



General Paleontology, Systematics, and Evolution (Invertebrate Palaeontology)

The oldest genus of the subfamily Sagrinae (Coleoptera: Chrysomelidae) from the Paleocene of Menat (France)



Le plus ancien genre de la sous-famille Sagrinae (Coleoptera : Chrysomelidae) dans le Paléocène de Menat (France)

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ABSTRACT

The new oldest representative of the subfamily Sagrinae, *Gallopsis perita* gen. et sp. n. from the Paleocene of Menat (France), is described and illustrated. It is distinguished from the genus *Neodiaphanops* Blackburn, 1899 by the metafemora without teeth, wider pronotum, weakly widened tibiae, bilobed tarsomere 2, subparallel elytra, and narrower metanepisterna. It differs from the Australian genus *Carpophagus* Macleay, 1826 in the head without rostrum, weakly widened metafemora without teeth, and gently sculptured pronotum and elytra. The new genus differs from the Eocene genus *Eosagra* Haupt, 1950 in the longer antennomere 2, wider pronotum and elytra, dense and diffuse elytral puncturation, and weakly inflated metafemora.

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R É S U M É

Gallopsis perita gen. et sp. n., représentant le plus ancien de la sous-famille Sagrinae, est décrit et illustré du Paléocène de Menat (France). Il se distingue du genre *Neodiaphanops* Blackburn, 1899 par des métafémurs sans dents, un pronotum plus large, des tibias faiblement élargis, des tarsomères 2 bilobés, des élytres subparallèles et des métanépisterna plus étroits. Il diffère du genre australien *Carpophagus* Macleay, 1826 par sa tête sans rostre, des métafémurs faiblement élargis sans dents et un pronotum et des élytres légèrement sculptés. Le nouveau genre diffère du genre éocène *Eosagra* Haupt, 1950 par un antennomère 2 plus long, un pronotum et des élytres plus larges, une puncturation élytrale diffuse et des métafémurs faiblement gonflés.

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1. Introduction

The clade Phytophaga consists of two superfamilies, Chrysomeloidea and Curculionoidea, characterized by the pseudotetramerous tarsi and aedeagus of cucujoid type (Crowson, 1955; Marvaldi et al., 2009). The monophyly of this group is supported by molecular data (Marvaldi et al., 2009). The superfamily Chrysomeloidea consists of seven families, Chrysomelidae, Megalopodidae, Orsodacnidae, Cerambycidae, Vesperidae, Oxypeltidae, Disteniidae (Reid, 2014). The determination of these families and in particular of many subfamilies is rather difficult and is based mostly on the characters that are poorly visible or not visible in fossil forms (Reid, 1995).

The oldest known cerambycids sensu lato are known from the Barremian of Yixian (Kirejtshuk et al., 2010; Wang et al., 2014; Yu et al., 2015). The oldest known leaf beetles were described from the Early Cretaceous of the Yixian Formation but were recorded from the border of the Middle-Upper Jurassic of Karatau (Kirejtshuk et al., 2015). Other findings of Chrysomelidae are sporadic in the Cretaceous. Undescribed leaf beetles are known from the Aptian–Albian of the Crato Formation (Wolf-Schwenninger and Schawaller, 2007). A putative leaf beetle larva was recorded from Cenomanian Burmese amber (Rasnitsyn and Ross, 2000). Valentin et al. (2014) found a chrysomelid from the Cenomanian of the western France. The oldest genus of the subfamily Bruchinae Latreille, 1802 was described from Campanian Canadian amber (Poinar, 2005). Nadein and Perkovsky (2018) described a new galerucine tribe from Taimyr amber. Representatives of the subfamilies Galerucinae Latreille, 1802 and Cryptocephalinae Gyllenhal, 1813 were described from the Paleocene of Menat (Piton, 1940). Two species of the subfamily Donaciinae Kirby, 1837 were described from the early Paleocene of the Russian Far East (Bienkowski, 2015) and the late Paleocene of Canada (Askevold, 1990). Chrysomelidae are more frequent in the Eocene and later (Askevold, 1990).

Fossil Sagrinae are very rare. The late Triassic *Mesosagrites* Martynov, 1935, described as “Sarginae,” seems to be a representative of the family Schizocoleidae of the suborder Archostemata (Kirejtshuk and Ponomarenko, 2018). The genus *Eosagra* Haupt, 1950 with two species was described from the Middle Eocene of Geiseltal in Germany (Haupt, 1950). This genus is also characterized by the putative plesiomorphic character ‘femora without teeth’ (Haupt, 1950: 144–145), but its metafemora are strongly swollen as in most sargines, and its first three tarsomeres are rather wide and comparable with those in the genus *Sagra* Fabricius, 1792. Later Haupt (1956: 64–66, text-figs. 73–76) described and figured new fossils under the name ‘*Eosagra* sp. 1950’ from Geiseltal. The metafemora are swollen but it is not possible to determine from the description and figures if they had teeth or not. About 30 specimens of Sagrinae are known from the Middle Eocene Eckfelder Maar in Germany, including some specimens looking very similar to *Eosagra* (Wappler, 2003a). Wappler (2003b: fig. 71) figured a hind leg he attributed to *Eosagra* sp. indet. from the same outcrop. No other data on fossil Sagrinae have been published.

Here we describe a new chrysomelid genus and species from Menat as the oldest representative of Sagrinae.

2. Material and methods

All specimens of the new species are deposited in the Menat Town Museum, Village of Menat, Puy-de-Dôme (further MTM). The specimens were studied using a stereomicroscope Olympus SCX9 in MNHN. The specimens were also examined 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 contains sedimentary rocks (spongo-diatomites) with remains of diverse aquatic and terrestrial flora and fauna (Nel, 1989, 2008; Piton, 1940; etc.). The composition of faunal and floral remains suggests that this lake was surrounded by a forest and the palaeoenvironment was warm and humid (Wedmann et al., 2018). Following the pollen, mammalian stratigraphic, and radiometric K/Ar analyses, the age of the Menat outcrop was estimated as 59 Ma. (Kedves and Russel, 1982; Nel, 2008). However, the new estimate based on macroflora postulated its age within 60–61 Ma (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: Chrysomelidae Latreille, 1802

Subfamily: Sagrinae Leach, 1815

Notes. The new genus belongs to the family Chrysomelidae based on the head not narrowed basally, without rostrum, filiform antenna (not clubbed), antennomere 1 (scape) about twice longer than antennomere 2, striate elytra, narrowly separated procoxal cavities, exposed pygidium and pseudotetramerous tarsi. The new genus differs from genera of the family Orsodacnidae in the transverse clypeus and striate elytra. *Gallopsis* is distinguished from representatives of the family Megalopodidae in the head not narrowed basally and distinctly striate elytra. The adsutural stria deeper than other elytral striae, metafemora larger than other femora, tarsomere 2 bilobed, prognathous head without middle sulcus show that the new genus belongs to the subfamily Sagrinae. The new genus cannot be linked with the subfamily Donaciinae Kirby, 1837 because of the deep adsutural stria, antennae not separated by median groove, pronotum with the largest width not at apex and bilobed tarsomere 2. The new genus differs from the genera of the subfamily Criocerinae Latreille, 1804 in the elongate antennomere 1, metafemora larger than other femora, wide metepimera,

and adsutural stria deeper than other elytral striae. From representatives of the subfamily Bruchinae Latreille, 1802, *Gallopsis* differs in the prognathous head not narrowed basally, with long temples and deep sutural stria.

Gallopsis gen. n.

Type species: *Gallopsis perita* sp. n.

Etymology. The name of the new genus derives from the ancient country name Gallia and Greek “ὄψις” (opsis – resembling a (specified) thing). Gender feminine.

Diagnosis. Head prognathous, without median sulcus, not narrowed basally, without rostrum. Mandibles large, curved. Clypeus transverse. Labrum free, almost semicircular, transverse. Eyes transverse oval, non-emarginate, probably convex. Temples short. Antennae 11-segmented, inserted before eye, filiform, reaching anterior third of elytra, not clubbed. Antennomere 1 (scape) about twice longer than antennomere 2. Pronotum widest before middle, with lateral carina. Elytra striate. Sutural stria deep, deeper than other striae. Precoxal portion of prosternum considerably longer than postcoxal portion. Procoxal cavities narrowly separated. Metaventricle rather short. Metepimera wide triangular (Fig. 2F). Abdomen with free ventrites. Ventricle 1 longer than ventrites 2 and 3 combined. Ventrites 2–5 subequal in length. Pygidium exposed. Procoxae subconical. Femora inflated, without distinctly teeth. Metafemora larger than other femora. Tibiae carinate. Tarsi pseudotetramerous. Tarsomeres 2 and 3 bilobed.

Comparison. The genera of Sagrae were revised by Crowson (1946) and Monrós (1960). The new genus is similar to the extant genera of the Australian fauna. From *Neodiaphanops* Blackburn, 1899 with long antennae, wide tarsomere 2, non-emarginate eye, and pronotum widest before the middle, *Gallopsis* gen. n. is distinguished in the metafemora without teeth, wider pronotum, weakly widened tibiae, bilobed tarsomere 2, subparallel-sided elytra, pronotum with lateral carinae, narrower metanepisterna and lack of pubescence on integument. It differs from *Carpophagus* Macleay, 1826 in the lateral carina in the head without rostrum, weakly widened metafemora without teeth, and gently sculptured pronotum and elytra. Besides, the new genus resembles the Eocene genus *Eosagra* Haupt, 1950 because of its long antennae, shape of the pronotum, striate elytra, and femora without teeth, but it differs from the latter in the longer antennomere 2, wider pronotum and elytra, and weakly inflated metafemora.

Gallopsis perita sp. n.

(Figs. 1–4)

Etymology. The name derives from Latin “peritus” (part. perf. from the verb “perere” to perish, to disappear, to vanish, to die).

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 southeast of the village of Menat.

Holotype: “MNT 06-886”, part and counterpart, well preserved on rather smooth pieces of rock; the specimen

shows the main parts of body sclerites in dorso-lateral view, but tarsi are missing. **Paratypes:** “MNT 05”, part and counterpart, well preserved: the specimen shows the main parts of body sclerites in dorsal view but the apex of head, forelegs, right mesotibia, left metatibia and tarsi are missing. “MNT 05-17”, part and counterpart, well preserved; rock with counterpart is cracked; the specimen shows the main parts of body sclerites in dorso-lateral view but the right antennae, part of the left antennae and tarsi (except right metatarsus) are missing. “MNT 06-2530”, presented by the counterpart of the right foreleg, partially pronotum and elytra in ventral view, preserved on piece of rock. **Additional specimen:** “MNT 06-3304”, with parts of the elytra and abdomen (dorsally), this specimen is attributed to the new species here described but without inclusion in the type series.

Description of holotype. Body brown. Mandibles large. Eyes oval, wider than length, convex. Temples short, shorter than eye. Antennae inserted before eye, filiform and long, reaching anterior third of elytra. Antennomeres 3–10 long-conical. Antennomere 3 twice as long as wide. Antennomeres 3–5 subequal in length. Antennomere 4 four times as long as wide, twice as long as antennomere 3. Antennomere 5 3.7 times as long as wide, little shorter than antennomere 4. Antennomere 6 3.9 times as long as wide, 1.2 times as long as and 1.2 times as wide as antennomere 5. Antennomeres 7 and 8 subequal in length. Antennomere 7 3.8 times as long as wide, 1.1 times as long as and 1.1 times as wide as antennomere 6. Antennomere 8 3.5 times as long as wide, little shorter than antennomere 7. Antennomere 9 3.4 times as long as wide, shorter and narrower than antennomere 8. Antennomeres 10 2.3 times as long as wide, 0.7 times as long as and subequal in length to antennomere 9. Antennomere 11 twice as long as wide, 0.8 times as long as and 0.9 times as narrow as antennomere 10, somewhat pointed to apex. Disc of pronotum moderately convex, finely and densely punctate. Elytra subparallel-sided, with weak humeri, finely striate. Fine and rather dense diffuse punctures. Mesocoxal cavities oval and narrowly separated. Distance between meso- and metacoxae subequal with length of metacoxal cavity. Metanepisterna about five times as long as wide in middle. Abdominal ventrite 1 long, about 1.3 times as long as ventrites 2 and 3 combined. Abdominal intercoxal process subtriangular. Ventricle 2 about 0.4 times as long as ventrite 1. Ventricle 3 equal in length to ventrite 2. Ventricle 4 about 0.8 times as long as ventrite 3. Ventricle 5 subequal in length to ventrite 4. Legs long. Pro- and mesofemora subequal in width. Metafemora larger than other femora, reaching ventrite 4. Metafemora without teeth. Tibiae weakly widened to apex, with two subparallel carinae and costate dorsal margin.

Body length 14.0 mm.

Variations and additions (paratypes). Clypeus transverse. Antennomere 2 shorter than antennomere 1. Antennomere 3 longer and wider than antennomere 1. Pronotum about 1.4 long as wide as precoxal portion of prosternum and distinctly longer than postcoxal portion. Sutural stria deep. Apices of elytra subtruncate. Metepimera wide triangular. Metafemora more inflated than pro- and mesofemora. Tarsi quite wide,

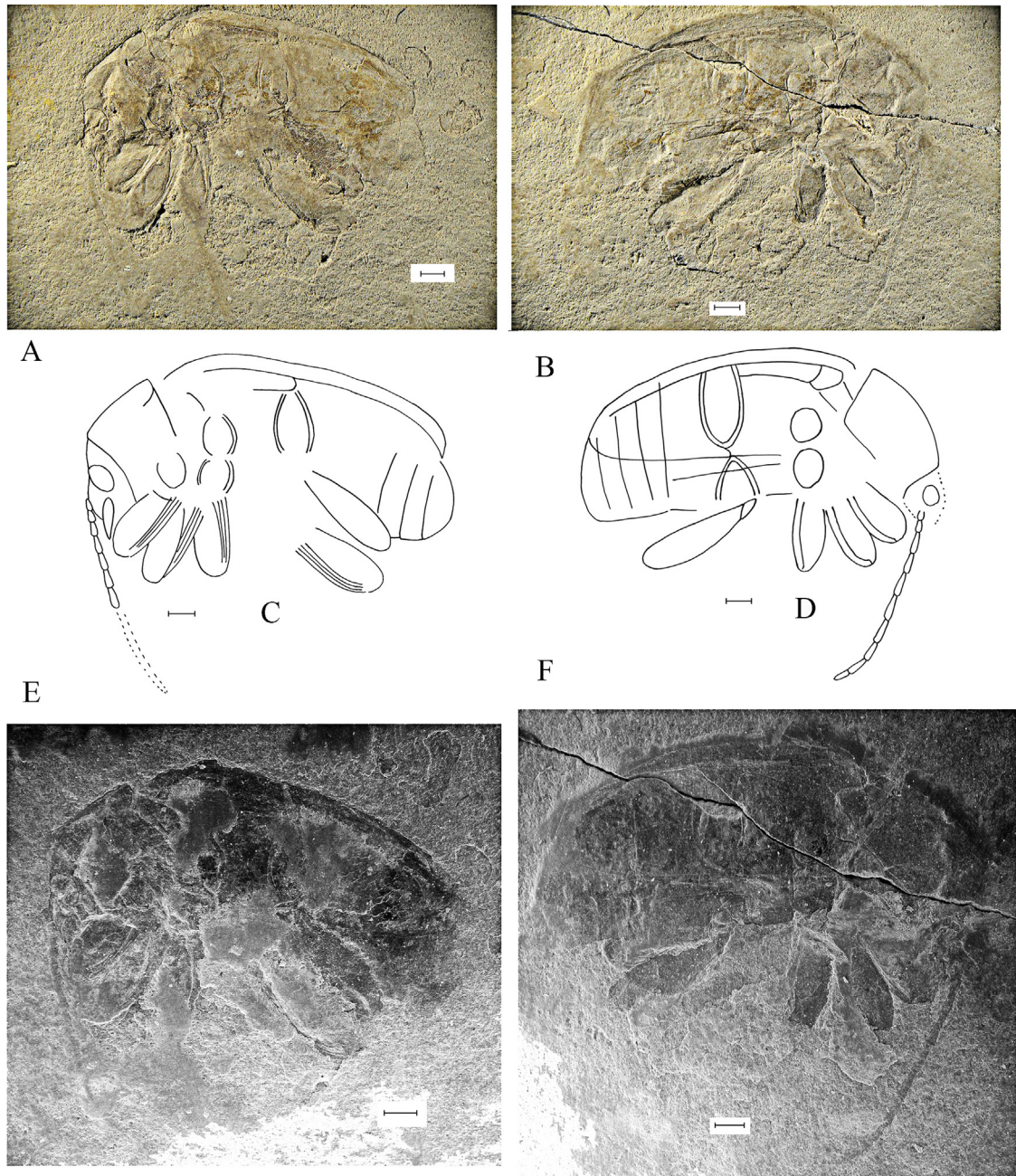


Fig. 1. *Gallopsis perita* gen. et sp. n. from the Paleocene of Menat, holotype. A. Body, part, lateral view. B. Body, counterpart, lateral view. C. Reconstruction drawing of body, part, lateral view. D. Reconstruction drawing of body, counterpart, lateral view. E. Body, part, lateral view, Tescan Vega LSU scanning electron microscope, LVSTD. F. Body, counterpart, lateral view, Tescan Vega LSU scanning electron microscope, LVSTD. Scale bar: 1.0 mm.

Fig. 1. *Gallopsis perita* gen. et sp. n., Paléocène de Menat, holotype. A. Corps, empreinte, vue latérale. B. Corps, contre-empreinte, vue latérale. C. Reconstruction du corps, empreinte, vue latérale. D. Reconstruction du corps, contre-empreinte, vue latérale. E. Corps, empreinte, vue latérale, microscope électronique à balayage Tescan Vega LSU, LVSTD. F. Corps, contre-empreinte, vue latérale, microscope électronique à balayage Tescan Vega LSU, LVSTD. Barre d'échelle : 1,0 mm.

pseudotetramerous. Tarsomere 1 conical. Tarsomere 2 bilobed. Tarsomere 3 wider than tarsomere 2. Tarsomere 5 longer than tarsomere 3. “MNT 05” has elytral integument showing nearly uniformly diffuse, fine and dense puncturation.

Body length 14.0–18.5 mm.

5. Discussion and conclusions

The Sagrinae (frog-beetles) is a small group of Chrysomelidae distributed in the Neotropical, Afro-Malagasy, Indo-Malayan, and Australian regions with the most diversity in Australia (Lawrence and Reid, 2014),

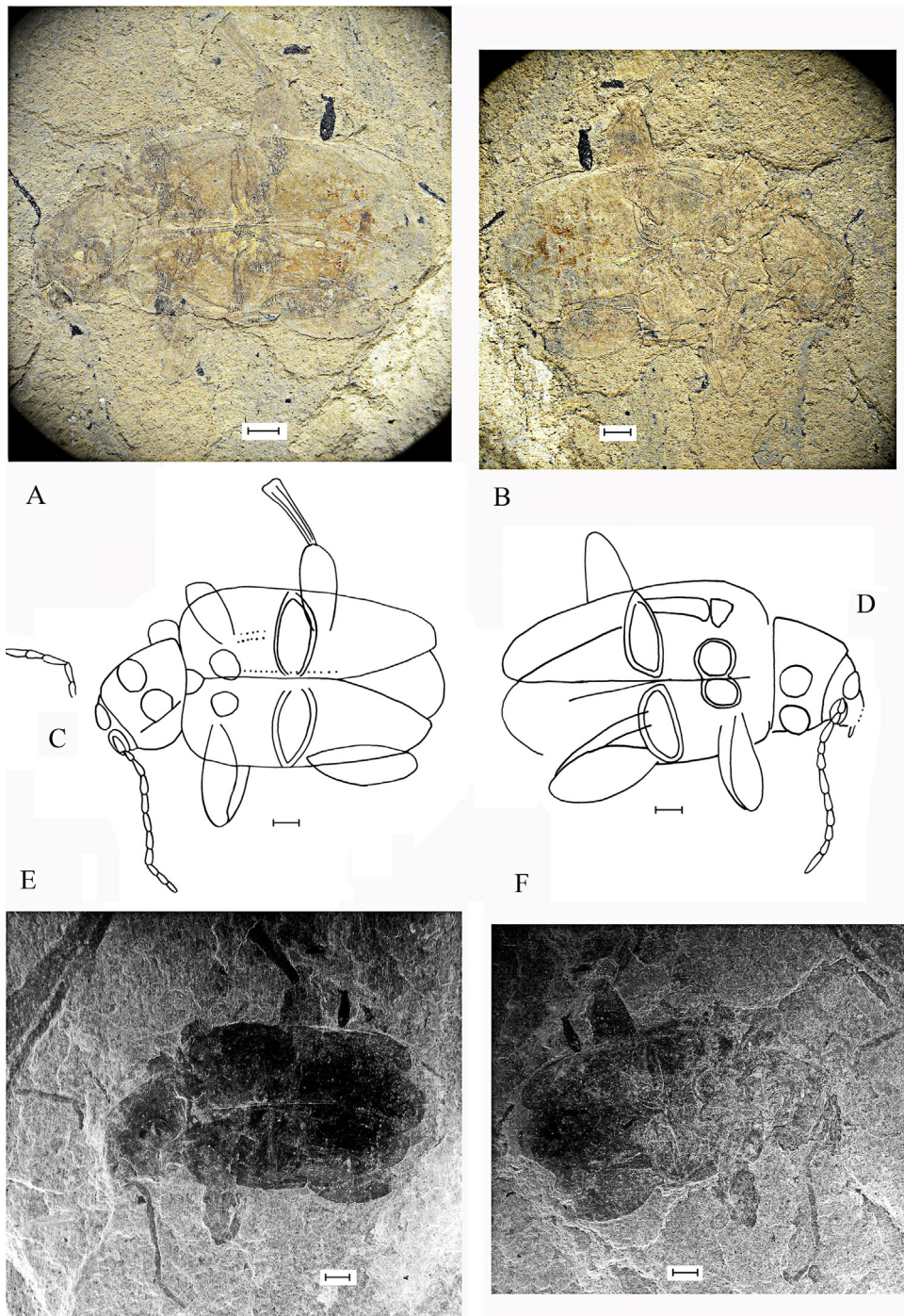


Fig. 2. *Gallopsis perita* gen. et sp. n. from the Paleocene of Menat, paratype, MNT 05. A. Body, part, dorsal view. B. Body, counterpart, ventral view. C. Reconstruction drawing of body, part, dorsal view. D. Reconstruction drawing of body, counterpart, ventral view. E. Body, part, dorsal view, Tescan Vega LSU scanning electron microscope, LVSTD. F. Body, counterpart, ventral view, Tescan Vega LSU scanning electron microscope, LVSTD. Scale bar: 1.0 mm.

Fig. 2. *Gallopsis perita* gen. et sp. n., Paléocène de Menat, paratype, MNT 05. A. Corps, empreinte, vue dorsale. B. Corps, contre-empreinte, vue ventrale. C. Reconstruction du corps, empreinte, vue dorsale. D. Reconstruction du corps, contre-empreinte, vue ventrale. E. Corps, empreinte, vue dorsale, microscope électronique à balayage Tescan Vega LSU, LVSTD. F. Corps, contre-empreinte, vue ventrale, microscope électronique à balayage Tescan Vega LSU, LVSTD. Barre d'échelle : 1,0 mm.

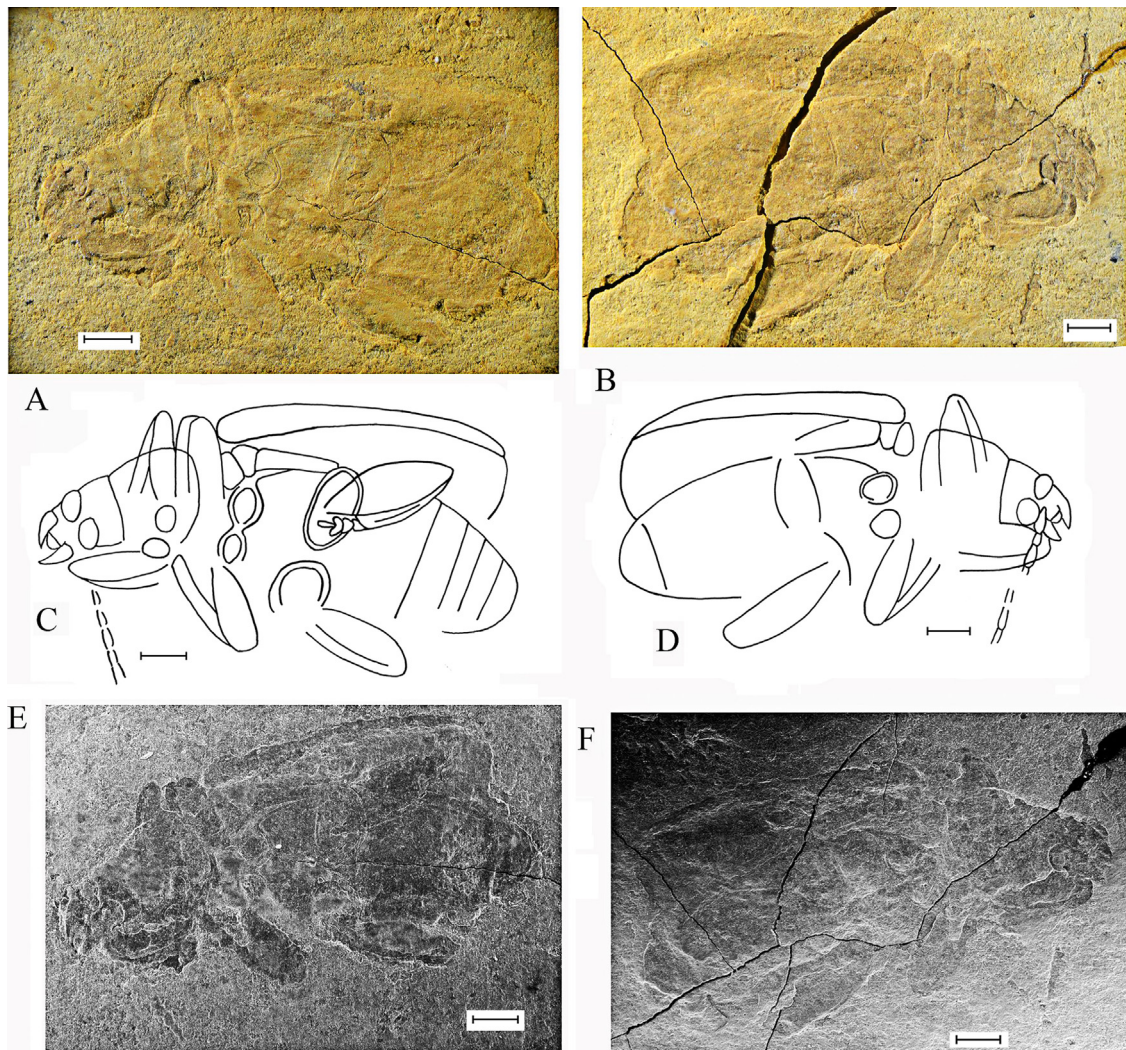


Fig. 3. *Gallopsis perita* gen. et sp. n. from the Paleocene of Menat, paratype, MNT 05-17. A. Body, part, dorsal view. B. Body, counterpart, ventral view. C. Reconstruction drawing of body, part, dorsal view. D. Reconstruction drawing of body, counterpart, ventral view. E. Body, part, dorsal view, Tescan Vega LSU scanning electron microscope, LVSTD. F. Body, counterpart, ventral view, Tescan Vega LSU scanning electron microscope, LVSTD. Scale bar: 1.0 mm.

Fig. 3. *Gallopsis perita* gen. et sp. n., Paléocène de Menat, paratype, MNT 05-17. A. Corps, empreinte, vue dorsale. B. Corps, contre-empreinte, vue ventrale. C. Reconstruction du corps, empreinte, vue dorsale. D. Reconstruction du corps, contre-empreinte, vue ventrale. E. Corps, empreinte, vue dorsale, microscope électronique à balayage Tescan Vega LSU, LVSTD. F. Corps, contre-empreinte, vue ventrale, microscope électronique à balayage Tescan Vega LSU, LVSTD. Barre d'échelle : 1,0 mm.

supporting a warm environment for the Menat paleobiota (Wedmann et al., 2018). The modern sagrine larvae develop in plant stems where they cause swellings or stem galls (Lawrence and Reid, 2014).

A sister relationship between Sagrinae and Bruchinae has been recovered in several phylogenetic analyses (Haddad and McKenna, 2016). These authors also indicated that 'Sagrinae often is recovered within a clade containing the other subfamilies of Chrysomelidae with bifid tarsal setae, except Cassidinae: Criocerinae, Donaciinae and Bruchinae'. The oldest known Bruchinae are late Cretaceous (Poinar, 2005). The earliest known Donaciinae are Paleocene (Bienkowski, 2015), while the oldest Criocerinae are Eocene Baltic amber (Bukejs and Schmitt, 2016).

The lack of Cretaceous discoveries of the mentioned subfamilies suggests a relatively recent diversification for this group.

The new genus is the oldest Sagrinae. Its several characters are present potential plesiomorphies for the subfamily: non-emarginate eyes, all femora lacking teeth, slightly thickened metafemora, tibiae slightly widened to apex, and elytra with distinct punctate striae. The subfamily Sagrinae is absent in landscapes with temperate climate of the Northern Hemisphere. The new Paleocene and earlier published Eocene finds of Sagrinae confirm the connections of Paleogene European faunas with the modern Indo-Malayan, Afrotropical, Australian, and Neotropical faunas.

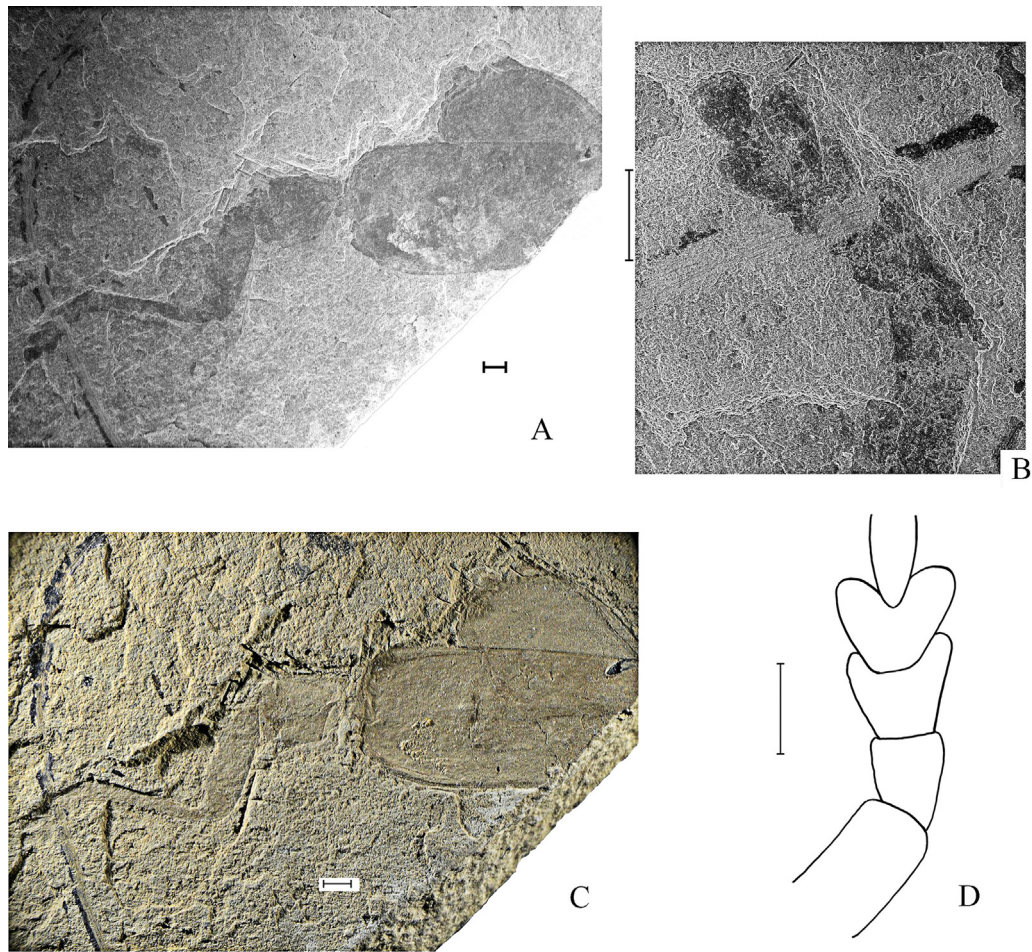


Fig. 4. *Gallopsis perita* gen. et sp. n. from the Paleocene of Menat, paratypes. A. Body, counterpart, ventral view, Tescan Vega LSU scanning electron microscope, LVSTD, MNT 06-2530. B. Protarsus, counterpart, ventral view, Tescan Vega LSU scanning electron microscope, LVSTD, MNT 06-2530. C. Body, counterpart, ventral view, MNT 06-2530. D. Protarsus, counterpart, ventral view, MNT 06-2530. Scale bar: 1.0 mm.

Fig. 4. *Gallopsis perita* gen. et sp. n., Paléocène de Menat, paratypes. A. Corps, contre-empreinte, vue ventrale, Tescan Vega LSU Microscopie électronique de balayage, LVSTD, MNT 06-2530. B. Protarse, contre-empreinte, vue ventrale, Tescan Vega LSU Microscopie électronique de balayage, LVSTD, MNT 06-2530. C. Corps, contre-empreinte, vue ventrale, MNT 06-2530. D. Protarse, contre-empreinte, vue ventrale, MNT 06-2530. Barre d'échelle : 1,0 mm.

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