

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

MARTIN FIKÁČEK^(1,2), JIŘÍ HÁJEK⁽²⁾ & JAKUB PROKOP^{(1)*}

⁽¹⁾ Charles University in Prague, Faculty of Science, Department of Zoology, Viničná 7, CZ – 128 44, Praha 2, Czech Republic

⁽²⁾ National Museum, Department of Entomology, Kunratic 1, CZ – 148 00 Praha 4, Czech Republic

* Corresponding author

Abstract. New Cenozoic aquatic beetles of the families Dytiscidae (*Cybister* cf. *rotundatus* Říha 1974 and *Cybister* sp.) and Hydrophilidae (*Hydrophilus* cf. *pistaceus* Laporte de Castelnau 1840 and *Hydrobiomorpha enspelense* Wedmann 2000) are described and compared with recent relatives based on external morphological structures. All specimens are preserved in Oligocene and Miocene fluvio-lacustrine deposits of the Krušné hory piedmont basins (Bílina Mine, Czech Republic) and the Hrádek Basin (Seifhennersdorf, Germany). Generic classification of *Cybister nicoleti* Heer 1862 (Miocene) is discussed. Based on the confirmation of generic identification of *Hydrobiomorpha enspelense*, the occurrence of the circumtropical recent genus *Hydrobiomorpha* Blackburn 1888 in European Miocene deposits is confirmed. Habitat preferences of recent relatives of all reported taxa support the local palaeoenvironmental conditions of both localities previously inferred from fossil flora.

Résumé. Nouvelles données de coléoptères aquatiques (Coleoptera : Dytiscidae, Hydrophilidae) des dépôts Oligocène-Miocène de l'Europe Centrale, avec la confirmation de l'appartenance générique de *Hydrobiomorpha enspelense* Wedmann 2000. De nouveaux coléoptères aquatiques cénozoïques appartenant aux familles Dytiscidae (*Cybister* cf. *rotundatus* Říha 1974 et *Cybister* sp.) et Hydrophilidae (*Hydrophilus* cf. *pistaceus* Laporte de Castelnau 1840 et *Hydrobiomorpha enspelense* Wedmann 2000) sont décrits et comparés aux taxons modernes proches à partir des structures de la morphologie externe. Tous les échantillons ont été trouvés dans des sédiments fluviaux-lacustres de l'Oligocène et du Miocène des bassins au pied des montagnes de Krušné hory (Mine de Bílina, République Tchèque) et du bassin de Hrádek (Seifhennersdorf, Allemagne). La classification générique de *Cybister nicoleti* Heer 1862 (Miocène) est discutée. L'identification générique d'*Hydrobiomorpha enspelense* est attestée, confirmant ainsi l'existence du genre *Hydrobiomorpha* Blackburn 1888 à distribution circumtropicale actuelle dans un gisement du Miocène de l'Europe centrale. Les préférences d'habitat de tous les taxons parents récents confirment ce qu'on savait des conditions paléoenvironnementales des deux localités, telles qu'on les avait déduites de la flore fossile.

Keywords: Insecta, *Cybister*, *Hydrophilus*, Tertiary, Cenozoic, Czech Republic, Germany.

In the Cenozoic fossil record, aquatic beetles became dominant in number of specimens for the first time after the Cretaceous, with a high diversity known mainly from the Miocene (Ponomarenko 1995). Many taxa are described from the Cenozoic lacustrine deposits and a few also from amber resin (Carpenter 1992, Hansen 1999, Miller & Balke 2003, Říha 1979), and fossils of aquatic beetle larvae are known as well (Klausnitzer 2003). The increase of the species diversity of these groups in the Oligocene-Miocene is attributed to the increase of the submerged macrophytes in lakes (Ponomarenko 1995). The vast majority of the fossils is represented by the taxa of the families Dytiscidae

(Adephaga: Dytiscoidea) and Hydrophilidae (Polyphaga: Hydrophiloidea) (Carpenter 1992).

Fossils of both mentioned families are known already from the Jurassic (Carpenter 1992). The taxonomic position of many Mesozoic fossils of both families remains, however, largely unsolved, and there is still not a wide consensus of whether these taxa represent basal branches of the above mentioned families or separate evolutionary branches within the superfamilies Dytiscoidea and Hydrophiloidea (see e.g. Carpenter 1992, Ponomarenko 1995, Arnol'di *et al.* 1992, Beutel 1995). On the other hand, the Cenozoic dytiscid and hydrophilid taxa seem mostly to represent recent genera. The fossil taxa described by older authors (e.g. Deichmüller 1886, Heer 1862) require a critical taxonomic revision.

E-mail: mfikacek@seznam.cz, jiri_hajek@nm.cz, jprokop@natur.cuni.cz

Accepté le 31 janvier 2008

Most of the published Cenozoic records of aquatic beetles as well as most described taxa originate from the classical palaeontological localities in Europe (i.e. Le Locle, Schonen, both in Switzerland (Heer 1862, 1878); Aix, Corent, Menat, all in France (Heer 1862, Oustalet 1874); Enspel, Hohengau, Nieder Flörsheim, Oeningen, Rott, all in Germany (Heyden & Heyden 1866, Statz 1940, Heer 1862, Wedmann 2000); Radoboj, Croatia (Heer 1847); Pochlovice, Uzgruň, both in the Czech Republic (Prokop *et al.* 2004, Říha 1974), in Shanwang, Shandong, China (Jungfeng 1989, Jungfeng *et al.* 1994), and in the U.S.A. (Green River, Wyoming and Florissant, Colorado, Scudder 1878, 1900; Wickham 1909, 1911, 1912, 1913, 1914).

Cenozoic insect fauna of northwestern Bohemia is preserved in fluvio-lacustrine deposits of the Krušné hory piedmont basins and the České středohoří Mts. About 16 localities representing several different palaeoenvironments dated from Upper Eocene to Lower Miocene were reviewed (Prokop 2003). The relatively diverse insect fauna from Lower Oligocene (Ruppelian/Chattian) of Seifhennersdorf near the boundary of the Czech Republic-Germany is preserved in several interbeds of the brownish diatomite of Středohoří Complex (equivalent of Ústí Formation) after Kvaček (2003) and Prokop & Fikáček (2007). Another famous site is the Bílina mine (the former Maxim Gorkij mine) situated in the Most Basin near the town of Bílina. The stratigraphical attribution is to the Most Formation of the Lower Miocene (Burdigalian) and insects are preserved in three fossiliferous horizons (Clayey Superseam Horizon, Delta Sandy Horizon, Lake Clayey Horizon), (Kvaček *et al.* 2004).

Taphonomy is another important aspect to be noticed. Among the fossils preserved at the Bílina

mine, especially the isolated elytra of large-sized representatives of various beetle families, including Dytiscidae or Hydrophilidae dominate in number of specimens in certain layers (e.g., Delta Sandy Horizon). Smith *et al.* (2006) show this phenomenon to be caused by the robustness and size of beetle exoskeletons correlating with sinking and disarticulation rate under different local palaeoenvironmental conditions. The fossil record of the three horizons from Bílina mine is biased by the latter two factors (Prokop 2003).

Material and methods

The fossil specimens were observed by stereomicroscope Olympus SZX-12 in dry state and under thin film of ethylalcohol improving the clarity. Photographs were made simultaneously by digital camera Olympus 5050 in the highest contrast by single sided cross-light pre-exposure.

The reference material from the Bílina mine was collected by Zdeněk Dvořák and deposited in collection of Doly Bílina in Bílina (inventory numbers prefixed by ZD). Examined specimen from Seifhennersdorf is housed in the collection of Staatliches Museum für Mineralogie und Geologie in Dresden (inventory number prefixed by SaT).

Body size of the described material as well as of the compared fossils and recent species are characterized by the following measurements (all in mm): TL – total length; EL – elytral length; EW – maximum combined width of both elytra; EW/2 – maximum width of an elytron; PW – width at posterior pronotal margin; PL – pronotal length at midwidth; HW – head width at the level of eyes. Based on our experience with teneral specimens of recent water beetle taxa, elytral width (EW and EW/2) is highly affected by compression and measurements of compressed specimens do not characterize their real body shape properly. Therefore, body shape is characterized by EL/PL and TL/PW ratios for the Hydrophilidae. In Dytiscidae, most fossils are preserved only as fragments of elytra or metathorax plus abdomen, and the ratios mentioned above are not usable. We therefore list EL/EW ratio although it may be significantly affected by fossilization, along with approximate TL for the genus *Cybister*. We used the TL/EL ration inferred from

Table 1. Body measurements (in mm) of fossil *Cybister* in comparison with recent European species (numbers in italics represent approximate body length, see also Material and methods).

	Taxon	TL	EL	EW	EL/EW
Fossil species	<i>C. agassizi</i>	37	27.4	20.1	1.36
	<i>C. atavus</i>	24-28	20.5	16.8	1.22
	<i>C. fractus</i>	34-39	28.5	20.7	1.38
	<i>C. imperfectus</i>	20-23	17	14	1.21
	<i>C. mancus</i>	23-27	20	14.3	1.40
	<i>C. nicoleti</i>	24-28	20.4	21.1	0.97
	<i>C. rotundatus</i>	26-30	22	17	1.30
	<i>C. cf. rotundatus</i>	27-31	22.8	17.3	1.32
	<i>C. sp.</i>	29	22.5	18.5	1.22
	Recent species	<i>C. lateralmarginalis</i>	29-36	24-29.5	16-20.5
<i>C. tripunctatus</i>		21-28	17.2-23.0	11.2-15.0	1.54
<i>C. vulneratus</i>		22-27	16.0-20.8	11.2-14.1	1.50

recent *Cybister* and *Megadytes* taxa (TL/EL = 1.19–1.35) for calculating of approximate TL of all fossil *Cybister* from their EL. Measurements of all recent taxa are based on the specimens housed in the collection of the Department of Entomology in the National Museum in Prague.

The supraspecific nomenclature follows Nilsson (2001) for Dytiscidae & Hansen (1991, 1999) for Hydrophilidae.

Results and discussion

Family Dytiscidae

Cybister cf. *rotundatus* Řiha 1974 (Figs. 2–3)

Material. Specimen ZD0253: fossil of mesothorax, metathorax and abdomen in ventral view preserved in fine grained claystone.

Occurrence. Early Miocene (Burdigalian), zone MN 3a of mammal fauna, Most Formation, Clayey Superseam Horizon (Kvaček *et al.* 2004); Břilina mine near Břilina, N 50°34'18.73", E 13°40'34.82"[GPS], Czech Republic.

Description. Body measurements summarized in Tab. 1. Mesothorax damaged basally, only mesocoxal cavities, and part of right mesepimeron perceptible. Metasternum well preserved; lateral process ("metasternal wing") very narrow, constricted in flexure, width sensu Larson (1975) 1.8 mm. Right metepisternum distinctly preserved. Metacoxal plates with well-preserved trochanter attachments, 6.1 mm wide. Metacoxal process preserved basally, apical part damaged. General shape of elytra regularly rounded with maximum width near midlength. Epipleuron 0.8 mm wide in humeral part. All six abdominal ventrites (sternites II–VII) perceptible. Lengths of ventrites II–VI (medially) as follows: 1.9 - 2.4 - 1.1 - 0.9 - 5.3 mm.

Cybister sp. (Figs. 4–6)

Material. Specimen ZD9705a (imprint) and ZD9705b (counter-imprint): fossil of the whole beetle in dorsal view, mouthparts and antennomeres except of left scapus missing; pronotum and elytra almost completely preserved; left protarsomeres and mesotarsomeres only weakly preserved, metatarsomeres well preserved. Specimen ZD9706a (imprint) and ZD9706b (counter-imprint): fragmentary parts of elytra, metathorax, abdomen and hind tarsi, most probably in dorsal view. All compressed fossils preserved in fine grained claystone.

Occurrence. Early Miocene (Burdigalian), zone MN 3a of mammal fauna, Most Formation, Clayey Superseam Horizon (Kvaček *et al.* 2004); Břilina mine near Břilina (Czech Republic).

Description. Specimen ZD9705: Body measurements summarized in Tab. 1. Head transverse, HW = 6.5 mm, clypeus with anterior margin almost straight; compound eyes slightly protruding laterad. Left antennal scape 0.75 mm long. Pronotum distinctly transverse, widest basally; lateral sides slightly rounded; anterior and posterior corners acutely projecting anteriorly and posteriorly, respectively. Elytron widest in 0.66 of its length; epipleuron 0.7 mm wide in humeral part. Structures of metasternum, metacoxa and abdominal

ventrites only indistinctly perceptible through the cast of elytra. Structure of pro- and mesotarsomeres not distinguishable. Apex of metatibia with row of flat setae. Metatarsomeres 1–3 with numerous long natatorial setae (ca. 2.2 mm long) perceptible on ventral side, metatarsomeres 1–4 with several stout setae dorsoapically, metatarsomere 5 with several short stout setae on dorsal side; lengths of metatarsomeres 1–5 as follows: 2.4 - 1.7 - 1.3 - 1.1 - 2.9 mm. Claws not perceptible.

Specimen ZD9706: Elytra continuously rounded posteriorly; epipleuron ca. 0.5 mm wide subapically. Structures of abdomen not perceptible. Metafemora wide and short, all metatarsomeres with long natatorial setae on ventral side.

Generic attribution. Morphological characters used for supraspecific classification of Dytiscidae (see e.g. Pederzani 1995) are not perceptible in our material. Based on the presence of long natatorial setae on metatarsomeres, and especially on large body length (more than 25 mm), the fossils belong into the subfamily Dytiscinae. Metatarsomeres 1–4 with apical margin bare (not bearing a row of flat setae) on posterior surface; elytra widened apically with maximum width behind the middle or in two thirds of its length respectively, and characteristic very narrow metasternal lateral process with constriction before apex (Fig. 3) allow us to classify the fossil more precisely into the tribe Cybistrini.

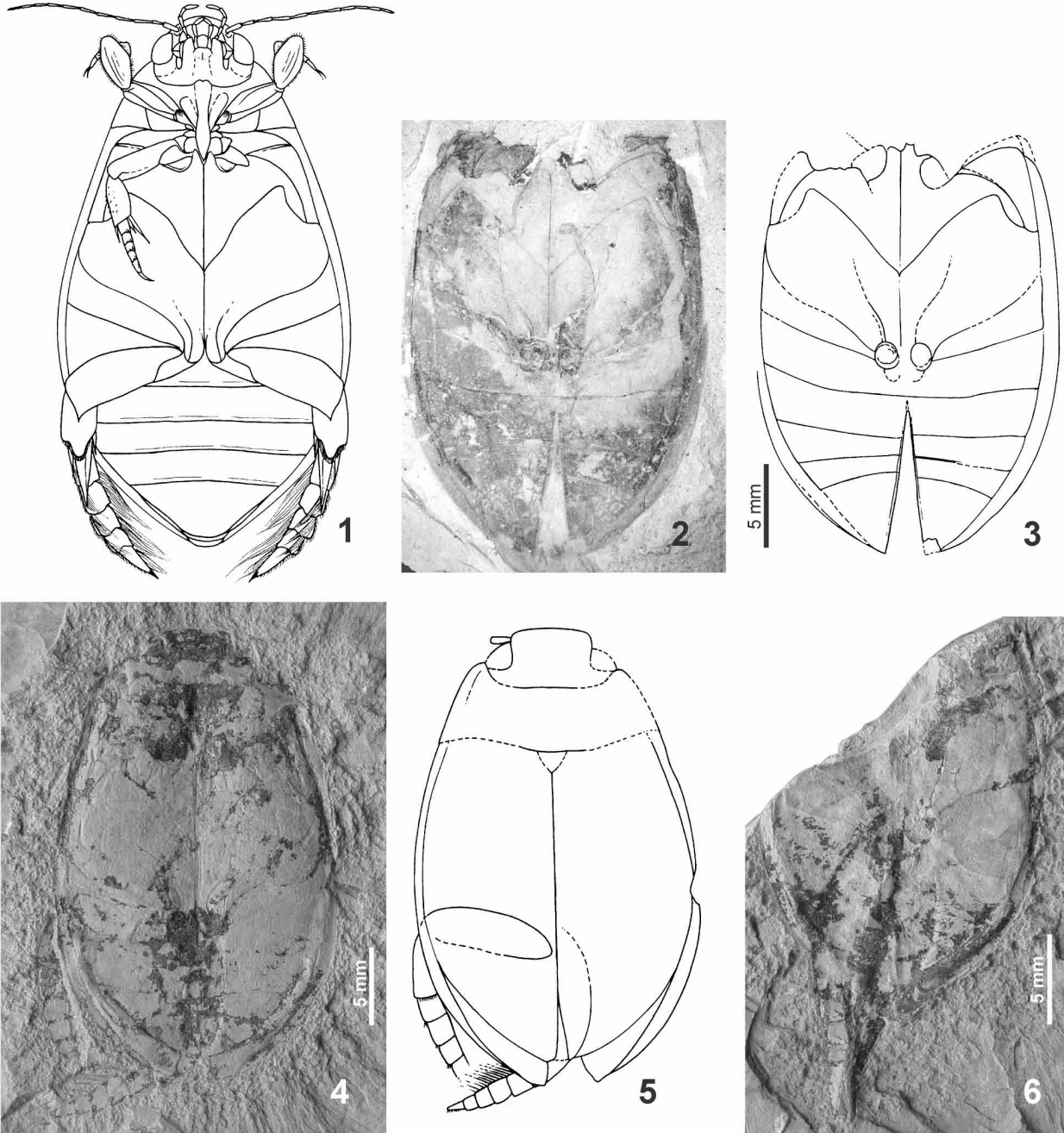
The latter tribe contains seven genera distributed world-wide (Nilsson 2001, Miller *et al.* 2007). Based on generic differential characters used by Brinck (1945), Pederzani (1995) and Miller *et al.* (2007), the generic identification is almost impossible for the fossils. However, only the genus *Cybister* Curtis 1827 occurs recently in the Palaearctic region, and all fossil specimens from the Palaearctic were originally attributed also to this genus. Of these taxa, Heer (1862) described *Cybister nicoleti* Heer, 1862 from the Miocene sediments of Oeningen and on the basis on the broad shape of elytra, he suggested its similarity with the South American species "*Cybister costalis* Oliv." (= *Cybister costalis* Fabricius 1775 sensu Olivier (1795); recently *Megadytes giganteus* Laporte de Castelnau 1835). Later, Guignot (1931–1933) noted that *C. costalis* is classified into the genus *Megadytes* Sharp 1882 and due to the similarity between the latter and the fossil species suggested by Heer (1862), he proposed the transfer of *C. nicoleti* into *Megadytes*. This opinion was subsequently adopted by Brinck (1945) and Nilsson (2001). Both genera could be only distinguished by the number of male metatarsal claws (one in *Cybister*, and two in *Megadytes*). This character is not preserved in most of fossils, and we are therefore not able to resolve the generic attribution properly. However, we consider the occurrence of Neotropical genus in the European Miocene as more improbable

and prefer to provisionally attribute all known Palaeartic fossil Cybistrini with the genus *Cybister*.

Comparison with fossil *Cybister*. Altogether seven species of ‘*Cybister*’ were described from Miocene of the western Palaeartic: *C. agassizi* Heer 1862, *C. atavus* Heer 1862 and *C. nicoleti* from Oeningen (Baden,

Germany); *C. fractus* Říha 1974 from Vishnevaya Balka (Stavropol, Russia); and *C. imperfectus* Říha 1974, *C. mancus* Říha 1974 and *C. rotundatus* Říha 1974 from Belyy Yar (Tomsk, Russia).

Most of the species were described based on single elytron, or metathorax and abdomen, which however



Figures 1–6
Cybister (Dytiscidae). **1**, *C. lateralmarginalis* (De Geer), ventral view; **2–3**, *C. cf. rotundatus* Říha, specimen ZD0253; **4–5**, *C. sp.*, specimen ZD9705a; **6**, *C. sp.*, specimen ZD9706a.

bear only few characters of taxonomic relevance. The characters used for identification of each species are usually (1) locality (sic!); (2) body length (length of elytra – see Tab. 1); (3) shape of elytra. Based on examination of recent species of *Cybister*, all three characters can vary: (ad 1) many recent *Cybister* in the intertropics and the temperate zone have large distributional areas (e.g. *Cybister vulneratus* Klug 1834 occurs in whole Africa and southwestern Palaearctic; *C. lateralimarginalis* (DeGeer 1774) occurs in the main part of Palaearctic, and finally *C. tripunctatus* (Olivier 1795) occurs in whole Old World intertropics, Nilsson 2003). There is therefore no reason to expect the fossil species to have their distribution restricted to small areas; (ad 2) variability of body length between smallest and biggest specimens of the same species reaches about 20% of TL in recent species (see Tab. 1 for measurements of selected recent species); (ad 3) shape of elytra in compressed fossils may be garbled with the fossilization process and the fossils seem to be wider than real dimensions of the beetles (see EL/EW for recent and fossil taxa in Tab. 1).

With the respect to facts mentioned above, we are not able to associate our species with previously described taxa undoubtedly. We assigned our first fossil to the Russian species *C. rotundatus*, because the fossil fits well in measurements and regularly rounded shape of elytra mentioned by Říha (1974). We leave the second fossil identified as *Cybister* sp., most similar with the German species *C. atavus*.

Comparison with recent species of *Cybister*. The cosmopolite genus *Cybister* currently contains 102 species (Nilsson 2001). The genus was usually classified

into three subgenera (Pederzani 1995), but the most recent revision (Miller *et al.* 2007) recognized four subgenera. Members of two of them occur recently in Europe. The characters used for identification of subgenera depend often on gender, and concern to presence/absence of adhesive setae on mesotarsus in male, natatorial setae on metatarsus in female, number of claws on metatarsus in female, male genitalia and body coloration. Unfortunately none of these characters are perceptible on fossil material, and we are not able to assign our fossils into any subgenus.

The comprehensive revision of *Cybister* species is still missing and comparison of our fossil with all recently described species is therefore very difficult. We compared it only with the *Cybister* species occurring recently in Europe: *C. lateralimarginalis*, *C. tripunctatus* and *C. vulneratus*. According to the data summarized in Tab. 1, our fossils could not be easily assigned to any of the recent European species. They are most similar to *C. lateralimarginalis*, which is however larger and more ovoid shaped (see Fig. 1).

Biology of recent *Cybister*. The representatives of recent European *Cybister* inhabit the littoral zone of larger, shallow, often thermophilous water bodies with rich submerged vegetation. Although they usually prefer stagnant water, their occurrence in slow flowing streams and rivers is not an exception. Larvae are predators of other insects – especially dragonflies larvae (Blunck 1922); adults are generally predators or scavengers on freshly dead animals.

Table 2. Body measurements (in mm) of fossil Hydrophilidae mentioned in this paper in comparison with type series of *Hydrobiomorpha enselense* (adapted from Wedmann 2000) and recent taxa (* – measurements inferred from photographs in Wedmann 2000; ** – approximate length because of missing elytral apex).

	TL	EL	EW/2	PW	PL	HW	EL/PL	TL/PW
<i>Hydrobiomorpha enselense</i> , holotype	–	–	5.8	8.8	3.7	4.7*	–	–
<i>Hydrobiomorpha enselense</i> , spec. no. 7311	21.9	14.7	5.7	9.0	4.0*	4.5*	3.7	2.3
<i>Hydrobiomorpha enselense</i> , spec. BAG	23.0	16.4	–	9.7	4.3	–	3.8	2.4
<i>Hydrobiomorpha enselense</i> , presented fossil	26.0	17.0	7.0	11.0	5.0	6.5	3.4	2.4
<i>Hydrophilus</i> cf. <i>pistaceus</i> spec. ZD9708	43.0	32.0**	11.0	18.0	7.0	10.0	4.3	2.4
<i>Hydrophilus</i> cf. <i>pistaceus</i> spec. ZD9709	–	35.0	12.0	–	–	–	–	–
<i>Hydrophilus pistaceus</i> , recent	33-40	28-31	9-10	14-16	5-6	8-10	4.8-5.2	2.4-2.6
<i>Hydrobiomorpha spinicollis</i> , recent	15-17	10.5-12	7-8.5	6-7	2.5-3	3.5-4	3.5-4	2.3-2.45

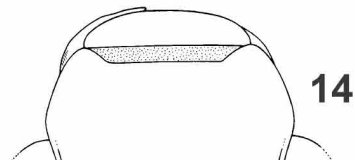
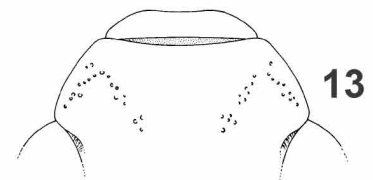
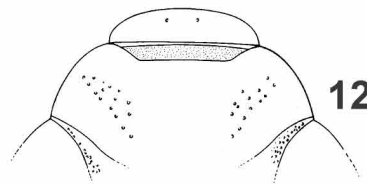
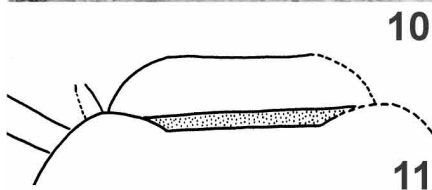
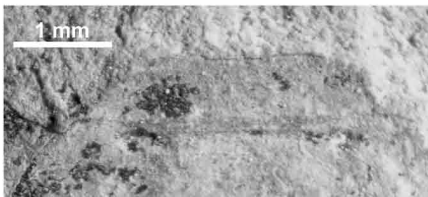
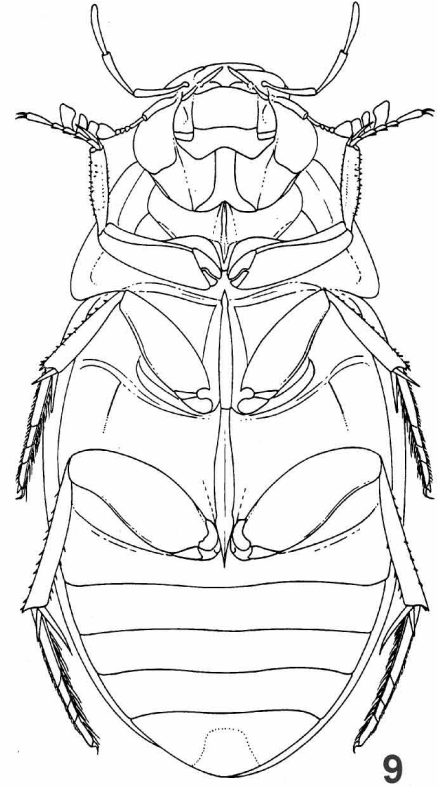
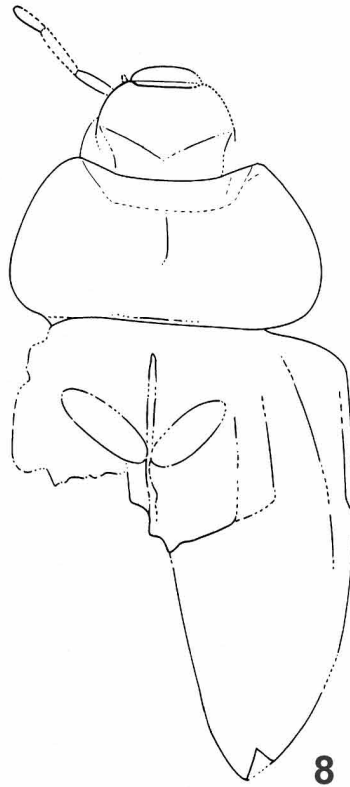
Family Hydrophilidae

Hydrobiomorpha enspelense Wedmann 2000
(Figs. 7–8, and 10–11)

Material. Specimen SaT 533: compressed fossil of whole beetle in ventral view, right part of head partly damaged, only left

maxillary palpus preserved, prothorax well-preserved, meso- and metathorax slightly deformed, legs absent, left elytron and abdomen missing, apical part of right elytron slightly deformed. Preserved in laminated diatomite.

Occurrence. Early Oligocene (Rupelian), Loučeň Formation (Hrádek Basin); Seifhennersdorf, N 50°55'59", E 14°36'0" [GPS], Germany.

**Figures 7–14**

Hydrophilidae. 7–8, 10–11, *Hydrobiomorpha enspelense* Wedmann, specimen SaT 533; 9, 12, *Hydrobiomorpha spinicollis* (Eschscholtz); 13, *Hydrochara caraboides* (Linnaeus); 14, *Hydrophilus pistaceus* Laporte de Castelnau. 7–8, general habitus; 9, ventral view; 10–14, detail of anterior emargination on clypeus.

Description. Body measurements summarized in Tab. 2. Head trapezoid in shape, eyes slightly protruding laterad. Clypeus widely emarginate at anterior margin, with posterior part triangular, divided from frons by distinct frontoclypeal sulci; superficial structure of head not preserved. Labrum well-sclerotized, 3 mm wide. Maxillary palpi 5 mm long, palpomere 2 slightly widened distally, palpomere 3 ca. 2.2 mm long, palpomere 4 slightly widened apically, 1.5 mm long. Pronotum slightly narrowed apicad, roundly emarginate anteriorly, antero- and posterolateral angles rounded. Prosternum with strong narrow longitudinal median carina in anterior half. Meso- and metaventrite with low median carina fused together, postcoxal median spine of metaventrite not preserved. Mesocoxal cavities widely oblique, narrowly separate from each other. Anepisternum 3 narrow, ca. 1.5 mm wide. Elytron narrowing apicad, pointed on apex; epipleuron not recognizable from pseudopipleuron, 1.75 mm wide basally when combined, narrowing apicad, ca. 1 mm wide at level of posterior margin of metathorax when combined. Superficial structure and elytral rows not preserved.

Comparison with type material of *H. enspelense*.

The fossil corresponds in most external characters with the type series of *H. enspelense*, except for its slightly longer and wider body size. Differences in EL/PL and TL/PW ratios (Tab. 2) correspond with the variability of these ratios observed in recent species (see Tab. 2 for measurements of recent Oriental species *Hydrobiomorpha spinicollis* (Eschscholtz 1822)) and suggest that the body shape of the new fossil specimen is very similar to that mentioned for *H. enspelense* by Wedmann (2000). The described specimen lacks the olive-green coloration of the body, which is probably caused by much worse preservation of superficial structures of the fossil.

Generic identification. Body size and shape of our material as well as the presence of the fused keel on mesoventrite and metaventrite of the fossil shows clearly that it belongs to the subtribe Hydrophilina of the family Hydrophilidae (Hansen 1991, Komarek 2003). Within the subtribe, only genera *Hydrochara* Berthold 1827 and *Hydrobiomorpha* Blackburn 1888 share the combination of narrow lamellar keel of prosternum and medium body size (Hansen 1991, Komarek 2003) – recent species of remaining Hydrophilina genera are either longer than 30 mm (*Hydrophilus* Geoffroy 1762) or shorter than 15 mm (*Sternolophus* Solier 1834, *Tropisternus* Solier 1834). Distinguishing of genera *Hydrochara* and *Hydrobiomorpha* is possible on the basis of the shape of the first club antennomere and the shape of anterior margin of clypeus. The difference in clypeal shape is not as strong as mentioned by Hansen (1991) (i.e. anterior margin of clypeus emarginate and articulation membrane exposed in *Hydrobiomorpha* whereas anterior margin of clypeus truncate, without exposed articulation membrane in *Hydrochara*) because a shallow emargination is present also in some

Hydrochara species. Nevertheless, the shape of clypeus of the described fossil seems to correspond to that present in most recent *Hydrobiomorpha*. Therefore, we ascribe the presented material to the latter genus. The size of the fossil seems to support this identification as recent *Hydrochara* are not longer than 20 mm according to Hansen (1991).

In the original description of *Hydrobiomorpha enspelense*, Wedmann (2000) mentioned two characters supporting the generic identification: (1) the shape of antennomere 9, and (2) deep anterior emargination of clypeus. The combination of these two characters is, however, not sufficient for reliable generic identification. Differential character (1) was misinterpreted by the Wedmann (2000), because the shape of antennomere 7 rather than antennomere 9 is crucial for recognition of the genera, whereas antennomere 9 does not show any considerable difference in the shape (see Figs. 8-11 in Komarek 2003). Character (2) is present in genera *Hydrobiomorpha* and *Hydrophilus* (Figs 12 and 14) and cannot be therefore used to separate these genera. In spite of this, the generic identification of the type series of *H. enspelense* seems to be correct based on the combination of the following characters preserved in the type specimens: medium body size (in contrast to recent *Hydrophilus*, *Sternolophus* and *Tropisternus*) and anterior margin of clypeus deeply emarginate (in contrast to *Hydrochara*, *Tropisternus*, and most *Sternolophus*).

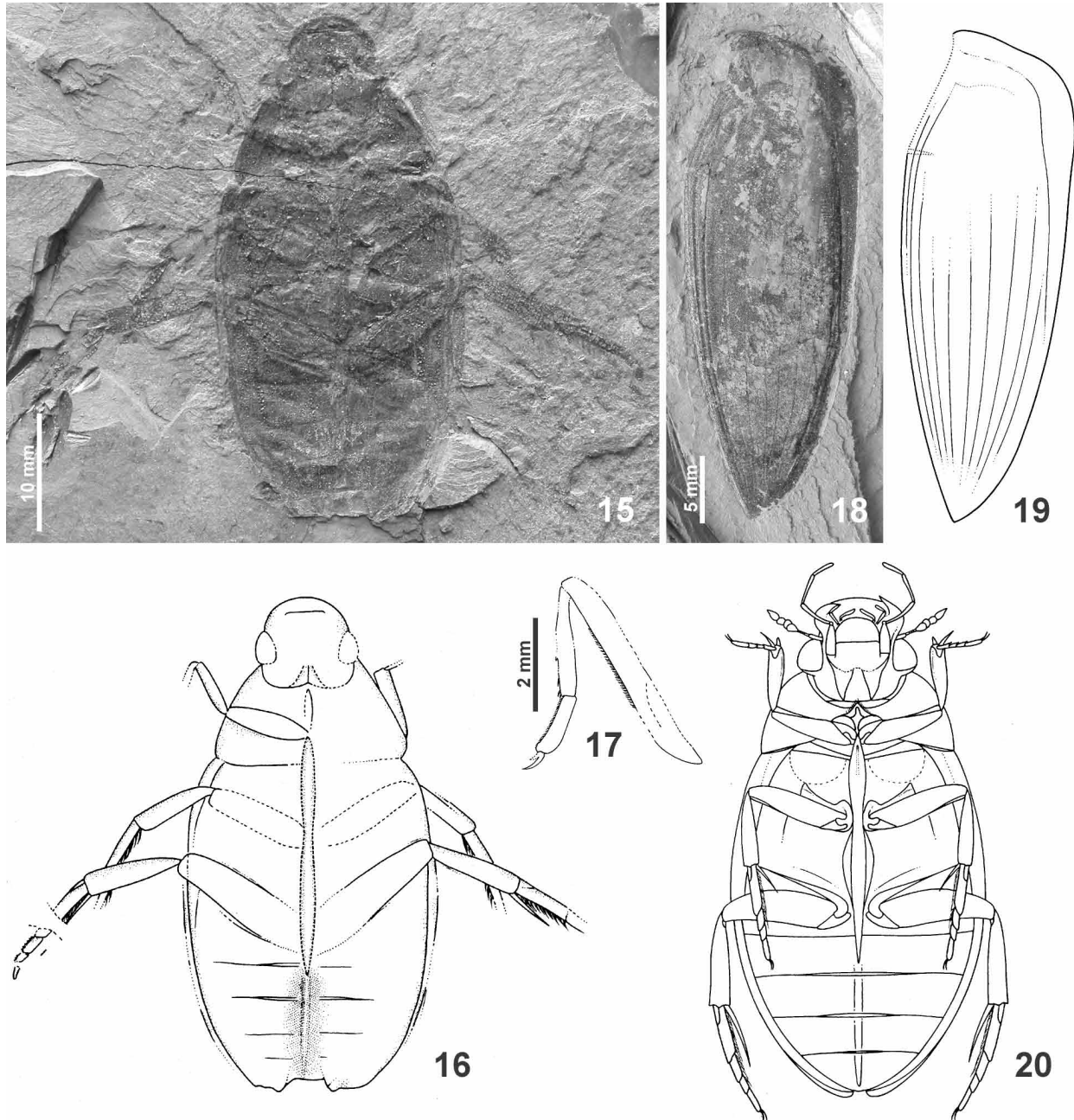
Based on the association of our material with the type series of *Hydrobiomorpha enspelense*, characters from both ventral and dorsal body-side can be combined. This allows us to confirm the generic identification of *H. enspelense*.

Comparison with recent species of *Hydrobiomorpha*. The taxonomy of the recent species of *Hydrobiomorpha* is based especially on the shape of prosternal carina, length of metathoracic postcoxal spine, pubescence of abdominal ventrites, punctuation of lateral parts of elytra, morphology of male genitalia and general body shape (Bachmann 1988, Hebauer 2006, Mouchamps 1959, Short 2004, Watts 1990). It is not possible to evaluate all these characters except of body shape in the fossil material and it is thus impossible to establish the relation of fossil *Hydrobiomorpha* to the recent species. Therefore, only the age of the fossils of *H. enspelense* as well as its distribution justifies its separate specific status. It seems, however, that *H. enspelense* is considerably larger than the recent Oriental and Australian *Hydrobiomorpha* species, corresponding in size with some Afrotropical (e.g. *H. deplanata* (Orchymont 1911) and *H. celata* Mouchamps 1959) as well as with many Neotropical

species (Bachmann 1988, Mouchamps 1959, Watts 1990).

Distribution and biology of recent *Hydrobiomorpha*. The recent genus *Hydrobiomorpha* has a circumtropical distribution, with most species occurring in Afrotropical and Neotropical regions

(Hansen 1999). Their distribution in the Old World is shown in Fig. 21. Adults and larvae live in permanent, shallow, well-vegetated water bodies. Larvae are predaceous, preying on various aquatic invertebrates (Archangelsky *et al.* 2004).



Figures 15–20

Hydrophilus (Hydrophilidae). 15–19, *H. cf. pistaceus* Laporte de Castelnau, fossil; 20, *H. pistaceus* Laporte de Castelnau, recent species. 15–16, specimen ZD9708a; 17, specimen ZD9708b; 18–19, specimen ZD9709; 20, specimen ZD9709.

***Hydrophilus* cf. *pistaceus* Laporte de Castelnau
1840 (Figs. 15–19)**

Material. Specimen ZD9708a: whole beetle in ventral view (imprint), head without preserved maxillary palpi, antennae only with left antennomere 9 partly preserved, apex of elytra not preserved; specimen ZD9708b: fragment of head and prothorax with completely preserved left leg and incompletely preserved right tibia and tarsus (counter-imprint); specimen ZD9709: left elytra (imprint) in ventral view, inner edge with a rupture in basal fourth. All compressed fossils preserved in fine grained claystone.

Occurrence. Early Miocene (Burdigalian), zone MN 3a of mammal fauna, Most Formation, Clayey Superseam Horizon (Kvaček *et al.* 2004); Břilina mine near Břilina (Czech Republic).

Description. Specimen ZD9708: Body measurements summarized in Tab. 2. Head slightly wider than long, eyes protruding laterad. Clypeus slightly emarginate at anterior margin. Labrum well-sclerotized, 5 mm wide. Submentum narrowing anteriorly. Pronotum narrowing anteriorly, lateral margins regularly rounded; anterolateral angle triangularly rounded, posterolateral angle rounded. Median part of

prosternum elevated, precise shape of elevation not preserved. Anterior leg with femur 7.5 mm long, 2.0 mm wide in widest part in basal third; tibia 5.5 mm long, 1.0 mm wide subapically; protarsus 4.5 mm long, without enlarged tarsomeres, tarsomeres 1-4 not distinguishable, forming basal 3.0 mm of tarsus; tarsomere 5 ca. 1.3 mm long, with numerous short and stout spines ventrally; claw 0.7 mm long, acute, evenly curved, with large thin basal tooth reaching ca. 0.5 of total claw length. Mesoventrite 18 mm wide anteriorly, bearing moderately broad median carina. Median part of metaventrite with elevated carina fused with mesothoracic carina to common sternal keel continuing into short and broad spine posteriorly; spine reaching anterior 0.33 of abdominal ventrite II. Elytron with epipleura 1.3 mm wide in humeral part, reaching level of insertion of hind legs. Middle legs with femora 9.0 mm long, 3.0 mm wide basally; tibia 7.0 mm long, 1.5 mm wide subapically, femoral spines not preserved. Both mesotarsi with ca. 1.5 mm long natatorial setae, tarsomeres not distinguishable. Claws not visible. Hind legs with femora 12.0 mm long, 3.5 mm wide in basal third; tibia 8.5 mm long, 2.0 mm wide apically; lateral spine of metatibia more than 4.0 mm long, apex not preserved; ventral spine not visible. Metatarsus ca. 10 mm long; tarsomeres 1 and 3-5 ca., 1.5 mm long, tarsomere 2 ca. 5.5 mm long; tarsomere 2 with distinct 1.2 mm long natatorial setae ventrally,

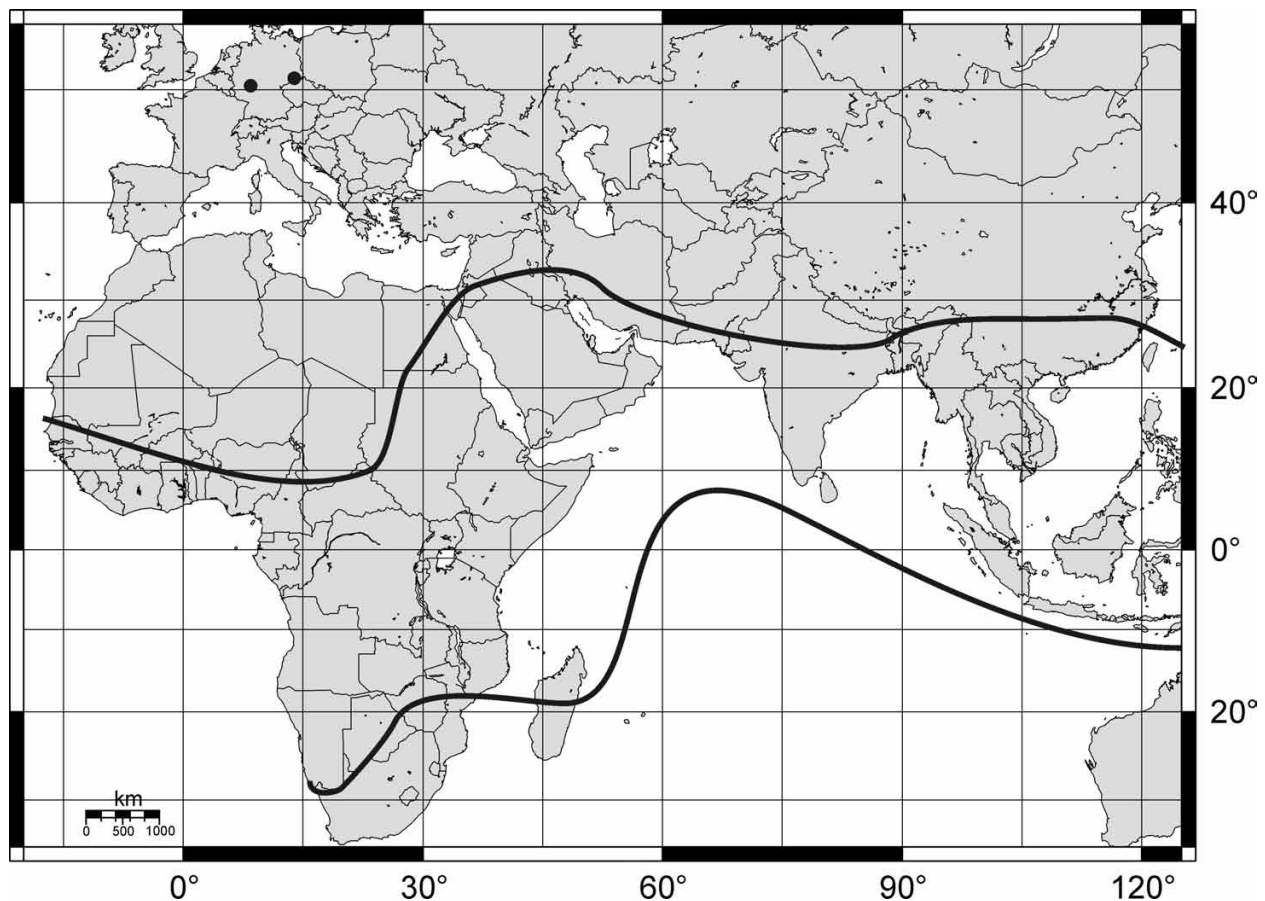


Figure 21
Distribution of recent *Hydrobiomorpha* (solid line) in comparison to the localities of fossil *H. enspelese* Wedmann (black dots).

tarsomeres 3 and 4 with distinct small spines dorsally; claws not preserved. Abdominal ventrites II-V preserved, ventrite V slightly damaged posteriorly. Length of ventrites II-IV: 3.5 - 2.6 - 3.0 mm. Median part of all ventrites with distinct elevated carina. Total length of abdomen (from insertion of hind legs to the notional apex of ventrite V) ca. 14.0 mm.

Specimen ZD9709: Measurements summarized in Tab. 2. General shape elongate; slightly narrowing from basal third to apex, slightly more abruptly narrowing in apical 0.15. Epipleuron 2.0 mm wide in humeral area, reaching ca. apical third of elytron. Superficial structure with 9 shallow furrows in apical 0.6; furrows situated close to sutural margin continuing more basad than remaining furrows. Apical part of elytron without trace of acute spine on apex or lateral spine on subapical part of lateral elytral margin.

Note. The isolate elytron (fossil ZD9709) was associated with whole beetle (fossil 9708) on the basis of similar size (the difference of the size of elytra and the whole beetles corresponds with the size variability observed in recent *Hydrophilus pistaceus* – see Tab. 2) The close attribution of both fossils is supported by indirect evidence of presence in the same fossiliferous layer.

Generic attribution. Genus *Hydrophilus* is characterized by these characters present in our material (partly according to Hansen 1991, Komarek 2003): mesoventrite elevated medially into a high keel and fused with median elevation of metaventrite, forming a common keel; metaventrite terminated with a spine going towards to abdomen; middle and hind tarsi with fringe of natatorial setae (all characters distinguish the subtribe Hydrophilina within the tribe Hydrophilini); sternal spine relatively long, reaching second abdominal ventrite (character shared by *Hydrophilus*, *Tropisternus*, and some *Sternolophus* within the Hydrophilina), superficial structure of elytra with striae distinct apically; size of the specimen overlaps 30 mm (distinguishing *Hydrophilus* within the Hydrophilina). See Fig. 20 for ventral view of recent *Hydrophilus*.

Comparison with recent species of *Hydrophilus*. In *Hydrophilus* there are three recent subgenera according to Hansen (1999), of which the subgenera *Temnopterus* Solier 1834 and *Dibolocelus* Bedel 1891 do not correspond with our material in the length of metathoracic spine and presence of spines on posterior part of elytra. Our species therefore belongs to the nominate subgenus *Hydrophilus*, which contains a few species groups characterized by external morphology according to Bedel (1891), Kuwert (1893) and Régimbart (1901). Based on external morphology we can eliminate both the “Asian group” of species (with very long metathoracic spine reaching beyond the posterior margin of ventrite II) and the “American group” of species (characterized by less distinct elytral striae, non-tectiform abdominal ventrites, and/or

presence of apical spine on elytron). Most species of the “Australian group” characterized by pattern of pubescence of ventrite I (not preserved in our material) cannot be excluded based on the preserved characters (Watts 1988), their presence in Europe during the Miocene is, however, lowly probable. That is why we considered that our material belongs to the “Palearctic group” of species.

Among recent Palearctic species only *H. pistaceus* bears the combination of abdominal ventrites tectiform medially and apex of elytron without sutural spine. This species corresponds with our fossil material also in general shape and size (see Tab. 2). *H. pistaceus* is distributed in western Mediterranean at present time (Italy, France, Spain, Portugal, Morocco, Algeria, Tunisia – Régimbart 1901 and Hansen 1999). In difference with the recent *H. pistaceus*, in which the sternal spine usually reaches or slightly overlaps half of the length of abdominal ventrite II, it reaches anterior third of this ventrite in the fossil material. However, as in recent material the length and shape of sternal spine is very variable within the species, this difference can be explained by the variability. The morphology of the anterior tarsus corresponds completely with female anterior tarsus of recent *H. pistaceus*.

The detailed taxonomy of recent *Hydrophilus* species is based mainly on secondary sexual characters of males, i.e. the shape of anterior claw and tarsus, and (in some species) the shape of maxillary palpi. As our fossil material is represented by a female specimen, none of these characters are present. For this reason, as well as for the absence of any other relevant characters distinguishing the fossil species from *H. pistaceus*, we leave the fossil material as an undescribed species closely similar to the latter recent species in its morphology.

Comparison with fossil *Hydrophilus*. Comparison with fossil species of the genus *Hydrophilus* is impossible for the time being. This is caused by the following reasons: (1) generic identification of most fossil species requires confirmation because old authors often did not pay appropriate attention to the reliable differential characters, (2) generic names *Hydrous* L. 1775, *Hydrophilus* and *Hydrochara* were used inconsistently in the old papers for the genera *Hydrophilus* and *Hydrochara* and the real generic attribution cannot be therefore derived from original descriptions; (3) many species are described only on the basis of an isolated elytron lacking reliable specific characters. The comparison of our material with at least some fossil taxa would be therefore possible only after solving the problems mentioned under (1) and (2).

Biology of recent *Hydrophilus*. The representatives of recent *Hydrophilus* inhabit the littoral zone of larger,

shallow, well-vegetated water bodies (Hebauer & Klausnitzer 1998). Larvae are predaceous, preying on various planorbiid and limnaeid snails (Archangelsky 1997; Fikáček, unpubl. data).

Conclusions

The locality of Bílina mine is well known by wealthy fossil record of Neogene's terrestrial and aquatic flora and fauna (see e.g., Kvaček & Sakala 1999, Prokop 2003, Sakala 2000). Various stages of ecosystem development and specific types of environment correlated with plant and animal assemblages have been previously recognized and evaluated (Kvaček *et al.* 2004). The current living conditions of extant relatives of both beetle taxa (Dytiscidae: *Cybister* sp., Hydrophilidae: *Hydrophilus* sp.) well fit to the environmental reconstructions of both fossiliferous horizons interpreted as shallow pond or oxbow lake with calm water in Delta Sandy Horizon and oligotrophic environment with developing connected mire in Clayey Superseam Horizon. The fossilized shells of the planorbiid genus *Planorbarius* or *Helisoma* were found at the Bílina Mine together with the above presented fossil of *Hydrophilus* cf. *pistaceus* (Z. Dvořák, pers. comm.). This confirms that the locality was not visited only temporarily by the adults, but can serve also for the reproduction of the beetles as the larvae of recent species prey on planorbiid or lymnaeid snails.

The locality of Seifhennersorf is characterized as a diatom lake with rich aquatic vegetation of submerged plants (*Potamogeton*, charophytes) and plants with floating leaves (? *Brasenia*) in littoral zone, surrounded with mixed broad-leaved deciduous forest and the climate corresponding to recent central China (Walther 1977, Z. Kvaček pers. comm.). This habitat corresponds with the habitat preferences of recent *Hydrobiomorpha* species. However, the occurrence of *Hydrobiomorpha* in the Oligocene of Central Europe is quite surprising as the distribution of the genus is recently confined to the tropical areas (ca. from 30° of northern latitude to 25° of southern latitude in both Old and New Worlds, Hansen 1999). In Oligocene, the distribution of the genus had to be much wider, reaching subtropical and temperate areas. Similar case of occurrence of subtropical/intertropical elements in temperate/subtropical Central Europe are known for termites (Hodotermitidae, *Ulmeriella* Meunier 1920) in the Miocene (Prokop & Nel 1999). Further examples of markedly different distribution during the Cenozoic can be also found in the following groups, among others: Odonata: Megapodagrionidae, Isoptera: Mastotermitidae (*Mastotermes* Froggatt 1896), and Diptera: Bibionidae (*Plecia* Wiedmann 1822) (Nel *et al.* 1996, 1997; Nel & Paicheler 1993; Wedmann 2000).

Acknowledgements. The authors are grateful to Zdeněk Dvořák (Doly Bílina) for the loan of the material from Doly Bílina collection. Our express thanks go to Zuzana Čadová (scientific illustrator) for the magnificent line drawings of the specimens. We are indebted to André Nel (Muséum national d'Histoire naturelle, Paris) for valuable comments on the manuscript. The preparation of this study was partly supported by a grant of the Charles University Grant Agency (GAUK) 203/2005/B-Bio/PrF, grants of the Grant Agency of the Czech Republic (205/03/D151 and 205/04/0099), a grant of the Ministry of Education of the Czech Republic (MŠMT ČR) 0021620828 and a grant of the Ministry of Culture of the Czech Republic (MK ČR) 00002327201.

References

- Archangelsky M.** 1997. Studies on the biology, ecology & systematics of the immature stages of New World Hydrophiloidea (Coleoptera: Staphyliniformia). *Bulletin of the Ohio Biological Survey, New Series* **12**: 1-207.
- Archangelsky M., Torres P.L. M., Michat M.C.** 2004. Immature stages of *Hydrobiomorpha spinosa* (Orchymont, 1928) (Coleoptera: Hydrophilidae). *Aquatic Insects* **26**: 253-264.
- Arnol'di L.V., Zherikhin V.V., Nikritin L.M., Ponomarenko A.G.** 1992. *Mesozoic Coleoptera*. Smithsonian Institution Libraries & The National Science Foundation, Washington D. C., 285 p.
- Bachmann A.O.** 1988. Las especies Americanas de *Hydrobiomorpha* (Coleoptera, Hydrophilidae). *Opera Lilloana* **36**: 5-62.
- Bedel L.** 1891. Synopsis des grands Hydrophiles (Genre *Stethoxus* Solier). *Revue d'Entomologie* **10**: 306-323.
- Beutel R.G.** 1995. The Adephaga (Coleoptera): phylogeny and evolutionary history, p. 173-217 in: **Pakaluk J., Ślipiński S.A. (Eds.)**. *Biology, phylogeny, and classification of beetles. Papers celebrating the 80th birthday of Roy A. Crowson. Volume one*. Muzeum i Instytut Zoologii PAN, Warszawa, XII + 558 p.
- Blunck H.** 1922. Zur Biologie des Tauchkäfers *Cybister lateralmarginalis* Deg. nebst Bemerkungen über *C. japonicus* Sharp, *C. tripunctatus* Oliv. und *C. brevis* Aubé. *Zoologischer Anzeiger* **55**: 45-66, 93-124.
- Brinck P.** 1945. Nomenklatorische und systematische studien über Dytisciden. III. Die Klassifikation der Cybisterinen. *Kungliga Fysografiska Sällskapets Handlingar* **56**: 1-20.
- Carpenter F.M.** 1992. *Treatise on Invertebrate Paleontology. Part R. Arthropoda 4. Volume 3: Superclass Hexapoda*. The Geological Society of America, Boulder & The University of Kansas, Lawrence, 655 p.
- Deichmüller J.V.** 1886. Die Insecten aus dem lithographischen Schiefer im Dresdener Museum. *Mitteilungen aus dem Koeniglichen Mineralogisch-Geologischen und Praehistorischen Museum in Dresden* **7**: 1-84.
- Franciscolo M.E.** 1979. Coleoptera, Halipidae, Hygrobiidae, Gyrinidae, Dytiscidae. *Fauna d'Italia* **14**: 1-804.
- Guignot F.** 1931-1933. *Les Hydrocanthares de France*. Les Frères Douladoure, Toulouse, 1057 p.
- Guignot F.** 1961. Revision des hydrocanthares d'Afrique (Coleoptera Dytiscoidea). 3. *Annales du Musée Royal du Congo Belge, Série 8vo (Sciences Zoologiques)* **90**: 659-995.
- Hansen M.** 1991. The hydrophiloid beetles. Phylogeny, classification and a revision of the genera (Coleoptera: Hydrophiloidea). *Biologiske Skrifter* **40**: 1-368.
- Hansen M.** 1999. Hydrophiloidea (s.str.) (Coleoptera). *World Catalogue of Insects* **2**: 1-416.
- Heer O.** 1847. Die Insektenfauna der tertiärgebilde von Oeningen und von Radoboj in Croatien. Erste Abtheilung: Käfer. *Neue Denkschriften der Allgemeinen Schweizerischen gesellschaft für die Gesammten Naturwissenschaften* **8**(5): 1-230 + 8 Pls.

- Heer O. 1862.** Beiträge zur Insektenfauna Oeningens. Coleoptera. Geodephagen, Hydrocanthariden, Gyriniden, Brachyelytren, Clavicornen, Lamellicornen und Buprestiden. *Natuurkundige Verhandelingen van der Hollandsche Maatschappij der Wetenschappen te Haarlem* **16**: 1-90 + 7 Pls.
- Heer O. 1878.** Ueber einige Insektenreste aus der raetischen Formation Schonens. *Geologiska Foerningens i Stockholm Foerhandlingar* **4**: 192-197 + Pl. 13.
- Hebauer F. 2006.** Aktualisierte Bestimmungstabelle für die afrikanischen Arten der Gattung *Hydrobiomorpha* Blackburn, 1888 (Coleoptera: Hydrophilidae). *Acta Coleopterologica* **22**: 31-37.
- Hebauer F., Klausnitzer B. 1998.** Süswasserfauna von Mitteleuropa 20/7, 8, 9, 10-I. *Insecta: Coleoptera: Hydrophiloidea (exkl. Helophorus)*. Spektrum Akademischer Verlag, Stuttgart, 134 p.
- Heyden C. v., Heyden L. v. 1866.** Käfer und Polypen aus der Braunkohle des Siebengebirges. *Palaeontographica* **15** (1865-68): 131-156 + Pls xxii-xxiv.
- Jungfeng Z. 1989.** *Fossil insects from Shawang, Shandong, China*. Shandong Science and Technology Publishing House, Jinan, 459 p.
- Jungfeng Z., Bo S., Xiyu Z. 1994.** *Miocene insects and spiders from Shanwang, Shandong*. Science Press, Beijing, 298 p.
- Klausnitzer B. 2003.** Käferlarven (Insecta: Coleoptera) in Baltischem Bernstein - Möglichkeiten und Grenzen der Bestimmung. *Entomologische Abhandlungen* **61**: 103-108.
- Komarek A. 2003.** Hydrophilidae: I. Check list and key to Palearctic and Oriental genera of aquatic Hydrophilidae, p. 383-395 in: **Jäch M. A., Ji L. (Eds.)**. *Water Beetles of China. Vol. III*. Zoologisch-Botanische Gesellschaft and Wiener Coleopterologenverein, Wien, VI + 572 p.
- Kuwert A. 1893.** Die grossen Hydrophiliden des Erdballs des Genus *Hydrous* Leach. *Deutsche entomologische Zeitschrift* (1893): 81-93.
- Kvaček Z., Sakala J. 1999.** Twig with attached leaves, fruits and seeds of *Decodon* (Lythraceae) from the Lower Miocene of northern Bohemia, and implications for the identification of detached leaves and seeds. *Review of Palaeobotany and Palynology* **107**: 201-222.
- Kvaček Z., Walther H. 2003.** Reconstruction of vegetation and landscape development during volcanic activity in the České Středohoří Mountains. *Geolines* **15**: 60-64.
- Kvaček Z., Böhme M., Dvořák Z., Konzalová M., Mach K., Prokop J., Rajchl M. 2004.** Early Miocene freshwater and swamp ecosystems of the Most Basin (northern Bohemia) with particular reference to the Bílina mine section [Spodnomiocenní sladkovodní a bažinné ekosystémy mostecké pánve (severní Čechy) se zvláštním zřetelem k profilu dolu Bílina]. *Journal of the Czech Geological Society* **49**: 1-40.
- Larson D.J. 1975.** The predaceous water beetles (Col. Dyt.) of Alberta: systematics, natural history and distribution. *Questiones Entomologicae* **11**: 245-498.
- Miller K. B., Balke M. 2003.** The unusual occurrence of aquatic Beetles in Amber, *Copelatus aphrodisiae* Balke, sp.n. and *C. predaveterus* Miller, sp.n., (Coleoptera: Dytiscidae: Copelatinae). *Proceeding of the Entomological Society of Washington* **105**: 809-815.
- Miller K. B., Bergsten J., Whiting M. F. 2007.** Phylogeny and classification of diving beetles in the tribe Cybistrini (Coleoptera, Dytiscidae, Dytiscinae). *Zoologica Scripta* **36**: 41-59.
- Mouchamps R. 1959.** Remarques concernant les genres *Hydrobiomorpha* Blackburn et *Neohydrophilus* Orchymont. *Bulletin et Annales de la Société Royale belge d'Entomologie* **95**: 295-335.
- Nel A., Arillo A., Martinez-Declos X. 1996.** New fossil Odonata from the Upper Miocene of France and Spain (Anisoptera and Zygoptera). *Neue Jahrbuch für Paläontologie, Abhandlungen* **199**(2): 167-219.
- Nel A., Martinez-Declos X., Papier F., Oudard J. 1997.** New Tertiary Fossil Odonata from France (Sieblosidae, Lestidae, Coenoagrionidae, Megapodagrionidae, Libellulidae). *Deutsche Entomologische Zeitschrift* **44**(2): 231-258.
- Nel A., Paicheler J. C. 1993.** Les Isoptera fossiles (Insecta, Dyctioptera). *Annales de Paléontologie* **1993**: 103-179.
- Nilsson A. N. 2001.** Dytiscidae (Coleoptera). *World Catalogue of Insects* **3**: 1-395.
- Nilsson A. N. 2003.** Family Dytiscidae, p. 35-78 in: **Löbl I., Smetana A. (Eds.)**. *Catalogue of Palearctic Coleoptera, 1. Archostemata – Myxophaga – Adepaga*. Apollo Books, Sternstrup, 819 p.
- Olivier A. G. 1795.** *Entomologie, ou histoire naturelle des insectes. Vol. 3. Coléoptères*. Lanneau, Paris, 557 p.
- Oustalet M. E. 1874.** Recherches sur les insectes fossiles des terrains tertiaires de la France. Deuxième partie. Insectes fossiles de l'Aix de Provence. *Annales des Sciences géologiques* **5**: 1-374 + Pls 1-6.
- Pederzani F. 1995.** Keys to the identification of the genera and subgenera of adult Dytiscidae (sensu lato) of the world (Coleoptera Dytiscidae). *Atti dell'Accademia Roveretana degli Agiati, Contributi della Classe di Scienze Matematiche, Fisiche e Naturali* (VII) **4B** (1994): 5-83.
- Ponomarenko A. G. 1995.** The geological history of beetles, p. 155-171 in: **Pakaluk J., Ślipiński S. A. (Eds.)**. *Biology, phylogeny, and classification of beetles. Papers celebrating the 80th birthday of Roy A. Crowson. Volume one*. Muzeum i Instytut Zoologii PAN, Warszawa, XII + 1-558.
- Prokop J. 2003.** Remarks on palaeoenvironmental changes based on reviewed Tertiary insect association from the Krušné hory piedmont basins and the České středohoří Mts in northwestern Bohemia (Czech Republic). *Acta Zoologica Cracoviensia* **46** (suppl.-Fossil Insects): 329-344.
- Prokop J., Fikáček M. 2007.** Early Oligocene insect fauna from Seiffenhensdorf (Saxony, Germany). *Acta Musei Nationalis Pragae, Series B, Historia Naturalis* **63**(2-4): 209-217.
- Prokop J., Nel A. 1999.** Tertiary termite from the Bílina mine locality in northern Bohemia (Isoptera: Hodotermitidae). *Klapalekiana* **35**: 141-144.
- Prokop J., Nel A., Hájek J., Bubík M. 2004.** First record of a fossil beetle (Coleoptera, Haliplidae) from the base of Paleocene flysch sediments in the Magura Unit (Outer Western Carpathians, Moravia). *Geologica Carpathica* **55**: 469-473.
- Régimbart M. 1901.** Revision de grands Hydrophiles. *Annales de la Société entomologique de France* **70**: 188-232+2 Pls.
- Říha P. 1974.** Neue fossile Schwimmkäfer aus dem Tertiär Europas und Westsibiriens (Coleoptera, Dytiscidae). *Acta Entomologica Bohemoslovaca* **71**: 398-413 + Pls I-VII.
- Říha P. 1979.** Bibliografie der tertiären Haliplidae, Hygrobiidae, Dytiscidae (inklusive Paleogyrinidae) und Gyrinidae der Welt. *Beiträge zur Entomologie, Berlin* **29**: 267-270.
- Sakala J. 2000.** Flora and vegetation of the roof of the main lignite seam in the Bílina Mine (Most Basin, Lower Miocene). *Acta Musei Nationalis Pragae, Series B - Historia Naturalis* **56**: 49-84.
- Sakala J. 2002.** First record of fossil angiosperm wood (Ulmoxylon, Ulmaceae) from the famous locality of Bílina (Czech Republic, Early Miocene). *Comptes Rendus Palevol* **1**: 161-166.
- Scudder S. H. 1878.** The fossil insects of the Green River shales. *Bulletin of the United States Geological Survey of the Territories* **2**: 77-87.
- Scudder S. H. 1900.** Adepagous and clavicorn Coleoptera from the Tertiary deposits at Florissant, Colorado with description of a few other forms and a systematic list of the non-rhynchophorous tertiary Coleoptera of North America. *United States Geological Survey, Washington* (1900): 1-148.
- Short A. E. Z. 2004.** Review of the Central American species of *Hydrobiomorpha* Blackburn (Coleoptera: Hydrophilidae). *Koleopterologische Rundschau* **74**: 363-366.
- Smith D., Cook A., Nufio C. R. 2006.** How physical characteristics of beetles affect their fossil preservation. *Palaios* **21**: 305-310.

- Statz G. 1939.** Geradflüger und Wasserkäfer der oligocänen Ablagerungen von Rott. *Decheniana* **99A**: 1-102.
- Walther H. 1977.** Versuch der Rekonstruktion einer tertiären Lokalflora an Beispiel von Seiffhennersdorf. *Abhandlungen und Berichte des Naturkundemuseums Görlitz* **51**: 23-35.
- Watts C.H.S. 1988.** Revision of Australasian *Hydrophilus* Muller, 1764 (Coleoptera: Hydrophilidae). *Records of the South Australian Museum* **22**: 117-130.
- Watts C.H.S. 1990.** Revision of Australian *Hydrobiomorpha* Blackburn (Coleoptera: Hydrophilidae). *Records of the South Australian Museum* **24**: 35-42.
- Wedmann S. 2000.** Die Insekten der oberoligozänen Fossilagerstätte Enspel (Westerwald, Deutschland). Systematik, Biostratonomie und Paläoökologie. *Mainzer Naturwissenschaftliches Archiv* **23**: 1-154 + VI + 9 pls.
- Wickham H.F. 1909.** New fossil Coleoptera from Florissant. *American Journal of Science and Arts* (4) **28**: 126-130.
- Wickham H.F. 1911.** Fossil Coleoptera from Florissant with descriptions of several new species. *Bulletin of the American Museum of natural History* **30**: 53-69.
- Wickham H.F. 1912.** A report of some recent collections of fossil Coleoptera from the Miocene shales of Florissant. *Bulletin from the Laboratories of Natural History of the State University of Iowa* **6**(3): 1-38 + 8 pls.
- Wickham H.F. 1913.** Fossil Coleoptera from the Wilson Ranch near Florissant, Colorado. *Bulletin of the Laboratories of Natural History of the State University of Iowa* **6**(4): 3-29.
- Wickham H.F. 1914.** New Miocene Coleoptera from Florissant. *Bulletin of the Museum of Comparative Zoology Harvard* **58**: 423-494 + 16 pls.