Report

Current Biology

# Early evolution of wing scales prior to the rise of moths and butterflies

## Highlights

- Lepidochlamidae fam. nov is the most basal lineage of Trichoptera with scales
- Support the Tarachoptera as a monophyletic group at the base of Amphiesmenoptera
- Scales are a monophyletic origin in the common ancestors of Endymenoptera
- Scales lost in Eutrichoptera, but evolved and further developed in moths and butterflies

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## In brief

Lepidochlamidae of Trichoptera and Tarachoptera in the mid-Cretaceous (99 Ma) have small and angustifoliate scales. Based on phylogenetic and morphometric analyses, Wang et al. suggest that scales are the ancestral state in Endymenoptera, followed by a major loss in Eutrichoptera and developed in moths and butterflies respectively.

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# Early evolution of wing scales prior to the rise of moths and butterflies

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## SUMMARY

Although scales are a defining and conspicuous feature of moths and butterflies (Lepidoptera),[1–3] their earliest evolution predates the group but is shrouded by a dearth of fossil evidence. Herein, we report two new species in mid-Cretaceous Kachin amber, representing lineages closely related to Lepidoptera: one represents the extinct Tarachoptera, with dense scales on the fore- and hindwings, while the other is an early lineage of caddisflies, with a hindwing covered by a single layer of angustifoliate scales. A novel phylogenetic analysis of 174 morphological characters and 73 extant and fossil representatives of Mecopterida demonstrates a monophyletic origin of scales in the common ancestor of Tarachoptera, Trichoptera, and Lepidoptera; that Tarachoptera are monophyletic but their scale morphology is plesiomorphic for the whole group; and that scales were lost early in caddisfly evolution before reappearing multiple times within the clade. Collectively, these fossils provide clarity into the origin and early evolution of scales before their diversification among the moths and butterflies.

## RESULTS

Butterflies and moths (order Lepidoptera) are famed for the often-stunning patterns of their wings, the result of a fine covering of scales, from which the order gets its name: *lepís* in Ancient Greek, meaning "scales." Although most often thought of in the context of wings, scales are not confined to the wings and typically cover the entire insect body from the antennae to the tip of the abdomen, and sometimes even elements of the genitalia. The scales are modified setae, effectively enlarged macrotrichia, which are socketed at their bases via short stalks and have an expanded bladelike surface composed of upper and lower lamina. The lower lamina is mostly smooth; the upper lamina has a complex lattice composed of primary longitudinal ridges interconnected by cross-ribbings. The scales give the organisms their coloration and serve a variety of functions ranging from thermoregulation and aerodynamics to increasing sensory space and communication.[1–8] The scales of Lepidoptera are one of their defining features and have been hypothesized to have been critical to the success of these insects.[1] Yet scales are not confined to Lepidoptera. Indeed, scales have evolved numerous times among various insects and can be found on springtails, silverfish, book lice, beetles, flies, and many other lineages.[9] While these groups are quite distantly related to Lepidoptera, some close relatives may also possess scales. Lepidoptera, along with their sister order Trichoptera (caddisflies)[10,11] and the extinct lineage Tarachoptera,[12,13] form the monophyletic superorder Amphiesmenoptera. Scales may at times be found in all three amphiesmenopteran groups, but the structures of the latter two differ markedly from those of Lepidoptera, suggesting that their scales either evolved independently or represent an early form prior to the appearance of the characteristic scales of moths and butterflies.[7,10,11]

The earliest fossil records of decidedly lepidopteran scales are isolated scales recovered from the Upper Triassic sediments of Germany.[14] These isolated scales predate the early fossils of moth wings, completed with their scales, from the Lower Jurassic of Germany and England[15–17] and the Upper Jurassic of Kazakhstan.[18] The morphological features of these scales are quite similar to those of the scales of extant Lepidoptera and therefore provide little insight into the early evolution of the scales.

The fossil record of scales in Tarachoptera and Trichoptera offers an opportunity to explore scale morphological evolution beyond Lepidoptera. Herein, we report a new species of Tarachoptera with dense scales on the fore- and hindwings and a new basal family of Trichoptera with a single layer of scales on the hindwings, both persevered in mid-Cretaceous Kachin amber. Based on the results of a phylogenetic analysis, using morphological characters of extant and fossil Amphiesmenoptera and the two new taxa, we reconstruct the early evolutionary history of scales for this iconic clade of insects.

### Systematic paleontology

Trichoptera Kirby, 1815

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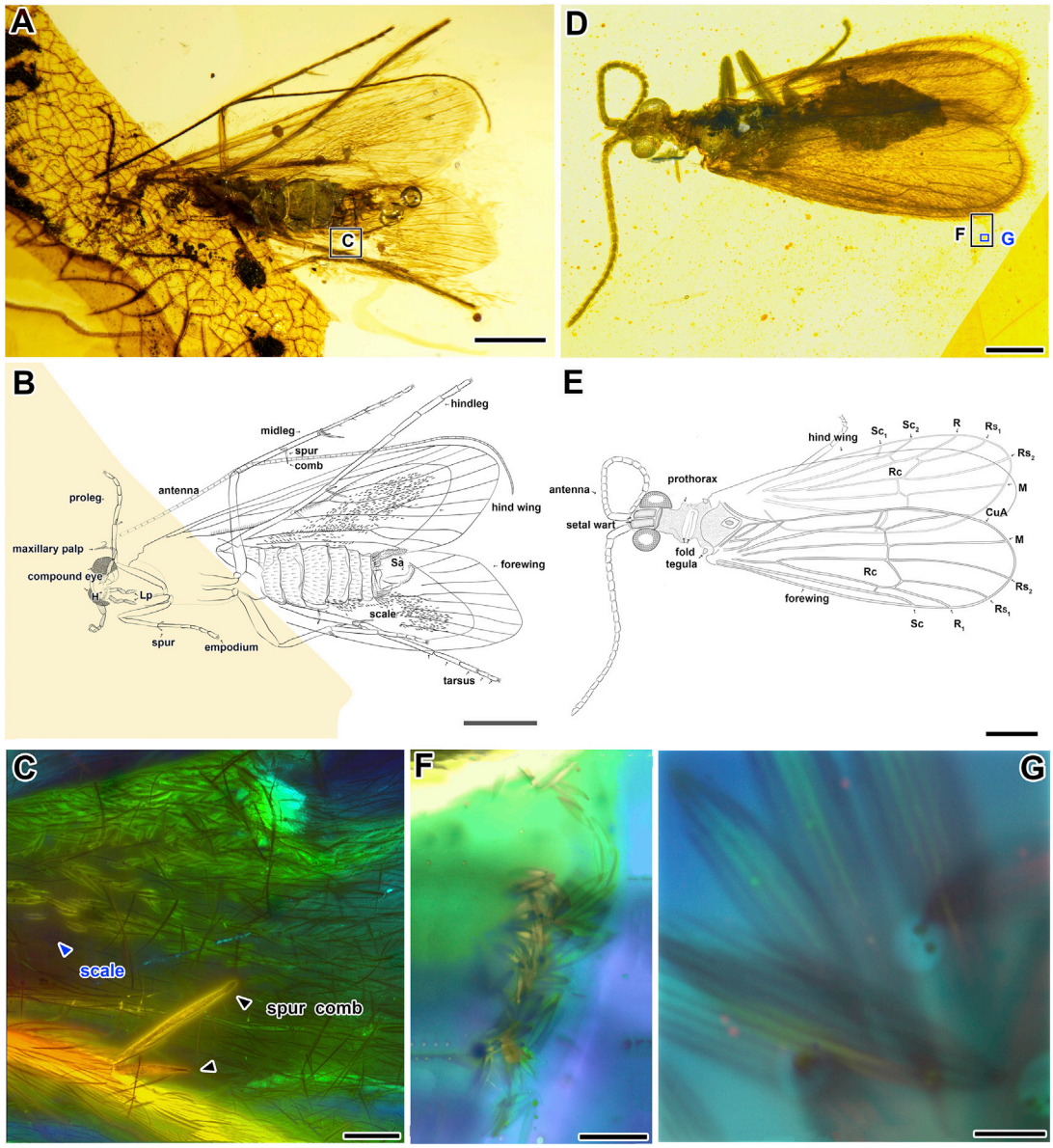


**Figure 1. Two specimens covered with scales in Burmese amber**

(A–C) *Lepidochlamus nodosa* gen. et sp. nov. holotype, CNU-TRI-MA-2015501, male.
(A) Specimen in ventral view.
(B) Line drawing of specimen in (A), in ventral view.
(C) Scales (blue arrow) covering the hindwing and combs (black arrows) at the tip of the spurs, under confocal laser-scanning microscopy (10×).
(D–G) *Kinitocelis dashengi* sp. nov. holotype, CNU-TAR-MA-2015502, male.
(D) Specimen in dorsal view.
(E) Line drawing of entire insect in (D), in dorsal view.
(F) Scales near forewing in (D), under confocal laser-scanning microscopy (20×).
(G) Microphotograph of the scales near forewing in (D) (40×).
Lp, labial palp; H, haustellum; Rc, radial cell; Sa, superior appendage. Scale bars represent 1,000 μm (A and B), 100 μm (C), 500 μm (D and E), 50 μm (F), and 15 μm (G). See also Figures S1 and S2.

Lepidochlamidae Wang, Engel, Shih, and Ren fam. nov.
Type genus: *Lepidochlamus* gen. nov. (Figures 1A, 1B, and S1)
Type species: *Lepidochlamus nodosa* gen. et sp. nov. (Figures 1A, 1B, and S1)

**Brief diagnosis (family, genus, and species)**

Antenna longer than forewing; maxillary palpus pentamerous, maxillary palpomere V longest, not annulated, shorter than combined lengths of preceding four palpomeres. Forewing with forks I, III, and V present; most cross-veins absent. Upper side of

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hindwing covered with a single layer of angustifoliate scales. Tibial spur formula 2-4-4.

### Etymology

The generic name is a combination of the Ancient Greek *lepídos* (λεπίδος, genitive of *lepís*, meaning "scale") and *khlamús* (χλαμύς, meaning "cloak" or "robe"), referring to the covering of scales on hindwings (gender: feminine). The specific epithet is taken from the Latin *nōdōsus*, meaning "knotty," referring to the shape of the antenna.

See Methods S1 for complete descriptions of Lepidochlamidae fam. nov. and *Lepidochlamus nodosa* gen. et sp. nov.

Tarachoptera Mey, Wichard, Müller, and Wang, 2017

*Kinitocelis dashengi* Wang, Engel, Shih, and Ren sp. nov. (Figures 1D, 1E, and S2)

### Brief diagnosis

Dense scales with uniform coloration on fore- and hindwings. Forewing Sc not forked; 1A and 2A fused and Y-shaped but not fused with 3A. Hindwing Sc forked. Dorsal plate IX of male terminalia nearly quadrangular.

### Etymology

The specific epithet is derived from "Dasheng," the title of the Monkey King, one of the famous heroes of classical Chinese literature. The curved antenna of the new species is similar to the long and curved feathers on the helmet of Dasheng.

See Methods S1 for a complete description of *Kinitocelis dashengi* sp. nov.

### Phylogenetic analysis of Amphiesmenoptera

A new morphological character matrix for the Amphiesmenoptera was set up in order to explore relationships of the extant and fossil Amphiesmenoptera. Fourteen fossil taxa and 59 extant taxa of this superorder were included in the data matrix and the family Osmylidae (Neuroptera) employed as an outgroup. Aside from the fossil taxa included, we specifically selected extant groups that are key families for understanding the morphological evolution and diversification within Mecopterida, especially the evolution of scales within Amphiesmenoptera. The results of our phylogenetic analysis of 174 morphological characters suggest that both Protomeroptera and Tarachoptera are monophyletic and positioned as progressively earlier diverging lineages of Amphiesmenoptera, consistent with the morphological classifications of earlier authors.[12,19] Protomeroptera are sister to Tarachoptera + Trichoptera + Lepidoptera (=Mirorder Endymenoptera Engel), and Tarachoptera are sister to Trichoptera + Lepidoptera (=Epiorder Stelloptera Engel). Lepidochlamidae are the earliest diverging Trichoptera with moderate support. Other extinct trichopteran families belong to Integripalpia. Eolepidopterigidae and Mesokristenseniidae are early-diverging lepidopteran taxa. Ascololepidopterigidae seem to be accommodated in Glossata and closely related to Neopseustidae (Figure 2).

See supplemental information for complete phylogenetic analysis of Amphiesmenoptera.

## DISCUSSION

### Morphological implications of scales

The results of our phylogenetic analysis indicate that Lepidochlamidae, whose hindwings are covered by scales, are the sister group to all other caddisflies (Eutrichoptera Wang, Engel, Shih, and Ren). *Lepidochlamus nodosa* has single-layered, mono-colored scales covering the hindwings. The scales of *L. nodosa* are relatively small, about 50–60 μm long, and angustifoliate with a sharp apex (Figures 3A–3C, 4B, S1C, S3K, and S3L). The number of ridges on these scales is about 6–8, but there is no cross-ribbing or herring-bone patterns between the ridges. The scales are stipitate, and the base of each scale is well situated in a socket (Figures 3B, S1C, S3J, and S3K).

Few species of extant Trichoptera (such as some species of Lepidostomatidae, Limnephilidae, Hydroptilidae, Glossosomatidae, etc.) possess scales, but when they do, these scales are restricted to the forewings.[10,11] The shapes of scales of extant Trichoptera are quite variable, ranging from wide (Lepidostomatidae) to strap-like (Glossosomatidae), but all have a rounded rectangular apex and are therefore markedly different from those observed in Lepidochlamidae. It is likely that the scales of Lepidochlamidae are plesiomorphic and that the sporadic distribution of scales among extant trichopteran lineages along with their variable forms indicate that those of extant Trichoptera are independently derived. However, the similarity of lepidochlamid scales with those of Tarachoptera indicates that these forms are likely symplesiomorphic for Endymenoptera (i.e., all Amphiesmenoptera excluding Protomeroptera).

The scales of Tarachoptera (Figures 3D–3F, 4A, and S3A–S3I) are quite different from those of Lepidoptera,[12,13] as they are angustifoliate, about 40–70 μm long, and all of the ridges end at the terminus of the scale (Figures 3E, 3F, 4A, and S3A–S3I). The number of ridges ranges from 3 to 12 (Figures 3E, 3F, and S3A–S3I), and there is no cross-ribbing or herring-bone pattern between the ridges, just as is the case in Lepidochlamidae. Previous studies have not implicated scales in the early evolution of the Trichoptera. The presence of a single layer of scales on the hindwings of Lepidochlamidae, the basal-most lineage of Trichoptera, greatly expands our understanding of the early evolution of caddisflies, as well as their loss and subsequent reacquisition of scales. The scales of Lepidochlamidae are similar to those of Tarachoptera rather than Lepidoptera or any of those found occasionally in extant Trichoptera. The scales of Lepidochlamidae and Tarachoptera share the relatively small size, the angustifoliate shape with a sharp apical end (Figures 3A–3F, 4A, 4B, and S3A–S3L), the smaller number of ridges, and the absence of cross-ribbing or herring-bone patterns between the primary ridges. These features are certainly plesiomorphic between Tarachoptera and Lepidochlamidae, suggesting that a potentially more basal clade originally possessed such scales.

The scales of Lepidoptera are considerably different from those of Lepidochlamidae and Tarachoptera.[20,21] Seven different shapes of scales have been reported in early micropterigid moths (Figures 3G–3I and 4C in this paper and Figure 3D in Zhang et al.[22]), the basal-most lineage of extant Lepidoptera. Most of the scales (cover scales and ground scales) are flat and blunt (Figures 3G–3I, 4C, and S3M–S3O), and few scales are angustifoliate and seta-like (Figures 3I and 4C; Table S1). In addition, the

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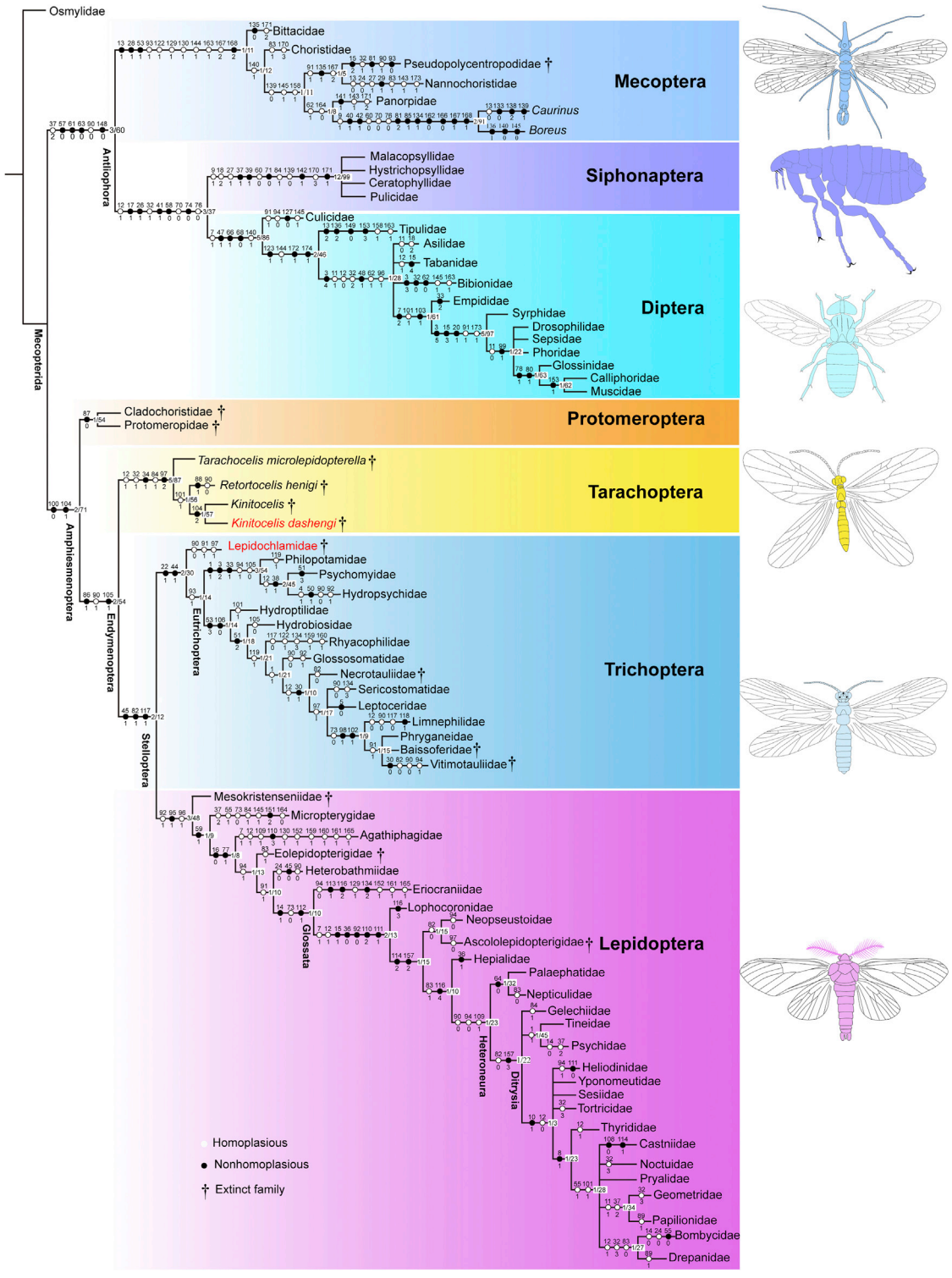


**Figure 2. Recovered topology from phylogenetic analysis, with characters and their states mapped by TNT Version 1.5**

(●) indicates unique character changes; (○) indicates parallelisms or reversals. The numbers above circles are characters; the numbers below the circles are character states. The numbers at the branch points are Bremer support values (front) and Bootstrap support values (back).

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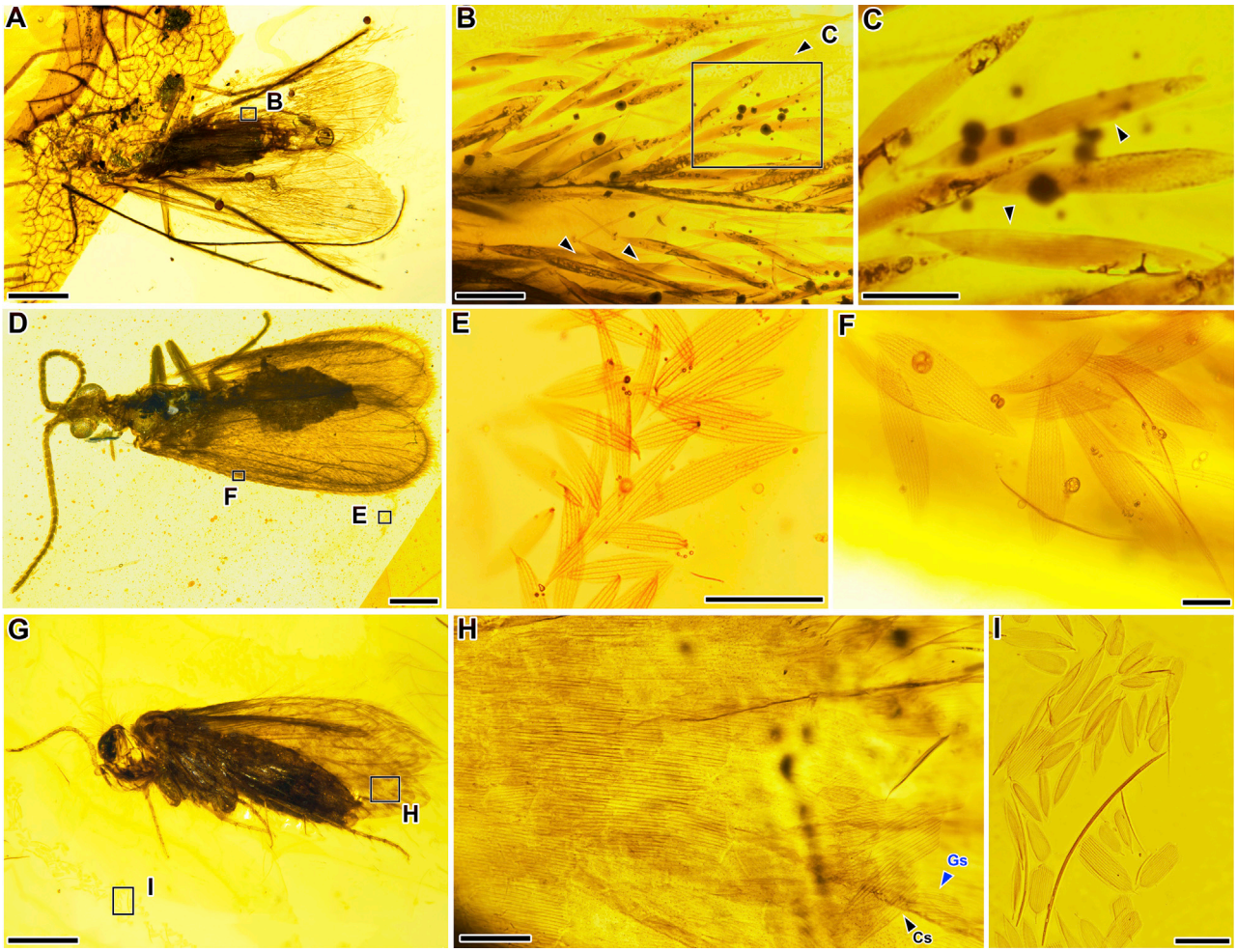


**Figure 3. The scales in different amphiesmenopteran orders**

(A) Specimen of *Lepidochlamus nodosa* gen. et sp. nov. in Lepidochlamidae fam. nov.
(B) Scales covering the hindwing in (A).
(C) Detail characters of scales in (B) (black arrows present the clear ridges on the scales).
(D) Specimen of *Kinitocelis dashengi* sp. nov. in Tarachoptera.
(E) Scattered scales away from the wing in (D).
(F) Scales covering the forewing in (D).
(G) Specimen of the Micropterigidae, using the scale of new specimen present the state in Lepidoptera.
(H) Details of scales covering the forewing in (G). Black arrow indicates Cs (cover scales) and blue arrow indicates Gs (ground scales).
(I) Scattered scales away from the wing in (G).
Scale bars represent 1,000 μm (A), 50 μm (B, E, H, and I), 25 μm (C and F), and 500 μm (D and G). See also Figure S3 and S4.

scales are decorated with elongate primary ridging, with a herring-bone pattern or cross-ribbing between the ridges (Figure S4). These characteristic features were already present in the earliest lepidopteran scales reported from the Late Triassic.[14] Lepidoptera usually have a scale bilayer (i.e., ground scales and cover scales; Figure 3H). The apical margin of the scale is notched or blunt,[7] with the primary ridges extending beyond the apical margin of the scale,[22] and the flutes run down the longitudinal ridges.[23]

It now seems apparent that scales are a groundplan feature of the broader clade of Endymenoptera (Tarachoptera + Trichoptera + Lepidoptera). Long and slender scales with fewer ridges and the absence of cross-ribbing or herring-bone patterns represent the groundplan condition for the Amphiesmenoptera excluding Protomeroptera. This form of scale is indicative of all Amphiesmenoptera excluding Protomeroptera. Scales were then subsequently lost in the early evolution of Eutrichoptera, with various forms reappearing in different derived extant lineages. Scales of Lepidochlamidae are present only on the hindwings, indicating that scales were perhaps first lost in the forewings. Ultimately, in the Lepidoptera, scales achieved their most complex form and a coat of scales consisting of two distinct layers evolved: those forming a ground-covering layer and those overlapping this basal layer (Figure 4). These scales facilitated the evolution of a spectacular array of species, e.g., extant moths and butterflies, which display the intricate patterns and stunning colors that enchant researchers and amateurs alike.

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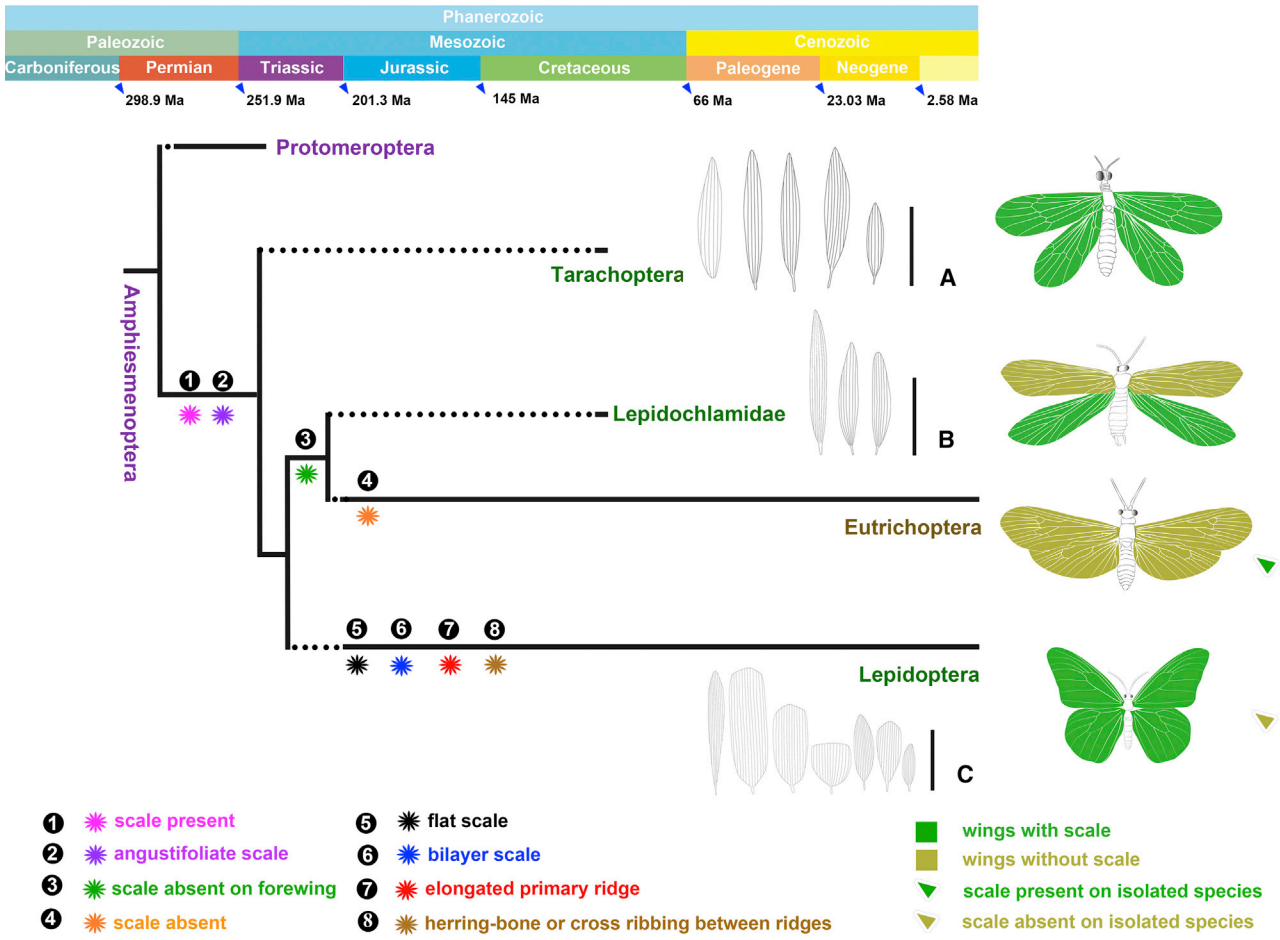


**Figure 4. The phylogeny of Amphiesmenoptera showing changes of the key characters of scales during the evolutionary history in Tarachoptera, Lepidochlamidae, and basal Lepidoptera**

This tree is simplified from the strict consensus recovered in present phylogenetic analysis. Solid lines indicate the known extent of the fossil records. The scale bars represent 50 μm (A–C).

## STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
  - Lead contact
  - Materials availability
  - Data and code availability
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
  - Optical microscopy, photography, and nomenlature
  - Confocal laser scanning microscopy
  - Phylogenetic analysis
- QUANTIFICATION AND STATISTICAL ANALYSIS

## SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2022.06.086.

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## AUTHOR CONTRIBUTIONS

D.R. designed the project; J.W., M.S.E., and D.R. performed the comparative and phylogenetic work; J.W. and X.S. collected the fossil data and took the pictures; J.W., M.S.E., and D.R. contributed to the phylogenetic analysis; J.W., C.S., and D.R. contributed to the discussion; and J.W., M.S.E., W.Z., C.S., and D.R. wrote and revised the manuscript and analyzed the results.

## DECLARATION OF INTERESTS

The authors declare no competing interests.

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## STAR★METHODS

### KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|---|---|---|
| Deposited data | | |
| Phylogenetic matrix | This paper | Supplemental information |
| Software and algorithms | | |
| TNT V. 1.5 | [24] | http://www.lillo.org.ar/phylogeny/tnt/ |

### RESOURCE AVAILABILITY

#### Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Dong Ren (rendong@mail.cnu.edu.cn).

#### Materials availability

Both the holotype of *Lepidochlamus nodosa* (CNU-TRI-MA-2015501) and *Kinitocelis dashengi* (CNU-TAR-MA-2015502) are housed in the College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University, China.

#### Data and code availability

All data used for analysis in this study are included in the Main text or the supplemental information of this published article. The newly proposed names are registered under the following doi numbers in ZooBank: Lepidochlamidae - urn:lsid:zoobank.org:act:804ECE46-5CE5-496C-AC75-08DC14D0F0A4; *Lepidochlamus* - urn:lsid:zoobank.org:act:B530E47E-DFA1-4AF2-BE7D-3E2DDA69E8BA; *Lepidochlamus nodosa* - urn:lsid:zoobank.org:act:143534EB-11D8-4258-ADF9-6EA803FF0900; *Kinitocelis dashengi* - urn:lsid:zoobank.org:act:5345CA73-6308-4842-A134-CCA60A26D8F0.

### EXPERIMENTAL MODEL AND SUBJECT DETAILS

Both the holotypes of *Lepidochlamus nodosa* (CNU-TRI-MA-2015501) and *Kinitocelis dashengi* (CNU-TAR-MA-2015502) were collected from mid-Cretaceous deposits in the Hukawng Valley, Tanai Township, Myitkyina District, Kachin State, north Myanmar approximately 100 km southwest of the Village of Tanai. All new specimens described herein were acquired by Mr Fangyuan Xia in 2015 and donated the amber specimens for this study in 2016, thus, in full ethical compliance for the study of Kachin amber.[25–27] The age of Kachin amber is dated by U-Pb to 98.79 ± 0.62 Mya, earliest Cenomanian, mid-Cretaceous.[28,29] Research on fossils preserved in Burmese amber has a long history, dating back more than a century. To date more than 1000 species of insects have been described from these deposits,[30] including beetles,[31] ants,[32] termites,[33] lacewing,[34] etc.

### METHOD DETAILS

#### Optical microscopy, photography, and nomenlature

The specimens were examined and photographed using Nikon SMZ 18 dissecting microscope with an attached Nikon DS-Ri2 digital camera system, and Nikon ECLIPSE Ni microscope with an attached Nikon DS-Ri2 digital camera system. In order to reduce the interference of the light, we fixed the specimen to the Blu-Tack and deposited it in glycerol. All the pictures were superimposed of Z-Stack. All the optical microscopes are in College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University, Beijing China.

#### Confocal laser scanning microscopy

We used a Zeiss LSM 780 Confocal laser scanning microscope (College of Life Sciences, Capital Normal University, Beijing, China) to observe and photograph detailed characters from the specimens. The laser wavelengths were 458 nm, 488 nm, 514 nm, with a green background. The specimens were stuck to the coverslip in an oil-free state. In order to acquire clear detailed characters, all specimens were controlled at about 0.5 mm. Because the specimen of *Lepidochlamus nodosa* is poorly preserved, with parts of the body preserved only as desclerotized integument, we used 3D textures and Depth Coding to get clearer pictures.

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### Phylogenetic analysis

The phylogenetic relationships of all the taxa were tested using a data matrix of published taxa and two new fossil species described in this paper. We chose 73 taxa and 174 characters (all taxa and characters are summarized in supplemental information: Morphological character descriptions), 93 characters from Beutel et al.,[35] 11 characters from Lambkin et al.,[36] and 70 newly identified and coded traits. The datasets were analyzed with Tree Analysis Using New Technology (TNT) version 1.5.[24] We used traditional search with tree bisection-reconnection (TBR) and 1,000 replicates, saving ten trees per replication. Bremer support values were obtained in the TNT V.1.5 using the 10,000 replicates. The analysis produced 27 equally parsimonious topologies of length 473 steps, and retention index (RI) and consistency index (CI) of 0.51 and 0.89, respectively. The Bootstrap values were evaluated by the Bootstrap algorithm with 100 replicates. The Bremer values were calculated using TNT version 1.5.[24] The morphological characters choosed for phylogenetic analysis and their descriptions are given in Methods S1. The dara matrix is shown in Data S1.

## QUANTIFICATION AND STATISTICAL ANALYSIS

The Phylogenetic analysis, which is described in detail under Method details, was performed using TNT V. 1.5.

**Current Biology, Volume *32***

## Supplemental Information

# Early evolution of wing scales prior to the rise of moths and butterflies

**Jiajia Wang, Weiting Zhang, Michael S. Engel, Xianyong Sheng, Chungkun Shih, and Dong Ren**

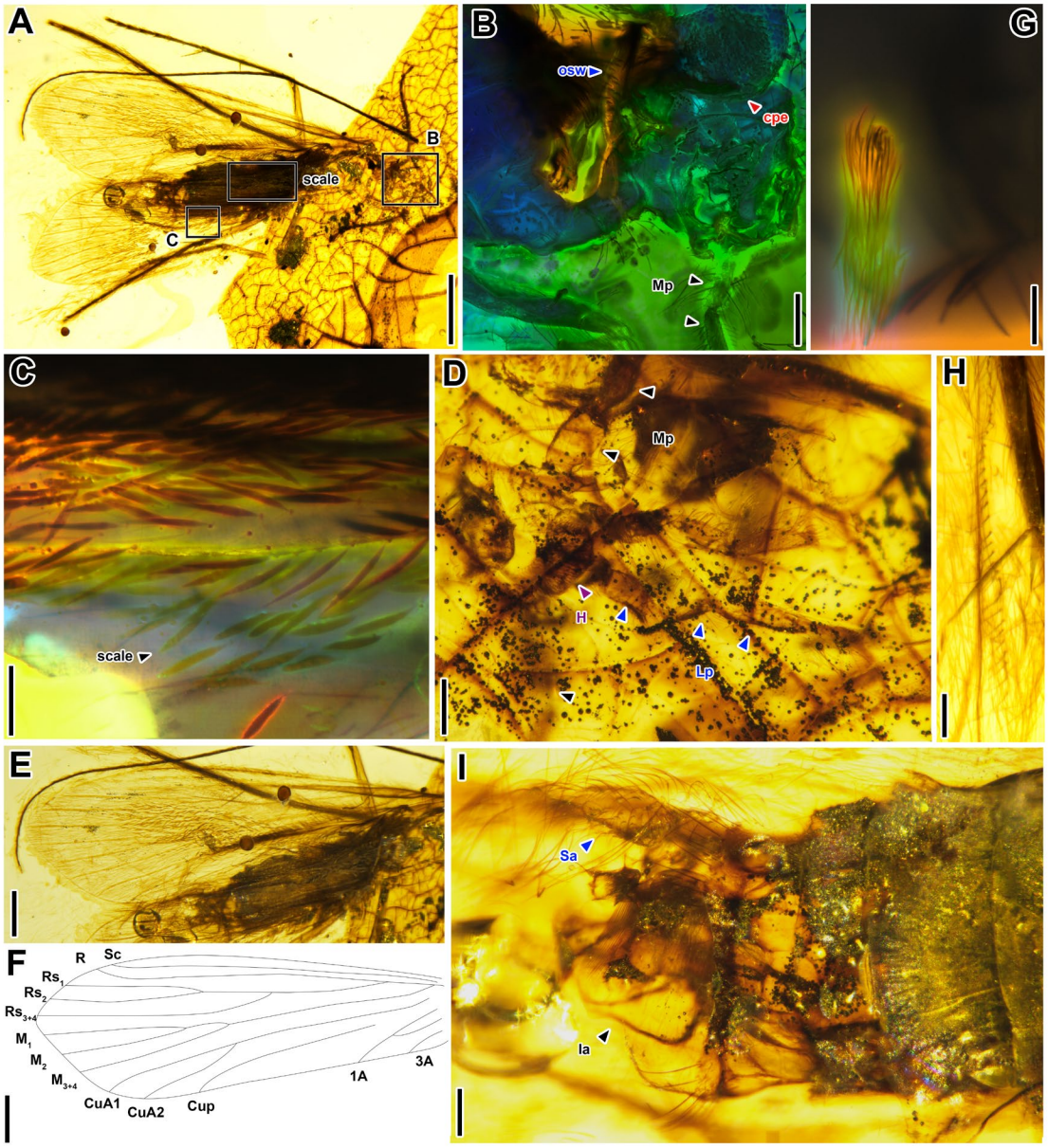


**Figure S1 | *Lepidochlamus nodosa* gen. et sp. nov. holotype, CNU-TRI-MA-2015501, male, related to Figure 1.** (A) Specimen in ventral view. (B) Microphotographs of the head, maxillary palpus (black arrow), compound eye (red arrow), occipital setal wart (blue arrow). (C) Microphotographs of scales from the other side of the amber at the location as marked in (A). (D) Mouthparts, maxillary palpus (black arrow), labial palpus (blue arrows) and the haustellum (purple arrow); Line drawing of forewing. (E) Forewing. (F) Line drawing of the forewing. (G) Pretarsi. (H) Coupling setae on hind wing. (I) Male genitalia (blue arrow showing superior appendage, black arrow showing the base of incompletely persevered inferior appendage), in ventral view. (B), (C) and (G) under confocal fluorescence.

Abbreviations are as follows: cpe, compound eye; osw, occipital setal wart; Mp, maxillary palpus; Lp, labial palp; H, haustellate; Sa, superior appendage; Ia, inferior appendage. Scale bars represent 1000 μm in A; 50 μm in B, C and D; 500 μm in E, F and G; 100 μm in H; and 200 μm in I.

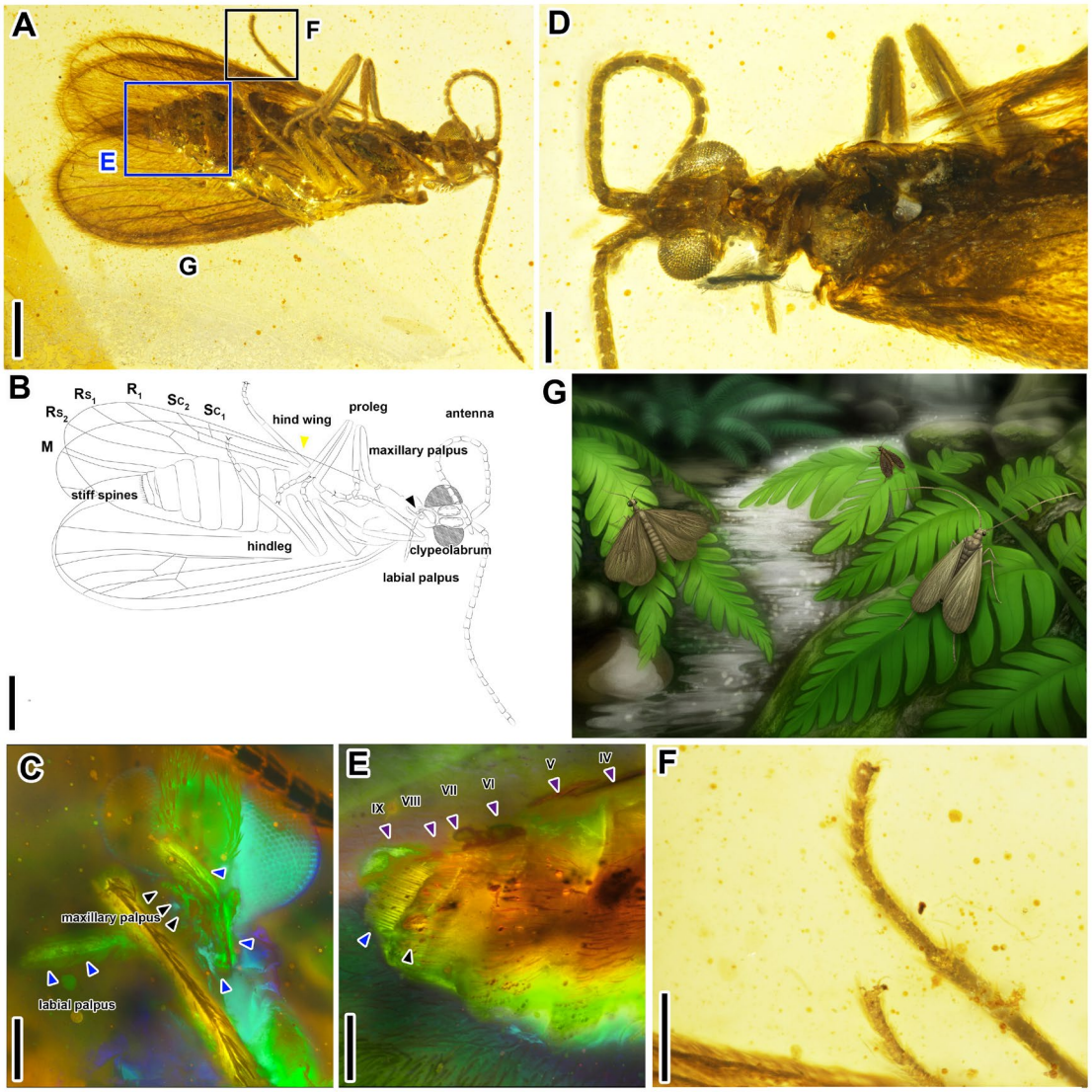


**Figure S2 | *Kinitocelis dashengi* sp. nov. holotype, CNU-TAR-MA-2015502, male, related to Figure 1.** (A) Specimen in ventral view. (B) Line drawing of *Kinitocelis dashengi* sp. nov. in (A), the yellow arrow shows the hind wing, in ventral view. (C) Mouthpart (black arrows show maxillary palpi and the blue arrows show the labial palpi), under confocal laser scanning microscopy, in ventral view. (D) Head and thorax. (E) Male genitalia (the blue arrow shows combs of stiff spines; the black arrow shows process from sternum VIII; the purple arrows show the sterna of IV–IX), under confocal laser scanning microscopy, in ventral view. (F) Tip of tarsomere V. (G) Ecological reconstruction of *Kinitocelis dashengi* sp. nov. in Tarachoptera (left), Micropterigidae Painted by Xiaoran Zuo. Scale bars represent 500 μm in (A) and (B); 200 μm in (C), (D) and (F); and 250 μm in (E).

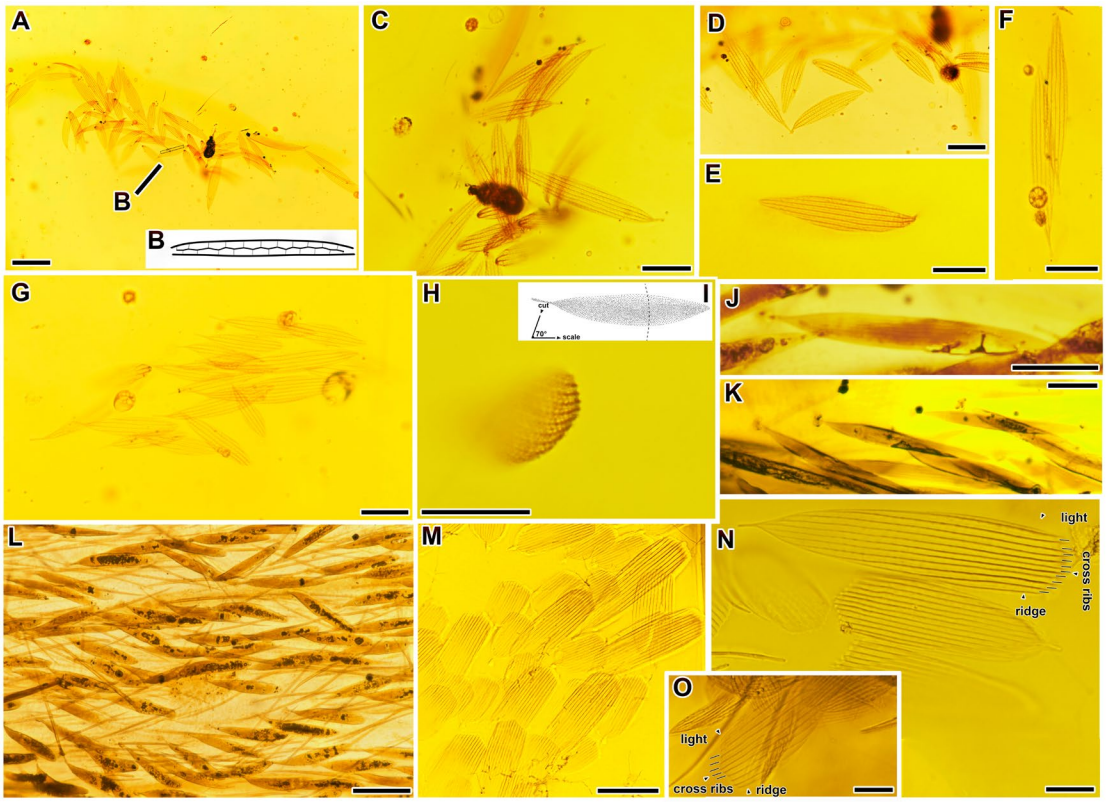


**Figure S3 | The additional figures of scales in different amphiesmenopteran orders, related to Figure 3.** (A)–(I) Scattered scales from the different view in *Kinitocelis dashengi* sp. nov.. (B) Line drawing of the scale, showing the detailed characters between ridges in (A). (H) cross-section of a single scale, the location of the cross section is shown in (I). (J)–(L) The details of hind wing scales in *Lepidochlamus nodosa* gen. et sp. nov. in different views. (M)–(O) The details of the scales in Micropterigidae. Scale bars represent 500 μm in (A), (J) and (K); 250 μm in (B)–(I); and 200 μm in (L) and (M).

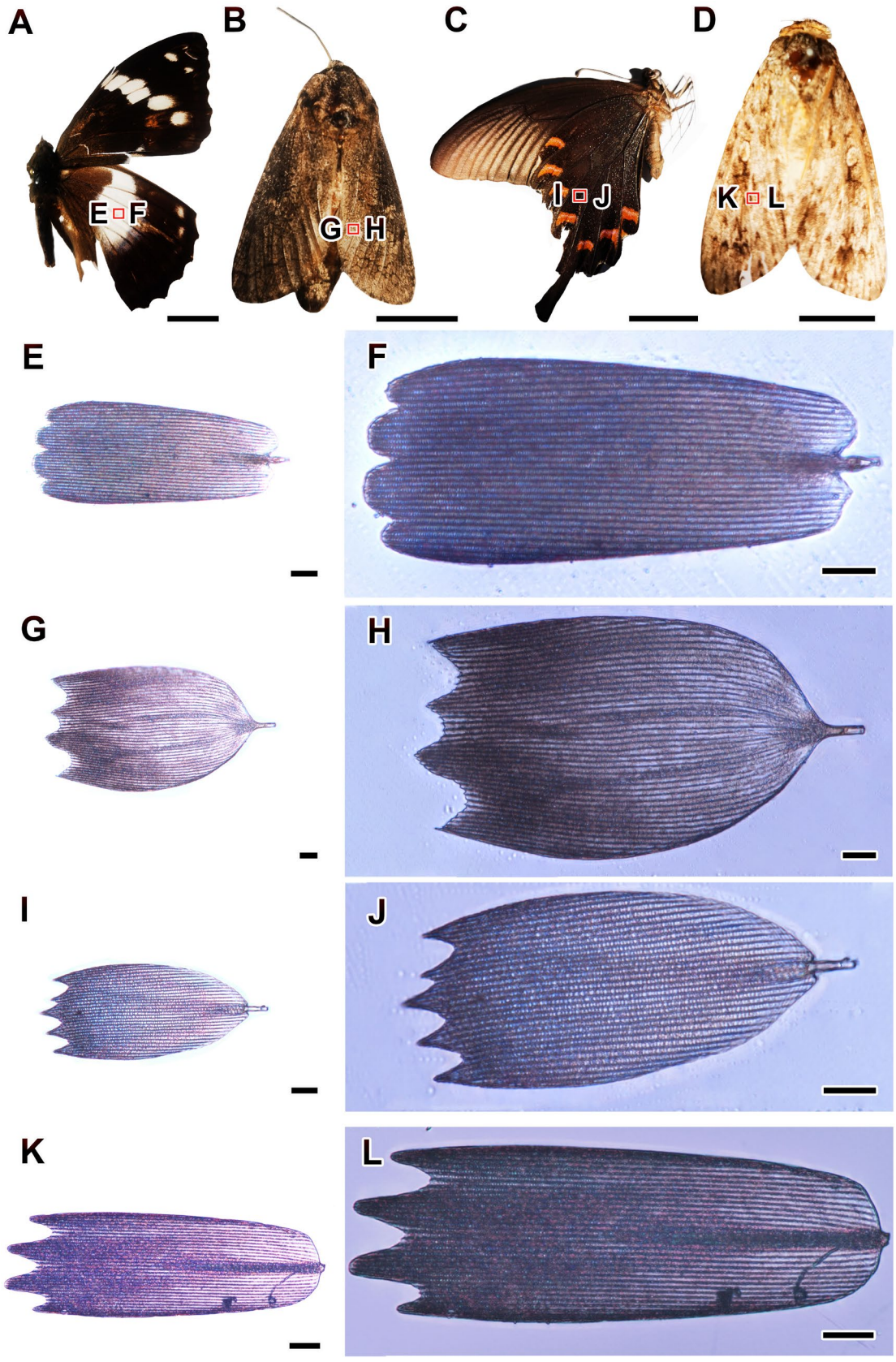


**Figure S4 | The extant lepidopteran specimens which offer the detailed figures of the scales, related to Figure 3.** (A), (E) and (F) Nymphalidae. (B), (G) and (H)

Noctuidae. (C), (I) and (J) Papilionidae. (D), (K) and (L) Notodontidae. Scale bars represent 1000 μm in (A)–(D). The scales under Nikon ECLIPSE Ni (×20 or ×40): (E), (G), (I) and (K) under the ×20; (F), (H), (J) and (L) under the ×40. Scale bars represent 20 μm in (E)–(L).

| Characteristics | Tarachoptera | Micropterigidae | | Lepidochlamidae | Derived Trichoptera |
|---|---|---|---|---|---|
| Types | Single layer | Bi-layer (Cs & Gs) | Fringed scale | Single layer | Single layer |
| Location | Fw & Hw | Fw & Hw | Margin of Fw & Hw | Hw | Fw |
| Size | 40–70 μm | >70 μm | >40 μm | 50–60 μm | |
| Morphology | One | Two | Two or more | One | One |
| Shape | Angustifoliate | Wide | Wide or piliform | Angustifoliate | |
| Apical margin | Sharp | Rounded or blunt | Rounded or blunt | Sharp | Rounded |
| Ridges | 3–13 | Most > 20 | >7 | 6–8 | |
| Elongated ridge | Absent | Present | Present | Absent | Absent |
| Bi-layer | Absent | Present | Present | Absent | Absent |
| Cross ridge | Absent | Present | Present | Absent | Absent |
| Herringbone pattern | Absent | Present | Present | Absent | Absent |
| Microribs | Absent | Present | Present | Absent | Absent |
| Structure | Solid | Soild | Soild | ? | Hollow |

**Table S1. The morphological and structural characteristics of scales in Tarachoptera, Micropterigidae, Lepidochlamidae fam. nov., and Eutrichoptera. Related to STAR Methods.**