



General palaeontology, Systematics, and Evolution (Invertebrate Palaeontology)

The oldest Cenozoic passandrid (Coleoptera: Cucujoidea: Passandridae) from the Paleocene of Menat (France)



Le plus ancien passandride cénozoïque (Coleoptera: Cucujoidea: Passandridae) du Paléocène de Menat (France)

Alexander G. Kirejtshuk^{a,*,c,d}, Alexey V. Kovalev^{a,*,b}, André Nel^{c,d}

^a Zoological Institute RAS, Universitetskaya nab., 1, 199034 Saint Petersburg, Russia

^b All-Russian Institute of Plant Protection of the Russian Academy of Agricultural Sciences, shosse Podbelskogo, 3, 196608 St. Petersburg-Pushkin, Russia

^c CNRS, MNHN, UPMC, EPHE, Muséum national d'histoire naturelle, Sorbonne Universités, 57, rue Cuvier, CP 50, Paris, France

^d Entomologie, 45, rue Buffon, 75005 Paris, France

ARTICLE INFO

Article history:

Received 17 May 2019

Accepted after revision 9 October 2019

Available online 23 November 2019

Handled by Annalisa Ferretti

Keywords:

Fossil record

Classification

New genus

New species

France

Mots clés :

Registre fossile

Classification

Nouveau genre

Nouvelle espèce

France

ABSTRACT

The new oldest representative of the subfamily Passandrinae (Passandridae) was found in materials from Menat (Puy-de-Dôme, France). It was preliminarily assigned to the genus *Passandra* Dalman in Schönherr, 1817, although the new species (?) *Passandra plenaria* sp. n., in contrast to other congeners, demonstrates an exposed labrum and an absence of preapical groove or impression on the hypopygidium. Some notes on fossil records and classification of the family Passandridae are made. The distinctiveness of the families Passandridae and Laemophloeidae in light of the new data on fossils is considered, and the attribution of *Mesopassandra* Jin, Ślipiński, Zhou and Pang, 2019 (type genus of Mesopassandrinae) to the family Passandridae is regarded as problematic.

© 2019 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

R É S U M É

Le nouveau représentant le plus ancien de la sous-famille Passandrinae (Passandridae) est décrit du Paléocène de Menat (Puy-de-Dôme, France). Il est attribué de manière préliminaire au genre *Passandra* Dalman in Schönherr, 1817, bien que la nouvelle espèce (?) *Passandra plenaria* sp. n., contrairement à ses congénères, possède un labrum exposé, mais n'a ni sillon préapical, ni impression hypopygiale. Le registre fossile et la classification des Passandridae sont discutés. La séparation entre les deux familles Passandridae et Laemophloeidae à la lumière des nouvelles données sur les fossiles est discutée. L'attribution de *Mesopassandra* Jin, Ślipiński, Zhou et Pang, 2019 (genre type des Mesopassandrinae) aux Passandridae est considérée comme problématique.

© 2019 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

* Corresponding authors.

E-mail addresses: kirejtshuk@gmail.com (A.G. Kirejtshuk), melasis313@gmail.com (A.V. Kovalev), andre.nel@mnhn.fr (A. Nel).

1. Introduction

The cucujoid family Passandridae Blanchard, 1845 is represented by somewhat more than one hundred of species of nine genera in the extant fauna, mostly from tropical and subtropical territories (Jin et al., 2019), with a reduced fossil record Kirejtshuk and Ponomarenko, 2019; Klebs, 1910; Menge, 1856, etc.). All recent members of this family seem to be associated with wood; the larvae are known as ectoparasites on wood-inhabiting insect larvae or pupae, such as longhorn beetles, bark and ambrosia beetles, weevils, and hymenopterans. One fossil species was described as a member of this family, *Passandra septentrionaria* Bukejs et al., 2016 from the Eocene Baltic amber. Jin et al. (2019) described a new species from the Upper Cretaceous Burmese amber, for which a new genus and a new subfamily were proposed (*Mesopassandra* Jin, Ślipiński, Zhou et Pang, 2019 (type genus of Mesopassandrinae Jin, Ślipiński, Zhou et Pang, 2019: see below § Discussion). Besides, one fossil species (*Catogenus punctatus* Ramírez, Consorini and di Orio, 2016 from the middle Eocene of Argentina), initially described as a passandrid (Ramírez et al., 2016), was later transferred to cucujids (Jin et al., 2019). In this paper, one new species is described from the Paleocene of Menat, which is the oldest member of the family Passandridae or of the subfamily Passandrinae *sensu stricto* (if *Mesopassandra* can really be placed in the passandrids).

2. Material and methods

The holotype of the new species is deposited in the Menat Town Museum, Village of Menat, Puy-de-Dôme, France (further MTM). This specimen was studied using a stereomicroscope Olympus SCX9 with an Olympus camera in MNHN, a stereomicroscope Nikon SMZ25, a camera Nikon D800, and also with a Tescan Vega LSU scanning electron microscope in MNHN with the Low Vacuum Secondary Electron TESCAN Detector (LVSTD).

3. Geological setting and locality information

The middle Paleocene Menat fossil site (Menat Basin, Puy-de-Dôme, France) is a volcanic maar containing a paleolake ca. 1 km in diameter (46°06' N; 2°54' E), which at present contains sedimentary rocks (spongo-diatomites) with remains of diverse aquatic and terrestrial flora and fauna (Piton, 1940; Nel, 1989, 2008; etc.). The composition of the faunal and floral remains makes it possible to conclude that this lake was surrounded by a forest. The palaeoenvironment was warm and humid (Wedmann et al., 2018). Following the pollen, mammalian stratigraphic, and radiometric K/Ar analyses, the age of Menat was estimated at 59 Myr (Kedves and Russel, 1982; Nel, 2008). However, the new estimate based on macroflora postulated its age within 60–61 Myr (Wappler et al., 2009). Some preliminary results of studies on the beetle fauna from Menat outcrop were published by Nabozhenko and Kirejtshuk (2014, 2017), Kirejtshuk et al. (2016), Legalov et al. (2017), and Kirejtshuk and Nel (2018).

4. Systematics

Family: PASSANDRIDAE Blanchard, 1845

Subfamily: PASSANDRINAE Blanchard, 1845

Passandra Dalman, 1817

Type species: *Passandra sexstriata* Dalman, 1817, by monotypy

= *Hectarthrum* Newman, 1838 (type species: *Hectarthrum curtipes* Newman, 1838, by monotypy)

Notes. The new species should be regarded as a member of the generic complex with 11-segmented antenna, a short tarsomere 1, and the absence of the median groove of the head (*Catogenus* Westwood, 1830, *Passandra*, *Passandrina* Reitter, 1878, *Nicolebertia* Burckhardt and Ślipiński, 1995). It is preliminarily assigned to the genus *Passandra* due to the smaller number of grooves on elytra and the probable absence of shoulder ribs (characteristic of *Catogenus* and *Nicolebertia*). Besides, the new species has no observable pronotal sublateral lines, present in almost all extant species of *Passandra* (except *Passandra sexstriata* Dalman, 1817). Also the Eocene species *P. septentrionaria* possesses these lines only in the basal one-third of the pronotum. However, the new species is distinct from the latter in the different configuration of the grooves on its head. The admedian grooves of the head of the new species are very weak to unclear and do not reach the occipital groove (as in *Passandra sexstriata*); while in other congeners they are distinct, more or less deep and reach the occipital groove (in general, the admedian grooves of the head of the new species are reminiscent of those in members of *Catogenus* and *Nicolebertia*). The abdominal ventrite 5 (hypopygidium) has no trace of preapical groove or impression observable in other species of the generic complex (*Catogenus*, *Passandra*, *Passandrina* and *Nicolebertia*) and most other passandrid genera, except for *Ancistria* Erichson, 1845 (Burckhardt and Ślipiński, 2003). Unfortunately, the presence or absence of the oblique keel of the ultimate antennomere is untestable in the holotype of the new species (the ultimate antennomere of the mentioned four genera with a sharp keel or “indistinctly keeled” in *Nicolebertia*: Burckhardt and Ślipiński, 2003). Finally, the Passandrinae is characterized by the small labrum inclined ventrally between mandibles and not visible from above. The labrum of the new species is shaped as in other passandrines, but clearly visible in the imprints of the holotype examined. Thus, the new species is most similar to the species of *Passandra* (defined by Burckhardt and Ślipiński, 2003; Ślipiński, 1987), although it demonstrates the exposed labrum and the absence of preapical groove or impression on its hypopygidium, and it is a reason why its attribution is here considered as preliminary.

(?) *Passandra plenaria* sp. n.

(Figs. 1–4)

Etymology. The species name derives from the Latin “*plenarius*” (complete, finished).

Type locality and stratum. Menat Basin, Puy-de-Dôme, France. Middle Paleocene (46°06' N; 2°54' E), collected in a new, small outcrop near the south-east of the village of Menat.

Holotype: “Nel 3036,” imprint and counterimprint (obliquely cracked through its mid-length), well preserved

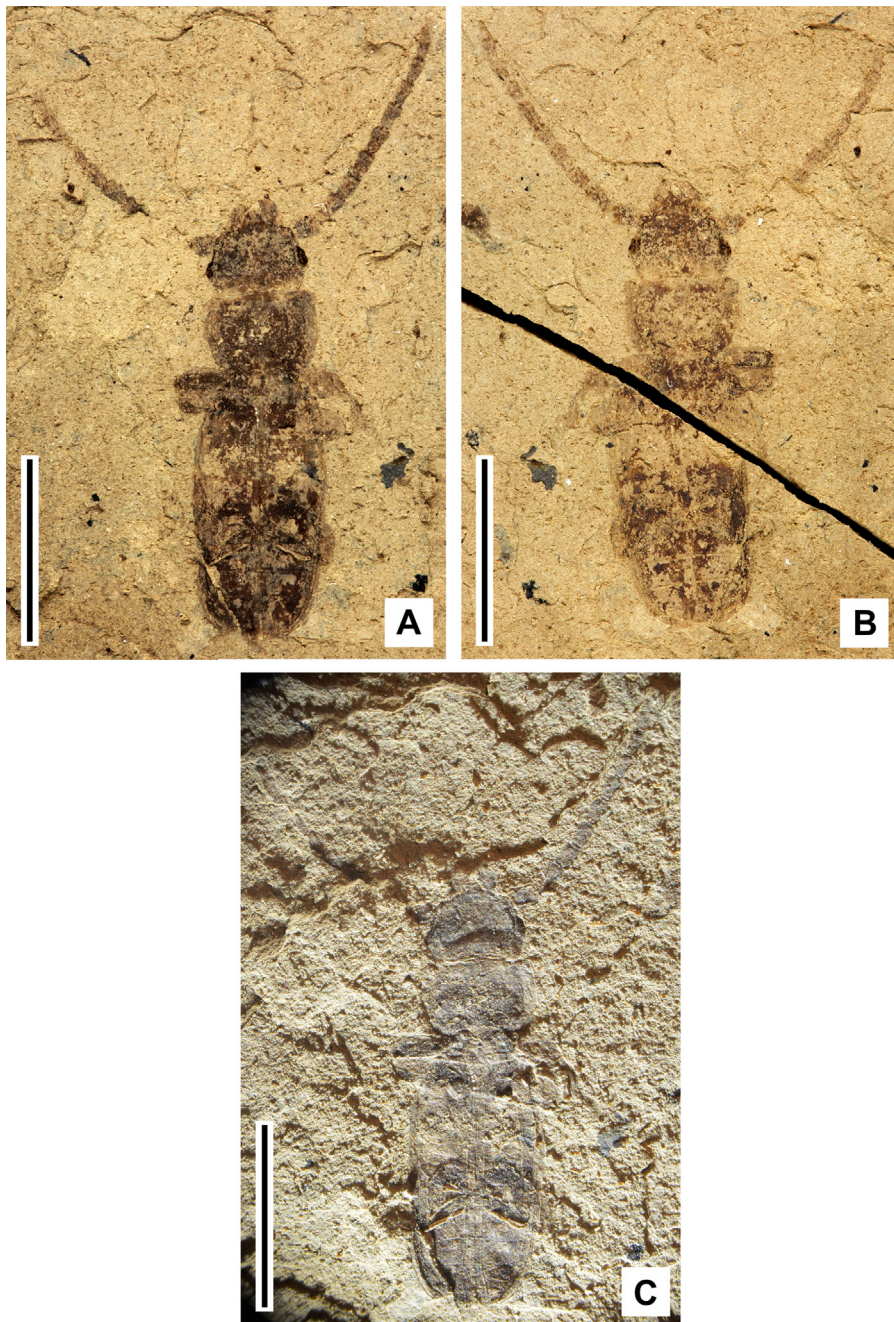


Fig. 1. (?) *Passandra plenaria* sp. n., holotype. Habitus. **A:** Imprint; **B:** counterimprint; **C:** imprint. Scales: 5.0 mm.

Fig. 1. (?) *Passandra plenaria* sp. n., holotype. Habitus. **A:** Empreinte ; **B :** contre-empreinte ; **C :** empreinte. Échelles : 5,0 mm.

on rather smooth piece of rock; the specimen shows the main parts of body sclerites in upper and lower views, but some left antennomeres, three tibiae and most tarsomeres are missing.

Description of holotype. Body length 11.8 mm, maximum width 3.6 mm. Body elongate-oval, 3.3 times as long as wide.

Head slightly narrower than pronotum; impunctate. Admedian grooves diverging anteriorly, expressed in

anterior third of head length and becoming obliterated posteriorly, sublateral grooves well developed throughout their entire lengths, curved along lateral angles of frons and joined posteriorly to the occipital groove; occipital groove clear, sinuate medially. Median projection of frons moderately narrow, with emarginate anterior margin (Fig. 2A and Fig. 4A). Eyes moderately small, apparently about as long as antennomere 1 (scape) wide, slightly prominent, moderately convex. Antennae long and slender, extending to the

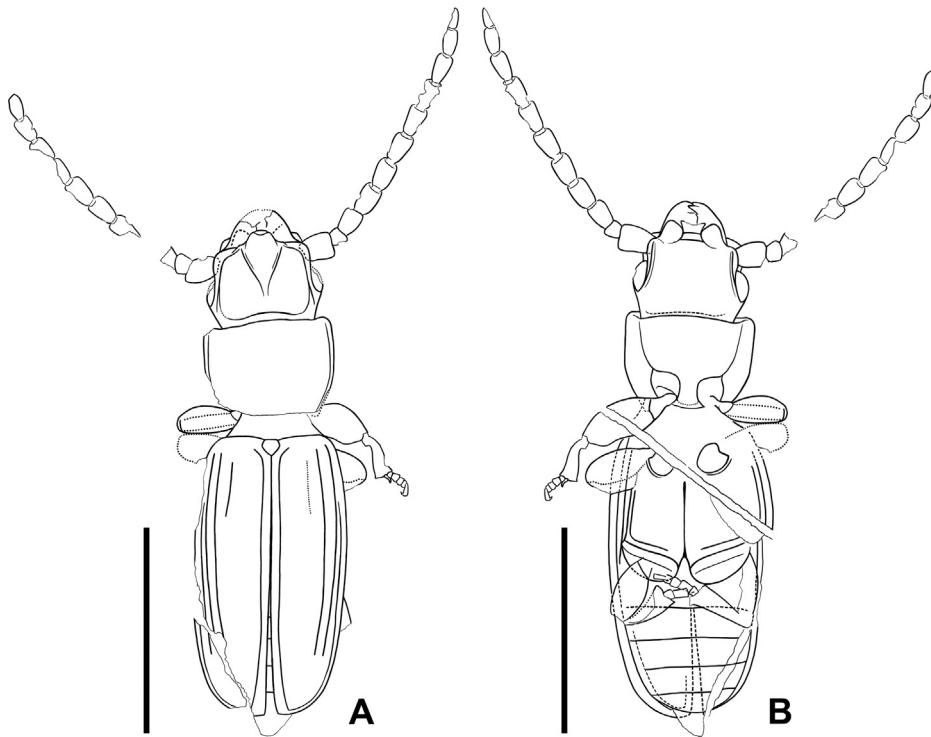


Fig. 2. (?) *Passandra plenaria* sp. n., holotype. Body reconstructions. **A:** Dorsal; **B:** ventral. Body length: 11.8 mm. Scales: 5.0 mm.

Fig. 2. (?) *Passandra plenaria* sp. n., holotype. Reconstruction du corps. **A :** Dorsale ; **B :** ventrale. Longueur du corps : 11,8 mm. Échelles : 5,0 mm.

basal one-third of the elytra; scape large, subcylindrical, about 1.2× as long as wide; pedicel small, about as long as wide and approximately 0.6 times as long as antennomere 3; antennomeres 3–10 subcylindrical and slightly thickened apically, about twice as long as wide; antennomere 11 elongate-oval, about twice as long as wide.

Pronotum slightly transverse, 1.1 times as wide as long, widest at anterior angles, sides subparallel in anterior two-thirds and distinctly narrowed posteriad. Anterior angles slightly protruding, subrectangular, narrowly rounded; anterior margin slightly bisinuate, with bordering joined to bordering of pronotal sides; pronotal sides with narrow and complete border. Disc impunctate; sublateral lines absent.

Scutellum moderately large, about as long as wide, pentagonal. Elytra about 1.8 times as long as their combined width; base markedly wider than the pronotal posterior margin. Elytra with three complete striae (1, 5, 6); stria 1 grooved throughout entire length and joined at apex to the bordering of the elytral sides; striae 5 and 6 grooved in basal four-fifths of the length; stria 4 distinct in basal fourth of the elytral length, striae 2 and 3 indistinct. Intervals smooth.

Legs short and robust. Femora rather thick. Protibia looking like moderately and metatibia rather wide. Pro- and metatarsi five-segmented. Tarsomere 1 of pro- and metatarsi short, distinctly shorter than tarsomere 2, partly covered by tibial apex; tarsomeres 2–4 short; protarsomere 5 about as long as tarsomeres 3–4 combined. Protarsal claws small.

Abdomen with five ventrites; ventrite 5 without visible groove or impression along the posterior margin.

5. Discussion and conclusions

The extant members of the family Passandridae are distributed mostly in tropical and subtropical territories beyond Europa. Only few species of *Passandra*, *Ancistria*, and *Aulonosoma* Motschulsky, 1858 have been recorded in the southern part of the Palearctic Asia, including South Korea, and Japan (Jin et al., 2019; Park et al., 2005), while two fossil species of the subfamily Passandrinae *sensu str.* originated from European outcrops of the Paleogene (Baltic amber: Alekseev et al. (2016) and Menat); however, one species of the subfamily Mesopassandrinae was found in the Albian–Cenomanian (most probably earliest Cenomanian) Burmese amber (Jin et al., 2019). The latter subfamily demonstrates some characters that make it possible to assign it to the family Passandridae as well as to the family Laemophloeidae, and its placement needs to be clarified by new data and arguments. Most diagnostic peculiarities of the Mesozoic subfamily (labrum broad and well exposed dorsally, mandibles narrow, strongly angled externally and bidentate apically, antennae with antennomere 3 distinctly longer than antennomeres 4 or 5, and male tarsal formula 5–5–4) occur in various members of Laemophloeidae. Crowson (1967) argued for the distinctiveness of the family Passandridae mostly by the presence of confluent gular sutures and of contiguous anterior tendons in adults, while all other “clavicornian” families (Cucujoidea *sensu lato*, including cerylonid-families or Coccinelloidea) have separate gular sutures. Crowson (1967) linked this family with Cucujidae (including Silvaninae, Phlaeostichinae,

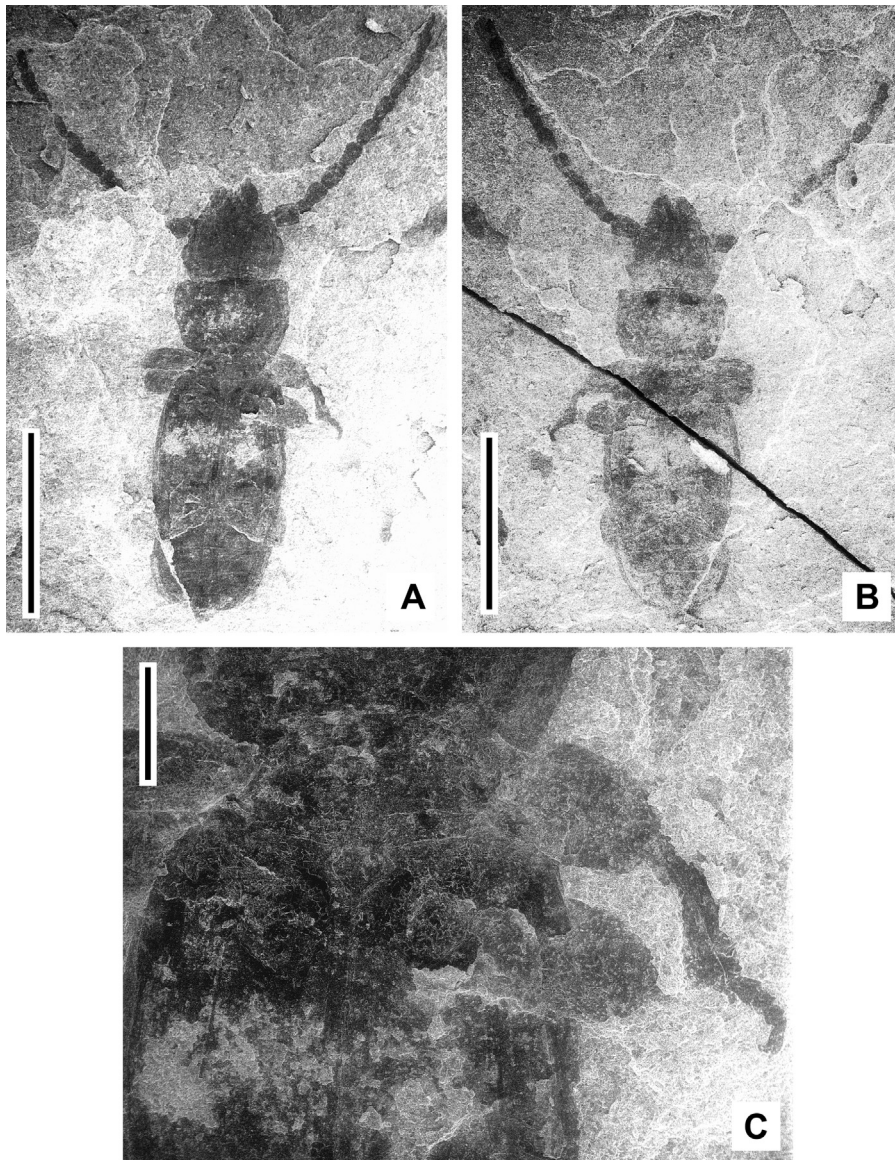


Fig. 3. (?) *Passandra plenaria* sp. n., holotype. Photographs under Tescan Vega LSU scanning electron microscope (LVSTD). **A:** Body, imprint; **B:** body, counterimprint; **C:** thorax, imprint. Scales: 5.0 mm for **A** and **B**, 1.0 mm for **C**.

Fig. 3. (?) *Passandra plenaria* sp. n., holotype. Photographies au microscope électronique à balayage Tescan Vega LSU (LVSTD). **A :** Corps, empreinte ; **B :** corps, contre-empreinte ; **C :** thorax, empreinte. Échelles : 5,0 mm pour **A** et **B**, 1,0 mm pour **C**.

Laemophloeinae, Prostominae). [Burckhardt and Ślipiński \(2003\)](#) added to the above-mentioned diagnostic characters of Passandridae also the “large mandibles with exposed articulation,” “usually closed mesocoxal cavities” and “strongly inequal tibial spurs”. However, the gular sutures that in Passandridae should be confluent at the base of the head are not observable in *Mesopassandra*. Moreover, the convergent paramedian longitudinal impressions behind the mentum can be traced in some passandrids and they are reminiscent of gular sutures of other cucujoids. [Lawrence and Ślipiński \(2013\)](#) indicated strongly projecting the genal process (“jugular lobes”) as an important passandrid character. Their presence in *Mesopassandra* was

interpreted by [Jin et al. \(2019\)](#) as a strong hint allowing to place it among passandrids. However, the development of these processes demonstrates a great variability in this family and scarcely can be a reliable indication of a passandrid attribution. Also, the tibial spurs of laemophloeids are unequal and generally much smaller than those of passandrids. Thus, the tibial spurs also are equivocal characters for this family. The same pertains the closed mesocoxal cavities and some other ambiguous structural peculiarities of *Mesopassandra* (bifid mandibular apices, wide and exposed labrum, narrowly separated meso- and metacoxae, etc.). The sexual dimorphism in tarsal formula can be interpreted as a scarcely plesiomorphic cucujoid character, as was

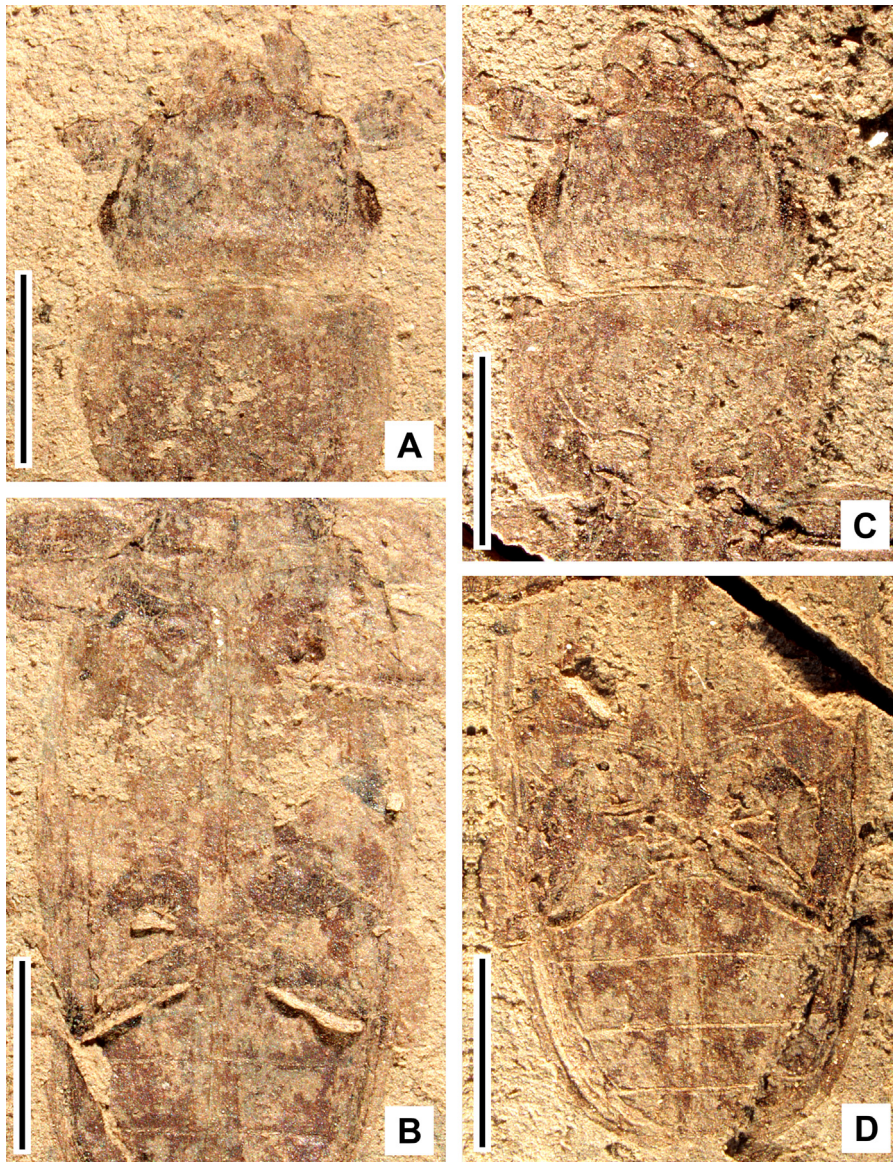


Fig. 4. (?) *Passandra plenaria* sp. n., holotype. Photographs under Olympus SCX9 with camera Olympus. **A:** Head and prothorax, imprint; **B:** pterothorax and abdomen, imprint; **C:** head and prothorax, counterimprint; **D:** pterothorax and abdomen, counterimprint. Scales: 2.0 mm.

Fig. 4. (?) *Passandra plenaria* sp. n., holotype. Photographies sous Olympus SCX9. **A :** Tête et prothorax, empreinte ; **B :** ptérothorax et abdomen, empreinte ; **C :** tête et prothorax, contre-empreinte ; **D :** ptérothorax et abdomen, contre-empreinte. Échelles : 2,0 mm.

supposed by Jin et al. (2019). As a result, only the “mandibles with exposed articulation” remain an argument to link this genus with passandrids. Therefore, it is reasonable to regard its attribution to Passandridae as rather problematic, needing further arguments thanks to additional fossil material. Besides, the distinctiveness between this family and Laemophloeidae also needs a detailed analysis.

Acknowledgments

Sylvain Pont (Laboratoire de minéralogie et de cosmochimie, MNHN) provided the authors with the

possibility of studying the holotypes by electronic microscopy. The authors had the pleasure to receive generous assistance from Clotilde Berger-Pompili and Mathilde Leygnac, directors of the EHPAD du Pays de Menat, for their kind help and authorisations to collect fossil insects in a small but rich outcrop near the village of Menat (Puy-de-Dôme, France). The work by the Russian co-authors was partly carried out under the framework of the Russian State research project No. AAAA-A19-119020690101-6, programs of the Presidium of the Russian Academy of Sciences “Evolution of organic world and planet processes,” Muséum national d’histoire naturelle (Paris), French Sorbonne Universités (Programme d’accueil de chercheurs

de haut niveau) and the Russian Foundation of Basic Research (grants Nos. 18-04-00243-a and 19-0400465-a). The authors greatly appreciate useful comments on an earlier version of the manuscript received from anonymous reviewers.

References

- Bukejs, A., Alekseev, V.I., McKellar, R.C., 2016. *Passandra septentrionaria* sp. nov.: the first described species of Passandridae (Coleoptera: Cucujoidea) from Eocene Baltic amber. *Zootaxa* 4144 (1), 117–123, <http://dx.doi.org/10.11646/zootaxa.4144.1.7>.
- Burckhardt, D., Ślipiński, S.A., 2003. Phylogeny and taxonomy of the world Passandridae (Coleoptera). In: Cuccodore, G., Leschen, R. (Eds.), *Systematics of Coleoptera: Papers celebrating the retirement of Ivan Löbl*. *Memoirs on Entomology, International*. Vol. 16, 99. Associated Publishers, Gainesville, FL, USA, pp. 753–883.
- Crowson, R.A., 1967. The natural classification of the families of Coleoptera. *EW. Classey Ltd., Middlesex*, 214 p.
- Jin, M., Ślipiński, A., Zhou, Y.-L., Pang, H., 2019. Mesopassandrinae subfam. nov., a basal group of parasitic flat beetle (Coleoptera: Passandridae) from the Cretaceous Burmese amber. *J. Syst. Palaeontol.*, <http://dx.doi.org/10.1080/14772019.2019.1584923>.
- Kirejtshuk, A.G., Nel, A., 2018. Nitidulidae (Coleoptera) from the Paleocene of Menat (France). *Zootaxa* 4402 (1), 1–41, <http://dx.doi.org/10.11646/zootaxa.4402.1.1>.
- Kirejtshuk, A.G., Nel, A., Kirejtshuk, P.A., 2016. Taxonomy of the reticulate beetles of the subfamily Cupedinae (Coleoptera, Archostemata), with a review of the historical development. *Invertebr. Zool.* 13 (2), 61–190, <http://dx.doi.org/10.15298/invertzool.13.2.01>.
- Kirejtshuk, A.G., Ponomarenko, A.G., 2019. Catalogue of fossil Coleoptera. In: *Beetles (Coleoptera) and Coleopterologists*. Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia, Updated May 2019 [updated at <http://www.zin.ru/Animalia/Coleoptera/rus/paleosys.htm>].
- Kedves, M., Russel, D.E., 1982. Palynology of the Thanetian layers of Menat. The geology of the Menat basin, France. *Palaeontographica B* 182, 87–150.
- Klebs, R., 1910. Über Bernsteineinschlüsse in allgemeinen und die Coleopteren meiner Bernsteinsammlung. *Schrift. d. Phys.-ökonom. Gesellsch. zu Königsberg* 51, 217–242.
- Lawrence, J.F., Ślipiński, S.A., 2013. *Australian Beetles. Morphology, Classification and Keys*, Volume 1. CSIRO Publishing, Collingwood, ON, Canada, 561 p.
- Legalov, A.A., Kirejtshuk, A.G., Nel, A., 2017. New and little known weevils (Coleoptera: Curculionoidea) from the Paleocene of Menat (France). *C. R. Palevol* 16, 248–256, <http://dx.doi.org/10.1016/j.crpv.2016.10.007>.
- Menge, A., 1856. *Lebenszeichen vorweltlicher, im Bernstein eingeschlossener Thiere*. In: *Programm der öffentlichen Prüfung der Schüler der Petrischule*. A.W. Kafemann, Danzig, 32 p.
- Nabozhenko, M.V., Kirejtshuk, A.G., 2014. New genus and species of the tribe Helopini (Coleoptera: Tenebrionidae) from Palaeocene of Menat (France). *C. R. Palevol* 13, 65–71, <http://dx.doi.org/10.1016/j.crpv.2013.09.005>.
- Nabozhenko, M.V., Kirejtshuk, A.G., 2017. The oldest opatrine terrestrial darkling beetle (Coleoptera: Tenebrionidae: Tenebrioninae) from the Paleocene of Menat (France). *Paläontol. Z.* 91, 307–313, <http://dx.doi.org/10.1007/s12542-017-0368-2>.
- Nel, A., 1989. Les Gyrinidae fossiles de France (Coleoptera). *Ann. Soc. Entomol. Fr. (N.S.)* 25 (3), 321–330.
- Nel, A., 2008. The oldest bee fly in the French Paleocene (Diptera: Bombyliidae). *C. R. Palevol* 7 (7), 401–405, <http://dx.doi.org/10.1016/j.crpv.2008.08.001>.
- Park, J.-S., Yang, K.-M., Ahn, K.-J., 2005. First Record of the Family Passandridae in Korea (Coleoptera: Cucujoidea). *Entomol. Res.* 35 (3), 173–175, <http://dx.doi.org/10.1111/j.1748-5967.2005.tb00155.x>.
- Piton, L., 1940. Paléontologie du gisement éocène de Menat (Puy-de-Dôme), flore et faune. *Mem. Soc. hist. nat. Auvergne, Clermont-Ferrand, France* 1, 1–303.
- Ramírez, L.C., Corsolini, J., Di Iorio, O., 2016. First fossil record of parasitic flat-bark beetle (Coleoptera: Passandridae) from the Eocene of Patagonia, Argentina. *Ameghiniana* 53, 160–169, <http://dx.doi.org/10.5710/AMGH.29.11.2015.2920>.
- Ślipiński, S.A., 1987. A review of the Passandridae of the World (Coleoptera, Cucujoidea). I—Genus *Passandra* Dalman. *Ann. Mus. Civ. Stor. Nat. Genova* 86, 553–603.
- Wappler, T., Currano, E.D., Wilf, P., Rust, J., Labandeira, C.C., 2009. No post-Cretaceous ecosystem depression in European forests? Rich insect feeding damage on diverse middle Palaeocene plants, Menat, France. *Proc. R. Society London (B)* 276, 4271–4277, <http://dx.doi.org/10.1098/rspb.2009.1255>.
- Wedmann, S., Uhl, D., Lehmann, T., Garrouste, R., Nel, A., Gomez, B., Smith, K.T., Schaal, S.F.K., 2018. The Konservat-Lagerstätte Menat (Paleocene; France) – an overview and new insights. *Geol. Acta* 16 (2), 189–213, <http://dx.doi.org/10.1344/GeologicaActa2018.16.2.5>.