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For Palaeoentomology

Description of a new fossil genus of conifer sawfly (Hymenoptera: Diprionidae) revealed by
UV light

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Abstract

Oligomonoctenus neytirii **gen. et sp. nov.**, the second fossil representative of the family Diprionidae from the uppermost Oligocene of Aix-en-Provence, France, is described on the basis of a well-preserved compression fossil. It is compared to the other extant and fossil diprionid genera. Its morphology and wing venation support an attribution to the subfamily Monocteninae. *Paleomonoctenus patriciae*, the other diprionid described from the same paleolake, also belongs to the Monocteninae. On the other hand, the Eocene-Lower Oligocene genus *Eodiprion* would be attributable to the Diprioninae but needs revision. This discovery suggests that the two diprionid subfamilies were already present and diversified during the Eocene – Oligocene.

Keywords: Insecta, Tenthredinoidea, Monocteninae, Cenozoic, sp. nov.

Introduction

The family Diprionidae is relatively small (i.e., less speciose) when compared to the Tenthredinidae (Taeger *et al.*, 2010). The fossil record of both families remains scarce, even if recent phylogenetic analyses have suggested a Cretaceous age for the diversification of both families (Nyman *et al.*, 2019; Niu *et al.*, 2021, 2022). This scarce fossil record is likely due to an expertise bias because fossil compressions or imprints of the Tenthredinoidea are rarely placed with confidence in a certain family or subfamily. This issue stems from the characters used to delineate the genera, tribes, or subfamilies that are often not preserved or visible on fossil compressions or imprints. For example, it is sometimes very difficult to discriminate whether a fossil sawfly is a diprionid or a tenthredinid because some representatives of both families are very similar. To overcome this problem inherent to the fossilization process, new methodologies have to be developed or used, mainly to access new characters not visible in

‘normal’ conditions. Recent use of ultraviolet (UV) light on fossil insect compressions or imprints has revealed many structures very hard to recognize under natural light and is promising for the study of fossil insects (Nel *et al.*, 2023). Herein, we apply this new methodology to a fossil readily attributed to the superfamily Tenthredinoidea in order to determine accurately its placement.

Recently, molecular phylogenies have retrieved the Diprionidae as the putative sister group of the Cimbicidae, the two families likely diverging during the Cretaceous (Nyman *et al.*, 2019: fig. 1; Niu *et al.*, 2022). However, these time divergence estimates have to be considered cautiously due to the extremely reduced fossil record of the Diprionidae constraining the available calibrations to young ages (a problem well known for Lepidoptera: Sohn *et al.*, 2015). Currently, only four fossils of the family Diprionidae are known, viz. ‘*Pteronus*’ *prodigus* Brues, 1908 from the lowermost Oligocene of Florissant (Colorado, USA), *Eodiprion groehni* Schedl, 2007 and *Eodiprion* sp. in Schedl (2008) from the Eocene-Lower Oligocene Baltic amber, and *Paleomonoctenus patriciae* Nel, 2005 from the uppermost Oligocene of Aix-en-Provence (France) (Nel, 2005; Taeger *et al.*, 2010).

Here we describe a new fossil sawfly from the Uppermost Oligocene lacustrine basin of Aix-en-Provence (Southern France) that we propose to attribute to the diprionid subfamily Monocteninae. We also briefly discuss the placement of *Eodiprion groehni*, *Eodiprion* sp., and ‘*Pteronus*’ *prodigus*.

Material and methods

Preparation and outcrop location

The holotype was collected in very tiny siliceous laminites of the insect horizon in a small outcrop situated near the locality Courtassy south of the village of Eguilles, west of the town

Aix-en-Provence. Another poorly preserved Tenthredinidae was also found in the same layer. ‘Symphyta’ are extremely rare in the paleolake of Aix. The previously found fossils come from the historical gypsum quarry of ‘Les Platrières’ at Aix-en-Provence, in a layer situated one meter below the one from which the new fossil comes. The new fossil was prepared using a sharp spine.

Imaging and morphological terminology

The fossil was photographed at CEREGE using a Camera Sony Alpha 7R IV (61.2MP, Full frame, Pixel Dimensions, 9504×6336) with a Zeiss Macro 90mm lens and dual Flash lighting. Pictures were recorded in RAW format for further post-processing. Colors have been calibrated with Xrite ColorChecker® Classic chart and ColorChecker Passport software. Raw photo development and editing for white balance, colors, and aberrations were made with Capture One 20 software. UV light photographs were taken with a Nikon D850 FX camera with an attached 60 mm/2.8 Micro-Nikkor lens. A UV light (365 nm) has been used to find different visible fluorescence contrasts with the sedimentary matrix and reveal hidden structures and putative ornamentations or patterns on the wing surface. UVA (365 nm rather than 390 nm) used for fossil insect studies is a new promising technique for enhancing observation with a simple, portable, and economical device (Nel *et al.*, 2023). It is a useful way to select specimens of interest for chemical analysis and imaging by more sophisticated techniques (e.g., X-ray synchrotron fluorescence, Georgiou *et al.* 2019). We follow the morphological terminology of Goulet & Huber (1993).

Geological setting

The well-known paleolake of Aix-en-Provence has been extensively studied since the beginning of the 19th century (e.g., Serres, 1829). Théobald (1937) proposed a revision of the entomofauna. Gaudant *et al.* (2017) proposed a general overview of the Konservat-Lagerstätte of Aix-en-Provence. Insects are found in a rather thin level of ca. 1.5 m thick of very delicate and thin laminites. Its stratigraphy was extensively studied by Nel (1991) and Peinado (2002) who indicated that the laminites were generated by microbial mat activities, a result that was later confirmed by Downen *et al.* (2022) when studying fossil Arachnida. The layer which has yielded the new fossil originates is very particular, being very rich in Silica, green-colored, with numerous dragonfly larvae, marine fishes, and Siphonophora, suggesting a putative marine influence at least in this Western part of the paleolake (Nel *et al.*, 1987; Nel, 1991).

Systematic paleontology

Order Hymenoptera Linnaeus, 1758

Family Diprionidae Rohwer, 1911

Subfamily Monocteninae MacGillivray, 1906

Genus *Oligomonoctenus* **gen. nov.**

Zoobank xxxx

Type species. *Oligomonoctenus neytirii* **sp. nov.**

Etymology. Named after the Oligocene age of the type species and the genus *Monoctenus* Dahlbom, 1835. Gender masculine.

Diagnosis. Lateral ocelli apparently as far apart as each is from an eye margin; 22 antennomeres, all short, shorter than wide, except for scape and pedicel that are slightly longer than wide, without visible serration; clypeus very short and transverse with distinct

supraclypeal furrow; anterior corner of mesoscutellum angular, slightly obtuse, triangularly protruding; mesoscutellar appendage narrow but distinct; cenchri very narrow and transversely extended, distance between them as long as their respective, and length about half as long as their respective width; vein M nearly straight; cell 1R1 large, well separated from cell Rs; no crossvein Sc1; crossvein 2r-rs absent; vein M meeting with vein R at point where vein Rs+M separates from vein R; crossvein 1cu-a oblique, meeting cell 1M beyond middle; proximal part of vein 2A+3A meeting with vein 1A, basal anal cell closed.

***Oligomonoctenus neytirii* sp. nov.**

(Figs 1-3)

Zoobank xxxx

Material. Holotype (female) MNHN.F.A71362 (part and counterpart of a nearly complete wasp, with legs and mouthparts missing, forewings well visible, but hind wings only partly preserved), stored at the Museum national d'Histoire naturelle, Paris, France.

Etymology. Named after Neytiri, princess of the Na'vi people from Pandora planet in the Avatar animation movie (James Cameron, 2009 and 2022), a blue and bioluminescent skin people who defend nature and life in all its forms.

Type locality and horizon. Aix paleolake, Eguille, Bouches-du-Rhone, France; Latest Oligocene, insect layers.

Diagnosis. As for the genus by monotypy.

Description. Female. Body 8.0 mm long; head deformed by compression, visible part 0.7 mm long, 1.8 mm wide; mouthparts not visible; right antenna well visible under UV light, not reaching posterior part of thorax, with 22 antennomeres, of decreasing lengths, nearly all wider than long, except for scape and pedicel; eyes 0.5 mm long, but deformed; ocelli partly

visible in profile, anterior margin of lateral ocellus at level with middle of median ocellus; lateral ocelli apparently as far apart as each is from an eye margin; clypeus very short and wide, at least four times as broad as middle length; epistomal furrow curved, distinct.

Thorax 4.5 mm long, 2.0 mm wide; posterior margin of pronotum in dorsal view strongly concave; anterior part of mesoscutellum angular, slightly obtuse, forming an angle of 110°; mesoscutellar appendage narrow but distinct; cenchri narrow and transverse, three times as wide as long; abdomen 4.7 mm long, 3.3 mm wide, with genital appendages partly preserved, ovipositor sheaths visible under UV light, acute and short, ca. 0.5 mm long, not expanded distad abdomen apex. Forewing 7.6 mm long, 2.9 mm wide; vein C not strongly swollen at apex; stigma broad; vein M separating from vein Cu at 2.2 mm of wing base; basal part of vein M nearly straight, ending in vein R very close to origin of vein Rs+M, thus length of vein R+M between junctions with veins M and Rs+M shorter than first sector of vein Rs; first sector of vein M and crossvein 1m-cu convergent toward stigma; vein R straight, not curved posteriorly before its junction with vein M; distance between junctions of vein M with vein M+Cu and junction of vein Rs+M with vein R 2.5 times the length of crossvein 1m-cu; vein 2m-cu strongly curved, joining cell 1Rs2 near vein 2r-m; cell 1M 1.6 mm long, 0.9 mm wide; vein 1cu-a in distal half of cell 1M; vein Rs+M straight; cell 1R1 rather large, well separated from cell Rs; cells Rs and 1Rs2 long; vein 2A+3A completely outlined (see forewing on right side in Fig.2B) and fused with 1A, forming a basal anal cell.

Discussion

Systematic placement

The antenna with 22 short antennomeres suggests an attribution of the new fossil to the Diprionidae (see Goulet & Huber, 1993). Some Tenthredinidae (e.g., *Fenella*, *Cladiucha*)

have 16 to 23 antennomeres but at least some of the flagellomeres are distinctly longer than wide. The anterior margin of the lateral ocellus at the level with the middle of median ocellus is also a character of the Diprionidae, and it can be used to separate this family from the Tenthredinidae (Goulet & Huber, 1993), although their relative position can be affected by compression. The Diprionidae have their antenna pectinate or bipectinate in males, and more or less serrate in females (even in the Baltic amber genus *Eodiprion* Schedl, 2007), *versus* apparently simply beaded in the new fossil. Moreover, in some cases, the serration can be difficult to see in fossil imprints or compressions and the shape of the antennae can be slightly deformed during the fossilization process. Therefore, we do not consider this character sufficient to preclude a placement into the family Diprionidae. Therefore, we propose to place the new fossil in the Diprionidae.

After Benson (1945, 1954), the new genus would fall into the subfamily Monocteninae because of the following forewing characters: anal cell divided into two cells; no anal crossvein (see also Smith 1974, 1988); lcu-a distinctly oblique.

Benson (1939) also divided the Diprionidae into two groups on the basis of the shape of the anterior part of mesoscutellum, viz. acute in front in the genera *Monoctenus* Dahlbom, 1835, *Augomonotenus* Rohwer, 1918, *Zadiprion* Rohwer, 1918, *Neodiprion* Rohwer, 1918, and *Microdiprion* Enslin, 1917, *versus* blunt in the other genera, including *Paleomonotenus* (Nel, 2005). But Benson (1954) revised this statement and indicated that the mesoscutellum of *Augomonotenus* is obtuse in front, at least more than in *Monoctenus*, but without precision on the exact difference between the two taxa. The new fossil has an anterior part of the mesoscutellum as obtuse as in *Monoctenus sanchezi* Smith (in Smith *et al.*, 2010: fig. 1).

The new fossil differs from *Augomonotenus* in its clypeus very short and broad (*vs.* longer and narrower in *Augomonotenus*), in its basally straight vein M, and its much more

numerous antennomeres, viz. 22 in the new fossil *versus* 12 in the female of *Augomonoctenus smithi* Xiao & Wu, 1983, 16 in the female of *Augomonoctenus pilosus* Middlekauff, 1967, and 16 in the female of *Augomonoctenus libocedrii* Rohwer, 1918 (Middlekauff, 1967; Xiao & Wu, 1983). The females of *Monoctenus* spp. have more antennomeres (up to 25) (Rohwer, 1918; Benson, 1954; Okutani, 1958; Goulet, 1992; Togashi, 2001; Japoshvili & Haris, 2022; De Lira-Ramos *et al.*, 2022). The new fossil differs from *Monoctenus* by the absence of the crossvein Sc1; from *Monoctenus* and *Rhipidoctenus* Benson, 1954 by the forewing vein M ending into R at the point where Rs+M separates from R. The new fossil shares with *Rhipidoctenus* the ‘cenchri close together so that the distance between them is scarcely more than the length of a cenchrus’ (Benson, 1954: 118). But it would share with *Monoctenus* the lateral ocelli as far apart as each is from an eye margin, unlike in *Rhipidoctenus* (Benson, 1954). *Paleomonoctenus patriciae* can also be attributed to the Monocteninae because of its forewing anal cell divided into two cells. However, it has only 16 antennomeres, and its forewing venation strongly differs from that of the new fossil in the small cell 1R1 and the vein 1cu-a close to the base of vein M (Nel, 2005).

Remarks on the other fossil Diprionidae

‘*Pteronus*’ *prodigus* was originally attributed to the Diprionidae (Brues, 1908). The genus *Pteronus* Jurine (in Panzer, 1801) is listed as a junior synonym of *Diprion* Schrank, 1802 in Taeger *et al.* (2010), but several extant taxa originally attributed to *Pteronus* are now in the tenthredinid genus *Nematus* Panze, 1801. Brues (1908: 262) compared *P. prodigus* to the ‘*P. ribesii* Scop. and *P. mendicus* Walsh.’, two species now in *Nematus*, suggesting that he considered that *P. prodigus* could rather be a Tenthredinidae. The photograph of the holotype (specimen PALE-2038, stored at Museum of Comparative Zoology (MCZ) at Harvard

University) clearly shows elongated antennomeres, excluding its attribution to the Diprionidae.

Schedl (2007) did not discuss precise arguments supporting the attribution of *Eodiprion groehni* Schedl, 2007 to the Diprionidae, and nothing was indicated on the crucial characters of the disposition of the ocelli and of the structure of the mesepimeron. Schedl (2008: fig. 2) described a male of *Eodiprion* sp. that shows several characters typical of the family, even of the Diprioninae (presence of a crossvein between 1A and 2A+3A in forewing). However, the female described by Schedl (2007: fig. 2a-b) as the holotype of the genus *Eodiprion* and of the species *E. groehni* Schedl, 2007 would have a long fusion between 1A and 2A+3A, a character suggesting that the male and female specimens attributed to *Eodiprion* could belong to two different genera or species. These two fossils need to be revised and redescribed.

Nevertheless, male and female currently attributed to *Eodiprion* differ from the new fossil in their longer fusion of M with R and their vein 1cu-a perpendicular to Cu (vs. oblique in the new fossil).

Serres (1829) listed an undescribed fossil representative of the genus '*Pteronus*' from the uppermost Oligocene of Aix-en-Provence. This fossil was never described and is probably lost.

Conclusion

The Diprionidae would have separated from the other 'symphytan' groups during the Cretaceous, and diversified during the early Paleocene and Eocene. These time divergence estimates are compatible with the presence of diprionid genera in the Oligocene. The fact that all the fossil Diprionidae belong to extinct genera suggests that the family was already quite

diverse during the Paleogene. It also supports the hypothesis that the extant genera appeared during the Oligocene or the Neogene.

The extant Monocteninae feed on Cupressaceae and Diprioninae on Pinaceae (Benson 1945). Both groups are present in the Oligocene of Aix-en-Provence, e.g., respectively frequent remains of *Callitris* sp. and *Pinus* sp. However, as for *Paleomonoctenus patriciae*, it is not possible to make any biological inference for the new fossil.

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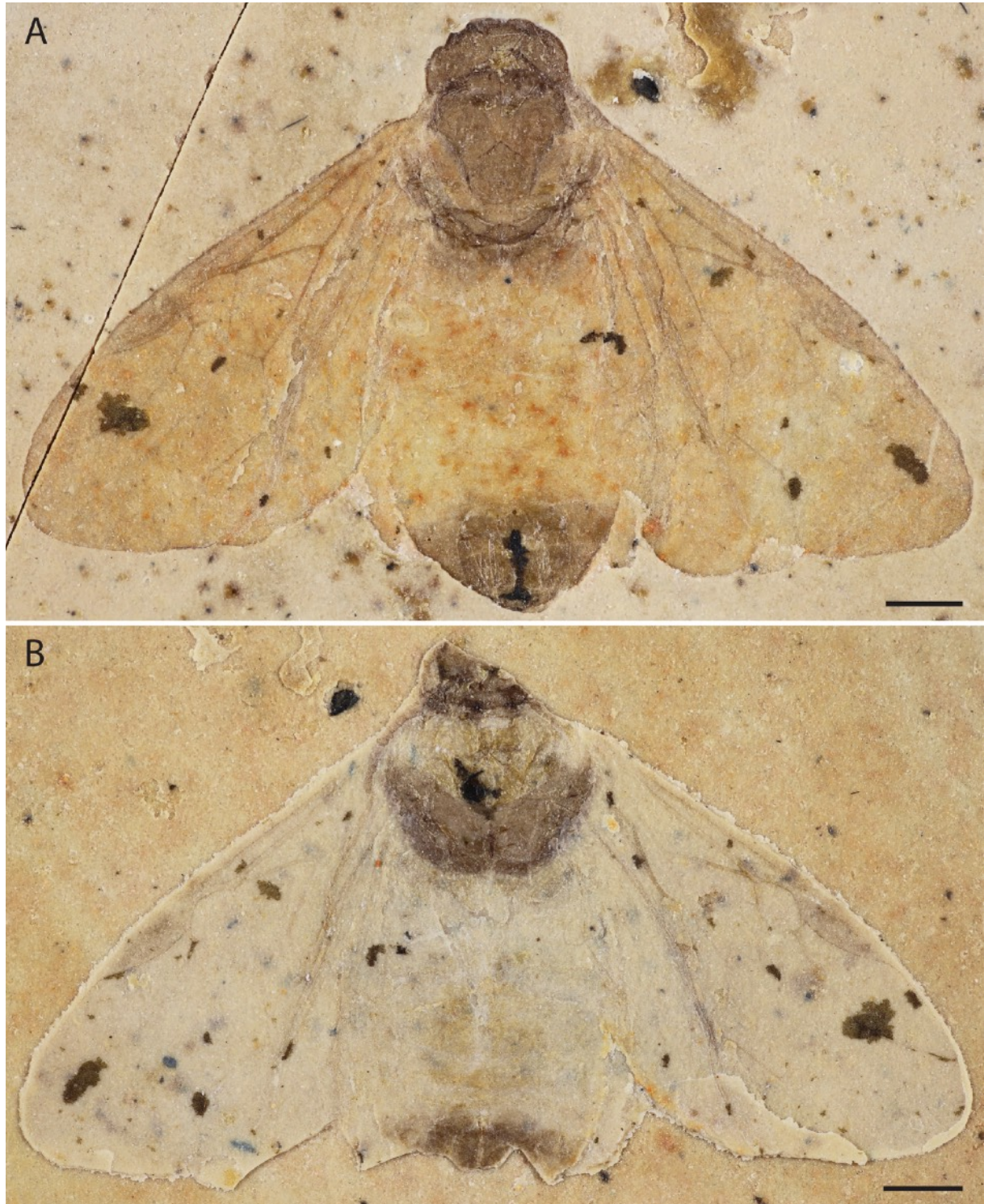


FIGURE 1. *Oligomonoctenus neytirii* **gen. et sp. nov.**, holotype MNHN.F.A71362. Habitus.

A, Imprint; B, Counterimprint. Scale bars = 1 mm.



FIGURE 2. *Oligomonoctenus neytirii* gen. et sp. nov., holotype MNHN.F.A71362. Habitus under ultraviolet light. A, Imprint; B, Counterimprint. Scale bars = 1 mm.

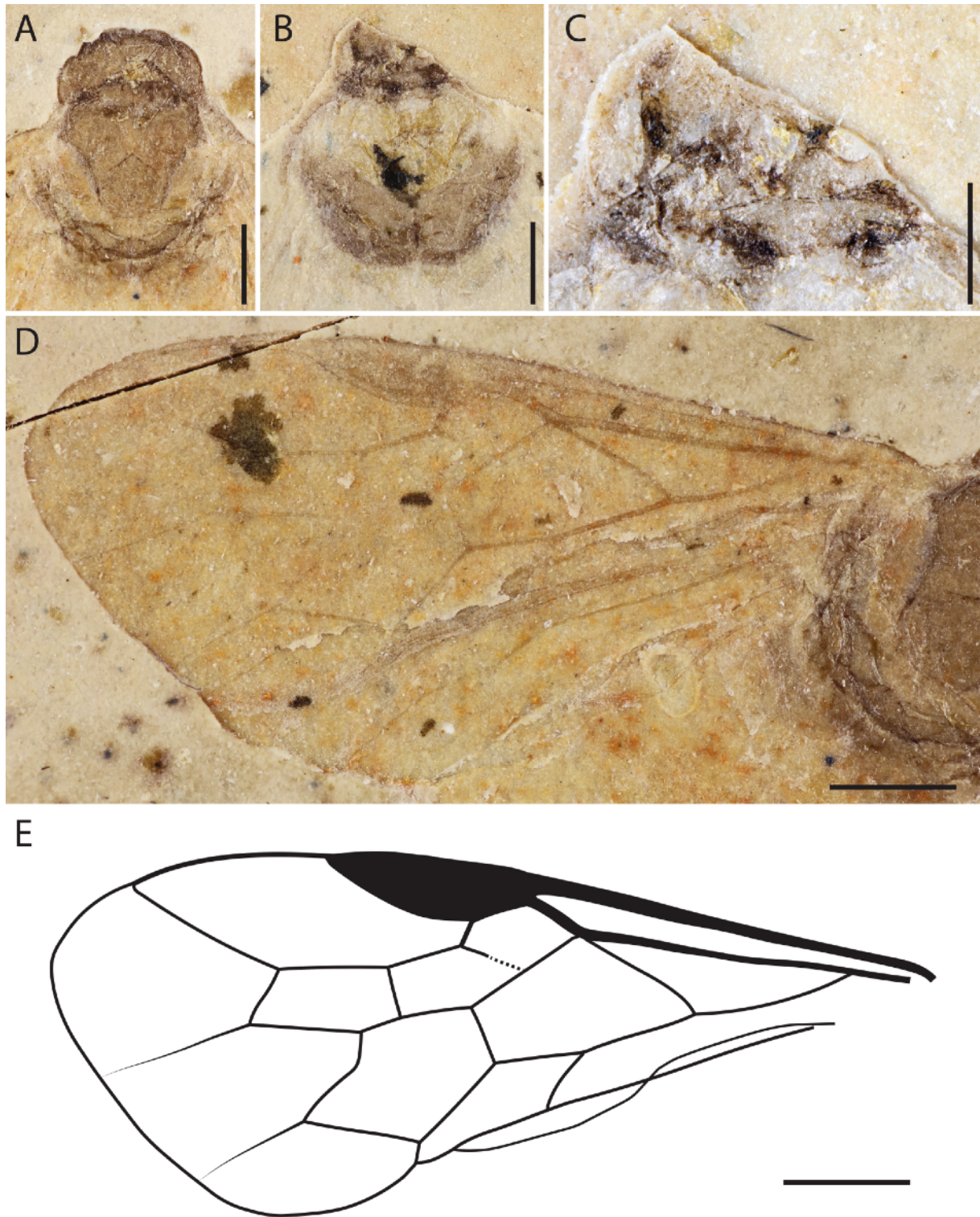


FIGURE 3. *Oligomonoctenus neytirii* gen. et sp. nov., holotype MNHN.F.A71362. A, Head and thorax, imprint; B, Head and thorax, counterimprint; C, Head, counterimprint; D, Fore- and hind wings; E, Reconstruction of forewing. Scale bars = 1 mm (A,B,D), 0.5 mm (C).