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First fossil Eriocottidae discovered in Eocene Baltic amber (Insecta: Lepidoptera)

VALERIE NGÔ-MULLER[1], MICHAEL S. ENGEL[2-3], ANDRE NEL[4] & JACQUES NEL[5]

[1] *UFR Sciences du Vivant, Université Paris Diderot, Université de Paris, Paris, France. E-mail: valerie.ngo-muller@univ-paris-diderot.fr;* https://orcid.org/0000-0002-9456-6667

[2] *Division of Entomology, Natural History Museum, and Department of Ecology & Evolutionary Biology, 1501 Crestline Drive – Suite 140, University of Kansas, Lawrence, Kansas 66045, USA*

[3] *Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024, USA. E-mail:* msengel@ku.edu*; https://orcid.org/0000-0003-3067-077X*

[4] *Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, CP 50, 57 rue Cuvier, 75005 Paris, France. E-mail: anel@mnhn.fr; https://orcid.org/0000-0002-4241-7651*

[5] *78 Avenue Gassion, F-13600 La Ciotat, France. E-mail: lucienne.nel@orange.fr; https://orcid.org/0000-0002-9803-0018*

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Abstract

Eocompsoctena macroptera **gen. *et* sp. nov**., the first fossil eriocottid moth, is described from Baltic amber and attributed to the Compsocteninae. Comparisons are provided with the related families Dryadaulidae, Meessiidae, Psychidae, and Tineidae. The new species confirms the antiquity of 'Tineoidea' grade diversification. The putative Gondwanan origin of Eriocottidae is discussed.

Key words: *Eocompsoctena macroptera* gen. *et* sp. nov., fossil, Tineoidea.

Introduction

The moth superfamily Tineoidea (= Tineidae, Eriocottidae, Acrolophidae, and Psychidae, *sensu* Robinson & Nielsen 1993) has been recently re-evaluated by Regier *et al.* (2015). These latter authors considered them as a grade of ditrysian moths as the base of the clade — (Meessiidae + (Psychidae + ((Eriocottidae + Dryadaulidae) + (Tineidae + 'other Ditrysia')))) — and also reclassified the Acrolophidae as a tineid subfamily. Kawahara *et al.* (2019) also recovered the same group of families as a grade basal among the Ditrysia and hypothesized that they originated during the 'mid'-Cretaceous and began to diversify during the Late Cretaceous. Fossil Tineidae and Meessiidae are found relatively frequently compared to other Lepidoptera, especially in Eocene Baltic amber and Miocene Dominican amber, although those from the Baltic are in need of careful revision (Kuznezov 1941; Skalski 1977; Kozlov 1987; Grimaldi & Engel 2005; Sohn *et al*. 2012). By contrast, the record of Psychidae is confined to a single adult and several larvae or larval cases, the latter showing sufficient diagnostic features to permit accurate attribution to particular subfamilies (Heer 1849; Menge 1856; Cockerell 1926; Rebel 1934; Lewis 1976; Kozlov 1988; Weitschat & Wichard 1998; Perkovsky *et al.* 2003; Nuorteva & Kinnunen 2008; Weitschat 2009; Sobczyk & Kobbert 2009; Sohn *et al*. 2012). *Adelopsyche frustrans* Cockerell, 1926, the unique putative adult psychid moth, is based on a rather well-preserved specimen from the Eocene-Oligocene boundary of Colorado, USA (UCM IP 15880, Florissant Fossil Bed National Museum, Florissant). Unfortunately, only the forewing venation is available, rendering its attribution to Psychidae tenuous. The fossil record of Dryadaulidae is similarly scant and restricted to an undescribed species in Miocene amber of the Dominican Republic (Kristensen & Skalski 1998). Of the remaining tineoid family, the Eriocottidae, there has hitherto been no available fossil occurrences.

Herein we describe the first adult fossil of Eriocottidae, from an adult preserved in Eocene Baltic amber, and conserved in the historical collection of amber of the Muséum national d'Histoire naturelle, Paris. We provide a comparison between this fossil and other tineoid families and provide comments on the implications of this fossil for understanding the groups' evolution. The discovery of a fossil for this family will also help to refine diversification estimates for the "Tineoidea" in future analyses.

Material and methods

The specimen is embedded in a small clear piece of amber together with two Acari, a worker of Formicidae, a Collembola, and an Aphididae. It has been prepared using a diamond disk or polished with a grinder polisher (Buehler EcoMet 30) by using a very thin silicon carbide sanding paper (grit size = 7000). The specimen was examined using a Nikon binocular microscope SMZ 1500 or a Leica MZ APO stereomicroscope. Photographs were taken with a Nikon camera D800 and a Canon 5D Mark II camera, and were digitally stacked photomicrographic composites of several individual focal planes, which were obtained using HeliconFocus. The figures were composed with Adobe Illustrator and Photoshop softwares.

We follow the morphological terminology of Arnscheid & Weidlich (2017) except with proper annotation for wing veins and using the following anatomical abbreviations: Sc - subcostal vein; R - radial vein, with branches R1, R2, R3, R4, R5; M - median vein, with branches M1, M2; ac - accessory cell; dc - discoidal cell; ic - intercalary cell; Cu – cubital vein, with branches Cu1, Cu2; CuP - cubitus posterior; A – anal vein, with branches A1, A2.

Systematic palaeontology

Order Lepidoptera Linnaeus, 1758

Superfamily "Tineoidea" Latreille, 1810

Family Eriocottidae Spuler, 1898

Subfamily Compsocteninae Dierl, 1970

Genus *Eocompsoctena* **gen. nov.**

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Type species. *Eocompsoctena macroptera* **sp**. **nov**.

Etymology. The new genus-group name is a combination of the prefix from Eocene and the generic name *Compsoctena* Zeller, 1852, type genus of the subfamily. The gender of the name is considered to be feminine.

Diagnosis. i) ocelli absent; ii) pecten on scape; iii) proboscis short, uncoiled and serrate; iv) maxillary palpus as long as proboscis and first labial palpomere; v) labial palpus with three palpomeres and ventral scale brush, third palpomere as long as second palpomere, longer than first palpomere; vi) ten veins arising separately from discal cell, all simple; vii) ac and ic present; viii) CuP elongate, surpassing level of discal cell apex, but not reaching wing margin; ix) hind wing ic present, shorter than that of forewing, x) six simple veins arising separately from discal cell; xi) epiphysis quite slender, arising from proximal half of tibia and extending beyond distal end of tibia; xii) tibial spur formula 0-1-2.

Eocompsoctena macroptera **sp. nov.**

(Figs 1–5)

Zoobank xxxx

Etymology. The specific epithet refers to the macropterous condition of the holotype's wings.

Material. Holotype MNHN.F.A71340 (a complete female), conserved in the Muséum national d'Histoire naturelle, Paris, France.

Age and outcrop. Eocene Baltic amber, exact country of origin unknown (historical collection at the MNHN).

Diagnosis. As for the genus (*vide supra*), with the following addition: macropterous female; forewing apparently with a darker zone along anterior margin and a light brown zone along vein CuP.

Description. Female. Head (fig. 2): frons bulged with erect scales; ocelli absent; antenna filiform, extending to a point slightly distal to half of forewing costa, with tufts of long thin setae on each flagellomere, a pecten present on scape with six long setae; proboscis as long as maxillary palpus but distinct, uncoiled and serrate; maxillary palpus with probably three (?) palpomeres, as long as proboscis and first labial palpomere; labial palpus with three palpomeres, first and second palpomeres with a ventral scale brush, third palpomere as long as second palpomere, longer than first palpomere. Forewing (figs 3–4) 7.6 mm long, 2.7 mm wide. Apparently dark blackish brown, possibly with microtrichia, ten veins arising from discal cell, all simple, with only R4 and R5 with common point of origin but lacking a combined stem (i.e., no R4+5), and all other veins well separated basally; R5 terminating on termen; ac and ic present, ic longer than ac; CuP distally effaced, not reaching posterior wing margin, but quite elongate, surpassing level of discal cell apex; anal veins beyond anal loop fused into A1+2; fringe not preserved.

Hind wing ca. 6.1 mm long, 2.8 mm wide, with six veins originating from discal cell, all simple and well separated basally; ic present; fringe not preserved; frenulum not visible.

Epiphysis quite slender, arising from proximal half of tibia and extending beyond distal end of tibia (fig. 5); meso- and metatibiae with one and two pairs of spurs, respectively; tarsomeres spinose.

Abdomen with possibly telescopic ovipositor, with anal tuft made up of long piliform scales (probably used to emit pheromones to attract males).

Discussion

The wing venation of *Eocompsoctena* **gen. nov**. is quite similar to those of some Psychidae of the subfamily Typhoniinae. Within ”Tineoidea”, Robinson & Nielsen (1993) argued that a group consisting of Eriocottidae, Acrolophidae, and Psychidae is ‘strongly supported’ by seven synapomorphies: i) bipectinate antennae in the male (unknown in *Eocompsoctena* **gen**. **nov**.); ii) reduced or absent maxillary palpus (shared with *Eocompsoctena* **gen**. **nov**.); iii) vein R5 terminating on the forewing termen (shared with *Eocompsoctena* **gen**. **nov**.); iv) male retinaculum arising between Sc and costa; v) female frenulum with supernumerary bristles; vi) thorn-like sensilla at apex of male sacculus; and vii) male valve with basal pulvillus. *Eocompsoctena* **gen**. **nov**. also shares with the Tineoidea the following characters: i) frons with erect scales; ii) proboscis short, uncoiled; and iii) a possibly telescopic ovipositor.

Regier *et al*. (2015) proposed a radically different phylogeny for Ditrysia in which the Acrolophidae were reduced to a subfamily of Tineidae, and Psychidae and Eriocottidae no longer formed a clade. The Meessiidae, Dryadaulidae, and Tineidae, except Acrolophinae, have wing venations completely different from that of *Eocompsoctena* **gen**. **nov**. (see Regier et al. 2015: figs 6, 7C, 10C, 11C). Furthermore, according to these authors, the Dryadaulidae have no pecten on the scape, a pentamerous maxillary palpus (possibly trimerous in *Eocompsoctena* **gen**. **nov**.), and a the labial palpus flattened apically. Somewhat similarly, the Meessiidae have also a pecten on the scape and a pentamerous maxillary palpus.

Following Davis & Robinson’s (1998) key to tineoid families, *Eocompsoctena* **gen**. **nov**. would not fall within Tineidae owing to forewing R5 terminating at the wing apex and the likely trimerous maxillary palpus. The pecten on the scape is a character present in some Tineidae, Meessiidae, and some Eriocottidae, but generally absent in other Tineoidea.

Some Acrolophinae (Tineidae), Eriocottidae, and Psychidae (Typhoniinae and some Arrhenophaninae) have wing venations quite similar to that of *Eocompsoctena* **gen**. **nov**. (Dierl 1970: fig. 1; Nielsen 1978: fig. 17; Davis & Robinson 1998: fig. 7.3L; Davis 2003). The proboscis is vestigial or absent in Acrolophinae (Hasbrouck 1964), and in Psychidae it is, “represented at most by minute projections that do not extend beyond head vesture”, and the maxillary palpi are also greatly reduced but can be, “3-segmented in most primitive forms, but usually reduced to minute, hairy tubercules" in Psychidae (Davis 1965: 28–29; but see also Walsingham 1914; Davis *et al*. 1986; Davis 2003). The presence of a relatively long serrate proboscis in *Eocompsoctena* **gen**. **nov**. excludes it from crown-group Psychidae, but it is clearly a plesiomorphic character state that may have been present in stem-group Psychidae. The psychid genera *Palaeophanes* Davis, 2003, *Antillopsyche* Núñez Aguila & Davis, 2016, and *Kearfottia* Fernald, 1904 have relatively long proboscides, at least when compared to those of other Psychidae (Davis 2003: fig. 3; Núñez Aguila & Davis 2016: 60), but are nonetheless still much shorter than that of *Eocompsoctena* **gen**. **nov**. Psychidae and Acrolophinae have no antennal pecten (the arrhenophanine genus *Notiophanes* Davis & Edwards (in Davis 2003) has only a slender scale tuft on the scape, and *Anatolopsyche* Sugimoto & Saigusa, 2003 has a pecten on the pedicel (Davis 2003; Sugimoto & Saigusa 2003)), also suggesting that *Eocompsoctena* **gen**. **nov**. is not related to these groups (but see also Meyrick 1916–1922; Walsingham, 1914; Nielsen 1978; Davis *et al*. 1986; Robinson & Nielsen 1993; Davis & Robinson 1998; Holloway *et al*. 2001).

Robinson (1988) proposed two synapomorphies for Eriocottidae, i) ovipositor with dorsal apophyses anteriores and ii) sternite VIII of female membranous, but these characters are not visible in the only available specimen of *Eocompsoctena* **gen**. **nov**. Nielsen (1978: figs 19–20) indicated that Eriocottidae have some microtrichia on their forewings, which is not the case for Psychidae. Some structures could correspond to such microtrichia on the forewing of *Eocompsoctena* **gen**. **nov**. (see arrows in Fig. 3), but they are somewhat dubious and we cannot confirm the presence of these microtrichia with considerable confidence.

Within Eriocottidae, *Eocompsoctena* **gen**. **nov**. falls within Compsocteninae owing to the following characters: i) rather large, broad wings; ii) ocelli absent; iii) maxillary palpi reduced; and iv) CuP distally effaced, not reaching forewing posterior margin (Dierl 1970; Nielsen 1978). Sobczyk & Mey (2019: 119–120) regarded the subdivision of the family into Compsocteninae and Eriocottinae to be clear and distinct (Davis & Robinson 1998). However, the discoveries of new taxa in recent years have provided new characters and character combinations that blur the distinctions between these groups and weaken the recognition of two subfamilies for the family, with the current system rendering the placement of new taxa a challenge. Accordingly, although there is greater affinity between the fossil and Compsocteninae, we prefer to compare *Eocompsoctena* **gen**. **nov**. with all eriocottid genera. A new phylogenetic analysis of the family is clearly needed to resolve and refine the classification.

Within Eriocottinae, *Eocompsoctena* **gen**. **nov**. does not fit with the enigmatic genus *Tetracladessa* Gozmány & Vári, 1975 (Afrotropical region), placed by De Prins & De Prins (2018) in this subfamily because it has “veins 5 and 6 in hind wing somewhat approximated at base” (Janse 1968: 109, pl. 61, fig. 1), and the “forewings elongate, rather narrow, costa gently arched, apex pointed”, none of which corresponds with the fossil taxon (Meyrick 1920: 303). *Crepidochares* Meyrick, 1922 (Neotropical region) has a pecten on the scape and a venation similar to that of *Eocompsoctena* **gen**. **nov**., except in the forewing CuP terminates at the wing margin the epiphysis is quite short and situated in the distal third, the proboscis and maxillary palpus are much longer (Davis 1990). Like the preceding genus, *Eriocottis* Zeller, 1847 (Palaearctic region) also has a short epiphysis arising from the proximal half of the tibia and the forewing CuP terminates at the wing margin, but this genus lacks a pecten on the scape (Nielsen 1978). The genus *Deuterotinea* Rebel, 1901 (Palaearctic region) differs from the fossil genus in that it, like the aforementioned genera, has a forewing CuP that terminates at the wing margin and also a hind wing ic cell that differs considerably in shape, quite longer and ending distally between crossveins r-m1 and m2-m3, instead between m1-m2 and m2-m3 (de Joannis, 1917: fig. 3). The genus *Dacryphanes* Meyrick, 1908 (India), transferred to Eriocottidae by Robinson & Tuck (1996), differs from the fossil in that it has ocelli and the last labial palpomere shorter than the second palpomere (Meyrick 1908: 154).Within the Compsocteninae, *Kruegerellus* Mey & Sobczyk, 2019 has a forewing venation similar to that of *Eocompsoctena* **gen**. **nov**. except CuP is shorter and only extends to the proximal third of the wing, the ocelli are present, the terminal labial palpomere is shortened, and the epiphysis is short and situated in the distal third of the tibia (Mey & Sobczyk 2019: 121, figs 9–10). *Filiramifera* Mey, 2019 (Madagascar) differs from *Eocompsoctena* **gen**. **nov**. in the absence of a proboscis, an epiphysis longer than the protibia, maxillary palpi that are absent, a shortened terminal labial palpomere, and in the shapes of the ac and ic cells (Mey 2019: 30–31, fig. 3). The genera *Cathalistis* Meyrick, 1917 (South Africa and Namibia) and *Picrospora* Meyrick, 1912 (South Africa, transferred to Eriocottidae by Mey (2011)) share with the fossil the presence of an elongate maxillary palpus and a labial palpus with a ventral scale brush, quite unlike *Compsoctena* Zeller, 1854 (Afrotropical and Indomalayan, north to China and Taiwan) (Davis 1990; Mey & Sobczyk 2019: 120). A further difference is that in the fossil the third labial palpomere is as long as the second palpomere, while it is distinctly shorter in *Compsoctena* (Dierl 1970: figs 4–22). Furthermore, *Cathalistis* and *Picrospora* have narrower fore- and hind wings. *Picrospora* has a pecten on the scape, but a distinctly elongate epiphysis that is as long as the protibia (Sobczyk & Mey 2007: figs 19–20; Mey 2011; Mey & Sobczyk 2019). In addition, *Cathalistis* has the bases of veins M1 and M2 strongly approximate in the hind wing, which is not the case in the fossil genus. Lastly, the genus *Eucryptogona* Lower, 1901 (Australia) has pecten on the scape, but also a short epiphysis situated in the distal third of the protibia, a greatly shortened maxillary palpus, a labial palpus with a long second palpomere and a minute third palpomere; a forewing CuP that terminates on the wing margin, and an elongate ic in the hind wing, unlike *Eocompsoctena* **gen**. **nov**. (Nielsen & Robinson 1990).

Conclusion

Sobczyk & Kobbert (2009) have shown that the Psychidae were already quite diverse by the middle Eocene, with four different subfamilies represented in Baltic amber. With the present discovery, we demonstrate that the putatively more ‘derived’ family Eriocottidae was also present by that time. *Eocompsoctena* **gen**. **nov**. seems to be more related to Compsocteninae than to Eriocottinae, but given the current challenges with the classification of the family and the need for a revised and expanded phylogenetic analysis, there remains much to be clarified regarding its true relationships, as well as those of most modern genera in the clade. The Compsocteninae are currently known from the Afrotropical, Madagascan, and Indo-Malesian regions with some extensions into southern China. Such a distribution could be indicative of an ancient Gondwanan origin, perhaps also supported by the presence of the genus *Crepidochares* in the Neotropical region. This hypothesis would be particularly well supported if *Crepidochares* were particularly basal in the group, but relationships need to be further explored. The discovery of Eriocottidae in Baltic amber demonstrates that the family was already present in Eurasia during the Paleogene. The family could have diverged from other basal ditrysian moths in Gondwana during the Late Cretaceous and then gradually expanded to the North, eventually spreading across Eurasia, for instance via an Apulia microplate (Ezcurra & Agnolin 2012: fig. 2). Regardless, the discovery of this new taxon should help provide greater precision in calibrating phylogenetic estimates for families of 'Tineoidea' as well as refining our understanding of their historical biogeography.

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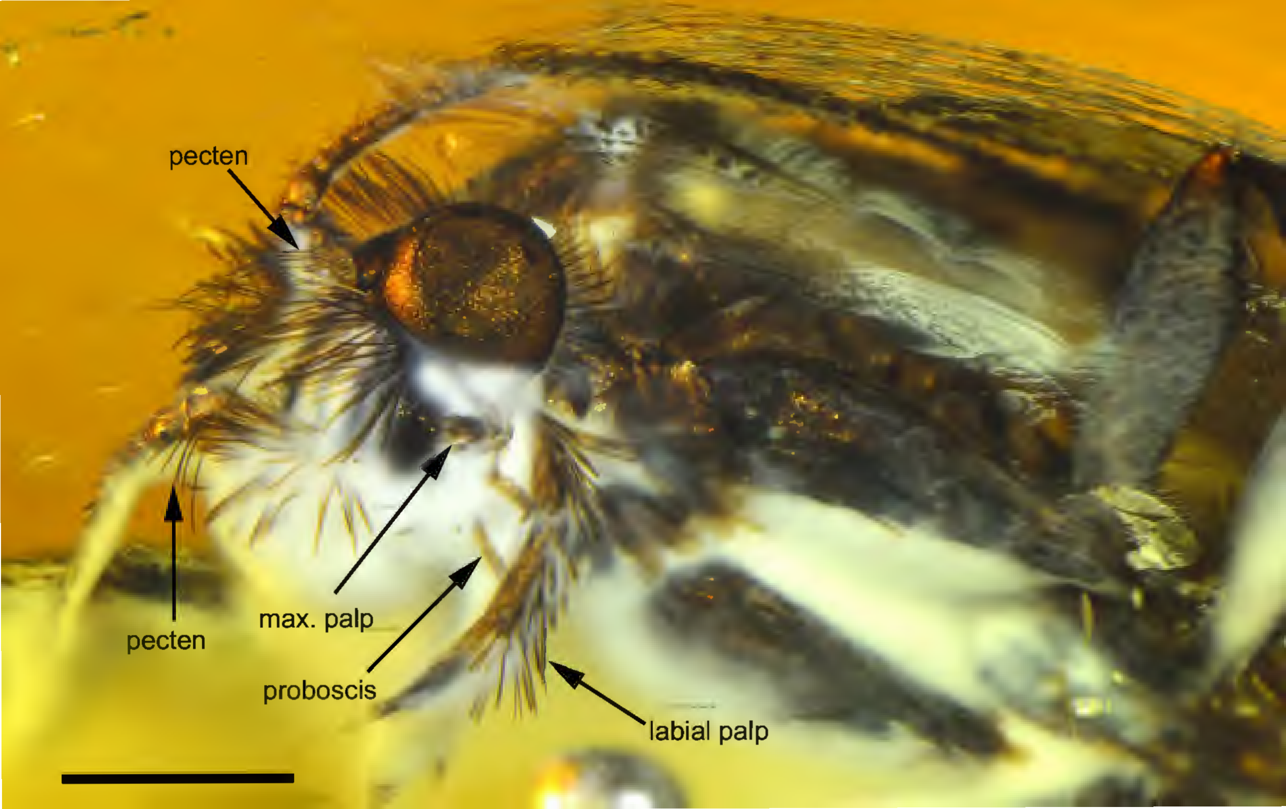
FIGURE 1. *Eocompsoctena macroptera* **gen**. et **sp**. **nov**., holotype MNHN.F.A71340. Habitus photograph. Scale bar = 1 mm.

FIGURE 2. *Eocompsoctena macroptera* **gen**. et **sp**. **nov**., holotype MNHN.F.A71340. Photograph of head. Scale bar = 0.5 mm.

FIGURE 3. *Eocompsoctena macroptera* **gen**. et **sp**. **nov**., holotype MNHN.F.A71340. Photograph of fore- and hind wings; small arrows indicate putative insertions of microtrichia; ac = accessory cell, ic = intercalary cell. Scale bar = 1 mm.

FIGURE 4. *Eocompsoctena macroptera* **gen**. et **sp**. **nov**., holotype MNHN.F.A71340. Reconstructions of fore- and hind wings; ac = accessory cell, ic = intercalary cell. Scale bar = 1 mm.

FIGURE 5. *Eocompsoctena macroptera* **gen**. et **sp**. **nov**., holotype MNHN.F.A71340. Photograph of fore legs from below. A, right leg; B, left leg. Scale bars = 0.5 mm.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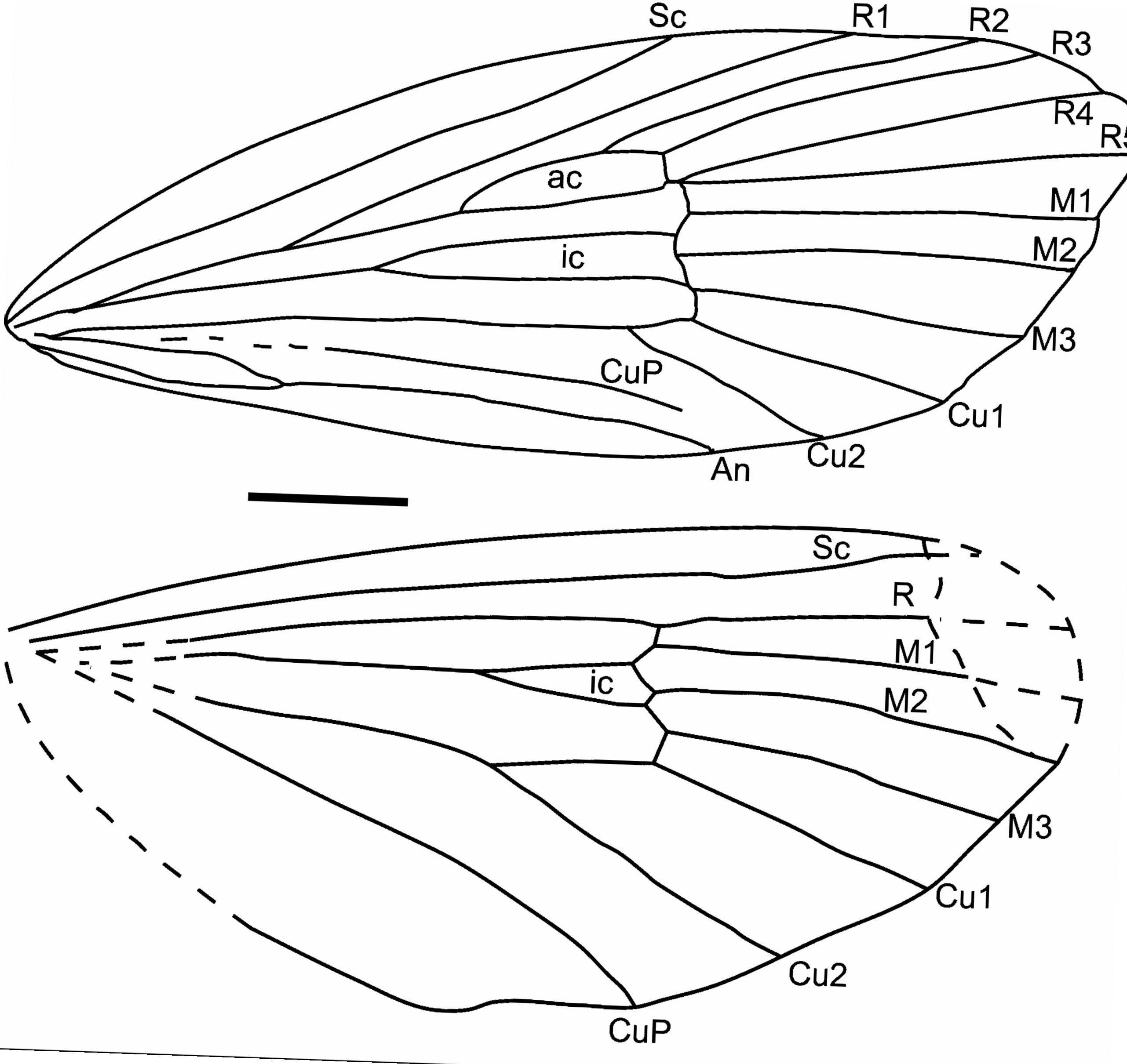
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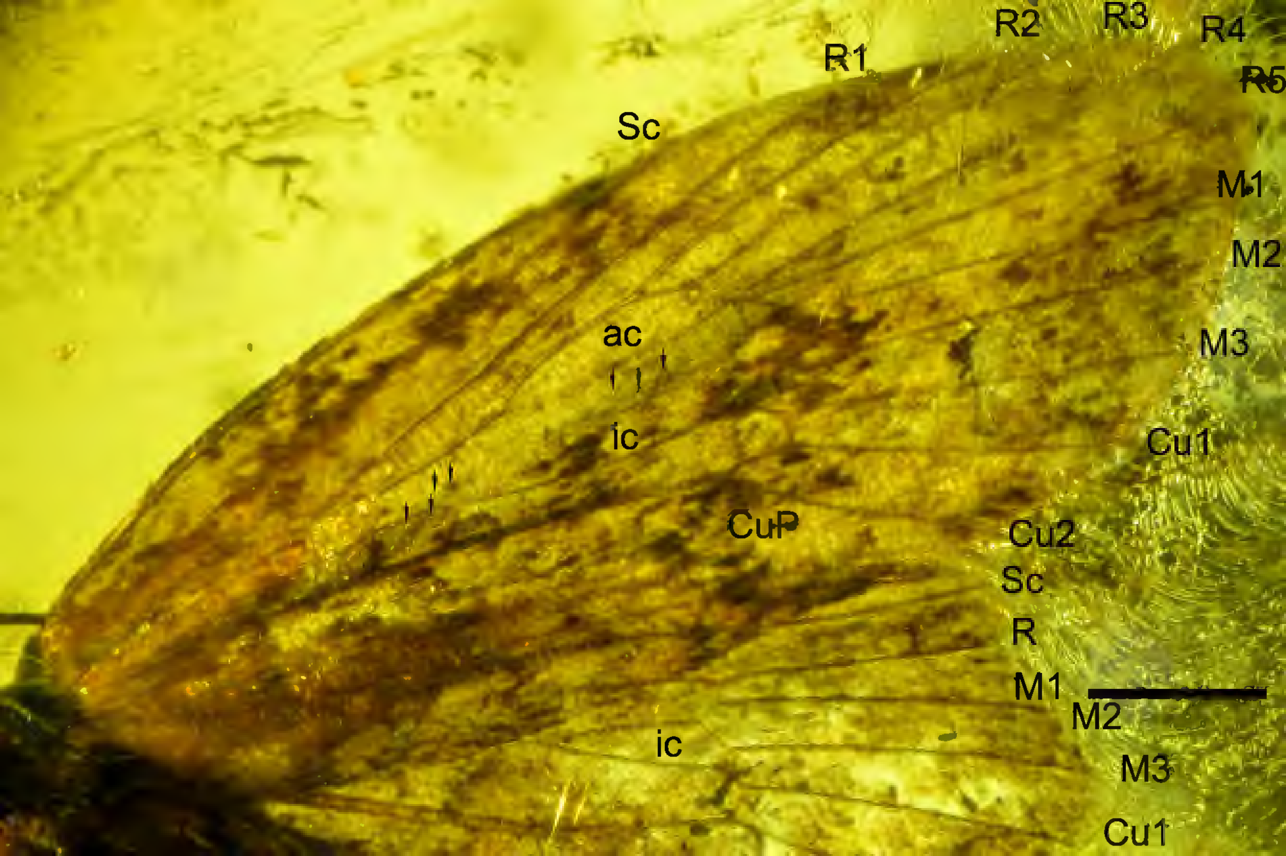
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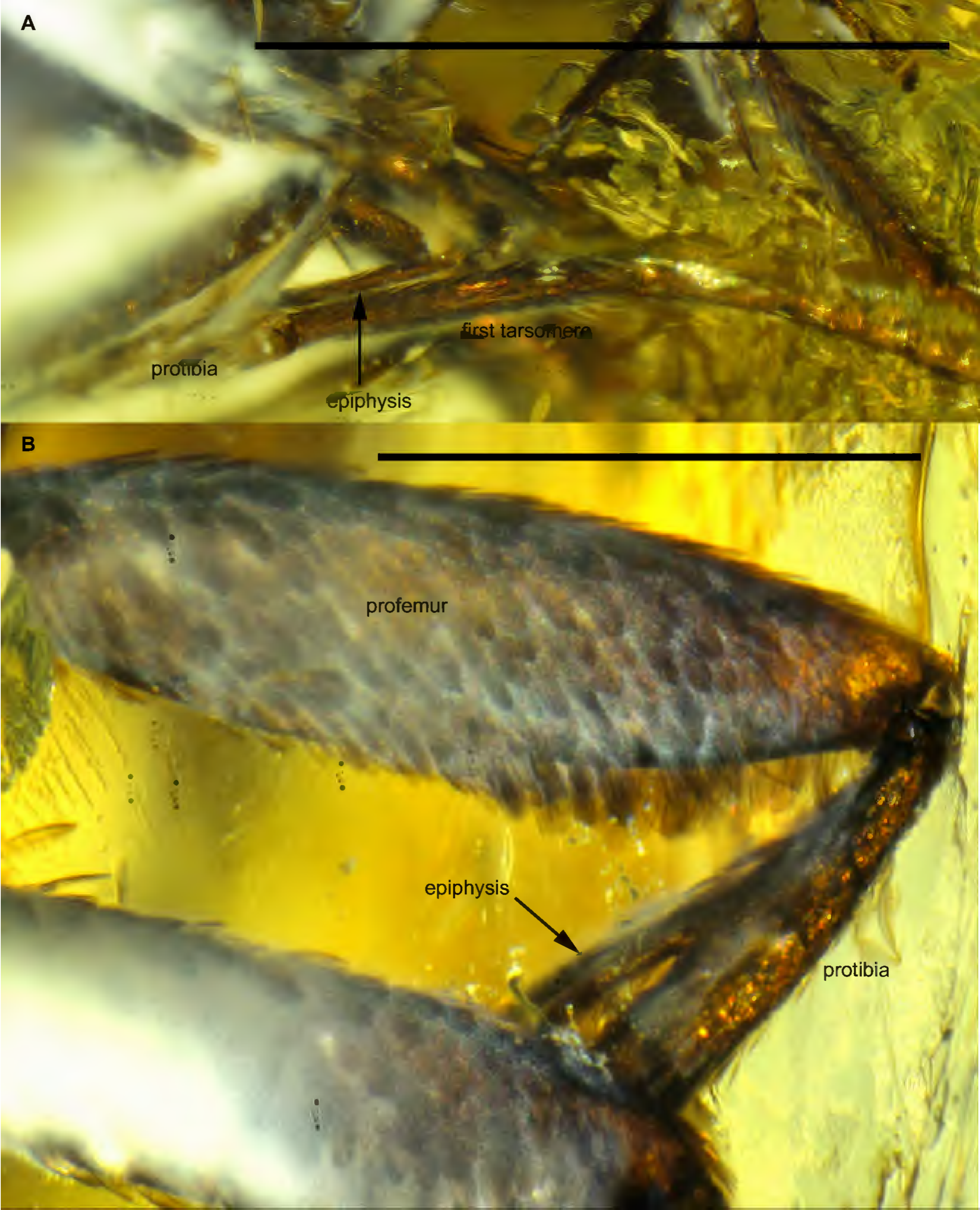
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