

## Fossil water scavenger beetles of the subtribe Hydrobiusina (Coleoptera: Hydrophilidae) from the Late Oligocene locality of Aix-en-Provence (France)

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**Abstract.** Two species assigned to the subtribe Hydrobiusina (Coleoptera: Hydrophilidae: Hydrophilinae: Hydrophilini) from the Late Oligocene locality of Aix-en-Provence (France) are examined: *Hydrobius obsoletus* Heer, 1856 is removed from the Hydrophiloidea and placed in Coleoptera *incertae sedis* based on the examination of its holotype. *Limnoxenus olenus* sp. nov. is described from two well-preserved fossil specimens. Based on a phylogenetic analysis combining the data of recent and fossil species, *L. olenus* sp. nov. is supported as belonging to the non-Hawaiian group of the genus *Limnoxenus* Motschulsky, 1853; it represents the first known fossil record of the genus.

**Keywords.** Coleoptera, Hydrophilidae, Hydrobiusina, fossil, Cenozoic, Oligocene, phylogenetic analysis, France

### Introduction

The subtribe Hydrobiusina of the family Hydrophilidae is represented by 22 recent species characterized by medium body size and primarily aquatic habits. The species are placed in five genera which are mostly rather restricted in geographic distribution. *Hydrobius* Leach, 1815 with eight recent species is confined to the Holarctic region, *Limnoxenus* Motschulsky, 1853 is represented in Europe (2 spp.), Australia and New Zealand (1 sp.), south Africa (1 sp.), and in the Hawaiian Islands where an adaptive radiation of seven species associated with habitat shifts from aquatic to semiaquatic or completely terrestrial habitats occurred

(SHORT & LIEBHERR 2007). The remaining three genera are represented by a single species each: *Hydramara* Knisch, 1925 in central Argentina, *Limnocyclus* Balfour-Browne, 1939 in New Caledonia, and *Hybograhius* d'Orchymont, 1942 in western Australia. Although the phylogeny of the Hydrobiusina is far from completely resolved, the recent phylogenetic analyses based on adult as well as larval characters (ARCHANGELSKY 2004, SHORT & LIEBHERR 2007) suggest its close relationships to the tribe Sperchopsini, but tentatively support its monophyly and bring the basic insight into phylogenetic relationships among the recent species.

Sixteen fossil species have been assigned to the genus *Hydrobius* (HEER 1847, 1852, 1856, 1862, 1870; GIEBEL 1856; SCUDDER 1878, 1890, 1900; WICKHAM 1911, 1913; THÉOBALD 1937) and therefore placed into Hydrobiusina. Consequently, the fossil record of the group seems to date back to the Lower Jurassic (ca. 197 millions of years ago) when the published data are considered. However, the Mesozoic fossils originally placed in *Hydrobius* are based on isolated elytra and were later transferred to the formal genus *Hydrobiites* Heer, 1865 by HEER (1865) and HANDLIRSCH (1908); their relationships to Hydrobiusina as well as to Hydrophiloidea remain doubtful (M. Fikáček, unpubl. data). The identity of the remaining fossil *Hydrobius* species requires a critical revision as many medium-sized elongate oval beetles have been attributed to the genus without considering any relevant characters (M. Fikáček, unpubl. data), as is illustrated by an example of *Hydrobius obsoletus* Heer, 1856 within this paper. No other fossil representatives of the subtribe have been described.

Four hydrophilid species were described from the Late Oligocene locality of Aix-en-Provence so far: *Hydrobius obsoletus*, *Hydrophilus antiquus* Oustalet, 1874, *Hydrophilopsis incerta* Oustalet, 1874, and *Laccobius vetustus* Oustalet, 1874 (HEER 1856, OUSTALET 1874, THÉOBALD 1937). In addition, two specimens of *Limnoxenus* and numerous specimens of a single species of *Berosus* Leach, 1817 were found in the unidentified material in the Laboratoire de Paléontologie in the Muséum National d'Histoire Naturelle, Paris. Within this paper, we are dealing with the representatives of the subtribe Hydrobiusina; the identity of the remaining species will be addressed in a future paper, pending on the examination of the type specimens.

### Locality and stratigraphy

The formation of Aix-en-Provence, the youngest of the Oligocene formations of the region around Marseille in Bouches-du-Rhône, is dated from the uppermost Oligocene (22.5 Ma). The deposit presents an alternation of limestone and marls with gypsum. This lacustrine formation was deposited in a very large but shallow-water lake, with variable salinity and near the marine coast (NURY 1990, NURY & THOMASSIN 1994).

This formation has yielded a diverse flora and fauna, with finely preserved fossils. The flora is represented by numerous plant remains (pollen, roots, wood, stems, leaves, seeds and flowers). The fauna of vertebrates is represented by abundant fishes (GAUDANT 1978), and some frogs, birds, and bats with preserved skin outlines. Some invertebrates are perfectly preserved, including jellyfish and shells of aquatic molluscs with original colors and ornamentations (NEL et al. 1987). Aquatic and terrestrial arthropods (insects and arachnids) are very diverse and frequently well preserved. The formation of the laminae is due to microbial, algal and

fungal activity (surface mats), with sedimentation figures (folds and ‘drapes’ on the surfaces of the laminae) similar to those of the Jurassic of Cerin (GALL et al. 1985).

While numerous fish and plant levels are known, just one layer with insects was identified. Specimens are particularly abundant, very well-preserved; often better than in other Oligocene outcrops of the region (Céreste, Bois d’Asson, Camoins-les-Bains and Aubagne-Fenestrelle near Marseille).

The ‘insect formation’ is 2.5 m thick, divided in two parts that correspond to two very different environmental conditions. The first (lower) episode is remarkable by its lateral monotony of facies on a distance of 6 km at least, in the outcrops observed on the northwest of Aix-en-Provence. This lower episode is distinguished from the rest of the ‘insect formation’ and from the whole formation of Aix-en-Provence by the presence of a very numerous thin limestone laminae. The second (upper) episode is remarkable by the presence of many silicified laminae. The fauna in this level is also very well preserved.

Aquatic insects are clearly less frequent than the terrestrial ones. The most abundant aquatic forms are dragonfly larvae (Libellulidae) which show considerable concentration on some laminae of the second episode where they are associated with numbers of marine jellyfish and fish (mass mortality due to the arrival of marine water in the lake). Aquatic bugs are very rare and represented by adults only (one Gerridae, one Notonectidae, two Naucoridae, one Belostomatidae; Nel, unpubl. data). Aquatic beetles are represented by few species of Hydrophilidae. One of them, an undescribed *Berosus*, is represented by hundred of adult specimens and is therefore the most frequent beetle in the outcrop. In spite of this, aquatic insects remain comparatively rare among the 30,000 fossil insects one of us (A.N.) collected at the locality.

## Material and methods

Fossils were examined in dry condition using a binocular microscope and photographed using the Nikon Coolpix P6000 digital camera attached to the ocular piece of the microscope. Drawings were prepared using a drawing tube and subsequently completed by comparison with the original specimen. Measurements were made from the photographs using tpsDig 2.10 software (ROHLF 2008). Morphological terminology follows HANSEN (1991), KOMAREK (2004) and SHORT & LIEBHERR (2007); nomenclature follows HANSEN (1999) and SHORT & LIEBHERR (2007). Fossil species which cannot be reliably assigned to genus (i.e., *Hydrobius obsoletus* in this study) are mentioned using the original combination of the name, with the generic name placed in quotation marks. Comparison with recent taxa is based on specimens deposited at National Museum (Prague, Czech Republic) and Natural History Museum (London, UK).

Phylogenetic analysis is based on the data matrix provided by SHORT & LIEBHERR (2007) containing 30 taxa (all species of Hydrobiusina sensu HANSEN (1999) plus selected species of subtribes Acidocerina and Hydrophilina and of the tribe Spermopsini, *Coleostoma orbiculare* Brullé, 1835 was used as outgroup taxon) and 55 morphological characters. *Limnoxenus olenus* sp. nov. was added to this matrix: only characters reliably seen on the fossil were included (see the Appendix), other characters were coded as missing (?). Data were analysed in the program TNT (GOLOBOFF et al. 2008) without any *a priori* considerations using the traditional (i.e. heuristic) search with 1000 replicates. This analysis resulted in four most parsimonous

cladograms of the length of 153 steps whose strict consensus was calculated. Subsequently the data were re-analysed using implied weighting (with default function of  $K=3.0$ ), which resulted in the single tree similar to the strict consensus tree of the previous analysis, but with resolved topology of *Hydramarca argentina* + *Limnocylus puncticeps* versus *Limnoxenus* clade. This tree (CI 0.44, RI 0.76) with collapsed unsupported branches is therefore used for this paper (Fig. 9); characters were mapped on this tree using the WinClada program (NIXON 2002). Data matrix in TNT format is available at the web site of the first author (<http://www.cercyon.eu/Publications.htm>).

## Taxonomy

### Family Hydrophilidae

#### *Limnoxenus olenus* sp. nov.

(Figs. 1–6)

**Type locality and horizon.** Aix-en-Provence (43°19'N 5°27'E), Bouches-du-Rhône, France; Aix-en-Provence Formation, Latest Oligocene, Late Chattian, about 22.5 million years ago.

**Type material.** HOLOTYPE: MNHN A32835 (part and counterpart; nearly completely preserved beetle in ventral view with preserved maxillary palpi and fore and hind legs). PARATYPE: MNHN A32836 (part and counterpart; nearly completely preserved beetle in ventral view with partly preserved legs); both deposited in Laboratoire de Paléontologie, Muséum national d'Histoire naturelle, Paris, France.

**Description.** Body elongate oval. For body measurements, see Table 1.

**Head.** Dorsal surface of head with visible frontoclypeal sutures arising very close to anterior margin of eyes; anterior margin of clypeus weakly emarginate. Eyes large, not protruding laterad of head outline, interocular distance 2.5 times the width of one eye in dorsal view. Gula weakly narrowing anteriorly, bearing distinct median longitudinal ridge posteriorly; genae with coarse granulate sculpture. Maxillary bases connected by sharp transverse ridge. Mentum transverse, 1.8 times as wide as long, anterior margin arcuately convex. Maxillary palpus slender, shorter than width of head; maxillary palpomere 2 longest, slightly bent inwards; palpomere 4 longer than palpomere 3.

**Thorax.** Pronotum weakly narrowing anteriorly, posterior corners rounded. Prosternum carinate medially; procoxal cavities contiguous medially; mesal portions of notopleural suture open. Transverse ridge below posterior margin of prothorax well developed, nearly reaching lateral margin. Mesoventrite divided from mesanepisternum by well developed anapleural sutures, shape of mesoventrite subtriangular with concave lateral margins ('trapezoidal' sensu SHORT & LIEBHERR (2007: Figs. 5A–C)); mesoventrite with high longitudinal median keel, anteromedian pit of mesoventrite ('mesoventrite depression' sensu SHORT & LIEBHERR (2007)) well developed. Scutellar shield large, triangular, ca. as long as wide. Elytra with sharply impressed sutural stria and nine longitudinal punctural series, series 7–10 (i.e., four lateral-most series) probably sharply impressed at least in posterior half. Mesocoxal cavities transverse, contiguous medially. Metaventrite slightly longer than mesoventrite; median portion longitudinally elevate, with sharp submedian arcuate ridges delimiting the median portion (both median elevation and submedian keels not seen in the paratype). Metanepisternum 3.2 times as long as wide, nearly equally wide throughout, with sharp transverse ridge anteriorly.

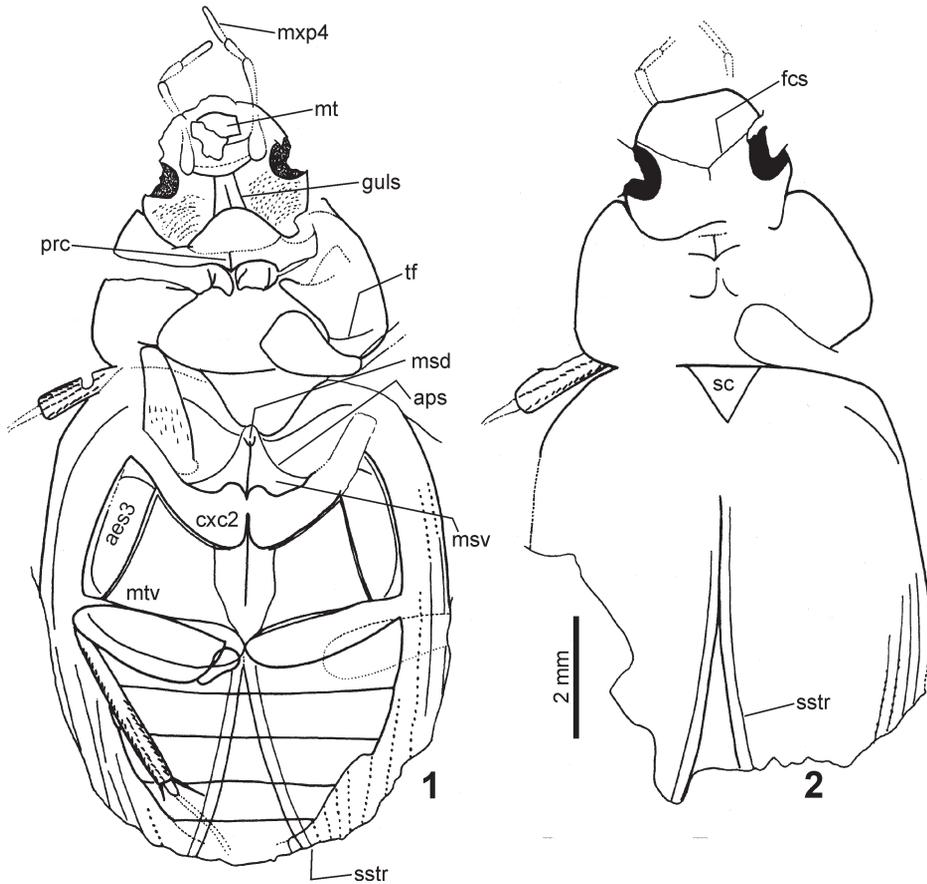
Table 1. Body measurements (in mm) of the fossil specimens examined for this study. Abbreviations: CW – clypeus width; EL – elytron length; HW – maximum head width; IOD – interocular distance; PL – length of pronotum at midline; PW – width of pronotum between posterior corners; TL – total body length.

Species / specimen	TL	HW	IOD	CW	PW	PL	EL
<i>Limnoxenus olenus</i> sp. nov.							
holotype	12.6	2.8	1.5	2.2	4.8	2.4	7.8
paratype	10.5	2.7	1.4	2.1	4.7	–	7.2
<i>'Hydrobius' obsoletus</i>							
holotype	8.4	2.3	–	–	5.0	–	6.1

*Abdomen* with five ventrites, ventrite 1 not carinate medially (apical portion of ventrite 5 not preserved and the presence or absence of the apical emargination cannot be therefore examined).

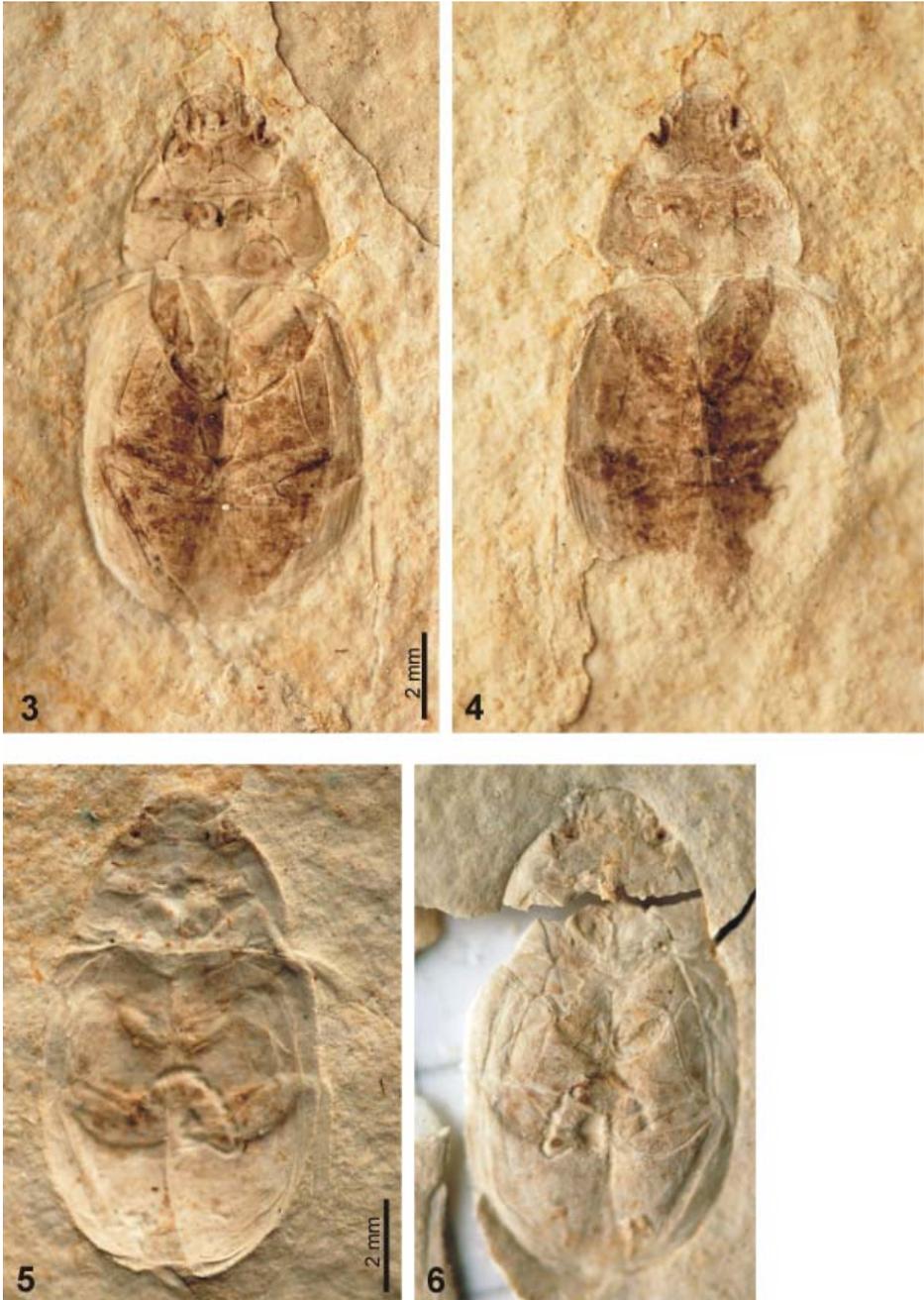
*Legs* slender, apices of femora not overlapping body outline. Metafemur 2.8 times as long as wide, facing metatrochanter only by posterior portion of proximal margin. Metatibia long, slender, bearing three longitudinal rows of spines; distal apex with two long spines. Metatarsomere 1 short but well developed.

**Generic attribution and phylogenetic analysis.** The position of *Limnoxenus olenus* sp. nov. within the Hydrophilidae is supported by the following characters: (1) clypeus large; (2) frontoclypeal sutures arising close to anterior margin of eyes; (3) maxillary palpi rather long; (4) anapleural sutures of mesothorax well developed, convergent anteriorly; (5) mesepisterna only narrowly divided anteromedially; (6) dorsal surface without granulate sculpture; (7) mesoventrite isolated from metaventrite by the mesocoxal cavity. Within Hydrophilidae, the placement in Hydrobiusina is supported by the following characters: (1) well developed anapleural sutures (in contrast to Megasternini, Omicrini, Sphaeridiini, Protosternini and Coelostomatini); (2) elytra with serial punctures (in contrast to some Chaetarthriini, many Anacaenini, some Laccobiini, many Acidocerina, and several groups of Sphaeridiinae); (3) mesoventrite with median longitudinal keel (in contrast to Rygmodini, Andotypini, some Sperchopsini, some Anacaenini, some Acidocerina); (4) metatarsomere 1 short (in contrast to Andotypini, Protosternini, Megasternini, Sphaeridiini, Omicrini, most Coelostomatini); (5) lateral margins of elytra not denticulate (in contrast to Sperchopsini); (6) scutellar shield ca. as long as wide (in contrast to Berosini); (7) body elongate oval and medium sized (in contrast to many Anacaenini, Chaetarthriini, Laccobiini, and Sphaeridiinae); (8) absence of the fused ventral keel on meso- and metaventrite (in contrast to the subtribe Hydrophilina); (9) maxillary palpomere 4 longer than palpomere 3 (in contrast to the subtribe Acidocerina and many Hydrophilina). The position of the fossil within Hydrobiusina is also supported by the results of the phylogenetic analysis, in which it is unambiguously placed within Hydrobiusina even though the representatives of other groups of Hydrophilini and Sperchopsini are included. The attribution of the fossil to the genus *Limnoxenus* is supported by the carinate prosternum, and median longitudinal carina on mesoventrite. Phylogenetic analysis supports the position of *L. olenus* sp. nov. within the genus *Limnoxenus*, precisely in the clade containing the non-Hawaiian species of the genus.

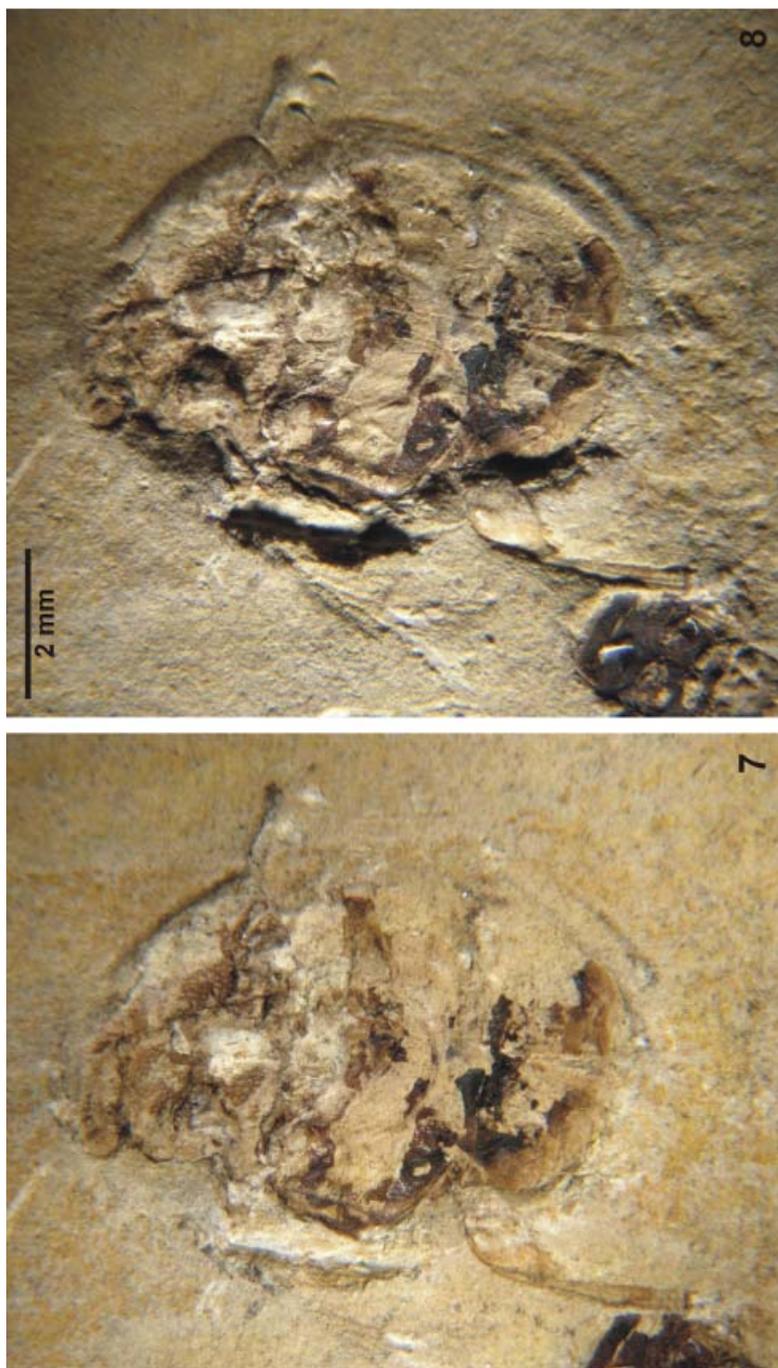


Figs. 1–2. *Limnoxenus olenus* sp. nov., holotype (1 – part, 2 – counterpart). Abbreviations: **aps** – anapleural suture; **aes3** – anepisternum 3; **cxc2** – mesocoxal cavities; **fcs** – frontoclypeal suture; **guls** – gular suture; **mxp4** – maxillary palpomere 4; **msd** – mesoventrite depression; **msv** – mesoventrite; **mt** – mentum; **mtv** – metaventrite; **prc** – prosternal carina; **sc** – scutellar shield; **sstr** – elytral sutural stria; **tf** – transverse fold of prothorax.

**Differential diagnosis.** The new species clearly differs from all representatives of the Hawaiian clade by the larger eyes (interocular distance less than 3.5, in contrast to interocular distance larger than 3.5 in all Hawaiian species), presence of the mesoventral depression (absent in all Hawaiian species) and wider posterior femora (metafemoral ratio 2.8, in contrast to 3.0 or more in *L. kauaiensis* Short & Lieberr, 2007, *L. semicylindricus* (Eschscholtz, 1822) and *L. nesiticus* (Sharp, 1908)). It seems to be very similar to recent *L. niger* (Gmelin, 1790), *L. olmoi* Hernando & Fresneda, 1994, *L. zealandicus* (Broun, 1880) and *L. sjostedti* Knisch, 1924 (based on the relatively large eyes and absence of characters defining the Hawaiian clade), from whose it differs mainly by larger body size (10.5–12.6 mm in *L. olenus* sp. nov., 8.0–10.0 in recent species); from *L. niger* and *L. olmoi* it also differs by slightly narrower



Figs. 3–6. *Limnoxenus olenus* sp. nov. 3–4 – holotype (3 – part, 4 – counterpart); 5–6 – paratype (5 – part, 6 – counterpart).



Figs. 7–8. '*Hydrobius*' *obscaletus* Heer, 1856, holotype (7 – photograph in the light from above; 8 – photograph in the light from side).

posterior femur (metafemoral ratio 2.80 in *L. olenus* sp. nov., less than 2.50 in *L. niger* and *L. olmoi*).

The only European Oligocene fossil taxa currently assigned to Hydrobiusina are those described within the genus *Escheria* Heer, 1847 by FÖRSTER (1891) from the locality of Brunstatt (they were transferred to *Hydrobius* by THÉOBALD (1937)). The identity of these species remains unknown pending the study of the type specimens, but all four species are much smaller than *Limnoxenus olenus* sp. nov. (with body length ranging between 5.0 and 9.0 mm) based on the original descriptions. Of the fossil species described from Aix-en-Provence, *Hydrobius obsoletus* is excluded from Hydrophilidae (see below) and *Hydrophilopsis incerta*, which may belong to Hydrobiusina based on some characters given in the original description, is much larger than *Limnoxenus olenus* (body length 20.0 mm). Even though these comparisons are based only on body size, they seem sufficient to exclude the possibility that the species is already described but incorrectly assigned to the genus.

**Etymology.** Olenus is a character of the Greek mythology; his wife Lethaea was turned to stone for her vanity and Olenus has chosen the same fate to stay forever with his beloved wife. Stands as noun in apposition.

### *Coleoptera incertae sedis*

#### *'Hydrobius' obsoletus* Heer, 1856

(Figs. 7–8)

*Hydrobius* sp.: CURTIS (1829: 294, 295), BRONN (1838: 811), HOPE (1847: 250, partim), GIEBEL (1856: 53, partim), SCUDDER (1891: 534), HANDLIRSCH (1908: 765, partim).

*Hydrobius obsoletus* Heer, 1856: 18, plate I: Fig. 19.

*Hydrobius obsoletus*: OUSTALET (1874: 128, translated description), SCUDDER (1891: 535, catalogue), HANDLIRSCH (1908: 765, catalogue), THÉOBALD (1937: Table XI, catalogue), STATZ (1939: 76, catalogue), HANSEN (1999: 319, catalogue).

**Type material.** HOLOTYPE: specimen no. NHM P(IV) 39859 (badly preserved fossil of whole specimen in ventral view, originally from the Murchison collection). Deposited in Department of Paleontology, the Natural History Museum, London.

**Description.** Body widely oval, for body measurements see Table 1. Head small, bearing globular eyes laterally. Prothorax rather large, pronotum ca. half as long as rest of body; pronotum wide posteriorly, strongly narrowing anteriorly. Prosternum small, prosternal process slightly protruding between procoxae (but see Discussion); ventral portion of prothorax with sparse and coarse punctation. Procoxae large, globular; procoxal cavities contiguous medially. Mesocoxae widely isolated from each other medially. Mesothoracic wings thickened and without conspicuous veins (i.e., transformed to elytra or hemelytra, see Discussion). Meta-ventrite rather short, transverse, metanepisternum developed. Metacoxae large, transverse, separated medially from each other. Mesotibia slightly widened at distal apex, mesotarsus nearly as long as mesotibia. Metafemur robust, widened, metatibia slightly widened distally, bearing at least one longitudinal row of setae or spines.

**Discussion.** In spite of a bad preservation of this fossil, the species can be reliably excluded from the superfamily Hydrophiloidea based on the large globular procoxae and medially separated meso- and metacoxae. The identity of this fossil remains unknown for the time being.

It partly resembles the aquatic groups of Heteroptera (especially the family Naucoridae) by the large procoxae and an acute projection between procoxae which might be alternatively interpreted as rostrum (it is interpreted as prosternal process in the redescription above). Mesothoracic wings not overlapping posteriorly may be present in some Nepidae and Naucoridae which bear the hemelytra with reduced membrane. However, *H. obsoletus* disagrees with aquatic Heteroptera in the ventral morphology, especially by well divided anepisterna laying at sides of metaventrite and separated meso- and metacoxae, and the specimen is therefore considered as Coleoptera *incertae sedis*. The body proportions and separated mesocoxae may resemble some groups of the Scarabaeoidea, but we refrain from placing the species to this group for the time being.

**Note on the records in old literature.** THE HOLOTYPE OF *Hydrobius obsoletus* comes from the Murchison collection. For that reason it may be concluded that the record of *Hydrobius* sp. from Aix-en-Provence by Curtis (1829) is most probably based on the same specimen. The record by Bronn (1838) has to be based on the Curtis's (1829) paper as well because *Hydrobius* is not mentioned by de Serres (1829) whose book is referred as a second source of data about fossils from Aix for Bronn's (1838) list. Hope (1847) adopted the data from Bronn (1838) and therefore still refer to the specimen mentioned by Curtis (1829), but he also mentioned additional specimens of *Hydrobius* deposited outside of Great Britain and therefore not coming from Murchison collection ('In my late visit to the Continent [...] my attention was also directed to those [insects] which for some period or periods have been entombed in fossil state' (Hope 1847: 250)); his data therefore only partly refer to the holotype of *Hydrobius obsoletus*. Giebel (1856) referred both to Curtis (1829) and Hope (1847) and supposed that their records of *Hydrobius* from Aix are based on the same specimen, which seems partly correct.

## Discussion

Two morphological groups may be recognized in recent species of *Limnoxenus*: (1) the Hawaiian clade containing seven endemic species characterized by a series of derived morphological characters (Fig. 9, see SHORT & LIEBHERR (2007) for details) and containing aquatic as well as terrestrial species, and (2) the group of less derived aquatic species represented by *L. niger*, *L. olmoi*, *L. sjostedti* and *L. zealandicus* which is resolved as a monophyletic clade in our analysis, but stands as a 'basal' group of *Limnoxenus* in the analysis by SHORT & LIEBHERR (2007) as well as in unpublished analyses based on molecular and morphological data (A. Short, unpublished data). The origin of the Hawaiian clade was estimated to date back to 5–28 million years ago based on the supposed time of emergence of recent Hawaiian islands or now submerged islands of the Hawaiian Archipelago (SHORT & LIEBHERR 2006), but no data about the age were available for non-Hawaiian group.

The Late Oligocene *Limnoxenus olenus* sp. nov. belongs to the non-Hawaiian group. It currently represents the oldest record of the genus, even though recent distribution of the *Limnoxenus* species suggest that the *Limnoxenus* clade is most probably much older, possibly dating back as far as to the Cretaceous. The Gondwanan origin was suggested for the 'stridulation file clade' (containing genera *Limnoxenus*, *Hydramara* and *Limnocyclus*, Fig. 9) based on the fact that most non-Hawaiian species of this clade occur in southern hemisphere

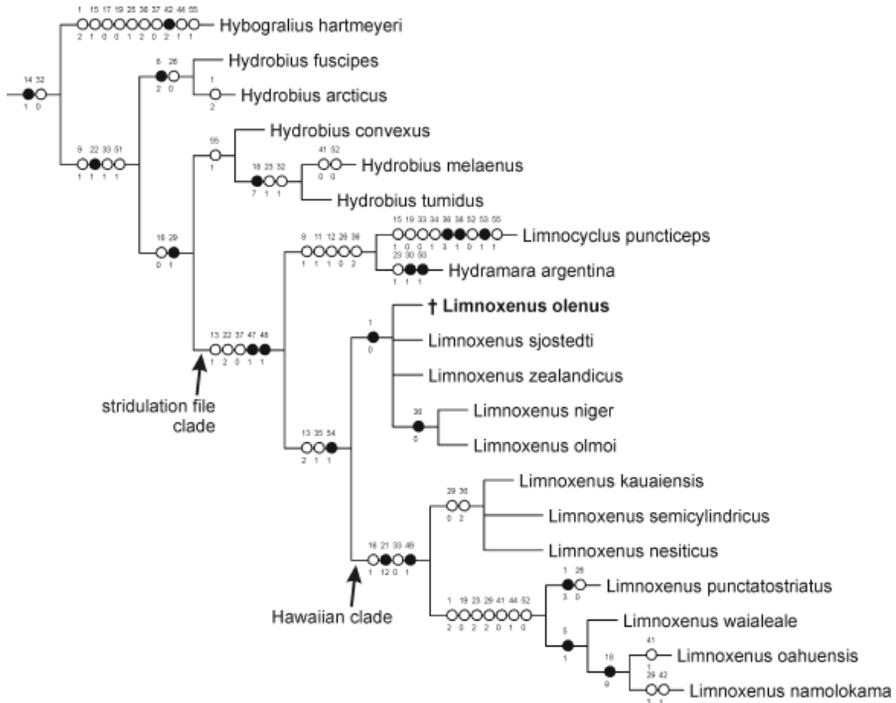


Fig. 9. Single most parsimonious tree of the analysis using implied weighting. Full dot: unique (syn)apomorphy, empty dot: homoplasy or reversal apomorphy. Only the part of the tree containing the species of Hydrobiusina is shown.

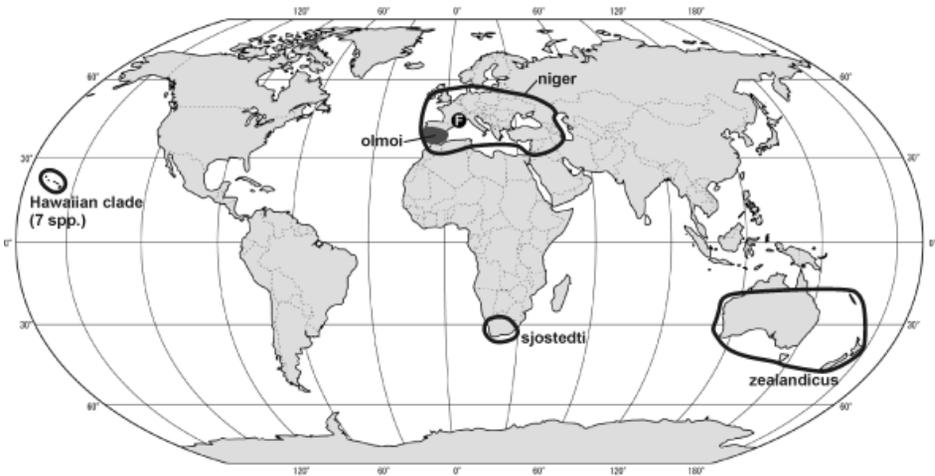


Fig. 10. Distribution of recent and fossil species of the genus *Limnoxenus*. F – Late Oligocene record of *L. olenus* sp. nov.

(Short, unpubl. data). If this is correct, the record of *L. olenus* sp. nov. from Aix-en-Provence indicates that the genus did colonize Europe and therefore the northern hemisphere at least during the Oligocene. As the recent distribution of the genus is confined to temperate zones, *Limnoxenus olenus* sp. nov. may be possibly considered as a temperate element of the European Late Oligocene insect fauna. Other records of fossil plants and insects from Aix-en-Provence indicate a rather warm environment, but with a distinct cooling in comparison to the Late Oligocene of Céreste (Lubéron, France) (GREGOR & KNOBLOCH 2001, COLLOMB et al. 2008).

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### Appendix: characters coded for *Limnoxenus olenus* sp. nov.

The list below contains only the characters preserved in the fossil (states coded for the fossil are highlighted in bold). For complete list of characters see SHORT & LIEBHERR (2007).

1. Interocular distance (narrowest width between eyes divided by the width of one eye when viewed dorsally): **(0)** less than 3.50; (1) 3.50–4.49; (2) 4.50–5.49; (3) greater than 5.49.
5. Maxillary palps: **(0)** longer than posterior margin of labrum; (1) equal to or shorter than posterior margin of labrum.
6. Second maxillary palpomere: **(0)** slightly to distinctly bowed inward; (1) bowed outward.
7. Apical maxillary palpomere: **(0)** longer than penultimate palpomere; (1) shorter than penultimate palpomere.
8. Mentum: **(0)** flat, at most slightly depressed anteromedially; (1) strongly depressed medially; (2) slightly convex medially.
13. Prosternum: (0) without carina; (1) with low median carina; **(2)** with strongly elevated carina; (3) nearly divided into two halves by anterior projection of the mesoventrite.
15. Mesoventrite: **(0)** trapezoidal; (1) triangular; (2) with anapleural sutures forming acute curve.
16. Mesoventrite depression: **(0)** distinct, well differentiated; (1) less differentiated or not distinguishable.
17. Mesoventrite: (0) flat, without distinct elevation; **(1)** elevated into a keel or tubercle (definition of states is corrected here to match the data matrix by SHORT & LIEBHERR (2007) who interchanged the states in their list).
20. Meso- and metaventrite: **(0)** not fused into a common keel; (1) fused into a common keel.
23. Metaventrite ratio (posterior width/median length): **(0)** less than 3.49; (1) 3.50–4.20; (2) greater than 4.20.
24. Elytral serial punctures: (0) absent; **(1)** present.
26. Elytral serial punctures: (0) set in distinct striae; **(1)** not set in striae (excluding sutural row).
27. Elytra: **(0)** with sutural stria (Fig. 6A); (1) without sutural stria.
31. Elytra: **(0)** with smooth margins; (1) with serrated margins.
36. Metafemoral ratio: (0) less than 2.50; **(1)** 2.50–2.99; (2) 3.00–3.99; (3) 4.00 or greater.
38. Metafemora: **(0)** with posterior margin evenly curved; (1) with posterior margin angulate.