Valenzuelo *et al.* (1981)).

The description of our collection fits very well with Singer's accounts of the species. However, the unusual habitat – growing on the stroma of a lignicolous Sordariomycetes (identified as *Phylacia poculiformis* (Mont.) Mont. by Jacques Fournier, pers. comm.) – does not align with the original description.

A comparison of the LSU sequence from this collection with our dataset of *Gloiocephala* sequences indicates that this species does not belong to the genus *Gloiocephala*. Instead, it should be assigned to the genus *Physalacria* (type species: *Physalacria inflata* (Fr.) Peck), supporting the polyphyletic nature of *Gloiocephala* as traditionally defined.

We suggest that the specific insertion of the stipe into the sterile part of the pileus - regardless of whether the hymenium is amphigenous - could be characteristic of *Physalacria*. In molecularly authenticated species of *Gloiocephala* with asymmetrical pilei, such as *G. menieri* and *G. cornelii*, the stipe attaches laterally via insertion into the hymenium. The fasciculate growth pattern observed in our collection, which is also known from several *Physalacria* species with amphigenous hymenia (notably the type species *P. inflata*), may be restricted to the genus *Physalacria* and excluded from *Gloiocephala*. The lacunose trama observed in our collection of *G. spathularia* aligns with Singer's (1986) circumscription. Furthermore, the lack of geotropism in the stipe - which could represent a pseudostipe - is noteworthy: our collection's fasciculate basidiomata were growing on the underside of wood, oriented in various directions toward the ground.

Another feature which could justify the exclusion of *P. spathularia* from *Gloiocephala s.s.* is the minute size of its basidiospores, which do not exceed 5 µm in our collection. Based on this same feature, Singer (1976) established a section *Spathulariae*, including *G. lutea* Singer, whose systematic position also needs a revision and which might also find its place within the genus *Physalacria s.s.* Buyck *et al.* (1998) recognized the affinities of *Laschia merulioides* R. Heim with section *Spathulariae* of the genus *Gloiocephala* and proposed its recombination in this genus. Given its anatomy, which is very similar to that of *G. spathularia*, it is also likely that this species should be transferred to *Physalacria*.

Based on the phylogenetic tree and its morphological characteristics, we introduce the following recombination: *Physalacria spathularia* (Singer) Corriol & Jargeat, comb. nov., basionym: *Gloiocephala spathularia* Singer, *Sydowia* 14: 271, 1976. Mycobank: MB861262.

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