

**Revision of Mesozoic fossils of the helophorid
lineage of the superfamily Hydrophiloidea
(Coleoptera: Polyphaga)**

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Abstract. A revision of the Mesozoic fossils belonging to the helophorid lineage of the superfamily Hydrophiloidea is performed and an adapted classification is suggested based on the phylogenetic analysis combining modern and fossil taxa of the lineage. Three genera are revealed as basal extinct Mesozoic clades of the helophorid lineage: *Hydrophilopsia* Ponomarenko, 1987, *Laetopsia* gen. nov. (adult forms) and *Cretotaenia* Ponomarenko, 1977 (larval form). *Mesosperchus* Ponomarenko, 1977 stat. nov. is resurrected from synonymy with *Zetemenos* Bode, 1953 and established as a formal subgenus of *Helophorus* Fabricius, 1775 containing probable stem taxa of that genus. *Mesohelophorus* Ponomarenko, 1977, stat. nov., is downgraded to a subgenus of *Helophorus*. Two new species are described: *Helophorus (Mesosperchus) inceptivus* sp. nov. (Sharteg, Mongolia, late Jurassic) and *H. (M.) yixianus* sp. nov. (Yixian Formation, China, Jurassic-Cretaceous boundary). *Mesohelophorus elongatus* Ponomarenko, 1990, syn. nov., is synonymised with *Mesosperchus tarsalis* Ponomarenko, 1977. The latter species and *Hydrophilopsia gracilis* Prokin, Ren & Fikáček, 2010 are transferred to *Helophorus (Mesosperchus)*, resulting in the following new combinations:

Helophorus (Mesosperchus) tarsalis (Ponomarenko, 1977), comb. nov. and *H. (M.) gracilis* (Prokin, Ren & Fikáček, 2010), comb. nov. *Mesohelophorus sibiricus* Ponomarenko, 1977 is transferred to *Helophorus (Mesohelophorus)* and the resulting secondary homonymy with *Helophorus sibiricus* (Motschulsky, 1860) is removed by proposing a new substitute name *Helophorus palaeosibiricus* nom. nov. for the former taxon. *Hydrophilopsia baissensis* Ponomarenko, 1987, *H. bontsaganica* Prokin, 2009, *H. hydraenoides* Prokin, Ren & Fikáček, 2010, *H. mongolica* Ponomarenko, 1987 and *H. shatrovskiyi* Prokin, Ren & Fikáček, 2010 are transferred to *Laetopsia* gen. nov. The inclusion of the fossil taxa into the helophorid lineage of the Hydrophiloidea made the slight adaptation of the diagnosis of the genus *Helophorus* necessary. Six fossil species included previously into the genera *Helophorus*, *Mesosperchus* and *Mesohelophorus* are excluded from the helophorid lineage: *Mesosperchus notatus* Ponomarenko, 1977, and *M. schultzi* Ponomarenko, 1985 (both transferred to *Polyphaga incertae sedis*), *Mesohelophorus mongolicus* Ponomarenko, 1986 (transferred to Buprestoidea), *Mesosperchus angulatus* Ponomarenko, 1985 (confirmed as not belonging to the Hydrophiloidea), *Tychon antiquum* (Giebel, 1856) (confirmed as *Coleoptera incertae sedis*) and *Helophoropsis brodiei* (Giebel, 1856) (transferred to *Coleoptera incertae sedis*). The genus *Zetemenos* Bode, 1953 is transferred to *Coleoptera incertae sedis* based on the examination of its type species, *Z. sexlineatus* Bode, 1953.

Key words. Hydrophiloidea, helophorid lineage, Helophoridae, *Helophorus*, Buprestoidea, new genus, new species, fossil record, Mesozoic, Jurassic, Cretaceous, China, Germany, Mongolia, Russia, United Kingdom

Introduction

Divergence times of principal coleopteran clades were estimated recently in the phylogenetic analyses performed by HUNT et al. (2007) and MCKENNA & FARRELL (2009) based on a molecular clock dated by selected Mesozoic fossils across the whole order. Although no hydrophiloid fossil was included, the origin of the hydrophiloid lineage was dated back to ca. 228 mya, i.e. the Late Triassic. Although the oldest fossils originally assigned to the Hydrophiloidea date back roughly to that time, coming from the Late Triassic deposits of the Blackstone Formation in Australia (TILLYARD 1916, DUNSTAN 1923, JELL 2004), Höganäs Formation in Sweden (HEER 1878), and Aust Cliff and Hasfield in United Kingdom (BRODIE 1845, GIEBEL 1856, HANDLIRSCH 1908), our initial study revealed that these fossils are mostly preserved as isolated elytra, and none of them bears any synapomorphy of the Hydrophiloidea (Fikáček, unpubl. data). These findings showed the necessity of a revision of the Mesozoic fossil record of the Hydrophiloidea prior to the application of the fossils for dating the phylogenies. For this reason, a project focused on the revision of previously described fossils assigned to Hydrophiloidea was undertaken.

After a series of papers concerning Tertiary fossils (FIKÁČEK et al. 2008, 2010a,b,c, 2011a,b; FIKÁČEK & ENGEL 2011) and descriptions of few Mesozoic species from Mongolian and Chinese deposits (PROKIN 2009, PROKIN et al. 2010), this contribution is the first detailed revision focused on the Mesozoic taxa. It is based on the initial study of described Mesozoic taxa which revealed that some of the fossils are similar to the recent genus *Helophorus* Fabricius, 1775. These fossils were examined in detail, compared with modern representatives of the helophorid lineage (i.e. genera *Helophorus*, *Georissus* Latreille, 1809 and *Epimetopus* Lacordaire, 1854; see also FIKÁČEK et al. 2011c) and a phylogenetic analysis combining modern and Mesozoic taxa has been performed. Results of the analysis clearly show that most of the fossils really belong to the helophorid lineage of the Hydrophiloidea and allow us to adapt the classification of the lineage in order to accommodate these fossil taxa. The comparison with modern taxa and the phylogenetic analysis are presented in a separate paper (FIKÁČEK et al. 2012). Here we summarize all taxonomic results, i.e. (re)describe all included fossil species, describe a new fossil genus, introduce necessary taxonomic changes and adapt the diagnosis of the genus *Helophorus* which became necessary after including the fossil taxa into the helophorid lineage of the Hydrophiloidea.

Material and methods

Described Mesozoic fossils assigned to the Hydrophiloidea and several undescribed specimens from Russian, Mongolian and Chinese deposits were examined by A. Prokin and M. Fikáček. Based on this initial study, only the species resembling the modern *Helophorus* in some characters were included in this study. All known specimens of these species were examined in order to obtain as many characters as possible. Specimens were examined either dry or under alcohol to enhance the contrast. Photographs of the fossils were made using a Canon MP-E 65 mm macro lens attached to a Canon EOS 550D camera or a Leica DFC420 camera attached to the Leica M165c microscope. Scanning electron micrographs of uncoated fossil specimens were taken using a Hitachi S-3700N environmental electron microscope in the Department of Paleontology, National Museum in Prague and Tescan Vega XMU in the Paleontological Institute of the Russian Academy of Sciences in Moscow.

The depository of the specimens examined is indicated by the following prefixes of their inventory numbers:

- CNU Capital Normal University, Beijing, China (D. Ren);
- NHM The Natural History Museum, Department of Paleontology (C. Mellish);
- NHMW Geologisch-Paläontologische Abteilung, Naturhistorisches Museum, Wien, Austria (A. Lukeneder);
- PIN Paleontological Institute of the Russian Academy of Science, Moscow, Russia (A. Ponomarenko);
- SMF Abteilung Paläontologie und Historische Geologie, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany.

The main purpose of this contribution is to revise the genus- and family-level attributions of the fossil taxa. Differences and synonymies at species level are only discussed in case that multiple species of the genus occur on the same locality or outcrop, or on localities of roughly same age situated close to each other.

Taxonomy

Basal extinct clades of the helophorid lineage

† *Hydrophilopsia* Ponomarenko, 1987

Hydrophilopsia Ponomarenko, 1987: 93.

Type species. *Hydrophilopsia longitarsalis* Ponomarenko, 1987 (by original designation).

Time range. Latest Jurassic, Tithonian, ca. 151–146 mya.

Diagnosis. Adult: Head and pronotum without setiferous granules, gula wide, pronotal flanks extremely wide, elytra without elevated costae, legs with dense series of swimming hairs on tibiae and tarsi; it is also probable that the pronotum lacks longitudinal grooves and that the median portion of frontoclypeal suture is not grooved (both these characters are incompletely preserved in the single specimen available). In the helophorid lineage, the extremely wide pronotal flanks delimited by a non-sinuate inner ridge are only developed in the modern *Helophorus* subgenera *Empleurus* Hope, 1838 and *Orphelophorus* Orchymont, 1927; both of them bear very distinct granulation on the head and pronotum, lack swimming hairs on legs and bear strongly costate elytra.

Taxonomic note. The genus is largely defined by plesiomorphies, but bears at least one autapomorphy, i.e. extremely wide pronotal flanks, hence it may represent an extinct late Jurassic clade of the helophorid lineage. All characters shared between *H. longitarsalis* (type species) and the remaining species assigned previously to this genus are plesiomorphic and *Hydrophilopsia* in its original concept seems to be paraphyletic or polyphyletic for that reason. In order to keep *Hydrophilopsia* monophyletic and easily diagnosable, we are excluding all other species into a separate genus *Laetopsia* gen. nov., which makes *Hydrophilopsia* a monotypic genus confined to the Latest Jurassic.

† *Hydrophilopsia longitarsalis* Ponomarenko, 1987

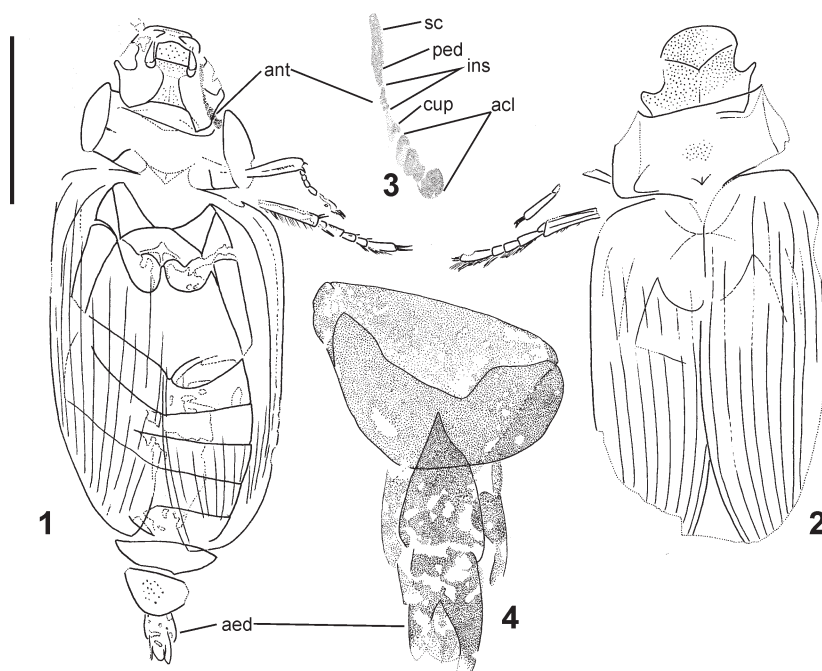
(Figs. 1–4, 42–48)

Hydrophilopsia longitarsalis Ponomarenko, 1987: 94.

Type locality and age. Russia, Chita Region, Daya outcrops [left bank of the Daya river above the Shiviya falls]. Latest Jurassic, Tithonian, ca. 151–146 mya (RASNITSYN 1990, SINITSHENKOVA & ZHERIKHIN 1996; Vasilenko, pers. comm. to A. Prokin, 2011).

Material examined (1 spec.). HOLOTYPE: PIN 3063/614 (piece and counterpiece).

Redescription (male). Body elongate oval, 9.7 mm long. Head with distinct lateral portions of frontoclypeal suture, median portion weakly preserved and probably not grooved, dorsal surface of head finely punctate, without setiferous granules. Narrow postocular bridge present. Mentum transverse, 1.5× wider than long, finely punctate. Gula wide, with fine median longitudinal ridge. Antenna with 9 antennomeres (i.e. with three intermediate antennomeres, Fig. 3), scape long, terminal three antennomeres forming a club. Pronotum slightly narrowing anteriorly, arcuate laterally, with protruding anterolateral corners, longitudinal grooves not preserved (probably absent), lateral margins smooth; pronotal flanks very wide, the ridge delimiting them from inner portion of hypomerone arcuate in shape. Mesanepisterna not meeting medially, mesoventrite strongly narrowing anteriorly, very narrow at anterior margin,



Figs. 1–4. *Hydrophilopsia longitarsalis* Ponomarenko, 1987 (holotype). 1 – piece, general view; 2 – counterpiece, general view; 3 – detail of antenna; 4 – detail of the aedeagus. Scale bar: 2 mm (corresponds to Figs. 1–2). Abbreviations: acl – antennal club; aed – aedeagus; ant – antenna; cup – cupule; ins – intermediate antennomeres; ped – pedicel; sc – scapus.

bearing a transverse ridge posteriorly. Mesocoxal cavities only very narrowly divided from each other. Elytron with 10 elytral series, scutellary stria not preserved, all elytral intervals of the same height, epipleuron narrow, subdivided into wider inner and narrower outer parts. Metaventricle much longer than mesoventricle, metanepisternum with oblique transverse ridge anteriorly. Mesotibia with sparsely arranged swimming hairs, its apex with several spines; mesotarsus with five tarsomeres, each with series of swimming hairs dorsally, tarsomere 1 shortest, tarsomere 2 longer than tarsomere 3, claws long, arcuate. Abdomen with five ventrites, posterior margin of ventrite 5 possibly with rectangular teeth. Aedeagus similar to *Helophorus* in general shape, phallobase with acute symmetrical manubrium.

† *Laetopsia* gen. nov.

Type species. *Hydrophilopsia shatrovskiyi* Prokin, Ren & Fikáček, 2011 (by present designation).

Time range. Early Cretaceous, ca. 145–112 mya.

Diagnosis. Adult: Head and pronotum without setiferous granules, with grooved median portion of frontal suture, gula wide, pronotal flanks narrow, elytra without elevated costae, pale with dark stripes along striae; pronotum with a median longitudinal groove. Within the

helophorid lineage, the genus is easily recognized according to the pale elytra with dark longitudinal stripes along elytral striae (unique character), narrow pronotal flanks (in contrast to wide flanks in *Hydrophilopsia*) and a pronotum with a single median longitudinal groove and without setiferous granules (in *Helophorus*, the subgenera *Orphelophorus* and *Mesohelophorus* bear a reduced number (i.e. less than five) of longitudinal pronotal grooves but always bear very distinct setiferous granules on the pronotum).

Etymology. From *laetus* (Latin), meaning joyful, pleasant, referring to the colourful elytra of this genus, plus the ending *-psia* derived from the genus *Hydrophilopsia* to which all species of the genus were assigned before. Gender: feminine.

Taxonomic note. All species included herein share plesiomorphic characters with *Hydrophilopsia* but lack its only autapomorphy, i.e. the extremely wide pronotal flanks. In addition, all of them are readily distinguishable by pale elytra bearing dark stripes along elytral striae, a character which may represent an unique autapomorphy of the genus (but is unfortunately not preserved in *Hydrophilopsia*). In absence of any additional data, both above differences indicate that the species with striped elytra form an easily diagnosable lineage separate from *Hydrophilopsia*, which is here described as *Laetopsia* gen. nov. The genus seems to have coexisted with *Helophorus* until the early Cretaceous and likely represents an extinct Mesozoic clade of the helophorid lineage.

† *Laetopsia baissensis* (Ponomarenko, 1987) comb. nov.

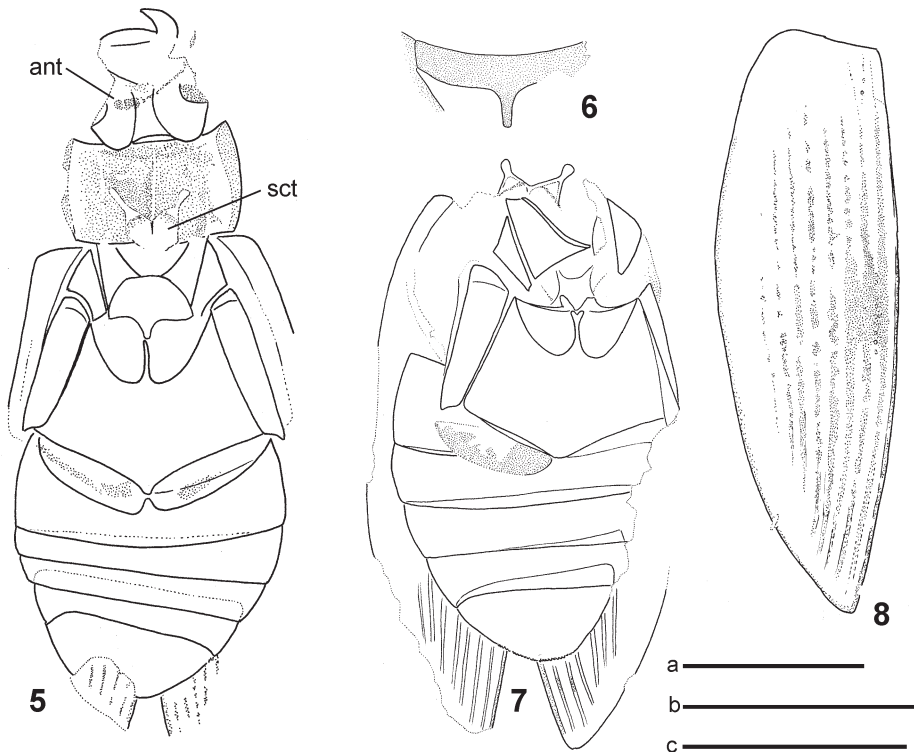
(Figs. 5–8, 53–56, 104–106)

Hydrophilopsia baissensis Ponomarenko, 1987: 95.

Type locality and age. Russia, Buryat Republic, Baissa outcrops [river Vitim below the mouth of the Baissa River]. Early Cretaceous, Berriasian to Hauterivian, ca. 146–135 mya (ZHERIKHIN et al. 1998; Vasilenko, pers. comm. to A. Prokin, 2011)

Material examined (23 spec.). HOLOTYPE: PIN 3064/6985 (piece and counterpiece). PARATYPES: PIN 3064/6979 (piece and counterpiece), PIN 3064/6984 (elytron), PIN 3064/6988 (piece and counterpiece), PIN 3064/6991 (piece only), PIN 3064/7002 (piece only), PIN 3064/7011 (piece only), PIN 3064/7018 (piece and counterpiece). OTHER MATERIAL (possibly including additional paratypes): PIN 3064/3037 (piece only), PIN 3064/6861 (fragment of an elytron), PIN 3064/6967 (piece only), PIN 3064/6968 (piece only), PIN 3064/6978 (piece only), PIN 3064/6981 (piece only), PIN 3064/6986 (piece and counterpiece), PIN 3064/6987 (piece only), PIN 3064/6989 (piece only), PIN 3064/6990 (piece only), PIN 3064/6997 (piece only), PIN 3064/7003 (fragment of an abdomen), PIN 3064/7009 (piece only), PIN 3064/7010 (piece only), PIN 3064/7017 (piece only).

Redescription. Body elongate oval, 6.7–7.7 mm long (holotype 7.4 mm). Head with narrow postocular bridge, mentum probably transverse, labrum transverse, attached on anterior margin of head, gula wide. Antenna with three-segmented club and well developed cupula, pedicel conical. Pronotum slightly narrowed basally, arcuate laterally, bearing a median longitudinal groove, lateral margins smooth. Prosternum well-developed, ca. as long as procoxal cavities, pronotal flanks narrow, slightly narrowing posteriad, ridge delimiting their inner margin sinuate. Mesanepisterna not meeting medially, mesoventrite strongly narrowing anteriad, sutures slightly arcuate, without transverse ridge posteriorly. Mesocoxal cavities only very narrowly divided from each other. Elytral series 1–8 darkened, scutellary stria absent, all elytral intervals of the same height; epipleuron subdivided into inner and outer portion, inner



Figs. 5–8. *Laetopsia baissensis* (Ponomarenko, 1987). 5 – PIN 3064/7018; 6 – PIN 3064/7010, detail of prosternum; 7 – PIN 3064/6987; 8 – PIN 3064/6984, elytron. Scale bars 2 mm (a: Fig. 5, b: Fig. 6, c: Figs. 7–8). Abbreviations: ant – antenna; sct – scutellum.

portion narrow. Metaventrite much longer than mesoventrite, metanepisternum with oblique transverse ridge anteriorly. Abdomen with five sparsely punctate ventrites, posterior margin of ventrite 5 with rectangular teeth.

Note. *Laetopsia baissensis* lacks the transverse ridge on the mesoventrite (Fig. 107) which is otherwise a synapomorphy shared by all representatives of the helophorid lineage. This might indicate that *L. baissensis* is not congeneric with the remaining *Laetopsia* species and may not even belong to the helophorid lineage. However, *L. baissensis* shares all remaining characters with *L. shatrovskiyi* (type species of *Laetopsia* gen. nov.), including the dark stripes on the elytra and a single median groove on pronotum. For this reason, we rather consider the species as an aberrant representative of *Laetopsia* gen. nov. which indicates that the morphology of the mesoventrite may have varied in *Laetopsia* gen. nov. in similar extent as it does in some modern hydrophiloid genera (e.g., in *Anacaena* Thomson, 1859, Hydrophilidae).

† *Laetopsia bontsaganica* (Prokin, 2009) comb. nov.

(Fig. 62)

Hydrophilopsia bontsaganica Prokin, 2009a: 54.

Hydrophilopsia bontsaganica: PROKIN (2009b: 660).

Type locality and age. Mongolia, Bayankhongor province, foothills of the Dund Ula Mts., S of Bööntsagaan Lake. Lower Cretaceous, Barremian or Aptian, ca. 130–112 mya (RASNITSYN & ZHERIKHIN 2002).

Material examined (1 spec.). HOLOTYPE: PIN 3559/6370 (piece only, specimen in dorsal view).

Redescription. Body elongate oval, 8.8 mm long. Head with very distinct frontoclypeal suture, its median portion grooved, anterior portion of clypeus straight. Pronotum slightly transverse, bearing median groove, lateral margins smooth, arcuate. Elytron with darkened striae. Abdomen with five ventrites.

Note. Although the only known specimen is poorly preserved, the combination of elytra with dark striae, the distinct frontoclypeal suture with grooved median portion and the presence of the median groove on the pronotum clearly assign the species to the genus *Laetopsia*.

† *Laetopsia hydraenoides* (Prokin, Ren & Fikáček, 2010) comb. nov.

(Figs. 9, 57, 61)

Hydrophilopsia hydraenoides Prokin, Ren & Fikáček, 2010: 178.

Type locality and age. China, Liaoning Province, Shangyuan County, Chaomidian Village, Huangbanjigou [the name of the village was misspelled in the original description]. Yixian Formation, Jurassic-Cretaceous boundary, Late Tithonian-Berriasian, ca. 145–140 mya (REN et al. 2010). An alternative dating was proposed by SWISHER et al. (1999): Lower Cretaceous, Aptian, 124.6 mya (see REN et al. (2010) for discussion on various datings of Yixian formation).

Material examined (3 spec.). HOLOTYPE: CNU 2010021 (piece only). PARATYPE: CNU 2010026 (piece only). ADDITIONAL NON-TYPE SPECIMEN: CNU 2009089 (piece only).

Redescription. Body elongate oval, 5.3–6.1 mm long (holotype 6.1 mm). Head with protruding eyes, frontoclypeal suture Y-shaped, with grooved median portion; anterior margin of clypeus straight; labrum transverse, tightly attached to anterior margin of clypeus; setiferous granules missing. Pronotum widest in anterior third, with distinctly angulate lateral margins; surface without setiferous granules, with median longitudinal groove; pronotal flanks narrow. Elytra with striae 1–7 darkened; scutellary stria absent. Mesocoxae contiguous, metaventrite much longer than mesoventrite. Abdomen with 5 ventrites. Legs relatively long.

Note. The species may be easily distinguished from all other *Laetopsia* species according to the distinctly angulate lateral margins of the pronotum. The additional specimen listed above is badly preserved and its assignment to the species is tentative.

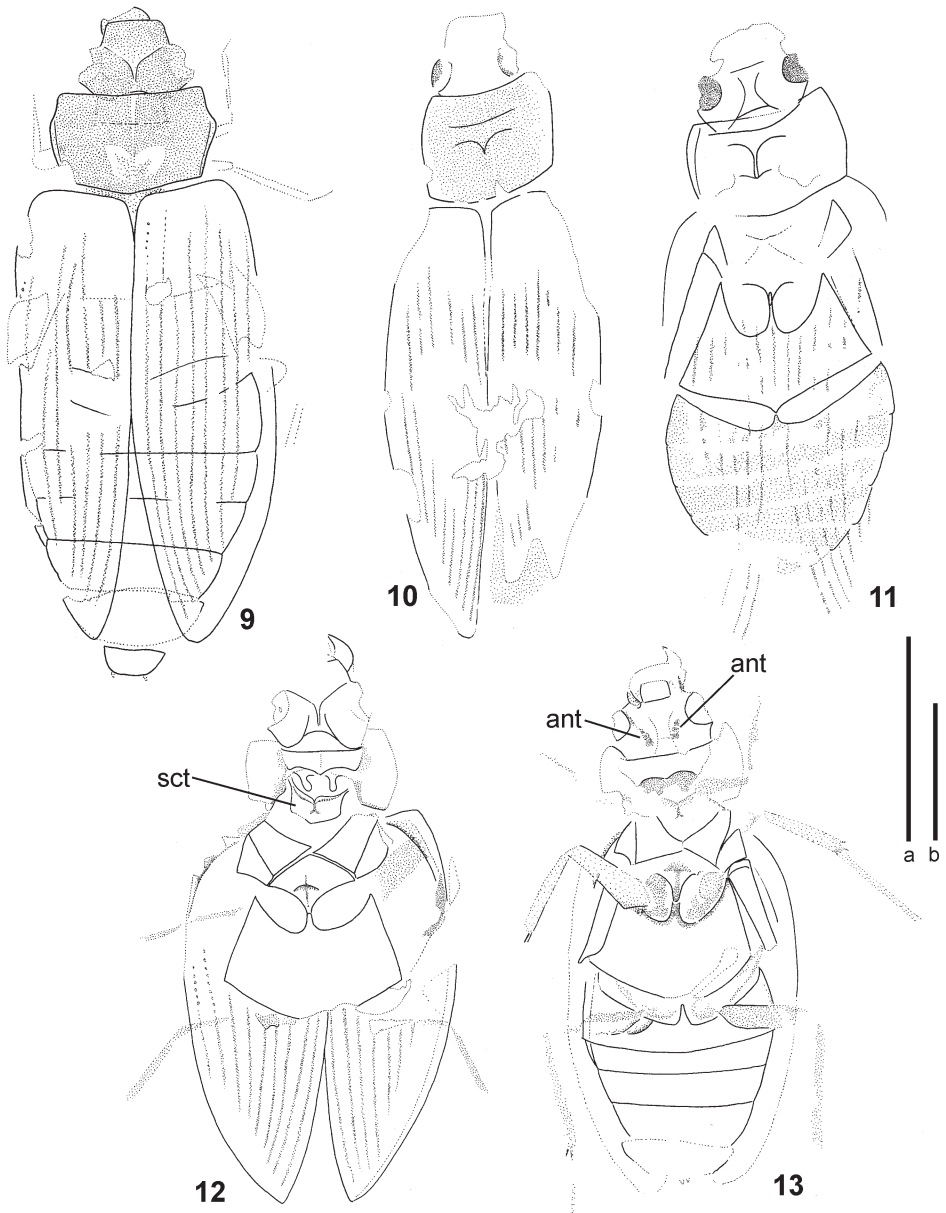
† *Laetopsia mongolica* (Ponomarenko, 1987) comb. nov.

(Figs. 10–11, 58–60)

Hydrophilopsia mongolica Ponomarenko, 1987: 97.

Type locality and age. Mongolia, Shin Khuduk, Middle-Gobi province. Lower Cretaceous, Hautervian to Barremian, ca. 136–125 mya (DURANTE & BAKULBEKOV 2009; Vasilenko, pers. comm. to A. Prokin, 2011).

Material examined (17 spec.). HOLOTYPE: PIN 3664/1567 (piece only). PARATYPES: PIN 3664/1480 (piece only); PIN 3664/1493 (piece only); 3664/1569 (piece only); PIN 3664/1573 (piece only); PIN 3664/1574 (piece only); PIN 3664/1583 (piece only); PIN 3664/1587 (piece only); PIN 3664/1642 (piece only); PIN 3664/1650 (piece only); PIN



Figs. 9–13. *Laetopsia* gen. nov. 9 – *L. hydraenoides* (Prokin, Ren & Fikáček, 2010), holotype. 10–11 – *L. mongolica* (Ponomarenko, 1987) (10 – PIN 3664/1567, holotype; 11 – PIN 3664/1661). 12–13 – *L. shatrovskiyi* (Prokin, Ren & Fikáček, 2010) (12 – CNU 2010199; 13 – CNU 2010242, holotype). Scale bars: 2 mm (a: Figs. 9, 12–13; b: Figs. 10–11). Abbreviations: ant – antenna; sct – scutellum.

3664/1655 (piece only); PIN 3664/1661 (piece only); PIN 3664/1663 (piece only); PIN 3664/1672 (piece only); PIN 3664/1683 (piece only); PIN 3664/1771 (piece only); PIN 3664/1772 (piece only); PIN 3664/1784 (piece only).

Redescription. Body elongate oval, 8.0–9.5 mm long (holotype 9.5 mm). Head with protruding eyes, frontoclypeal suture Y-shaped, with grooved median portion; anterior margin of clypeus straight; labrum transverse, tightly attached to anterior margin of clypeus. Gula slightly constricted but gular sutures still widely separate. Pronotum with median longitudinal groove, pronotal flanks narrow, widest anteriorly, narrowing posteriad; prosternum long anterior to procoxae. Elytral striae 1–8 darkened; scutellary stria absent. Mesocoxae contiguous, meta-ventrite much longer than mesoventrite, metepimeron wide. Abdomen with 5 ventrites.

Note. The specimens examined show a wide variation in body proportions which are likely the result of deformations during the fossilization process. Besides these differences, we did not find any indication that more species should be present at the locality. Therefore, in agreement with the original description, we treat all specimens as a single species. *Laetopsia mongolica* clearly differs from both *Laetopsia* species from the Yixian formation which is considered as roughly of the same age as Shin Khuduk by some authors (SWISHER et al. 1999) and was/is moreover rather close to it geographically – it has continually arcuate lateral margins of pronotum (in contrast to angulate margins in *L. hydraenoides*) and rather narrow prosternum in front of procoxae (in contrast to long precoxal portion of prosternum in *L. shatrovskiyi*).

† *Laetopsia shatrovskiyi* (Prokin, Ren & Fikáček, 2010) **comb. nov.**

(Figs. 12–13, 49–52)

Hydrophilopsia shatrovskiyi Prokin, Ren & Fikáček, 2010: 178.

Type locality and age. China, Liaoning Province, Shangyuan County, Chaomidian Village, Huangbanjigou [the name of the village was misspelled in the original description]. Yixian Formation, Jurassic-Cretaceous boundary, Late Tithonian-Berriasian, ca. 145–140 mya (REN et al. 2010). An alternative dating was proposed by SWISHER et al. (1999): Lower Cretaceous, Aptian, 124.6 mya (see REN et al. (2010) for discussion on various datings of Yixian formation).

Material examined (3 spec.). HOLOTYPE: CNU 2010242 (piece only). PARATYPES: CNU 2010016+CNU 2009199 (piece and counterpiece); CNU 2010012 (piece only).

Redescription. Body elongate oval, body 5.0–5.5 mm long (holotype 5.4 mm). Head with protruding eyes, clypeus subquadrate, with labrum attached to its anterior margin; frontoclypeal suture distinct, Y-shaped, slightly grooved medially; head surface with weak granulation. Mentum slightly wider than long, gula slightly constricted but with well-separated gular sutures. Antennae with three-segmented antennal club. Pronotum arcuate laterally, pronotal flanks narrow, narrowing posteriad. Prosternum long anterior to procoxae. Mesanepisterna probably nearly connecting anteriorly, mesoventrite extremely narrow at anterior margin; posterior portion of mesoventrite with very distinct transverse ridge. Mesocoxae large, contiguous. Elytron with striae 1–7 darkened; epipleuron narrow, subdivided into inner and outer portion, inner portion narrow. Meta-ventrite longer than mesoventrite, metepimeron with oblique transverse ridge anteriorly. Metacoxae transverse, abdomen with 5 ventrites. Legs rather long, tibiae slightly longer than femora, tibial apices with strong spines.

Note. One paratype of this species (CNU2010004) was found not to be conspecific with the remaining specimens and is described below as *Helophorus (Mesosperchus) yixianus* sp. nov.

† *Cretotaenia* Ponomarenko, 1977

Cretotaenia Ponomarenko, 1977a: 92.

Type species. *Cretotaenia pallida* Ponomarenko, 1977 (by original designation).

Time range. Early Cretaceous, Berriasian to Hauterivian, ca. 146–135 mya.

Diagnosis. Larva: Head hyperprognathous; nasale simply triangular, epistomal lobes large, slightly overlapping nasale, bearing series of setae; mandible with two retinacular teeth; labium without ligula; each parietale with 6 stemmata situated in area of darker cuticle; all thoracic segments with large dorsal tergite; abdominal segments 1–8 each with a pair of dorsal sclerites and a pair of minute sclerites on each side above spiracle; tracheal system holopneustic, spiracular atrium absent; urogomphi large, 3-segmented.

Note. The genus was originally described as *Adephaga incertae sedis* by PONOMARENKO (1977a), but CROWSON (1981) later noted that it may rather be related to *Helophorus*. A detailed comparison of all preserved characters including those not mentioned in the original description confirmed this opinion: *Cretotaenia* precisely matches modern *Helophorus* larvae in nearly all preserved characters except the labium which does not protract as much anteriorly, different arrangement of abdominal sclerites (two small sclerites are present laterally of dorsal large sclerite and dorsally of the spiracle in *Cretotaenia*, whereas *Helophorus* has a single large sclerite in this position) and the dorsally situated occipital foramen (situated posteriorly in *Helophorus*). The phylogenetic analysis by FIKÁČEK et al. (2012) also confirms that *Cretotaenia* is related to the Helophoridae, and the genus is therefore included into the helophorid lineage in the present work. ZHERIKHIN et al. (1998) hypothesized that *Cretotaenia pallida* is likely a larval form of *Laetopsia baissensis*, which cannot be confirmed or rejected by our analyses even though both genera seem to represent basal extinct clades of the helophorid lineage.

At first view, the number of stemmata seems to be five on each parietale in the specimens examined. However, the arrangement of stemmata in the fossils precisely fits that in modern *Helophorus* (see FIKÁČEK et al. 2012, Fig. 1H) in which five stemmata are situated dorsally in the area of darkened cuticle (and hence preserved in the fossils), whereas the largest stemma is rather isolated from the others, situated more ventrally outside of the area of darkened cuticle (and is therefore not preserved in the fossil). For that reason we consider *Cretotaenia* having 6 stemmata on each parietale.

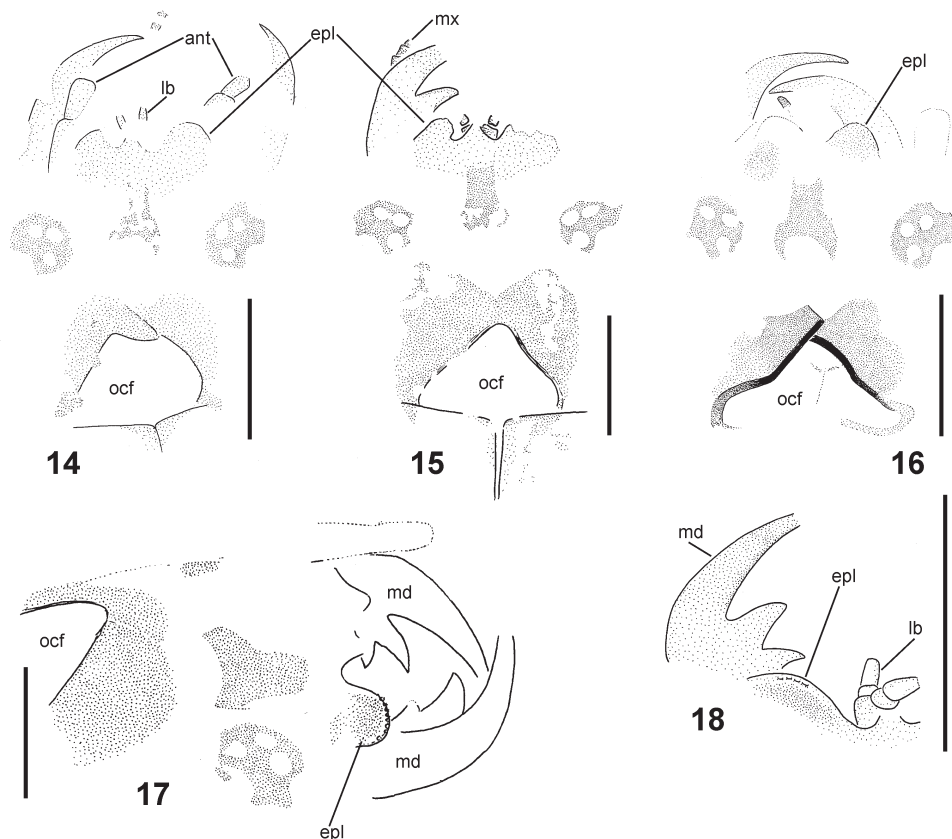
† *Cretotaenia pallida* Ponomarenko, 1977

(Figs. 14–25, 63–72)

Cretotaenia pallida Ponomarenko, 1977a: 93.

Type locality and age. Russia, Buryat Republic, Baissa outcrops [river Vitim below the mouth of the Baissa river]. Early Cretaceous, Berriasian to Hauterivian, ca. 146–135 mya (ZHERIKHIN et al. 1998; Vasilenko, pers. comm. to A. Prokin, 2011)

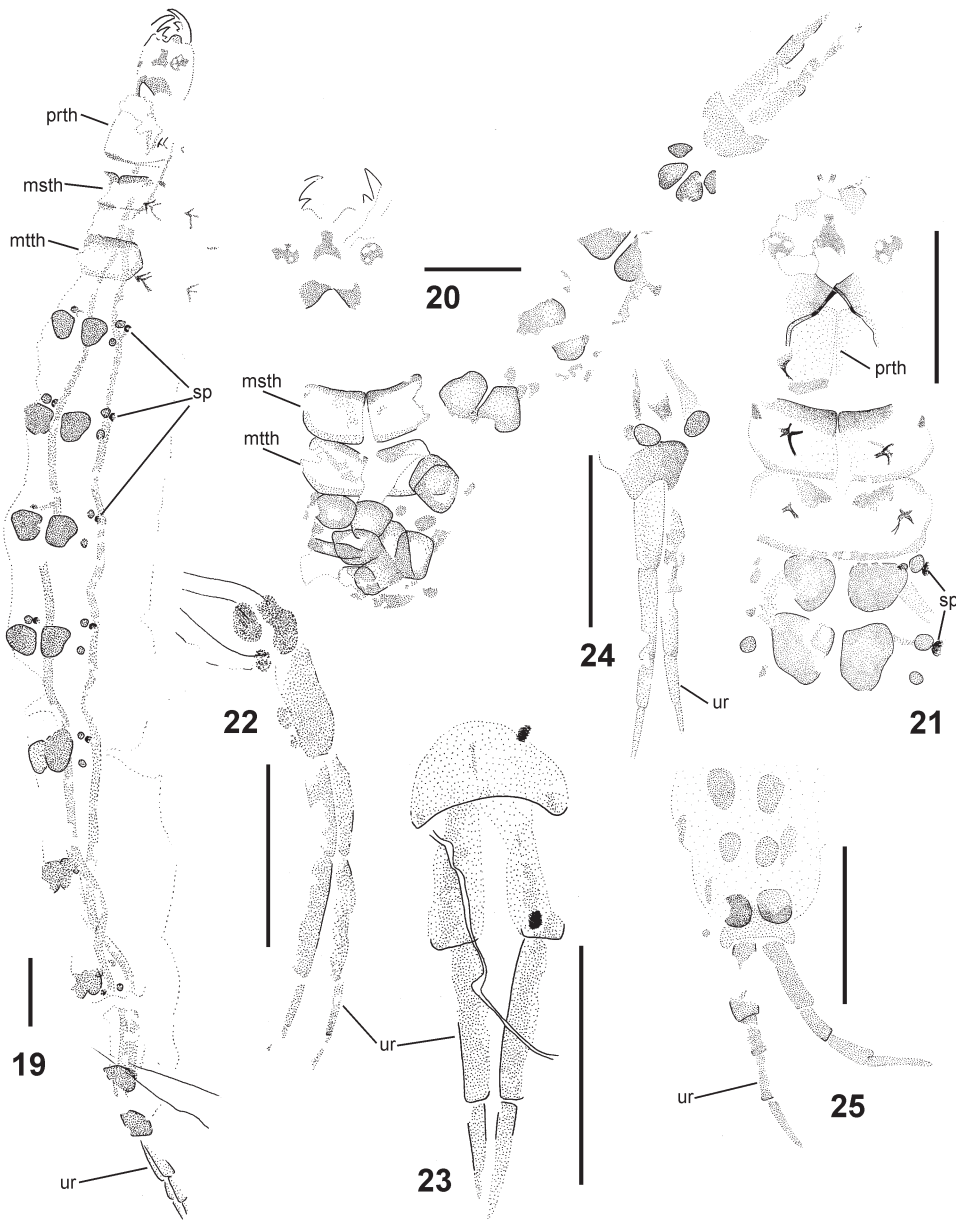
Material examined (36 spec.). HOLOTYPE: PIN 1989/2890 (piece and counterpiece). PARATYPES: PIN 1989/2889 (piece and counterpiece), PIN 1989/2903 (piece only), PIN 1989/2893 (piece only), PIN 1668/1837 (piece only), PIN 1989/2892 (piece only), PIN 1989/2900 (piece only). ADDITIONAL NON-TYPE SPECIMENS: PIN 4210/589 (piece only), PIN 4210/594 (piece only), PIN 4210/595 (piece only), PIN 4210/596 (piece and counterpiece), PIN 3064/930 (piece and counterpiece), PIN 1989/2887 (piece only), PIN 1989/2902 (piece only), PIN 3064/6847 (piece and counterpiece), PIN 3064/6848 (piece and counterpiece), PIN 3064/6855 (piece only), PIN 3064/6858 (piece only),



Figs. 14–18. *Cretotaenia pallida* Ponomarenko, 1977 (details of the head). 14 – PIN 3064/6899; 15 – PIN 4210/595; 16 – PIN 3064/6898; 17 – PIN 3064/6848, detail of the head in dorsolateral position; 18 – PIN 3064/6872, detail of right mandible and nasale. Scale bars: 2 mm. Abbreviations: ant – antenna; epl – epistomal lobe; lb – labium; md – mandible; mx – maxilla; ocf – occipital foramen.

PIN 3064/6865 (piece only), PIN 3064/6871 (piece only), PIN 3064/6872 (piece only), PIN 3064/6882 (piece only), PIN 3064/6883 (piece only), PIN 3064/6892 (piece only), PIN 3064/6894 (piece only), PIN 3064/6895 (piece only), PIN 3064/6897 (piece only), PIN 3064/6898 (piece only), PIN 3064/6899 (piece only), PIN 3064/6908 (piece only), PIN 3064/6909 (piece only), PIN 3064/6914 (piece only), PIN 3064/6925 (piece only), PIN 3064/6927 (piece only), PIN 3064/6942 (piece only), PIN 3064/6947 (piece only), PIN 3064/6949 (piece only), PIN 3064/6952 (piece only), PIN 3064/6953 (piece only).

Redescription. Body elongate oval, body length 6.2–14.5 mm (holotype 8.8 mm), width of head capsule 0.85–0.97 mm (holotype 0.97 mm). Head hyperprognathous, occipital foramen shifted dorsally. Head capsule slightly widening anteriorly, frontoclypeus symmetrical; nasale triangular, epistomal lobes semicircular, slightly overlapping nasale, bearing series of pits (setal articulations) along anterior margin indicating that series of setae was present originally; parietale with darkened stemmatal area bearing 5 stemmata (see the note under generic diagnosis for discussion of the number of stemmata of *C. pallida*), posterior portions



Figs. 19–25. *Cretotaenia pallida* Ponomarenko, 1977. 19 – PIN 3064/6848, larva in dorsolateral position; 20 – PIN 1989/2890 (holotype), general view; 21 – PIN 3064/6883, head, thorax and abdominal segments 1–2; 22 – PIN 1989/2900, urogomphi; H: 23 – PIN 3064/6871, urogomphi; 24 – PIN 3064/6953, urogomphi; 25 – PIN 3064/6897, urogomphi. Scale bars: 1 mm. Abbreviations: msth – mesothorax; mtth – metathorax; prth – prothorax; sp – spiracle; ur – urogomphus.

of parietale darkened; frontal sulci V-shaped, coronal sulcus probably at most very short. Antenna probably attaching on dorsal head surface, scape longer than pedicel. Mandible large, falcate, with two retinacular teeth, distal one larger than proximal one. Maxillae longer than mandibles. Labium not projecting far anteriad, without ligula, labial palpi rather short. Hypostomal sclerite subtrapezoid. All thoracic segments largely sclerotised dorsally, tergites subdivided by a fine median suture; thoracic pleura not sclerotised. Abdominal segments 1–8 each with a pair of large dorsal sclerites, each pleuron with two minute sclerites situated above spiracle; spiracles open, tracheal system holopneustic with large tracheal trunks; abdominal segment 9 with single dorsal sclerite, bearing large 3-segmented urogomphi.

Note. PONOMARENKO (1977a) mentioned that two size categories may be distinguished in the material available to him at the time of the description. Several dozens of additional specimens were collected in Baissa outcrops since that time (of which only better preserved specimens examined in detail for this study are listed above). We have measured body length and head width (measured as the distance between lateralmost portions of dark ocular area) of 19 well-preserved specimens (Table 1). Body length is highly variable among the specimens as the larvae were probably macerated to variable extent before fossilization and their membranous parts (especially the abdomen) were deformed. In contrast, head width shows a tendency to fall into three size categories with prevailing values of 0.87 mm, 0.91 mm and 0.97 mm (Fig. 26). Although the distinctness of these categories cannot be tested due to the low number of specimens available, the measurements seem to indicate that three larval instars were present in *C. pallida*. This corresponds with the presence of three larval instars known for the vast majority of modern *Helophorus* species (the only exceptions are two species inhabiting semidesert areas in which only two instars are present corresponding to the first and third instar of the species with normal living cycle; ANGUS 1992, 1998).

Table 1. Body measurements of well-preserved specimens of *Cretotaenia pallida* Ponomarenko, 1977 (n = 19).

Specimen (PIN no.)	Body length (mm)	Head width (mm)
1989/2889	12.4	0.97
1989/2890	8.8	0.97
1989/2990	8.0	0.95
1989/2903	6.2	–
3064/930	10.7	0.86
3064/6847	6.3	0.91
3064/6848	14.5	–
3064/6883	8.2	–
3064/6858	7.6	0.85
3064/6865	9.1	0.91
3064/6872	6.9	0.91
3064/6883	8.4	0.87
3064/6894	9.2	0.85
3064/6895	12.1	0.96
3064/6898	8.8	0.96
3064/6899	–	0.94
3064/6908a	8.0	–
3064/6908b	–	0.97
3064/6909	–	0.90

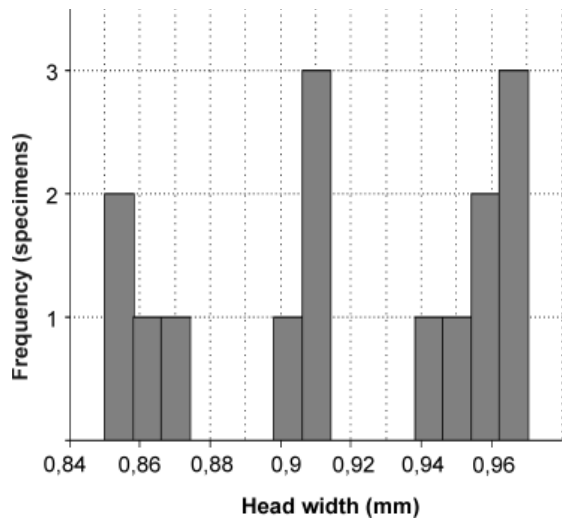


Fig. 26. Frequency histogram of head width of the examined specimens of *Cretotaenia pallida* (n = 15).

Family Helophoridae

Helophorus Fabricius, 1775

Type species. *Silpha aquatica* Linnaeus, 1758 (= *Helophorus* (s. str.) *aquaticus* (Linnaeus, 1758) (modern)), designated by LATREILLE (1810).

Time range. Late Jurassic (ca. 150–146 mya) to recent.

Diagnosis. Adult: Head and pronotum at least partly with setiferous granules in most species (granulation totally reduced in few species only); frontoclypeal suture very distinct, its median portion grooved; mentum distinctly transverse or only slightly wider than long; gula usually strongly constricted (moderately wide with well-separated gular sutures in few species only); pronotum with one to five longitudinal grooves (if less than five grooves are present, then all pronotal intervals bear large and very distinct setiferous granules); lateral margin of pronotum at least slightly crenulate; anterolateral portion of hypomeron with antennal groove; mesanepisterna not meeting mesally; mesoventrite very narrow at anterior margin, bearing a transverse ridge posteromedially; elytra of variable coloration, but never pale with dark stripes along elytral series; elytra in some species with elevated or costate alternate intervals.

Larva: Head prognathous; nasale simply triangular or with lobate lateral margins; epistomal lobes large, slightly overlapping nasale, bearing series of stout setae; mandible with two retinacular teeth; labium without ligula; each parietale with 6 stemmata situated in area of darker cuticle; all thoracic segments with large dorsal tergite; abdominal segments 1–8 each with a pair of dorsal sclerites and an additional large sclerite laterally of them on each side; tracheal system holopneustic, spiracular atrium absent; urogomphi large, three-segmented.

Subgenus † *Mesosperchus* Ponomarenko, 1977 stat. nov.

Mesosperchus Ponomarenko, 1977b: 108.

Mesospercheus (incorrect subsequent spelling): ARNOLDI et al. (1992: 148, name changed by translators).

Type species. *Mesosperchus tarsalis* Ponomarenko, 1977 (by original designation).

Time range. Late Jurassic (ca. 150–146 mya) to Jurassic–Cretaceous boundary (ca. 145–140 mya).

Diagnosis. Adult: Head and pronotum with setiferous granules; frontoclypeal suture very distinct, its median portion grooved; gula moderately wide, with well-separated gular sutures; pronotum with five longitudinal grooves; pronotal flanks narrow; elytra with sutural stria; all elytral intervals flat, alternate ones never elevated, costate or bearing tubercles.

Taxonomic notes. The subgenus *Mesosperchus* is understood here as a paraphyletic formal taxon defined solely by the absence of the apomorphies of any other subgenus of *Helophorus* (hence, it is defined by plesiomorphies only). It is designed to accommodate fossil species which can be clearly assigned to the genus *Helophorus*, but lack any characters allowing further subgeneric assignment. As such, *Mesosperchus* may be understood as a formal taxon containing Late-Jurassic stem taxa of the genus *Helophorus*. We are, however, unable to distinguish between fossil species in which additional apomorphies have been really absent from those in which they are only not preserved. Hence, *Mesosperchus* may also contain

species representing extinct basal lineages of *Helophorus* (rather than stem taxa) or even species which would be classified as a part of an other subgenus recognized at present if their preservation was better.

PONOMARENKO (1992) synonymised *Mesosperchus* with the genus *Zetemenos* Bode, 1953, previously containing a single species, *Z. sexlineatus* Bode, 1953. The re-examination of the holotype of this species (see below for details) showed that the specimen is very poorly preserved and does not bear any synapomorphy indicating its assignment to the Helophoridae or Hydrophiloidea. For that reason, the synonymy of *Mesosperchus* with *Zetemenos* is rejected here and *Mesosperchus* is re-established as a valid taxon.

Taxa excluded from *Mesosperchus*. *Mesosperchus angulatus* Ponomarenko, 1985, *M. notatus* Ponomarenko, 1977 and *M. schultzi* Ponomarenko, 1985 (for details see under Taxa excluded from the Hydrophiloidea).

† *Helophorus (Mesosperchus) inceptivus* sp. nov.

(Figs. 27, 81–82, 107, 111)

Type locality and age. Mongolia, Gobi-Altai Province, SE Ajbogd-uul Range, S of Mount Shar-Teg, fossil site Shar-Teg, exposure 442/2; Shar-Teg sequence, Late Jurassic, Tithonian, ca. 150–145 mya (GUBIN & SINITZA 1996; RASNITSYN & ZHERIKHIN 2002; YAN & ZHANG 2010).

Material examined (1 spec.). HOLOTYPE: PIN 4270/1008 (piece only).

Description. Adult: Body rather wide, body length 3.9 mm. Frons partly bearing weak granulation, gula wide, antenna with three-segmented antennal club. Pronotum transverse, with simply arcuate lateral margins and slightly angulate posterior margin; surface bearing five longitudinal grooves, all pronotal intervals with well-developed (through mostly only weakly preserved) granulation; anterolateral corners of pronotum probably not projecting. Prothoracic antennal grooves probably present. Elytron with 10 series of punctures, all series finely impressed; elytral intervals flat. Mesocoxal cavities very narrowly separated from each other, metaventrite slightly longer than mesoventrite. Mesotibia with several longitudinal series of spines, bearing few larger spines on distal margin; abdomen with five ventrites.

† *Helophorus (Mesosperchus) tarsalis* (Ponomarenko, 1977) comb. nov.

(Figs. 29–37, 73–79, 83–84)

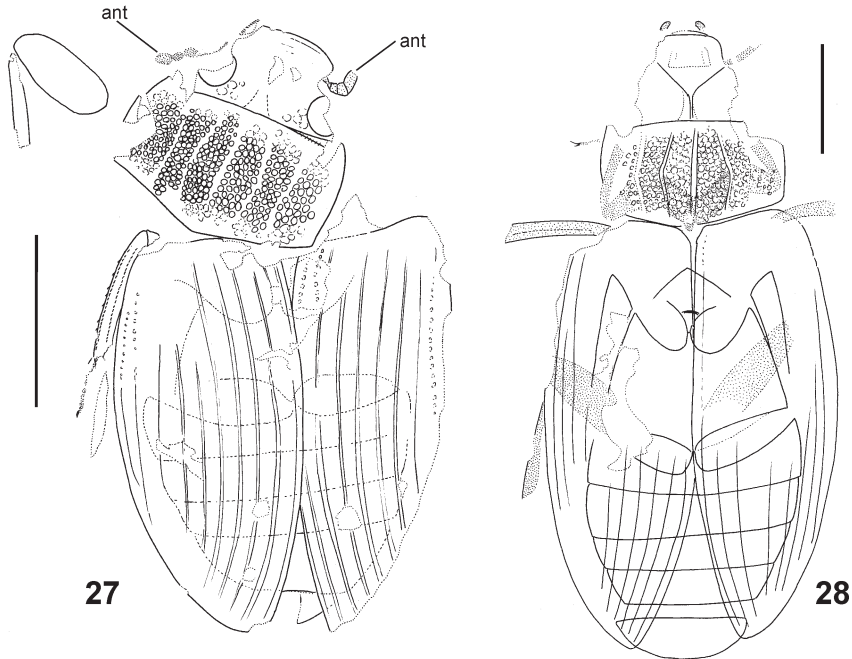
Mesosperchus tarsalis Ponomarenko, 1977b: 109.

Mesohelophorus elongatus Ponomarenko, 1990: 48, **syn. nov.**

Type locality and age (both for *Mesosperchus tarsalis* and *Mesohelophorus elongatus*). Russia, Zabaykalskiy Kray, Baley district, right bank of the Unda river 2 km upstream of the Zhidka village (outcrops Unda and Daya), Glushkovo Formation, Latest Jurassic, Tithonian, ca. 151–146 mya (RASNITSYN 1990, SINITSHENKOVA & ZHERIKHIN 1996; Vasilenko, pers. comm. to A. Prokin, 2011).

Material examined (8 spec.). *Mesosperchus tarsalis*: HOLOTYPE: PIN 3015/367 (piece and counterpiece). PARATYPE: PIN 3063/116 (piece and counterpiece). *Mesohelophorus elongatus*: HOLOTYPE: PIN 3063/735 (piece and counterpiece). ADDITIONAL NON-TYPE SPECIMENS: PIN 3063/2192 (Daya, piece and counterpiece), PIN 3063/2194 (Daya, piece and counterpiece), PIN 3015/1769 (Unda, piece and counterpiece), PIN 3063/2195 (Daya, piece and counterpiece), PIN 3063/2197 (Daya, piece and counterpiece).

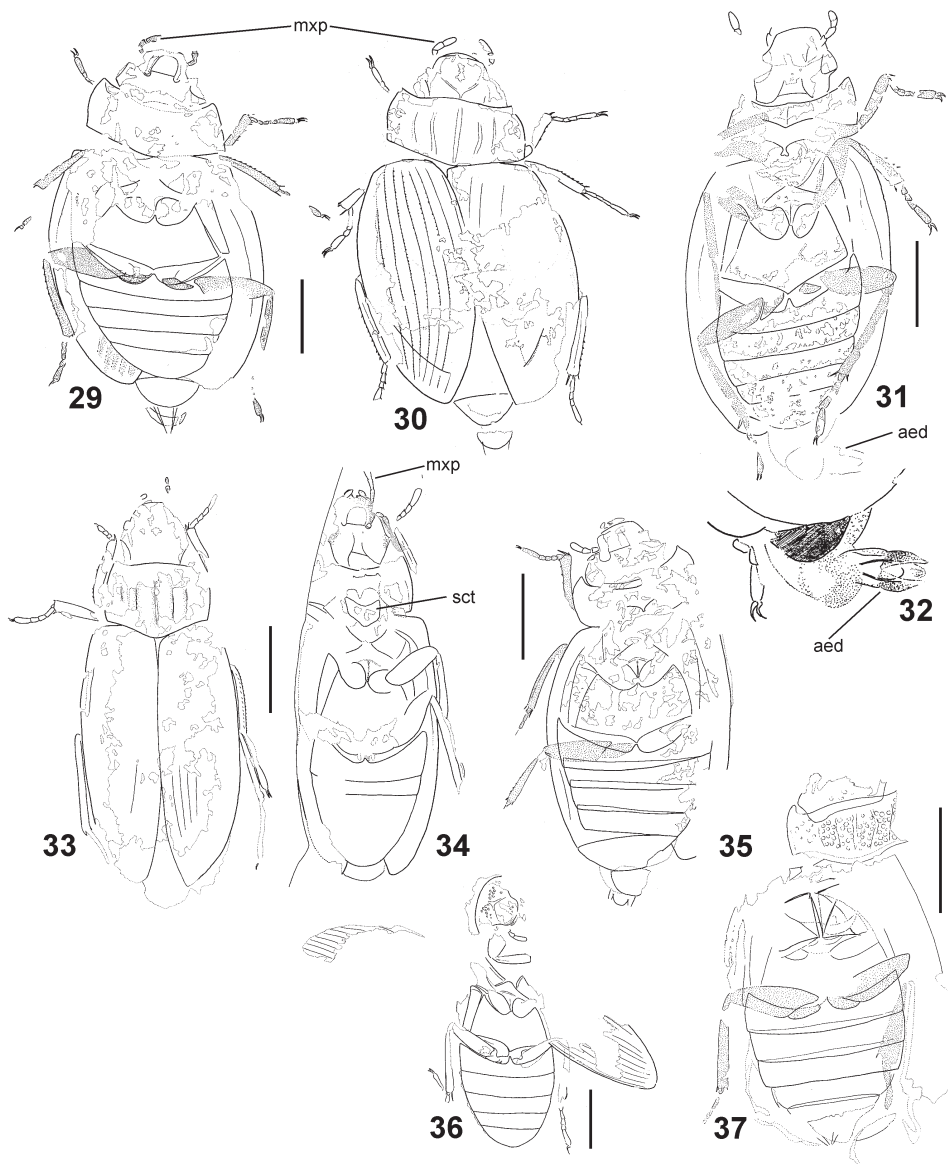
Redescription. Adult: Body elongate oval, 3.1–3.7 mm long (holotype ca. 3.2 mm). Head with very distinct frontoclypeal suture, its median portion grooved; both frons and clypeus bearing



Figs. 27–28. Representatives of *Helophorus*, subgenus *Mesosperchus* Ponomarenko, 1977. 27 – *H. (M.) inceptivus* sp. nov. (PIN 4270/1008, holotype); 28 – *H. (M.) yixianus* sp. nov. (CNU 2010004, holotype). Scale bars: 1 mm. Abbreviations: ant – antenna.

distinct granulation; eyes protruding laterad, narrow postocular bridge present. Mentum narrow, ca. $1.3\times$ wider than long; gula wide. Maxillary palpi long, palpomere 4 most probably asymmetrical. Pronotum transverse, bearing five longitudinal grooves, pronotal intervals with sparse but distinct granulation; prosternum long anterior to procoxae, antennal groove present; pronotal flank narrow. Mesoventrite narrowing anteriorly, with distinct transverse ridge posteromedially. Metaventrite twice as long as mesoventrite, metepimera rather wide, with oblique transverse ridge anteriorly. Elytron with finely punctate and impressed striae, scutellar stria absent. Legs rather long, tibiae with several longitudinal series of fine spines, bearing larger spines on distal apices; tarsi slightly shorter than tibiae, basal tarsomere very short, tarsomere 2 longer than tarsomere 3; swimming hairs absent or not preserved both on tibiae and tarsi. Abdomen with five ventrites. Aedeagus rather short and wide, phallobase symmetrical with basal manubrium, ca. twice as long as parameres, parameres slightly arcuate, gradually narrowing from base to apex, median lobe widely rounded apically, with basal struts ca. twice as long as its distal portion.

Taxonomic notes. Two species were originally described from the outcrops of Unda and Daya, both belonging to the Glushkovo Formation and situated closely apart: *Mesosperchus tarsalis* defined by its widely oval body, short and thick tarsi and the absence of pronotal grooves (hence its assignment to *Mesosperchus*; PONOMARENKO 1977b), and *Mesohelophorus*



Figs. 29–37. *Helophorus (Mesosperchus) tarsalis* (Ponomarenko, 1977). 29–30 – PIN 3063/2194, piece and counterpiece; 31–32 – PIN 3063/2192 (31 – general view of the piece, 32 – detail of genitalia of the counterpiece); 33–34 – PIN 3063/735, holotype of *Mesohelophorus elongatus* Ponomarenko, 1990, piece and counterpiece; 35 – PIN 3063/116; 36 – PIN 3015/367, holotype of *Mesosperchus tarsalis* Ponomarenko, 1977; 37 – PIN 3015/1769. Scale bars: 1 mm. Abbreviations: aed – aedeagus; mxp – maxillary palpus; sct – scutellum.

elongatus defined by its narrowly elongate body, long and slender tarsi and a pronotum with longitudinal furrows (hence its assignment to *Mesohelophorus*; PONOMARENKO 1990). The re-examination of the type and additional material from the Unda and Daya outcrops revealed that both taxa are actually extremely similar in all preserved characters and we failed to find any character other than the body proportions which would distinguish both species from each other. Body proportions seem to vary considerably among the examined specimens and the extremely elongate form of the holotype of *Mesohelophorus elongatus* seems to be caused by deformation during the fossilization process (much in the way present also in *Laetopsia mongolica* and discussed above). The difference in the presence / absence of pronotal grooves seems to be artificial as well, caused by generally bad preservation of the prothorax in the type specimens of *Mesosperchus tarsalis*. For all these reasons as well as due to the high proximity of both outcrops, both forms seem to be conspecific and we therefore consider *Mesohelophorus elongatus* as a junior subjective synonym of *Helophorus (Mesosperchus) tarsalis*.

† *Helophorus (Mesosperchus) gracilis* (Prokin, Ren & Fikáček, 2010) comb. nov.

(Fig. 80)

Hydrophilopsia gracilis Prokin, Ren & Fikáček, 2010: 178.

Type locality and age. China, Liaoning Province, Shangyuan County, Chaomidian Village, Huangbanjigou [the name of the village was misspelled in the original description]. Yixian Formation, Jurassic-Cretaceous boundary, Late Tithonian-Berriasian, ca. 145–140 mya (REN et al. 2010). An alternative dating was proposed by SWISHER et al. (1999): Lower Cretaceous, Aptian, 124.6 mya (see REN et al. (2010) for discussion on various datings of Yixian formation).

Material examined (4 spec.). HOLOTYPE: CNU 2010018 (piece only). PARATYPES: CNU 2010067 (piece only); CNU 2010068 (piece only); CNU 2010030 (piece only).

Redescription. Body elongate oval, 4.2–4.9 mm long (holotype 4.9 mm). Head with distinct Y-shaped frontoclypeal suture. Anterior margin of clypeus straight, attached to well sclerotized transverse labrum. Eyes moderately large, protruding laterad, postocular bridge present. Maxillary palpus rather long, ultimate palpomere asymmetrical. Gula wide, gular sutures widely separate. Pronotum subrectangular, with weakly arcuate lateral margins and without projecting anterolateral corners. Prosternum rather long anterior to procoxae, procoxal cavities contiguous, pronotal flanks narrow, slightly narrowing posteriad. Mesoventrite with transverse ridge posteromedially. Elytron pale, with several elytral series, without dark longitudinal stripes; epipleuron well developed, narrow. Metaventrite ca. twice as long as mesoventrite. Legs rather long, protibia slightly widening apically. Abdomen with 5 ventrites.

Note. The species is known from several rather poorly preserved specimens and was originally assigned to the genus *Hydrophilopsia* due to its overall similarity to *Hydrophilopsia shatrovskiyi* and *H. hydraenoides* (PROKIN et al. 2010). In this study we transfer both latter species to the genus *Laetopsia* defined by characters not preserved in *H. gracilis* (i.e. the absence of pronotal granulation and presence of the single median pronotal furrow) and by dark longitudinal stripes on elytra which seem to be absent from *H. gracilis* (even though this may also be due to bad preservation of the specimens). Hence, we found that the placement of *H. gracilis* in *Laetopsia* was not justified by any preserved character.

On the other hand, the species agrees in all preserved characters with *Helophorus* (*Mesosperchus*) as it is redefined here. Hence, we are tentatively transferring *Hydrophilopsia gracilis* to *Mesosperchus*, although the crucial character, i.e. the sculpture of pronotum, is not preserved and this placement will require confirmation once additional specimens of this species are available.

The species co-occured with *Helophorus* (*Mesosperchus*) *yixianus* sp. nov. described below, the reasons for considering them as separate taxa are given under the latter species.

† *Helophorus* (*Mesosperchus*) *yixianus* sp. nov.

(Fig. 28, 85–86)

Hydrophilopsia shatrovskiyi (paratype CNU 2010004, misidentification): PROKIN et al. (2010: 178)

Type locality and age. China, Liaoning Province, Shangyuan County, Chaomidian Village, Huangbanjigou [the name of the village was misspelled in the original description]. Yixian Formation, Jurassic-Cretaceous boundary, Late Tithonian-Berriasian, ca. 145–140 mya (REN et al. 2010). An alternative dating was proposed by SWISHER et al. (1999): Lower Cretaceous, Aptian, 124.6 mya (see REN et al. (2010) for discussion on various datings of Yixian formation).

Material examined (1 spec.). HOLOTYPE: CNU 2010004 (piece only).

Description. Body elongate oval, 5.6 mm long. Head with distinct frontoclypeal suture, its median portion grooved; anterior margin of clypeus straight, closely attached to labrum; gula wide, mentum probably transverse. Pronotum with five longitudinal furrows, pronotal intervals bearing dense and fine granulation. Mesoventrite strongly narrowing anteriorly, bearing a transverse ridge posteromedially; mesocoxal cavities very narrowly separated; metaventrite ca. twice as long as mesoventrite; metepimeron narrow. Elytron with fine longitudinal series. Abdomen with five ventrites. Legs rather long.

Taxonomic note. The only known specimen was originally considered as a part of the type series of *Hydrophilopsia shatrovskiyi* (= *Laetopsia shatrovskiyi* in our concept) by PROKIN et al. (2010). Re-examination of the specimen revealed that it distinctly differs from the holotype of *Laetopsia shatrovskiyi* in the following characters: (1) pronotum with five longitudinal furrows (only a median furrow present in *L. shatrovskiyi*), (2) pronotal surface with granulation (without granulation in *L. shatrovskiyi*), and (3) elytral series not darkened (darkened in *L. shatrovskiyi*). Moreover, the above characters indicate that the specimen does not belong to *Laetopsia* but to *Helophorus*, and due to the lack of synapomorphies of other *Helophorus* subgenera it should be assigned to the subgenus *Mesosperchus*. For that reason, the specimen is described here as a new species, *Helophorus yixianus*.

The species co-occurs with *Helophorus* (*Mesosperchus*) *gracilis*. Both species seem to differ by body measurements (*H. yixianus* is much larger than *H. gracilis*), more detailed comparison is impossible at the moment due to the bad preservation of the fossils on which the description of *H. gracilis* was based. Hence, we prefer to assign the above specimen bearing all important diagnostic characters to a separate species, rather than to assign it to *H. gracilis* which generic placement is only tentative due to the bad preservation of all available specimens and which moreover differs from *H. yixianus* by its body size.

Subgenus † *Mesohelophorus* Ponomarenko, 1977 stat. nov.

Mesohelophorus Ponomarenko, 1977b: 113.

Type species. *Mesohelophorus sibiricus* Ponomarenko, 1977 (= *H. palaeosibiricus* nom. nov.) (by original designation).

Time range. Early Cretaceous, Berriasian – Hauterivian, ca. 146–135 mya.

Diagnosis. Adult: Body rather wide; mentum ca. as wide as long; gula constricted, gular sutures joint at a point; maxillary palpomere 4 symmetrical; pronotum with three longitudinal furrows; pronotal intervals bearing very distinct granulation; pronotal flanks narrow; elytron with rather long scutellar stria; alternate elytral intervals not elevated or costate; epipleuron well-developed, wide anteriorly.

By the rather wide body, strongly granulate pronotum, constricted gula and symmetrical maxillary palpomere 4, *Mesohelophorus* resembles the species of the modern subgenera *Empleurus* Hope, 1838, *Transithelophorus* Angus, 1970, *Eutrichelophorus* Sharp, 1915 and *Kyphohelophorus* Kuwert, 1886. It may be easily distinguished from them by the presence of only three pronotal furrows (five in the modern subgenera), elytra without elevated alternate intervals or tubercles (elevated in *Empleurus*, *Transithelophorus* and *Eutrichelophorus*, bearing tubercles in *Kyphohelophorus*) and wide elytral epipleura (extremely narrow in modern taxa). In addition, it differs from *Empleurus* by narrow pronotal flanks (very wide in *Empleurus*). *Mesohelophorus* also resembles the modern *H. (Orphelophorus) arcticus* Brown, 1937 by the reduced number of pronotal grooves and strong pronotal granulation, but may be easily distinguished from it by the rather long scutellar stria on the elytron (the scutellary stria is absent, or very rarely consists of one or two punctures only in *H. arcticus*).

Taxonomic note. Due to the presence of all diagnostic characters of *Helophorus*, we downgrade *Mesohelophorus* to a subgenus of *Helophorus* which seems to be confined to the early Cretaceous only. Three species of *Mesohelophorus* have been described till now, of which only *M. palaeosibiricus* nom. nov. belongs to the subgenus. *Mesohelophorus elongatus* is synonymised with *Helophorus (Mesosperchus) tarsalis* above, and *Mesohelophorus mongolicus* Ponomarenko, 1986 is transferred to the Buprestoidea below.

† *Helophorus (Mesohelophorus) palaeosibiricus* nom. nov.

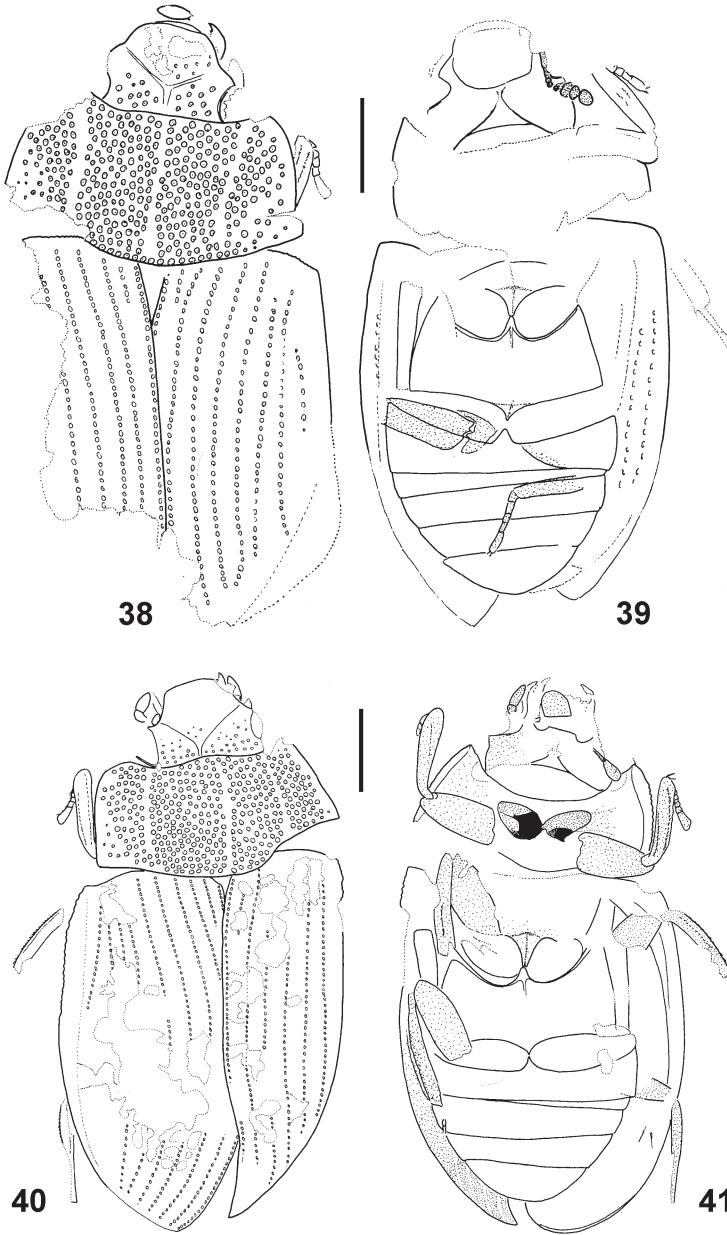
(Figs. 38–41, 87–90, 108–110, 112)

Mesohelophorus sibiricus Ponomarenko, 1977b: 113 (secondary homonym of *Helophorus (Gephelophorus) sibiricus* (Motschulsky, 1860)).

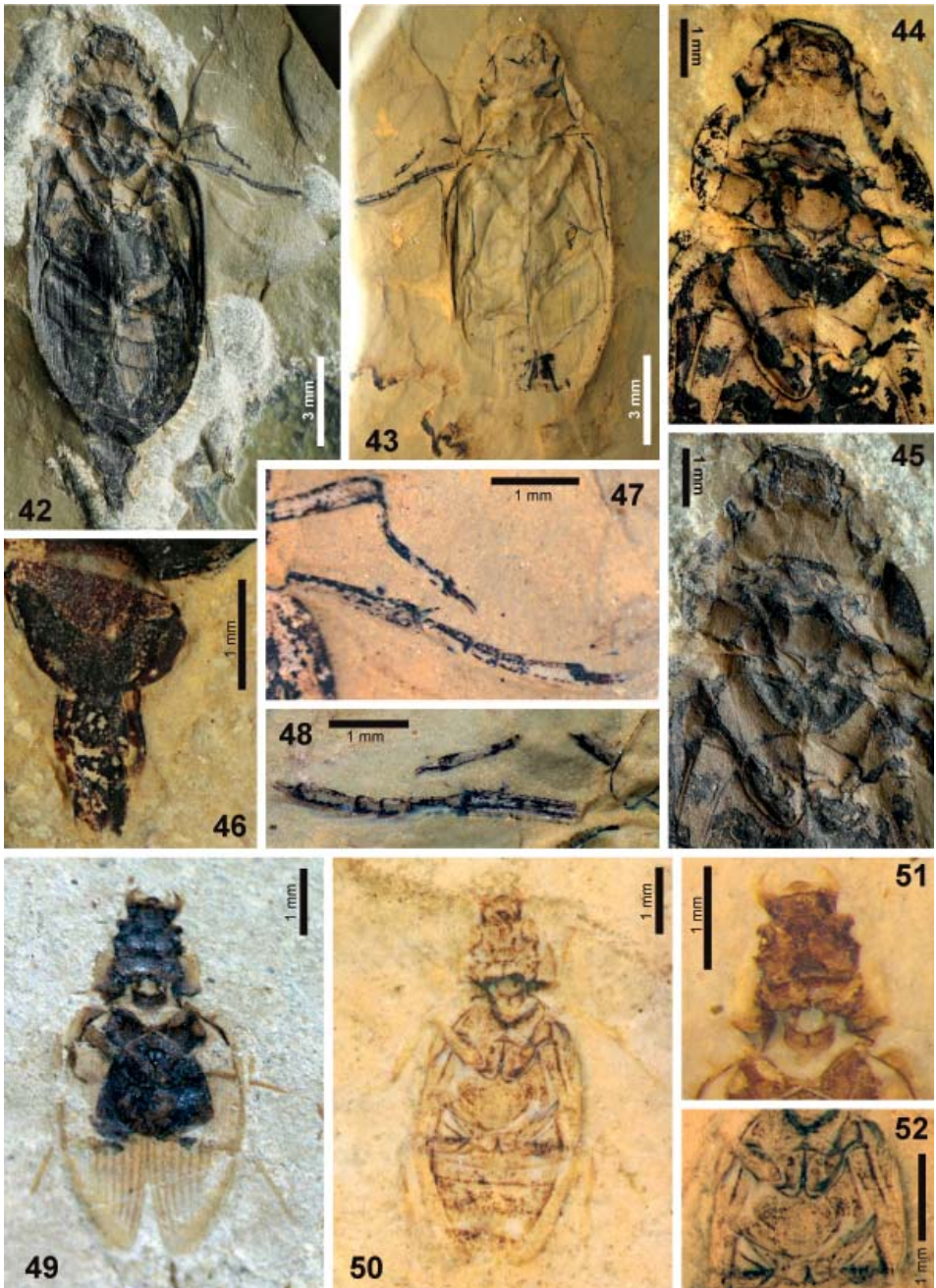
Type locality and age. Russia, Buryat Republic, Baissa. Early Cretaceous, Berriasian to Hauterivian, ca. 146–135 mya (ZHERIKHIN et al. 1998; Vasilenko, pers. comm. to A. Prokin, 2011).

Material examined (8 spec.). HOLOTYPE: PIN 3064/841 (piece and counterpiece). PARATYPES: PIN 3064/931 (piece and counterpiece), PIN 1989/2998 (piece only). ADDITIONAL NON-TYPE SPECIMENS: PIN 3064/6983 (piece and counterpiece), PIN 3064/884 (piece and counterpiece), PIN 3064/6976 (piece and counterpiece), PIN 3064/6980 (piece and counterpiece), PIN 1989/3038 (piece only).

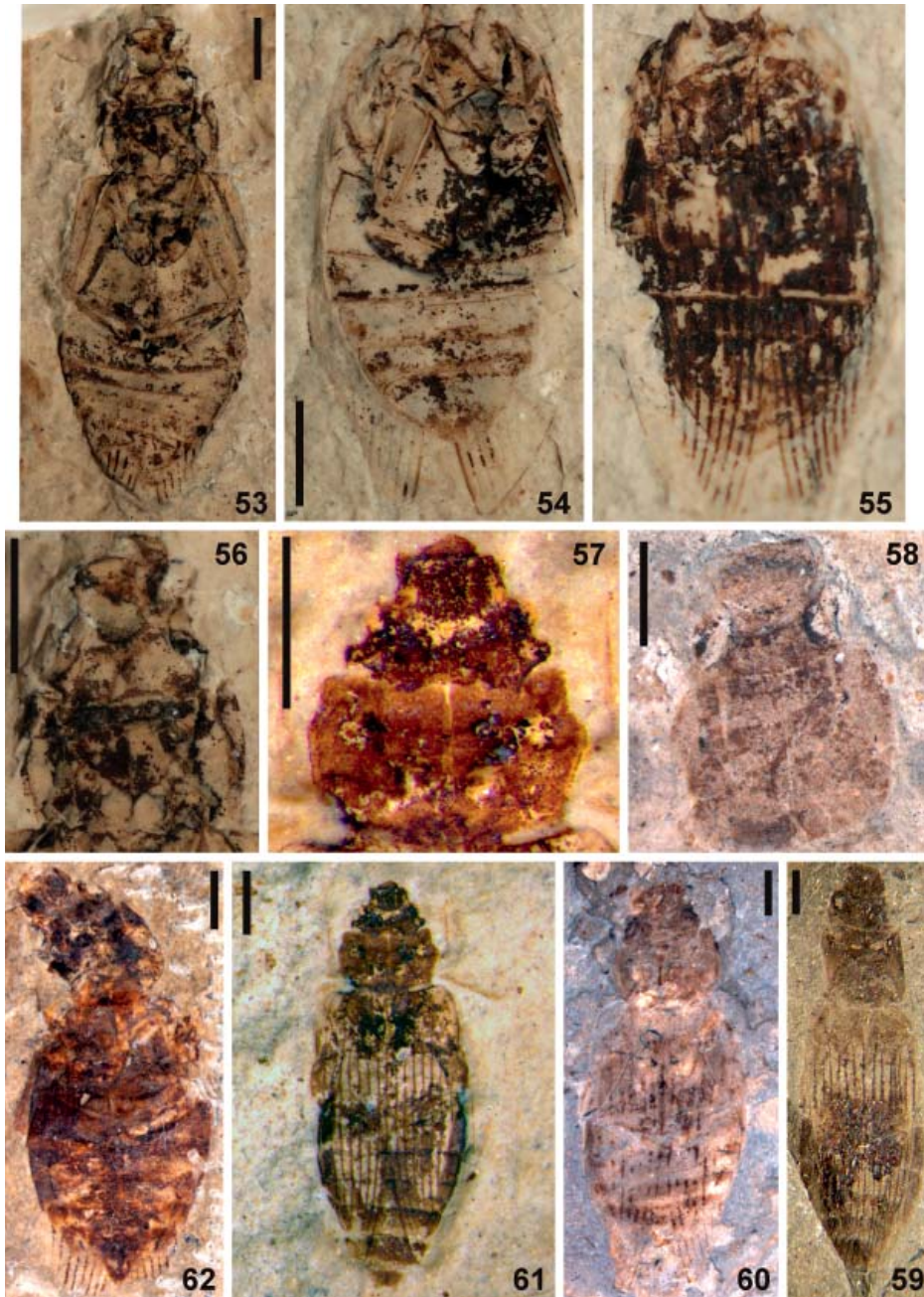
Redescription. Adult: Body widely elongate, 3.2–3.6 mm long (holotype 3.3 mm). Head with very distinct slightly grooved frontoclypeal suture, clypeus and frons bearing sparse but



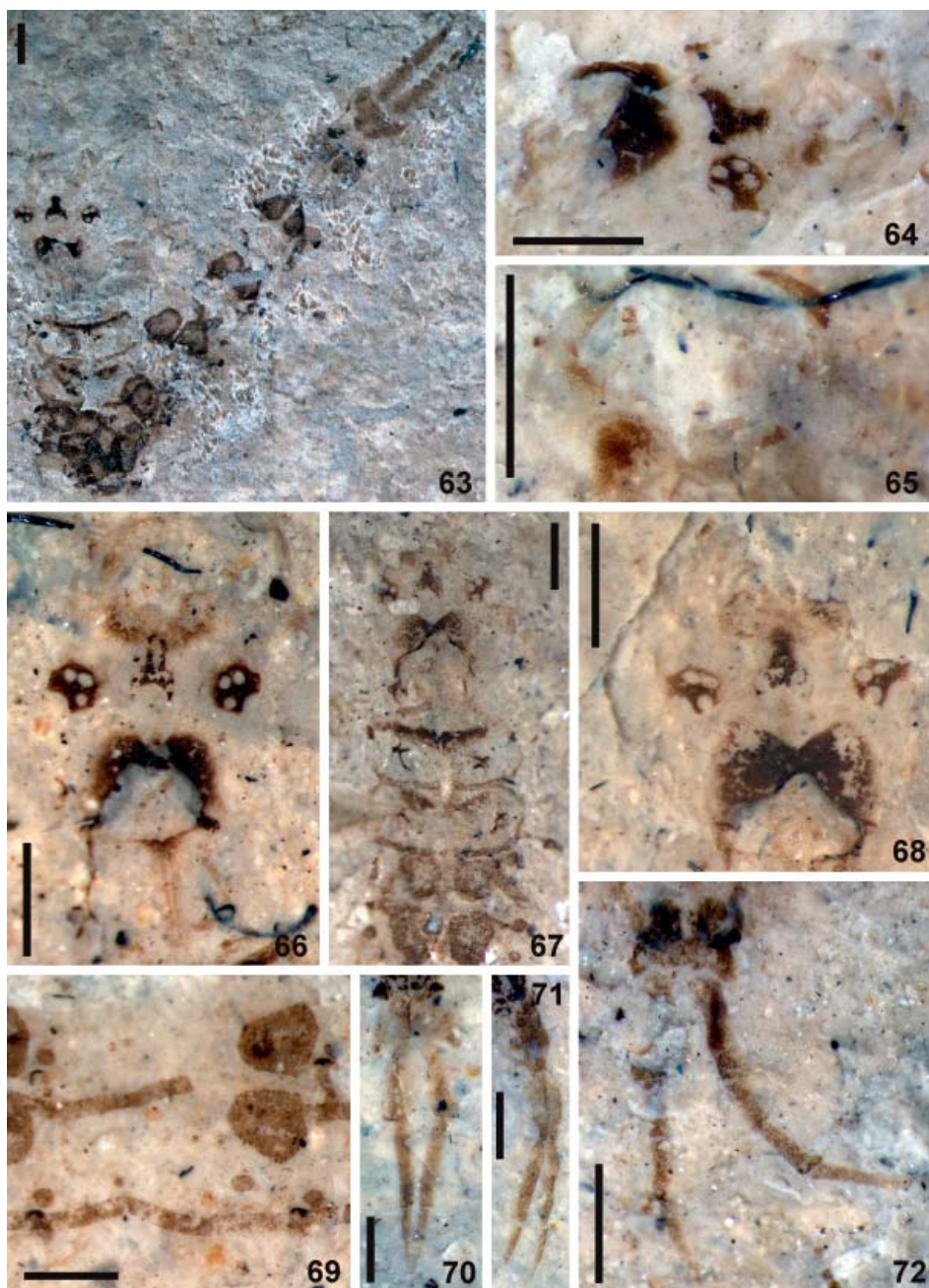
Figs. 38–41. *Helophorus (Mesohelophorus) palaeosibiricus* nom. nov. 38–39 – PIN 3063/841, holotype, piece and counterpiece; 40–41 – PIN 3064/6981, piece and counterpiece. Scale bars: 0.5 mm.



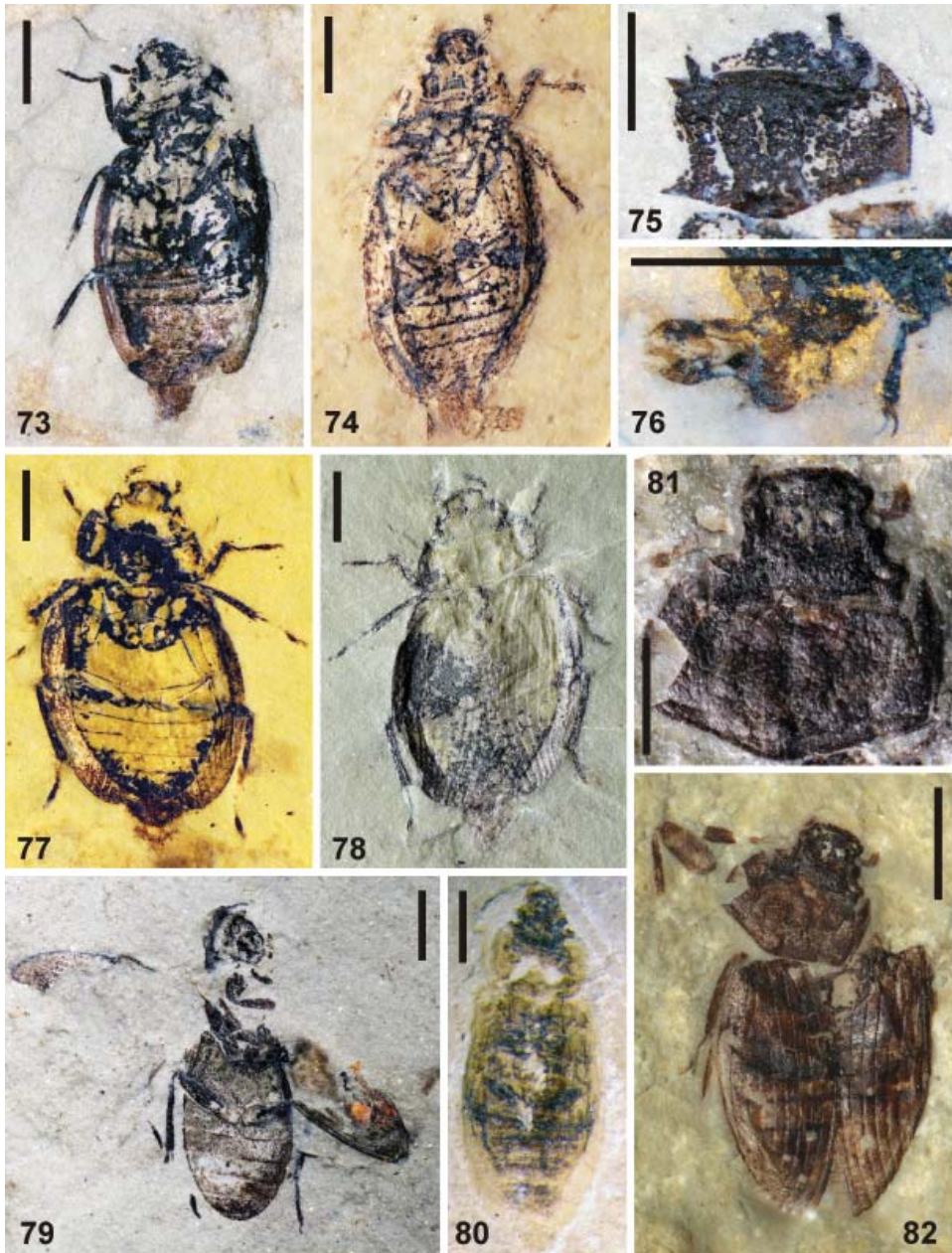
Figs. 42–52. Representatives of *Hydrophilopsis* Ponomarenko, 1986 and *Laetopsia* gen. nov. 42–43 – *Hydrophilopsis longitarsalis* Ponomarenko, 1986, holotype (42–43 – piece and counterpiece, general views; 44 – detail of the head and thorax, photo under alcohol; 45 – same, photo in dry state; 46 – detail of aedeagus; 47 – legs of piece, 48 – legs of counterpiece). 49–52 – *Laetopsia shatrovskiyi* (Prokin, Ren & Fikáček, 2010) (49, 51 – CNU 2009199; 50, 52 – CNU 2010242).



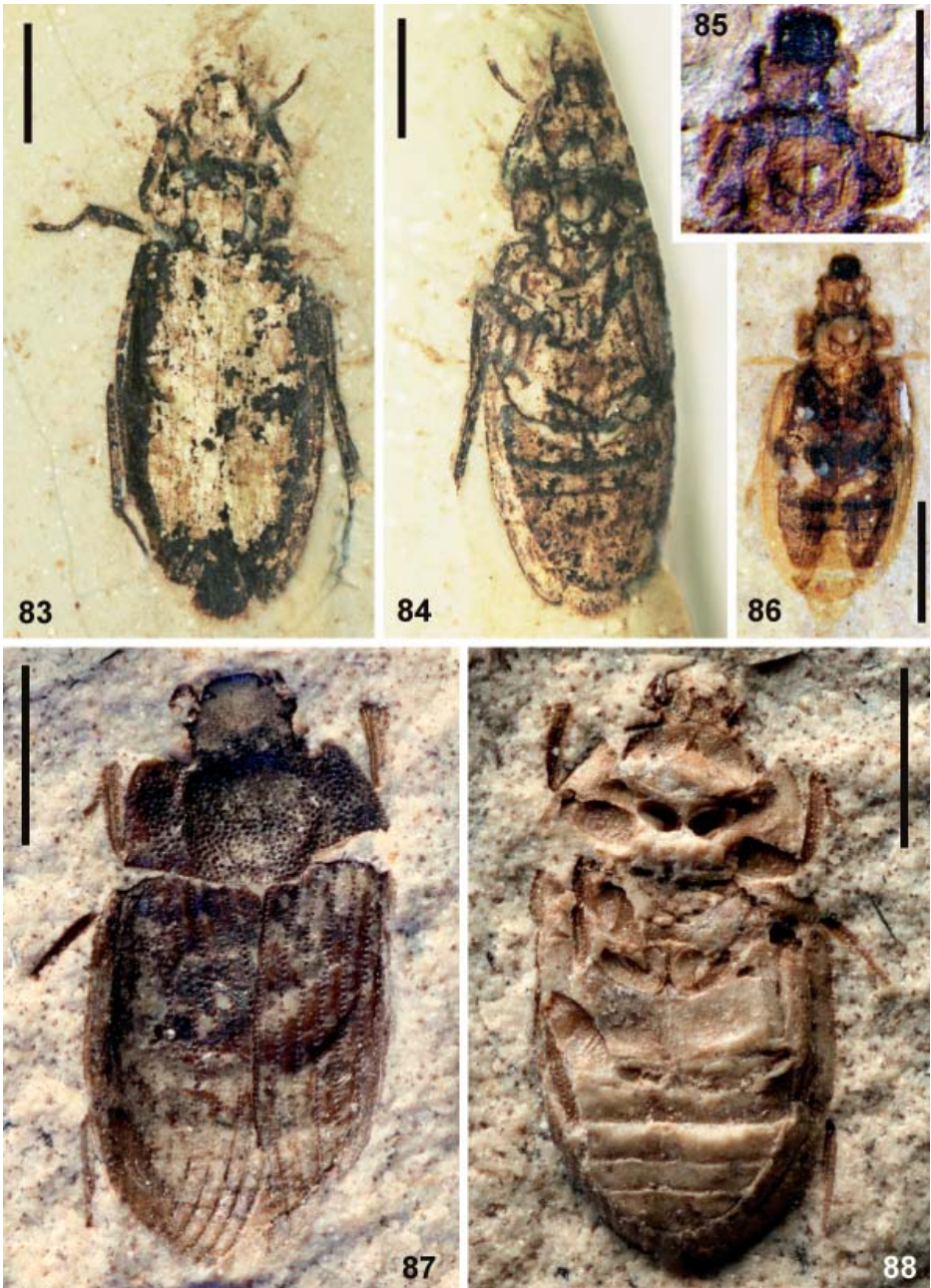
Figs. 53–62. Representatives of *Laetopsia* gen. nov. 53–56 – *L. baissensis* (Ponomarenko, 1986) (53 – PIN 3064/7016; 54–55 – PIN 3064/6987, piece and counterpiece; 56 – detail of PIN 3064/6987). 57, 61 – *L. hydraenoides* (Prokin, Ren & Fikáček, 2010), CNU 2010021, holotype (57 – detail of head and pronotum; 61 – general view). 58–60 – *L. mongolica* (Ponomarenko, 1987) (58 – PIN 3664/1661, detail of head and pronotum; 59 – PIN 3664/1772; 60 – PIN 3664/1567, holotype). 62 – *L. bontsaganica* (Prokin, 2009), holotype. Scale bars: 1 mm.



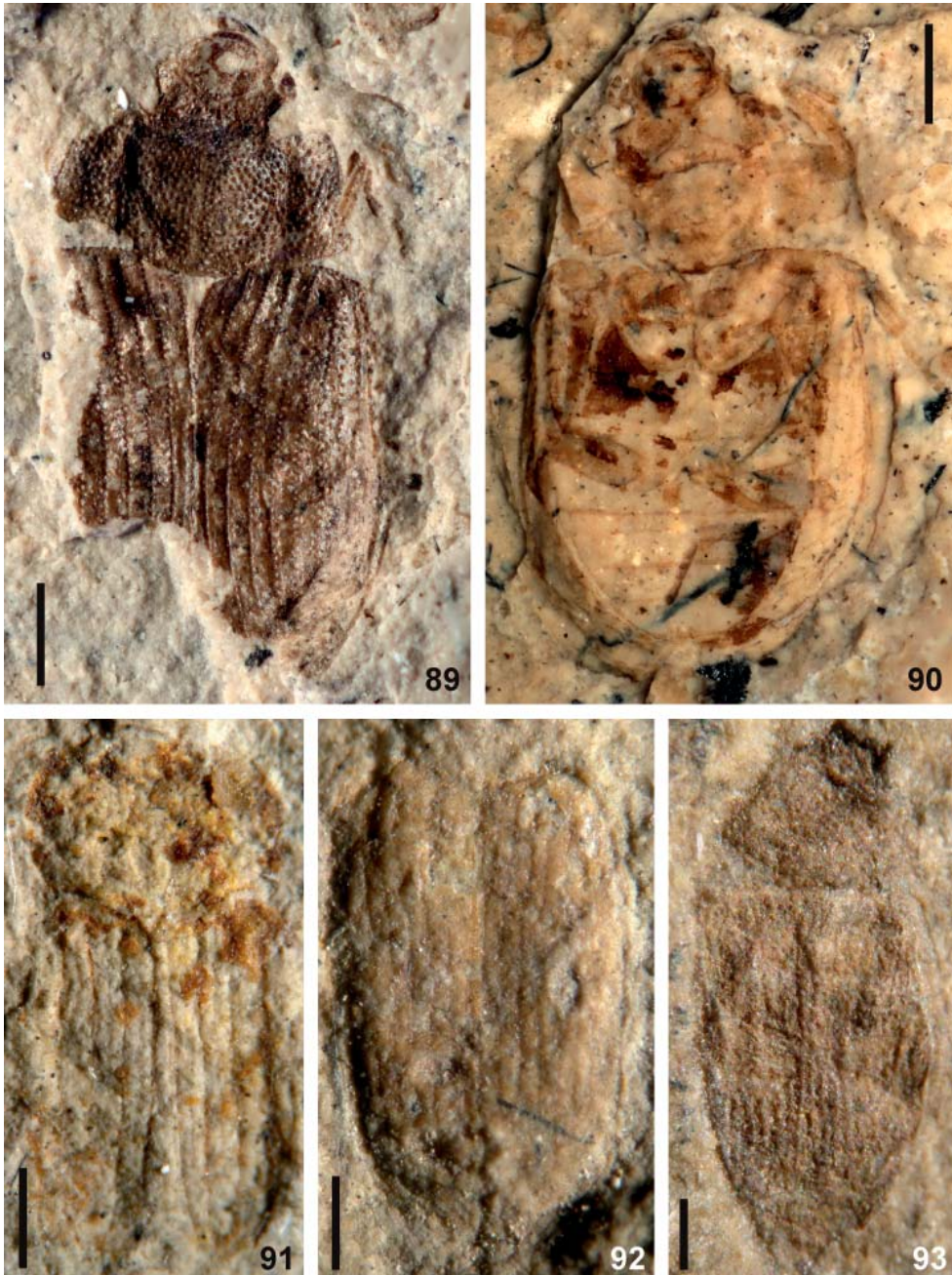
Figs. 63–72. *Cretotaenia pallida* Ponomarenko, 1977. 63 – PIN 1989/2890 (holotype), general view; 64 – PIN 3064/6848, detail of the head in dorsolateral view; 65 – PIN 3064/6872, detail of anterior portion of the head; 66 – PIN 3064/6899, head and prothorax; 67 – PIN 3064/6883, head, thorax and abdominal segments 1–2; 68 – PIN 4210/595, detail of the head; 69 – PIN 3064/6848, detail of abdominal segments in lateral view; 70 – PIN 3064/6871, urogomphi; 71 – PIN 1989/2900, urogomphi; 72 – PIN 3064/6897, urogomphi. Scale bars: 0.5 mm.



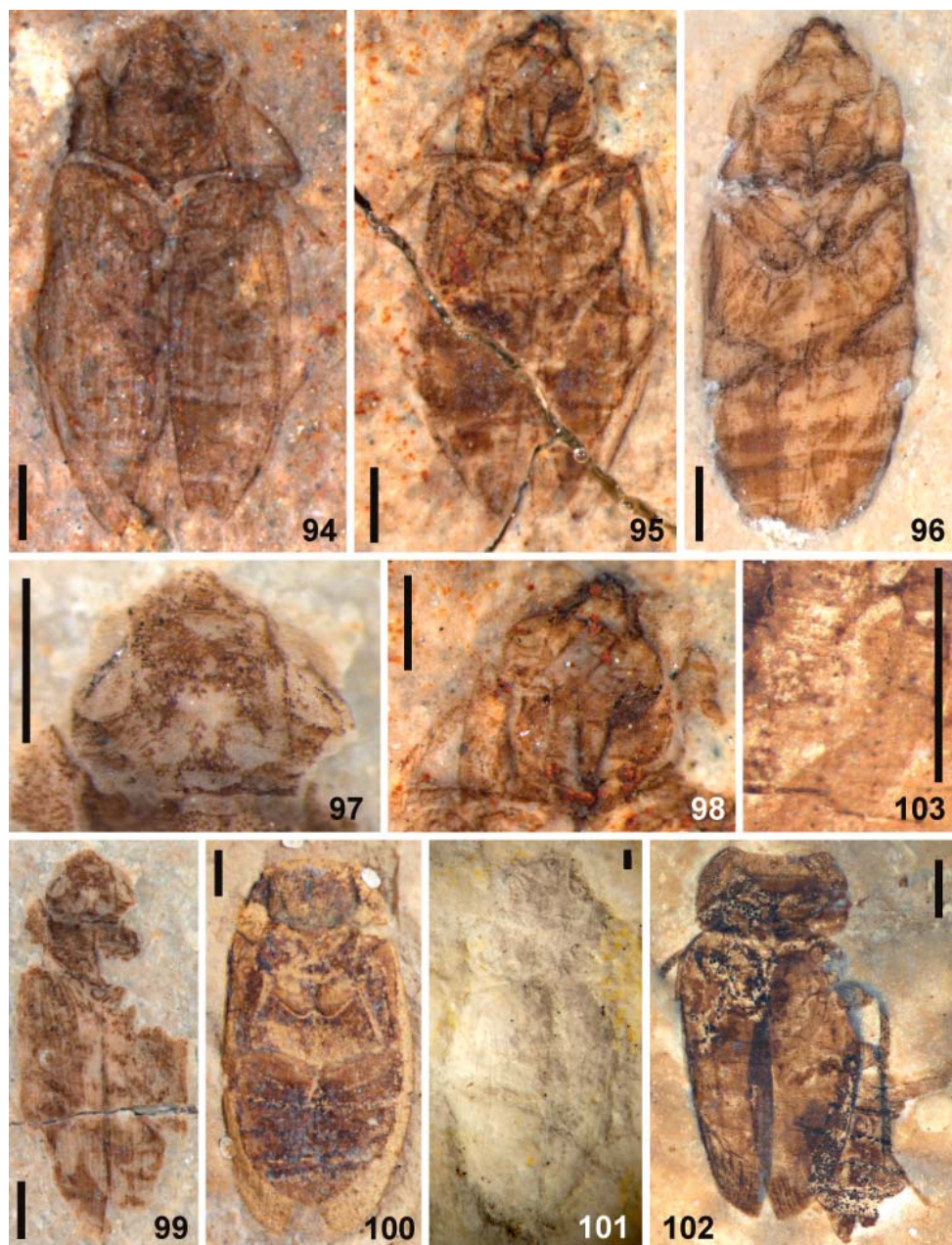
Figs. 73–82. Representatives of *Helophorus*, subgenus *Mesosperchus* Ponomarenko, 1977. 73–79 – *Helophorus tarsalis* (Ponomarenko, 1977) (73 – PIN 3063/116, paratype; 74 – PIN 3063/2192, piece, general view; 75 – PIN 3015/1769; 76 – PIN 3063/2192, counterpiece, detail of male genitalia; 77 – PIN 3063/2194, piece under alcohol; 78 – same specimen, counterpiece in dry condition; 79 – PIN 3015/367, holotype). 80 – *Helophorus gracilis* (Prokin, Ren & Fikáček, 2010), CNU 2010018, holotype. 81–82 – *Helophorus inceptivus*, PIN 4270/1008 (81 – detail of head and pronotum; 82 – general view). Scale bars: 1 mm (Figs. 73–80, 82); 0.5 mm (Fig. 81).



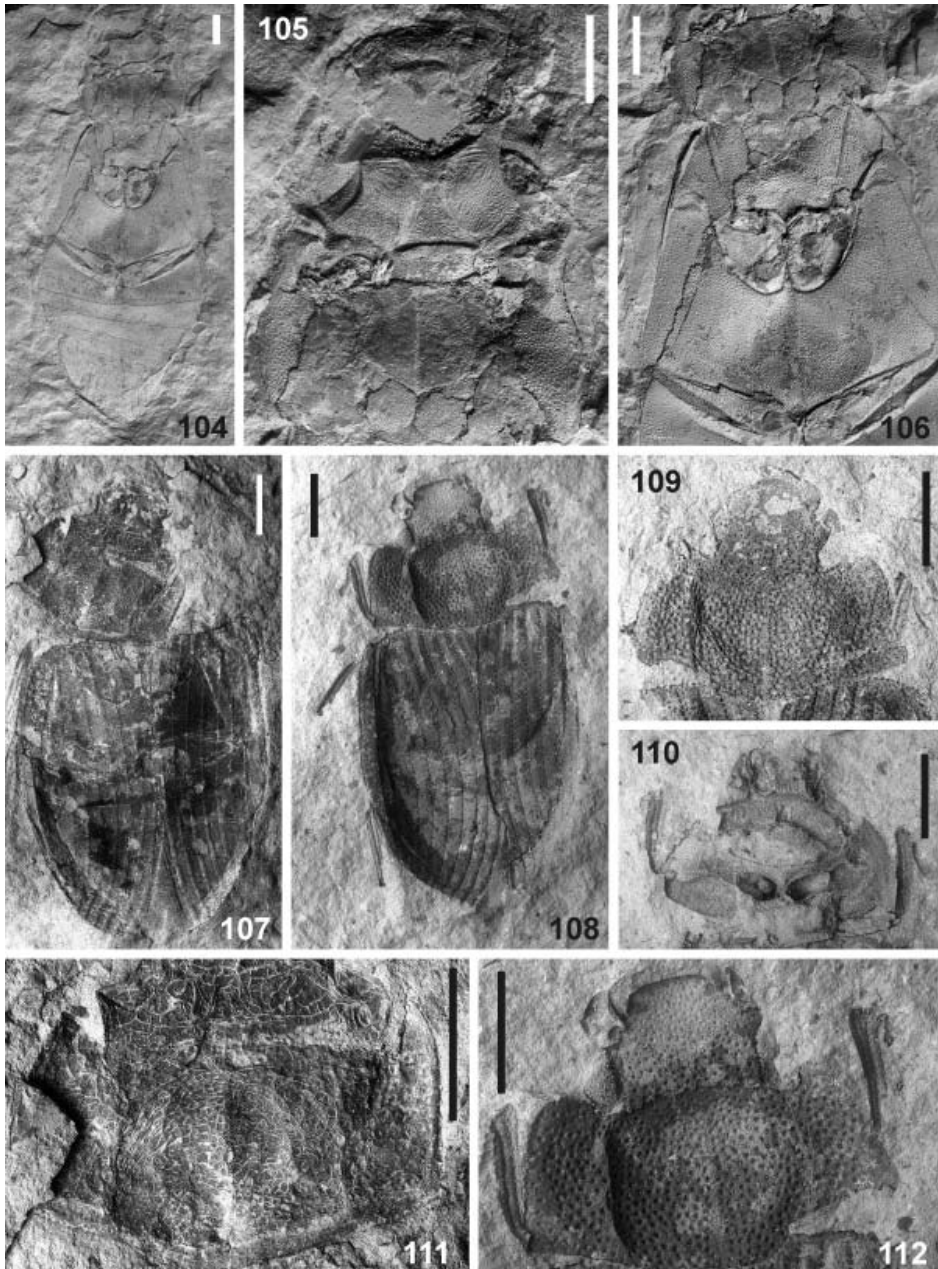
83–88. Representatives of *Helophorus*, subgenera *Mesosperchus* Ponomarenko, 1977 (83–86) and *Mesohelophorus* Ponomarenko, 1977 (87–88). 83–84 – PIN 3063/735, holotype of *Mesohelophorus elongatus* Ponomarenko, 1990 (= *Helophorus tarsalis* (Ponomarenko, 1977)) (piece and counterpiece). 85–86 – *Helophorus yixianus* sp. nov., CNU 2010004, holotype (85 – detail of head and pronotum; 86 – general view, under alcohol). 87–88 – *Helophorus palaeosibiricus* nom. nov., PIN 3064/6981, piece and counterpiece. Scale bars: 1 mm.



Figs. 89–93. Representatives of *Helophorus*, subgenus *Mesohelophorus* Ponomarenko, 1977 (89–90) and taxa excluded from the helophorid lineage (91–93). 89–90 – *Helophorus palaeosibiricus* nom. nov., PIN 3063/841, holotype, piece and counterpiece; 91 – *Helophoropsis brodiei* (Giebel, 1856), holotype. 92 – *Tychon antiquum* (Giebel, 1856), holotype. 93 – *Zetemenos sexlineatus* Bode, 1953, holotype. Scale bars: 0.5 mm.



Figs. 94–103. Taxa excluded from the hydrophilid lineage. 94–99 – *Mesohelophorus* *mongolicus* Ponomarenko, 1986 (94–95 – PIN 3152/4355, holotype, piece and counterpiece; 96, 99 – PIN 3152/4312, piece and counterpiece; 97 – same specimen, detail of head in dorsal view; 99 – head and prosternum of the holotype). 100 – *Mesosperchus* *angulatus* Ponomarenko, 1985, holotype; 101 – *Mesosperchus* *schultzi* Ponomarenko, 1985, holotype, piece; 102–103 – *Mesosperchus* *notatus* Ponomarenko, 1977, holotype (102 – general view; 103 – detail of elytral structure). Scale bars: 0.5 mm.



Figs. 104–112. Mesozoic representatives of the helophorid lineage, scanning electron micrographs. 104–106 – *Laetopsia baissensis* (Ponomarenko, 1986), PIN 3064/7018 (104 – general view; 105 – detail of head and pronotum; 106 – detail of meso- and metathorax). 107, 111 – *Helophorus (Mesosperchus) inceptivus* sp. nov. (107 – general view; 111 – detail of pronotum). 108–112 – *Helophorus (Mesohelephorus) paleosibiricus* nom. nov. (108 – PIN 3064/6981, general view; 109 – PIN 3063/863, holotype, 110 – PIN 3064/6981, detail of prothorax, ventral view; 112 – same, dorsal view).

very distinct granulation. Mentum ca. as wide as long, gula strongly constricted, gular sutures joint in a point; antenna with three-segmented club. Pronotum slightly narrowing anteriorly, with slightly arcuate lateral margins; pronotal surface with three longitudinal grooves, intervals bearing strong and rather dense granulation; pronotal flanks narrow, slightly narrowing posteriorly, divided from hypomeron by sinuate ridge. Prosternum moderately long, ca. half as long as procoxal cavity. Mesoventrite very narrow at anterior margin, bearing transverse ridge posteromedially. Metaventrite slightly longer than mesoventrite, metepimeron rather narrow. Elytron with 10 punctate series, scutellary stria well developed, consisting of more than five punctures; elytral intervals not elevated or costate; epipleuron wide anteriorly, subdivided in inner and outer portions of equal width. Abdomen with 5 ventrites. Legs rather short and stout.

Taxonomic note. By transferring the species to the genus *Helophorus*, *Mesohelophorus sibiricus* Ponomarenko, 1977 becomes the secondary homonym of a modern species *Helophorus* (*Gephelophorus*) *sibiricus* (Motschulsky, 1860). In order to eliminate the homonymy, we are hereby proposing a new substitute name for the fossil species, *H. palaeosibiricus* nom. nov.

Mesozoic taxa excluded from the helophorid lineage of Hydrophiloidea

† *Helophoropsis brodiei* (Giebel, 1856)

(Figs. 91, 113)

Helophorus (species not identified): BRODIE (1845: 116, Pl. iii: Fig. 2).

Helophorus Brodiei Giebel, 1856: 51.

Helophoropsis brodiei: HANDLIRSCH (1908: 543, Pl. XLV: Fig. 6, transferred to *Helophoropsis* Handlirsch, 1908).

Helophorus brodiei: HANSEN (1999: 318).

Type locality. United Kingdom, Wiltshire, Vale of Wardour, Middle Purbeck. Early Cretaceous, Middle Berriasian, 145.5–140.2 mya (CLAPHAM 2011a).

Material examined. HOLOTYPE: NHM I-3524 (piece only).

Taxonomic note. The holotype, which is the only available specimen of this species, is badly preserved and only few characters are therefore available: elytra are elongate with alternating highly and lowly carinate intervals and the pronotum is extremely large, possibly projecting into the anterolateral lobes and possibly bearing a slight median longitudinal depression. No characters of the ventral side are preserved. Except for the costate elytra, which may resemble some *Helophorus* species of the subgenera *Empleurus*, *Transithelophorus* and *Orphelophorus* but are also present in many other groups of beetles, the specimen does not bear any preserved characters which would indicate its placement within the Hydrophiloidea. For that reason, we are transferring here the species as well as the monotypic genus *Helophoropsis* Handlirsch, 1908 to which it belongs in Coleoptera *incertae sedis*. The body proportions, extremely large pronotum and elytral sculpture resemble some Mesozoic species of the family Cupedidae, but we cannot rule out that *H. brodiei* belonged to some group of the Polyphaga.

† *'Mesohelophorus' mongolicus* Ponomarenko, 1986

(Figs. 94–99, 120–123)

Mesohelophorus mongolicus Ponomarenko, 1986: 94.

Type locality and age. Mongolia, Kobdo province, Mayngad, section 221/17 (current GPS coordinates 48.1°N 91.6°E). Gurvan-Eren Formation, early Cretaceous, Berriasian, 145.5–140.2 mya (CLAPHAM 2011c).

Material examined. HOLOTYPE: PIN 3152/4355 (piece and counterpiece). PARATYPE: PIN 3152/4312 (piece and counterpiece).

Taxonomic note. Both examined type specimens are very well preserved and show enough characters to be reliably placed into the superfamily Buprestoidea: eyes large and globular, antennae elongate without club, mentum situated rather anteriorly, narrowing anteriorly, prosternum massive, with large (but not wide) prosternal process, mesoventrite with groove for reception of prosternal process, mesocoxae narrowly but distinctly isolated, metepimeron narrow posteriorly, largely widened anteriorly, metacoxae massive and subtriangular, five abdominal ventrites. Two characters would seemingly contradict the assignment in the Buprestoidea and indicate the possible placement in the Elateroidea: antennae are not serrate (but we suppose this is due to incomplete preservation causing that the detailed morphology of antennae cannot be estimated) and the prosternal process is rather narrow posteriorly (however, the shape of the process actually largely varies in the Buprestoidea, although a wide prosternal process is often considered as typical for the Buprestoidea; see e.g. COBOS 1986). We have also discussed the placement of *M. mongolicus* with the specialists on modern Buprestoidea (S. Bílý, V. Kubáň & M. Kalashian, pers. comm. to M. Fikáček, 2012) who all considered the placement to the Buprestoidea as well justified. For that reason, we are excluding the species from the Hydrophiloidea and transferring it to Buprestoidea.

† *'Mesosperchus' angulatus* Ponomarenko, 1985

(Figs. 100, 114)

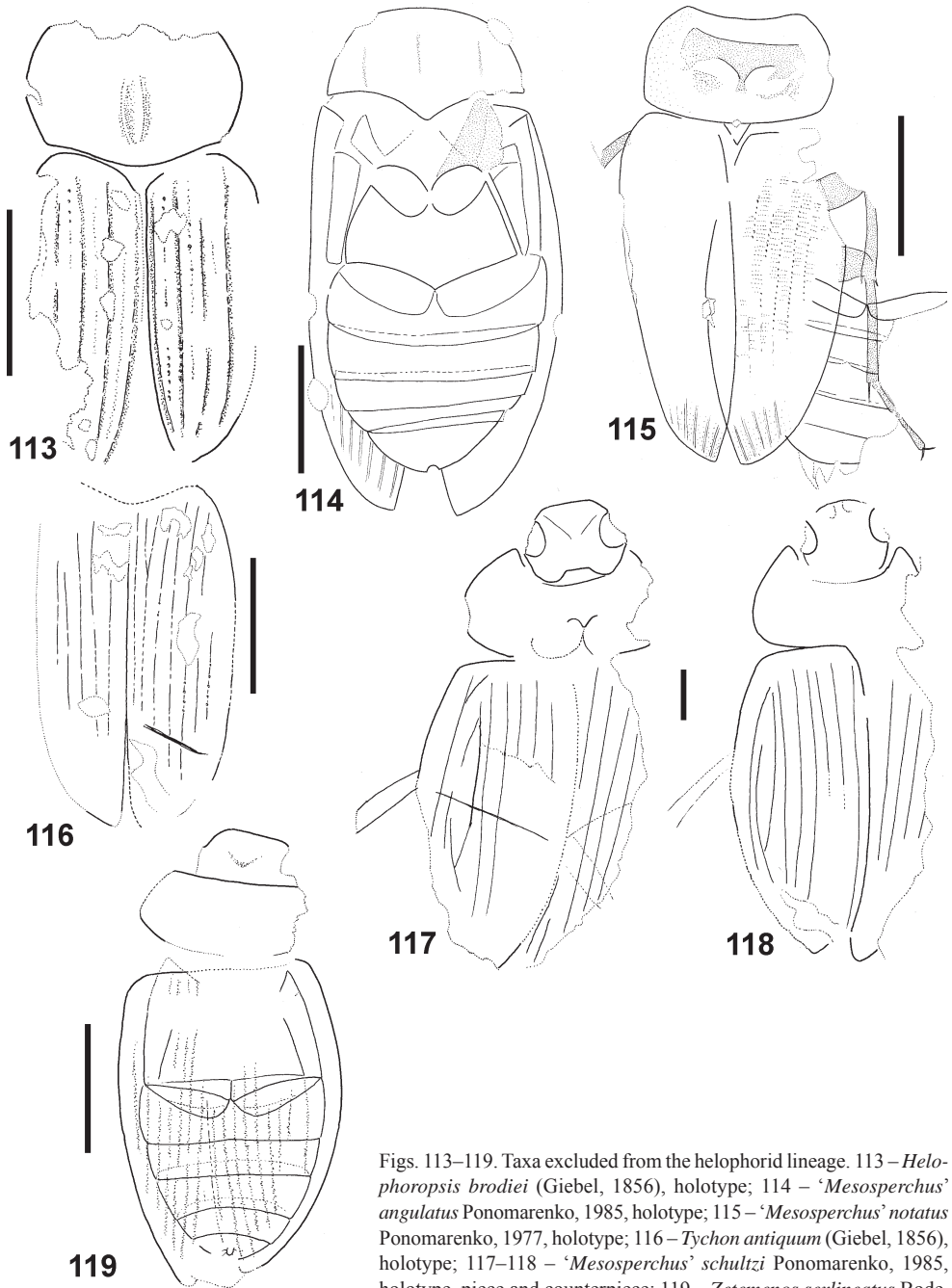
Mesosperchus angulatus Ponomarenko, 1985b: 63.

Mesosperchus angulatus: PERKOVSKY (1998: 114, synonymized with *Mesecanus communis* (Ponomarenko, 1977)).

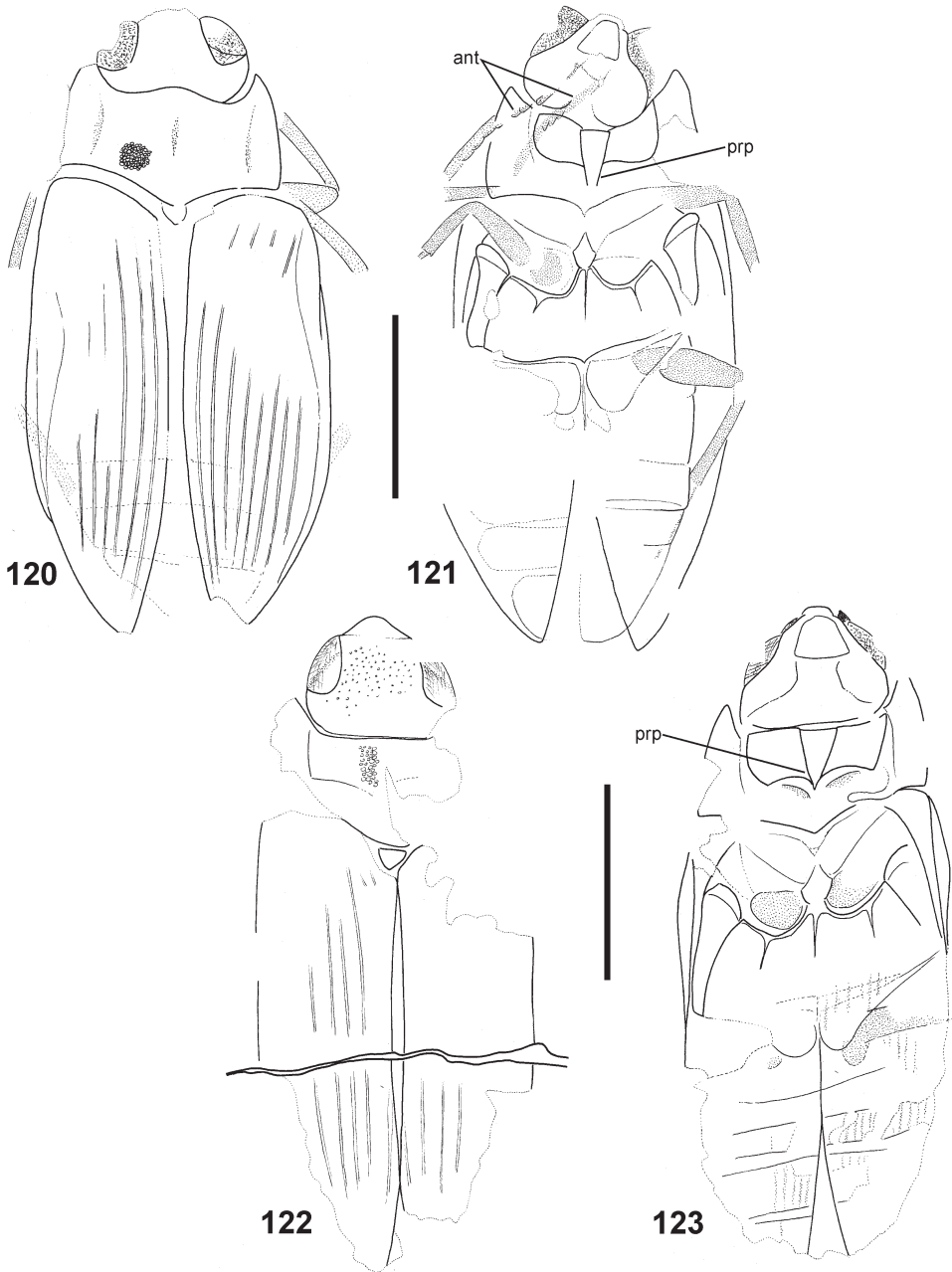
Type locality and age. Russia, Buryat Republic, Novospasskoye village (current GPS coordinates 51.3°N 108.1°E). Ichetuy Formation, Late Jurassic, Oxfordian, 161.2–155.7 mya (CLAPHAM 2011d).

Material examined. HOLOTYPE: PIN 3000/921 (piece only).

Taxonomic note. The holotype, which is the only preserved specimen, is a rather well-preserved fossil in ventral view, which however does not bear any apomorphy or combination of characters indicating its placement in the Hydrophiloidea. The apical emargination of the abdominal ventrite 5 resembles that present in some groups of the Hydrophilidae but is not enough to justify the placement of the species to this family. At the same time, the presence of the abdominal emargination excludes the placement in the helophorid lineage of the Hydrophiloidea irrespectively to the real placement of the fossil, as abdominal ventrite 5 is entire on posterior margin in all modern and fossil groups of the lineage. Based on the comparison with other fossils from the locality of Novospasskoye, PERKOVSKY (1998) synonymized *Mesosperchus angulatus* with *Mesecanus communis* (Ponomarenko, 1977) (considered as



Figs. 113–119. Taxa excluded from the helophorid lineage. 113 – *Helophoropsis brodiei* (Giebel, 1856), holotype; 114 – ‘*Mesosperchus angulatus*’ Ponomarenko, 1985, holotype; 115 – ‘*Mesosperchus notatus*’ Ponomarenko, 1977, holotype; 116 – *Tychon antiquum* (Giebel, 1856), holotype; 117–118 – ‘*Mesosperchus schultzi*’ Ponomarenko, 1985, holotype, piece and counterpiece; 119 – *Zetemenos sexlineatus* Bode, 1953, holotype. Scale bars: 1 mm.



Figs. 120–123. *Mesohelophorus* *mongolicus* Ponomarenko, 1986 (120–121 – PIN 3152/4355, holotype, piece and counterpiece; 122–123 – PIN 3152/4312, paratype, piece and counterpiece). Scale bars: 1 mm. Abbreviations: ant – antenna; prp – prosternal process.

belonging to the Agyrtidae by PONOMARENKO (1977b) and NEWTON (1997), and to Leiodidae by PERKOVSKY (1998). We are not able to comment on the correctness of the species synonymy or family assignment of *Mesosperchus angulatus*, but we can confirm here that the species does not belong to the Hydrophiloidea. The species may possibly belong to the Elateriformia according to Ch.-Y. Cai (pers. comm. to M. Fikáček, 2012).

† ‘*Mesosperchus*’ *notatus* Ponomarenko, 1977

(Figs. 102–103, 115)

Mesosperchus notatus Ponomarenko, 1977b: 110.

Type locality and age. Russia, Buryat Republic, Novospasskoye village (current GPS coordinates 51.3°N 108.1°E). Ichety Formation, Late Jurassic, Oxfordian, 161.2–155.7 mya (CLAPHAM 2011d).

Material examined. HOLOTYPE: PIN 3000/923 (piece only). PARATYPE: PIN 3000/912 (piece only).

Taxonomic note. Both preserved specimens lack the head and the only preserved ventral structures are prosternum and parts of abdomen. The preserved parts do not bear any apomorphy or combination of characters which would indicate the placement of the species in the Hydrophiloidea. For that reason, it is here transferred to *Polyphaga incertae sedis*. The superficial structure of elytra with fine transverse ridges on elytral intervals somewhat resembles some groups of the Leiodidae.

† ‘*Mesosperchus*’ *schultzi* Ponomarenko, 1985

(Figs. 101, 117–118)

Mesosperchus schultzi Ponomarenko, 1985a: 142.

Type locality and age. Germany, Bavaria, Solnhofen (current GPS coordinates 48.0°N 11.0°E). Solnhofen Formation, Late Jurassic, Early/Lower Tithonian, 150.8–145.5 mya (LABANDEIRA 2003).

Material examined. HOLOTYPE: NHMW 1985/20 (piece and counterpiece).

Taxonomic note. The holotype, which is the only available specimen of this species, is preserved as a three-dimensional impression in a whitish limestone without any fossilized organic remnants, which makes it rather difficult to examine. Unfortunately, except the contiguous procoxae, only dorsal characters are preserved and the precise taxonomic assignment of the species is therefore impossible. The shape of the head and the presence of the large clypeus and distinct frontoclypeal suture resembles some groups of Hydrophilidae, but a study of better preserved specimens would be necessary to confirm this placement as the Hydrophilidae are not known from the Jurassic so far. Hence, we are considering the species as *Polyphaga incertae sedis* with possible affinity to the Hydrophiloidea for the time being.

† *Tychon antiquum* (Giebel, 1856)

(Figs. 92, 116)

Helephoridae? [sic!]: BRODIE (1845: 117, Pl. vi: Fig. 13).

Helophorus antiquus Giebel 1856: 51.

Tychon antiquum: HANDLIRSCH (1908: 563, Pl. XLV: Fig. 76; transferred to *Tychon*).

Helophorus antiquus: HANSEN (1999: 318).

Type locality. United Kingdom, Wiltshire, Vale of Wardour, Middle Purbeck. Early Cretaceous, Middle Berriasian, 145.5–140.2 mya (CLAPHAM 2011a).

Type material: HOLOTYPE: NHM I-11967 (piece only).

Taxonomic note. The holotype, which is the only available specimen of the species, is a badly preserved fossil with partly preserved elytra in dorsal view, whereas all remaining body parts are missing. Hence, the fossil does not bear any apomorphy or combination of characters indicating its placement within the Hydrophiloidea. The assignment to the Hydrophiloidea was supposed as unjustified even by HANDLIRSCH (1908) who also considered the species to be of an unclear placement within Coleoptera. We are confirming this opinion here and exclude the species as well as the monotypic genus *Tychon* Handlirsch, 1908 to which it belongs from the Hydrophiloidea to Coleoptera *incertae sedis*.

†*Zetemenos sexlineatus* Bode, 1953

(Figs. 93, 119)

Zetemenos sexlineatus Bode, 1953: 230.

Zetemenos sexlineatus: PONOMARENKO (1992: 186).

Type locality and age. Germany, Niedersachsen, Grassel at Braunschweig (current GPS coordinates: 52.4°N 10.6°E. Posidonia Shale Formation, Early Jurassic, Early Toarcian, 183.0–182.0 mya (CLAPHAM 2011b).

Material examined. HOLOTYPE: SMF VI 1399 (piece only).

Taxonomic note. The holotype, which is the only available specimen of this species, is a badly preserved fossil in dorsal view showing an elongate beetle with striate elytra. Other characters are not preserved, except for the abdomen with five ventrites, narrow and elongate metepimera, and possibly the frontoclypeal suture (however, the impression on the head may also represent some ventral head structures). The latter character would be also the only possible indication of the position of the species in the Hydrophiloidea. However, due to the bad preservation we do not consider this character as adequate to justify the superfamily assignment of the fossil. For that reason, the species including the currently monotypic genus *Zetemenos* Bode, 1953 to which it belongs are excluded from the Hydrophiloidea and transferred to Coleoptera *incertae sedis*.

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References

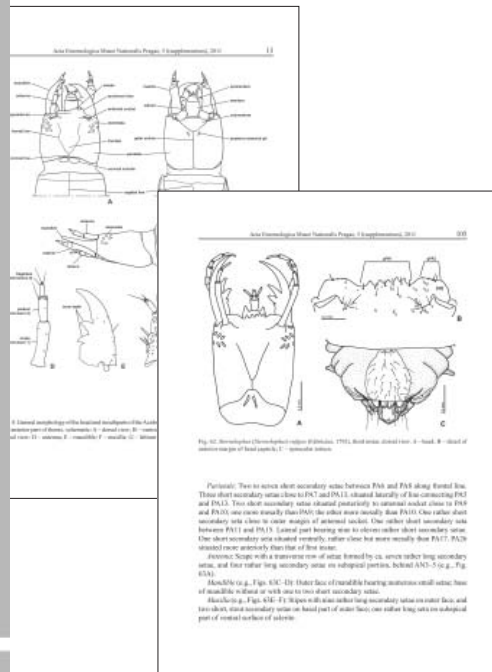
- ANGUS R. B. 1992: *Süsswasserfauna von Mitteleuropa. Bd. 20/10 – 2: Insecta, Coleoptera, Hydrophilidae, Helophorinae*. Spectrum Akademischer Verlag, Heidelberg – Berlin, 144 pp.
- ANGUS R. B. 1998: *Helophorus pallidipennis* Mulsant & Wachanru and *H. kervillei* d’Orchymont as good species (Coleoptera: Helophoridae). *Koleopterologische Rundschau* **68**: 189–196.
- ARNOLDI L. V., ZHERIKHIN V. V., NIKRITIN L. M. & PONOMARENKO A. G. (eds.) 1992: *Mesozoic Coleoptera*. Smithsonian Institution Libraries & The National Science Foundation, Washington, 285 pp.
- BODE A. 1953: Die Insektenfauna des ostniedersächsischen oberen Lias. *Palaeontographica, Abteilung A* **103(1–4)**: 1–375.
- BRODIE P. B. 1845: *A history of the fossil insects in the secondary rocks of England. Accompanied by a particular account of the strata in which they occur, and of the circumstances connected with their preservation*. John van Voorst, London, xviii + 130 pp. + 12 pls.
- CLAPHAM M. 2011a: *Dinton, Vale of Wardour, Middle Purbeck*. Paleobiology Database Collection No. 104008 [for Paleobiology Database homepage see <http://paleodb.org>]. Visited on 21st February 2012.
- CLAPHAM M. 2011b: *Grassel, Braunschweig*. Paleobiology Database Collection No. 107321 [for Paleobiology Database homepage see <http://paleodb.org>]. Visited on 21st February 2012.
- CLAPHAM M. 2011c: *Myangad locality, Section 221/17*. Paleobiology Database Collection No. 104054 [for Paleobiology Database homepage see <http://paleodb.org>]. Visited on 21st February 2012.
- CLAPHAM M. 2011d: *Novospasskoye village (PIN collection 3000)*. Paleobiology Database Collection No. 105017 [for Paleobiology Database homepage see <http://paleodb.org>]. Visited on 21st February 2012.
- COBOS A. 1986: *Fauna iberica de coleopteros Buprestidae*. Aguirre, Madrid, 364 pp.
- CROWSON R. A. 1981: *The biology of the Coleoptera*. Academic Press, London, 802 pp.
- DUNSTAN B. 1923: Mesozoic Insects of Queensland. Part I. – Introduction and Coleoptera. *Geological Survey of Queensland Publication* **273**: 1–89.
- DURANTE M. V. & BAKULBEKOV N. M. 2009: *Paleontology of Mongolia. Flora of the Phanerozoic*. Geos, Moscow, 356 pp (in Russian).
- FIKÁČEK M. & ENGEL M. S. 2011: An aquatic water scavenger beetle in Early Miocene amber from the Dominican Republic (Coleoptera: Hydrophilidae). *Annales Zoologici (Warszawa)* **61**: 621–628.
- FIKÁČEK M., HÁJEK J. & PROKOP J. 2008: New records of the water beetles (Coleoptera: Dytiscidae, Hydrophilidae) from the central European Oligocene-Miocene deposits, with a confirmation of the generic attribution of *Hydrobiomorpha* *enspelense* Wedmann 2000. *Annales de la Société Entomologique de France (Nouvelle Série)* **44**: 187–199.
- FIKÁČEK M., PROKOP J. & NELA. 2010a: Fossil water scavenger beetles of the subtribe *Hydrobiusina* (Coleoptera: Hydrophilidae) from the Upper Oligocene locality of Aix-en-Provence. *Acta Entomologica Musei Nationalis Pragae* **50**: 445–458.
- FIKÁČEK M., SCHMIED H. & PROKOP J. 2010b: Fossil hydrophilid beetles (Coleoptera: Hydrophilidae) of the Late Oligocene Rott Formation (Germany). *Acta Geologica Sinica (English Series)* **84**: 732–750.

- FIKÁČEK M., WEDMANN S. & SCHMIED H. 2010c: Diversification of the greater hydrophilines clade of giant water scavenger beetles dated back to the Middle Eocene (Coleoptera: Hydrophilidae: Hydrophilina). *Invertebrate Systematics* **24**: 9–22.
- FIKÁČEK M., PROKIN A. & ANGUS R. B. 2011a: A long-living species of the hydrophiloid beetles: *Helophorus sibiricus* from the early Miocene deposits of Kartashevo (Siberia, Russia). *ZooKeys* **130**: 239–254.
- FIKÁČEK M., HÁJEK J. & SCHMIED H. 2011b: On the identity of the fossil aquatic beetles from the Tertiary localities in the southern part of the Upper Rhine Graben (Coleoptera, Hydrophilidae, Dytiscidae). *ZooKeys* **78**: 15–25.
- FIKÁČEK M., BARCLAY M. V. L. & PERKINS P. 2011c: Two new species of the *Epimetopus mendeli* species group and notes on its adult and larval morphology (Coleoptera: Hydrophiloidea: Epimetopidae). *Acta Entomologica Musei Nationalis Pragae* **51**: 477–504.
- FIKÁČEK M., PROKIN A., ANGUS R. B., PONOMARENKO A., YUE Y., REN D. & PROKOP J. 2012: Phylogeny and the fossil record of the Helophoridae reveal Jurassic origin of modern hydrophiloid lineages (Coleoptera: Polyphaga). *Systematic Entomology* **37**: in press. DOI: 10.1111/j.1365-3113.2012.00630.x
- GIEBEL C. G. 1856: *Fauna der Vorwelt mit steter Berücksichtigung der lebenden Thiere. Zweiter Band: Gliederthiere. Erste Abtheilung: Insecten und Spinnen*. F. A. Brodhaus, Leipzig, xviii + 511 pp.
- GUBIN Y. M. & SINITZA S. M. 1996: Shar Teg: a unique Mesozoic locality of Asia. In: MORALES M. (ed.): *The Continental Jurassic. Museum of Northern Arizona Bulletin* **60**: 311–318.
- HANDLIRSCH A. 1908. *Die fossilen Insekten und die Phylogenie der rezenten Formen. Ein Handbuch für Paläontologen und Zoologen*. Wilhelm Engelmann, Leipzig, 1430 pp + 51 plates.
- HANSEN M. 1999: *World Catalogue of Insects. Volume 2. Hydrophiloidea (s.str.) (Coleoptera)*. Apollo Books, Stenstrup, 416 pp.
- HEER O. 1878: Ueber einige Insektenreste aus der raetischen Formation Schonens. *Geologiska Foerhingens i Stockholm Foerhandlingar* **4**: 192–197.
- HUNT T., BERGSTEN J., LEVKANIČOVÁ Z., PAPADOPOULOU A., ST. JOHN O., WILD R., HAMMOND P. M., AHRENS D., BALKÉ M., CATERINO M. S., GÓMEZ-ZURITA J., RIBERA I., BARRACLOUGH T. G., BOČÁKOVÁ M., BOČÁK L. & VOGLER A. P. 2007: A comprehensive phylogeny of beetles reveals the evolutionary origins of superradiation. *Science* **318**: 1913–1916.
- JELL P. A. 2004: The fossil insects of Australia. *Memoirs of the Queensland Museum* **50**: 1–124.
- McKENNAD. D. & FARRELL B. D. 2009: Beetles (Coleoptera). Pp. 278–289. In: BLAIR HEDGES S. & KUMAR S. (eds.): *The timetree of life*. Oxford University Press, New York, 572 pp.
- NEWTON A. F. 1997: Review of Agyrtidae (Coleoptera), with a new genus and species from New Zealand. *Annales Zoologici (Warszawa)* **47**: 111–156.
- LABANDEIRA C. 2003: *Solnhofen*. Database Collection No. 29012 [for Paleobiology Database homepage see <http://paleodb.org>]. Visited on 21st February 2012.
- LATREILLE P. A. 1810: *Considérations générales sur l'Ordre naturel des Animaux composant les Classes des Crustacés, des Arachnides, et des Insectes*. F. Schoell, Paris, 444 pp.
- PERKOVSKY E. E. 1998: Evolutionary development of the specific antennal structure in leiodid beetles and systematic position of Jurassic *Mesecanus communis* and *Polysitum elongatum* (Coleoptera: Staphylinoidea, Leiodidae). Pp. 111–115. In: *Proceedings of the first international paleoentomological conference, Moscow 1998*. AMBA Projects International, 121 pp.
- PONOMARENKO A. G. 1977a: Podotryad Adephaga. [Suborder Adephaga]. Pp. 17–104. In: ARNOLDI L. V., ZHERIKHIN V. V., NIKRITIN L. M. & PONOMARENKO A. G. (eds.): *Mezozoiskie zhestkokrylye*. [Mesozoic Coleoptera], Nauka, Moskva, 204 pp (in Russian). [for English translation see ARNOLDI et al. 1992].
- PONOMARENKO A. G. 1977b: Infraotryad Staphyliniiformia. [Infraorder Staphyliniiformia]. Pp. 106–119. In: ARNOLDI L. V., ZHERIKHIN V. V., NIKRITIN L. M. & PONOMARENKO A. G. (eds.): *Mezozoiskie zhestkokrylye*. [Mesozoic Coleoptera]. Nauka, Moskva, 204 pp (in Russian). [For English translation see ARNOLDI et al. (1992)].
- PONOMARENKO A. G. 1985a: Fossil insects from the Tithonian „Solnhofener Plattenkalke“ in the Museum of Natural History, Vienna. *Annalen des Naturhistorischen Museums in Wien* **87A**: 135–144.
- PONOMARENKO A. G. 1985b: Zhestkokrylye iz Yury Sibiri i zapadnoy Mongolii. [Beetles from the Jurassic of Siberia and Western Mongolia]. *Trudy Paleontologicheskogo Instituta* **211**: 47–87 (in Russian).

- PONOMARENKO A. G. 1986: Zhestkokrylye. Scarabaeida (= Coleoptera). Pp. 84–105. In: *Nasekomye v rannye-myelovykh ekosistemakh Zapadnoy Mongolii*. Nauka, Moskva, 214 pp. (in Russian).
- PONOMARENKO A. G. 1987: Novye mezozoiskye vodnye zhestkokrylye (Insecta, Coleoptera) iz Azii. [New Mesozoic aquatic beetles (Insecta, Coleoptera) from Asia]. *Paleontologicheskii Zhurnal* **1987**: 83–97 (in Russian).
- PONOMARENKO A. G. 1990: Zhuki (Scarabeida). [Beetles (Scarabeida)]. Pp. 39–87. In: RASNITSYN A. P. (ed.) *Pozdne-mezozoiskie nasekomye Vostochnogo Zabaikalya*. Nauka, Moskva, 200 pp (in Russian).
- PONOMARENKO A. G. 1992: Upper Liassic beetles (Coleoptera) from Lower Saxony, Germany. *Senckenbergiana Lethaea* **72**: 179–188.
- PROKIN A. 2009: New water scavenger beetles (Coleoptera: Hydrophilidae) from the Mesozoic of Mongolia. *Paleontological Journal* **43**: 660–663.
- PROKIN A., REN D. & FIKÁČEK M. 2010: New Mesozoic water scavenger beetles from the Yixian Formation in China (Coleoptera, Hydrophiloidea). *Annales Zoologici (Warszawa)* **60**: 173–179.
- RASNITSYN A. P. 1990: *Pozdne-mezozoiskie nasekomye Vostochnogo Zabaikalya*. Nauka, Moskva, 200 pp (in Russian).
- RASNITSYN A. P. & ZHERIKHIN V. V. 2002: Alphabetic list of selected insect fossil sites – Impression fossils. Pp. 437–444. In: RASNITSYN A. P. & QUICKE D. L. J. (eds.): *History of Insects*. Kluwer Academic Publishers, Norwell, 517 pp.
- REN D., TAN J. J., SHIH C. K. & GAO T. P. 2010: The upper Mesozoic stratigraphic characteristics in northeastern China. Pp. 12–21. In: REN D., SHIH C. K., GAO T. P., YAO Y. Z. & ZHAO Y. Y. (eds.): *Silent stories – Insect fossils treasures from dinosaur era of northeastern China*. Science Press, Beijing, 322 pp.
- SWISHER C. C. III, WANG Y.-Q. & WANG X. L. 1999. Cretaceous age for the feathered dinosaurs of Liaoning, China. *Nature* **400**: 58–61.
- SINICHENKOVA N. D. & ZHERIKHIN V. V. 1996: Mesozoic lacustrine biota: extinction and persistence of communities. *Paleontological Journal* **30**: 710–715.
- TILLYARD R. J. 1916: Mesozoic and Tertiary Insects of Queensland and New South Wales. *Geological Survey of Queensland Publication* **1916**: 1–49.
- YAN E. V. & ZHANG H. C. 2010: New beetle species of the formal genus *Artematopodites* (Coleoptera: Polyphaga), with remarks on the taxonomic position of the genera *Oviovagina* and *Sinonitidulina*. *Paleontological Journal* **44**: 451–456.
- ZHERIKHIN V. V., MOSTOVSKI M. B., VRŠANSKÝ P., BLAGODEROV V. A. & LUKASHEVICH E. 1998: The unique Lower Cretaceous locality Baissa and other contemporaneous fossil sites in North and West Transbaikalia. Pp. 185–191. In: *Proceedings of the first international paleontological conference, Moscow 1998*. AMBA Projects International, 121 pp.

BOOK ANNOUNCEMENT

Larval morphology of the Japanese species of the tribes Acidocerini, Hydrobiusini and Hydrophilini (Coleoptera: Hydrophilidae)



MINOSHIMA Y. & HAYASHI M. 2011: Larval morphology of the Japanese species of the tribes Acidocerini, Hydrobiusini and Hydrophilini (Coleoptera: Hydrophilidae). *Acta Entomologica Musei Nationalis Pragae* 51(supplementum): 1–118.

The volume contains a detailed treatment of larvae of three tribes of the water scavenger beetles (Hydrophilidae) of Japan. Larvae of 11 species belonging to 7 aquatic genera are described, including the information about larval chaetotaxy and transformations of morphological characters between larval instars. The volume also contains an identification key to the Japanese genera of the Hydrophilidae based on larval characters, and 67 high-quality plates illustrating all characters mentioned in the text.

The volume can be ordered from the Department of Entomology, National Museum, Prague, Czech Republic (aemnp.editors@gmail.com).