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An old familiar face: *Tremella anaptychiae* sp. nov. (Tremellales, Basidiomycota)

JUAN CARLOS ZAMORA¹, PAUL DIEDERICH², ANA M. MILLANES³ & MATS WEDIN⁴

¹Departamento de Biología Vegetal II, Facultad de Farmacia, Universidad Complutense de Madrid, E-28040, Madrid, Spain (jcsenoret@gmail.com)

²Musée national d'histoire naturelle, 25 rue Munster, L-2160 Luxembourg, Luxembourg (paul.diederich@education.lu)

³Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, E-28933 Móstoles, Spain

⁴Department of Botany, Swedish Museum of Natural History, P.O. Box 50007, SE-10405 Stockholm, Sweden

Abstract

Tremella anaptychiae, a lichenicolous fungus growing on *Anaptychia ciliaris*, is described as new. Both morphological and molecular data (DNA sequences from the ITS and 28S regions) are used to characterize and distinguish it from other *Tremella* s. l. species. *Tremella anaptychiae* is closely related to *T. parmeliarum* but comparatively distantly related to other previously recognized lichenicolous species groups.

Key words: *Anaptychia*, lichenicolous fungi, morphology, phylogenetic analyses, *Tremella*, Tremellomycetes

Introduction

The genus *Tremella* Persoon (1794) : Fries (1821) has traditionally been considered a huge and non-monophyletic assembly of mycoparasitic fungi. *Tremella* s. l. is characterised by certain morphological synapomorphies; dolipore septa with cupulate-vesiculose parenthesomes, basidia that are often septate and in which each hypobasidial cell grows to form a single and distinct epibasidium, and usually the presence of specialized cells, called haustoria, involved in the parasitic activity (Bandoni 1984, Diederich 1996, Chen 1998, Millanes *et al.* 2011). More than 50 species are known to exclusively parasitize specific lichenized fungal hosts, and the number is continuously increasing (Diederich 1986, 1996, 2003, 2007, Diederich & Marson 1988, Diederich & Christiansen 1994, Sérusiaux *et al.* 2003, Zamora *et al.* 2011, 2016, Millanes *et al.* 2012, 2014a, 2015, Diederich *et al.* 2014, Ariyawansa *et al.* 2015, Lindgren *et al.* 2015). This big heterogeneous group has recently been divided into several monophyletic genera (Liu *et al.* 2016), but most lichenicolous species still remain as “*Tremella* s. l.” awaiting a better resolved phylogeny and further research to find morphological or physiological synapomorphic characters.

One of these lichenicolous species is known to grow associated with the lichen-forming fungus *Anaptychia ciliaris* (Linnaeus 1753: 1144) Körb. ex Massalongo (1853: 35). It was first noted and shortly described and illustrated by Diederich (1996), who left it unnamed as “*Tremella* sp. 5” due to the scarcity of the material (a single basidioma) available at that time. During subsequent years, more specimens have been collected, and the aim of the present paper is to formally describe this taxon.

Material and methods

Morphology

The morphological study was based on nine specimens collected either by the authors or collaborators. General methodology and terminology follows Diederich (1996) and Zamora *et al.* (2016). Micromorphological study was done using hand-cut sections mounted and stained with Congo red in 10% ammonia, phloxin B in 5% KOH or a mixture of Congo red and phloxin B in 5% KOH. Spore amyloidity was tested with Melzer's reagent. Measurements were made in KOH solution. Basidiospore length:width ratio was expressed as Q, and basidiospore shape terminology follows Bas (1969). Microscopic photographs were taken using a Leitz Orthoplan microscope coupled to a Canon EOS 50D digital camera.

DNA extraction, PCR amplification, sequencing, and phylogenetic analyses

Taxon sampling consisted of three specimens of the new species, in addition to specimens of *Tremella* s. l. species parasitizing Caliciales (*T. christiansenii* Diederich (1996: 60), *T. dirinariae* Diederich, Millanes & Wedin in Ariyawansa *et al.* (2015: 239), *T. phaeophysciae* Diederich & M.S. Christ. in Diederich (1996: 143)) plus other representative specimens of the Tremellales (TABLE I). These included: (i) the type species of the genus *Tremella* (*Tremella mesenterica* (Schaeffer 1774: 108) Retzius (1769: 249)); (ii) *Tremella fuciformis* Berkeley (1856: 277) as representative of the Fuciformis group distinguished by Chen (1998); (iii) representatives of the Aurantia and Indecorata groups distinguished also by Chen (1998), which have recently been assigned the generic names *Naematelia* Fries (1818: 370) and *Pseudotremella* X.Z. Liu, F.Y. Bai, A.M. Yurkov, M. Groenew. & Boekhout in Liu *et al.* (2016: 129), respectively (Liu *et al.* 2016); (iv) representatives of three groups of lichenicolous species distinguished by Millanes *et al.* (2011), and (v) lichenicolous taxa with a micro or macromorphology similar to that of the new species. *Cryptotrichosporon anacardii* Okoli & Boekhout in Okoli *et al.* (2007: 348) and *Trichosporon ovoides* Behrend (1890: 467) were used as outgroup based on Liu *et al.* (2016). Species names, voucher information, and GenBank accession numbers are provided (TABLE I).

TABLE 1. Sequences newly produced (bold), or downloaded from GenBank, with culture reference, or specimen data. Two strain numbers for *Saytozyma podzolica* correspond to replicates of the same culture deposited in different collections with distinct identification codes. Two strain numbers for *Sterigmatosporidium polymorphum* correspond to two conspecific strains according to Kirschner *et al.* (2001).

Species name	Culture	Specimen data	ITS	nLSU
<i>Carcinomyces effibulatus</i>		Sweden, Santos s.n. (S-F40014)	AF444315	AF189842
<i>Cryptococcus neoformans</i>	B-3501A		BR000310	BR000310
<i>Naematelia aurantia</i>	CBS 6965		AF444315	AF189842
<i>Pseudotremella moriformis</i>	RJB 2846-8		AF042426	AF042244
<i>Saytozyma flava</i>	CBS 331		AF444338	AF075497
<i>Saytozyma podzolica</i>	JCM 10452/CBS 6819		AB035576	AF075481
<i>Sterigmatosporidium polymorphum</i>	CBS 8088/IGC 5647		AF444320	AY032662
<i>Tremella anaptychiae-a</i> (Type)		Spain, Zamora & Zamora s.n. (AM499; holotype MAF-Lich. 21306)	KY950297	KY950300
<i>Tremella anaptychiae-b</i>		Spain, 2005, Pérez-Ortega s.n. (AM130; MAF-Lich)	KY950298	KY950301
<i>Tremella anaptychiae-c</i>		Sweden, 2012, Knutsson s.n. (AM493; S)	KY950299	KY950302
<i>Tremella caloplacae</i>		France, Sérusiaux s.n. (S-F102489)	JN053469	JN043574
<i>Tremella cetrariicola</i>		Finland, Suija s.n. (S-F102413)	JN053490	JN043596
<i>Tremella christiansenii</i>		Denmark, Christiansen 607 (herb. Diederich)	-	JN043577
<i>Tremella cladoniae</i>		Estonia, Suija 872 (TU-45019)	JN053477	JN043583
<i>Tremella coppinsii</i>		Estonia, Suija 38a (TU-38637)	JN053496	JN043602
<i>Tremella dirinariae</i>		U.S.A., Harris 37673 (NY)	KR058780	KR058785
<i>Tremella hypogymniae</i>		Sweden, Wedin 6892 (UPS)	JN053484	JN043590
<i>Tremella fuciformis</i>	CBS 6970		JN053466	JN043571
<i>Tremella lobariacearum</i>		Madeira, Diederich 4935 (S-F102418)	JN053473	JN043579
<i>Tremella mesenterica</i>		Sweden, Ryman 9146 (S-F102411)	JN053463	JN043568
<i>Tremella parmeliarum</i>		Canary Islands, Diederich 16574 (S-F102497)	JN053511	JN043618
<i>Tremella pertusariae</i>		France, Diederich 16331 (S-F102502)	JN053494	JN043600
<i>Tremella phaeophysciae</i>		Luxembourg, Diederich 12429 (S-F102505)	JN053479	JN043585
<i>Trimorphomyces papilionaceus</i>	CBS 443.92		AF444483	AF075491
Outgroup				
<i>Cryptotrichosporon anacardii</i>	CBS 6241		AF190007	AF075498
<i>Trichosporon ovoides</i>	CBS 7556		AF444439	AF075523

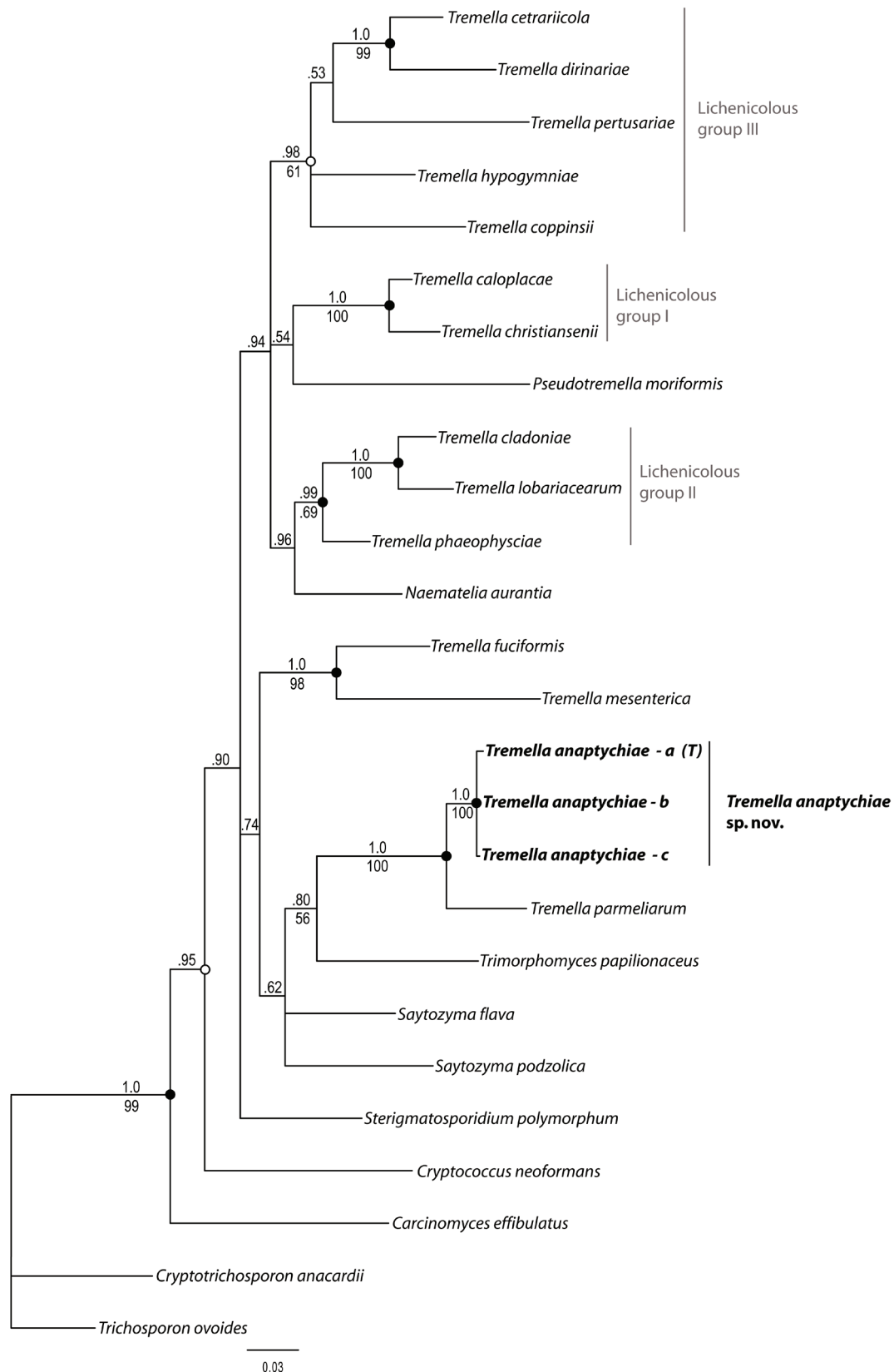


FIGURE 1. Fifty-percent majority rule Bayesian consensus phylogram with average branch lengths, from the combined analyses of ITS1, 5.8S, ITS2, and 28S datasets. Bayesian Posterior Probability values are indicated over the branches, and bootstrap values obtained in the maximum likelihood analysis are added below the branches. White circles represent nodes supported only in the Bayesian analysis. Black circles represent nodes supported in both Bayesian and ML analyses. BPP values ≥ 0.5 are indicated above the branches, and ML bootstrap values $\geq 50\%$, below branches. The newly described species is highlighted in bold font, and the type specimen is indicated with (T). Some lichenicolous groups distinguished by Millanes *et al.* (2011) are indicated in grey in the right margin. Branch lengths are scaled to the expected number of nucleotide substitutions per site.

DNA extractions and PCR amplifications were achieved following Millanes *et al.* (2012). We amplified the nuclear rDNA internal transcribed spacer 1 (ITS1), 5.8S, internal transcribed spacer 2 (ITS2) and a fragment of approximately 500 bp in the rDNA 28S region with the primer pair ITS1F (Gardes & Bruns 1993)/BasidLSU3-3 (Millanes *et al.* 2011). An additional and overlapping fragment of the rDNA 28S region, of approximately 1000 bp, was amplified with the primer pair BasidLSU1-5 (Millanes *et al.* 2011)/LR5 (Vilgalys & Hester 1990). Sequence alignments (TreeBase accession 20905) were performed following Millanes *et al.* (2012). Dataset congruence was assessed manually by analyzing the datasets separately by maximum likelihood bootstrapping. Conflict among clades was considered significant if a significantly supported clade (bootstrap support $\geq 70\%$; Hillis & Bull 1993) for one marker was contradicted with significant support by another. Datasets were combined if no incongruences were found.

Bayesian analyses were conducted following Millanes *et al.* (2012) with minor modifications. We considered ITS1, 5.8S and ITS2 independent partitions, as was suggested by Gaya *et al.* (2011) and Petkovits *et al.* (2011). Likelihood models were selected for each of the three gene regions with the Akaike information criterion (AIC) as implemented in jModeltest (Posada 2008). A GTR+ Γ model was selected for the ITS1, a SYM+I model was selected for the 5.8S, a SYM+ Γ model was selected for ITS2 and a GTR+I+ Γ model was selected for 28S. Three parallel runs were executed, each with five chains four of which were incrementally heated with a temperature of 0.15. The analysis was diagnosed for convergence every 100 000 generations, measured as the average standard deviation of splits across runs in the last half of the analysis. Every 100th tree was saved. The first half of the run was discarded as burn-in.

Maximum likelihood (ML) analyses were conducted in RAxMLGUI 1.3 (Silvestro & Michalak 2012), a graphical front-end for RAxML (Stamatakis 2006), with the GTRGAMMA model of nucleotide substitution applied to all partitions. We performed a thorough ML search with 100 runs and assessed node support thorough bootstrap using 1000 bootstrap pseudo-replicates. Significant support is considered as BPP values ≥ 0.95 in the Bayesian analysis, and bootstrap values $\geq 70\%$ in the ML analysis.

Results

Phylogenetic results

We generated six new sequences, which were aligned together with sequences already available in GenBank (Table 1). Two data matrices were produced, one including ITS and one including 28S rDNA. The combined matrix contained 1262 characters (ITS1: 1–78; 5.8S: 79–231; ITS2: 232–335; 28S rDNA: 336–1262). The ln-likelihood value of the best tree obtained from the ML analysis was -7993.068784. The Bayesian analysis halted after 1 600 000 generations. The average standard deviation of split frequencies across runs was 0.009 (<0.01), which indicated convergence of the three runs. A majority-rule consensus tree was constructed from the 24 000 trees of the stationary tree sample.

The consensus 50% majority-rule phylogram of the Bayesian analysis and the ML phylogram yielded the same topology concerning significantly supported clades. Therefore, only the Bayesian phylogram is shown, with BPP and ML bootstrap values indicated at branches (Fig. 1). The three specimens of the new species (*Tremella anaptychiae*) formed a strongly supported clade (1.0 BPP, 100% BS), being sister to one specimen of *T. parmeliarum* Diederich (1996: 125). This last relationship also received full support (1.0 BPP, 100% BS). The lichenicolous species groups defined by Millanes *et al.* (2012) were also recovered here, the lichenicolous group I with full support (1.0 BPP, 100% BS), while the lichenicolous groups II and III received significant support only from the Bayesian analysis (0.96 and 0.98 BPP, respectively). The clade formed by *T. anaptychiae* and *T. parmeliarum* is not closely related to any of those lichenicolous groups (Fig. 1).

Taxonomy

Tremella anaptychiae J.C. Zamora & Diederich, *sp. nov.* (Fig. 2)

Mycobank MB 821018.

Diagnosis:—Basidiomata growing parasitically on different parts of the thallus of *Anaptychia ciliaris*, cream-coloured to blackish, 0.2–2 mm in diameter; context hyphae clamped, thick-walled; basidia two-celled and stalked, stalk 2–21(24) μm long, basidial upper part 15–20 \times 10–15 μm , septum oblique or longitudinal, more rarely transverse; basidiospores 5.5–9 \times 5–9 μm ; further distinguished by its characteristic ITS–28S rDNA sequences.

Etymology:—Growing on *Anaptychia*.

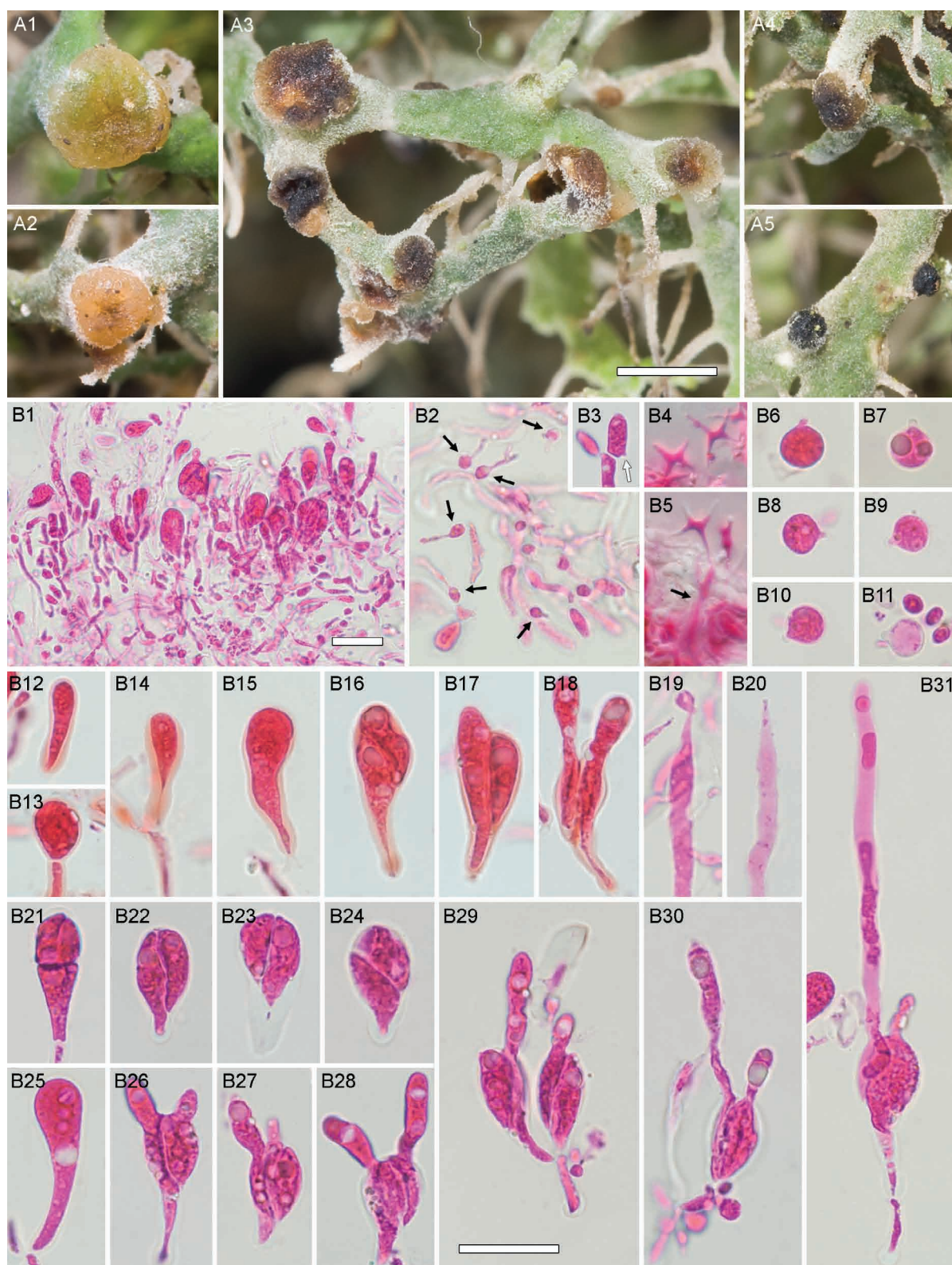


FIGURE 2. Morphological characteristics of *T. anaptychia*, **A** morphological variation of the basidiomata on the host thallus, **B** micromorphological features; B1 hymenium; B2 young hyphae with haustorial branches (black arrows); B3 young cell (perhaps a probasidial initial) with a spur-like basal swelling (white arrow); B4–B5 asteroconidia and conidiogenous cell (black arrow); B6–B11 basidiospores, in B11 collapsed basidiospore with yeast-like cells; B12–B18 basidial development, note that basidia are often thick-walled, particularly towards the stalk; B19–B20 epibasidia with an apical sterigma, in B19 with an asymmetrically attached young basidiospore; B21–B24 basidia with transverse (B21), almost longitudinal (B22) or oblique (B23, B24) septa; B25 young long-stalked basidium. B26–B31; mature basidia with epibasidia in different degrees of development; B1–B11 and B19–B31, phloxin B in 5% KOH; B12–B18, Congo red and phloxin B in 5% KOH. Scale bars: A=1 mm (all photographs at the same scale), B=20 μ m (B2–B31 at the same scale). B4–B5 from *E. Zimmermann* 1065, all other photographs from the holotype.

Type:—SPAIN. Castilla-La Mancha: Guadalajara, El Cardoso de la Sierra, near Jarama river, 41°6'15" N, 3°29'20" W, 1260 m, on *Anaptychia ciliaris* thallus, on *Crataegus monogyna* branches, 16.4.2011, J.C. Zamora & B. Zamora s.n., holotype MAF-Lich. 21306 (DNA: AM499), isotypes in AH, MA-Fungi, S, and herb. Diederich.

Description:—Basidiomata subglobose to somewhat tuberculate when old, waxy-gelatinous, cream-coloured, pinkish, brownish or blackish, rarely with greenish shades, 0.2–2 mm diam, growing on the thallus (both surfaces), including cilia of the host, more rarely on the margin of apothecia (Fig. 2A). Context hyphae and subbasidial hyphae thick-walled, slender, (2.5)3–5.5(6.5) µm diam., clampless, but small spur-like swellings (perhaps pseudoclamps) have been seen at few septa, exceptionally with clamps. Haustorial branches very abundant, mother cell subglobose to broadly ellipsoid, 3–4 × 3–3.5 µm diam., haustorial filament 1.5–7(11) × 1 µm, unbranched or with few and short apical branches (Fig. 2B2). Hymenium well-developed, hyaline or with a subtle brownish tinge, containing numerous probasidia (Fig. 2B1). Hyphidia absent or indistinct. Probasidial initials mostly claviform to narrowly ellipsoid, rarely subglobose, with a long, thick-walled stalk, clampless, but often with an asymmetric attachment to the subtending hypha, rarely with a small spur-like swelling (perhaps a pseudoclampe, Fig. 2B3, 2B12–B15). Mature basidia two-celled, with often longitudinal or oblique septa, sometimes transverse, stalked, thick-walled (walls thicker towards the base); stalk 2–21(24) µm long; upper part (without stalk) ellipsoid, claviform or subglobose, 15–20 × 10–15 µm; epibasidia subcylindrical or slightly dilated close to the apex, 3–4(5) × 10–30(60) µm, developing an apical sterigma, 3–5 µm long (Fig. 2B16–B31). Basidiospores globose to subglobose, sometimes broadly ellipsoid, 5.5–9 × 5–9 µm, inamyloid, germinating by repetition to form ballistoconidia (similar to basidiospores but slightly smaller) and blastic conidia (yeast-like cells), the latter ellipsoid, 4–6 × 3–5 µm (Fig. 2B6–B11). Asteroconidia sometimes present, with 4 arms, 10–15 µm in diam., individual arms 3.5–8 µm long, basal arm often longer and connected to the conidiogenous cell; conidiogenous cells 17–26 µm long, 1.5–4 µm in diam., with a few or several branches close to the apex up to 4 µm long, very numerous in the hymenium of some basidiomata in which basidia are sparse (Fig. 2B4–B5).

Additional specimens examined (on *Anaptychia ciliaris*, unless otherwise indicated):—ITALY. Calabria: Cosenza, Pollino timpa di Porac, 1300 m, [no date], [no collector] (CLU). MACEDONIA. Sar planina: Rudoka, Popova sapka W Tetovo, Hänge W der Bergstation der Bergbahn, 8.9.1977, J. Hafellner 3906 (herb. Hafellner at GZU). SPAIN. Canary Islands: Gran Canaria, Strasse GC150 Tejado-Pico de las Nieves, nahe Forsthaus, 27.988839° N, 5.593184° W, 1600 m, 2014, E. Zimmermann 1065 (herb. Diederich). La Palma, Cumbre vieja, Puntade los Roqus, BE exp. Felswand, 2000 m, [no date], F. Berger 10454 (herb. Berger). SPAIN, Iberian Peninsula. Castilla-La Mancha: Guadalajara, Condemios de Arriba, Aldeanueva de Atienza, 31.10.2009, J.C. Zamora s.n. (MAF-Lich. 21307). La Rioja, Villoslada de Cameros, hayedo cerca de Puente Ra, 1260 m, 42°03' N, 02°42' W, 30.3.2005, S. Pérez-Ortega s.n. (MAF-Lich.) (DNA: AM130). Navarra, Lezaun, entrada al puerto de Lizárraga, [no date], J. Etayo s.n. (MA-Lichen 4014). País Vasco, Ullibarri, [no date], Etayo s.n. (herb. Etayo). SWEDEN. Gotland: Fårösund, Lake Hau, 57°53'28.50" N, 18°58'51.17" E, 14.6.2012, T. Knutsson s.n. (S) (DNA: AM493).

Ecology and distribution:—The new species is known from Italy, Macedonia, Spain (incl. Canary Islands), and Sweden. It seems to be confined to *Anaptychia ciliaris*. As for most lichenicolous fungi, the distribution is primarily dependent on the host. *Anaptychia ciliaris* is a palearctic species, known from Scandinavia, the British Isles, Central and Southern Europe, north Africa, the Canary Islands and eastern Europe including Turkey, with scattered Asian records (Rose 1998), growing mainly within the “temperate broadleaf and mixed forests” and the “Mediterranean forest, woodlands and scrub” biomes (Olson *et al.* 2001). Since the studied samples of *T. anaptychiae* indeed cover an important part of this distribution, it is expected that it may be present in any place where the host is common.

Discussion

Tremella anaptychiae is a well-delimited species, mainly characterized by the clampless hyphae, thick-walled, stalked, two-celled basidia, relatively small basidiospores, and by growing on different parts of the thallus of *Anaptychia ciliaris*, but not on the hymenium of the host. One of us (PD) has studied a specimen on *A. setifera* (Mereschk.) Räsänen (1931: 123) (Canary Islands: La Gomera, Valle Gran Rey, Felsgrat W ober Arure, 17°18'40" W, 28°07'30" N, 800 m, an W-exponierten Steiflächen, 21.2.1991, J. Hafellner 33596 [herb. Hafellner at GZU]) that has much darker, almost black basidiomata, but is immature, and therefore has provisionally not been included within *Tremella anaptychiae*, awaiting more material on that host.

The new species forms a strongly supported clade with *T. parmeliarum* (Fig. 1), a species normally also inducing the formation of very conspicuous, often dark galls or basidiomata on the thallus of *Parmotrema* spp. (but see Diederich (1996) concerning some specimens of *T. parmeliarum* on *Parmotrema perforatum* (Wulfen in Jacquin 1786: 116) Massalongo (1860: 248)), with basidia of about the same size and a similar septation pattern, and lacking true clamp-connections, as in *T. anaptychia*. However, in addition to parasitizing a different host, *T. parmeliarum* is distinguished by its sessile to shortly stalked, 2–4-celled basidia (Diederich 1996). Both taxa are relatively isolated from a phylogenetic point of view, although their precise phylogenetic placement is unclear due to the low support of the backbone.

There are a number of lichenicolous species that may resemble *T. anaptychia* in several morphological features. One of them is *T. pertusariae* Diederich (1996: 133), because of the clearly stalked basidia, often with thickened walls towards the base and the stalk, slender subbasidial hyphae, with less numerous septa than in most lichenicolous species, and the absence of clamp connections. However, *T. pertusariae* is well separated by the much larger 2–4-celled basidia, larger basidiospores, and by growing mostly in the hymenium, more rarely on the thallus, of *Pertusaria* spp. (Diederich 1996). *Tremella harrisii* Diederich (1996: 85) also has many characteristics in common: in this species basidia are about the same size and shape but are provided with basal clamp-connections and are 2–4-celled. It has been found parasitizing the genera *Trypethelium* and *Polymeridium*, being one of the few lichenicolous heterobasidiomycetes known on different host genera. The yet undescribed *Tremella* sp. 6 in Diederich (1996: 175) has two-celled stalked basidia that are smaller than in *T. anaptychia* and have basal clamp-connections; it also differs in the host selection, as it parasitizes a *Leptogium* species.

Finally, since recent studies have shown that host specificity is important to characterize certain evolutionary lineages in this group of fungi (Millanes *et al.* 2014b; Zamora *et al.* 2016), *T. anaptychia* has to be compared with the other *Tremella* species known to parasitize *Caliciales* hosts. None of them is morphologically similar to *T. anaptychia*, since *T. phaeophysciae* and *T. rinodinae* Diederich & M.S. Christ. in Diederich (1996: 154), growing on *Phaeophyscia orbicularis* (Necker 1771: 88) Moberg (1977: 44) and *Rinodina gennarii* Baglietto (1861: 17) respectively, have two-celled basidia with a transverse septum (very rarely longitudinal in *T. rinodinae*), while *T. christiansenii*, growing on *Physcia* spp., has larger basidiospores and mostly two-celled, sessile basidia, in which each cell elongates and grows independently before forming the epibasidia. According to our phylogenetic analyses, neither *T. phaeophysciae* nor *T. christiansenii* are closely related to *T. anaptychia* (Fig. 1), while for *T. rinodinae* molecular data are not available yet. *Tremella dirinariae*, a species known only from the type specimen on *Dirinaria* in Florida, has smaller basidiomata, rarely exceeding 0.35 mm in diam., and slightly smaller basidia, 17–24 × 6.5–10 µm (stalk included), with a basal clamp; in addition, it is phylogenetically distant to *T. anaptychia*, but related to the clade including *T. cetrariicola* Diederich & Coppins in Diederich (1996: 57), *T. coppinsii* Diederich & G. Marson (1988: 175), and *T. hypogymniae* Diederich & M.S. Christ. in Diederich (1996: 90) (lichenicolous group III, Fig. 1).

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