

## **First Fossil Record of Polypore Fungus Beetles from Lower Cretaceous Amber of France**

Authors: Soriano, Carmen, Pollock, Darren, Néraudeau, Didier, Nel, Andre, and Tafforeau, Paul

Source: Acta Palaeontologica Polonica, 59(4) : 941-946

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2012.0074>

---

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](http://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# First fossil record of polypore fungus beetles from Lower Cretaceous amber of France

CARMEN SORIANO, DARREN POLLOCK, DIDIER NÉRAUDEAU, ANDRE NEL,  
and PAUL TAFFOREAU



Soriano, C., Pollock, D., Néraudeau, D., Nel, A., and Tafforeau, P. 2014. First fossil record of polypore fungus beetles from Lower Cretaceous amber of France. *Acta Palaeontologica Polonica* 59 (4): 941–946.

The first fossil genus and species of Tetratomidae (Coleoptera) is described, from the Lower Cretaceous amber deposits of France. The new genus represents the first insect to be recognized inside an opaque piece of amber, through the use of propagation phase contrast X-ray microtomography using synchrotron radiation. This new finding proves the capabilities of this imaging technique in amber inclusions, as well as increases the knowledge of fossil tenebrionoids, a group scarcely recognized in the Cretaceous fossil record.

Key words: Coleoptera, Tetratomidae, amber, propagation phase contrast X-Ray microtomography, synchrotron, Cretaceous, Charentes, France.

Carmen Soriano [carmen.soriano@gmail.com] and Paul Tafforeau [paul.tafforeau@esrf.fr], European Synchrotron Radiation Facility, 6 rue Jules Horowitz, 38043 Grenoble, France;

Darren Pollock [darren.pollock@enmu.edu], Department of Biology, Eastern New Mexico University, NM 88130 Portales, USA;

Didier Néraudeau [didier.neraudeau@univ-rennes1.fr], Géosciences Rennes and CNRS UMR 6118, Campus de Beaulieu, bâtiment 15, 263 Avenue du Général Leclerc, 35042 Rennes Cedex, France;

Andre Nel [anel@mnhn.fr], CNRS UMR 7205, Muséum National d'Histoire Naturelle, CP50, Entomologie, 45 Rue Buffon, 75005 Paris, France.

Received 30 May 2012, accepted 29 July 2013, available online 9 August 2013.

Copyright © 2014 C. Soriano et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

## Introduction

Beetles are the most diverse group of animals, constituting more than 20% of the total animal biodiversity on Earth. The first record of this order is from the Asselian to earliest Sakmarian of Grögelborn/Saarland (Germany) and the Artinskian of Obora (Czech Republic) as the putative Pennsylvanian beetle from Mazon Creek (USA) (after Béthoux 2009) does not belong to this clade (Ponomarenko 2002; Kirejtshuk et al. 2014). In Triassic deposits, beetles already comprise the major part of the insect diversity in most outcrops. In the Upper Cretaceous entomofauna, about 50% of the Recent families are already recognized (Ponomarenko 1995, 2002).

Even though beetles are very common as fossils, the study of the anatomy and systematics of these specimens is scarce, especially for Mesozoic fossils. This has been attributed to several factors, such as the incompleteness of the fossil specimens, the lack of sufficient diagnostic characters in many families (descriptions based only on Recent material) and the autapomorphic states of characters in many Mesozoic fossil

beetles (Ponomarenko 1995, 2004; Krell 2006). Therefore, beetles are generally excluded from most of the monographs on fossil localities where insects are found, and thousands of specimens remain unstudied in collections all over the world.

The use of some new three-dimensional imaging techniques, such as Synchrotron X-Ray microtomography (Tafforeau et al. 2006; Lak et al. 2008; Soriano et al. 2010), can render and characterize the maximum level of anatomical detail of fossil beetles, thus making it possible to study the systematic position of these specimens.

The specimen described was collected from the Archingeay-Les Nouillers amber locality (herein simplified as Archingeay), the most fossiliferous Cretaceous French amber deposit (Perrichot and Néraudeau 2009). The Late Albian–Cenomanian period is one of the warmest of the last 140 million years. The climate was warm and humid, and the amber forest was located close to the sea shore or was at least temporarily under marine influence, probably an easturine area (Néraudeau et al. 2002; Girard et al. 2009). The resin is of gymnosperm origin.

The deposit is unique in that a large percentage of the inclusions represent litter fauna (Néraudeau et al. 2002; Adl et al. 2011). Coleopteran inclusions are not very frequent in this amber; members of the families Bostrichidae, unidentified Cucujoidea, Curculionidae, Limnichidae, Nemonychidae, Ripiphoridae, Staphylinidae, and Tetratomidae have been recognized or described (Perrichot et al. 2004, 2010).

Tetratomidae is a small family of Tenebrionoidea (13 genera and about species) (Nikitsky 1998; Lawrence and Leschen 2010), the members of which were formerly placed in numerous other families. Extant species of the subfamily Eustrophinae, of which this new taxon is a member, are known from the Nearctic, Neotropical, Afrotropical (including Madagascar) and Oriental regions; they are notably absent from Australia and New Zealand (Pollock 2012).

*Institutional abbreviations.*—ESRF, European Synchrotron Radiation Facility, Grenoble, France; IGR.ARC, Laboratory of Palaeontology, University of Rennes I, France.

## Material and methods

The specimen is included in a completely opaque piece of amber from the Lower Cretaceous of France. Due to the impossibility of surveying the interior of the piece due to the opacity, propagation phase contrast X-ray synchrotron microtomography (afterwards PPC-SR $\mu$ CT) was used to recognize any possible inclusion inside the amber. The specimen was scanned following the protocols described in Lak et al. (2008) with a set energy of 30 keV (using a double Si 111 Bragg monochromator) and 960 mm of distance between the camera and the sample. Scan acquisition consisted of 1999 images over 180°, with 0.7 s of exposure time, and 5.06  $\mu$  of voxel size. After the scan, the slices were reconstructed using a filtered back-projection algorithm adapted for local tomography applications (PyHST software, ESRF). The later three-dimensional processing was made using VGStudioMax 2.1 software (Volume Graphics, Heidelberg, Germany).

By using this method it is possible not only to examine the habitus of the fossil under all desirable angles, but also to see internal structures which are usually not available in fossil insects (structure of the head, thorax, abdomen and hidden hind wings). This method is especially interesting for future studies of the inclusions in Mesozoic amber which is very frequently opaque. More than 80% of the amber of French Late Albian is opaque and cannot be studied using conventional methods.

All the data regarding the scan acquisition parameters, including original reconstruction of the scan, parameters of acquisition, VGStudioMax segmentation file, stereolithographic surface file for 3D printing, plates and animations are available online in the ESRF Paleontological Database (<http://paleo.esrf.eu>) following the recommendation in Lak et al. 2008. Three ABS plus plastic models of this specimen have been produced, one housed in the University of Rennes

I, one at Eastern New Mexico University and one at the European Synchrotron Radiation Facility.

The original specimen is housed in the Laboratory of Palaeontology of the University of Rennes I, under the collection number IGR.ARC-330.1. The specimen is in the same piece with four other inclusions: one Hemiptera (Aphidoidea), one Lepidoptera, one Hymenoptera (?Chrysoidea), and one undetermined insect.

## Systematic paleontology

Order Coleoptera Linnaeus, 1758

Family Tetratomidae Billberg, 1820

Subfamily Eustrophinae Gistel, 1856

Tribe Holostrophini Nikitsky, 1998

Genus *Synchrotronia* Soriano and Pollock nov.

*Etymology:* After the European Synchrotron Radiation Facility in Grenoble, where the specimen was detected and reconstructed. This specimen is the first one ever discovered in opaque amber using a synchrotron.

*Type species:* *Synchrotronia idinineteena* Soriano and Pollock sp. nov. here designated by monotypy.

*Diagnosis.*—Eyes widely separated, distance between them greater than diameter of single eye, slightly emarginate around antennal insertion; antennae elongate, extended posteriorly well beyond posterior pronotal margin, antennomeres 4–10 distinctly triangular, longer than wide, subequal in width, without distal club; prosternal process elongate, narrowed and rounded posteriorly, extended to midlength of mesoventrite, received in concavity on mesoventrite; tibiae simple, without series of transverse furrows; dorsal body surface seemingly glabrous, without obvious deep, coarse punctation or striation; base of pronotum without distinct pair of impressions.

*Synchrotronia idinineteena* Soriano and Pollock sp. nov.

Fig. 1.

*Etymology:* After beamline ID19, in which the specimen was detected and imaged.

*Holotype:* Specimen IGR.ARC-330.1, figured in Tafforeau et al. (2006), but no description was provided.

*Type locality:* Archingeay-Les Nouillers, Charente-Maritime, southwest France.

*Type horizon:* Uppermost Albian, Lower Cretaceous (Néraudeau et al. 2002).

*Diagnosis.*—As for genus.

### Description

*Body.*—Length 3.2 mm, width 1.4 mm, antennal length 1.3 mm, elytra length 2.2 mm. Body subovate, elongate, dorsally convex.

*Head.*—About two times narrower than base of pronotum. Labrum visible, about two times as wide as long. Three-seg-

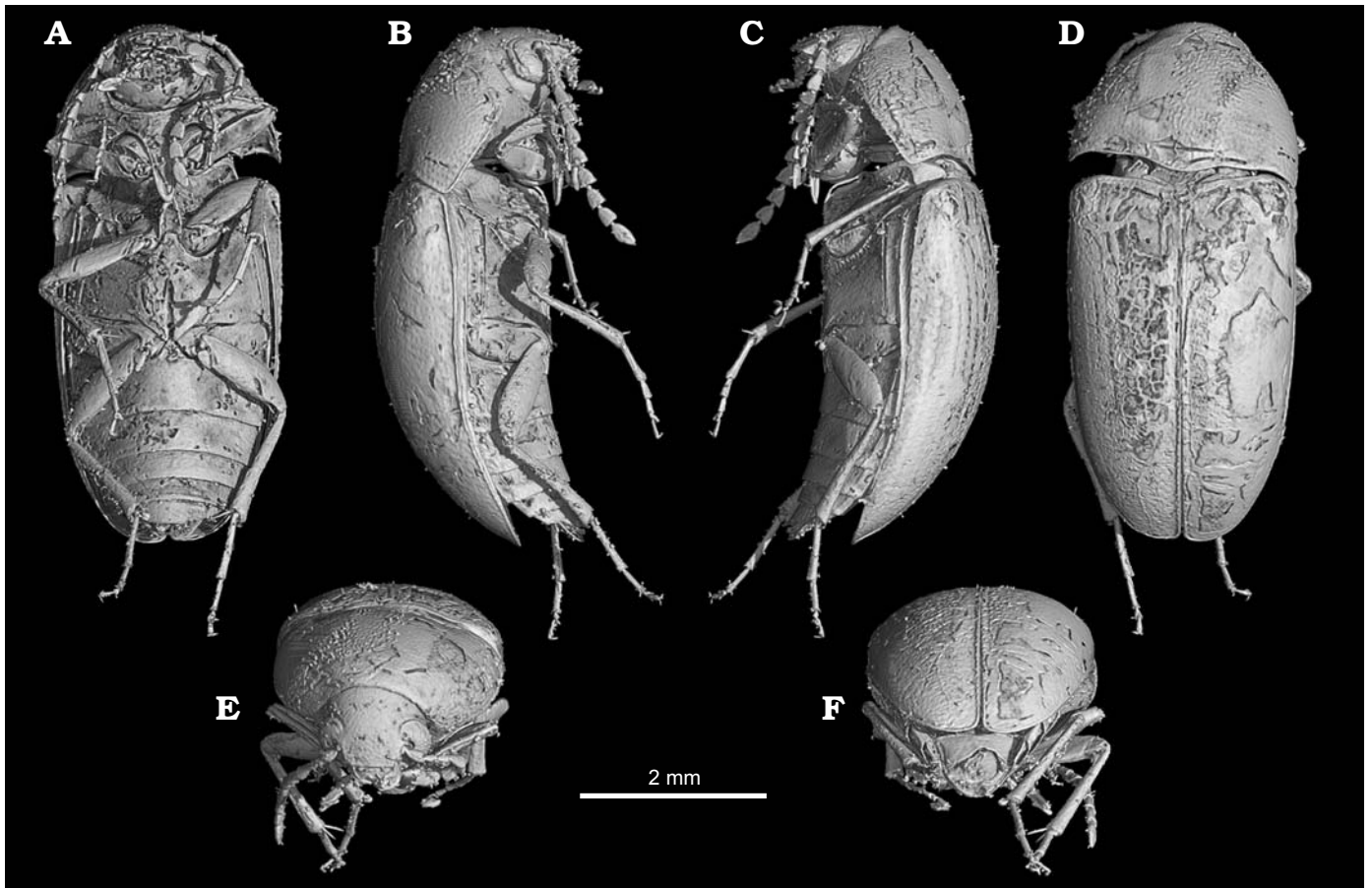


Fig. 1. 3D reconstruction of the holotype of polypore fungus beetle *Synchrotronia idinineteena* Soriano and Pollock gen. et sp. nov., University of Rennes I, Archingeay-Les Nouillers, Albian. Specimen tomographed in beamline ID19 of the ESRF, at 30 keV and 5.06  $\mu$  voxel size. In ventral (A), lateral (B, C), dorsal (D), frontal (E), and posterior (F) views.

mented maxillary palpi: first palpomere two times as long as second, and nearly three times shorter than third, which is securiform and twice as broad as the two others. Eyes laterally inserted, very close to antennae, shallowly emarginate anteriorly. Antennae widely separated, subserrate, antennomeres 4–10 distinctly triangular, widest distally, without club. Antennomeres 1.3–2 times as long as wide, and 1.8–3 times wider distally than proximally, except for last one which is quite elliptical (two times as long as wide). First antennomere twice as long as wide and with a constriction at its basal third. Second and third antennomeres the shortest (scarcely half the length of first antennomere) and the narrowest, about 1.3 times as long as wide. Fourth and sixth as long as first one and slightly broader, 1.4 times as long as wide. Fifth antennomere slightly shorter and narrower than fourth and sixth however with similar proportion length/width. Antennomere 7–10 with same length as fourth, fifth, and sixth, while they are slightly wider, with proportion comparable to those of second and third antennomeres. Neck-like constriction not distinct, visible in sagittal cut (Fig. 2), but with a posterior carina meeting anterior margin of pronotum.

**Prothorax.**—1.7 times wider than long, anteriorly rounded, widest posteriorly, broader than elytra at shoulders, with a

lateral carina in its posterior 3/4; posterior margin bisinuate, posterolateral angles acute, but without groove; prosternal process long (3/4 of prosternum) and narrowed apically; sutures not visible; procoxal cavities seem to be closed and separated from each other. Mesothorax slightly shorter than prothorax; mesocoxal cavities rounded, a little longer than wide, separated by an elongate concavity for insertion of prosternal process; mid coxal cavities closed laterally by sterna. Metathorax parallel-sided, as long as pro- and me-

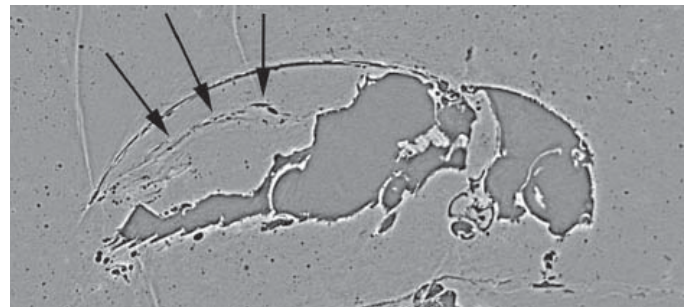


Fig. 2. Sagittal cut of the 3D volume of the holotype of polypore fungus beetle *Synchrotronia idinineteena* Soriano and Pollock gen. et sp. nov., University of Rennes I, Archingeay-Les Nouillers, Albian. Arrows mark the wings preserved under the collapsed notum.

sothorax combined and approximately 1.8 times wider than long; metepimeron about two times as wide as long; metepisterna elongate and anteriorly narrowed; discrimen dividing metaventre along half of its length from its posterior edge.

*Prothoracic coxae*.—very large and protruding; metacoxae transverse (about three times as wide as mesocoxae), extending laterally to elytra. Trochanters obliquely attached to femora, so that femora abut coxa. Meso- and metafemora almost as long as maximal length of metathorax; profemora slightly shorter; all femora three times as long as wide, quite flattened, slightly broadened from base to apical third, then narrowing more abruptly. Tibiae about twice as narrow as femora in widest part; protibiae curved in distal fourth, with a strong apical hook; meso- and metatibiae conical with apex two times as wide as base; two tibial spurs on each meso- and metatibia, approximately as long as widest part of tibia. Tarsal formula 5-5-4; last tarsomere with two short claws. Prothoracic tarsi with tarsomere 1 about four times shorter than prothoracic tibia, cylindrical with apex slightly bulging, tarsomeres 2, 3 and 4 each 0.5 times as long as tarsomere 1, tarsomeres 2 and 4 quite triangular; tarsomere 2 longer than wide and tarsomere 4 slightly wider than long; tarsomere 3 wider than long and bilobed; tarsomere 5 conical with widest part at apex. Mesothoracic and metathoracic tarsomeres cylindrical with apex slightly bulging, except for bilobed mesothoracic tarsomere 4 and metathoracic tarsomere 3; mid tarsomere 1 approximately 1.8 times as short as mesotibia; tarsomeres 2, 3 and 5 about two times shorter than tarsomere 1. Metathoracic tarsomere 1 almost two times as short as metatibia; tarsomere 2 two times as short as tarsomere 1; tarsomere 4 two times as short as tarsomere 2.

*Abdomen*.—Approximately as long as meta- and mesothorax together, with apex slightly rounded and five ventrites; tergites deformed because the abdomen is completely desiccated under the elytra.

*Elytra*.—Without striations or insertion of setae, probably smooth, approximately three times as long as wide, parallel-sided from their anterior margin for 2/3 of their length, then gradually narrowed; epipleurae visible on ventral face whole length of elytra, each approximately nine times as long as wide, strongly narrowing posteriorly and slightly curved; maximal epipleural width approximately equal to maximal width of metathoracic femora. Elytra covering most of pygidium. Metathoracic wings present, macropterous, hidden under elytra but visible in sagittal cut (Fig. 2).

*Discussion*.—Tetratomidae is an example of a relatively obscure group whose classification has become better understood through increased study of the larvae (e.g., Nikitsky 1998); historically, its constituents (especially the Eustrophinae) were placed in Melandryidae, but now have separate family status. The five subfamilies comprise 13 genera and approximately 140 species. As far as is known, all species are associated with decaying trees and/or tree-rotting fungi (Young and Pollock 2002; Lawrence and Leschen 2010; Pol-

lock 2012), like the new fossil species *S. idinineteena* (Adl et al. 2011). Adults are active nocturnally and can be seen crawling on dead trees and fungal fruiting bodies.

The species of Eustrophinae are all rather uniform in shape: subovate to oval, with convex dorsal surface. The Palaearctic fauna presently comprises four genera in two tribes: Holostrophini (*Pseudoholostrophus* Nikitsky, 1983, *Holostrophus* Horn, 1888) and Eustrophini (*Eustrophus* Illiger, 1802 and *Synstrophus* Seidlitz, 1898) (Nikitsky 1998; Young and Pollock 2002). The Holostrophini have an Asiatic distribution, with three Nearctic species and about 20 from Russian Far East to the Oriental region. The Palaearctic Eustrophini are known from the Holarctic and Oriental regions, with only a single species—*Eustrophus dermestoides* (Fabricius, 1792)—known from western Europe. This species is widespread (ranging from Spain to Turkey) (Nikitsky 2008) and is the only one presently sympatric with the type locality of *Synchrotronia*. However, as discussed below, the holotype of *S. idinineteena* has greater affinity to the Holostrophini than to the Eustrophini.

The 5-5-4 tarsal formula exhibited by the type specimen place this new genus/species within Tenebrionoidea (= Heteromera auct.); other salient anatomical features place this taxon in Tetratomidae (sensu Nikitsky 1998), like the simple narrow tarsi of all legs, procoxae separated by a prosternal process combined with the simple metacoxa and the relatively short spurs of the metatibiae, and more specifically within the subfamily Eustrophinae. Two characters that are important in separating the two tribes within Eustrophinae are (i) furrowing (or lack) on meso- and metatibiae, and (ii) size and separation of eyes. Other characters, such as presence or absence of laminae on the metendosternite, are not ordinarily visible on amber inclusions. According to Nikitsky (1998), members of Holostrophini are characterized as having no tibial furrows and also smaller, more widely separated eyes. These latter characters are also present on the holotype of *S. idinineteena*; other features that lend support for a placement among the Eustrophinae (Holostrophini) include the subovate body shape, which is distinctly convex dorsally, the rather large prosternal process, and the bisinuate posterior pronotal margin.

Three features that are often considered diagnostic for this family are noteworthy, in relation to the single examined specimen of *S. idinineteena*: antennomere shape, basal pronotal impressions, and upper elytral surface. The antennae of *S. idinineteena* are unique among eustrophines, in that they are not clubbed, and that antennomeres 4–10 are distinctly triangular, and very similar in structure to each other. Adults of extant species possess antennae that range from slightly to distinctly clubbed (Nikitsky 1998; Pollock 2008, 2012); no phylogenetic analysis has been done for the Eustrophinae, or the Tetratomidae, but perhaps the clubbed antenna represent an apomorphic state.

According to Nikitsky (1998) a key character for members of Eustrophinae is the presence of short, paired longitudinal impressions along the posterior margin of the prono-

Table 1. Cretaceous fossil record of superfamily Tenebrionoidea (Insecta: Coleoptera).

Family	Genus and species	Age	Country
Tetratomidae Billberg, 1820	<i>Synchrotronia idininiteena</i> Soriano and Pollock gen. et sp. nov.	Lower Cretaceous–Albian	France
Melandryidae Leach, 1815	<i>Pseudohallomenus cretaceus</i> Nikitsky, 1977	Upper Cretaceous–Santonian	Russia
	<i>Archaeoxylita zherichini</i> Nikitsky, 1977	Upper Cretaceous – Santonian	Russia
	<i>Archaeserropalpus cretaceus</i> Nikitsky, 2002	Upper Cretaceous–Turonian	USA
	<i>Pseudocuphosis tristis</i> Nikitsky, 2002	Upper Cretaceous–Turonian	USA
Mordellidae Latreille, 1802	<i>Praemordella martynovi</i> Scegoleva-Barovskaya, 1929	Upper Cretaceous–Oxfordian	Kazakhstan
	<i>Cretanaspis lushangfenensis</i> Huang and Yang, 1999	Lower Cretaceous–Barremian	China
	<i>Liaoximordella hongii</i> Wang, 1993	Upper Jurassic or Lower Cretaceous	China
	<i>Mirimordella gracilicruralis</i> Liu, Lu, and Ren, 2007	Upper Jurassic or Lower Cretaceous	China
	<i>Bellimordella capitulifera</i> Liu, Zhao, and Ren, 2008	Upper Jurassic or Lower Cretaceous	China
	<i>Bellimordella longispina</i> Liu, Zhao, and Ren, 2008	Upper Jurassic or Lower Cretaceous	China
	<i>Bellimordella robusta</i> Li, Zhao, and Ren, 2008	Upper Jurassic or Lower Cretaceous	China
Scraptiidae Mulsant, 1856	<i>Scraptiomima brachycornis</i> Medvedev, 1969	Lower Cretaceous	Russia
	<i>Scraptiomima minima</i> Ponomarenko and Ryvkin, 1990	Lower Cretaceous	Russia
Rhipiphoridae Geminger and Harold, 1870	<i>Macrosiagon ebooi</i> Perrichot, Nel, and Neraudeau, 2004	Lower Cretaceous–Cenomanian	France
	<i>Cretaceoripidius burmiticus</i> (Cockerell, 1917)	Lower Cretaceous–Aptian	Myanmar
	<i>Paleoripiphorus deploegi</i> Perrichot, Nel, and Neraudeau, 2004	Lower Cretaceous–Albian	France
Tenebrionidae Latreille, 1802	<i>Jurallecula grossa</i> Medvedev, 1969	Upper Cretaceous–Oxfordian	Kazakhstan
	<i>Alphitopsis initialis</i> Kirejtshuk, Nabozhenko, and Nel, 2012	Lower Cretaceous	China
	<i>Cretaceites jingxiensis</i> Wang, 1998	Lower Cretaceous	China
	unnamed species of Geertsma and Van den Heever (2000)	Upper Cretaceous	South Africa
	unnamed species of Kirejtshuk et al. (2010)	Upper Jurassic–Lower Cretaceous	China
Anthicidae Latreille, 1819	<i>Eurygenius wickhami</i> Cockerell, 1917	Lower Cretaceous–Aptian	Myanmar
	<i>Camelomorpha longicervix</i> Kirejtshuk and Azar, 2008	Lower Cretaceous–Albian	Lebanon

tum; these vary from being only slightly impressed, to being distinctly incised. The holotype of *S. idininiteena* seems not to have these impressions, however.

The fact that the holotype of *S. idininiteena* seems to be glabrous dorsally could be an artifact of the preservation process. However, it seems obvious that the elytra are not distinctly striate. Within Eustrophinae, members of Holostrophini also share this non-striate condition, whereas most members of Eustrophini have distinctly impressed elytral striae (Pollock 2008).

In summary, although based on only a single specimen, the holotype of *S. idininiteena* is sufficiently complete, and exhibits enough diagnostic features to warrant its placement within Tetratomidae: Eustrophinae: Holostrophini. The combination of features definitely indicates a new (and extinct) species, which cannot be placed into any described genus. Based on overall structural similarity, it seems closest to *Pseudoholostrophus* Nikitsky, 1983. It seems probable that the feeding preferences of the Cretaceous *Synchrotronia* are very similar to those of extant species of this tribe, i.e., various wood-rotting fungi.

This new finding represents the first record of the family Tetratomidae in the Cretaceous. Table 1 lists the other species of superfamily Tenebrionoidea described from this period. Nevertheless, the systematic position of many of these fossil taxa remains doubtful, due to the lack of anatomical characters. Future implementation of Synchrotron X-Ray tomog-

raphy will surely aid to reconstruct the anatomy and more precise systematic placement of new insect taxa preserved in Cretaceous amber.

## Acknowledgements

The authors would like to express their gratitude for their support and help to the staff of ID19 beamline, especially to Jose Baruchel and Elodie Boller (ESRF, France). We are grateful to Malvina Lak and Simon Defortis for their assistance in the original scanning and segmentation of this specimen. Rich Leschen (New Zealand Arthropod Collection, Auckland New Zealand) and Dan Young (University of Wisconsin-Madison, USA) provided useful comments on an earlier version of this paper. DAP thanks especially Jaroslaw Stolarski for his patience during the publication of this manuscript. Partial support for this work was provided by the AMBRACE Project of the French National Research Agency (ANR-BLAN07-1-184190), and by the ESRF through attribution of in-house beam-time on the beamline ID19.

## References

- Adl, S., Girard, V., Breton, G., Lak, M., Maharning A., Mills, A., Perrichot, V., Trionnaire, M., Vullo, R., and Néraudeau, D. 2011. Reconstructing the soil food web of a 100 million-year-old forest: the case of the mid-Cretaceous fossils in the amber of Charentes (SW France). *Soil Biology and Biochemistry* 43: 726–735.

- Béthoux, O. 2009. The earliest beetle identified. *Journal of Paleontology* 83: 931–937.
- Falin, Z. H. and Engel, M.S. 2010. Notes on Cretaceous Ripidiini and revised diagnoses of the Ripidiinae, Ripidiini, and Eorhipidiini (Coleoptera: Ripiphoridae). *Alavesia* 3: 35–42.
- Geertsma, H. and Van den Heever, J.A. 2000. First record of a Late Cretaceous–Palaeocene tenebrionid from southern Africa. *South African Journal of Science* 96: 553–555.
- Girard, V., Schmidt, A.R., Struwe, S., Perrichot, V., Breton, G., and Néraudeau, D. 2009. Taphonomy and palaeoecology of mid-Cretaceous amber-preserved microorganisms from southwestern France. *Geodiversitas* 31: 153–162.
- Kirejtshuk, A.G., Nabozhenko, M.V. and Nel, A. 2012. First Mesozoic representative of the subfamily Tenebrioninae (Coleoptera: Tenebrionidae) from the Lower Cretaceous of Yixian (China, Liaoning). *Entomological Review* 92: 97–100.
- Kirejtshuk, A.G., Ponomarenko, A.G., Prokin, A.A., Chang, H.-L., Nilolajev, G.V., and Ren, D. 2010. Current knowledge of Mesozoic Coleoptera from Daohugou and Liaoning (northeast China). *Acta Geologica Sinica* (English edition) 84: 783–792.
- Kirejtshuk, A.G., Poschmann, M., Prokop, J., Garrouste, R., and Nel, A. 2014. Evolution of the elytral venation and structural adaptations in the oldest Palaeozoic beetles (Insecta: Coleoptera: Tsherkardocoleidae). *Journal of Systematic Palaeontology* 12: 575–600.
- Krell, F.T. 2006. Fossil record and evolution of Scarabaeoidea (Coleoptera: Polyphaga). *Coleopterists Society Monograph* 5: 120–143.
- Lak, M., Néraudeau, D., Nel, A., Cloetens, P., Perrichot, V., and Tafforeau, P. 2008. Phase contrast X-ray synchrotron imaging: Opening access to fossil inclusions in opaque amber. *Microscopy and Microanalysis* 14: 251–259.
- Lawrence, J.F. and Leschen, R.A.B. 2010. Tetratomidae Billberg, 1820. In: R.A.B. Leschen, R.G. Beutel, and J.L. Lawrence (eds.), *Handbook of Zoology. Coleoptera, Beetles Vol. 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)*, 514–520. De Gruyter, Berlin.
- Liu, M., Lu, W., and Ren, D. 2007. A new fossil mordellid (Coleoptera: Tenebrionoidea: Mordellidae) from the Yixian Formation of Western Liaoning Province, China. *Zootaxa* 1415: 49–56.
- Néraudeau, D., Perrichot, V., Dejax, J., Masure, E., Nel, A., Philippe, M., Moreau, P., Guillocheau, F. and Guyot, T. 2002. Un nouveau gisement à ambre insectifère et à végétaux (Albien terminal probable): Archingeay (Charente-Maritime, France). *Géobios* 35: 233–240.
- Nikitsky, N.B. 1998. *Generic Classification of the Beetle Family Tetratomidae (Coleoptera, Tenebrionoidea) of the World, with Description of New Taxa. Pensoft Series Faunistica* 9. 80 pp. Pensoft, Moscow.
- Nikitsky, N.B. 2008. Tetratomidae. In: I. Lobl and A. Smetana (eds.), *Catalogue of Palaearctic Coleoptera* 5: 62–64. Apollo Books, Stenstrup.
- Perrichot, V. and Néraudeau, D. 2009. Foreword. Cretaceous ambers from southwestern France: geology, taphonomy, and palaeontology. *Geodiversitas* 31: 7–11.
- Perrichot, V., Nel, A., and Néraudeau, D. 2004. Two new wedge-shaped beetles in Albo-Cenomanian ambers of France (Coleoptera: Ripiphoridae: Ripiphorinae). *European Journal of Entomology* 101: 577–581.
- Perrichot, V., Néraudeau, D., and Tafforeau, P. 2010. Charentese amber. In: D. Penney (ed.), *Biodiversity of Fossils in Amber from the Major World Deposits*, 192–207. Siri Scientific Press, Manchester.
- Pollock, D.A. 2008. Review of the Canadian Eustrophinae (Coleoptera, Tetratomidae). *ZooKeys* 2: 261–290.
- Pollock, D.A. 2012. Review of the Eustrophinae (Coleoptera, Tetratomidae) of America north of Mexico. *ZooKeys* 188: 1–153.
- Ponomarenko, A.G. 1995. The geological history of beetles. In: J. Pakaluk and S.A. Ślipiński (eds.), *Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson*, 155–171. Muzeum i Instytut Zoologii PAN, Warszawa.
- Ponomarenko, A.G. 2002. Superorder Scarabaeiformia. In: A.P. Rasnitsyn and D.L.J. Quicke, (eds.), *History of Insects*, 164–182. Kluwer Academy Publications, Dordrecht.
- Ponomarenko, A.G. 2004. Beetles (Insecta, Coleoptera) of the Late Permian and Early Triassic. *Paleontological Journal* 38 (Special Volume 2): 185–196.
- Soriano, C., Archer, M., Azar, D., Creaser, P., Delclòs, X., Godthelp, H., Hand, S., Jones, A., Nel, A., Néraudeau, D., Ortega-Blanco, J., Pérez-De La Fuente, R., Perrichot, V., Saupe, E.E., Solórzano Kraemer, M.M., and Tafforeau, P. 2010. Synchrotron X-ray imaging of inclusions in amber. *Comptes Rendus Palevol* 9: 361–368.
- Tafforeau, P., Boistel, R., Boller, E., Bravin, A., Brunet, M., Chaimanee, Y., Cloetens, P., Feist, M., Hoszowska, J., Jaeger, J.J., Kay, R.F., Lazzari, V., Marivaux, L., Nel, A., Nemoz, C., Thibault, X., Vignaud, P., and Zabler, S. 2006. Applications of X-ray synchrotron microtomography for non-destructive 3D studies of paleontological specimens. *Applied Physics A: Materials Science and Processing* 83: 195–202.
- Wang, W.-L. 1998. Some fossil insects (Coleoptera) of western Beijing with discussion of development and succession of the Late Mesozoic insect fauna. *Memoirs of the Beijing Natural History Museum* 56: 199–206.
- Young, D.K. and Pollock, D.A. 2002. Tetratomidae Billberg 1820. In: R.H. Arnett, M.C. Thomas, P.E. Skelley, and J.H. Frank (eds.), *American Beetles. Vol. 2. Polyphaga: Scarabaeoidea through Curculionoidea*, 413–416. CRC Press, Boca Raton.