# Lichen mimesis in mid-Mesozoic lacewings

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**Abstract**

Animals mimicking other organisms or using camouflage to deceive predators are vital survival strategies. Modern and fossil insects can simulate diverse objects. Lichens are an ancient symbiosis between a fungus and an alga or a cyanobacterium that sometimes have a plant-like appearance and occasionally are mimicked by modern animals. Nevertheless, lichen models are almost absent in fossil record of mimicry. Here, we provide the earliest fossil evidence of a mimetic relationship between the moth lacewing mimic *Lichenipolystoechotes* gen. nov. and its co-occurring fossil lichen model *Daohugouthallus ciliiferus*. We corroborate the lichen affinity of *D. ciliiferus* and document this mimetic relationship by providing structural similarities and detailed measurements of the mimic's wing and correspondingly the model's thallus. Our discovery of lichen mimesis predates modern lichen-insect associations by 165 million years, indicating that during the mid-Mesozoic, the lichen-insect mimesis system was well established and provided lacewings with highly honed survival strategies.

## Introduction

Modern insects have dramatic morphological specializations that match various objects of the environment. For instance, the specializations occurring in katydids and butterflies that mimic leaves, stick insects and inchworms that resemble twigs, and orchid mantids that duplicate orchid flowers, provide ecological insights for understanding mimetic associations between insect mimics and their plant models (*Stevens and Merilaita 2011*; *Gullan and Cranston 2014; Maran, 2017*). These and other fascinating cases reveal that mimesis or camouflage is highly effective when cryptic insects resemble closely the appropriate self-similar background, indicating the complexity of ecological relationships between insect mimics and their imitating models. When and how insects first evolved such an ingenious survival strategy is unclear. A Permian katydid exhibiting a mimicking pattern of wings similar to the modern relatives was considered the oldest case of insect mimicry (*Garrouste et al., 2016*). However, evidence for a contemporaneous mimetic relationship in this Permian deposit was scarce, and there was no quantitative or other useful data to track the mimetic interactions among the insect, model and predator. More recent cases of insect mimicry have been recorded from the Mesozoic, indicating the existence of several such effective survival strategies. As in morphological specializations involving masterly deceit found in modern insects, several Mesozoic insect taxa developed remarkable structural adaptations resulting in highly accurate resemblances to co-existing models (*Wang Y et al., 2012; Wang M et al., 2014; Yang et al., 2020*). Prominent among these mimetic insects are Neuroptera (lacewings, antlions and relatives), a nonspeciose relic order consisting of ca. 6000 extant species that engaged in several, impressive instances of mimicry that reveal novel and specialized strategies of deception, of which many are absent today. Striking examples are the Jurassic lacewing *Bellinympha* (Saucrosmylidae), a compression fossil, mimicking cycadophyte leaves (*Wang Y et al., 2010*), and larvae of the green lacewing *Phyllochrysa* (Chrysopidae) from amber, modified to

resemble co-occurring liverworts (*Liu et al., 2018*). Besides mimicry, other deceptive modes of appearance have been documented among Mesozoic lacewings, such as camouflaged larvae of chrysopid (green lacewing) and myrmeleontoid (antlion relative) neuropterans in amber, which evolved distinctive debris-carrying behaviors to enhance their predatory effectiveness (*Pérez-de la Fuente et al., 2012, 2018; Wang B et al., 2016; Badano et al., 2018*). These cases collectively have promoted understanding of the early evolution of insect mimicry, but also have revealed that the currently species poor Neuroptera had evolved a significant repertoire of specializations involving morphologies and behaviors that adapted to a variety of Mesozoic settings.

In this report, we found an exceptional system of the first lichen mimesis by a fossil lacewing. These occurrences are from the Daohugou 1 locality of Inner Mongolia in northeastern China. The new lichen-like-mimicking insects represent a new genus with two new species and exhibit remarkable wing patterns that accurately resemble the contemporaneous lichen species *Daohugouthallus ciliiferus* Wang, Krings *et* Taylor, 2010 (*Wang X et al., 2010*). The lichen affinity of the *D. ciliiferus* model previously was doubted due to the absence of evidence for fungal and algal connections that would indicate the presence of lichenization and thus the presence of a mutualistic symbiosis (*Honegger et al., 2013; Lücking and Nelsen, 2018*). Our SEM results corroborate the actual presence of hyphae connected to algal cells on the *D. ciliiferus* specimens, indicating the foliose and subfruticose lichen growth forms were in existence during the Middle Jurassic. Present-day lichen-mimicking insects are widely recorded among several diverse orders, especially Coleoptera (beetles), Lepidoptera (moths and butterflies) and Orthoptera (grasshoppers, katydids and crickets), which have evolved unusual specializations of morphology and behavior consistent with co-occurring lichens and other habitation- or appearance similar organisms such as liverworts (*Gerson, 1973; Lücking, 2001; Capinera, 2008;*

*Cannon, 2010; Lücking et al., 2010*). An extraordinary orthopteran, the lichen dragon katydid from the modern Ecuadorian Andes, provides an excellent disguise of lichens (*Braun, 2011*). Other predatory and extant chrysopid larvae have a body mask adorned with affixed lichen fragments, an example of aggressive mimicry or the "wolf in sheep's clothing" syndrome (*Skorepa and Sharp, 1971; Slocum and Lawrey, 1976; Wilson and Methven, 1997; Tauber et al., 2014*). Importantly, lichen-mimetic or -camouflaged insects have established a specialized lichen-association for feeding or sheltering to obtain survival advantage (*Gerson, 1973*). Our finding documents the earliest lichen-mimicking insect and reveals that this strategy of mimicry among insects has been in existence for minimally 165 Mya. This ancient association also will provide new insight for exploring the predator–prey relationships among insects and lichens, and the role of habitat during mid-Mesozoic time.

## Results

### Reanalysis of the previously suspected lichen fossil *Daohugouthallus ciliiferus*

We have studied five fossil lichen specimens, PB23120, B0474, B0476P/C, CNU-LICHEN-NN2019001 and CNU-LICHEN-NN2019002P/C, all of which were collected from the Daohugou 1 locality of Inner Mongolia. The newly collected specimens were identified to be *Daohugouthallus ciliiferus* based on careful observations of its distinctive morphology.

**Genus** *Daohugouthallus* Wang, Krings *et* Taylor, 2010

**Species** *Daohugouthallus ciliiferus* Wang, Krings *et* Taylor, 2010

**Emended diagnosis**. The diagnosis is as follows and adds to the previous assessment (*Wang X et al.*,

*2010*). Thallus foliose to subfruticose; lobes ca. 20–30 mm long, irregularly branched, margin sometimes revolute; lateral and terminal branches ca. 0.5–5.0 mm long, tips tapered; upper surface smooth, partly broken; aggregated black spots often present, punctiform; cilia sometimes present near the branch tips, forming filiform appendages; lobules occasionally present (*Figure 1*).

Besides the external morphology, certain anatomic characters also were determined. Upper cortex conglutinate, comprising one cell layer, very thin, ca. 1 μm thick (*Figure 2A*); algal cells globose to near globose, one-celled, mostly 1.5–2.1 μm in diameter, some in framboidal form, interconnected (*Figure 2A, B, F*) by or adhered (*Figure 2C, D, E–G, H*) to the fungal hyphae with simple wall-to-wall mycobiont-photobiont interface; fungal hyphae filamentous, some shriveled, septate (*Figure 2B, C, G, H*), 1.2–1.5 μm wide. These additional features (*Figure 2*) support the above diagnoses that this specimen is a fossil lichen.

**Remarks.** This adpression lichen fossil was reported by Wang X *et al*. (2010) as a new genus and new species of lichen, i.e. *Daohugouthallus ciliiferus*. However, there were no anatomic characters including both fungal and algal components that was provided and consequently its lichen affinity was doubted and thought as ambiguous (*Honegger et al., 2013; Lücking and Nelsen, 2018*). Actually, the lichen fossil now has been well defined and should accord with three important criteria: presence of a mycobiont component, presence of a photobiont component, and presence of spatial connections between both components (*Lücking and Nelsen, 2018*). Accordingly, thallus sections were made in this study and relevant anatomic details can be observed. First, the upper cortex occasionally was present (*Figure 2A*), and the septa of fungal hyphae also is documented (*Figure 2C, D*). Second, the algal cells are globose and occasionally have a spherical assembly of microcrystals in framboidal form similar to *Trebouxia* of *Chlorolichenomycites salopensis* in morphology but much smaller (*Honegger et al.*,

*2013*). Third, the spatial connections between fungal hyphae and algal cells have been observed, mostly consisting of fungal hyphae interweaved with algal cells (*Figure 2A, C, D, F*). The above-mentioned characters of *Daohugouthallus ciliiferus* accords well with the definition of lichen fossil and indicate a strong affinity to a lichen. From the external morphology, *Daohugouthallus ciliiferus* would be easily associated with extant *Everniastrum cirrhatum*, a conclusion that requires further study in the near future.

**Systematic Paleontology**

The lichen-mimicking insects represent a new genus and two new species affiliated to Ithonidae of the order Neuroptera. The terminology of venation follows Breitkreuz *et al*. (2017).

**Order** Neuroptera Linnaeus, 1758

**Family** Ithonidae Newman, 1853 *sensu* Winterton *et* Makarkin, 2010

**Genus** *Lichenipolystoechotes* Fang, Zheng *et* Wang, gen. nov.

**Included species.** *Lichenipolystoechotes angustimaculatus* Fang, Zheng *et* Wang, sp. nov. (type species), *Lichenipolystoechotes ramimaculatus* Fang, Ma *et* Wang, sp. nov.

***Etymology***. The new genus name is a combination of *lichen* and *Polystoechotes* (a genus name of Ithonidae) in reference to the lichen-mimesis of the genus. The gender is masculine.

***Diagnosis***. Forewing ellipsoidal shaped, medium length, slightly narrow with length-width ratio 3.25–3.5; membrane bearing coralliform pattern with unclosed diaphanous U-shaped fenestrae along the margin in forewing; costal space slightly broad basally, then narrowed towards wing apex; ScA and

recurved humeral veinlet present; costal cross-veins simple in proximal half, and then distally forked; ScP and RA fused distally, ending close to the wing apex, no cross-veins present in this area; cross-veins in area between RA and RP scattered; RP with about 18 branches, RP1 a single branch, few cross-veins scattered at the radial sector; M forked beyond the separation point of RP1, MA and MP with the similar branched pattern, the number of MP branches slightly more than MA; CuA distinctly multi-forked, with 7–10 pectinate branches; CuP bifurcated.

***Remarks.*** The new genus can easily be assigned to Ithonidae by the following characters: medium body size, prolonged forewing, relatively narrow costal space, and presence of ScA and recurrent humeral veinlet. In addition, its forewing characters, including Sc and R1 fused distally, few cross-veins except for a row of well-defined outer gradate series in radial sector, MP forked beyond MA divergence, conforming to a polystoechotid affiliation (*Zheng et al., 2016*). It also is distinguished from other polystoechotid genera by the distinctive coralliform markings of the forewings.

***Lichenipolystoechotes angustimaculatus*** **Fang, Zheng *et* Wang, sp. nov.** (*Figures 3A–D, 4E*)

***Etymology.*** The specific name comes from the Latin words "*angusta*" and "*macula*" referring, respectively, to the narrow, linear and pigmented swaths on the forewing, and the spot-like patterns present on those swaths.

***Material.*** *Holotype*. CNU-NEU-NN2016040P/C (*Figures 3A–C, 4E*), *paratype*. CNU-NEU-NN2016041 (*Figure 3D*).

***Type locality and horizon.*** Daohugou 1, near Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China. Jiulongshan Formation, Callovian–Oxfordian boundary interval, latest Middle Jurassic.

***Diagnosis*.** Forewing, humeral veinlet strongly recurved; ScA present; cross-veins in area between RA and RP scattered except for the middle gradate series; RP with about 18 branches; MA and MP with similarly distal pectinate branches; CuA pectinately branched in distal half; CuP deeply bifurcated at anterior half.

***Description and comparison*.** Only forewing present. Forewing elongate, oval shaped, about 21.3 mm long, 6.5 mm wide; membrane bearing irregular coralloid markings of pigmentation, forming many diaphanous marginal fenestrae; costal space slightly broad basally, then narrowed towards the wing apex; costal cross-veins scarcely branched in proximal half of wing, and then forming bifurcated branches in distal half; sc-ra cross-vein absent; space between RA and RP relatively narrow with seven cross-veins; RP with 18 pectinate branches, and each branch bifurcated near wing margin; cross-veins in radial sector relatively scarce except for the middle gradate series; M forked slightly beyond the separation of RP1; MA and MP forming 7 pectinate branches each; CuA pectinate branched in distal half part, forming 7 pectinate branches; CuP first bifurcated at the proximal half, then forming the distal simple forks; A1–A3 forming several pectinate branches; a few cross-veins present among MA and A3.

***Lichenipolystoechotes ramimaculatus* Fang, Ma *et* Wang, sp. nov.** (*Figures 3E–H, 4A, G*)

***Etymology*.** The specific name comes from the Latin word *rami* and *macula*, referring, respectively, to the narrow, branched and pigmented swaths traversing the forewing, and the spot-like patterns present on those branched swaths.

***Material.*** *Holotype*. CNU-NEU-NN2019006P/C (*Figures 3E–H, 4A, G*).

***Type locality and horizon.*** Daohugou 1, near Daohugou Village, Shantou Township, Ningcheng

County, Inner Mongolia, China. Jiulongshan Formation, Callovian–Oxfordian boundary interval, latest Middle Jurassic.

***Diagnosis*.** The marginal diaphanous fenestrae significantly open, surrounded by pigmented zones; MA forming the distal dichotomizing fork, MP with 6 pectinate distal branches; CuA branched nearly at the middle, forming about 11 pectinate branches, CuP bifurcated beyond the middle portion of the vein.

***Description and Comparison*.** Only forewing preserved. Forewing elongate, oval shaped, about 22.8 mm long, 6.5 mm wide; costal space slightly broadened, then narrowed towards wing apex; subcostal veinlets relatively widely spaced, scarcely branched medially, forming multiple bifurcated branches distally; areas between Sc and RA narrow, without crossveins; space between RA and RP relatively narrow with sparse crossveins; RP with about 22 pectinate branches; RP1 branched from RP near wing base, single until wing margin; M forked basally, MA forming 2 distal dichotomous branches, and MP forming 6 distal pectinate branches; CuA pectinate medially to distally, forming 11 pectinate branches; CuP bifurcated at middle; A1–A3 partly preserved.

## Discussion

The two new species of *Lichenipolystoechotes* exhibit a very similar appearance, but they easily can be separated by the distinct differences of branches of the MA and CuA veins. *Lichenipolystoechotes* species are conspicuous based on their highly prominent, homologous, pigmentation pattern of their forewings, which implies that these insects evolved a similar defensive strategy. The closest extant relatives of *Lichenipolystoechotes* are Ithonidae (moth lacewings), of which their ecological and biological features are poorly documented (*New, 1989*). The forewings of the two new species demonstrate a high similarity in their overall appearance, such as the forewing branching pattern

(*Figure 3A, E, 4A*) that matches the thallus branches of the co-occurring foliose to subfruticose lichen *Daohugouthallus ciliiferus* (*Figure 4B–D*) (*Wang X et al., 2010*). The entire forewing forms an irregular branching pattern amid rounded, diaphanous fenestrae (windows) that are distributed along the wing center and as U-shaped extensions occurring around the wing border. The pigmented branch pattern of the wings has uneven widths and is angulated outwardly. The variation in width of each forewing vein branch conforms well to the variation in width of the lichen's branches, indicating a morphological similarity between the wing markings and lichen thallus (*Figure 4F; Figure 4–figure supplement 1; Supplementary file 1: Table S1*). Lichens often have punctiform pycnidia (asexual reproductive structures) with black spots appearing on their thallus, especially in extant foliose lichen families such as Parmeliaceae (*Thell et al., 2012*). In *Daohugouthallus ciliiferus* specimens, punctiform black spots occur, but whether they are pycnidia is uncertain. It is noteworthy that a specimen of *L. ramimaculatus* displays similar, scattered spots on its wings that resemble the dark spots on the lichen thallus of *D. ciliiferus* (*Figure 4G–I*), potentially strengthening the similarity between *L. ramimaculatus* and *D. ciliiferus*. Collectively, these details of insect morphology likely enhanced the similarity of the insect with a co-occurring lichen, providing a reasonable inference that the forewing is mimetic with the lichen thallus.

It is generally known that lichens are stable, symbiotic associations of fungi and algae (*Lücking and Nelsen, 2018*). At the same time, lichens are regarded as pioneers in the colonization of novel surfaces such as bark, rock and soil, which dominate about 7% of the earth's terrestrial surface (*Larson, 1987*), and have a distribution from the polar regions to the tropics (*Lumbsch and Rikkinen, 2017*). They are prominent in arctic-alpine vegetation types in wet and higher montane forests (*Lumbsch and Rikkinen, 2017*). Many extant foliose or fruticose lichens such as taxa of Parmeliaceae are known to be

227 epiphytic or corticolous, and bark surfaces are one of the most common substrates (*Lumbsch and*
228 *Rikkinen, 2017*). *Daohugouthallus ciliiferus* is considered an epiphytic foliose to subfruticose lichen,
229 and often is found entangled with gymnosperm seed cones (*Figure 1C, 4D*) (*Wang X et al., 2010*).
230 When *Lichenipolystoechotes* moth lacewings reposed in a habitat rich in *D. ciliiferus*, a near perfect
231 match of their appearances would assist their concealment. Among extant Neuroptera, similar
232 appearances of lichen-camouflage or related cases have been recorded in some larvae of green
233 lacewings that carry packets of lichen material on their backs to hide themselves (*Slocum and Lawrey,*
234 *1976; Wilson and Methven, 1997*). Although *Lichenipolystoechotes* probably lacked the same life-habit
235 as modern lichen-carrying chrysopoid larvae, the Jurassic taxa likely acquired a similar survival
236 advantage when they occupied a lichen-rich habitat. Some extant *Thyridosmylus* species of Osmylidae,
237 another archaic lineage of Neuroptera, possess similar complex wing markings and often occur on
238 moss-laden surfaces of rocks, tree bark and indurated soil surfaces (*Winterton et al., 2017: fig. 2B*),
239 which exhibit an impressive consistency with their surroundings (pers. observ. by Yongjie Wang).
240 Although *Lichenipolystoechotes* is a member of Ithonidae, phylogenetically distant to Osmylidae, we
241 infer that their concealment strategy of mimicking cryptogam plants in certain habitats has a deep
242 geochronologic history among ancient lacewing lineages.
243 Unlike the models of other, co-occurring, plant-mimicking insects, lichen-mimesis of
244 *Lichenipolystoechotes* appears highly specialized (*Figure 5*). Modern lichens can produce a variety of
245 lichenic acids (*Gerson, 1973*) that are unpalatable to many insects and enhance the protective sheltering
246 for animals. Consequently, lichens and lichen-tolerant animals, such as lichen feeding insects and mites,
247 constitute a unique micro-ecosystem. We hypothesize that such a micro-ecosystem existed 165
248 million-years-ago in Northeastern China that accommodated these trophic, sheltering, defensive and

mimetic interactions. Although lichen mimesis is not well documented among extant insects, the most iconic such case of lichen and insect resemblance is the industrial melanism of the peppered moth *Biston betularia* in nineteenth century Britain (*Gerson, 1973; Stevens and Merilaita, 2011*). The Industrial Revolution caused elevated levels of soot laden air pollution that resulted in disappearance of lichen shelters for the light-colored morph of *B. betularia*, as their corresponding habitation sites were changed from lightly tinged to dark-hued lichen surfaces that led to their greater vulnerability to predation. This change resulted in the abrupt increase of the dark colored morph of *B. betularia*. When lightly hued lichens returned after aerial pollution was thwarted, *B. betularia* again became dominant as the lightly colored morph. The industrial melanism of *B. betularia* was believed as a textbook example of Darwinian evolution in action, though it was questioned by some authors (*Sargent, 1968, 1969; Coyne, 1998; Cook and Saccheri, 2013*). Nevertheless, other studies demonstrated that selection pressures such as predation by birds genuinely affected the differential survival of the pale and dark colored morphs of *B. betularia* under differently hued backgrounds (*Howlett and Majerus, 1987; Liebert and Brakefield, 1987; Majerus, 2009; Walton and Stevens, 2018*). It is possible that the Jurassic *Lichenipolystoechotes* could have gained survival advantage from mimesis of a lichen similar to that of modern *B. betularia*–lichen mimesis. Specifically, if lichen models were present in the habitat occupied by *Lichenipolystoechotes*, survival of the mimic would be assured. It is noteworthy that the winged adults of *Lichenipolystoechotes* would not have been always in the shelter of a lichen model; however, when they were, the conditions of mating, laying of eggs and dispersal would be paramount for survival. If so, high-contrast lichen-like markings could contribute to concealment of the insects. Alternatively, such high-contrast markings of *Lichenipolystoechotes* species also can be interpreted as disruptive coloration, which would confuse the boundaries of moth lacewing and lichen to prevent the

detection of a body part essential for survival (*Stevens and Merilaita, 2011*). Consequently, the lichen-like markings of *Lichenipolystoechotes* could likely bring the double protections to the insects-background mimicry and disruptive coloration.

Was there possible benefit to *D. ciliiferus* from its mimetic association with *Lichenipolystoechotes*? This is an open question that could raise multiple alternative explanations. Some modern insects such as ants, dipterans and larva of green lacewings are considered to potentially contribute to dispersal of lichens by transporting lichen propagules to new sites of colonization (*Gerson, 1973; Keller and Scheidegger, 2016; Ronnås et al., 2017*). In a comparison with such relatively small, lichen-carrying insects, *Lichenipolystoechotes* possessed a considerably larger body size that likely was convenient for dispersal of lichen propagules. Notably, sexual reproductive organs such as apothecia have not been found on the *D. ciliiferus* thallus based on light-microscopic morphological and SEM anatomical observations; neither were vegetative propagules such as soredia or isidia seen except along marginal lobules that occasionally were present. This hypothesis of zoochory requires additional evidence for support. However, our alternative hypothesis of benefiting *D. ciliiferus* is based on trophic interactions. As predaceous insects, *Lichenipolystoechotes* inhabited a lichen-rich environment to evade their predators, but they also could have predated and consumed smaller lichen-feeding animals while simultaneously decreasing herbivore damage to the *D. ciliiferus* thallus. This latter hypothesis would require additional verification from evidence of a small ecological web of predator, shelter, defensive and mimetic interactions associated with *Daohugouthallus* and *Lichenipolystoechotes* in the same deposit.

The accepted oldest lichen fossil was reported from the Early Devonian and lichens have existed minimally for 410 million years (*Taylor et al., 1995; Honegger et al., 2013; Lücking and Nelsen, 2018*),

as have the apterygote insects (*Misof et al., 2014*). Both archaic Devonian lineages have evolved more derived, diverse clades of lichens and pterygote insects resulting in a myriad of associations among their modern lineages (*Figure 6*). Although there is virtually no evidence to suggest when and how such associations began; in this report, we describe the oldest examples of lichen mimesis that involved two lacewing species resembling a contemporaneous lichen from the same, latest Middle Jurassic deposit. These insect lineages have acquired mimicry associations with lichens in less than half of the time (40 %) of the duration of both major lineages since the early Devonian (Figure 6). This new finding documents a unique survival strategy among mid-Mesozoic Neuroptera, and others await discovery.

## Materials and methods

***Geological Context***. Specimens were collected from the Daohugou 1 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, 2019*).

***Specimen Repository***. CNU-NEU-NN2016040P/C and CNU-NEU-NN2016041 of *Lichenipolystoechotes angustimaculatus* sp. nov., and CNU-NEU-NN2019004P/C of *Lichenipolystoechotes ramimaculatus* sp. nov. are housed in the College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University (CNU), Beijing, China. Lichen specimens of *Daohugouthallus ciliiferus* Wang, Krings *et* Taylor, 2010: PB23120 is housed in the paleobotanical collection of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, in

Nanjing, China; B0474 and B0476P/C are housed in the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, in Beijing, China; CNU-LICHEN-NN2019001 and CNU-LICHEN-NN2019002P/C are housed 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.

***Experimental Methods.*** The insect and lichen fossils were examined and photographed using a Nikon SMZ25 microscope attached to a Nikon DS-Ri2 digital camera system at the Key Lab of Insect Evolution and Environmental Changes at Capital Normal University in Beijing, China. Lichen compression specimens from the Daohugou 1 locality were soaked in water for several seconds, dried on filter paper, and then a fragment was lifted up by the edge of a razor blade. One isolated, dried slice was examined and photographed using a Zeiss Axioscope2 compound microscope attached to a Nikon D5100 digital camera system at the State Key Laboratory of Mycology, Institute of Microbiology, at the Chinese Academy of Sciences in Beijing. That piece of lichen fossil then was sputter-coated with gold particles using an Ion Sputter E-1045 (HITACHI), and SEM images were recorded using a scanning electron microscope (Hitachi SU8010) with a secondary electron detector operated at 5.0 kV. Overlay drawings were prepared by Corel DRAW. Box plots were made with Origin 2018 software, which is used to display the distribution of the data of branch width of *L. ramimaculatus*'s forewing pattern and lichen thallus of *D. ciliiferus*. The box plots are formed by two quartiles showing the high frequency of values, and the upper and lower points of the boxes are the maximum and minimum values. All figures were composited in Adobe Photoshop.

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475 **Figure captions**

476 **Figure 1.** Photos of the lichen *Daohugouthallus ciliiferus* Wang, Krings *et* Taylor, 2010. (A) Specimen
477 B0476P, with arrows indicating the lobules. (B) Specimen CNU-LICHEN-NN2019001, with arrows
478 indicating the lobules. (C) Specimen CNU-LICHEN-NN2019002P. Scale bars: 5 mm in A–C.

479

480 **Figure 2.** Scanning electron microscopy (SEM) micrographs of lichen fossil
481 (CNU-LICHEN-NN2019001). (A) Thallus longitudinal section containing the cortex, with white
482 arrows pointing to the fungal hyphae, and black ones to the algal cells. The fungal hyphae are
483 interweaved with algal cells. (B–D, F–H) Fungal hyphae indicated by white arrows; algal cells are
484 indicated by black arrows showing entanglement and encirclement by fungal hyphae; septa shown in B,
485 C, G, H. (E) One algal cell indicated by the black arrow, displaying adherence to other fungal hyphae
486 indicated by the white arrow. Scale bars: 5 μm in A, C, D, G, H; 10 μm in B; 3 μm in E; 4 μm in F.

487

488 **Figure 3.** Photos and line drawings of *Lichenipolystoechotes angustimaculatus* gen. *et* sp. nov., and *L.*
489 *ramimaculatus* gen. *et* sp. nov. (A–C) Holotype CNU-NEU-NN2016040P/C of *L. angustimaculatus*,
490 photo of part in (A). Accompanying overlay drawing in (B). Photo of counterpart in (C). (D) Photo of
491 the paratype CNU-NEU-NN2016041 of *L. angustimaculatus*. (E-H) The holotype
492 CNU-NEU-NN2019006P/C of *L. ramimaculatus*, with a lichen mimicking forewing pattern. Photo of
493 part in (E); accompanying overlay drawing in (F); photo of counterpart in (G); and accompanying
494 overlay drawing in (H). Scale bars: 5 mm in A–H.

495

496 **Figure 4.** The lichen mimicking lacewing *Lichenipolystoechotes ramimaculatus* gen. *et* sp. nov. and *L.*

*angustimaculatus* gen. *et* sp. nov., and fossils of the contemporaneous lichen *Daohugouthallus ciliiferus* Wang, Krings *et* Taylor, 2010. (A) Photo of part of *L. ramimaculatus*, with a lichen mimicking forewing pattern, CNU-NEU-NN2019004P. (B–C) Photos of the lichen thallus *D. ciliiferus*, PB23120; thallus segment in (B); and entire thallus in (C). Photos A–C are at the same scale. (D) Photo of a nearly intact lichen thallus of *D. ciliiferus*, B0474. (E) Photo of *L. angustimaculatus* with a lichen mimicking wing pattern; CNU-NEU-NN2016040P. (F) Box scatter plots of measurement data displaying lower and upper extremes, lower and upper quartile, median and average (in the blue dotted line) of branch widths of *L. ramimaculatus*'s forewing pattern (CNU-NEU-NN2019004C) and thallus branch widths of lichen *D. ciliiferus* (PB23120, B0474) separately. (Black, red and green dots represent measurement results of branch pattern widths of lichen-mimicking lacewing and thallus widths of the two lichen specimens, respectively.) (G) Part of the wing pattern of *L. ramimaculatus*, with irregular wing spots. (H, I) Portion of the thallus of *D. ciliiferus*, with irregular spot-like punctiform pycnidia, B0474 (H), B0476P (I) The dark arrows indicate the spots on wing of *L. ramimaculatus* and thallus of *D. ciliiferus*. Scale bars: 5 mm in A–E, 1 mm in G–I.

**Figure 4–figure supplement 1.** Measuring lines on lichen-mimicking *L. ramimaculatus* and lichen *D. ciliiferus.* (A) Measuring lines on the forewing of lichen-mimicking *L. ramimaculatus*, CNU-NEU-NN2019004P. (B) Measuring lines on lichen specimen PB23120. (C) Measuring lines on lichen specimen B0474. Measuring lines are indicated by their red color. Scale bars: 5 mm in A–C.

**Figure 5.** Habitus reconstruction of the lichen mimicking lacewing *Lichenipolystoechotes ramimaculatus* gen. *et* sp. nov. on the lichen *Daohugouthallus ciliiferus* Wang, Krings *et* Taylor, 2010.

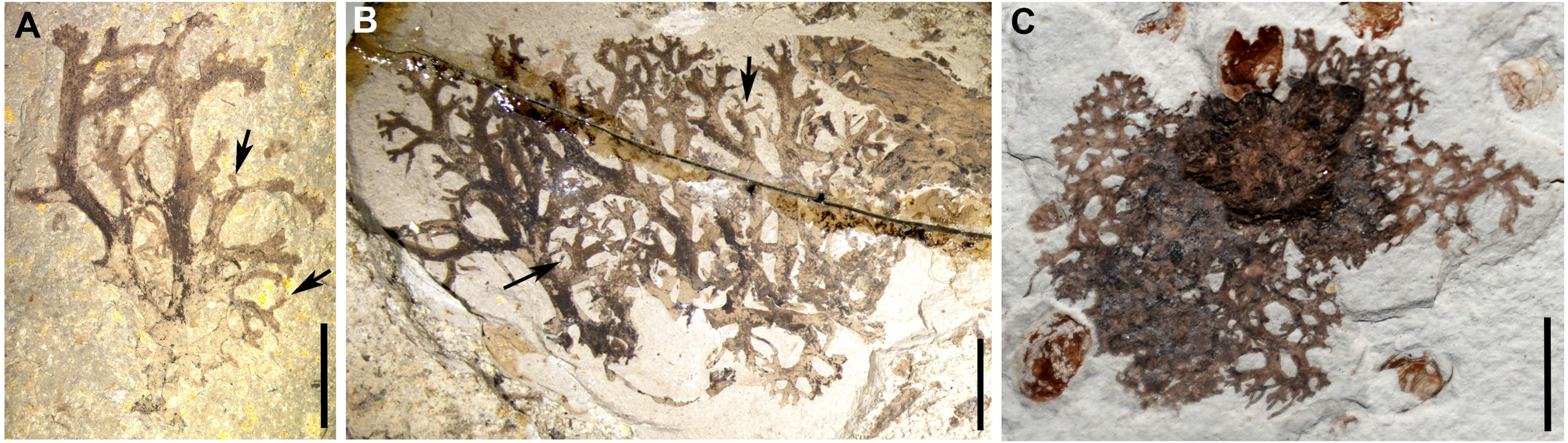
The colors used in the drawing of *D. ciliiferus* is Taupe, referring to the color of extant lichen *Everniastrum cirrhatum*. The body of the *L. ramimaculatus* is reconstructed based on living ithonid species, and the wing is based on the fossil of holotype CNU-NEU-NN2019006P/C. The color of insect is yellowish-brown based on the general coloration of extant polystoechotids. Xiaoran Zuo did the reconstruction drawing.

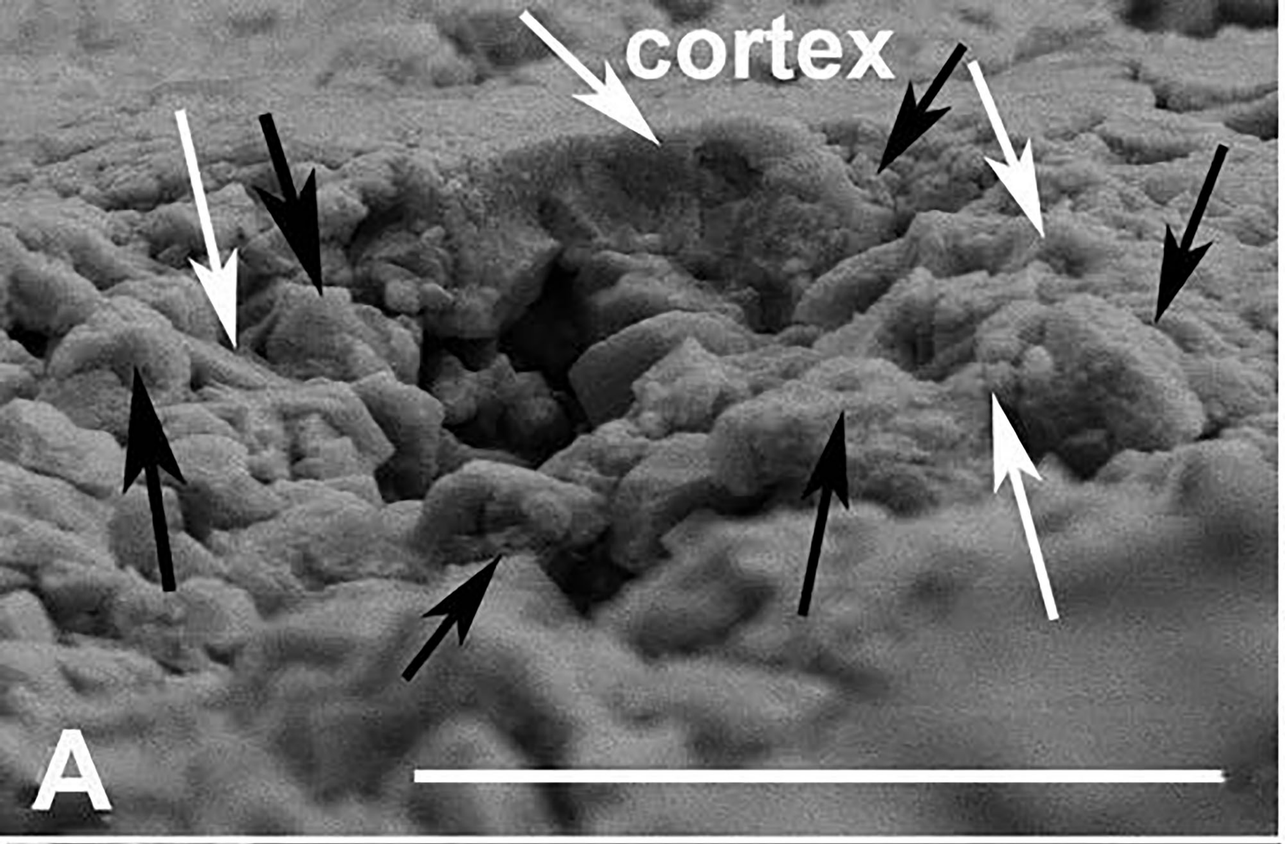
**Figure 6.** Lichen mimicry and camouflage by insects across major insect lineages. Time-dated chronogram based on *Misof et al.* (*2014*). Specific examples of fossil and modern lichen mimesis by various insect taxa are provided at right. Black dots represent modern insect–lichen-mimetic associations; the star represents the fossil *Lichenipolystoechotes*–lichen mimicry of this study.

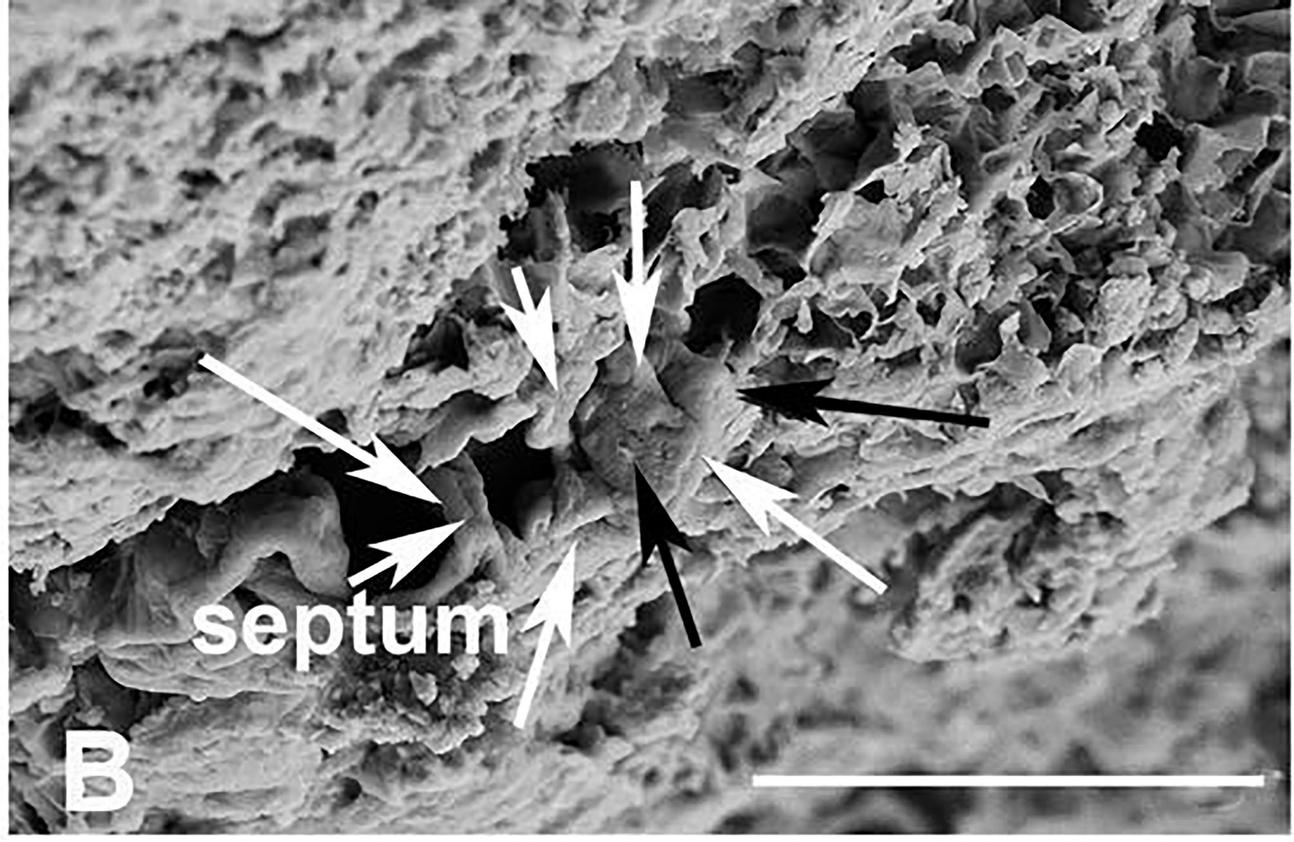
**Additional files**

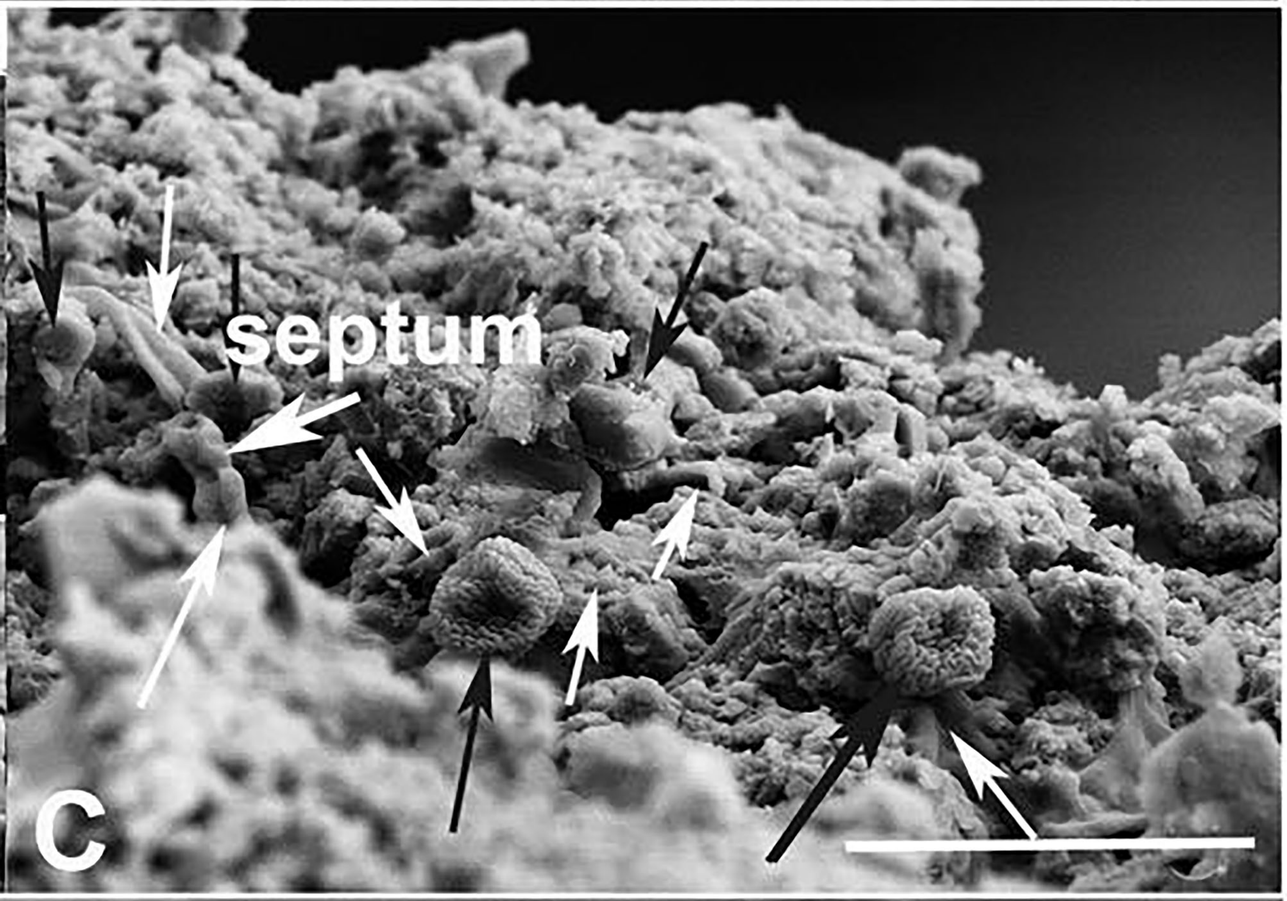
Supplementary files

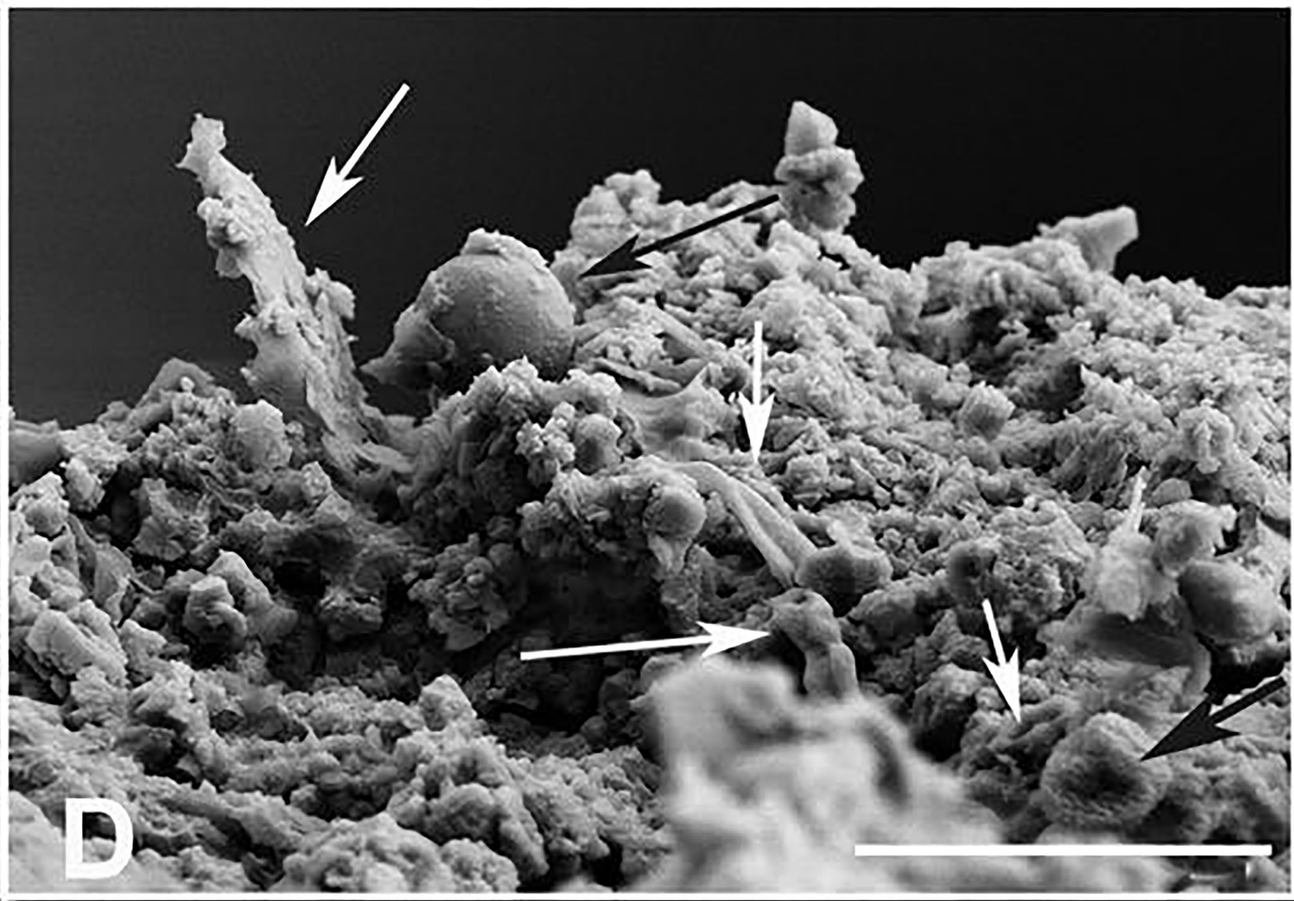
- Supplementary file 1. Table S1 Branch width of forewing pattern of *Lichenipolystoechotes ramimaculatus* and lichen thallus of *Daohugouthallus ciliiferus*

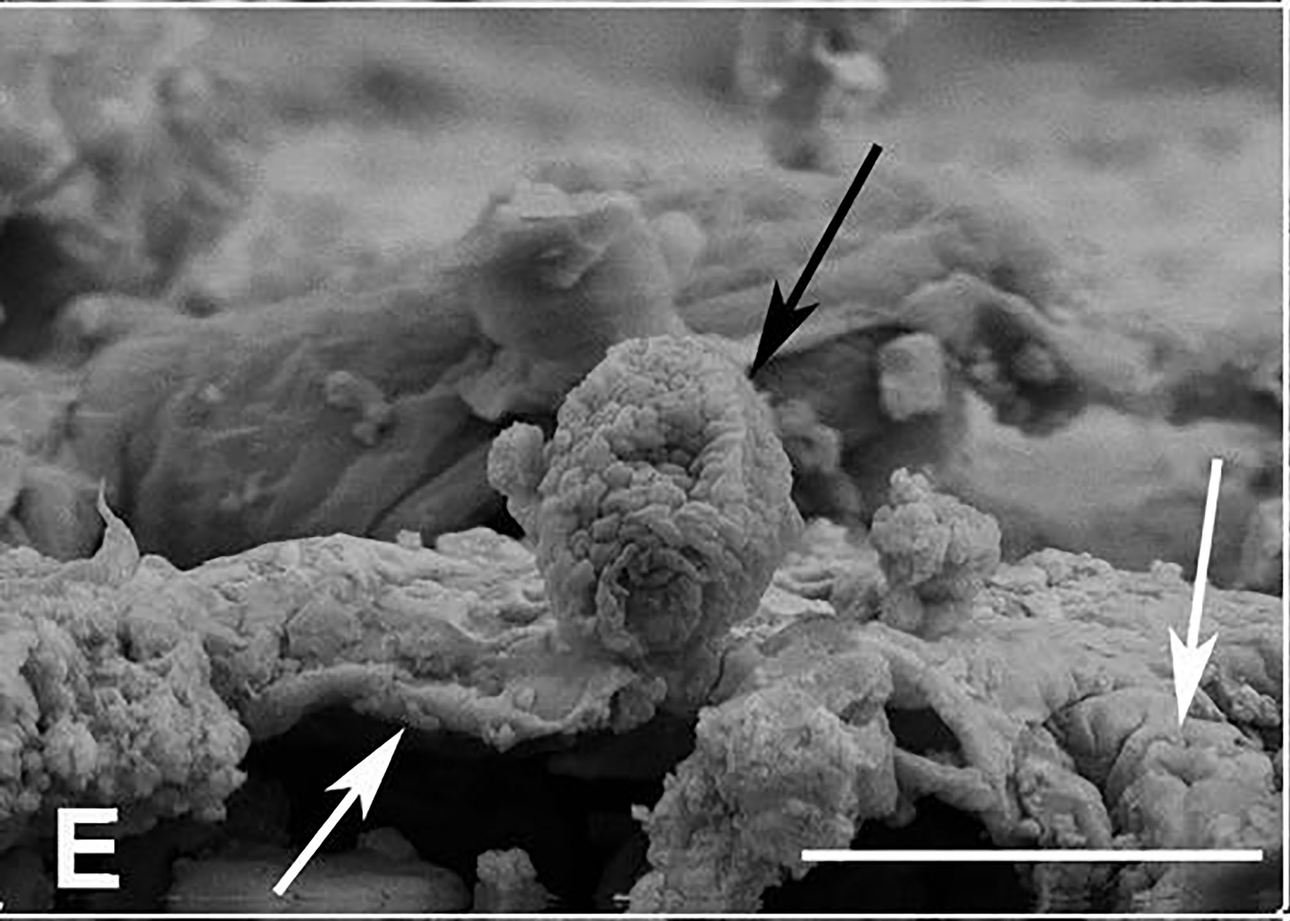

A
B
C


cortex
A


septum
B


septum
C


D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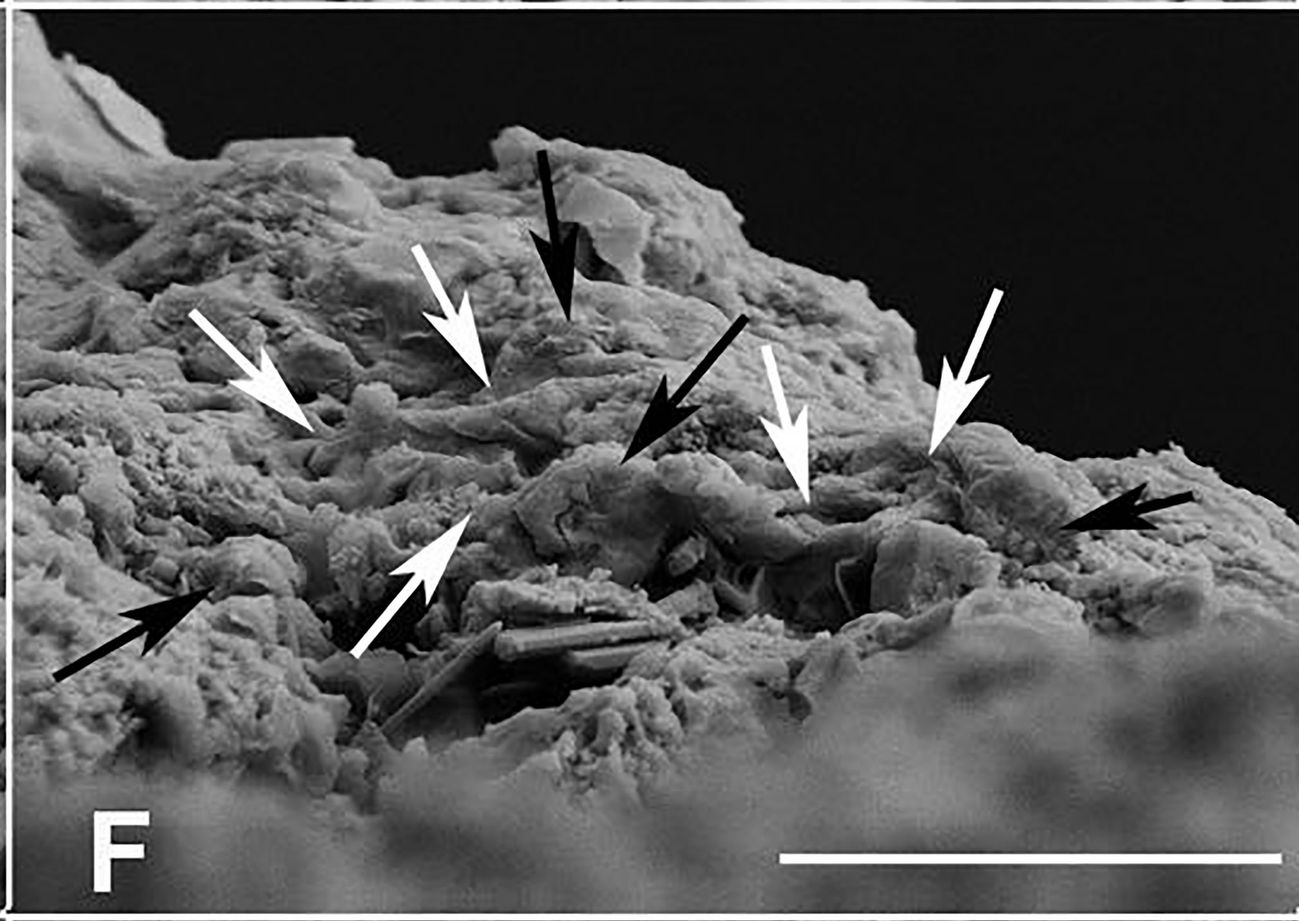
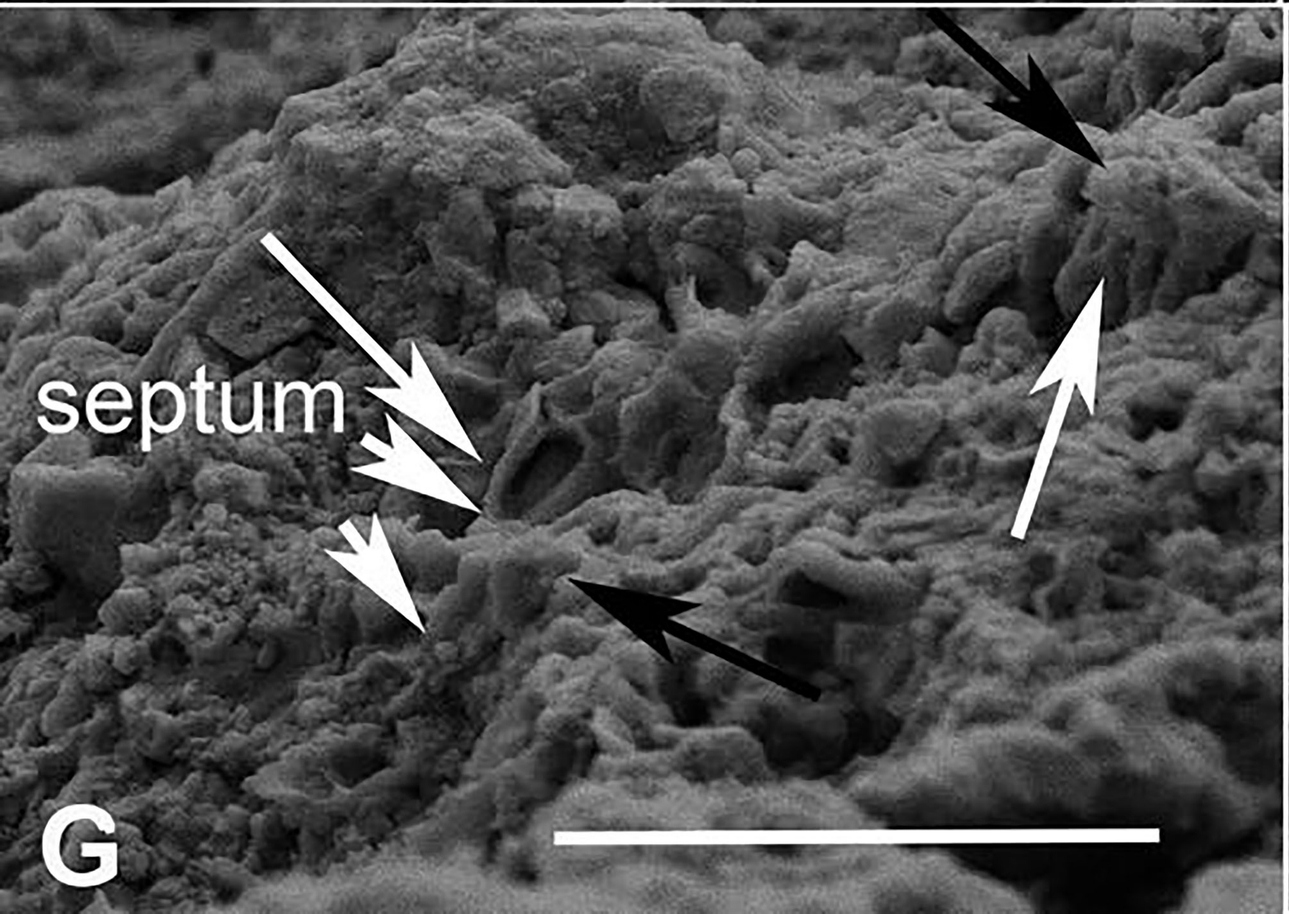

F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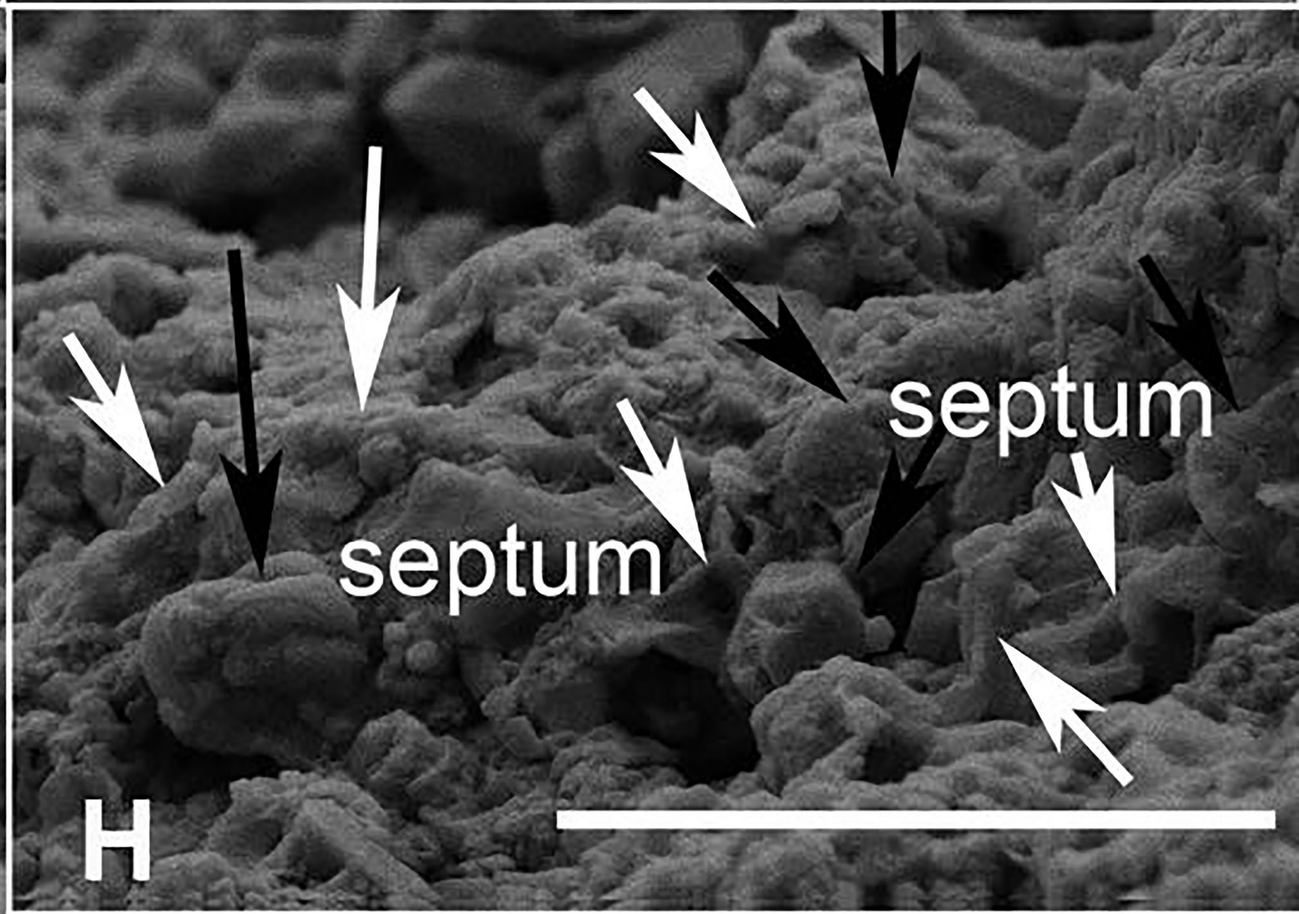
G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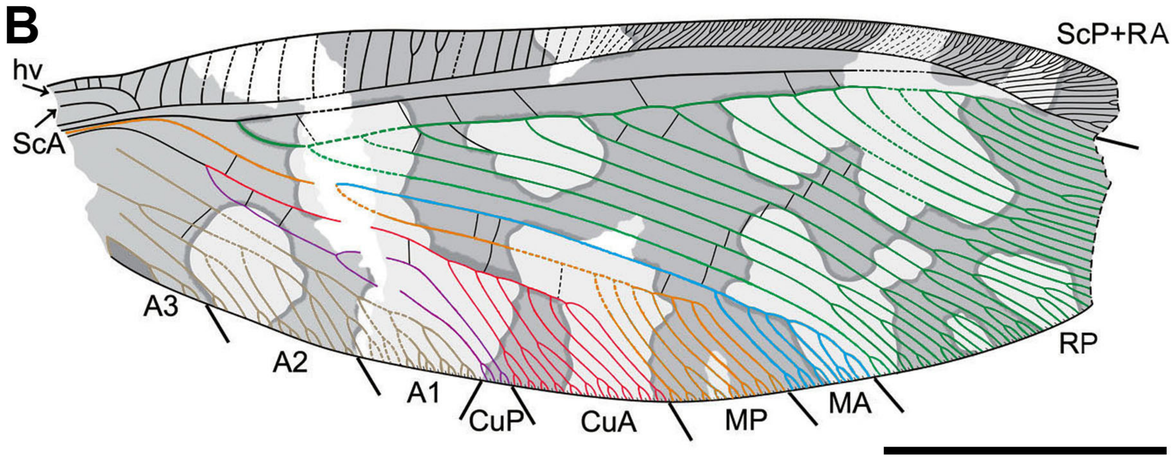
septum
H

A


B
hv
ScA
ScP+RA
A3
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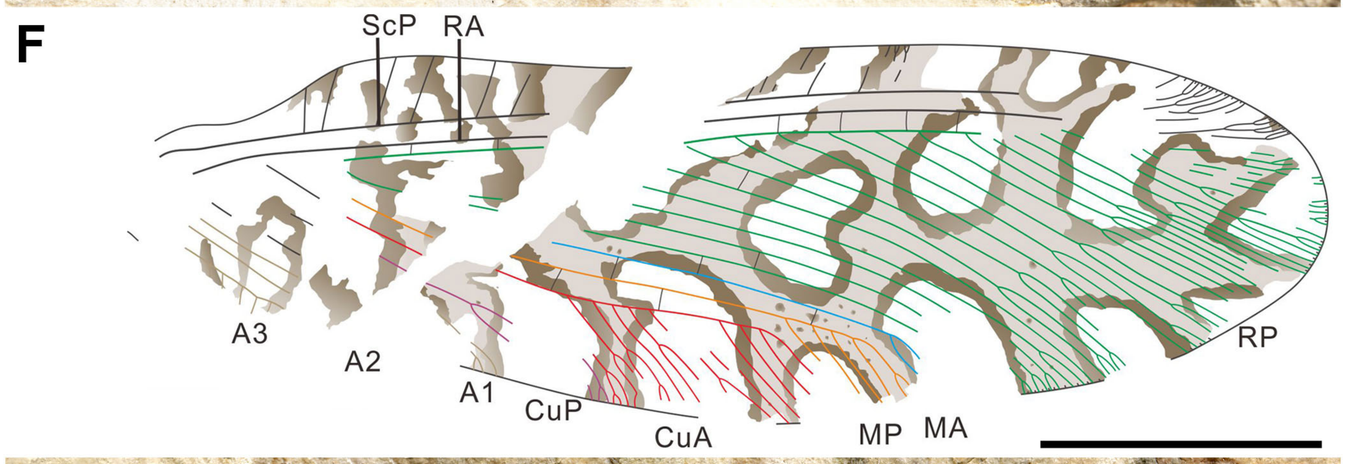
RP

C

D

E


F
ScP
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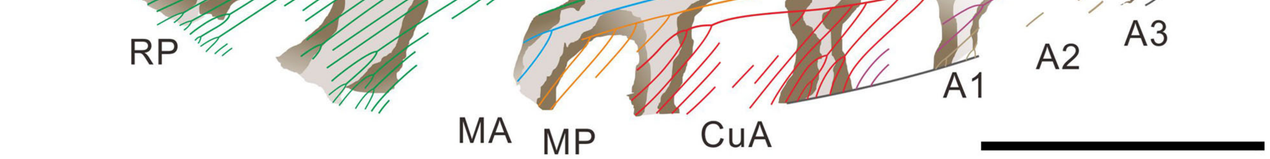
H
RP
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A1
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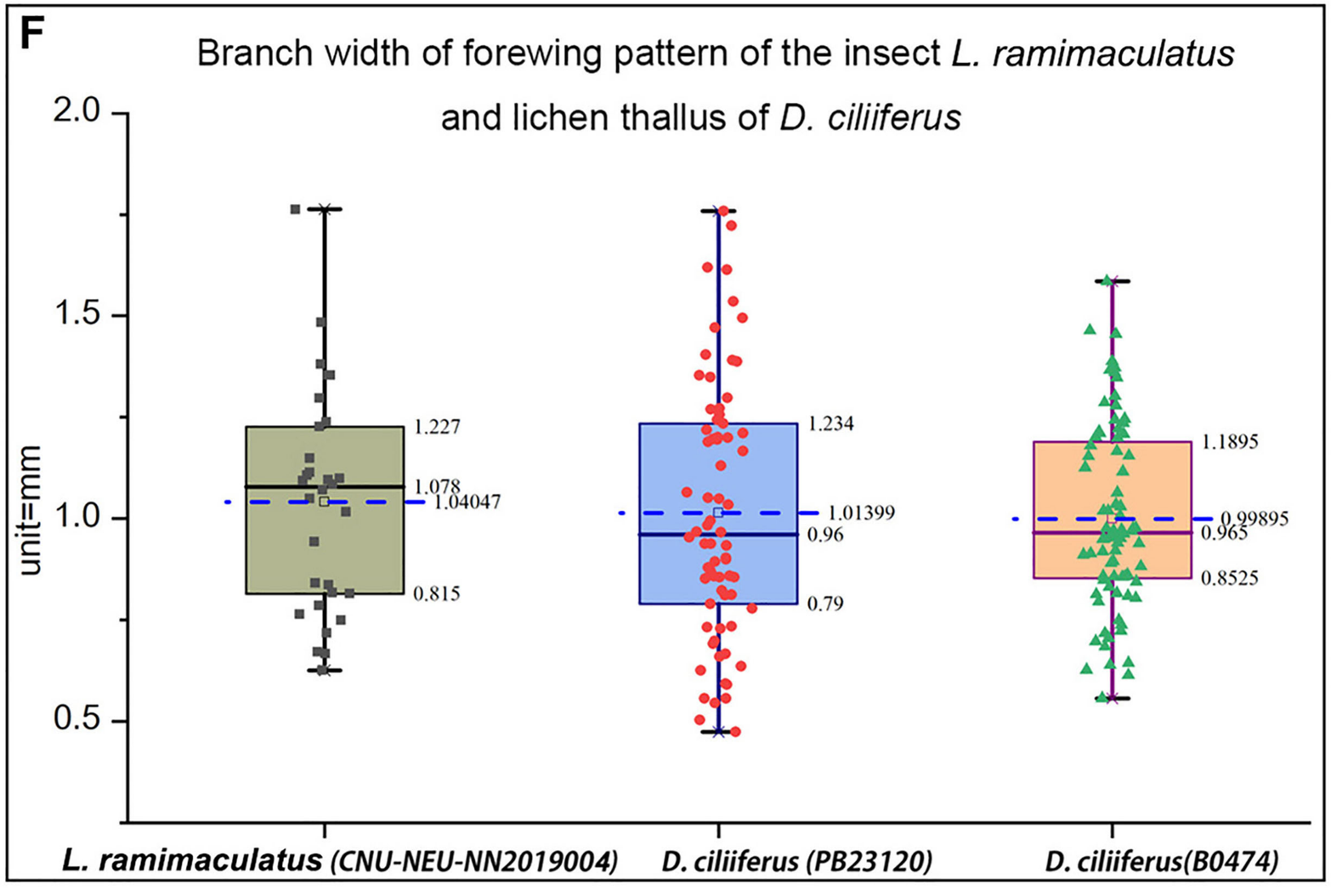
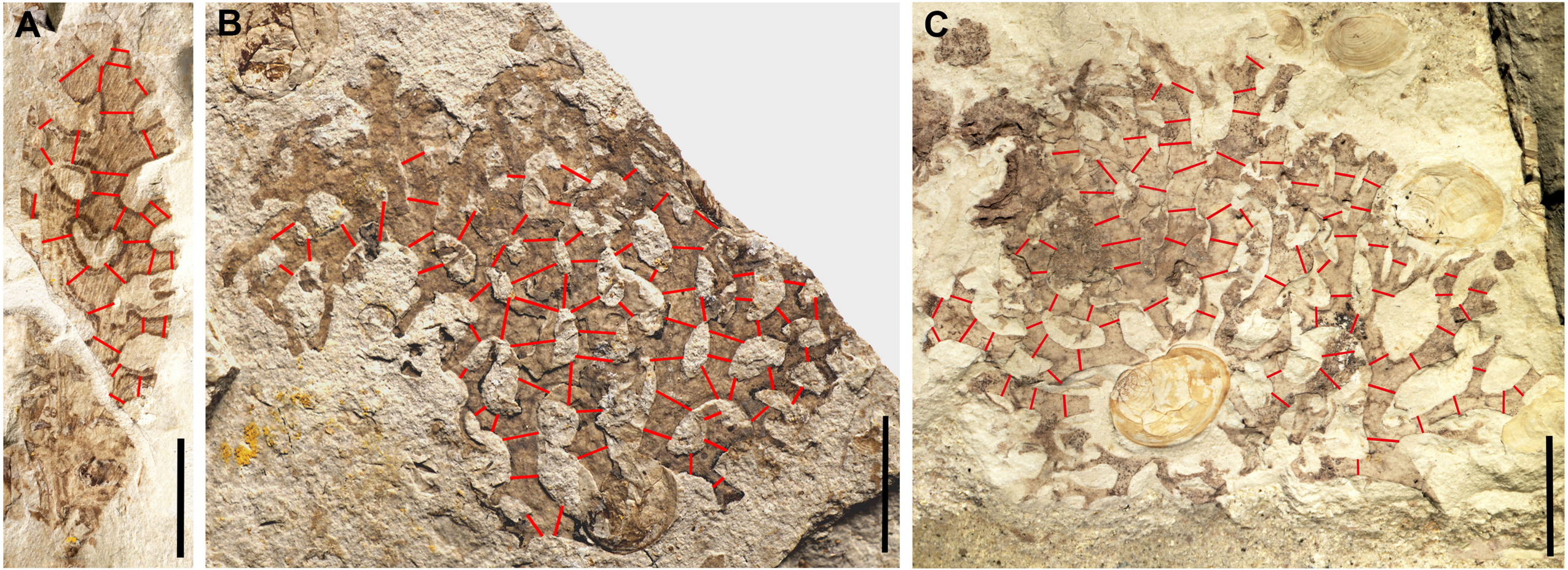
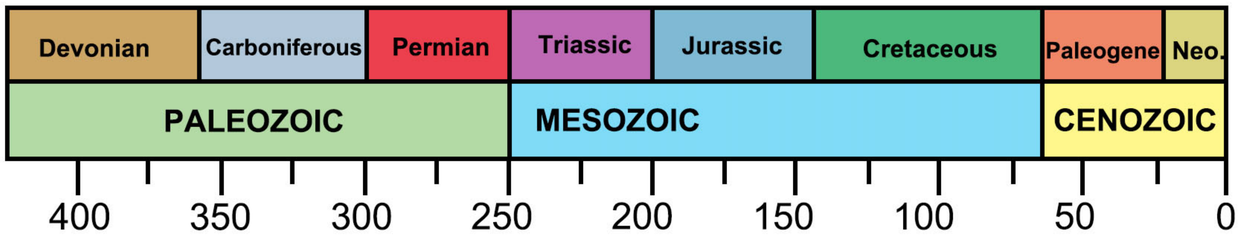

Branch width of forewing pattern of the insect L. ramimaculatus
and lichen thallus of D. ciliiferus
unit=mm
2.0
1.5
1.0
0.5
1.227
1.078
1.04047
0.815
1.234
1.01399
0.96
0.79
1.1895
0.99895
0.965
0.8525
L. ramimaculatus (CNU-NEU-NN2019004)
D. ciliiferus (PB23120)
D. ciliiferus(B0474)

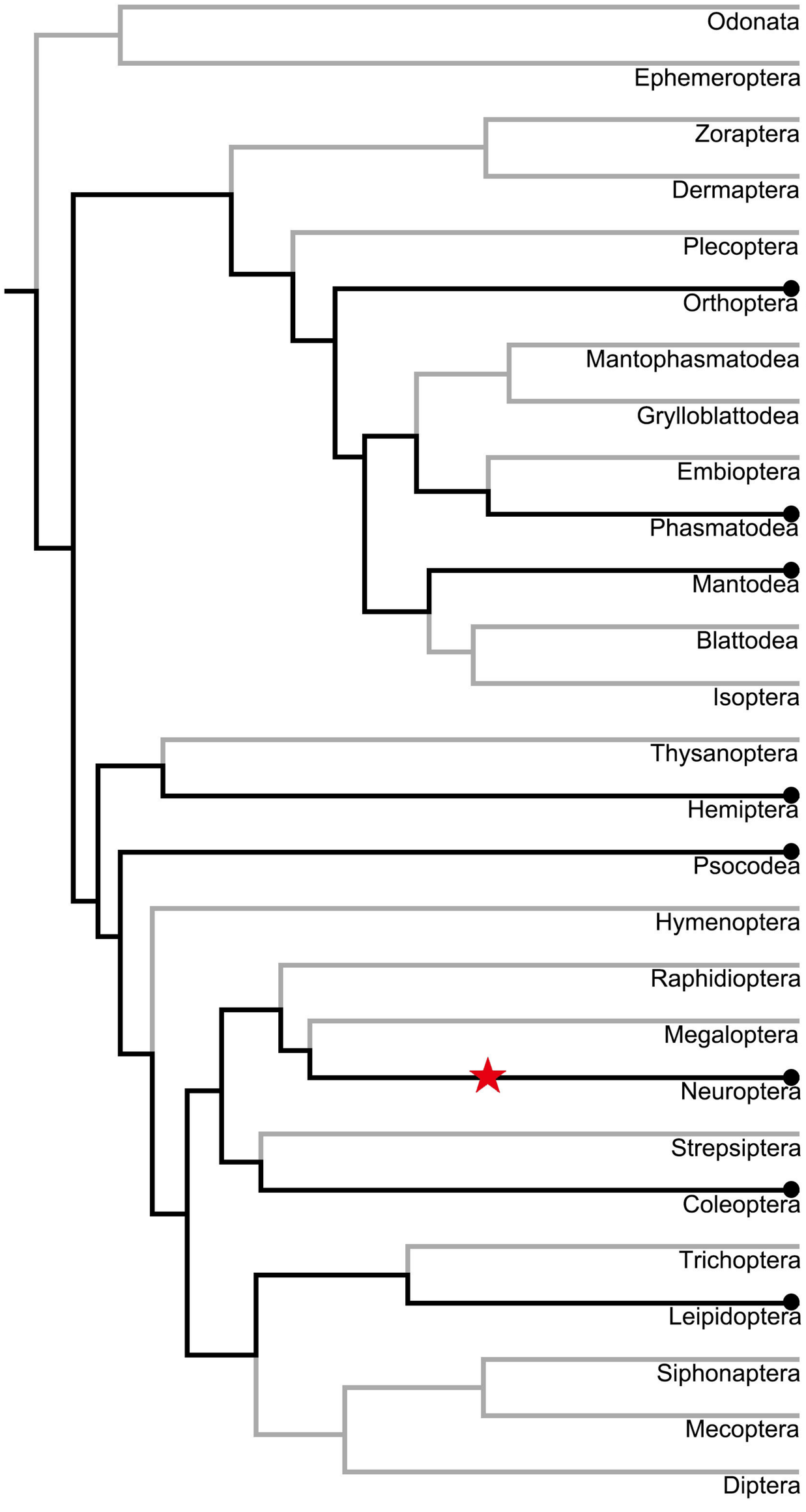
G

H

I


A
B
C




Grasshoppers and katydids:

*Leuronotina, Lichenodraculus, Lichenagraecia* etc.

Stick insects:

*Extatosoma, Pseudodiacantha, Onchestus* etc.

Mantids:

*Gonatista*

Bugs:

*Phytocoris*

Psocids:

*Trichadenotecnum*

Lacewing larvae and adults:

debris-carrying *Leucochrysa* and *Ceraeochrysa*,

fossil *Lichenpolystoechotes*

Beetles and weevils:

*Pristoderus, Synaphaeta, Pissodes*

Moth larvae and adults:

*Catocala, Macrurocampa, Leuconycta, Griposia* etc.