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Phylogenetic placement and new data on the morphology and ecology of *Calathella eruciformis* (*Agaricales*, *Basidiomycota*), a cyphelloid fungus new to Poland

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Abstract. *Calathella eruciformis*, a species hitherto unknown in Poland, is reported from four localities in the north-eastern part of the country. This wood-inhabiting saprotroph was found on dead decorticated but still attached twigs and branches of living *Populus tremula* in an oak-hornbeam forest (*Carpinion betuli*). Macro- and microcharacters of the recently collected material are presented in detail, together with selected illustrations. Examination of ITS rDNA sequences indicated that *Calathella* is not monophyletic and that the type species of the genus *C. eruciformis* is alien to the heterogeneous genus *Flagelloscypha*. Furthermore, molecular evidence is provided for a close relationship between *C. eruciformis* and the type species of the genus *Sphaerobasidioscypha*, *Sphaerobasidioscypha citrispora*.

Key words: *Flagelloscypha*, morphology, ITS sequences, phylogeny, Poland

Introduction

The macrofungi biota of Wigry National Park (NE Poland) is rich and varied. The known number of macromycetes species found in the area so far is nearly 1000, but research is ongoing (Romański 2005, 2009; Halama 2010; Halama & Romański 2010a, b; Krzysztofiak et al. 2010; Halama & Kudławiec 2014; Halama & Rutkowski 2014; Halama et al. 2014; Staniaszek-Kik et al. 2014; Halama et al. 2015, unpubl. data), so this number will certainly increase.

A research project on the biodiversity of cryptogams on Eurasian aspen *Populus tremula* in the Wigry National Park was conducted in 2018. The main purpose of the project was to estimate the diversity of various organisms associated with living aspen trees, including lichens, micro- and macrofungi, mosses, liverworts and algae. This work is part of a bigger project comprising studies of the biodiversity of cryptogams on various living tree species, and the vertical distribution of the cryptogams over the entire tree height. During the project, several finds of *Calathella eruciformis* were noted. This cyphelloid fungus seems to be rare in Europe and was not found in Poland until now (Krieglsteiner 2001; Kujawa 2018). The paper briefly describes the Polish finds, gives information on its distribution, and discusses its ecology. Molecular data are still lacking for *C. eruciformis*, as the species has not been included in any DNA study of the broadly defined genus *Flagelloscypha* and allies (Hibbett & Binder 2001; Bodensteiner et al. 2004; Matheny et al. 2006; Yamaguchi et al. 2009; Læssøe et al. 2016). Hence, we used a phylogenetic analysis of nuclear ribosomal DNA (ITS) sequences to tentatively determine the phylogenetic position of this elusive species.

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Materials and methods

Field research

We used 60 specimens of Eurasian aspen randomly picked in patches of an oak-hornbeam forest association (*Tilio cordatae-Carpinetum betuli*, *Carpinion betuli*). Each tree was at least 15 m high, the tallest ones being 35 m high; circumference at breast height was at least 110 cm. All trees were healthy, without any visible damage, with straight, not tilted trunks. Biodiversity data were collected using climbing techniques from trunks, boughs (branches >4 cm in diameter) and twigs (branches < 4 cm in diameter) from all accessible places within seven height zones: I (0–2 m), II (2–6 m), III (6–10 m), IV (10–14 m), V (14–18 m), VI (18–22 m) and VII (22–26 m). Fieldwork, including collection of mycological data, was carried out from May to September 2018.

Morphological studies

Descriptions of macro- and micromorphological characters are based on three collections from Poland (voucher numbers: MH-2018-0187, MH-2018-0190, MH-2018-0494). Fresh basidiomata were observed and their photographs were analysed in order to prepare a macromorphological description. Micromorphological characters were observed in dried specimens with a Nikon Eclipse E–400 light microscope equipped with a Nikon digital camera (DS-Fi1). Freehand sections from dry basidiomata were examined in squash preparations separately in 5% $NH_3 \cdot H_2O$, 5% KOH, 1% Phloxine B in 5% $NH_3 \cdot H_2O$ and Melzer's reagent, all of them after rehydration with 96% alcohol and distilled water. Image-grabbing and biometric analyses were done with NIS-Elements D 3.1 imaging software. Microcharacter dimensions are given as (minimum) 10–90 percentile (maximum) values (n = sample size per preparation). Statistical computations employed Statistica software (StatSoft). Spore length to width ratio is reported as Q. For basidiospore size measurements, randomly selected mature spores were measured without the apiculus. Basidia length was measured excluding sterigmata. Morphological terminology follows Vellinga (1988). Nomenclature follows Matuszkiewicz (2001) for plant communities, The Plant List (http://www.theplantlist.org) for vascular plants, and Agerer (2018) for fungi. The collected material is deposited in the private herbarium of one of the authors (MH).

DNA extraction, PCR amplification, and DNA sequencing

The ITS rDNA region (containing ITS1-5.8S-ITS2 sequences), which is commonly used for separation and identification of agaric species (e.g. Miller & Buyck 2002; Zhang et al. 2004; Borovička et al. 2012; Schoch et al. 2012; Adamčík et al. 2017), was used to confirm the taxonomic affiliation of the collected material and to infer the evolutionary relationships among *C. eruciformis* and other representative taxa in this study. Genomic DNA was extracted from dried specimens by using the CTAB procedure of Murray & Thompson (1980). Spectrometric DNA concentration measurements were conducted with NanoDrop ND 2000C (Thermo Scientific). Then the extracted DNA was purified with a Syngen DNA clean-up Kit (Syngen Biotech) and spectrometric measurements were repeated. ITS rDNA regions were amplified using primers ITS1F and ITS4 (White et al. 1990; Gardes & Bruns 1993). The PCR-reactions were performed in 20 µl volumes containing template DNA, primers and PCR mix (Q5™ High-Fidelity Polymerase, NewEngland-Biolabs Ltd.) according to the manufacturer's protocol. The reactions were carried out in a T-100 thermal cycler (Bio-Rad Inc.), with 35 cycles in the following conditions: denaturation (98°C, 10 sec), annealing (52°C, 30 sec), extension (72°C, 45 sec) and final extension (72°C, 2 min). Amplification products were visualised by gel electrophoresis in 2% agarose gel in TBE buffer. The size standard was 50 bp DNA Ladder (New England Biolabs Ltd.). Then the bands were cut out from the gel and the PCR products were purified with a QiaQuick Gel Extraction Kit (Qiagen N.V.), and the DNA concentration was measured.

Sanger sequencing was carried out with a BrilliantDye™ Terminator v3.1 Kit (Nimagen B.V.). Reactions were set with fourfold dilution of the reaction premix and addition of BrilliantDye® Terminator 5X Sequencing Buffer (Nimagen B.V.) according to the producer's instructions. Four sequencing reactions were run: for both samples and with each primer. Sequencing products were separated by capillary electrophoresis on an Applied Biosystems™ 310 Genetic Analyzer (Thermo Fisher Scentific). Capillary electrophoresis was performed in a 50 cm long capillary filled with POP-7 Polymer (Applied Biosystem). Separation time was 1 h 40 min, and run voltage was 6kV with 60 sec and 2kV sample injection. Two reads for each sequencing with ITS1-f primer reaction and a single read for each sequencing with ITS4 primer reaction were collected. For basecalling, Sequence Scanner Software v2.0 was utilised, and peak quality was also checked with the Sanger Quality Check App (Thermo Fisher Scientific). Two identical sequences were generated for this molecular and phylogenetic analysis, along with additional sequences obtained from GenBank NCBI (https://www.ncbi.nlm.nih.gov).

Sequence alignment and phylogenetic analysis

The sequences obtained from *C. eruciformis* were assembled in a data matrix with sequences of cyphelloid species (*Calathella*, *Cyphellopsis*, *Flagelloscypha*, *Halocyphina*, *Henningsomyces*, *Lachnella*, *Maireina*, *Merismodes*, *Nia*, *Phaeosolenia*, *Woldmaria*) and a non-cyphelloid member of Marasmiaceae (*Marasmiellus*), which were retrieved from GenBank. ITSx (Bengtsson-Palme et al. 2013), as implemented on the PlutoF web-based workbench (Abarenkov et al. 2010), was then used to extract the ITS1-5.8S-ITS2 region from all sequences. Prior to the phylogenetic analyses, all assembled sequences were aligned using MAFFT (Katoh et al. 2002; Katoh et al. 2005) on the MyHits gateway (http://myhits.isb-sib.ch), with default conditions for gap openings and gap

extension penalties, and subsequently adjusted by eye in MEGA 6.06 (Tamura et al. 2013). The alignment was then entered into Gblocks v.0.91b (Castresana 2000; Talavera & Castresana 2007) to objectively eliminate poorly aligned positions and divergent regions using the least stringent parameters. Phylogenies were estimated using the maximum likelihood (ML) and Bayesian inference (BI) optimality criteria, with RAxML-NG via web-server (Kozlov et al. 2018) and MrBayes ver. 3.2.2 (Ronquist et al. 2012), respectively. jModelTest ver. 2.1.1 (Posada 2008) was used to identify the sequence evolution model that fit the dataset, using the Bayesian information criterion (BIC). Finally, HKY+I+G (ITS1), TPM3+G (5.8S) and TPM2uf+G (ITS2) models of nucleotide substitution were used in ML analysis and BI inference. *Marasmiellus ramealis* (KJ416235) was chosen as the outgroup taxon for the analysed dataset. For ML analysis to perform a tree inference and to search for optimal topology, an automatic number of replicates option was chosen using the bootstrapping cutoff procedure (0.03). Support values from bootstrapping runs (MLB) were reported on the best-scoring/best-known ML tree. BI was performed with four (three incrementally heated, one cold) Monte Carlo Markov chains (MCMC) that were independently run twice, sampling one tree every 100 generations for 2×10^6 generations, starting with a random tree. Completion was determined by the average standard deviation of split frequencies falling below 0.003. Convergence of runs was estimated by assessment of the average standard deviation of split frequencies value (ASDSF), following instructions given by Hall (2008). Convergence and stationarity was additionally assessed using Tracer ver. 1.6 (Rambaut et al. 2014). The first 25% of generations were discarded as burn-in, whereas the remaining trees were used to calculate a 50% majority-rule tree and to determine the posterior probabilities (BPP) of individual branches. Significance thresholds were set above 50% for bootstrap and 0.90 for posterior probability. Consensus trees were visualized and compared using TreeGraph ver. 2.14b (Stöver & Müller 2010).

Results

Calathella eruciformis (P. Micheli *ex* Batsch: Fr.) D.A. Reid, Persoonia 3: 123 (1964) [as '*erucaeformis*'] Figs 1–2

≡ *Flagelloscypha eruciformis* (P. Micheli ex Batsch) Singer, Beih. Nova Hedwigia 29: 151 (1969). For complete synonymy see (Reid 1964).

Illustrations: Pilát (1933: 48, fig. 3); Reid (1964: 121, fig. 22–29; 129, fig. 31a-c); Agerer (1973: 433, fig. 38 a-d); Ryman & Holmåsen (1992: 343, lower photo); Knudsen (2012: 305, fig. C).

Description. Cyphelloid basidiocarps most frequently gregarious, often widely scattered over substrate, occasionally may appear to be aggregated into small, dense colonies as the result of proliferation of single fruitbodies. Basidiocarps varying in shape from almost tubular or narrowly funnel-shaped when young to campanulate

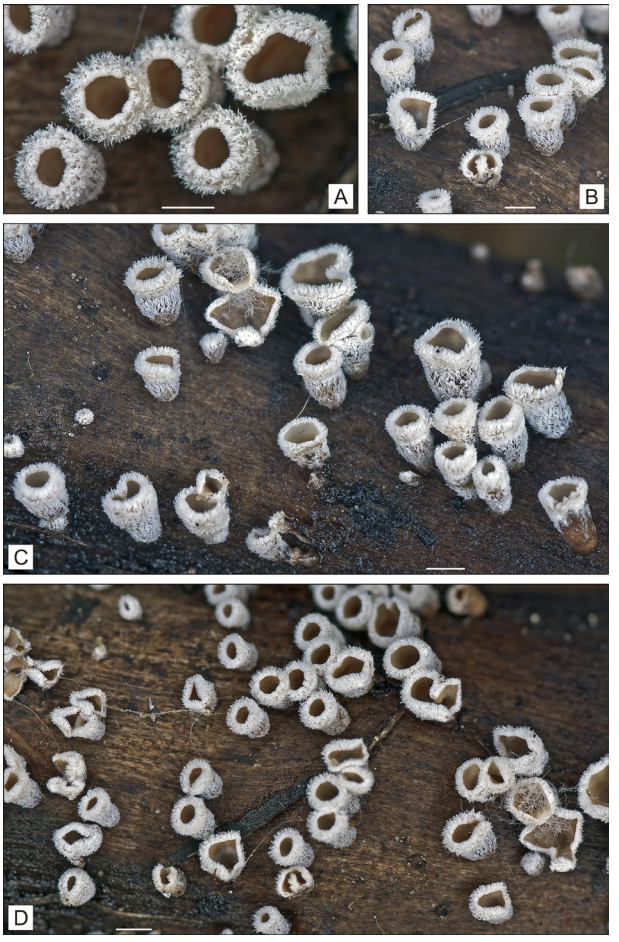

Figure 1. *Calathella eruciformis* (P. Micheli *ex* Batsch: Fr.) Reid. A–D – basidiomata on dead branch of living *Populus tremula* (MH-2018-0190). Scale bars = 0.5 mm.

or turbinate with a constricted base, and inrolled margin when dry, 0.4–2 mm high, 0.4–1.2 mm wide ($n=43$), tending to be rather tough. Outside and margin minutely hirsute due to the presence of long and stiff hairs, at first white, then becoming ochraceous brown, greyish brown to grey from below in living material (sometimes outer covering becoming greenish due to the presence of green algae). Hymenophore plane, hymenium lining a deep cavity, extending almost to base of basidiocarp, pale cream to dirty cream. Basidiospores (5.2)6.9–8.5(10.7), 7.8±0.7 × (2.4)2.5–3(3.5), 2.7±0.2 µm, Qw = (2.1)2.6–3.1(3.6), 2.8±0.2 ($n=152$), varying from narrowly ellipsoid, subcylindrical, cylindrical to suballantoid, with apiculus, thin-walled, smooth, inamyloid. Basidia (8.4)12.3–22.2(24.6), 16.3±3.7 × (2.7)4.7–5.8(6.6), 5.1±0.7 µm ($n=34$) µm, 2- and 4-sterigmate, clavate to constricted, clamped at base. Cystidia not found. Hyphal system monomitic. Hairs cylindrical, with obtuse or tapering apex, up to 320 × 3–6 µm, sinuous, helically coiled, thick-walled, fragile, at first colourless but in older specimens becoming brownish toward base, finely to coarsely incrusted over their whole length or glabrous (encrustation dissolves in 5% KOH and NH_4OH solution), at base with clamp, sometimes secondarily septate, irregularly swollen in 5% KOH, many of them dextrinoid, of a rather narrow although distinct lumen, except toward apex where walls may thin out. Context compact, consisting of thin-walled, clamped

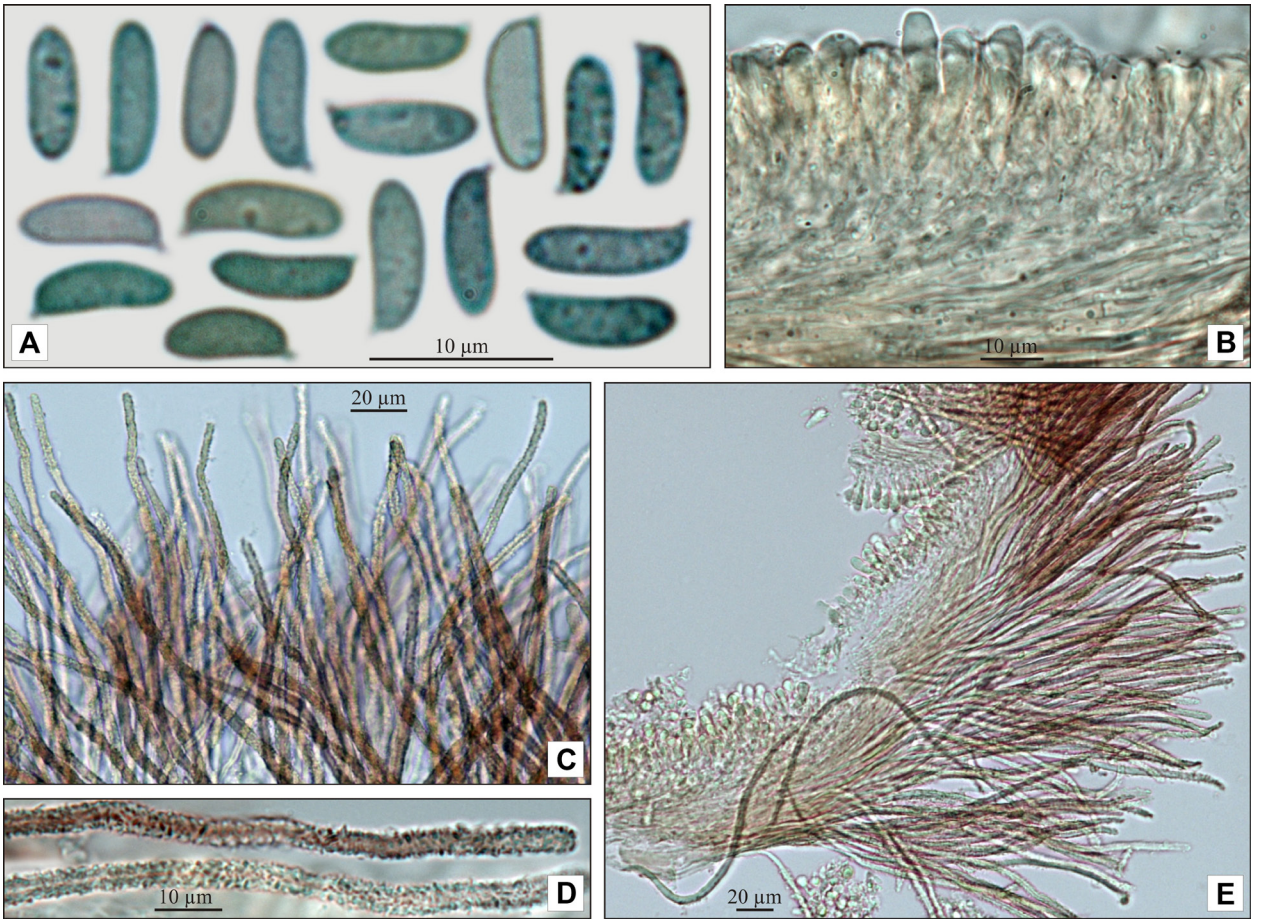

Figure 2. *Calathella eruciformis*. A – basidiospores, B – hymenium and subhymenial layer, C, D – marginal hairs, E – fragment of longitudinal section of basidiocarp, with hymenium and outer haired surface (all photographed from MH-2018-0187).

hyphae 1.6–4 µm in diameter. Subhymenial hyphae 1.5–2.5 µm in diameter, hyaline, clamped, thin-walled.

Specimens examined. POLAND, Eastern Suwałki Lakeland, Wigry National Park: ~1.7 km NE of Sobolewo village (54°04′16″N 23°0′51″E), *Tilio cordatae-Carpinetum betuli*: on dead, sun-exposed, still attached bough of *Populus tremula* tree, 15 Aug. 2018, leg. M. Halama (MH-2018-0187); ibidem: on dead, sun-exposed, still attached branch of living *Populus tremula* tree, 15 Aug. 2018, leg. M. Halama (MH-2018-0190); ~1.6 km NE of Sobolewo village (54°04′14″N 23°0′50″E), *Tilio cordatae-Carpinetum betuli*: on dead, sun-exposed, still attached branch of living *Populus tremula* tree (on bark), 16 Aug. 2018, leg. M. Halama (MH-2018-0231); ibidem: on dead, sun-exposed, still attached branch of living *Populus tremula* tree (on bark), 16 Aug. 2018, leg. M. Halama (MH-2018-0233); ~1.3 km E of Sobolewo village (52°03′58″N 23°0′50″E), *Tilio cordatae-Carpinetum betuli*: on dead, sun-exposed, still attached branch of living *Populus tremula* tree, 3 Sep. 2018, leg. M. Halama (MH-2018-0373); ~1.8 km S of Mikołajewo village (54°02′09″N 23°8′22″E), *Tilio cordatae-Carpinetum betuli*: on dead, sun-exposed, still attached branch of living *Populus tremula* tree, 6 Sept. 2018, leg. M. Halama (MH-2018-0494); ibidem: on dead, sun-exposed, still attached branch of living *Populus tremula* tree, 6 Sept. 2018, leg. M. Halama (MH-2018-0495); ibidem: on dead, sun-exposed, still attached branch of living *Populus tremula* tree, 6 Sept. 2018, leg. M. Halama (MH-2018-0504).

Molecular characterization. Sequencing of the ITS rDNA region of two *C. eruciformis* collections (MH-2018-0190, MH-2018-0187) yielded fragments 623 bp and 613 bp long, respectively. The two new sequences generated for this study are available from GenBank under accession numbers MK434305 and MK434306. The aligned ITS complete dataset consisted of 29 sequences (one as outgroup) representing 23 taxa and 1020 characters. After exclusion of ambiguous (mainly terminal) ITS-regions of the dataset, 954 characters remained for the final analysis. Of these, 193 were constant, 611 were variable sites, 470 were parsimony-informative and 126 were singletons. Maximum likelihood (ML) and Bayesian inference (BI) analyses revealed nearly identical tree topologies, and so only the tree inferred from the BI strategy is shown in Figure 3. The general topology of our phylogenetic tree shows *Calathella* as traditionally circumscribed, non-monophyletic with its available taxa widely separated and placed in several variously supported not-sister groups. *Calathella eruciformis* forms a strongly supported clade (BPP = 1.0, MLB = 98) together with *Flagelloscypha austrofilicis* and *Flagelloscypha* sp. In turn, *Calathella mangrovei* is nested separately within the broadly understood *Nia* clade with moderate to strong support (BPP = 0.99, MLB = 72), while *Calathella columbiana* occupies an independent, poorly supported position in the tree and its phylogenetic relationships remain unresolved. A monophyletic, strongly supported clade is formed by the members of *Lachnella* (BPP = 1.0, MLB = 100). Representatives of *Flagelloscypha* are placed

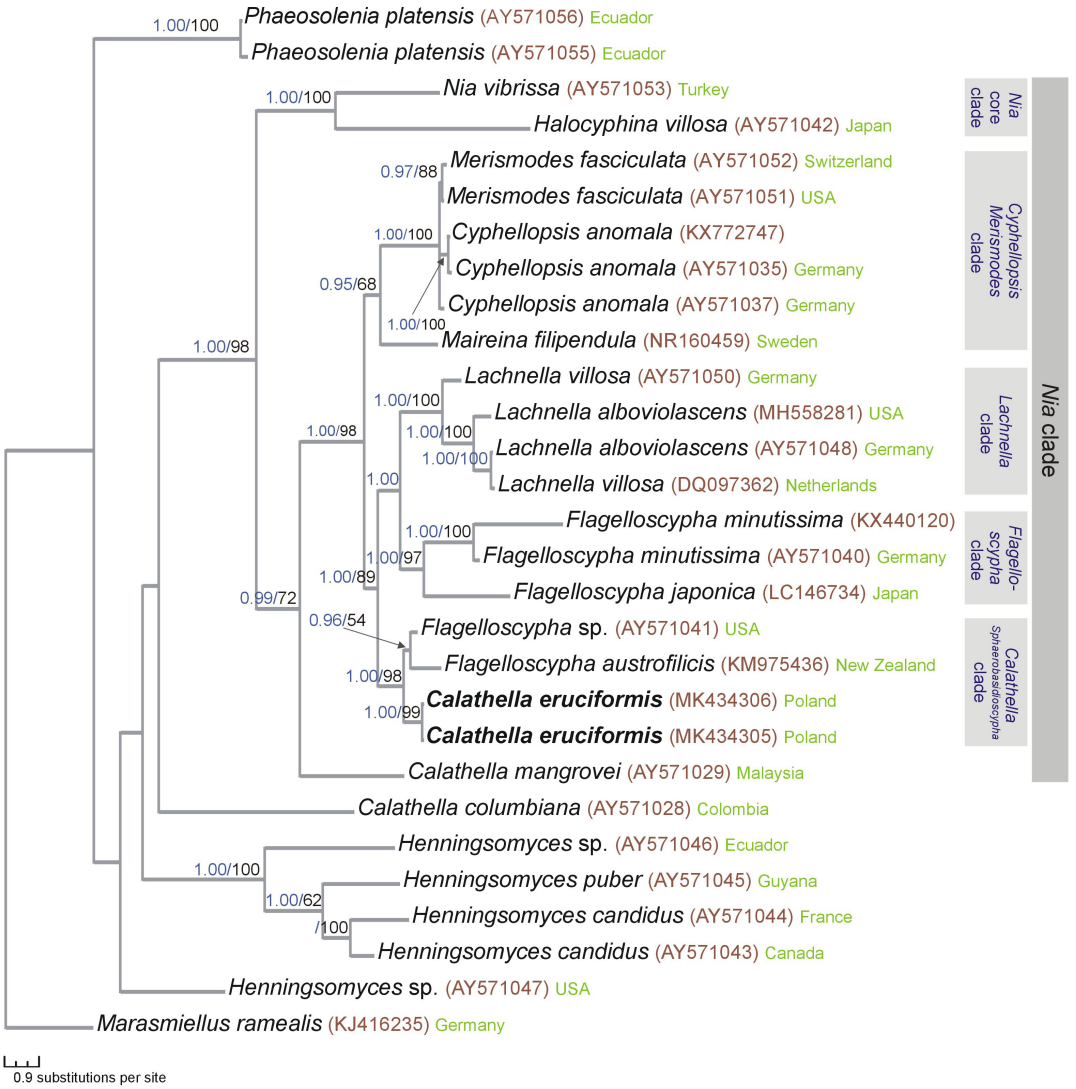

Figure 3. Phylogenetic placement of *Calathella eruciformis* inferred from ITS rDNA data. The best tree resulting from Bayesian inference analysis is presented, with BPP values ≥ 0.90 and MLB ≥ 50 displayed on the branches. Bolded sequences were obtained during this study. GenBank accession number for each sequence is given in brackets next to the species name. *Marasmiellus ramealis* was used as outgroup.

in two separate, strongly supported lineages. Sequences of *Flagelloscypha minutissima* and *Flagelloscypha japonica* form a very well-supported clade (BPP = 1.0, MLB = 97), sister to the group of *Lachnella*.

Discussion

Morphological variability, phylogeny and taxonomic implications

Cyphelloid fungi are one of the more complex groups in terms of classification and identification, and numerous taxonomic schemes have been proposed (e.g. Donk 1959; Cooke 1961; Donk 1962, 1966; Agerer 1973, 1975, 1983; Singer 1986). In the past it was common to assign the fungi to the artificial and entirely superseded order Aphyllophorales, but the currently widely accepted interpretation is that many of the species represent reduced series of agarics (Singer 1986; Bodensteiner et al. 2004; Agerer 2018). The delimitation of cyphelloid fungi is based on morphological characters (e.g. Donk 1959; Cooke 1961; Donk 1962; Reid 1964; Donk 1966; Singer 1986; Horak 2005; Bodensteiner 2006) and mainly upon characteristics of the hyphae that cover the outer surface of the basidiocarp (e.g. Agerer 1973, 1975, 1983). This kind of hypha has evolved to protect basidiocarps, and they are usually called "surface hairs" or "surface hyphae" (Agerer 1986). Their important characteristics include colour, mode of ramification, and shape of apices, but also their extension, density, wall thickness, and the presence or absence of a crystal covering (Agerer 1973, 1975, 1983, 1986). However, basidia, spores, tramal hyphae and patterns of basidiocarp development are also essential features for the taxonomy of the smallest hymenomycetous fungi (Agerer 1975, 1983, 1986; Singer 1986; Knudsen & Vesterholt 2012). Agerer's (1975, 1983) introduction of a useful, rather narrow genus concept and, consequently, small genera, cannot change the fact that the cyphelloid fungi are still a heterogeneous, polyphyletic assemblage (Donk 1959, 1964; Agerer 1986; Singer 1986; Binder et al. 2001; Bodensteiner et al. 2004; Yamaguchi et al. 2009), and the morphological limits between the generic entities of the group are sometimes difficult to draw (Singer 1986).

For a time, *C. eruciformis* was considered to be within the genera *Cyphella*, *Solenia* or *Chaetocypha* (e.g. Reid 1964), until Reid (1964) transferred it to a new genus, *Calathella*. The concept conceived by Reid has been accepted by later authors (e.g. Agerer 1983; Hansen & Knudsen 1992; Krieglsteiner 2001; Horak 2005; Knudsen 2008), although Singer (1969, 1986) was the first to decide to place the species in *Flagelloscypha*. Recently, Knudsen (2012) used a much broader generic concept than Agerer's (1983, 1986) and placed in *Flagelloscypha* several species usually considered to be members of the genera *Cephaloscypha*, *Nochascypha*, *Seticyphella*, and also *Calathella*. Based on the key provided by Knudsen (2012), *C. eruciformis* is clearly distinct, based on its tubular to bell-shaped basidiocarps which are constricted at the base and whitish to greyish hairy outside, the presence of cylindrical (with obtuse tips), thick-walled, encrusted, partly dextrinoid, fragile surface hairs, cylindrical to narrowly ellipsoid, hyaline, smooth basidiospores, clavate to suburniform basidia, clamped hyphae, and a distinct affinity of the fungus for aspen wood. All material from Wigry National Park fits well with the data given by Knudsen (2008) and earlier authors (Reid 1964; Agerer 1983) for *C. eruciformis*, as regards both the macro- and microcharacters.

The genus *Calathella* was emended by Agerer (1983). It currently contains nine species worldwide, distributed in Asia, Europe, North America and South America (Kirk et al. 2008; Sulzbacher et al. 2008; Baltazar et al. 2009). The combination of incrusted surface hairs with rounded tips, constricted (suburniform) basidia, oblong-elliptical to cylindrical, rarely subglobose to short-ellipsoid (never ellipsoid to naviculate) basidiospores, and coalescent or even proliferating basidiocarps is considered diagnostic for the genus (Agerer 1983; Bodensteiner et al. 2001; Bodensteiner & Agerer 2003). However, the taxonomic circumscription of *Calathella* has been problematic, and the phylogenetic position of the genus remains unsettled (Sulzbacher et al. 2008). The name *Calathella* introduced by Reid (1964) is governed by the International Code of Nomenclature for algae, fungi, and plants (Turland et al. 2018). Applying Arts 53 and 54, *Calathella* D.A. Reid is interpreted as a later homonym (cf. Florin 1929) under the ICN and hence illegitimate (Art. 53.1). A new genus name to replace the illegitimate homonym has not been introduced yet. Molecular phylogenetic analyses based on partial nuclear LSU rDNA involving three species of *Calathella* (terrestrial *C. columbiana*, *C. gayana*, marine, salt-tolerant *C. mangrovei*) indicate unresolved phylogenetic relationships of the fungi and suggest that the genus *Calathella* is not monophyletic (Bodensteiner et al. 2004; Yamaguchi et al. 2009; Læssøe et al. 2016). The results of our molecular analyses (Fig. 3) agree with those of previous molecular data that suggested close relationships between aquatic homobasidiomycetes represented by the *Nia* core clade and terrestrial cyphelloid taxa (Binder et al. 2001; Hibbett & Binder 2001; Bodensteiner et al. 2004; Yamaguchi et al. 2009; Læssøe et al. 2016). Moreover, our studies continue to demonstrate the polyphyly not only of *Calathella* (Agerer 1983) but apparently also broadly understood *Flagelloscypha* (Fig. 3) (Knudsen 2012; Cooper 2015). This conclusion rejects the opinion published (without arguments) by Cooper (2015) that *Sphaerobasidioscypha citrispora* is a member of *Flagelloscypha*. The phylogenetic analysis showed that *C. eruciformis* (type species of *Calathella*) is closely related to the type species of the genus *Sphaerobasidioscypha*, that is, *S. citrispora* (named here *Flagelloscypha austrofilicis*), from which it can easily be distinguished on the basis of the greater (8–12.5 × 5–7.5 µm), lemoniform basidiospores, spherically clavate, ± stipitate (pedunculate) basidia and tapering surface hairs in the latter species (Agerer 1983). Moreover, both of the mentioned species form a separate monophyletic assembly which appears sufficiently distant both from the *Flagelloscypha minutissima* group and from the *Lachnella* group to treat the branch *Calathella*/*Sphaerobasidioscypha* as an independent evolutionary lineage, which possibly consists of two different phylogenetic relationships. The presented data indicate clearly that *C. eruciformis* is not closely related to *C. mangrovei* and *C. columbiana*. Similarly to previous findings (Bodensteiner et al. 2004; Yamaguchi et al. 2009; Læssøe et al. 2016), the marine *C. mangrovei* is located in the *Nia* clade, whereas *C. columbiana* is placed separately. The latter species appears as sister to the *Nia* clade. Unfortunately, the ITS data do not provide the phylogenetic information necessary to resolve the deeper nodes of the phylogram with significant support.

Since the genus *Calathella*, as currently defined (Agerer 1983), is not monophyletic (Bodensteiner et al. 2004; Yamaguchi et al. 2009; Læssøe et al. 2016; this study), it should be recircumscribed in a strict sense, including (at least for now) the species currently allocated to the *Calathella* clade (Fig. 1). At the same time, the new name *Calathella* should be introduced to replace the illegitimate homonym. Furthermore, it appears that at least two new genera should be erected to accommodate *C. mangrovei* and *C. columbiana*. Until the relationships of *Sphaerobasidioscypha* can be resolved with more confidence, we feel that this genus should be retained. We agree, however, with Bodensteiner et al. (2004), that before the taxonomic treatment and new combinations, some further investigations including sequences of six other described species of *Calathella* are required to fully resolve the status of the genus. We stress that the inferences drawn from the provided ITS molecular analyses are only provisional, pending multi-gene analyses utilizing multiple loci such as nLSU rDNA, rpb and tef, which may support, change or negate the conclusions reported above.

Ecology

Calathella eruciformis grows saprotrophically on dead wood of various kinds of trees. Wood of *Populus tremula* and other *Populus* species (*P. balsamifera*, *P. nigra*, *Populus* sp., *P. tremuloides*, *P. trichocarpa*) is typical, being the most common substrate for the fungus (Cooke 1961; Reid 1964; Ginns & Lefebvre 1993; Horak 2005; Knudsen 2012). Occasionally it is found on other

deciduous trees such as *Acer* sp., *Alnus incana* subsp. *tenuifolia*, *Malus domestica*, *Myrica* sp., *Robinia pseudoacacia*, *Salix caprea*, *Salix* sp. and *Sorbus aucuparia* (Cooke 1961; Reid 1964), though also on *Tilia* sp. and *Fraxinus* sp. (Singer 1969; Engel 1993). The *C. eruciformis* material that we collected and saw in Wigry National Park were exclusively from *P. tremula*. In that area the fungus occurs solely on dead but still attached, decorticated branches and twigs in the canopy of the sampled trees. It was recorded on four sampled trees, where it was observed in height zones III (one record), IV (four records), V (three records) and VI (one record). Although Reid (1964) noted that *C. eruciformis* is usually found on fallen branches, the fungus seems to be a tree crown specialist, growing on sun-exposed wood; thus it can easily be overlooked when only the first two meters of the tree trunk or only fallen wood material are sampled. Wakefield (1952) and Cooke (1961) listed some further host plants of *C. eruciformis* (syn. *Cyphella albocarnea*), such as *Galium aparine* and *Juncus* sp.; in addition to those hosts, Kirk and Spooner (1984) gave the evergreen perennial *Phormium tenax*. However, these unusual data are well outside the normal host range of the fungus and are probably misidentifications of the fungal collections (Legon et al. 2005). Nevertheless, we note that some wood-destroying fungi are capable of secondary colonization of herbaceous plants and non-lignified substrata (Zmitrovich et al. 2015).

Distribution

Calathella eruciformis has a large-scale distribution but is nowhere characterized as common (Krieglsteiner 2001). It is known from some localities scattered throughout Europe (cf. below), Western Asia (Turkey), North America (USA: Idaho, Michigan, Utah; Canada: Alberta, British Columbia, Manitoba, Ontario), the Caribbean (Guadeloupe) and South America (Argentina) (Pilát 1933; Cooke 1961; Reid 1964; Singer 1969; Redhead 1973; Sesli & Denchev 2008). It would appear that the distribution of *C. eruciformis* is largely determined by the occurrence of widely distributed and abundant *Populus* species, but the fact that the fungus was neither recorded by Ginns & Lefebvre (1993) in their studies on basidiomycetes that decay aspen in North America, nor discussed by Jahn (1966), suggests more limiting factors. The large majority of records of *C. eruciformis* are from Europe (Belgium, Estonia, Finland, France, Germany, Hungary, Italy, Luxembourg, Macedonia, Norway, Spain, Sweden, Czech Republic, Scotland), where the species seems to be scattered to rare in warmer regions and more common in northern areas (e.g. Pilát 1925; Bourdot & Galzin 1927; Laurila 1939; Cooke 1961; Reid 1964; Agerer 1973, 1983; Ulvinen et al. 1989; Engel 1993; Krieglsteiner 1994; Parmasto 1999; Krieglsteiner 2001; Legon et al. 2005; Rubio et al. 2006; Knudsen 2012; Lehmann 2015–2016; Pancorbo et al. 2017). The distribution pattern of *Calathella eruciformis* in Poland is not known, as it was not recognised or found there in the past. It seems to be a rare species in the country, but may be overlooked due to its occurrence in unusual habitats seldom explored by mycologists. During investigations of forest habitats and scattered tree patches, attention should be paid to this tiny fungus that may be more common than we think.

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