UNIVERSITY OF HELSINKI

https://helda.helsinki.fi

Subfamily Palaeoxeninae from the Middle Jurassic Jiulongshan Formation of China (Coleoptera, Eucnemidae)

Li, Haolun; Chang, Huali; Muona, Jyrki; Ren, Dong

2023-09-15
Wiss. Verl. Peks
http://hdl.handle.net/10138/569933
Li, H, Chang, H, Muona, J & Ren, D 2023, 'Subfamily Palaeoxeninae from the Middle Jurassic Jiulongshan Formation of China (Coleoptera, Eucnemidae)', Entomologische Blätter für Biologie und Systematik der Käfer, vol. 118, pp. 1-6.

Downloaded from Helda, University of Helsinki institutional repository. https://helda.helsinki.fi
This is an electronic reprint of the original article.
This reprint may differ from the original in pagination and typographic detail.
Please cite the original version.

Entomologische Blätter und Coleoptera

Ent. Bl. Col. (2022/2023) 118: 001 - 006 ISSN 0013-8835 © Wissenschaftlicher Verlag Heinz Peks OHG

Subfamily Palaeoxeninae from the Middle Jurassic Jiulongshan Formation of China (Coleoptera, Eucnemidae)

Haolun Li[1], Huali Chang[2], Jyrki Muona[3]* and Dong Ren[1]

Abstract
The eucnemid *Palaeoxenus clavatus* sp. nov. is described from the Middle Jurassic Jiulongshan Formation of Inner Mongolia, China. This is the second record of eucnemids from the Jiulongshan Formation and the first record of the subfamily Palaeoxeninae Muona from the Jurassic. This discovery confirms that all basal lignicolous Eucnemidae subfamilies, Schizophilinae, Pseudomeninae, Anischiinae and Palaeoxeninae, had evolved in the Jurassic before the angiosperm radiation. Palaeoxeninae being the sister-group of the clade (Melasinae, Eucneminae, Macraulacinae), the "Derived Eucnemidae", DE for short, this new record proves that the DE clade originated in the Jurassic as well. On the basis of fossil evidence, the modern Eucnemidae diversity appears to be connected with the angiosperm radiation in Upper Cretaceous to Paleocene. However, this diversification was facilitated by the larval special adaptations for extraoral feeding inside gymnosperm wood, a feature already present in the Jurassic.

Key words
Coleoptera, Eucnemidae, fossil, Middle Jurassic, Jiulongshan Formation, China,

Simple summary
The false click-beetle subfamily Palaeoxeninae includes only one extant species, Dohrn's Elegant Eucnemid found in Southern California mountain region. This evolutionary lineage forms the sister-group of all other 1800 described extant eucnemids. Fossil species belonging to this group are known from Myanmar amber, 100 Ma, as well as Middle Cretaceous deposits, 125 Ma. This new Chinese discovery pushes the age of the group to the Jurassic, some 170 Ma. This proves that the ancestors of the other extant false click-beetles existed at that time as well and the group started its known diversification no later than in the Middle Jurassic, long before the angiosperm main radiation.

Introduction

The first Jurassic eucnemid fossil published was *Paradesmatus baiae* Chang, Kirejtschuk & Ren, originally placed in Elateridae and later transferred in the Eucnemidae subfamily Schizophilinae Muona (Chang et al., 2009; Muona et al., 2020), collected from the Middle Jurassic Daohugou beds, Jiulongshan Formation, Ningcheng County, Inner Mongolia, China (Ren et al., 2019). We now report another eucnemid species belonging to another subfamily from the same formation.

The geological section at the Daohugou Village is composed of grey tuffaceous sandstone and sandy mudstone. Ren & Krzeminski (2002) reconstructed the palaeoenviroment of this locality as a volcanic region with mountain streams and lakes. The paleontological data were interpreted as indicating a humid and warm-temperate climate (Tan & Ren, 2002). A comparative study of the fossils and a detailed analysis of the lithology indicated that Daohugou Village in Middle Jurassic was at the edge of a shallow lake. The terrain was flat and the lake was surrounded by lush forests and grasslands with a warm, moist climate and plenty of moisture in the soil (Zheng, 2010). The water bodies were formed on the surface of volcanic ash layers and they were characterized by small size, shallow depth and temporal nature. The constant cycle between shores and shallow water created a marsh-like habitat (Yang & Jiang, 2015).

According to the International Chronostratigraphic Chart (v2016/04), the age of the strata is regarded as Middle Jurassic, between 163.5 ±1.0 and 174.1±1.0 Mya.

Material and methods

This study is based on one fossil Eucnemidae specimen collected from the Jiulongshan Formation. The specimen was examined using a Nikon SMZ25 dissecting microscope and the line drawings were produced with the software Adobe Illustrator 17.0. Photographs were acquired with a Nikon SMZ25 Digital Camera. Body length was measured along the midline from the

anterior edge of the mandible to the apex of the abdomen, and the width was measured across the broadest part of the elytra. The length of the pronotum was measured along the midline; the width was measured across the broadest part at its posterior angles.

Antennal parts are referred to as consisting of a scape, a pedicel and a flagellum, which consists of nine flagellomeres. These are referred to as "f" and the appropriate number from 1 to 9.

Systematic paleontology

Class Insecta Linnaeus, 1758
Order Coleoptera Linnaeus, 1758
Superfamily Elateroidea sensu stricto (the clicking elateroids)
Family Eucnemidae Eschscholtz, 1829
Subfamily Palaeoxeninae Muona, 1993
Genus Palaeoxenus Horn, 1891

Elateroidea sensu stricto synapomorphy: promesothoracic clicking mechanism present.

Elateroidea sensu stricto diagnostic other features: body elongated, flattened; metacoxal plates enlarged, metaventrite without transverse suture (Fig. 1).

Eucnemidae synapomorphies: elytra with sutural and lateral striae with apical enlarged punctures (Fig. 2); pedicel attached to scape subapically (Fig. 3).

Eucnemidae other diagnostic feature: f7-f9 enlarged, forming a loose club; pronotal hind angles without dorsal short carinae; all abdominal ventrites connate (Fig. 3).

Palaeoxenus synapomorphies: f7-f9 flattened, apically excavated (Fig. 3)

Palaeoxenus other diagnostic characters: Body parallel sided and flat; legs robust; claws and tarsi simple; lateral ridge of pronotum simple (Fig. 1).

Genus Palaeoxenus Horn, 1891

Species: *Palaeoxenus clavatus* Li, Chang & Muona new species

Etymology "clavatus" refers to the antennal club formed by enlarged f7-f9.

Diagnosis

The pro-mesothoracic clicking mechanism places this species on the superfamily Elateroidea s.str. The subapically attached pedicel and the apically deeper sutural elytral striae with enlarged punctures place it in the family Eucnemidae. Within Eucnemidae it is characterized by parallel sided and flattened body, 3-segmented antennal club with apically excavated antennomeres and small head, placing it in the subfamily Palaeoxeninae. Compared with the only extant species, *Paleoxenus dohrni* (Horn), the pedicel is proportionately larger, f1-f6 more elongated and f7-f9 more strongly expanded and flattened, reminding of the antennae of *Phyllocerus lambertoni* Fleutiaux (see Muona, 1993b).

Holotype

CNU-COL-NN2018348 housed in the fossil insect collection of the Key Laboratory of Insect Evolution & Environmental Changes, College of Life Science, Capital Normal University, Beijing, China.

Description

Body length 19.44 mm; head width 2.53 mm; pronotum width 6.13 mm (visible); pronotum length 4.22 mm; elytron length, 14.46 mm; combined elytral width 3.76 mm.

Body flattened and elaterid-like, wide and elongate, parallel-sided, widest at pronoto-elytral junction and narrowing anteriorly and posteriorly (Fig. 1).

Head subquadrilateral, transverse, small, pronotum 2.6 times as wide as head. Distance between antennal insertions appears to be wide, but not fully visible. Antennae short, about one-fifth as long as body (fig. 1, 3). Scape poorly visible except of apex, elongated, oval, longer than the subapically attached pedicel. F1 exceptionally elongate, twice as long as pedicel. F2-f6 about equal, longer than wide, subconical. F7-f9 distinctly wider than long, f9 slenderer and shorter than f7 or f8, all three apically excavated.

Pronotum 1.46 times as wide as long and about 2.6 times as wide as head (left hind corner broken off), hind angles produced and acute, caudal margin forming interlocking system with base of elytra.

Scutellum poorly defined, apparently transverse and small. Elytra elongate, 1.9 times as long as wide and about 3.4 times as long as pronotum with fine, distinct striae, interstices convex at apex, sutural striae widening and with larger punctures close to apex (Fig. 3). Proleg slender, femur simple, tibia long, tarsus with five simple tarsomeres (fig. 1). Metacoxae contiguous, abruptly narrowing before middle towards sides, metafemora and -tibiae poorly visible, metatarsi missing.

Discussion

The great majority of modern Eucnemidae (99% of species) belong to three subfamilies: Eucneminae, Macraulacinae and Melasinae. Muona & Teräväinen (2020) called this clade "Derived Eucnemidae" or DE for short. With very few exceptions these species breed in angiosperm wood infected with bracket fungi. Numerous DE fossils are known from both the Cenomanian Myanmar amber and the Eocene Baltic amber (Muona, 1993a; 2020), but the composition

of these two faunas are different. The Eocene fauna is like a sample of the present world fauna, whereas the Cenomanian fauna does not include any species belonging to the most specious present clade, the tribe Macraulacini Fleutiaux (Muona, 2020).

The basal lignicolous Eucnemidae clades, Pseudomeninae, Schizophilinae, Anischiinae and Palaeoxeninae include only about a dozen modern species (Muona, 1993b, 2010; Muona & Teräväinen, 2020). The rich Mesozoic fossil deposits from China have provided an unexpected and most welcome surprise – several different eucnemid fossils belonging to these four subfamilies (Chang et al., 2016; Muona et al., 2020; Li et al., 2021). *Palaeoxenus clavatus* n. sp. from the same deposits as *Paradesmatus baiae* is the latest one to be added in this list.

The known history of the eucnemid subfamily Palaeoxeninae now spans over 163 million years: *Palaeoxenus clavatus* n. sp. (Jurassic China), *Palaeoxenus sinensis* Chang, Muona & Teräväinen (Early Cretaceous China), *Cupressicharis elongatus* Muona (Cenomanian Myanmar) and *Palaeoxenus dohrni* (Horn) (alive and clicking in Southern California).

Such an evolutionary series may appear to be of marginal specialist interest only, but the phylogenetic implications are wider. First, Palaeoxeninae is the sister-group of the presently dominant DE clade. Pseudomeninae, Schizophilinae and Anischiinae have split of this combined clade before DE and Paleoxeninae diverged. By combining the result of the phylogenetic analyses with the Chinese fossil records it now can be established that all these extant eucnemid clades existed at least 163 million years ago.

Second, although the majority of extant eucnemids, the DE clade, breed in white-rot angiosperm wood infested by bracket fungi, the origins of this clade are from the time when no angiosperms existed. As the specialized *Palaeoxenus* larval structures are similar to the ones found in the DE group larva, they all reflect adaptation to something not related to co-evolution with the angiosperms. The obvious answer is in the mode of feeding (Muona & Teräväinen, 2008). The eucnemid larvae specialized in feeding extraorally fungal hyphae from solid substrate, the wood of gymnosperms. Once the angiosperms became dominant, the eucnemids invaded them together with the fungi. As pointed out earlier (Muona, 2021), this innovation may be connected with the fact that some fungi are able to infest both gymno- and angiosperms.

Both the absence of modern type eucnemid fossils before late Cretaceous (Otto, 2018; Muona, 2020) as well as their significant diversity in Eocene amber (Muona, 1993a) support DE clade diversification during the angiosperm explosion. However, the ability to succeed in doing so was tied to the co-evolution with fungi, not the type of plant the fungi attacked.

Finally, we wish to stress that morphological adaptations as extreme as the ones found in the derived eucnemid larval types can evolve in a context different from what we observe today. Although prevalent in angiosperms today, it originated in species utilizing fungi in gymnosperms. Functional preadaptation is a possibility one should not ignore when discussing evolutionary scenarios.

Acknowledgements

This work was supported by grants from the National Natural Science Foundation of China (42288201, 32020103006), Support project for high -ranking teachers at urban universities in Beijing (BPHR20220114) (D.R.) as well as grants (H.L.C.) from the National Natural Science Foundation of China [grant no. 41702021] and (JM) the Finnish Academy of Sciences (grant 79243) and the Entomological Society in Helsinki (JM).

References

Chang, H, Kirejtschuk, AG, Ren, D. & Shih, C. 2009. First Fossil Click Beetles from the Middle Jurassic of Inner Mongolia, China (Coleoptera: Elateridae). Annales Zoologici, 59(1):7-14.

Chang, H., Muona, J., Pu H., Xu, L., Wang C., Teräväinen, M., Ren, D., Yang, Q., Zhang, X. & Jia S. 2015. Chinese Cretaceous larva exposes a southern Californian living fossil (Insecta, Coleoptera, Eucnemidae). Cladistics - the international journal of the Willi Hennig Society. 32:211–214. https://doi.org/10.1111/cla.12124

Li, H.; Chang, H.; Muona, J.; Zhao, Y.; Ren, D. 2021. Subfamily Anischiinae (Coleoptera: Eucnemidae) in Early Cretaceous of Northeast China. Insects, 12, 105. https://doi.org/10.3390/insects12020105

Muona, J. 1993a. Eucnemidae and Throscidae in Baltic Amber. Entomologische Blätter für Biologie und Systematik der Käfer 89, 15–45.

Muona, J. 1993b. Review of the phylogeny, classification and biology of the family Eucnemidae (Coleoptera). Entomologica Scandinavica. Supplement 44: 1–133.

Muona, J. 2010. 4.5. Eucnemidae. In: Beutel, R., Lawrence, J. F., Leschen, R. (toim.). Handbuch der Zoologie/Handbook of Zoology, Band IV. Arthropoda: Insecta. Teilband, Part 42. Coleoptera, Beetles. De Gruyter, Berlin.Volume 2: 61–68.

Muona, J. 2020. The late Cretaceous amber Eucnemidae fossils from Myanmar. Entomologische Blätter und Coleoptera. 2020, 116, 27–55.

Muona, J. 2021. How do Vanhorniidae (Hymenoptera) parasitize Eucnemidae? (Coleoptera). Insecta Mundi 0867: 1–10.

Muona, J., Chang, H, & Ren, D. 2020. The Clicking Elateroidea from Chinese Mesozoic Deposits (Insecta, Coleoptera). Insects 2020, 11, 875.

Muona, J., Teräväinen, M. 2008. Notes on the biology and morphology of false click-beetle larvae (Coleoptera: Eucnemidae). Coleopterists Bulletin 62; 475–479.

Muona, J., Teräväinen, M. 2020. A Re-evaluation of he Eucnemidae larval characters (Coleoptera). Papéis Avulsos de Zoologia, 60.special-issue: e202060(s.i.).28, 13 pp. http://doi.org/10.11606/1807-0205/2020.60.special-issue.28

Otto R. L. 2018. Descriptions of two new elateroid beetles (Coleoptera: Eucnemidae, Elateridae) from Burmese amber. Insecta Mundi, 702: 1–6.

Ren, D.; Shih, C.; Gao, T.; Wang, Y.; Yao, Y. 2019. Rhythms of Insect Evolution—Evidence from the Jurassic and Cretaceous in Northern China; John Wiley et Sons: Hoboken, NJ, USA. 710p.

Ren, D. & Krzeminski, W. 2002. Eoptychopteridae (Diptera) from the Middle Jurassic of China. Annales Zoologici, 52(2), 207–210.

Tan, J.J. & Ren, D. 2002. Palaeoecology of insect community from Middle Jurassic Jiulongshan Formation in Ningcheng County, Inner Mongolia, China. Acta Zootaxonomica Sinica, 27, 428–434. (in Chinese.)

Yang, Z. & Jiang, B. 2015. Paleoenvironmental reconstruction of the Middle-Late Jurassic Daohugou Biota in Ningcheng County, Inner Mongolia, Northeast China [A]. Palaeontological Society of China. Abstact Volume, The 28th Annual Conference of the Palaeontological Society of China [C]. Palaeontological Society of China: Palaeontological Society of China, 2015:2.

Zheng, N. 2010. Geological period and Environmental Change of Daohugou Biota [D]. China University of Geosciences (Beijing).

Author's adresses

Jyrki Muona
Finnish Museum of Natural History
P.O.Box 17
FIN-00014 University of Helsinki
jyrki.muona@helsinki.fi
0000-0003-2771-1171

[1] College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University, Xisanhuanbeilu 105, Haidian District, Beijing 100048, China; rendong@cnu.edu.cn (D.R.); 2190802111@cnu.edu.cn (H.L.)

[2]Henan Geological Museum, Jinshuidonglu 18, Zhengdongxin Dsitrict, Zhengzhou 450016, China; changxinyin07@gmail.com

[3]Entomology Team, Zoology Unit, Finnish Museum of Natural History, FIN-00014 University of Helsinki, 00100 Helsinki, Finland; jyrki.muona@helsinki.fi
ORCID: https://orcid.org/0000-0003-2771-1171

* Correspondence: jyrki.muona@helsinki.fi

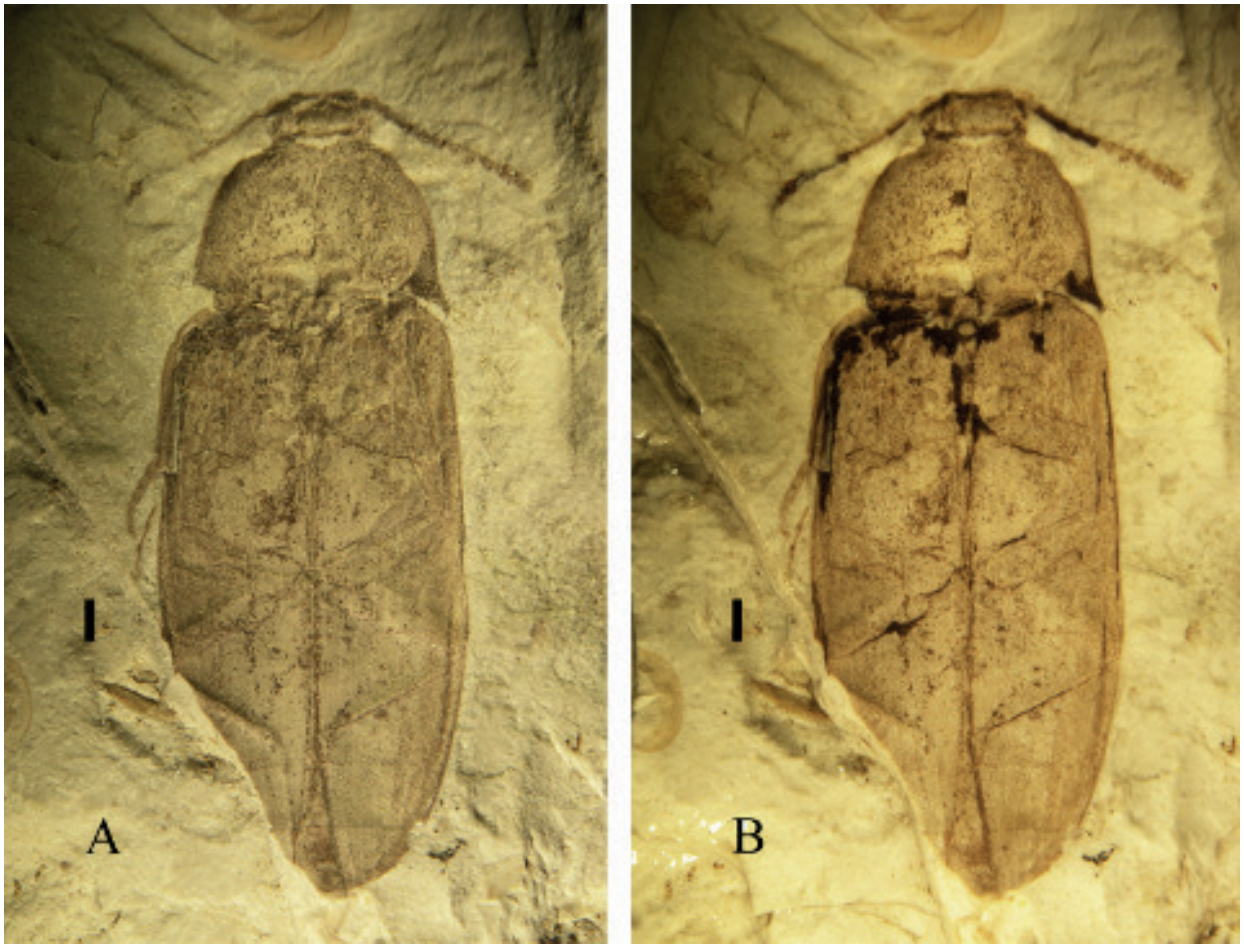


Fig. 1. *Palaeoxenus clavatus* n. sp. Holotype CNU-COL-NN2018348. Dorsal view. A: Dry fossil. B: Fossil covered in ethanol. Scale bar = 1mm.

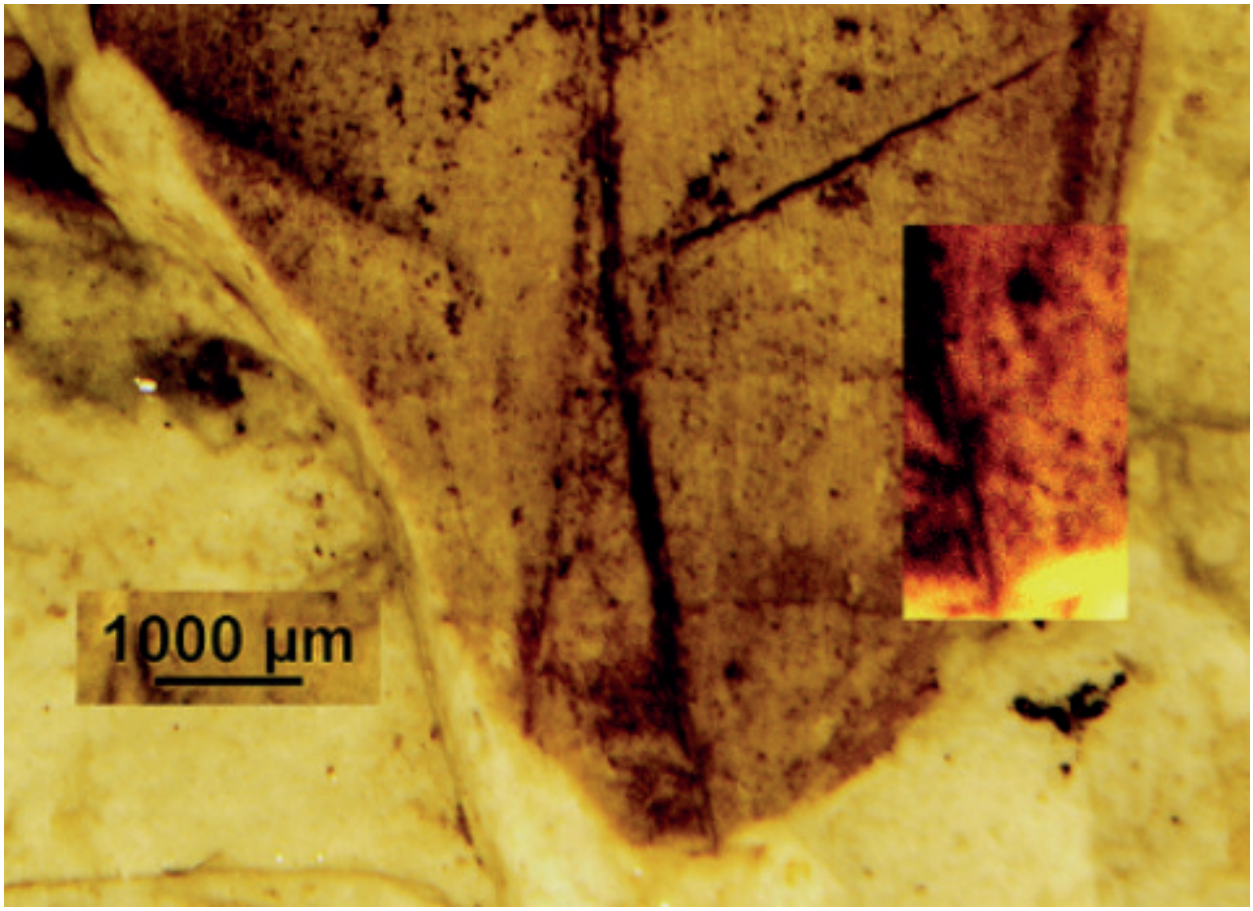


Fig. 2. *Palaeoxenus clavatus* n. sp. Holotype CNU-COL-NN2018348. Tip of elytra. A magnification of the extreme apical part of right elytron on right showing a pale row of enlarged excretory punctures along apex of sutural stria. Scale bar = 1mm.

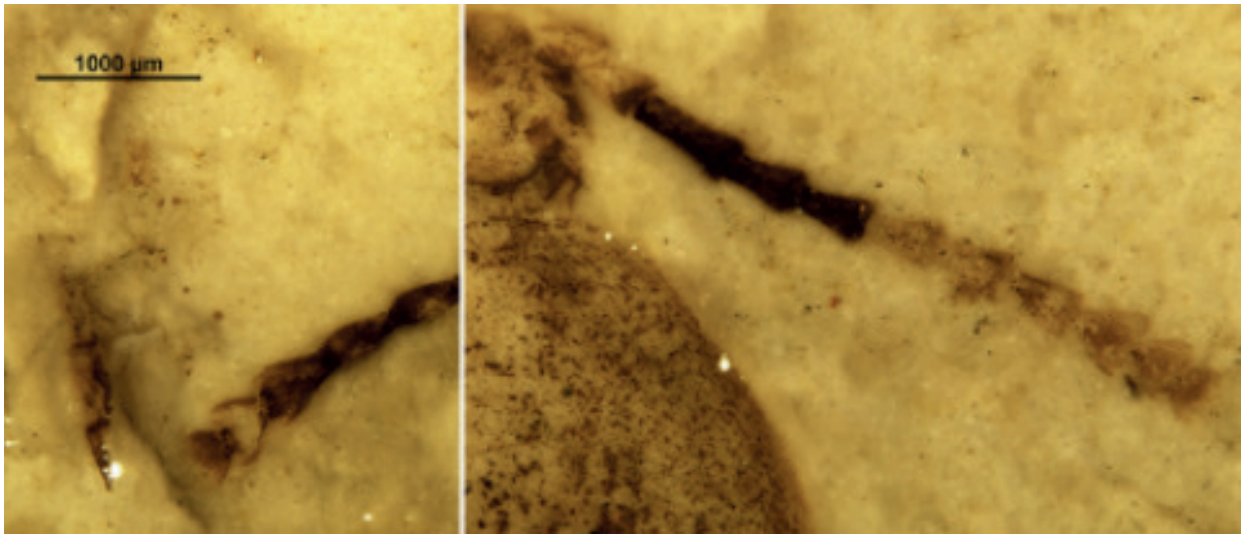


Fig. 3. *Palaeoxenus clavatus* n. sp. Holotype CNU-COL-NN2018348. Antennae. Left: apex of left antenna with apically excavated flagellomeres 7-9. Right: complete right antennae with subapically attached pedicel and elongated flagellomeres 1-6. Scale bar = 1mm