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[urn:lsid:zoobank.org:pub:10628DAB-42D7-4B92-9204-4276F958BE05](https://zoobank.org/pub:10628DAB-42D7-4B92-9204-4276F958BE05)

**The first fossil representative of the water strider subfamily
 Ptilomerinae (Heteroptera: Gerromorpha: Gerridae)
 in the Oligocene paleolake of Murs (southern France) with some
 palaeoecological considerations**

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Abstract. *Oligoptilomera luberonensis* gen. et sp. nov., first fossil representative of the gerrid subfamily Ptilomerinae, is described and figured from the Oligocene of Murs (Vaucluse, Southern France). Extant Ptilomerinae live in streams in warm climates, of the Indo-Malaysian, eastern Palaearctic, and Papouan regions. The discovery of this Oligocene French Ptilomerinae is in accordance with the putative age of the subfamily, at least older than the Eocene, and with the Indo-Malaysian affinities previously recorded for some other insects from the Oligocene of France. The two insect assemblages of Murs and Céreste are compared and the differences discussed. Although of similar ages, that from Murs was possibly corresponding to a more shallow water paleolake than that of Céreste.

Keywords. Insecta, Hemiptera, fossil record, biogeography, paleoecology.

Nel A., Menecart B., Spasojevic T., Viertler A., Maridet O., Costeur L., Garrouste R. & Coster P. 2023. The first fossil representative of the water strider subfamily Ptilomerinae (Heteroptera: Gerromorpha: Gerridae) in the Oligocene paleolake of Murs (southern France) with some palaeoecological considerations. *European Journal of Taxonomy* 888: 124–136. <https://doi.org/10.5852/ejt.2023.888.2235>

Introduction

Gerridae Leach, 1815 or water striders (Heteroptera: Gerromorpha) constitute today the second most species-rich family of semiaquatic and aquatic Heteroptera Latreille, 1810. However, in comparison to fossil Nepomorpha, an infraorder of aquatic Heteroptera of comparable extant species richness and fossil representatives from the Triassic, fossil Gerridae Leach, 1815 are relatively scarce. The oldest known Gerridae is *Cretogerris albianus* Perrichot *et al.*, 2005 from mid-Cretaceous amber of France. Damgaard (2008a) summarized all described fossil Gerromorpha Popov, 1971. Cai *et al.* (2019) re-actualized the list of references, the periods, and the countries from which fossil Gerridae have been described, forgetting the Paleocene *Cylindrostethus gaudanti* Hartung *et al.*, 2016. To date, only the subfamilies Gerrinae Leach, 1815, Halobatinae Bianchi, 1896, Charmatometrines Andersen, 1975, Cylindrostethinae Andersen, 1975, and the fossil Electrobatinae Andersen & Poinar, 1992 are known in the fossil record (Damgaard 2008a; Hartung *et al.* 2016; Cai *et al.* 2019). Interestingly, no fossil Ptilomerinae Bianchi, 1896 is currently known, even if a representative of its sister group Halobatinae is recorded from the Eocene of Italy (Damgaard 2008a, 2008b), suggesting at least an Eocene age for Ptilomerinae, too.

Here, we describe the first Oligocene record of a Gerridae in the system of paleolakes of the Luberon region, an area extremely rich in fossil insects, but with very few discoveries of aquatic taxa. The new fossil can be referred to the Ptilomerinae. Some ‘*Gerris*’ have been cited in very ancient publications from the latest Oligocene of Aix-en-Provence, a different Basin south of the Luberon (Serres 1829, 1843, 1845). Meunier (1913) indicated that this material is stored in the collection of the University of Lyon (France) and added that this material is very poorly preserved. During years of collecting in the layers of Aix-en-Provence, we could only find one Gerridae among 6000 insects. In addition, we have never found any Gerridae from the early Oligocene locality of Céreste in the Luberon out of a collection of 7000 insects.

Although excavations made at Murs are only preliminary, some significant differences in the entomofaunas can be found between the paleolakes of Murs and Céreste, even if they are of similar ages.

Material and methods

Sampling of specimen

The fossil was collected in 2021, during a first exploratory field investigation of the locality ‘Les Vergiers’ in Murs, Vaucluse. It was prepared using a sharp knife. A first excavation was made during a week in September 2021, allowing the collection of around one hundred insects.

Imaging and morphological terminology

The fossil was photographed at CEREGE using a Sony Alpha 7R IV camera (61.2MP, Full frame, Pixel Dimensions, 9504 × 6336) with a Zeiss Macro 90 mm lens and dual Flash lighting. Pictures were recorded in RAW format for further post-processing. Colors have been calibrated with XRite ColorChecker® Classic chart and ColorChecker Passport software. Raw photo development and editing for white balance, colors, and aberrations made with Capture One 20 software. UV light photographs were taken with a Nikon D850 FX camera with a 60 mm / 2.8 Micro-Nikkor. UV light (365 nm) was used to find differential chemical composition with different visible fluorescence contrast with sedimentary matrix and revealed putative ornamentations or patterns on the wing surface. High definition images (45 MP sensor) permitted cropping into images. UVA (365 nm rather than 390 nm) use for fossil insect studies is a new useful and promising technique for enhancing observation with a simple, portable and economic device. It is a useful way to select specimens of interest for chemical analysis and imaging by more sophisticated techniques (e.g., X-ray synchrotron fluorescence, Georgiou *et al.* 2019). We follow the morphological terminology of Andersen (1982).

Geological setting

The new fossil fauna from ‘Les Vergiers’ comes from the graben of Murs (also known as Basin of Sénanque-Murs) (Blanc *et al.* 1975), which is located between Apt and Carpentras (Vaucluse, France; Fig. 1A). The locality of ‘Les Vergiers’ is situated north of the Murs village, 200 m NW of the historic locality of ‘le Puy’ that is protected by the National Geological Reserve of Luberon. This basin develops over marine Aptian sediments (Early Cretaceous). The graben is filled with Eocene and Oligocene fluvio-lacustrine sediments (Blanc *et al.* 1975). In ‘Les Vergiers’, a succession of Rupelian deposits has been observed (Fig. 1B), thanks to prospecting in 2018, an exploratory survey in 2021, and the excavation in 2022. The base of the Rupelian deposits is marked by limestones alternating with marls including some remains of the molluscs *Brotia laurae* (Matheron, 1843) and *Cyrenes* s. lat. typical for the Formation ‘Calcaires à Brotia laurae’ (Blanc *et al.* 1975). The transition between this Formation and the greenish fluvatile sand and sandstones of the ‘Sables et grès verts de la Valette-de-Pernes’ consists of a few meters of gray marls with caliches including one pink, massive limestone layer. In Murs, the ‘Sables et grès verts de la Valette-de-Pernes’ extend up to four meters in its southern part in the ‘La Sablière’ outcrop (Costeur *et al.* 2019), while they only reach 20–30 centimeters at its northern margin in ‘Les Vergiers’. These fluvatile sediments have provided a very rich and well-preserved terrestrial vertebrate fauna in the southern part of Murs (Rémy 2000; Mennecart 2012; Costeur 2019). One rodent incisor has been found in these sandstones at ‘Les Vergiers’ in 2021. The transition between the sands of the ‘Sables et grès verts de la Valette-de-Pernes’ and the laminated limestones of the ‘Laminites à Poissons de Murs’ is marked by ca 1.5 meters of gray to beige marls from the base to the top. The fossil Gerridae comes from the ‘Laminites à Poissons de Murs’. This formation is about 3 meters thick (Blanc *et al.* 1975; pers. obs.). Contrary to Blanc *et al.* (1975), we have observed that the series starts with 40 centimeters of finely laminated limestones rich in marls. Then 20 cm of massive plattenkalk are overlaid by 20 cm of marls. For the rest of the series, the limestones become more finely laminated and the proportion of marls increases toward the top of the Formation to finally become only beige marls. These beige marls are full of plant remains. This Formation is sealed by a massive green sandstone belonging to the ‘Marnes et grès verts de Murs’ (Blanc *et al.* 1975).

The laminated limestones of ‘le Puy’ fossil locality in Murs have been exploited by fossil collectors until the Luberon geological reserve was created in 1987. The nature reserve regulations formulate administrative, scientific and organizational conditions for excavations. Extraction and collection of fossils and minerals is prohibited without prior special authorization. Up to now, mostly fishes (*Dapalis macrurus* (Agassiz, 1834)) and some plant remains are known from the ‘Laminites à Poissons de Murs’ (Blanc *et al.* 1975). The new excavation allows refining the faunal list and the stratigraphy of the fossils. The massive bank in the lower part of the Formation provided the remains of an unidentified large fish (more than 20 cm), evidence of regurgitations (exploratory survey), and one tooth of a pike fish *Esox* sp. (prospecting). The excavation site at Les Vergiers (2021 and 2022) is located on the top of the ‘Laminites à Poissons de Murs’ in finely laminated limestones intercalated with marly banks. It provides a rich fauna composed of small fish (maximum 10 cm), *Prolebias* sp., plant remains, some rare gastropods, some purported lacustrine jellyfishes, and the studied larvae and insects. This Formation has been dated by Blanc *et al.* (1975) to the ‘middle Oligocene’-Stampian. The underlying formation of the ‘Sables et grès verts de la Valette-de-Pernes’ contains remains of the rodent *Blainvillimys helmeri* Vianey-Liaud, 1972 (Thaler 1966; Vianey-Liaud 1972; Costeur *et al.* 2019) consistent with an age of MP23, similar to Itardies (ca 31 Ma). No unconformity has been observed in the fields indicating that the ‘Laminites à Poissons de Murs’ may be MP23 (similar to Céreste limestones) or slightly younger.

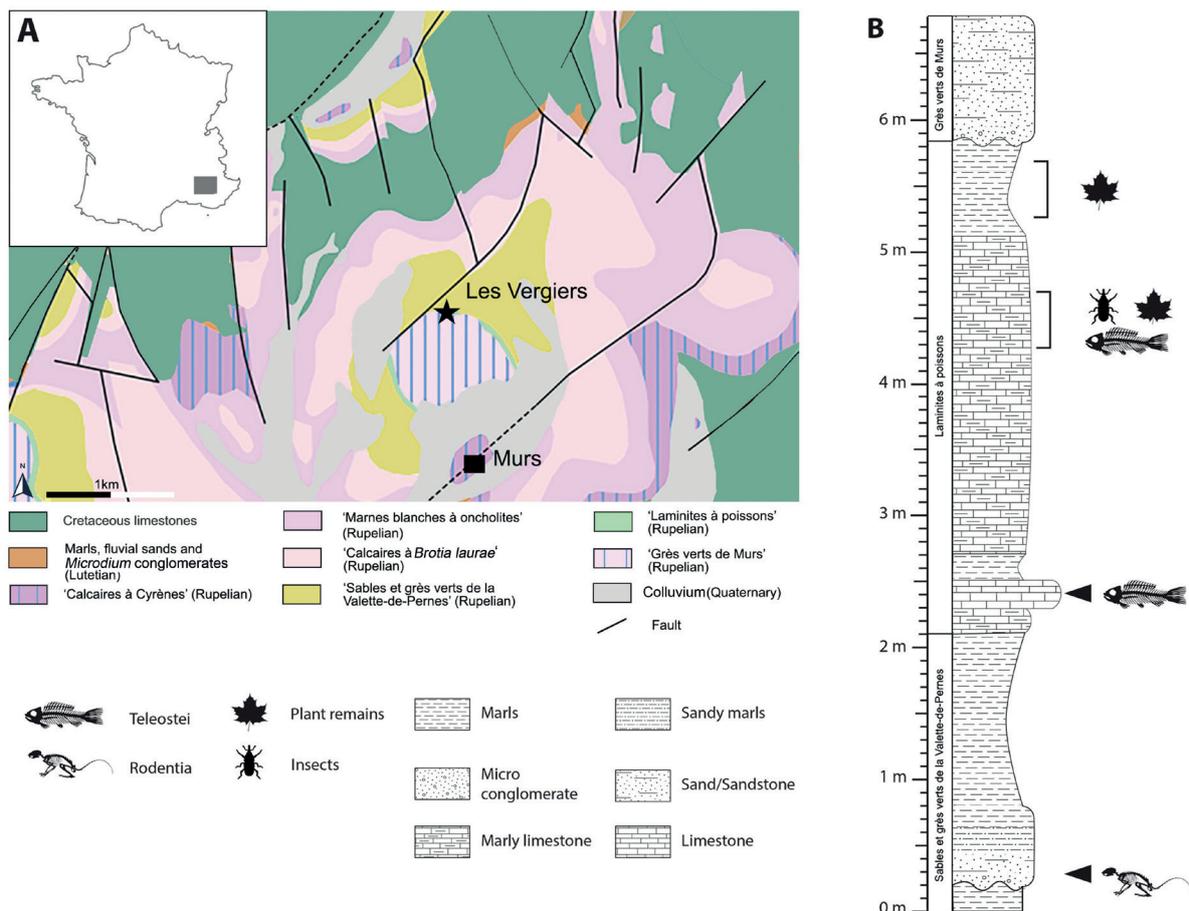


Fig. 1. Location map and geological context of the ‘Les Vergiers’ fossiliferous locality in Murs (Vaucluse, France). **A.** Geographical position of Murs in France and within the National Natural Reserve of Luberon. **B.** Stratigraphic log of the ‘Les Vergiers’ from the ‘Sables et grès verts de la Valette-de-Pernes’ to the ‘Marnes et grès verts de Murs’.

Results

Taxonomy

Class Insecta Linnaeus, 1758
Order Hemiptera Linnaeus, 1758
Clade Gerromorpha Popov, 1971
Family Gerridae Leach, 1815
Subfamily Ptilomerinae Bianchi, 1896

Oligoptilomera gen. nov.

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Type species

Oligoptilomera luberonensis gen. et sp. nov.

Diagnosis

Fore tarsus only slightly shorter than fore tibia; hind femur probably as long as mid one; first antennomere shorter than three following antennomeres together; antenna shorter than body; abdomen slightly shorter than thorax; no lateral wing of suranal plate; proctiger not exposed; a very large first genital segment; second genital segment well visible.

Etymology

Named after the Oligocene period and the extant genus name ‘*Ptilomera*’.

Oligoptilomera luberonensis gen. et sp. nov.

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Figs 1–4

Diagnosis

As for the genus, by monotypy.

Etymology

Named after the lacustrine Luberon basin.

Holotype

FRANCE • part and counterpart of a complete body with antennae and legs partly preserved; stored in the collection of the Geology Museum, Parc naturel régional du Luberon, Apt, France; PNRL 2715.

Age and outcrop

‘Laminites à Poissons de Murs’, Rupelian, Oligocene (Cautru & Gigot, 1982; Apostolescu & Dellenbach 1999), MP23 (or slightly younger), ca 31 Ma; Les Vergiers, Murs, Monts du Vaucluse, Vaucluse, France.

Description

Apterous, body dark to pale brown, with longitudinal white bands along lateral margins of mesothorax and three white spots on head, body 9.3 mm long, 3.7 mm wide; head 1.3 mm long, 1.3 mm wide; antenna 9.3 mm long; antenna as long as body; first antennomere 3.8 mm long, shorter than three following antennomeres together; fourth antennomere dorsoventrally flattened; thorax 4.2 mm long, 3.7 mm wide; pronotum short, not developed into pronotal lobe; mesothorax distinctly prolonged;

mesopostnotal margin straight; primary intersegmental suture between meso- and metathorax making two lateral curved lines; primary intersegmental suture between meso- and metathorax not obliterated laterally; coxal axes rotated to almost horizontal inclination; fore tarsus very long, 3.4 mm long, as long as fore tibia; mid coxa in posterior position; middle femur slender, 8.0 mm long; hind femur with distal part widened, at least 6.3 mm long, as long as mid one as it is preserved; abdomen slightly shorter than thorax, 3.8 mm long, 2.4 mm wide; no lateral wing of suranal plate; proctiger not exposed; large first genital segment but not covering second genital segment.

Discussion

Systematic relationships

This fossil has the characters of Gerridae as proposed by Andersen (1982, 2000): mesothorax distinctly prolonged; middle and hind coxae laterally inserted on thorax, coxal axes rotated to almost horizontal inclination. The shape of the thorax plus the absence of wings both indicate that it is a wingless form or a nymph. The second option is unlikely because of the very large apical abdominal segments that fit quite well with those of an adult male, especially of Ptilomerinae, rather than a nymph (Cheng & Fernando 1969: figs 168–169; Andersen 1982). Within Gerridae, Gerrinae and Charmatometrinae are excluded because the pronotum is short, not developed into a pronotal lobe. The presence of a straight mesopostnotal margin excludes Halobatinae, while the primary intersegmental suture between meso- and

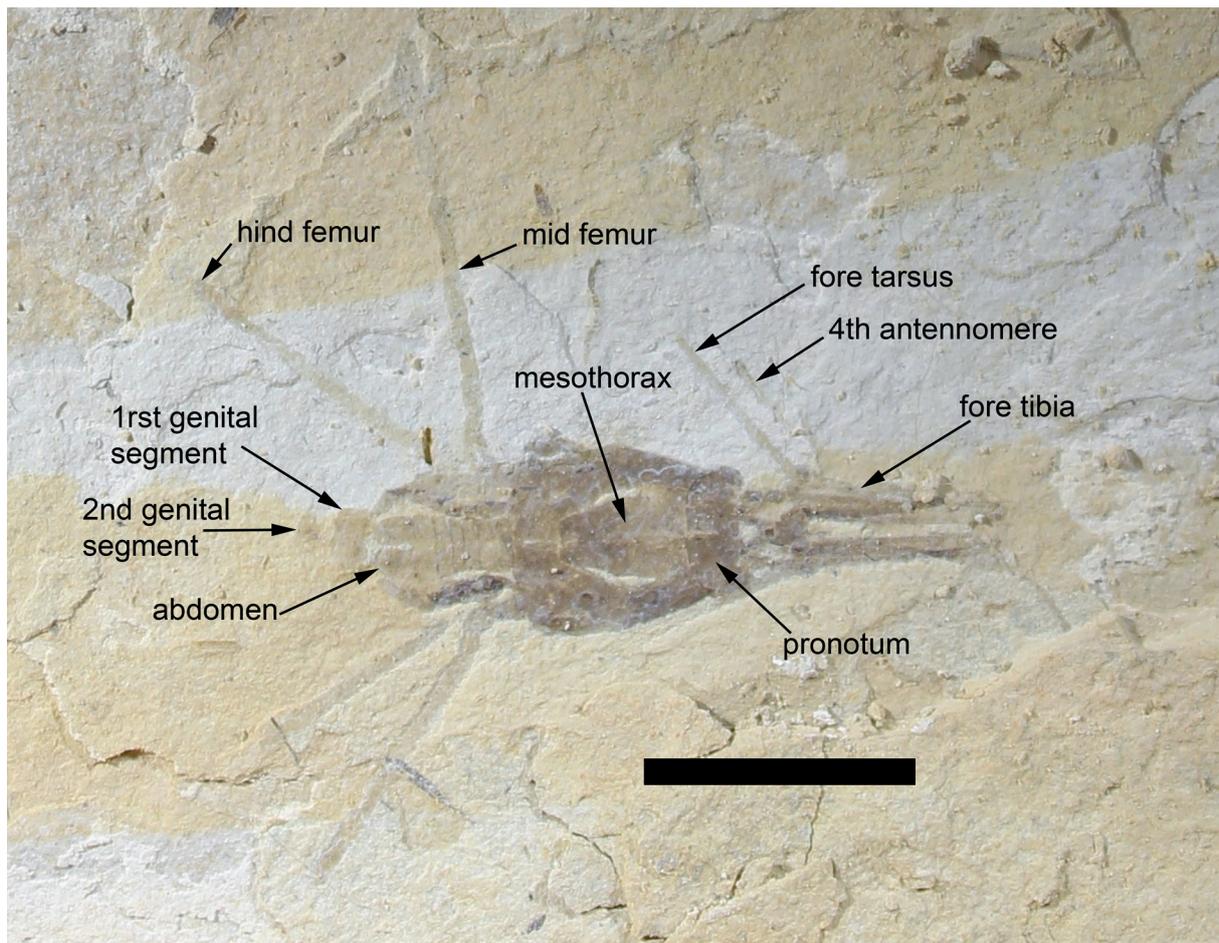


Fig. 2. *Oligoptilomera luberonensis* gen. et sp. nov., holotype (PNRL 2715), part, photographed under normal light. Scale bar = 5 mm.

metathorax making two lateral curved lines excludes the extinct subfamily Electrobatinae (Andersen & Poinar 1992). The slender middle femur further excludes the Trepobatinae Matsuda, 1960 (Andersen 1982). These shapes of the mesopostnotal margin and of the intersegmental suture are however present in Ptilomerinae, Cylindrostethinae, and Eotrechinae Matsuda, 1960 sensu Andersen (1982: fig. 395). The primary intersegmental suture between meso- and metathorax not laterally obliterated, because the mid coxa is in a posterior position, is a character of Ptilomerinae and Eotrechinae. The dorsoventrally flattened fourth antennomere is a synapomorphy of the Ptilomerinae, also the very long fore tarsus, nearly as long as the fore tibia is a character of this subfamily (Andersen 1982; Damgaard 2008).

After the key to ptilomerine genera of Andersen (1982), the new fossil shares with the extant genus *Potamometra* Bianchi, 1896 the fore tarsus only slightly shorter than the fore tibia. But its first antennomere is shorter than three following antennomeres together vs longer in *Potamometra*, and its abdomen is nearly as long as the thorax vs much shorter in *Potamometra* (Drake & Hoberlandt 1965; Chen *et al.* 2016; Zheng *et al.* 2019).

The first antennomere shorter than the three following antennomeres together suggests an affinity with *Rheumatogonus* Kirkaldy, 1909, *Jucundus* Distant, 1910, *Floresiobates* Polhemus & Polhemus, 2008, and *Pleciogonus* Chen, Nieser & Wattanachaiyingcharoen, 2002, while it is longer in the other genera (Esaki 1927; Zettel & Chen 1996; Zettel & Thirumalai 2001a, 2001b; Chen & Nieser 2002; Chen *et al.* 2002; Polhemus & Polhemus 2008; Zettel 2009; Zettel & Laciny 2021). However, *Rheumatogonus*, *Jucundus*, *Floresiobates*, and *Pleciogonus* have the fore tarsus distinctly shorter than the tibia. *Floresiobates* also has an abdomen as long as the thorax.



Fig. 3. *Oligoptilomera luberonensis* gen. et sp. nov., holotype (PNRL 2715), counterpart, photographed under ultra-violet light. Scale bar = 5 mm.

The genus *Ptilomera* Amyot & Serville, 1843 would be excluded because the hind femur is apparently as long as the mid one in the new fossil vs much longer in *Ptilomera*, but it is possible that the hind femora are incompletely preserved in the fossil. Their apical enlargement may be the evidence of the end of the leg segment, but it is not absolutely conclusive. The males of the subgenus *Ptilomera* have a lateral wing of suranal plate and a subtriangular proctiger which is mostly exposed, which is not the case in the new fossil (Hungerford & Matsuda 1965; Jehamalar & Chandra 2018). But the males of the subgenus *Proptilomera* Hungerford & Matsuda, 1958 (one species, *Ptilomera (Proptilomera) himalayensis* Hungerford & Matsuda, 1958) have an apical part of the abdomen very similar to that of the fossil, with no lateral wing of suranal plate and a proctiger not exposed (Hungerford & Matsuda 1958). Notwithstanding, *Proptilomera* has a ‘very large first genital segment that almost covers the second genital segment’, which is not the case in the new fossil in which the second genital segment is well visible (Hungerford & Matsuda 1965: fig. 2). The male and female of *Ptilomera (Proptilomera) himalayensis* also have an abdomen distinctly shorter than the thorax, unlike the new fossil.

Thus, the new fossil does not fit in any extant ptilomerine genus known so far. We attribute it to the new genus *Oligoptilomera*.

The extant Ptilomerinae are restricted to Madagascar, Southeast Asia, China, and New Guinea, absent from the New World and West Palearctic, ‘adapted to the life in the lotic sections of tropical and subtropical rivers’ (Zettel 2009: 26). Affinities of the Oligocene Western European entomofauna with the extant ones of the Indomalaysia and eastern Palearctic regions have been noticed since a long time (Théobald 1937). Thus, the discovery of a Gerridae with such affinities is not surprising. The presence of an extant Ptilomerinae in Madagascar also supports a past distribution much wider than the extant one.

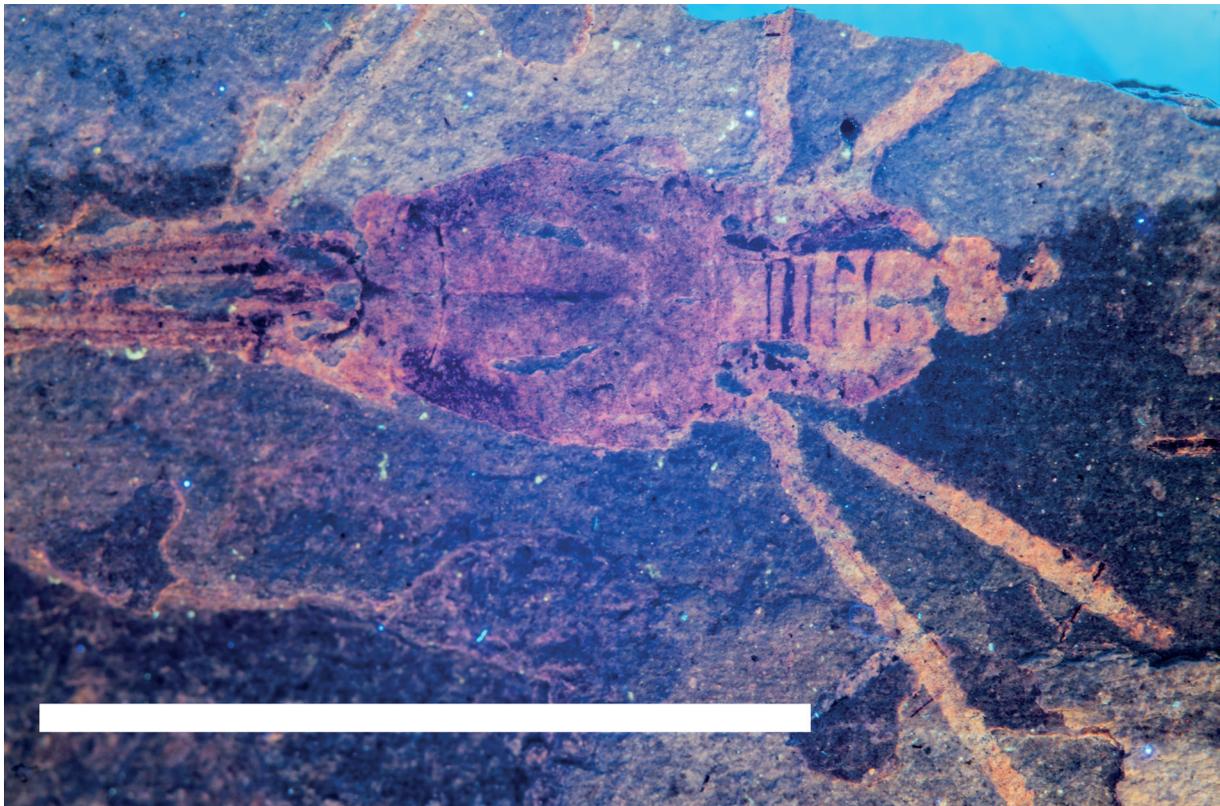


Fig. 4. *Oligoptilomera luberonensis* gen. et sp. nov., holotype (PNRL 2715), part, photograph of body under ultra-violet light. Scale bar = 5 mm.

Comparison of the insect assemblages of Murs and Céreste

The insect assemblage from Les Vergiers can be compared to the abundant entomofauna of the laminated lacustrine limestones at Céreste (e.g., Théobald 1937), dated to the Rupelian (biohorizon MP23) (Cautru & Gigot 1982). The insects seem to be less abundant at Les Vergiers than at Céreste. We have collected 110 determinable insects at Les Vergiers mostly during four days of extensive research made by four persons in average. This quantity of insects can be easily collected by two persons during three days at Céreste. Preservation in more marly sediments may explain this discrepancy.

Some insects seem to be taxonomically very close in the two assemblages (e.g., a very frequent small Heteroptera), but some others are newly found at Murs, especially the Gerridae and a very large Curculionidae Latreille, 1802, which were never found at Céreste, despite the great quantity of weevils we could collect there.

Among the 110 insects of Les Vergiers, we have found 52 Coleoptera (48%), 27 Diptera (24%), 24 Hemiptera (22%), six Hymenoptera (5%), and one Trichoptera (larval cast) (1%). At Céreste, Nel (1991) established on 7467 insects, there were 40.8% of Diptera, 36% of Coleoptera, 15.5% of Hemiptera, 6.3% of Hymenoptera. The rest of insects at Céreste are mainly Thysanoptera (0.5%), Orthoptera (0.3%), Odonata (0.2%), Lepidoptera (0.2%), while each other order represents less than 0.04% of the abundance (0.03% of Trichoptera). Of course, the quantity of insects collected at Les Vergiers is too low to consider that the percentages of the different orders have the same significance as those for Céreste. Nevertheless, in both outcrops, beetles dominate in diversity and abundance, with the main part being represented by Curculionidae. The following well-represented orders are also the Hemiptera and the Diptera in both outcrops. The Hymenoptera are clearly less well represented too. At Céreste and Les Vergiers, the most abundant Hemiptera is one type of small Heteroptera that we tentatively attribute to the aquatic family Veliidae Amyot & Serville, 1843. They clearly represent half of the total Hemiptera in the two outcrops.

The most obvious differences in the insect diversity between the outcrop of Les Vergiers and that of Céreste are as follows:

- 1) A very weak quantity of Bibionidae Newman, 1834 at Les Vergiers (six specimens, 22% of Diptera) compared to Céreste, where this family represents more than 60% of all the flies. The Bibionidae are mainly *Plecia* sp. (five specimens for only one *Bibio* sp.), which is similar to the proportion between the Pleciinae Duda, 1930 and Bibioninae Newman, 1834 at Céreste.
- 2) Presence of six fly larvae at Les Vergiers, five of which belong to the family Stratiomyidae Latreille, 1802, while these are extremely rare at Céreste (only two specimens among more than 10 000 insects found during 35 years of collection). These fly larvae have a terminal abdominal segment with a terminal coronet of long setae apical in position, a character of the Stratiomyinae Latreille, 1802 (James 1981). These setae are hydrofuge in the extant larvae that are aquatic, sometime in brackish, hypersaline, or high temperature waters. Stratiomyinae larvae colonize stagnant waters or rivers near the shores, seeking the richest vegetation, algae, and debris.

The important difference in the abundance of these stratiomyine larvae between Les Vergiers and Céreste suggests a difference in the quality of water. Ducreux & Tachet (1985) cited a layer in the Vachère Formation (near Sigonce, Luberon) in which there is an impressive accumulation of stratiomyid larvae, mainly head capsules. They considered that it corresponds to a palustrine paleoenvironment. The discovery of a Gerridae at Les Vergiers, while this family has not been recorded at Céreste among several thousands of insects, also marks a significant difference in the paleoenvironment and the water quality. The great abundance of small fish of the genus *Prolebias* Sauvage, 1874 in both outcrops shows that these animals could live in these waters even if they also certainly died in great quantity during some episodes, maybe related to microbial blooms that probably consumed a great part of the dissolved

oxygen and caused the death of the aquatic life. As the geological section suggests, the uppermost layers excavated at the site of Les Vergiers possibly correspond to a shallower paleolake than at Céreste, allowing the abundance of stratiomyid larvae. This interpretation is supported by the more marly nature of the laminated limestones at Les Vergiers than at Céreste, indicating a more proximal habitat, and by the sequence ending in beige marls just above the ‘Laminites à Poissons de Murs’, with abundant plant remains topped by a river system that deposited the ‘Grès Verts de Murs’ Formation.

Conclusion

The rarity of the Gerridae in the paleolakes of Luberon and Aix-en-Provence areas remains unexplained, in particular if we compare with their frequency in the Paleocene of Menat and the Oligocene of Tibet (ca 20 specimens recorded in both outcrops). Nevertheless, Gerridae are clearly infrequent in the Eocene to Miocene paleolakes of Western Europe, even unrecorded in many lacustrine outcrops otherwise very rich in insects (e.g., Late Eocene of Monteils, Gard, France; Oligocene of Camoins-les-Bains, France; Rott, Germany; Miocene maar paleolakes of Sainte-Reine or Montagne d’Andance, France) (pers. obs.). Therefore, the rarity of these insects seems to be more the rule than the exception for these Cenozoic lacustrine outcrops.

The present description of the oldest known representative of Ptilomerinae in the Oligocene of France is in accordance with its wider distribution in the past, also suggested by the presence of an extant representative in Madagascar.

Lastly, the insect assemblages at Murs and Céreste seem to differ, especially in the lower quantity of Bibionidae and the greater quantity of stratiomyid larvae at Murs than at Céreste. Thus the aquatic entomofauna at Murs could correspond to a more shallow lake than at Céreste, what also seems to be supported by the difference in sedimentology. Future sampling in the field will be necessary to confirm these tendencies.

Acknowledgments

We sincerely thank two anonymous referees for their useful comments on the first version of the paper. We thank the landowner, M. Guillen, for authorizing the fieldwork. O.M. is supported by a grant from the Swiss National Science Foundation (FNS-CRSK-2_190584).

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Manuscript received: 16 January 2023

Manuscript accepted: 16 March 2023

Published on: 15 August 2023

Topic editor: Marie-Beatrice Forel

Section editor: Daniel Stec

Desk editor: Eva-Maria Levermann

Printed versions of all papers are also deposited in the libraries of the institutes that are members of the *EJT* consortium: Muséum national d'histoire naturelle, Paris, France; Meise Botanic Garden, Belgium; Royal Museum for Central Africa, Tervuren, Belgium; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Leibniz Institute for the Analysis of Biodiversity Change, Bonn – Hamburg, Germany; National Museum of the Czech Republic, Prague, Czech Republic.