The first epiphytic macrolichen and its implication to the interacting with Mesozoic forest ecosystem

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Abstract

Lichens are well known as pioneer organisms or stress-tolerant extremophiles playing a core role in the early formation of terrestrial ecosystems, of which epiphytic lichens make a distinct contribution to the water-cycle and nutrient cycling in forest ecosystem. But due to the scarcity of relevant fossil records, the evolutionary history of epiphytic lichens is poorly documented. Herein, based on the new material of *Daohugouthallus ciliiferus*, we demonstrated that the hitherto oldest macrolichen inhabited a gymnosperm branch, representing the first unambiguous Jurassic epiphytic lichen. Combing the fossil and extant macrolichen representatives, we performed the geometric morphometric analysis and comprehensive comparison to infer the systematic status of this rare Jurassic macrolichen. The results declared that *D. ciliiferus* cannot be assigned to any known macrolichen lineages for its elder age and particular habits, and therefore a new family, Daohugouthallaceae was proposed. This work updated the current knowledge to the historical evolution of epiphytic lichens, implying the macrolichens may have diversified much earlier than the generally accepted K–Pg boundary. In addition, our new finding also provided direct evidence for tracing the continuing joint development of epiphytic lichens and forest ecosystem since the Jurassic of 165 Mya.

Introduction

Lichens are a stable symbiosis composed of fungi and algae and/or cyanobacteria; they also include a diverse microbiome (Spribille et al., 2016; Lücking and Nelsen, 2018; Hawksworth and Grube, 2020). Lichens are components of mostly terrestrial ecosystems from the polar regions to the tropics (Lumbsch and Rikkinen, 2017), growing on all kinds of substrates, including bark, rock, leaves and soil (Belnap et al., 2001; Nash, 2008). Lichens play important roles in ecosystem function, including weathering of rock and accelerating formation of soil (Lindsay, 1978; Chen et al., 2000), fixing carbon and nitrogen from the atmosphere (Wu et al., 2011), and as food source for animals (including humans, Cornelissen et al., 2007). Due to their sensitivity to environmental changes, lichens also are widely used as bioindicator of air pollution and environmental health. The evolutionary history of lichen-forming fungi is poorly understood, due to the sparse fossil record, and has been primarily reconstructed based on molecular dating analyses (Lücking et al., 2017; Kraichak et al., 2018; Huang et al., 2019; Nelsen et al., 2020). Although these approaches proposed a framework to illustrate how the lichen symbiosis may have evolved, the fossil evidence is indispensable in testing and supplementing the current understandings especially when the earlier fossil was discovered.

To date, only about 190 fossils are accepted to represent genuine lichens, and a few are considered ambiguous, i.e. potentially representing lichens (Lücking and Nelsen, 2018). The earliest accepted lichen are two crustose lichens from Devonian fossils, i.e. *Cyanolichenomycites devonicus* and *Chlorolichenomycites salopensis* (419–411 Mya), which were inferred to be saxicolous or terricolous (Lücking and Nelsen, 2018). The other earlier lichen is from the Lower Cretaceous, i.e. *Honeggeriella complexa* (ca. 133 Mya) that was suggested as a squamulose or foliose lichen, although no larger pieces showing its architecture are preserved (Matsunaga et al., 2013; Honegger et al., 2013). Other than this fossil, lichens with foliose and fruticose thalli, the principal forms of macrolichens, have no unambiguous fossil record before Cretaceous-Paleogene (K–Pg) boundary 65 Mya (Lücking and Nelsen, 2018), which represents one of the most dramatic turnover events in the fossil record (Renne et al., 2013). Diverse macrolichen fossils including foliose and fruticose Parmeliaceae from Eocene Baltic amber (38–44 Mya) seem to corroborate the fact (Kaasalainen et al., 2017). Actually, some presumed Mesozoic macrolichens were also mentioned from the Keuper formation (230–200 Mya) (Ziegler, 2001), but this work had not received much attention and was overlooked by lichenologists due to the absence of voucher information (Lücking and Nelsen, 2018). Until recently, a study with the convincing evidence demonstrated the occurrence of macrolichen, *Daohugouthallus ciliiferus* from the Middle Jurassic (ca. 165 Mya), unequivocally provided an opportunity to catch a glimpse of the earlier evolution of macrolichens (Fang et al., 2020).

Macrolichens evolved independently in various classes of Basidiomycota (Agaricomycetes: e.g., *Cora*) and Ascomycota, such as Arthoniomycetes (e.g., *Roccella*) and Lichinomycetes (e.g., *Thyrea*). However, most macrolichens are found in the largest class of lichenized Ascomycota, the Lecanoromycetes, which includes 78% of all known lichen fungi (Lücking et al., 2017).
Considering the diverse ecological interactions with environments especially for the epiphytic macrolichens that were most focused concerning their distinct contributions to balancing the water-cycle and nutrient cycling in forest ecosystem dynamics (Ellis, 2012), the evolution of macrolichens is of particular interest.

Given that macrolichens have evolved in convergent fashion in multiple, unrelated lineages in Basidio- and Ascomycota, it is vital to clarify the position of *Daohugouthallus ciliiferus* in reconstructing and understanding the evolution of macrolichens. Unfortunately, diagnostic features, such as hamathecium, ascus, and ascospore structure, are not known from this fossil, which renders its exact classification challenging. However, techniques such as automated image recognition have allowed to at least analyze morphometric features in a way that allow a quantitative approach to hypothesis testing when placing macrofossils. In the present study, we therefore provide an updated morphological assessment of new material of *Daohugouthallus ciliiferus*, corroborating it as the first Jurassic epiphytic macrolichen. And moreover, we employed image-based, geometric morphometric analysis to compare the fossil with a range of extant macrolichens. In parallel, we used the large molecular clock analysis by Nelsen et al. (2020), which due to the comprehensive sampling offers a much broader framework than other molecular clock studies including lichen formers (e.g. James et al., 2006; Lutzoni et al., 2018; Kraichak et al., 2018), to reassess stem and crown node ages for major clades of macrolichen formers in the Lecanoromycetes, in comparison to the age of the fossil. As a result, we propose a new family, Daohugouthallaceae, for this fossil, and reveal the Jurassic lichens with particular association with the contemporaneous gymnosperm plants, possibly play an important role in the early Jurassic forest ecosystem.

**Results**

**Geometric morphometric analysis**

The geometric morphometric analysis of 140 images (Fig. S1) resulted in cumulative values for all the principal components were listed in Table S1. The cumulative eigenvalues for the main axes (principal components) with the cumulative variance of the first four principal components amounting to 61.1% (Table S1), meeting the requirements for geometric morphometric analysis. Among the canonical variate analysis (CVA) for four combinations of the four principal components (individual variances 24.4, 18.0, 10.8,8.0; Fig. 1), the plot combining the first two principal components (cumulative variance 42.4) showed that the fossil *Daohugouthallus ciliiferus*, in group 2, appeared morphologically closest to foliose Parmeliaceae, in group 3, including the genera *Hypotrachyna* and *Hypogymnia* and two foliose Parmeliaceae fossils (Kaasalainen et al., 2017; Lücking and Nelsen, 2018). However, placement of the fossil within the family Parmeliaceae is not possible, as the inferred stem age of Parmeliaceae is much younger than the age of the fossil (Kraichak et al., 2018; Nelsen et al., 2020). Therefore, a new family, Daohugouthallaceae is proposed, which is tentatively placed in the order Lecanorales given the close morphological similarity to Parmeliaceae.

**Molecular clock assessment**

We used the detailed molecular clock tree provided by Nelsen et al. (2020) to illustrate inferred ages for selected family-level clades in the Lecanoromycetes that include macrolichens (Fig. 2). Most of these families have stem node ages relative to the macrolichen genera contained therein substantially younger than 100 Mya, including Caliciaceae, Cladoniaceae, Pannariaceae, Parmeliaceae, Physciaceae, Ramalinaceae, Sphaerophoraceae, Stereocaulaceae and Teloschistaceae. The stem node ages of a few families including macrolichens were reconstructed as between 150 and 100 Mya, including Baeomycetaceae, Coccocarpiaceae, Collemataceae, Pannariaceae, Peltigeraceae, and Umbilicariaceae. However, all these families have a crown node age significantly younger than 165 Mya, the age of Daohugouthallaceae (Fig. 3). The only macrolichen family older than the fossil is Icmadophiliaceae, with an inferred crown node age of approximately 200 Mya (Figs. 2–3). However, members of this family differ strongly in morphology from Daohugouthallaceae (Fig. 3), and its substrate ecology is also different, its members preferring terrestrial such as acid soil or peat (Rambold et al., 1993). In addition, the macrolichen genera within Icmadophiliaceae distinctly diversified after the K–Pg boundary: *Siphula* approximately 48 Mya and *Thamnolia* about 16 Mya (Fig. S2). If these estimates are correct, the Jurassic macrolichen cannot
be included in any extant family containing macrolichens, and so the occurrence of Daohugouthallaceae in the Jurassic may reflect a scenario of early macrolichen evolution long before the diversification of extant lineages of epiphytic macrolichens.

**Daohugouthallaceae** X.L. Wei, X. Wang, D. Ren & J.C. Wei, fam. nov. (Fig. 4)

---Fungal Names FN570853

**Diagnosis**

Thallus corticolous, foliose to subfruticose, lobes irregularly branching, lateral black cilia and lobules present. Fungal hyphae thin, photobiont cells globose, one celled.

*Type genus:* Daohugouthallus Wang, Krings & Taylor (Wang et al., 2010)

*Type species:* Daohugouthallus ciliiferus Wang, Krings & Taylor (Wang et al., 2010)

Thallus foliose to subfruticose, about 5 cm high, 3 cm wide (Fig. 4A, E); lobes slender, about 5 mm long and 0.5–1.5 mm wide, tips tapering, nearly dichotomous to irregular branching, with lateral rhizinate cilia, concolorous to thallus to black, 0.5–1.5 mm long (Fig. 4B); black spots present in some areas; lobules present (Fig. 4B); unknown disc-like structure superficial, or nearly terminal, 0.25–0.5 mm in diam., sometimes immersed (Fig. 4C). Upper cortex conglutinate, comprising one cell layer, very thin, c. 1 µm thick (Figs. 5A-B); photobiont cells globose to near globose, one-celled, mostly 1.5–2.5 µm in diameter (Figs. 4I, G; Figs. 5C-F), anastomosed by or adhered to the fungal hyphae with simple wall-to-wall mycobiont-photobiont interface; fungal hyphae filamentous, some shriveled, septate, mostly less than 1.25 µm wide (Figs. 4I-K; Figs. 5A-C).

**Substrate**

An unidentified gymnosperm branch (Fig. 4D).

**Specimens examined**

China, Inner Mongolia, Ningcheng County, Shantou Township, near Daohugou Village, Daohugou 1, Jiulongshan Formation, Callovian–Oxfordian boundary interval, latest Middle Jurassic. CNU-LICHEN-NN2019001, CNU-LICHEN-NN2020001 (part and its counterpart), CNU-LICHEN-NN2020002, B0476P.

*Remarks:* Daohugouthallus ciliiferus was first published almost a decade ago (Wang et al., 2010), and its lichen affinity was recently corroborated based on anatomical characters from scanning electron microscopy (Fang et al., 2020). Due to limitations of the available material, the systematic relationships of *D. ciliiferus* have not been explored in more detail up to the present. The newly available material allowed to better assess the phenotypic characters of *D. ciliiferus*, including morphology and anatomy, furthermore, to gather new information about its substrate ecology as the most direct evidence of this oldest macrolichen.

**Discussion**

**Phylogenetic placement of Daohugouthallaceae**

The new family based on the fossil lichen *Daohugouthallus ciliiferus* is tentatively placed in Lecanorales, although sexual reproductive structures are missing that would allow to test this placement. Ascomata, asci and ascospores are crucial to assess systematic affinities within Lecanoromycetes (Hafellner, 1994) and have ever been demonstrated in fungal fossils as old as 400 Mya (Taylor et al., 2005). Apothecia-like structures seem to be present in the fossil (Fig. 4C), but no structures interpretable as asci and ascospores were detectable. In fact, the thin nature of compression fossils like *Daohugouthallus ciliiferus* (Fig. 4H) makes it difficult for such structures to be preserved, if they were indeed present in the organism. Molecular phylogeny has also shaped the systematics of Lecanoromycetes (Leavitt et al., 2015; Magain et al., 2017). DNA has been
presumably extracted and amplified from fossils as old as 250 Mya (Cano et al., 1993; Fish et al., 2002), but these findings have been challenged and considered artifactual (Pääbo et al., 2004). Successful DNA extraction from permineralized or compression fossils as old as *Daohugouthallus ciliiferus* seems impossible and so this is not an avenue that could be followed to clarify the systematic affinities of this and other lichen or fungal fossils.

In lieu of sexual reproductive structure evidence to clarify the potential affinities of Daohugouthallaceae, our geometric morphometric analysis seems a suitable alternative to provide at least a hypothesis based on quantitative data. This approach, based on homologous landmarks or structural outlines (Rohlf and Marcus, 1993), was here apparently used for the first time in this context but has been widely used in entomology (Bai et al., 2014; Ren et al., 2017). However, it requires a careful approach to data assessment (Fox et al., 2020). The CVA plots (Fig. 1) based on the comparison with homologous landmarks of 59 extant macrolichens and two Parmeliaceae fossils showed that Daohugouthallaceae are most similar to foliaceous Parmeliaceae (Lecanorales). Given the much younger stem age of the latter (and other related families such as Physciaceae), the introduction of a new, monogeneric family for this fossil therefore seems justified.

Too thin and incomplete save status of the new fossil material led to intact and stratified thallus structures unavailable, but fortunately, Energy Dispersive X-Ray Spectroscopy (EDX/EDS) helped to distinguish the lichen fossil areas, including fungal hyphae and photobiont cells, from the rock areas including rock particles in this study, which showed they obviously differed in the main elements contained and lichen affinities of the new fossil are further confirmed (*Table S2; Fig. S3*). The apparently smaller photobiont cells (1.5–2.5 µm in diam.) (Figs. 4I, K; Figs. 5C-F) and thinner fungal hyphae (mostly less than 1.25 µm wide) in *Daohugouthallus ciliiferus* (Figs. 4I-K; Figs. 5A-C) compared to extant Lecanoromycetes, suggest that Daohugouthallaceae may have also originated from a relict clade outside Lecanoromycetes. The morphology of some photobiont cells exhibited a framboidal form like in some degree (Figs. 5D, F), similar to the description of presumed green algal cells in other lichen fossils (Honegger et al., 2013). While we cannot exclude the possibility of the photobiont cells to represent cyanobacteria, this seems unlikely, as in extant lichens cyanobacterial cells are usually arranged in clustered fashion.

**An updated macrolichens evolution from Daohugouthallaceae**

The new family Daohugouthallaceae suggest that epiphytic macrolichens already existed in the Jurassic. Extant lichenized clades that are largely epiphytic have been dated back to as far as the early Jurassic, such as microlichens in the Graphidaceae, Pyrenulaceae, and Trypetheliaceae (Lücking et al., 2013; Kraichak et al., 2018; Nelsen et al., 2020). However, the oldest extant macrolichen clade, *Umbilicaria*, is almost exclusively rock-dwelling (saxicolous), and while extant macrolichens vary greatly in substrate choice (Belnap et al., 2001; Nash, 2008), extant epiphytic macrolichen clades are consistently younger than the K–Pg boundary and only since then have evolved to form the conspicuous elements of terrestrial woody ecosystems they are today (McCune et al., 2000; Spribille and Muggia, 2013; Wei et al., 2017), which have been well supported by the diversity of European Palaeogene fossil macrolichens of Lecanoromycetes (Kaasalainen et al., 2017).

The divergent time of Lecanoromycetes, the main class including epiphytic macrolichens, has been estimated at 300–250 Mya (*Nelsen and Lücking*, 2018; Kraichak et al., 2018; Lutzoni et al., 2018; Nelsen et al., 2020), and so it is conceivable that epiphytic macrolichens even older than *Daohugouthallus ciliiferus* may have existed. The diversification of Lecanoromycetes coincides with the period after the end-Permian extinction. Before that time, diverse Permian forests existed around the world (Gulbranson et al., 2012; Wang et al., 2012). While these could have provided potential environments for epiphytic macrolichens, there is no fossil record that would support such an assumption. The end-Triassic mass extinction 200 Mya greatly affected marine and terrestrial organisms (Erwin, 2001; Damborenea et al., 2017), but its effect on lichenized fungi is unclear. The ecology of terrestrial vegetation at that time, with diverse forests already in the Late Triassic and into the Jurassic (Rees et al., 2004; Bonis and Kürschner, 2012), would certainly have supported the existence of epiphytic macrolichens, but again, no unambiguous fossil record exists that would support such a hypothesis.

The Mid-Mesozoic era was a cooling and greenhouse period (Willis and Niklas, 2004) and the paleoenvironment of the Daohugou formation has been described as humid, warm-temperate and montane (Ren and Krzeminski, 2002), thus favoring
the potential growth of epiphytic macrolichens, as shown by the ecology of extant macrolichen lineages in the tropics. Foliose macrolichens are also known for their ability to explore additional niche spaces (Huang et al., 2019), and gymnosperms such as conifers could have provided suitable new substrata helping the macrolichens away from the constraints of substrate surface as common in microlichens, promoting the better growth and spreading of this kind of macrolichen, thus laying an important foundation for the advance of the earlier evolution of epiphytic macrolichens, especially during the life recovery period just after the end-Triassic mass extinction. The presence of a fossil macrolichen such as Daohugouthallus ciliiferus is therefore not surprising and we expect that more macrolichen morphotypes may be found in this and other formations of the Mesozoic, hopefully expanding the evidence for the diversification of macrolichen lineage well before the most recent mass extinction event, the K–Pg boundary.

Interactions of Daohugouthallaceae and Mesozoic forest ecosystem

Extant epiphytic macrolichens are crucial components of terrestrial woody ecosystems (McCune et al., 2000; Spribille and Muggia, 2013; Wei et al., 2017), which play an important role in the forest water-cycle and nutrient cycling (Klein et al., 2021). More importantly, epiphytic lichen diversity can be regarded as a biodiversity indicator of forest ecosystems (Klein et al., 2021). There exists a significant interaction between epiphytic lichen diversity and tree species composition (McMullin et al., 2010; Király et al., 2013; Frisch et al., 2015; Klein et al., 2021). But when this relationship between epiphytic lichens and trees began was unknown until the discovery of Daohugouthallaceae.

Among the new specimens of Daohugouthallus ciliiferus collected from the type locality, one thallus was found attached to the branch of an unidentified cone-bearing gymnosperm fossil. The Daohugou paleoenvironment has been analyzed to be a gymnosperm-dominated forest vegetation (Ren and Krzeminski, 2002; Zhang et al., 2006), and Daohugouthallus ciliiferus has been reconstructed to be epiphytic on gymnosperms due to its association with a small seed cone (Wang et al., 2010), but in the original study the two fossils were not directly connected. Our new specimen (Figs. 4A, E) clearly shows the thallus growing directly on a thin branch of a gymnosperm with an associated cone (Fig. 4D), possibly representing a conifer, suggesting that gymnosperms may have served as substrate for epiphytic macrolichens already in the Jurassic.

The fossil record and molecular clock studies indicated that gymnosperms diverged around 315 Mya (Nie et al., 2020), while conifers originated approximately 300 Mya and diversified between 190–160 Mya in the Early to Middle Jurassic (Leslie et al., 2018) into the various families recognized today. The Jurassic epiphytic macrolichen Daohugouthallus ciliiferus became the just right connection between the diversification of Lecanoromycetes represented by Daohugouthallaceae and gymnosperms represented by conifers during the recovery period after the end-Permian extinction, and the connecting event was that Daohugouthallus ciliiferus selected gymnosperms as its substrates. Notably, various other groups of organisms underwent radiations in this period, such as mammals or the avian stem lineage (Benson et al., 2014; Close et al., 2015).

The emergence of epiphytic macrolichen in Jurassic may indicate that the internal relationships and energy flows of forest ecosystems in this period were more diverse and complex, however, in order to reveal the interaction between epiphytic macrolichens diversity, tree species composition and succession, and the forest ecosystems pattern and function, further exploration of Mesozoic epiphytic macrolichens and paleobotany are still greatly needed in the future.

Materials And Methods

Geological context

Specimens in this study were collected from the Daohugou locality of the Jiulongshan Formation, near Daohugou Village, Ningcheng County, approximately 80 km south of Chifeng City, in the Inner Mongolia Autonomous Region, China (119°14.318′E, 41°18.979′N). The age of this formation is 168–152 Ma based on $^{40}$Ar/$^{39}$Ar and $^{206}$Pb/$^{238}$U isotopic analyses (He et al., 2004; Liu et al., 2006; Ren et al., 2019).

Experimental methods


The lichen fossils were examined and photographed using an Olympus SZX7 Stereomicroscope attached to a Mshot MD50 digital camera system. For selected fossil we made cross sections using a stonecutter, one piece was embedded in EXAKT Technovit 7200 one-component resin, then cut using an EXAKT 300CP cutting system. The thin sections were grinded and polished to the thickness of about 20 µm using an EXAKT 400CS variable speed grinding system with P500 and P4000 abrasive papers; one piece was sputter-coated with gold particles using Ion Sputter E-1045 (HITACHI). SEM images were recorded using a scanning electron microscope (Hitachi SU8010) with a secondary electron detector operated at 5.0 kV; one piece was analyzed with a Zeiss MA EVO25 scanning electron microscope under a high vacuum mode by using an accelerating voltage of 20kV. Energy Dispersive X-Ray Spectroscopy (EDX/EDS) spectra were obtained with an Oxford X-act detector. The working distance was kept between 8-10 mm. Acquisition time was set up to 60 seconds for each EDS spectrum. Plates were composed in Adobe Photoshop. Most lab work was performed at the Institute of Microbiology, except the stonecutter was operated at the Institute of Geology and Geophyscis, and the fossil thin slicing and EDX were taken at the Institute of Vertebrate Paleontology and Paleoanthropology. All the above three Institutes are in Beijing and subordinate to Chinese Academy of Sciences.

**Specimen repository**

Fossil specimens of *Daohugouthallus ciliiferus* (CNU-LICHEN-NN2019001, CNU-LICHEN-NN2020001 (part and its counterpart), CNU-LICHEN-NN2020002, B0476P) are deposited in the Key Lab of Insect Evolution and Environmental Changes, College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University, in Beijing, China.

**Geometric morphometrics:** For this purpose, 140 images (Fig. S1) of 59 representative extant macrolichen species were selected from 12 families and 6 orders of Lecanoromycetes (*Table S3*), including specimens deposited in HMAS-L, photos provided by Robert Lücking, and pictures downloaded from the CNALH (Consortium of North American Herbaria) Image Library https://lichenportal.org/cnalh/imagelib/ and the Hypogymnia Media Gallery http://hypogymnia.myspecies.info/gallery, among which 13 species had more than 2 samples and images, 15 species had only one sample each but more than 2 images, and 31 species had one image each, together with two images of accepted Parmeliaceae fossils (Kaasalainen et al., 2017), and 25 sub-images cut from the images of *Daohugouthallus ciliiferus* fossil. The sampling number of images in this study comprehensively considered the quality requirement for the geometric morphometric analysis, representativeness and availability of the discernable topology of thallus lobes or branches. The whole image set was divided into five groups according to lobes types: microfoliose group, the *Daohugouthallus ciliiferus* fossil group, a long branches group, a wide-lobed group, and a fruticose group (*Table S4*). The selected images were two-dimensional graphs with two views of the front or back of the thallus where the branch tips were clearly recognizable. To orientate the images in the same direction, they were adjusted so that the end of the branches faced right. Images were named in a unified format: growth type-order-family-genus-species (sample number) except for the two selected reference fossil images only corresponding to family name.

The external forms were represented by one curve extracted from the end of branches or lobes and the curve was resampled into 60 semi-landmarks by length (Fig. S4). The starting point of the curve was selected as a point on the upper edge of the lobe or branch near the center or substrate, and after describing the outline of the whole lobe or branch, the end point returning to the lower edge near the starting point. The curves and semi-landmarks were digitized using TPS-DIG 2.05 (Rohlf, 2006). To merge all semi-landmarks into the same data file to produce the data set for morphological analysis, the data file was opened as text file to convert the semi-landmarks to landmarks, by deleting the line with the curve number and point number and replacing the landmark number by the point number (Tong et al., 2021).

MORPHO J 1.06a (Klingenberg, 2011) was used for subsequent analysis of the data set. Through Procrustes analysis, the morphological data of all test features were placed in the same dimensional vector space to screen out physical factors such as size. Principal component analysis (PCA) and geometric modeling of the mathematical space formed by PC axis were used to coordinate the shape changes of the entire dataset. We then selected the data set to generate a covariance matrix. In this context, the first two principal components corresponding to the highest cumulative variance represent the best variation
pattern of test shape. The relationships among different morphological groups were then visualized through canonical variate analysis (CVA).

Declarations

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**Author contributions**: QXY: Literatures investigation, geometric morphometric analysis, molecular data collection and analysis, original draft editing; YYW: SEM photos taking and analysis, molecular data analysis, original draft editing; RL: Conceptualization, molecular analysis, validation, draft review and editing; TL: Conceptualization, validation, draft review and editing; XW: Fossil lichen and plant identification, draft review and editing; ZYD: molecular analysis; YKC: Geometric morphometric analysis; MB: Geometric morphometric analysis, draft review and editing; DR: Conceptualization, resources collection, supervision, project administration, validation, funding acquisition, draft review and editing; JCW: Conceptualization, supervision, validation, draft review and editing; HL: Conceptualization, molecular analysis, validation, draft review and editing; YJW: Conceptualization, resources collection, supervision, funding acquisition, validation, draft review and editing; XLW: Conceptualization, supervision, geometric morphometric analysis, SEM photos taking and analysis, data curation, funding acquisition, project administration, validation, original draft writing, review and editing.

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**Figures**

**Figure 1**

*CVA plots based on the geometric morphometrics analysis (the first four principal components). (A).* CVA plot based on the highest Cumulative value 42.385 corresponding to the sum of the first principal component with the Variance value 24.433 and the second (17.952). *(B).* CVA plot based on the Cumulative value 35.271 corresponding to the sum of the first principal component with the Variance value 24.433 and the third (10.838). *(C).* CVA plot based on the Cumulative value 32.457 corresponding to the sum of the first principal component with the Variance value 24.433 and the fourth (8.024). *(D).* CVA plot
based on the Cumulative value 28.79 corresponding to the sum of the second principal component with the Variance value 17.952 and the third (10.838). Different colors represented different groups (Table S3). The distance showed the degree of similarity between different groups. Group 1 in red: FO-C-Physcia (Physciaceae, Caliciaceae)/FO-P-Coccocarpia (Coccocarpiaceae, Peltigerales)/FO-P-Pannaria (Pannariaceae, Peltigerales), group 2 in purple: FO-L-Daohugouthallus, group 3 in green: FO-L-Accepted foliose Parmeliaceae fossil/Hypotrachyna/Hypogymnia (Parmeliaceae, Lecanorales), group 4 in blue: FO-P-Peltigera (Peltigeraeae,Peltigerales)/Lobaria/Sticta (Lobariaceae, Peltigerales)/FO-U-Umbilicaria (Umbilicariaceae, Umbilicariales), group 5 in orange: FR-L-Accepted fruticose Parmeliaceae fossil/Cladonia (Cladoniaceae, Lecanorales)/Evemia (Parmeliaceae, Lecanorales)/Ramalina (Ramalinaceae, Lecanorales)/Sphaerophorus (Sphaerophoraceae, Lecanorales)/FR-P-Siphula (Icmadophilaceae, Pertusariales)/FR-T-Teloschistes (Teloschistaceae, Teloschistales).

Figure 2

Time-calibrated ML phylogeny of 3,373 Lecanoromycetes fungi (based on Nelsen et al., 2020). Macrolichen lineages are indicated in orange and the corresponding families are indicated. The temporal placement of the Daohugouthallus ciliiferus fossil is marked by the bold gray circle. For details see Suppl. Fig. S2.
Figure 3

**Distribution of inferred divergence times for the oldest extant macrolichen families** (based on Nelsen et al., 2020). The external morphology of selected representatives of each family is depicted to the right. The dotted line indicates the temporal placement of the *Daothugouthallus ciliiferus* fossil. The first three families are likely as old or older than the fossil but do not fit morphologically and/or ecologically. The best morphological and ecological fit are Peltigeraeaceae, in particular lobaroid lineages, but that family is significantly younger.
Photos of lichen *Daohugouthallus ciliiferus*, CNU-LICHEN-NN2020001. (A). External morphology of lichen thallus directly growing on the gymnosperm branch. (B). Marginal rhizinate cilia and lobules marked by white and black arrows, respectively. (C). Superficial and nearly immersed unknown disc-like structure. (D). Gymnosperm branch with seed cones marked by black arrow. (E). The counterpart of A. (F). Local zoom of the marked area of E. Light microscopy of *Daohugouthallus ciliiferus* (G). Part of lobes in F with rock embedded in the light-cured resin for cross slicing, the arrows indicating the location of lobes. (H). Cross section of the fossil, the arrows indicating the dark areas corresponding to the lobes, about 10μm high, absence of thallus structure. (I). Temporary slide of fossil fragments showed some photobiont cells, and conglutinated hyphae and single hypha, which are indicated by black arrows, white circles and white arrow, respectively. (J). A single hypha (same to the one in photo I) and a possible hollow photobiont cell indicated by white and black arrow, respectively. (K). Enlarged image of photobiont cells and conglutinated hyphae same to ones in photo I which are indicated by black and white circle and arrows, respectively. Scale bars: A, B, E, F=1cm; C=5mm; D=1mm; H= 100μm; I, K=10μm; J=20μm.
Figure 5

Scanning electron microscopy (SEM) of *Daohugouthallus ciliiferus*. (A). Lichen upper cortex composed of conglutinated hyphal strand, CNU-LICHEN-NN2020001. (B). Morphology of upper cortex seen from lower side, conglutinated, stratiform and shriveled, CNU-LICHEN-NN2020001. (C). The hyphae with obvious septum observed in CNU-LICHEN-NN2020001, which is a diagnostic character of Ascomycota fungi. (D-E). Fungal and photobiont cell and their contact, CNU-LICHEN-NN2020001. (F). Fungal and photobiont cell and their contact, the photobiont cell is in framboidal form like, similar to the suspected green algae reported by Honegger et al. 2013 in some degree, CNU-LICHEN-NN2019001. Scale bars: The fungal hyphae and photobiont cells indicated by white and black arrows, respectively; A, C, D=5μm; B=3μm; E=4μm; F=2μm.
Figure 6

Habitus reconstruction of the lichen *Daohugouthallus ciliiferus* growing on gymnosperm branches. Drawing by Xiaoran Zuo.

**Supplementary Files**

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- SupplementaryMaterialsThefirstepiphyticmacrolichenandsimplificationtotheinteractingwithMesozoicforestecosystem.pdf