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Standard Paper

Five new species in the *Tremella caloplacae* complex

Sandra Freire-Rallo[1], Paul Diederich[2], Ana M. Millanes[1] and Mats Wedin[3]

[1]Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, Móstoles, Spain; [2]Musée national d'histoire naturelle, L-2160 Luxembourg, Luxembourg and [3]Department of Botany, Swedish Museum of Natural History, SE-10405 Stockholm, Sweden

Abstract

Tremella caloplacae (Zahlbr.) Diederich is a species complex including at least nine different species. Here, we formally describe the new species *Tremella elegantis*, *T. nimisiana*, *T. parietinae*, *T. pusillae* and *T. sorediatae*. *Tremella elegantis* induces galls in the hymenium of *Rusavskia elegans* and forms 2-celled basidia, where cells rarely elongate and sometimes give the appearance of two immature, independent basidia. *Tremella nimisiana* has small basidiomata (less than 1 mm diam.), narrowly ellipsoid to pyriform 2-celled, occasionally clavate to subcylindrical 3-celled basidia, and grows in the hymenium of *Xanthocarpia* species. *Tremella parietinae* is characterized by the exclusive growth in the hymenium of *Xanthoria parietina*, the broadly fusiform to ellipsoid probasidia, and the subspherical, pyriform or ellipsoid 2(−3)-celled basidia. *Tremella pusillae* has ellipsoidal probasidia, 2(−3)-celled pyriform or ellipsoidal basidia that sometimes are constricted at the septum, and grows only on *Calogaya pusilla*. *Tremella sorediatae* is characterized by inducing galls on the thallus of *Rusavskia sorediata* and by pyriform to ellipsoid basidia that sometimes are constricted at the septum. Three species are not formally described and are left unnamed as *Tremella* sp. 13 on *Calogaya biatorina*, *Tremella* sp. 14 on *Calogaya decipiens* and *Tremella* sp. 15 on *Polycauliona* sp. *Tremella caloplacae* in the strict sense is re-circumscribed as a species confined to *Variospora* species.

Keywords: basidiomycetes; lichenicolous fungi; molecular phylogeny; species complex; taxonomy; *Tremellales*

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Introduction

Tremella Pers. (*Tremellales*, *Agaricomycotina*) is a widespread genus with more than 300 species that grow associated with other fungi, including lichenized fungi. Lichenicolous *Tremella* species were neglected and poorly studied until the publication of the first monograph on lichenicolous heterobasidiomycetes by Diederich (1996). Since then, the number of formally described lichenicolous species has increased to 117, and we expect this number to continue increasing in the coming years (Diederich *et al.* 2022). Species delimitation is often complicated in this group due to the scarcity of morphological characters (Diederich 1996). Still, lichenicolous *Tremella* species are highly specific towards their hosts, usually growing on a single species or genus (Diederich *et al.* 2018), which has been useful for species circumscription (Diederich 1996; Millanes *et al.* 2015; Zamora *et al.* 2016; Diederich *et al.* 2022). Evidence suggests that speciation is driven by host selection rather than by geographical isolation (Werth *et al.* 2013; Millanes *et al.* 2014, 2015, 2016; Diederich & Ertz 2020; Diederich *et al.* 2022).

A large amount of still overlooked diversity in lichenicolous tremellalean fungi is hidden in several species complexes (Diederich *et al.* 2022). *Tremella caloplacae* (Zahlbr.) Diederich was first described as a hyphomycete with large, 1-septate conidia (as *Lindauopsis caloplacae* Zahlbr.; Zahlbruckner 1906). The description was based on a specimen growing in the hymenium of *Caloplaca callopisma* (Ach.) Th. Fr. (currently *Variospora aurantia* (Pers.) Arup *et al.*), collected in Crete. In his monograph of lichenicolous heterobasidiomycetes, Diederich (1996) described a species of lichenicolous *Tremella* growing in the hymenium of specimens of *Caloplaca* collected in Austria and Great Britain, but he left the species unnamed as *Tremella* sp. 1 due to the lack of taxonomically useful morphological characters of the specimens and the impossibility of finding differences between this species and *Tremella rinodinae* Diederich & M.S. Christ. The species was not formally described until 2003 (Sérusiaux *et al.* 2003), when enough material from new localities had been collected and studied. Sérusiaux *et al.* (2003) studied the type of *Lindauopsis caloplacae* Zahlbr. and concluded that the structures that Zahlbruckner (1906) illustrated in great detail (and interpreted as conidia) in reality correspond to tremelloid basidia with one transverse primary septum. The species corresponds to '*Tremella* sp. 1' (*sensu* Diederich 1996) and was combined in *Tremella* and reported on several species of *Caloplaca* s. lat. by Sérusiaux *et al.* (2003). Later, Diederich (2007) reported the species growing on *Xanthoria sorediata* (Vain.) Poelt from Canada and Greenland. The two collections on *X. sorediata* could not be distinguished microscopically from the material on *Caloplaca* s. lat., although they were macroscopically very distinct. That led Diederich (2007) to suggest that *Tremella caloplacae* could represent a species complex needing further study, also considering the polyphyly of both *Caloplaca* and *Xanthoria*, which was

Corresponding author: Mats Wedin; Email: mats.wedin@nrm.se
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already acknowledged at that time by Gaya *et al.* (2003). The first molecular data obtained from *Tremella caloplacae* also supported this hypothesis (Millanes *et al.* 2011), although this was not discussed by those authors.

Freire-Rallo *et al.* (2023) studied the phylogenetic relationships and species boundaries of 52 specimens of *Tremella caloplacae* s. lat. growing on different hosts of the *Teloschistaceae*. That study showed that *Tremella caloplacae* s. lat. is indeed a species complex including at least six putative new species, each of them restricted to grow and develop on a single host species or genus. The specimens analyzed in Freire-Rallo *et al.* (2023), to which we refer here for practical reasons as the *Tremella caloplacae* species complex, are studied in this work at a morphological level. In addition, we have sequenced two specimens of *Tremella* growing on *Calogaya biatorina* (A. Massal.) Arup *et al.* and on *Polycauliona* sp., and these are also included in this study to test their phylogenetic position.

The aim of this work is to formally describe five species and to tentatively describe three other species within the *Tremella caloplacae* complex, combining morphological, ecological and molecular data, and studying the phylogenetic relationships within the group.

Materials and Methods

Morphological studies

Specimens studied are housed in the ANGUC, BR, GZU, MARSSJ, S and UBC herbaria (abbreviations according to Index Herbariorum http://sweetgum.nybg.org/science/ih/) or the private collection of Javier Etayo (Table 1). Macroscopic characters were observed using an Olympus SZX16 or a Leica MZ 7.5 dissecting microscope. Images of macroscopic traits were captured with either a Sony Alpha A6000 camera on an Olympus SZX16 dissecting microscope or a Canon 6D camera with Nikon BD Plan 5 or 10 microscope objectives, using StackShot (Cognisys) and Helicon Focus (HeliconSoft) for increasing the depth of field. The samples were first moistened with distilled water and then the surface of the gall cut with a razor blade to maximize the amount of tremellalean hyphae taken. Sections were pretreated with a solution of KOH (5%) and stained with phloxine B (1% in water), following the methods used by Diederich (1996). Microscopic photographs were captured with a Sony Alpha A6000 or an Olympus DP23 camera on an Olympus BX51 microscope, or a Leica EC3 camera on a Leica DMLB microscope, without or with DIC optics. Values of the measured structures were rounded to the nearest 0.5 µm. The basidiospore apiculus is not included in the measurements. Microscopic images were adjusted with Helicon Focus to increase the depth of field. Measurements are presented with a range representing the 69% probability interval; within parentheses the smallest and largest measurements are specified followed by the mean ($\bar{x}$) minus and plus the standard deviation (SD) as follows: (min–) ($\bar{x} - \mathrm{SD}$) – ($\bar{x} + \mathrm{SD}$) (–max). Basidiospore length/width ratio is expressed as Q. The total number of measurements (n) is given within parentheses. Mycological terminology used follows Diederich (1996), Kirk *et al.* (2008) and Diederich *et al.* (2022).

Molecular studies

DNA extraction, amplification and sequencing. DNA was extracted directly from the specimens studied (Table 1), either freshly collected or herbarium material. Total DNA extraction was performed using the Qiagen DNeasy Plant Mini Kit, following the manufacturer's instructions but repeating the final elution of 50 µl with water twice.

For PCR amplification, we combined general fungal primers with others specifically designed to amplify DNA from the tremellalean fungi (Millanes *et al.* 2011; Freire-Rallo *et al.* 2023). To perform the PCRs, we used the primers ITS1F (Gardes & Bruns 1993), BasidLSU3-3 (Millanes *et al.* 2011) and TRMcal_R2 (Freire-Rallo *et al.* 2023) to amplify the internal transcribed spacer I, the 5.8S rDNA gene and the internal transcribed spacer II gene. PCR reactions were carried out using Illustra™ Hot Star PCR beads, according to the manufacturer's instructions. For ITS1F/BasidLSU3-3 and ITS1F/TRMcal_R2, we ran an initial denaturing at 95 °C for 5 min; four cycles of 95 °C for 40 s, 53 °C for 40 s and 72 °C for 90 s; four cycles of 95 °C for 30 s, 50 °C for 30 s and 72 °C for 90 s; 32 cycles of 95 °C for 30 s, 47 °C for 30 s and 72 °C for 90 s; a final extension step of 72 °C for 10 min. For PCR samples we added 2 µl of DNA extraction and 0.5 µl of each primer (primer concentration 10 µM). Before sequencing, we purified PCR products using 5 µl of Exo-sap-IT© (USB Corporation) added to 22 µl volume of amplification product. Sequencing was performed at the Molecular Systematic Laboratory of the Swedish Museum of Natural History, at the Genomic Unit in Rey Juan Carlos University, or by Macrogen Europe (Amsterdam, the Netherlands) or Macrogen Spain (Madrid, Spain).

Sequence alignment and phylogenetic analysis. Newly produced sequences were assembled and edited with Geneious Prime® v. 2021.0.3. (https://www.geneious.com). A data matrix was produced for subsequent phylogenetic analyses using sequences of the ITS1, 5.8S, ITS2 and LSU nuclear rDNA produced by us or retrieved from GenBank (Table 1). *Tremella candelariellae* was used as outgroup (Table 1) based on previous literature (Millanes *et al.* 2011; Liu *et al.* 2015) and from preliminary trees. Sequences were aligned using the Q-INS-I algorithm as implemented in MAFFT v. 7 (Katoh *et al.* 2019). Misaligned positions, major insertions and ambiguous and/or divergent regions were identified and deleted with Gblocks v. 0.91b (Castresana 2000), following the relaxed conditions described by Talavera & Castresana (2007). Alignments were then checked with Mesquite (Maddison & Maddison 2021) and terminal gaps were converted to missing data.

We considered four independent partitions, ITS1, 5.8S, ITS2 and nuLSU, in all analyses. Each partition was analyzed individually by maximum likelihood ultrafast bootstrap (UF-BS) in IQ-TREE to assess for conflicts. Strongly supported clades (IQ-TREE UF-BS > 95%) in disagreement were considered to be an indication of significant conflict (Mason-Gamer & Kellogg 1996; Hoang *et al.* 2018). Since no conflict was detected in our data sets, they were combined and then analyzed using maximum likelihood (ML) and Bayesian approaches. Maximum likelihood analyses were carried out in IQ-TREE (Nguyen *et al.* 2015). Model selection for each partition was achieved using ModelFinder in IQ-TREE (Kalyaanamoorthy *et al.* 2017), with the corrected Akaike information criterion (AICc). Following this scheme, the TIM2e + I model was selected for ITS1 and 5.8S, TIM2e + Γ4 for ITS2, and TIM3 + F + Γ4 for nuLSU. We assessed node support by standard bootstrap using 1000 bootstrap pseudoreplicates. Bayesian analyses were performed by Markov chain Monte Carlo (MCMC) sampling as implemented in the software MrBayes v. 3.2.7a (Ronquist *et al.* 2012). Since

Table 1. *Tremella* sequences newly generated in this study (bold), or downloaded from GenBank, with specimen data. Type specimens are indicated by '(T)'.

Species names (DNA extraction number)	Host	ITS	LSU	Specimen data
Tremella caloplacae (SF148)	*Variospora aurantia*	OQ192947	OQ176395	Ukraine. *Kukwa* 1851 (S-F117262)
T. caloplacae (SF302)	*Variospora aurantia*	OQ192959	OQ176407	Spain. *Millanes* 1370 & *Freire-Rallo* (S)
T. caloplacae (AM780)	*Variospora dolomiticola*	OQ192948	OQ176396	Greece. *Diederich* 18575 (BR)
T. caloplacae (SF305)	*Variospora dolomiticola*	OQ192960	OQ176408	Spain. *Millanes* 1371 & *Freire-Rallo* (S)
T. caloplacae (AM782)	*Variospora flavescens*	OQ192949	OQ176397	Luxembourg. *Diederich* 18559 (BR)
T. caloplacae (SF149)	*Variospora flavescens*	OQ192950	OQ176398	Sweden. *Westberg, Košuthová, Prieto* GTL24 (S-F268002)
T. caloplacae (SF243)	*Variospora flavescens*	OQ192951	OQ176399	Sweden. *Freire-Rallo* S37 (S)
T. caloplacae (SF254)	*Variospora flavescens*	OQ192952	OQ176400	Sweden. *Freire-Rallo* S41 (S)
T. caloplacae (SF257)	*Variospora flavescens*	OQ192953	OQ176401	Sweden. *Freire-Rallo* S42 (S)
T. caloplacae (SF260)	*Variospora flavescens*	OQ192954	OQ176402	Sweden. *Freire-Rallo* S43 (S)
T. caloplacae (SF266)	*Variospora flavescens*	OQ192955	OQ176403	Sweden. *Freire-Rallo* S45 (S)
T. caloplacae (SF272)	*Variospora flavescens*	OQ192956	OQ176404	Sweden. *Freire-Rallo* S46 (S)
T. caloplacae (SF279)	*Variospora flavescens*	OQ192957	OQ176405	Sweden. *Freire-Rallo* S50 (S)
T. caloplacae (SF150)	*Variospora thallincola*	OQ192958	OQ176406	United Kingdom. *Kärnefelt* 970901 (S-L5870)
T. elegantis (AM315E)	*Rusavskia elegans*	OQ192939	OQ176388	Sweden. *Millanes* 908 (S-F255314)
T. elegantis (AM349E)	*Rusavskia elegans*	OQ192940	OQ176389	Norway. *Millanes* 808 (S-F255312)
T. elegantis (AM443)	*Rusavskia elegans*	OQ192941	OQ176390	Norway. *Millanes* 1085 (S)
T. elegantis (AM444) (T)	*Rusavskia elegans*	OQ192942	OQ176391	Norway. *A. Millanes* 1113 (S)
T. elegantis (AM554)	*Rusavskia elegans*	OQ192943	OQ176392	Sweden. *Millanes* 904 (S-F255313)
T. elegantis (SF161)	*Rusavskia elegans*	OQ192944	-	Sweden. *Odelvik, Hedenäs* & *Rönblom* 14-453 (S-F253739)
T. nimisiana (SF155)	*Xanthocarpia ferrarii*	OQ192962	OQ176410	Estonia. *Thor* 8202 (S-F70137)
T. nimisiana (AM558)	*Xanthocarpia lactea*	OQ192961	OQ176409	Austria. *Hafellner* 24839 (GZU)
T. nimisiana (SF291) (T)	*Xanthocarpia marmorata*	OQ192964	OQ176412	Spain. *Millanes* 1365 & *Freire-Rallo* (S)
T. nimisiana (SF156)	*Xanthocarpia* sp.	OQ192963	OQ176411	Estonia. *Thor* 8202 (S-F70137)
T. nimisiana (SF292)	*Xanthocarpia* sp.	OQ192965	OQ176413	Spain. *Millanes* 1356 & *Freire-Rallo* (S)
***T. nimisiana* (SF414)**	*Xanthocarpia* sp.	**OQ418449**	-	France. *B. de Lesdain* 1906 (ANGUC)
T. parietinae (AM310)	*Xanthoria parietina*	OQ192966	OQ176414	Austria. *Obermayer* 12148a (GZU)
T. parietinae (AM311)	*Xanthoria parietina*	OQ192967	OQ176415	Austria. *Fleischhacker* 11010 (GZU)
T. parietinae (AM352E)	*Xanthoria parietina*	OQ192968	OQ176416	Spain. *Zamora, Zamora* & *Señoret* 8-v-2010 (G)
T. parietinae (AM353E)	*Xanthoria parietina*	OQ192969	OQ176417	Spain. *Vivas, Zamora* & *Zamora* 18-xii-2011 (G)
T. parietinae (AM446)	*Xanthoria parietina*	OQ192970	OQ176418	Spain. *Millanes* 1192 & *Westberg* (S)
T. parietinae (AM447)	*Xanthoria parietina*	OQ192971	OQ176419	Spain. *Millanes* 1197 & *Westberg* (S)
T. parietinae (AM553)	*Xanthoria parietina*	OQ192972	OQ176420	Sweden. *Millanes* 849 (S)
T. parietinae (AM555)	*Xanthoria parietina*	OQ192973	OQ176421	Sweden. *Millanes* 833 (S)
T. parietinae (AM559)	*Xanthoria parietina*	OQ192974	OQ176422	Austria. *Obermayer* 12148a1 (GZU)
T. parietinae (AM561)	*Xanthoria parietina*	OQ192976	OQ176424	Austria. *Hafellner* 77075 (GZU)
T. parietinae (AM562)	*Xanthoria parietina*	OQ192977	OQ176425	Austria. *Obermayer* 12148a1 (GZU)
T. parietinae (AM563)	*Xanthoria parietina*	OQ192978	OQ176426	Austria. *Obermayer* 12446 (GZU)
T. parietinae (AM564)	*Xanthoria parietina*	OQ192979	OQ176427	Austria. *Hafellner* 77065 (GZU)
T. parietinae (AM565)	*Xanthoria parietina*	OQ192980	OQ176428	Slovenia. *Hafellner* 77507 (GZU)
T. parietinae (AM638)	*Xanthoria parietina*	OQ192981	OQ176429	Luxembourg. *Diederich* 17385 (BR)
T. parietinae (AM639)	*Xanthoria parietina*	OQ192982	OQ176430	Luxembourg. *Diederich* 17455 (BR)

(*Continued*)

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Table 1. (*Continued*)

Species names (DNA extraction number)	Host	ITS	LSU	Specimen data
T. parietinae (AM640)	*Xanthoria parietina*	OQ192983	OQ176431	Luxembourg. *Diederich* 17473 (BR)
T. parietinae (AM641)	*Xanthoria parietina*	OQ192984	OQ176432	Luxembourg. *Diederich* 17740 (BR)
***T. parietinae* (SF390) (T)**	*Xanthoria parietina*	**OQ418450**	-	Spain. *Millanes* 1328 (S)
***T. parietinae* (SF391)**	*Xanthoria parietina*	**OQ418451**	-	Spain. *Millanes* 1364 (S)
***T. parietinae* (SF392)**	*Xanthoria parietina*	**OQ418452**	-	Spain. *Millanes* 1304 (S)
***T. parietinae* (SF394)**	*Xanthoria parietina*	**OQ842302**	-	Spain. *Freire-Rallo* S128 (S)
***T. parietinae* (SF397)**	*Xanthoria parietina*	**OQ842303**	-	Spain. *Etayo* 31851 (hb. Etayo)
T. pusillae (SF234) (T)	*Calogaya pusilla*	OQ192934	OQ176384	Sweden. *Freire-Rallo* S33 (S)
T. pusillae (SF237)	*Calogaya pusilla*	OQ192935	OQ176385	Sweden. *Freire-Rallo* S34 (S)
T. pusillae (SF263)	*Calogaya pusilla*	OQ192936	OQ176386	Sweden. *Freire-Rallo* S44 (S)
T. pusillae (SF269)	*Calogaya pusilla*	OQ192937	OQ176387	Sweden. *Freire-Rallo* S45 (S)
T. servidiatae (AM32) (T)	*Rusavskia sorediata*	OQ192945	OQ176393	Greenland. *Kukwa* 4385a (UGDA)
T. sorediatae (AM642)	*Rusavskia sorediata*	OQ192946	OQ176394	Canada. *Goward* 01-608 (UCB)
***Tremella* sp. 13 (SF401)**	*Calogaya biatorina*	**OQ418453**	-	Spain. *Etayo* 20762 (hb. Etayo)
Tremella sp. 14 (AM556)	*Calogaya decipiens*	OQ192933	OQ176383	Sweden. *Millanes* 850 (S-F253110)
***Tremella* sp. 15 (SF399)**	*Polycauliona* sp.	**OQ418454**	-	Spain. *Etayo* 19125 (hb. Etayo)
***T. candelariellae* (AM384)**	*Candelaria concolor*	**OQ418455**	**OQ410474**	Spain. *Zamora* 13-iii-2010 (G)

not all models tested by ModelFinder in IQ-TREE can be directly implemented in MrBayes, for the Bayesian analyses we selected from a subsample of substitution models using the corrected Akaike information criterion (AICc) as implemented in jModelTest 2 (Darriba *et al.* 2012), allowing only three substitution schemes, using full likelihood optimization and four discrete gamma categories. In this case, JC was selected for ITS1 and 5.8S, and SYM + Γ for ITS2 and nuLSU rDNA. The combined analyses treated the different regions as separate partitions with topology linked across partitions but separate model parameter values and proportional rates across partitions. For each combined data set, two parallel runs were performed, each with four chains, three of which were incrementally heated with a temperature of 0.15. The analyses were diagnosed for convergence every 100 000 generations and were set to halt automatically when the average standard deviation of splits across runs in the last half of the analysis descended below 0.01. Every 100th tree was saved. The first 50% of each run was discarded as burn-in. Both ML and Bayesian analyses were performed on the CIPRES Web Portal (Miller *et al.* 2015).

Results and Discussion

Nine sequences of the ITS region and one sequence of the nuLSU region were newly produced for this study. The alignment included these newly generated sequences, combined with sequences of ITS and nuLSU sequenced by Freire-Rallo *et al.* (2023) or retrieved from GenBank (Table 1). A data matrix corresponding to the ITS and nuLSU regions was generated with a total of 1360 characters (ITS1, 1–122; 5.8S, 123–276; ITS2, 277–595; nuLSU, 596–1360). The best tree obtained from the ML analysis had a ln-likelihood value of −2998.5609. The Bayesian analysis halted after 900 000 generations, at which time the average standard deviation of split frequencies across runs was 0.0098, indicating that the three runs had converged (< 0.01). A majority-rule consensus tree was constructed from the 9000 trees of the stationary tree sample. No incongruences were found among the topologies of the trees obtained with ML and Bayesian inference and therefore only the best tree from the ML analysis is shown in Figure 1.

The phylogenetic analyses showed at least nine distinct lineages. Most of them coincide with the species delimitation analyses performed by Freire-Rallo *et al.* (2023), who discussed at least nine different species growing on different hosts: 1) on *Xanthoria parietina* (L.) Th. Fr., 2) on *Xanthocarpia lactea* (A. Massal.) A. Massal., 3) on *Xanthocarpia* sp., 4) on *Calogaya decipiens* (Arnold) Arup *et al.*, 5) on *Calogaya pusilla* (A. Massal.) Arup *et al.*, 6) on *Rusavskia elegans* (Link) S.Y. Kondr. & Kärnefelt, 7) on *Rusavskia sorediata* (Vain.) S.Y. Kondr. & Kärnefelt, 8) on *Variospora* sp., and 9) on *Leproplaca xantholyta* (Nyl.) Nyl. Not all the species delimited in Freire-Rallo *et al.* (2023) will be formally described in this work. The specimen of *T. caloplacae* s. lat. on *Leproplaca xantholyta* is in a very poor condition so it has not been possible to obtain sufficient morphological data for a full description. Although *T. caloplacae* s. lat. on *Calogaya decipiens* is one of the species delimited in Freire-Rallo *et al.* (2023), we refrain from describing a species based on a single specimen and instead leave it unnamed as *Tremella* sp. 14, until more specimens are available. The same applies to *Tremella* sp. 13 on *Calogaya biatorina* and *Tremella* sp. 15 on *Polycauliona* sp. The latter two samples were not included in Freire-Rallo *et al.* (2023) and were sequenced for the first time in this study. The specimens growing on *Xanthocarpia* species are all included in the newly described *Tremella nimisiana,* although our current and previous phylogenetic results (Freire-Rallo *et al.* 2023) clearly show that

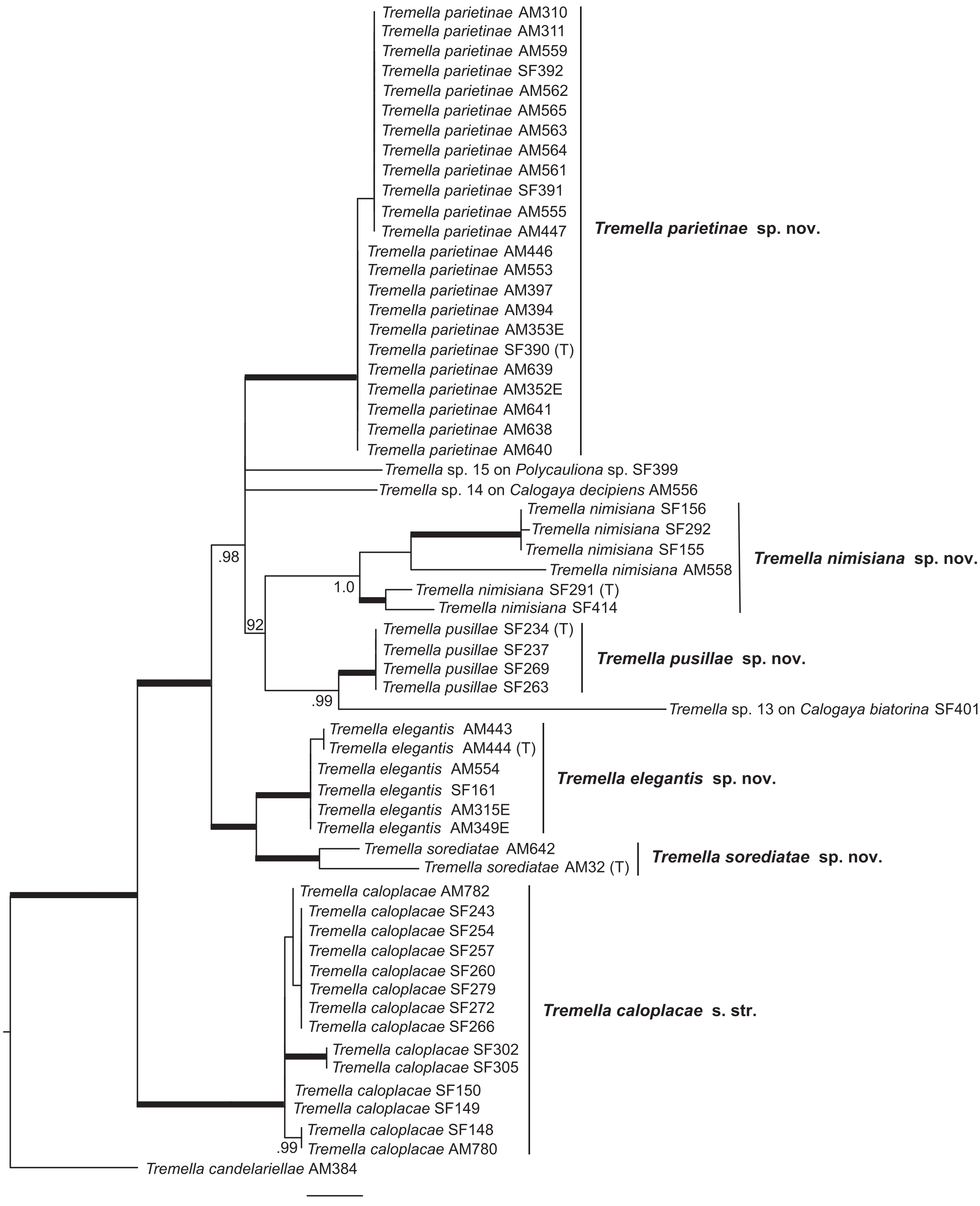

Figure 1. Phylogram based on ITS and nuLSU sequences of *Tremella* species, corresponding to the best tree recovered in the maximum likelihood analysis (ML), with information on the Bayesian posterior probability (PP) values added. Branches in bold indicate nodes supported by both PP≥ 0.95 and ML bootstrap (ML-BS) values ≥ 70. When nodes received support only from one of the two methods, ML-BS values ≥ 70 are indicated above branches and PP values ≥ 0.95, below branches. Species names are indicated in the right margin. Types are indicated with '(T)'. Branch lengths are scaled to the expected number of substitutions per site.

Tremella material growing on *Xanthocarpia* represents a species complex. This conservative decision was made owing to the low number of specimens available growing on each *Xanthocarpia* host, and to the scarcity of diagnostic characters, which makes a morphological characterization based on a small number of samples challenging.

There are also other lichenicolous *Tremella* species known to grow on *Teloschistaceae* hosts (Diederich *et al.* 2022):

Tremella teloschistis Diederich *et al.*, which is phylogenetically not close to *Tremella caloplacae* s. lat., on *Teloschistes exilis*; *T. occultixanthoriae* Diederich *et al.* on *Xanthoria parietina*; *T. pisutiellae* Diederich & W. R. Buck on *Pisutiella conversa*; *T. xanthomendozae* Diederich *et al.* on *Xanthomendoza weberi* (S.Y. Kondr. & Kärnefelt) L. Lindblom; and *Tremella* sp. 11 on *Pyrenodesmia chalybaea* (Fr.) A. Massal., from which there are no sequences and which is therefore not included in this work. These species are, however, included in our key to facilitate the identification of the newly described species, and to complement recently published keys (Diederich *et al.* 2022).

Key to *Tremella* species

1 Basidia devoid of epibasidia; on the lower thallus surface of *Xanthoria parietina* . . . . . **T. occultixanthoriae**
Basidia with epibasidia 2

2(1) Basidiomatal galls on the host thallus 3
Basidia immersed in the hymenium of the host 5

3(2) Basidiomatal galls elongated; on *Teloschistes exilis* . . . . . **T. teloschistis**
Basidiomatal galls subspherical; on other hosts 4

4(3) Basidia transversely or obliquely septate, 5.5–9 µm wide; basidiospores 5–7.5 × 4.5–6 µm; on *Xanthomendoza weberi* . . . . . **T. xanthomendozae**
Basidia transversely or obliquely septate, 8.7–13 µm wide or longitudinally septate, 13.2–16.2 µm wide; basidiospores slightly smaller; on *Rusavskia sorediata* . . . . . **T. sorediatae**

5(2) Infected apothecia without visible symptoms or only slightly swollen; basidia 2-celled, transversely septate 6
Infected apothecia strongly swollen at maturity, with convex basidiomatal galls; basidia 2-celled or rarely 3-celled 7

6(5) Basidia 17–24 × 7–10 µm; on *Pisutiella conversa* . . . . . **T. pisutiellae**
Basidia shorter, 12–18 × 7–9 µm; on *Pyrenodesmia chalybaea* . . . . . **Tremella** sp. 11

7(5) Basidiomata often > 1 mm diam. 8
Basidiomata < 1 mm diam. 11

8(7) Clamped hyphae not or rarely observed; probasidia subspherical to ellipsoidal, not fusiform 9
Clamped hyphae present; probasidia ellipsoidal to broadly fusiform 10

9(8) Basidia 2-celled; basidiospores 3.8–9.6 × 3.8–7.9 µm; on *Variospora* spp. . . . . . **T. caloplacae**
Basidia 2-celled or rarely 3-celled; basidiospores 7.6–9.2 × 6.7–10.2 µm; on *Calogaya pusilla* . . . . . **T. pusillae**

10(8) Basidia 2-celled or rarely 3-celled, not elongating separately; basidiospores 6.5–11.9 × 5.7–11.9 µm; on *Xanthoria parietina* . . . . . **T. parietinae**
Basidia 2-celled, when longitudinally septate, cells occasionally elongating and growing separately; basidiospores smaller (one measurement of 5.5 × 6.0 µm); on *Rusavskia elegans* . . . . . **T. elegantis**

11(7) Clamped hyphae not observed; basidia with transverse septa often constricted at the septum 12
Clamped hyphae present; basidia with transverse septa rarely constricted at the septum 13

12(11) Basidia 2-celled or rarely 3-celled; basidiospores 8.7–10.2 × 8.2–10.3 µm; on *Calogaya biatorina* . . . . . **Tremella** sp. 13
Basidia 2-celled, when transversely septate sometimes upper part subglobose and wider than the lower part; basidiospores smaller (one measurement of 5.5 × 4.5 µm); on *Calogaya decipiens* . . . . . **Tremella** sp. 14

13(11) Basidia 2-celled and ellipsoid to pyriform, rarely 3-celled and clavate to subcylindrical; basidiospores 7.5–10.3 × 6.9–10.1 µm; on *Xanthocarpia* spp. . . . . . **T. nimisiana**
Basidia 2-celled, elongate, very narrowly ellipsoid to ellipsoid; basidiospores smaller (one measurement of 6.5 × 7.0 µm); on *Polycauliona* sp. . . . . . **Tremella** sp. 15

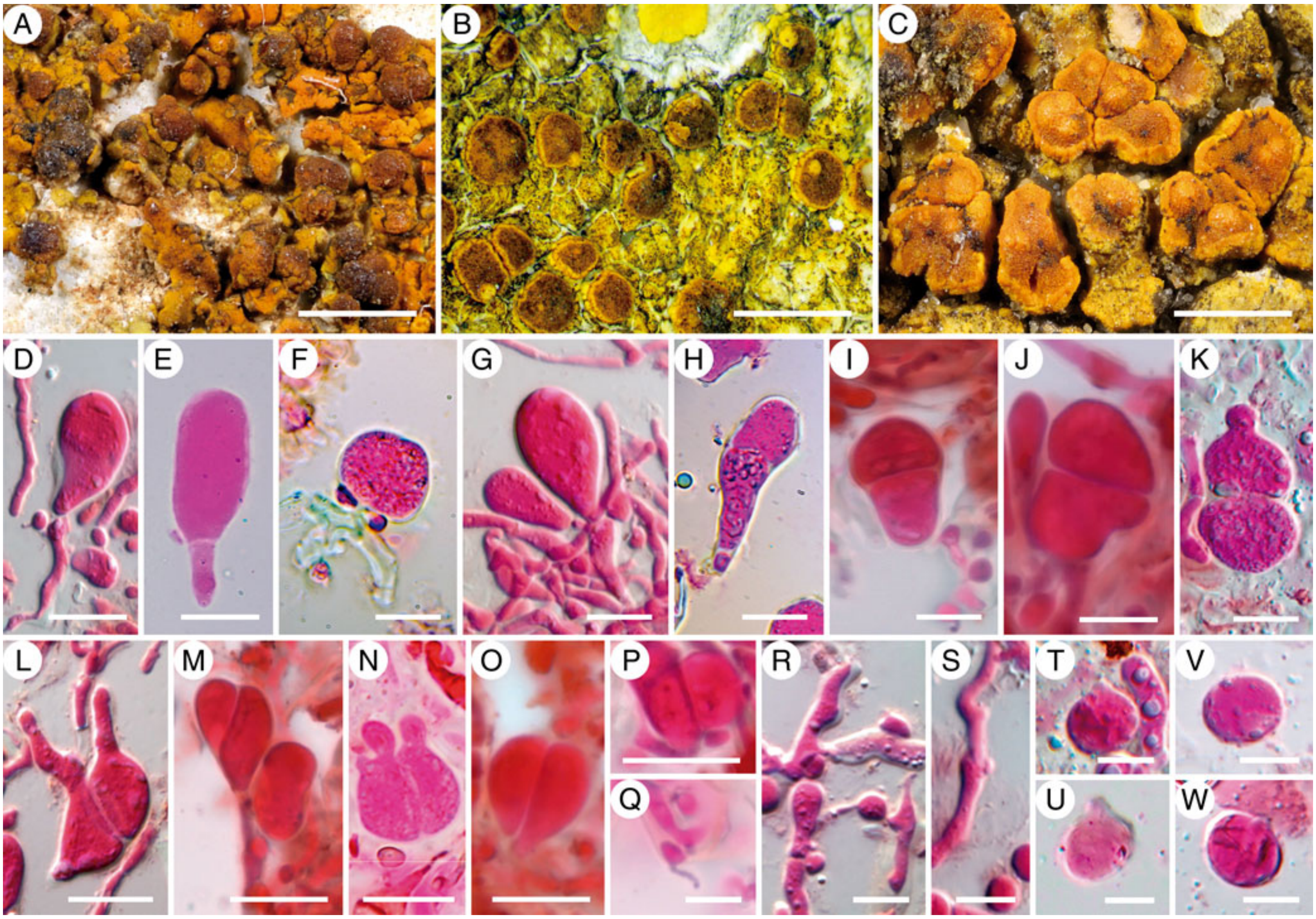

Figure 2. *Tremella caloplacae* (A, I, J, M & O, lectotype on *Variospora aurantia*; B & E, *Diederich* 12328 on *V. flavescens*; K, T, U & W, *Freire-Rallo* S43 on *V. flavescens*; N, *Freire-Rallo* S37 on *V. flavescens*; C, D, G, L, R & S, *Sérusiaux* iv 1983 on *V. dolomiticola*; F, H, P, Q & V, *Millanes* 1371 & *Freire-Rallo* on *V. dolomiticola*). A–C, variation in gall morphology. D–G, probasidia showing basal clamp connections and haustoria. H–K, transversely septate basidia. L–M, obliquely septate basidia. N–P, longitudinally septate basidia. Q–S, haustoria and hyphal clamp connections. T–W, basidiospores. Scales: A–C = 1 mm; D–R = 10 µm; S–W = 5 µm. In colour online.

Taxonomy

Tremella caloplacae (Zahlbr.) Diederich

In Sérusiaux *et al.*, *Lejeunia n. s.* **173**, 31 (2003).—*Lindauopsis caloplacae* Zahlbr., *Ber. Deutsch. Bot. Ges.* **24**, 145 (1906); type: Crete, 'an Kalkfelsen bei Kristallenia', 1904, *R. Sturany* (W 11196, lichenicolous fungus in apothecia of *Variospora aurantia*: lectotype, designated by Sérusiaux *et al.* (2003)).

= *Tremella* sp. 1, in Diederich, *Bibl. Lichenol.* **61**, 167 (1996).

(Fig. 2)

Basidiomata reduced, inducing the formation of convex, sometimes hemispherical, smooth, uniform or irregular, light yellow to brown galls in the hymenium of the host, sometimes a single gall occupying the whole surface of the hymenium obscuring the thalline margin, often scattered all over the hymenium or forming conglomerates, (0.06–)0.1–0.5(–1.8) mm diam. (n = 404). *Hyphae* rarely with clamp connections, thin-walled, up to 3 µm diam.; haustorial branches present, tremelloid, rarely with a bifurcated filament or with two filaments, mother cell (2–)2.7–4.8(–7) µm diam. (n = 114), filament up to 9.5 µm in length. *Hymenium* reduced when young but developed when old, containing numerous subspherical to ellipsoid, rarely cylindrical probasidia with a basal clamp connection. *Basidia* subspherical to ellipsoid, 2-celled when mature, with one transverse, sometimes oblique, rarely longitudinal septum, when transversely septate sometimes constricted at the septum, or upper part subglobose and wider than the lower part, (11–)14.5–27.2(–46) × (5.5–)8.0–21.2(–23) µm (n = 508) [transversely septate: (11–)15.6–27.2(–46) × (5.5–)8.8–14.5(–21) µm (n = 401); obliquely septate: (12.5–)14.5–25.7(–34) × (6.5–)8.0–15.8(–22) µm (n = 89); longitudinally septate: (11–)15.1–22.0(–25.5) × (9–)13.3–21.2(–23) µm (n = 18)]; epibasidia elongate, (1.5–)2.3–5.8(–8.5) µm diam. (n = 77), up to at least 37 µm in length. *Basidiospores* subspherical to ellipsoid, apiculus present, (3.5–)3.8–9.6(–14) × (3–)3.8–7.9(–9.5) µm (n = 13).

Ecology and distribution. *Tremella caloplacae* s. str. is known to grow only in the hymenium of *Variospora aurantia*, *V. dolomiticola*, *V. flavescens* and *V. thallincola*. The species is known from France, Greece, Luxembourg, Spain, Sweden, Ukraine and the United Kingdom.

Notes. The description above refers to *Tremella caloplacae* s. str. and is based on the description by Diederich (1996), slightly modified according to the material recently studied and the exclusion of the newly described species. *Tremella caloplacae* s. str.

grows exclusively on *Variospora* spp. and differs from other species in the *T. caloplacae* complex by the size of the basidiomata (often > 1 mm diam.), the rarity of hyphae with clamp connections, and the subspherical to ellipsoidal probasidia. Other species growing in the hymenium of *Teloschistaceae* hosts are *T. pisutiellae* and *Tremella* sp. 11 (Diederich *et al.* 2022) but these are not known to induce galls, in contrast to the rest of intrahymenial species in the *T. caloplacae* complex. Species with a micromorphology resembling that of *T. caloplacae* s. str. (i.e. 2-celled basidia transversely, obliquely or only rarely longitudinally septate) are *T. dirinariae* Diederich *et al.*, *T. montis-wilhelmii* Diederich and *T. rinodinae* Diederich & M.S. Christ. However, they differ in host selection and only *T. rinodinae* grows intrahymenially. The recent specimens of *T. caloplacae* from Crete have been collected 2.5 km NNE of the type locality and are thus likely to be genetically very similar to the type. The circumscription of *Tremella caloplacae* s. str. may be modified in the future when there is better knowledge of the species complex.

Additional specimens examined. **France:** *Pas-de-Calais*: Audresselles, Cran-aux-Oeufs, falaise maritime, sur rochers arénacés face à la mer, on *Variospora dolomiticola*, 1983, *Sérusiaux* (BR, LG, S). *Vaucluse*: 2 km S of Gordes, col de Gordes, on *V. flavescens*, 1995, *Diederich* 12328 (BR).—**Great Britain:** *England*: **V.C. 3,** South Devon, Torbay, Berry Head, locally abundant, on *V. thallincola*, 50°25′N, 3°32′W, 1997, *Kärnefelt* 970901 (S).—**Greece:** *Crete*: S of Malia, Lasithi Plateau, 500 m NW of Tzermiado, 35°12′16″N, 25°28′58″E, 890 m, on *V. dolomiticola*, 2016, *Diederich* 18575 (BR); *ibid*., on *V. aurantia*, 2016, *Diederich* 18576 (BR).—**Luxembourg:** Luxembourg City, ancient city wall S of Rumm and W of the railway bridge, 49°36′28″N, 6°8′20″E, 245 m, on *V. flavescens*, 2016, *Diederich* 18559 (BR).—**Spain:** *Guadalajara*: Valdegrudas, Páramos de la Alcarria Occidental, cliff next to a crop area, on *V. aurantia*, 40°43′03″N, 3°00′32″W, 962 m, 2017, *Millanes* 1370 & *Freire-Rallo* (S); *ibid*., on *V. dolomiticola*, *Millanes* 1371 & *Freire-Rallo* (S).—**Sweden:** *Gotland*: Hangvar par., Irevik, along the small road towards Svarthäll on the east side of Irevik, on *V. flavescens*, 57°50′14″N, 18°36′22″E, 2014, *Westberg, Košuthová* & *Prieto* GTL24 (S). *Öland*: Jordhamn, on *V. flavescens*, 57°5′52″N, 16°53′13″E, 8 m, 2017, *Freire-Rallo* S37 (S); *ibid*., *Freire-Rallo* S41, S42, S43, S46, S50 (S).—**Ukraine:** *Khmel'nyts'ka Oblast*: Posil's'ki Tovtry National Park, Kamyanets'-Podil's'kyi Rayon, Kitaygorod Village, 15 km SE of Kamyanets'-Podil's'kyi, canyon of Ternava River, 48°38′25″N, 26°46′59″E, 141 m, on *V. aurantia*, 2003, *Kukwa* 1851 (S).

Tremella elegantis Freire-Rallo, Diederich, Millanes & Wedin sp. nov.

MycoBank No.: MB 847663

Differs from *Tremella caloplacae* in the higher frequency of hyphae with clamp connections, the presence of broadly fusiform probasidia, the formation of basidia with longitudinal septa in which cells elongate and grow separately, and in developing only on *Rusavskia elegans*.

Type: Norway, Finnmark, Vadsø, Store Ekkerøya, 70°04′14″N, 30°06′26″E, 50 m, on calcareous rock, on *Rusavskia elegans*, 2014, *Millanes* 1113 (S—holotype). DNA voucher: AM444; GenBank Accession nos: OQ192942 (ITS), OQ176391 (LSU).

(Fig. 3)

Basidiomata reduced, inducing the formation of convex, orange or reddish orange to brown galls in the hymenium of the host, sometimes subspherical, irregular and rough, often forming gall conglomerates, sometimes a single gall occupying the whole surface of the hymenium obscuring the thalline margin, (0.1)0.13–0.68(1.15) mm diam. ($n = 80$). *Hyphae* sometimes with clamp connections, thin-walled, up to 3 μm diam.; haustorial branches present, tremelloid, mother cell (2)2.5–4.1(5) μm diam. ($n = 34$), filament up to 7 μm in length. *Hymenium* reduced when young but developed when old, containing numerous broadly fusiform to ellipsoid probasidia with a basal clamp connection. *Basidia* subspherical to ellipsoid or pyriform, 2-celled when mature, with one transverse, oblique, or longitudinal septum, when transversely septate, sometimes constricted at the septa, when longitudinally septate, rarely cells elongating and growing separately, (10.5)13.6–31.8(39) × (7)8.4–15.0(23) μm ($n = 140$) [transversely septate: (13)18.0–31.8(39) × (7.5)9.7–14.2(18) μm ($n = 38$); obliquely septate: (10.5)14.8–27.4(36) × (7)8.9–15.0(21) μm ($n = 62$); longitudinally septate: (11)13.6–20.0(24.5) × (8.5)8.4–16.3 (23) μm ($n = 40$)]; epibasidia elongate, (2.5)2.9–5.7(10.5) μm diam. ($n = 68$), up to at least 40 μm in length. *Basidiospores* subspherical, apiculus present, 5.5 × 6.0 μm ($n = 1$).

Etymology. From *Rusavskia elegans*, the host lichen.

Ecology and distribution. Tremella elegantis is known to grow only in the hymenium of *Rusavskia elegans*. The species is known from Norway and Sweden.

Notes. Tremella elegantis resembles *T. caloplacae* s. str. since it induces the formation of convex galls in the hymenium of its host. *Tremella elegantis*, however, grows exclusively on *Rusavskia elegans* and also differs from other species in the *T. caloplacae* complex in the size of the basidiomata (often > 1 mm diam.), the higher frequency of hyphae with clamp connections, the ellipsoidal to broadly fusiform probasidia, and the formation of basidia with cells elongating and growing separately when they are longitudinally septate. Both *T. elegantis* and *T. sorediatae* sometimes produce basidia with longitudinal septa where the cells grow separately, but basidia are smaller in *T. elegantis*. Species also showing basidia with these characteristics are *T. christiansenii* Diederich, *T. diederichiana* Pérez-Ort. *et al.*, *T. hypocenomycis* Diederich, *T. mayrhoferi* J.C. Zamora *et al.* and *T. tuckerae* Diederich, but these differ in the larger (*T. christiansenii*, *T. diederichiana*, *T. mayrhoferi* and *T. tuckerae*) or smaller (*T. hypocenomycis*) basidia, and in that basidia can be 2–4-celled except for *T. tuckerae* (also 2-celled). The new species *T. elegantis* is phylogenetically homogeneous and is sister to *T. sorediatae*.

Additional specimens examined (all on Rusavskia elegans*).* **Norway:** *Finnmark*: Vardø, Bukkemoltangen, Dolomites area, 70°25′33″N, 30°45′19″E, 25 m, 2014, *Millanes* 1085 (S). *Oppland*: Lom, Runningsgrende, Kleive, 61°42′57″N, 8°14′03″E, 750 m, 2013, *Millanes* 808 (S).—**Sweden:** *Ångermanland*: Grundsunda sn, Skagsudden, 2550 m S om Skags kapell, Skagsudde, 250 m WSW om fyren, 63°11′12″N, 19°01′11″E, 2 m, 2013, *Odelvik, Hedenäs* & *Rönblom* 14-453 (S). *Torne Lappmark*: Jukkasjärvi, Mt Paddos, 68°19′8″N, 18°51′54″E, 596 m, at the base of a cliff, 2013, *Millanes* 908 (S); Jukkasjärvi, Mt Paddos, 68°19′10″N, 18°51′56″E, 625 m, 2013, *Millanes* 904 (S).

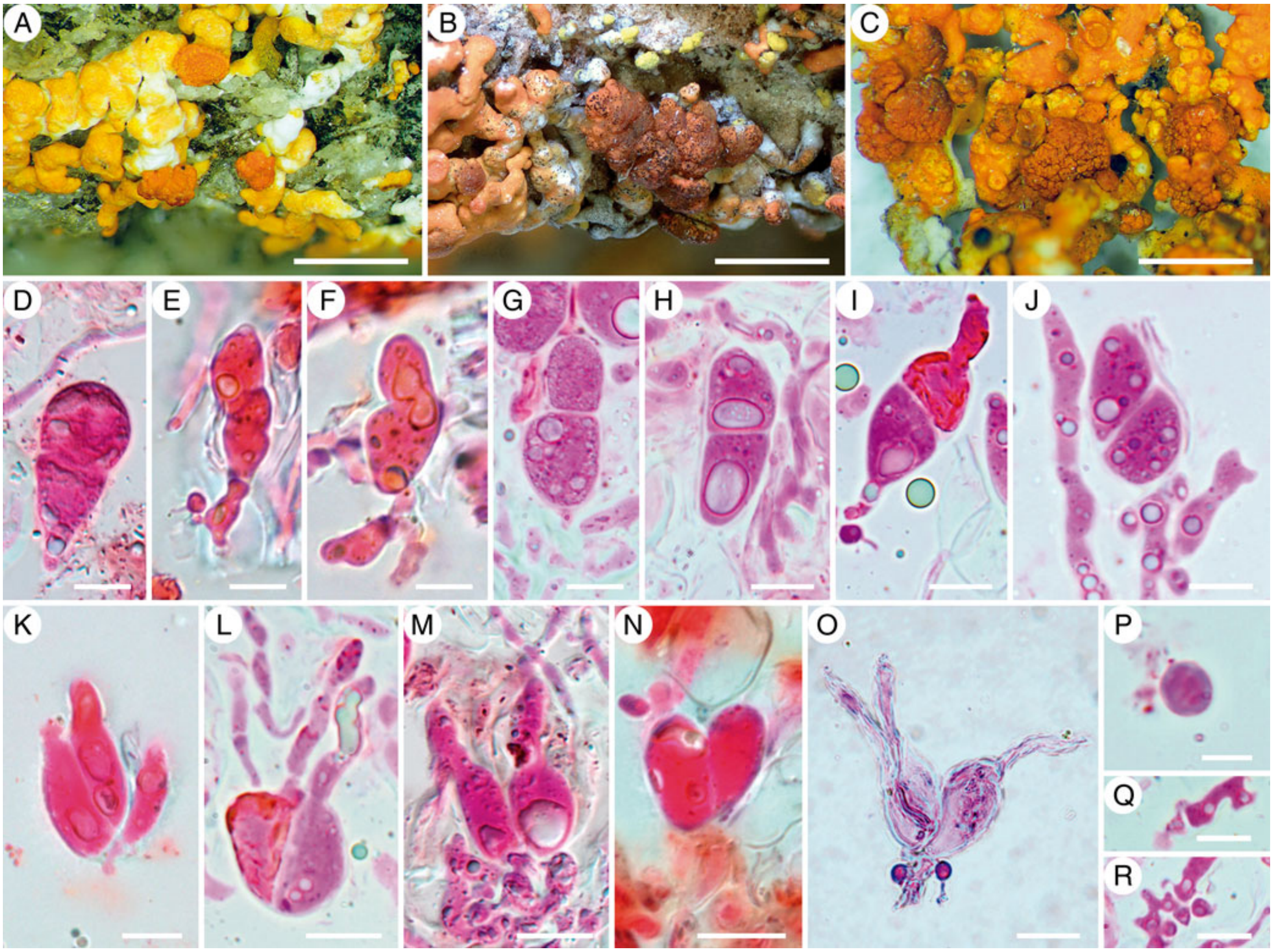

Figure 3. *Tremella elegantis* on *Rusavskia elegans* (A, D & M, *Millanes* 808; B, E & F, *Millanes* 908; C, G, H, J, Q & P, holotype; I & L, *Millanes* 1085; K, N & R, *Millanes* 904; O, *Odelvik, Hedenäs* & *Rönblom* 14-453). A–C, variation in gall morphology. D–H, 2-celled transversely septate basidia with one haustorium. I–K, obliquely septate basidia with one haustorium. L–O, longitudinally septate basidia with haustoria. P, basidiospore. Q & R, hyphae with clamp connections. Scales: A–C = 1 mm; D–O = 10 μm; P–R = 5 μm. In colour online.

Tremella nimisiana Freire-Rallo, Diederich, Millanes & Wedin sp. nov.

MycoBank No.: MB 847664

Differs from *Tremella caloplacae* in the size of the basidiomata (< 1 mm diam.), the higher frequency of hyphae with clamp connections, larger basidiospores (7.5–10.3 × 6.9–10.1 μm), and in developing only on *Xanthocarpia* spp.

Type: Spain, Guadalajara, Tendilla, Páramos de la Alcarria Occidental, 40°31′44″N, 2°58′60″W, 910 m, on calcareous rock, on *Xanthocarpia marmorata*, 2017, *Millanes* 1365 & *Freire-Rallo* (S—holotype). DNA voucher: SF291; GenBank Accession no: OQ192964 (ITS).

(Fig. 4)

Basidiomata reduced, inducing the formation of convex, yellowish orange to dark brown galls in the hymenium of the host, sometimes hemispherical, irregular and rough, sometimes smooth, often forming gall conglomerates, sometimes a single gall occupying the whole surface of the hymenium, (0.08–)0.07–0.30(–0.66) mm diam. *Hyphae* sometimes with clamp connections, thin-walled, up to 3 μm diam.; haustorial branches present, tremelloid, rarely with a bifurcated filament, mother cell rarely triangular, (2.5–)2.7–5.2(–7) μm diam. ($n = 74$), filament up to 17 μm in length. *Hymenium* reduced when young but developed when old, containing numerous broadly fusiform to ellipsoid probasidia with a basal clamp connection. *Basidia* narrowly elongate ellipsoid to pyriform, 2-celled when mature, with one transverse, rarely oblique or longitudinal septum, when transversely septate often stalked, rarely constricted at the septa, exceptionally 3-celled, with 2 transverse septa, clavate to subcylindrical, resembling *Biatoropsis* basidia, (17–)17.1–37.9(–55.5) × (7–)9.6–13.6(–17) μm ($n = 142$) [transversely septate: (17–)23.8–37.9(–55.5) × (7–)9.6–13.4(–17) μm ($n = 132$); obliquely septate: (18–)17.1–35.2(–48) × (11–)10.6–13.6(–15) μm ($n = 8$); longitudinally septate: (21.5–)21.0–23.6(–23.5) × (8–)6.9–11.9(–11.5) μm ($n = 2$)]; epibasidia elongate, (2.5–)2.9–5.7(–11.5) μm diam. ($n = 62$), up to at least 40 μm in length. *Basidiospores* subspherical to ellipsoid, apiculus present, (7–)7.5–10.3(–12) × (6–)6.9–10.1(–11.5) μm ($n = 38$).

Etymology. Named after Pier Luigi Nimis, Italian lichenologist, in recognition of his great work and contribution to lichenology.

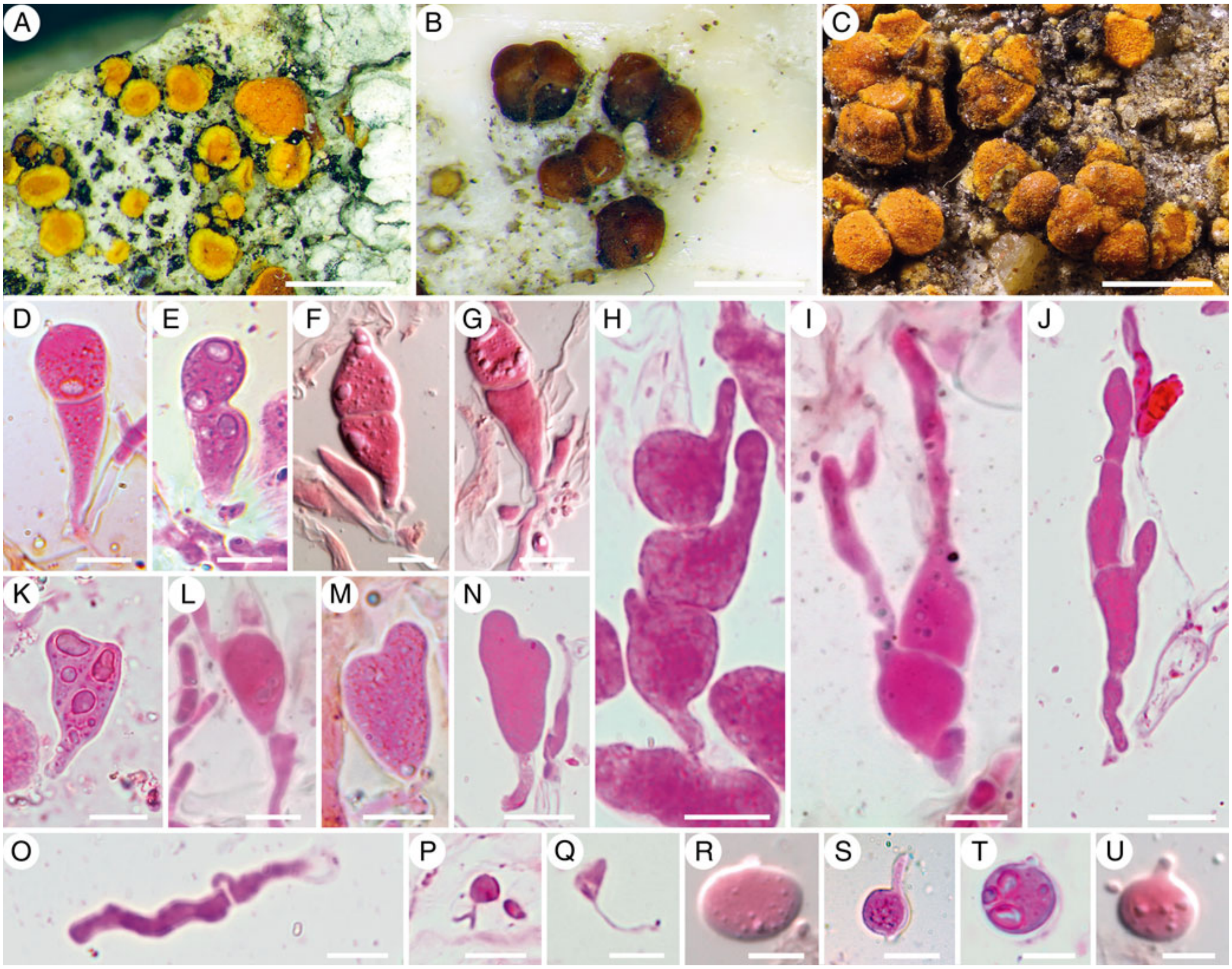

Figure 4. *Tremella nimisiana* (A, E, M & S, holotype on *Xanthocarpia marmorata*; B, H, I, J, L, N–Q, *B. de Lesdain* 1906 on *Xanthocarpia* sp.; C, F, G, R & U, *Hafellner* 24839 on *X. lactea*; K & T, *Thor* 8202 on *X. ferrarii*). A–C, variation in gall morphology. D–G, I & J, 2-celled transversely septate basidia with haustoria and clamp connections. H, transversely septate 3-celled basidium. K & L, obliquely septate basidia. M & N, longitudinally septate basidia. O, hypha with clamp connection. P & Q, haustoria. R–U, basidiospores. Scales: A–C = 1 mm; D–N = 10 μm; O–U = 5 μm. In colour online.

Ecology and distribution. *Tremella nimisiana* is known to grow in the hymenium of *Xanthocarpia ferrarii* (Bagl.) Frödén *et al.*, *X. lactea*, *X. marmorata* (Bagl.) Frödén *et al.* and *Xanthocarpia* sp. The species is known from Austria, Estonia, France and Spain.

Notes. *Tremella nimisiana* resembles *T. caloplacae* s. str. since it induces the formation of convex galls in the hymenium of its host. *Tremella nimisiana*, however, grows exclusively on *Xanthocarpia* spp. and also differs from other species in the *T. caloplacae* complex by the size of the basidiomata (often < 1 mm diam.), the higher frequency of hyphae with clamp connections, and the formation of 2-celled ellipsoid to pyriform basidia, or rarely 3-celled clavate to subcylindrical basidia. Other species within the *T. caloplacae* complex with occasionally 3-celled basidia are *T. parietinae*, *T. pusillae* and *Tremella* sp. 13, but these can be distinguished from *T. nimisiana* by their shorter and wider basidia. Another species commonly producing 3-celled basidia is *Tremella phaeographinae* Diederich & Aptroot, but this differs in the smaller basidia. The genetic differences among the specimens of *T. nimisiana* suggest that it is a potential species complex, which will probably be confirmed when there is a better knowledge of the species. The circumscription of *Tremella nimisiana* s. str. may therefore need to be modified in the future.

Additional specimens examined. **Austria:** *Burgenland*: Mühlgraben SW von Jennersdorf, bei den Gehöften, am Bachufer, 310 m, auf Beton einer alten Brücke, on *Xanthocarpia lactea*, 1990, *Hafellner* 24839 (GZU).—**Estonia:** *Harjumaa*: Tallinn Botanic Garden, Kloostiimetsa, 59°28′N, 24°52′E, 24 m, on *X. ferrarii* and *Xanthocarpia* sp., 1989, *Thor* 8202 (S).—**France:** *Nord*: Bray-Dunes à la frontière belge, sur les vieilles coquilles, on *Xanthocarpia* sp., 1906, *B. de Lesdain* (ANGUC—holotype of *Caloplaca lactea* f. *ostreaeseda* (Harm.) Zahlbr.) (Navarro-Rosinés & Hladun 1996).—**Spain:** *Zaragoza*: Belchite, La Lomaza de Belchite, road to Nª Sª del Rosario, 625 m, calcareous knoll, on *X. marmorata*, 2003, *Etayo* 20387 (hb. Etayo).

Tremella parietinae Freire-Rallo, Diederich, Millanes & Wedin sp. nov.

MycoBank No.: MB 847665

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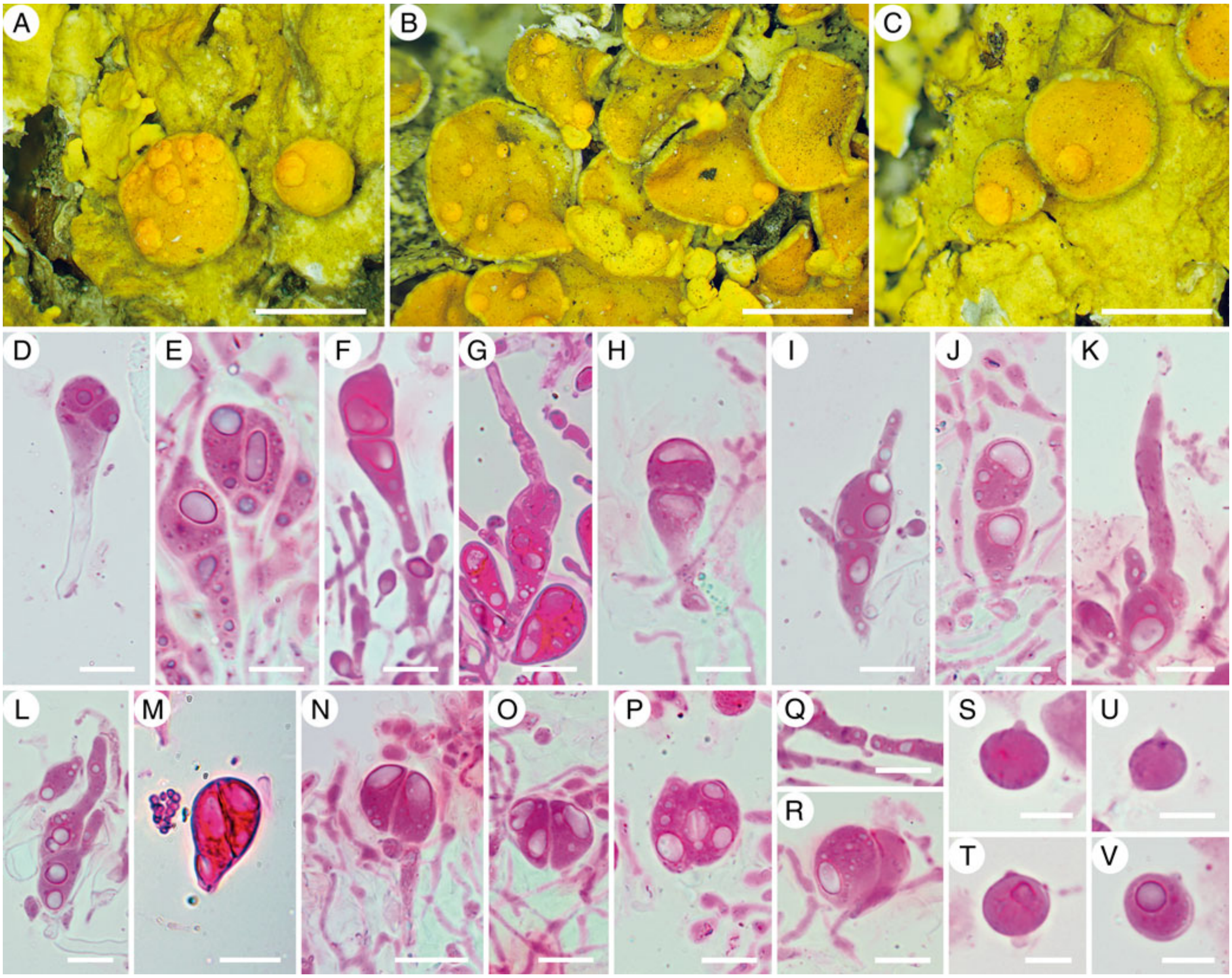

Figure 5. *Tremella parietinae* on *Xanthoria parietina* (A, D, E, K, T & U, *Diederich* 17385; B, F, J, L, P & S, holotype; C, H, I, N, O & R, *Diederich* 17740; G, M, Q & V, *Obermayer* 12148a). A–C, variation in gall morphology. D & E, 3-celled basidia and transversely septate 2-celled basidium. F–J, transversely septate basidia with haustoria and clamp connections. K–N, obliquely septate basidia with haustoria and clamp connections. O, P & R, longitudinally septate basidia. Q, hypha with clamp connection. S–V, basidiospores. Scales: A–C = 1 mm; D–R = 10 µm; S–V = 5 µm. In colour online.

Differs from *Tremella caloplacae* in the higher frequency of hyphae with clamp connections, the broadly fusiform probasidia, the rarely 3-celled basidia, bigger basidiospores (6.5–11.9 × 5.7–11.9 µm), and in developing only on *Xanthoria parietina*.

Type: Spain, Madrid, Villaviciosa de Odón, Área Recreativa El Sotillo, 40°22′03″N, 3°56′44″W, 580 m, on the bark of *Fraxinus* sp., on *Xanthoria parietina*, 2017, *Millanes* 1328 (S—holotype). DNA voucher: SF390; GenBank Accession no: OQ418450 (ITS).

(Fig. 5)

Basidiomata reduced, inducing the formation of convex, yellow to orange galls in the hymenium of the host, often hemispherical, smooth, uniform and scattered all over the hymenium, sometimes irregular and forming conglomerates, (0.05–)0.10–0.42(–1.18) mm diam. ($n = 330$). *Hyphae* sometimes with clamp connections, thin-walled, up to 3 µm diam.; haustorial branches present, tremelloid, rarely with a bifurcated filament, mother cell (2–)3.0–5.3(–6.5) µm diam. ($n = 116$), filament up to 10 µm in length. *Hymenium* reduced when young but developed when old, containing numerous broadly fusiform to ellipsoidal probasidia with a basal clamp connection. *Basidia* subspherical, pyriform or ellipsoid, 2-celled when mature, with one transverse, sometimes oblique, rarely longitudinal septum, when transversely septate sometimes constricted at the septum, or upper part subglobose and wider than the lower part, rarely basidia 3-celled with two oblique septa or one transverse and another oblique septum, rarely with a distinct stalk, (11–)14.0–34.3(–47.5) × (5–)9.7–21.5(–22) µm ($n = 408$) [transversely septate: (12–)20.7–34.3(–47.5) × (5–)10.1–14.3(–18.5) µm ($n = 315$); obliquely septate: (15–)19.6–30.3(–40) × (7.5–)9.7–14.6(–20.5) µm ($n = 84$); longitudinally septate: (11–)14.0–21.2(–23) × (14–)16.7–21.5(–22) µm ($n = 9$)]; epibasidia elongate or cylindrical, (2–)2.9–5.1(–7.5) µm diam. ($n = 136$), up to at least 43.5 µm in length. *Basidiospores* subspherical, apiculus present, (4–)6.5–11.9(–14.5) × (3–)5.7–11.9(–14.5) µm ($n = 46$).

Etymology. From *Xanthoria parietina*, the host lichen.

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Ecology and distribution. *Tremella parietinae* is known to grow only in the hymenium of *Xanthoria parietina*. The species is known from Austria, Luxembourg, Portugal, Slovenia, Spain and Sweden but probably has a broader distribution as it seems not to be rare where *Xanthoria parietina* is present.

Notes. *Tremella parietinae* resembles *T. caloplacae* s. str. since it induces the formation of convex galls in the hymenium of its host, but it grows exclusively on *Xanthoria parietina* and also differs from other species in the *T. caloplacae* complex by the size of the basidiomata (often > 1 mm diam.), the higher frequency of hyphae with clamp connections, the ellipsoidal to broadly fusiform probasidia, and the formation of 2-celled or rarely 3-celled basidia. *Tremella occultixanthoriae* is another species growing on *X. parietina*, but it grows on the lower surface of the thallus and produces 4-celled basidia with longitudinal septa devoid of epibasidia. Differences among *T. nimisiana*, *T. parietinae*, *T. pusillae* and *Tremella* sp. 13 are discussed in the notes of *T. nimisiana*. The new species *T. parietinae* is phylogenetically homogeneous.

Additional specimens examined (all on Xanthoria parietina*).* **Austria:** *Kärnten*: Zentralalpen, 46°50′05″N, 14°47′10″E, 550 m, 2010, *Hafellner* 77065 (GZU). *Steiermark*: Nordalpen, Dachstein-Gruppe, Ramsau, 47°25′16″N, 13°38′10″E, 1170 m, 2011, *Obermayer* 12148a (GZU); *ibid*., 2012, *Obermayer* 12446 (GZU); *ibid*., 47°25′35″N, 13°39′10″E, 1180 m, 2011, *Obermayer* 12147 (GZU); Oststeirisches Hügelland, Graz, Andritz, Pfanghofweg 40a, 47°06′57″N, 15°26′18″E, 410 m, 2011, *Pinter* 11010 (GZU); Oststeirisches Hügelland, Graz, Ragnitztal, 47° 4′35″N, 15°28′50″E, 380 m, 2010, *Hafellner* 77075 (GZU).—**Luxembourg:** Pétange, Fuussbësch, 2012, *Diederich* 17385 (BR); Belvaux, Metzerbierg, 2012, *Diederich* 17455 (BR); Belvaux, Kiemreech, 2012, *Diederich* 17473 (BR); Strassen, Tossebierg, 2014, *Diederich* 17740 (BR).—**Portugal:** *Lisboa*: Monsanto Natural Park, 38°43′44″N, 9°10′54″W, 180 m, 2019, *Etayo* 31826 (hb. Etayo).—**Slovenia:** Southern Alps, Julian Alps, Cezsoča S of Bovec SE above the village, 46°19′10″N, 13°33′20″E, 380 m, 2003, *Hafellner* 77507 (GZU).—**Spain:** *Castilla y León*: Burgos, Santo Domingo de Silos, 41°57′30″N, 3°24′00″W, 1130 m, 2019, *Etayo* 31851 (hb. Etayo); Burgos, between Santo Domingo de Silos and Espinosa de Cervera, 41°54′16″N, 3°28′04″W, 1145 m, 2019, *Etayo* 31889 (hb. Etayo); Burgos, road from Lerma to Santo Domingo de Silos, 2019, *Etayo* 31970 (hb. Etayo); Segovia, San Ildefonso, 40°52′22″N, 4°01′07″W, 1220 m, 2010, *Zamora*, *Zamora* & *Señoret* 2010 (G). *Extremadura*: Cáceres, Monfragüe National Park, Villareal de San Carlos, 39°50.91′N, 6°02.48′W, 290 m, 2014, *Millanes* 1192 & *Westberg* (S); Cáceres, Monfragüe National Park, from Salto del Gitano to Fuente del Francés, 39°49′42″N, 6°03′02″W, 320 m, 2014, *Millanes* 1197 & *Westberg* (S). *Madrid*: El Escorial, 2011, *Vivas, Zamora* & *Zamora* (G); Pinilla, 40°55′42″N, 3°48′57″W, 1100 m, 2014, *Millanes* 1190 (S); same locality as the type, 2017, *Millanes* 1297, 1304, 1364 (S); 2019, *Freire-Rallo* S128 & *Millanes* (S); *ibid*., 2011, *Zamora* (BR).—**Sweden:** *Östergötland*: Nässja Parish, 58°27′53″N, 14°48′47″E, 109 m, 2013, *Millanes* 833, 849 (S).

Tremella pusillae Freire-Rallo, Diederich, Millanes & Wedin sp. nov.

MycoBank No.: MB 847666

Differs from *Tremella caloplacae* in the presence of ellipsoid probasidia, the rare presence of 3-celled basidia, the size of the basidiospores (7.6–9.2 × 6.7–10.2 μm), and in developing only on *Calogaya pusilla*.

Type: Sweden, Öland, Jordhamn, 57°05′53″N, 16°53′13″E, 6 m, on calcareous rock, on *Calogaya pusilla*, 2017, *Freire-Rallo* S33 (S—holotype). DNA voucher: SF234; GenBank Accession nos: OQ192934 (ITS), OQ176384 (LSU).

(Fig. 6)

Basidiomata reduced, inducing the formation of convex, light orange to brown galls in the hymenium of the host, hemispherical, irregular and rough, rarely smooth and uniform, often forming gall conglomerates in the hymenium of the host, sometimes the thalline margin of the host is not visible, (0.13–)0.14–0.55(–1.5) mm diam. ($n = 84$). *Hyphae* thin-walled, up to 3 μm diam., clamp connections not observed; haustoria rarely observed, haustorial branches tremelloid, mother cell (2.5–)2.3–4.8(–5) μm diam. ($n = 3$), filament up to 4 μm in length. *Hymenium* reduced when young but developed when old, containing numerous ellipsoid probasidia. *Basidia* ellipsoid or pyriform, 2-celled when mature, rarely 3-celled, often with one transverse or oblique, rarely longitudinal septum, when transversely septate, sometimes constricted at the septum, (13–)15.6–26.7(–30) × (6.5–)9.5–19.3(–18.5) μm ($n = 58$) [transversely septate: (13–)18.6–26.7(–30) × (6.5–)9.5–13.0(–15.5) μm ($n = 38$); obliquely septate: (13.5–)19.2–26.2(–28) × (9–)9.6–14.4(–18.5) μm ($n = 18$); longitudinally septate: (17–)15.6–23.3(–22.5) × (15–)14.2–19.3(–18.5) μm ($n = 2$)]; epibasidia cylindrical to elongate, (2.5–)2.9–5.2(–6) μm diam. ($n = 16$), up to at least 34 μm in length. *Basidiospores* subspherical, apiculus present, (7–)7.6–9.2(–9.5) × (7–)6.7–10.2(–11) μm ($n = 10$).

Etymology. From *Calogaya pusilla*, the host lichen.

Ecology and distribution. *Tremella pusillae* induces galls in the hymenium of *Calogaya pusilla*. It is known only from Sweden.

Notes. *Tremella pusillae* resembles *T. caloplacae* s. str. since it induces the formation of convex galls in the hymenium of its host. *Tremella pusillae*, however, grows exclusively on *Calogaya pusilla* and also differs from other species in the *T. caloplacae* complex by the size of the basidiomata (often > 1 mm diam.), the absence of hyphae with clamp connections, the subspherical to ellipsoidal probasidia, and the formation of 2-celled or rarely 3-celled basidia. Differences among *T. nimisiana*, *T. parietinae*, *T. pusillae* and *Tremella* sp. 13 are discussed in the notes of *T. nimisiana*. The new species *T. pusillae* is phylogenetically homogeneous and is closely related to *Tremella* sp. 13.

Additional specimens examined (all in Calogaya pusilla*).* **Sweden:** same locality as the type, 2017, *Freire-Rallo* S34, S44, S45 (S). *Östergötland*: Nässja parish, 58°27′53″N, 14°48′47″E, 112 m, on calcareous rocks on the church wall, 2013, *Millanes* 835 (S).

Tremella servediatae Freire-Rallo, Diederich, Millanes & Wedin sp. nov.

MycoBank No.: MB 847667

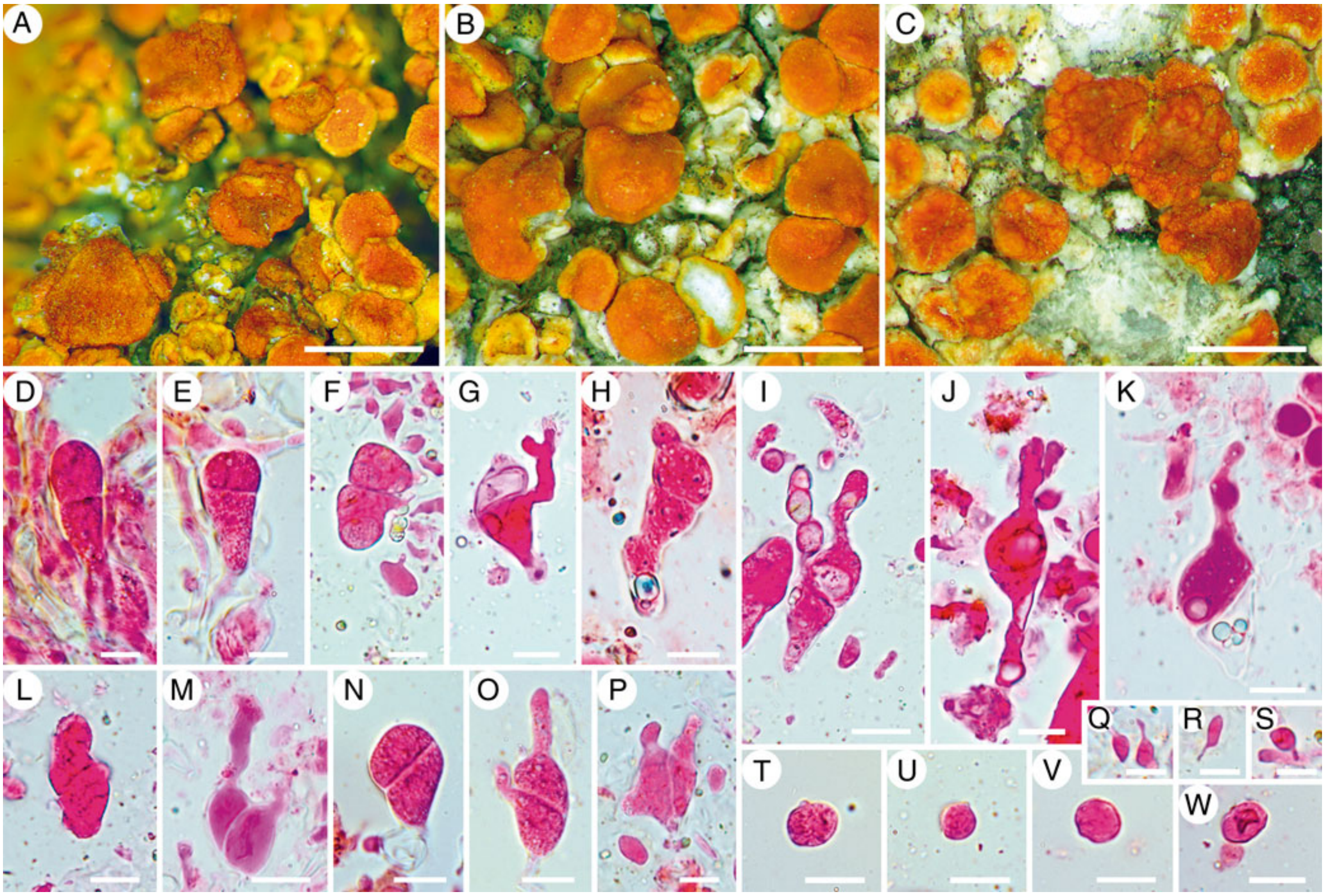

Figure 6. *Tremella pusillae* on *Calogaya pusilla* (A, F, G, I, J, L, P–S, holotype; B, D, E, N, O, T, U & W, *Freire-Rallo* S37; C, K & M, *Freire-Rallo* S44; H & V, *Freire-Rallo* S45). A–C, variation in gall morphology. D–J, 2-celled transversely septate basidia. K–O, obliquely septate basidia. P, longitudinally septate basidium. Q–S, haustoria. F, T–W, basidiospores. Scales: A–C = 1 mm; D–P, T–W = 10 µm; Q–S = 5 µm. In colour online.

Differs from *Tremella caloplacae* and from other species in the *T. caloplacae* complex in the development of basidiomatal galls on the host thallus instead of the hymenium, and in the presence of basidia with longitudinal septa with cells elongating and growing separately.

Type: Greenland, Qagssiarsuk, open area, 61°10′N, 45°35′W, on rock, on *Rusavskia sorediata*, 2005, *Kukwa* 4385a (UGDA—holotype; BR, S—isotypes). DNA voucher: AM32; GenBank Accession nos: OQ192945 (ITS), OQ176393 (LSU).

(Fig. 7)

Basidiomata growing on the host thallus, inducing the formation of convex, orange to brown galls, more or less subspherical, irregular and rough, often forming gall conglomerates, (0.19–)0.15–0.66(–1.34) mm diam. ($n = 29$). *Hyphae* thin-walled, up to 3 µm diam., clamp connections not observed; haustorial branches present, tremelloid, mother cell (2–)2.2–3.9(–4.5) µm diam. ($n = 21$), filament up to 7 µm in length. *Hymenium* reduced when young but developed when old, containing numerous ellipsoid probasidia with a basal clamp connection. *Basidia* ellipsoid, pyriform, 2-celled when mature, often with one transverse or oblique, rarely longitudinal septum, when transversely septate, sometimes constricted at the septum, when longitudinally septate, sometimes cells elongating and growing separately, (12–)15.0–22.6(–24.5) × (7.5–)8.7–16.2(–16) µm ($n = 42$) [transversely septate: (12–)16.5–22.6(–24.5) × (7.5–)8.7–12.7(–14.5) µm ($n = 18$); obliquely septate: (12.5–)15.0–21.3(–24.5) × (8–)8.8–13.0(–15) µm ($n = 20$); longitudinally septate: (16–)16.7–19.3(–19) × (13–)13.2–16.2(–16) µm ($n = 4$)]; epibasidia elongate, (2–)2.1–4.1(–4) µm diam. ($n = 20$), up to at least 25 µm in length. Sterigma not observed. *Basidiospores* subspherical to ellipsoid, apiculus present, (4–)4.1–5.7(–6) × (3–)3.0–4.5(–5) µm ($n = 8$).

Etymology. From *Rusavskia sorediata*, the host lichen.

Ecology and distribution. Tremella sorediatae induces galls on the thallus of *Rusavskia sorediata*. The species is known from Greenland and Canada.

Notes. Tremella sorediatae grows exclusively on *Rusavskia sorediata* and differs from other species in the *T. caloplacae* complex by being the only species that induces galls on the thallus of its host. It is similar to *T. xanthomendozae*, a species apparently confined to *Xanthomendoza weberi*, that induces the formation of galls on the thallus of its host, but differs in the smaller size of its basidia and basidiospores. Differences with *T. elegantis* are discussed in the notes of this species. We have studied only two specimens of *T. sorediatae* and they form a supported monophyletic lineage. However, the genetic differences between the two samples suggest that further material and studies are needed to clarify whether this is a single species or a species complex.

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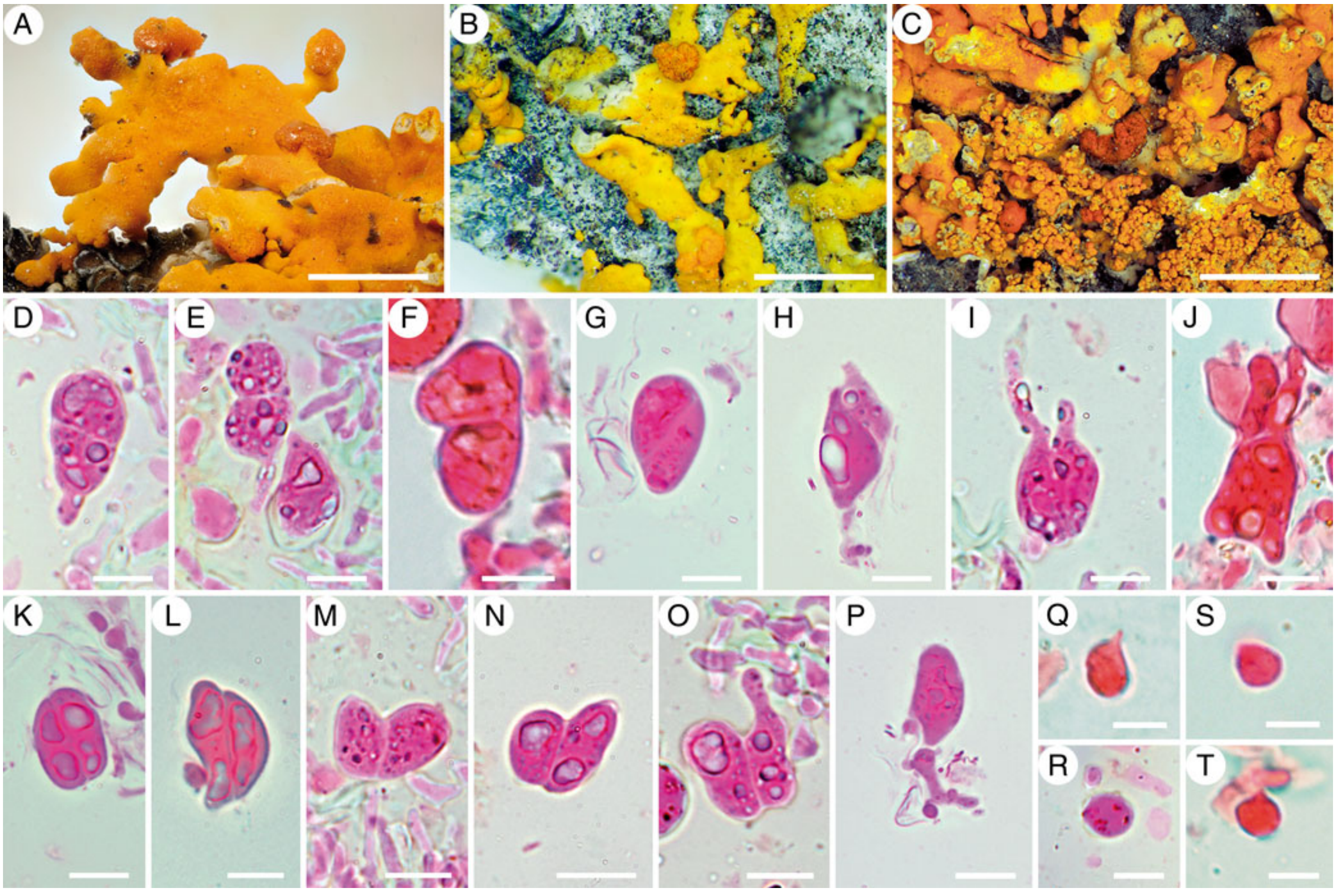

Figure 7. *Tremella sorediatae* on *Rusavskia sorediata* (A, C, F, G, J, K, L, P, Q, S & T, holotype; B, D, E, H, I, M, N, O & R, *Goward* 01-608). A–C, morphological variation in gall morphology. D–F, 2-celled transversely septate basidia. G–J, obliquely septate basidia. K–O, longitudinally septate basidia. P, probasidium with haustorium and clamp connection. Q–T, basidiospores. Scales: A–C = 1 mm; D–P = 10 μm; Q–T = 5 μm. In colour online.

Additional specimen examined. **Canada:** *British Columbia*: Crown Lake, Marble Canyon Provincial Park, 25 km NE of Lillooet, 600 m, on *Rusavskia sorediata*, 2001, *Goward* 01-168 (BR, UBC).

Tremella sp. 13 (on *Calogaya biatorina*)

(Fig. 8)

Basidiomata reduced, inducing the formation of convex, light to dark orange galls in the hymenium of the host, hemispherical, smooth and uniform, often several galls on the same apothecium but not forming aggregates, (0.12–)0.17–0.35(–0.48) mm diam. ($n = 35$). *Hyphae* thin-walled, up to 3 μm diam., clamp connections not observed; haustoria rarely observed, haustorial branches tremelloid, mother cell (3.5–)3.6–5.5(–6) μm diam. ($n = 11$), filament up to 5 μm in length. *Hymenium* reduced when young but developed when old, containing numerous broadly fusiform to ellipsoid probasidia. *Basidia* narrowly elongate ellipsoid to subspherical, pyriform, 2-celled when mature, rarely 3-celled, often with one transverse septum, rarely with oblique or longitudinal septum, when transversely septate, sometimes constricted at the septum, (19–)20.0–33.3(–41.5) × (10.5–)11.4–16.8(–17) μm ($n = 47$) [transversely septate: (19–)24.2–33.3(–41.5) × (10.5–)11.4–14.5(–17.5) μm ($n = 38$); obliquely septate: (23.5–)24.0–31.2(–33.5) × (12.5–)12.6–16.2(–17) μm ($n = 6$); longitudinally septate: (20–)20.0–21.4(–21.5) × (14.5–)14.6–16.8(–17) μm ($n = 3$)]; epibasidia elongate, (3.5–)4.1–5.8(–7) μm diam. ($n = 29$), up to at least 61 μm in length. *Basidiospores* subspherical, apiculus present, (8.5–)8.7–10.2(–10.5) × (8–)8.2–10.3(–10.5) μm ($n = 5$).

Ecology and distribution. *Tremella* sp. 13 induces galls in the hymenium of *Calogaya biatorina*. It is known only from Spain.

Specimen examined. **Spain:** *Huesca*: ascent slope to Góriz, 1990 m, on *Calogaya biatorina*, 2003, *Etayo* 20762 (hb. Etayo).

Tremella sp. 14 (on *Calogaya decipiens*)

(Fig. 9)

Basidiomata reduced, inducing the formation of convex, dark yellow to light brown galls in the hymenium of the host, subspherical, irregular, (0.09–)0.08–0.39(–0.81) mm diam. ($n = 23$). *Hyphae* up to 3 μm diam., clamp connections not observed; haustoria rarely observed, haustorial branches tremelloid, mother cell (2–)2.0–4.1(–4) μm diam. ($n = 2$), filament up to 3 μm in length. *Hymenium* reduced when young but developed when old, containing numerous ellipsoid probasidia. *Basidia* ellipsoid to subspherical, 2-celled when mature, with one transverse septum, rarely obliquely or longitudinally septate, when transversely septate, sometimes upper part subglobose and wider than the lower part, (11–)13.2–19.4(–23) × (8–)8.3–11.4(–14.5) μm ($n = 39$) [transversely septate:

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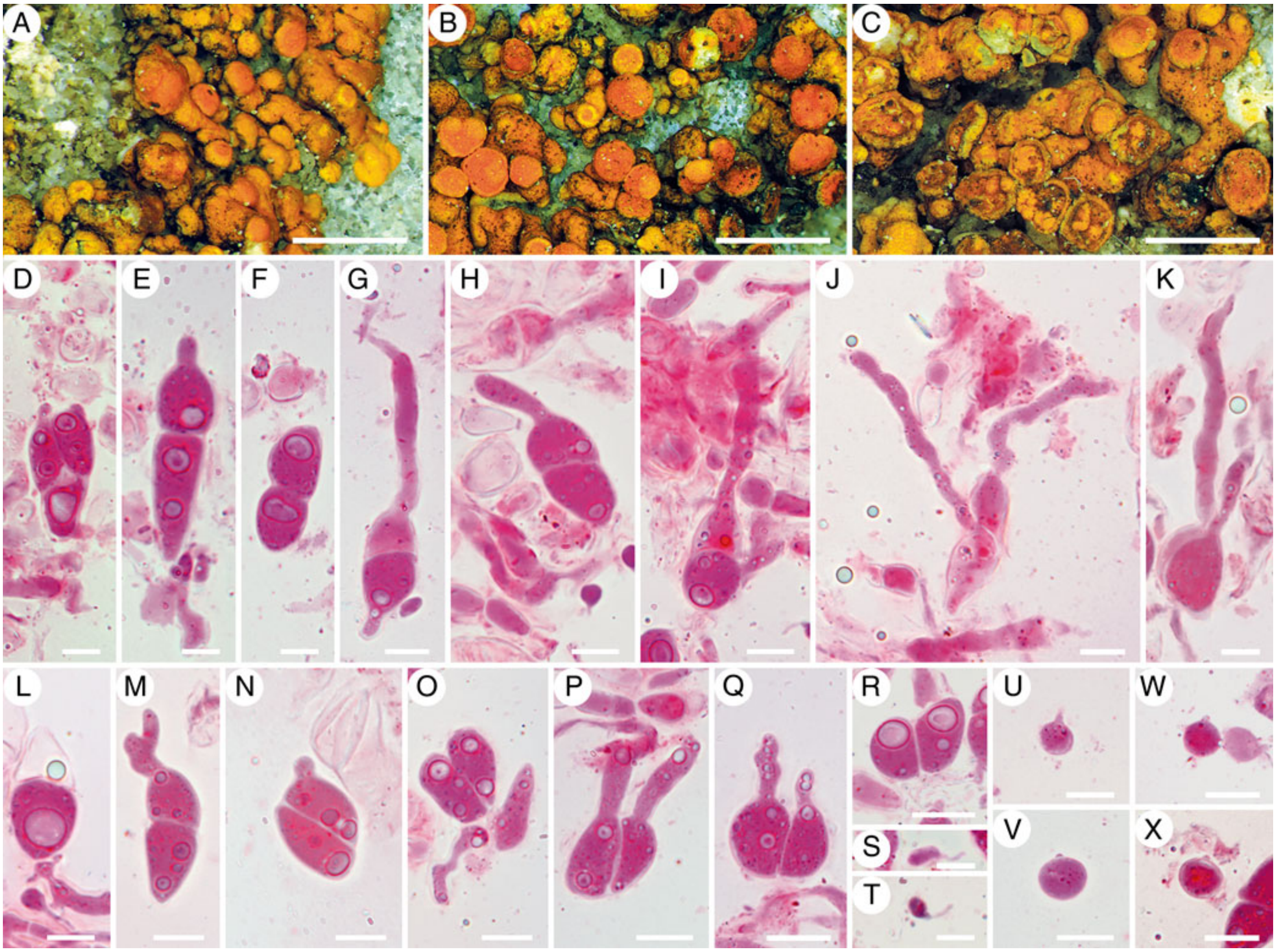

Figure 8. *Tremella* sp. 13 on *Calogaya biatorina* (*Etayo* 20762). A–C, variation in gall morphology. D, 3-celled basidium. E–J, L & M, 2-celled transversely septate basidia with haustoria and clamp connections. N & O, obliquely septate basidia. K, P–R, longitudinally septate basidia. S & T, haustoria. U–X, basidiospores. Scales: A–C = 1 mm; D–R = 10 μm; S–X = 5 μm. In colour online.

(11–)13.2–18.9(–23) × (8–)8.4–11.1(–14.5) μm (n = 33); obliquely septate: (16.5–)16.0–19.4(–20) × (8.5–)8.3–10.4(–10.5) μm (n = 4); longitudinally septate: (14–)13.7–16.9(–16.5) × (9–)8.8–11.4(–11) μm (n = 2)]; epibasidia elongate, (2–)2.4–3.2(–3.5) μm diam. (n = 16), up to at least 24 μm in length. *Basidiospores* subspherical, apiculus present, 5.5 × 4.5 μm (n = 1).

Ecology and distribution. *Tremella* sp. 14 induces galls in the hymenium of *Calogaya decipiens*. It is known only from Sweden.

Specimen examined. **Sweden:** *Östergötland*: Nässja parish, historically interesting area with an ancient stone circle, a churchyard, and a church, 58°27′53″N, 14°48′47″E, 109 m, on *Calogaya decipiens*, 2013, *Millanes* 850 (S).

Tremella sp. 15 (on *Polycauliona*)

(Fig. 10)

Basidiomata reduced, inducing the formation of convex, dark orange galls in the hymenium of the host, hemispherical, smooth and uniform, sometimes irregular, scattered all over the hymenium but sometimes forming gall conglomerates, (0.07–)0.08–0.25(–0.82) mm diam. (n = 18). *Hyphae* sometimes with clamp connections, up to 3 μm diam.; haustoria rarely observed, haustorial branches tremelloid, rarely with two filaments or one bifurcated filament, mother cell (2–)2.6–4.7(–5.5) μm diam. (n = 13), filament up to 7.0 μm in length. *Hymenium* reduced when young but developed when old, containing numerous broadly fusiform to ellipsoid, pyriform probasidia. *Basidia* narrowly elongate ellipsoid to ellipsoid, 2-celled when mature, with one transverse septum, rarely obliquely septate, when transversely septate, sometimes stalked, sometimes laterally elongated cells resembling *Biatoropsis* basidia, (20.5–)26.5–40.5(–52) × (8–)10.5–13.6(–15) μm (n = 54) [transversely septate: (20.5–)26.5–40.5(52) × (8–)10.5–13.6(–15) μm (n = 53); obliquely septate: 25.5 × 13.5 μm (n = 1)]; epibasidia elongate, (2.5–)3.3–4.9(–5) μm diam. (n = 19), up to at least 37 μm in length. *Basidiospores* subspherical, apiculus present, 6.5 × 7.0 μm (n = 1).

Ecology and distribution. *Tremella* sp. 15 induces galls in the hymenium of *Polycauliona* sp. It is known only from Spain.

Specimen examined. **Spain:** *Teruel*: between Rubielos and Mora, Fuentes del Ocino, 1100 m, on *Polycauliona* sp., 2002, *Etayo* 19125 (hb. Etayo).

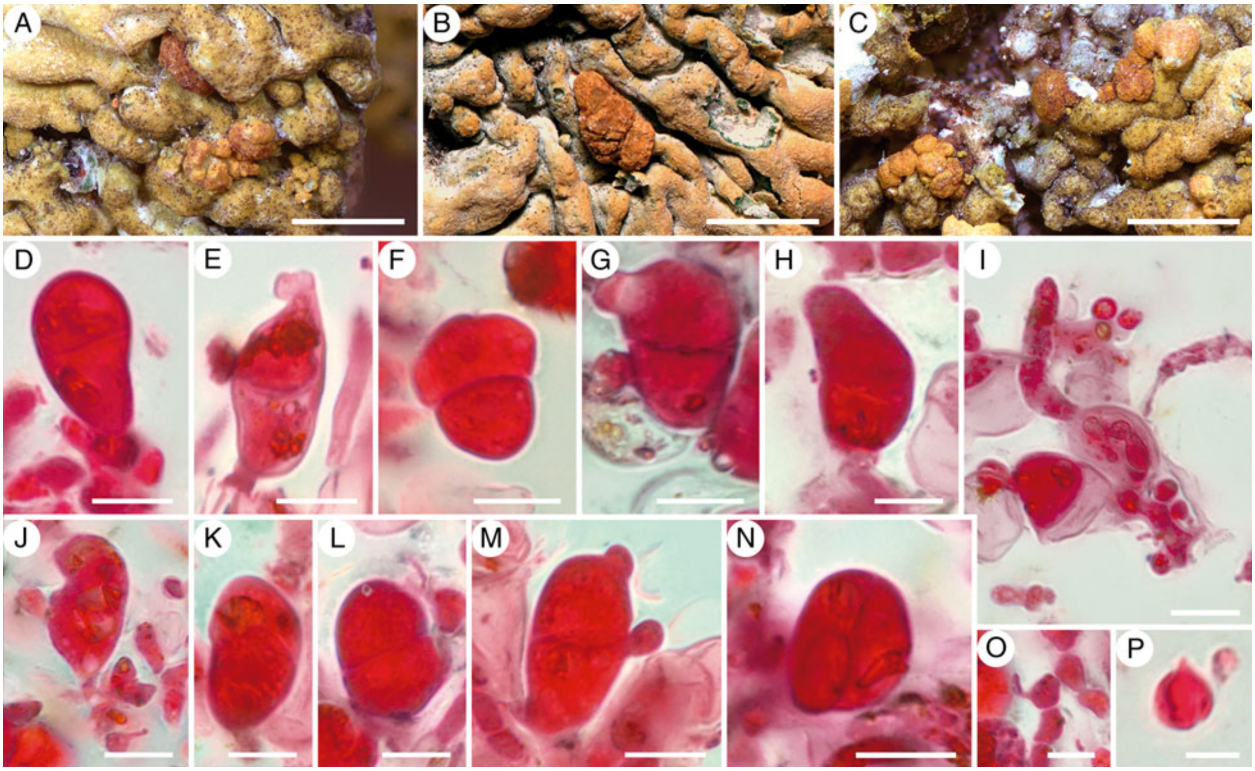

Figure 9. *Tremella* sp. 14 on *Calogaya decipiens* (*Millanes* 850). A–C, variation in gall morphology. D–K, 2-celled transversely septate basidia with haustoria and clamp connections. L & M, obliquely septate basidia. N, longitudinally septate basidium. O, haustorium. P, basidiospore. Scales: A–C = 1 mm; D–N = 10 μm; O & P = 5 μm. In colour online.

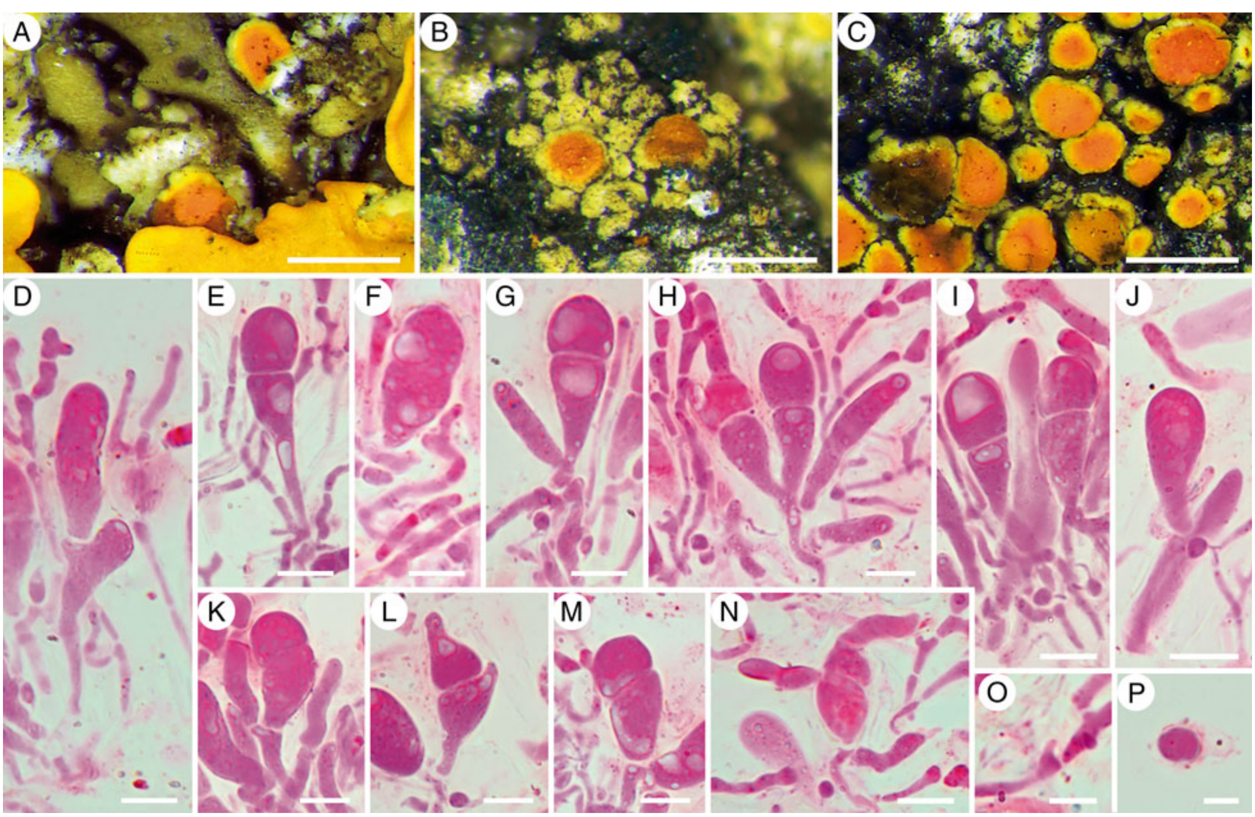

Figure 10. *Tremella* sp. 15 on *Polycauliona* sp. (*Etayo* 19125). A–C, variation in gall morphology. D–I, 2-celled transversely septate basidia with haustoria and clamp connections. K–N, obliquely septate basidia with haustoria and clamp connections. J, probasidia with haustorium. O, hypha with clamp connection. P, basidiospore. Scales: A–C = 1 mm; D–N = 10 μm; O & P = 5 μm. In colour online.

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Author Contribution. S. Freire-Rallo: conceptualization, investigation, resources, formal analysis, writing (original draft, review and editing). P. Diederich: conceptualization, investigation, resources, supervision and writing (review and editing). A. Millanes and M. Wedin: conceptualization, investigation, resources, supervision, writing (review and editing) and funding acquisition.

Author ORCIDs. Sandra Freire-Rallo, 0000-0003-1576-0507; Paul Diederich, 0000-0003-0357-7414; Ana M. Millanes, 0000-0001-5003-4186; Mats Wedin, 0000-0002-8295-5198.

Competing Interests. Nothing to declare.

Data Accessibility. Newly generated sequences have been deposited in GenBank. Nomenclatural novelties have been deposited in MycoBank.

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