

Notes on *Helophorus* (s.str.) *kozlovi* ZAITZEV, 1908, with description of two new species, re-evaluation of *Helophorus* s.str. FABRICIUS, 1775 and *Trichohelophorus* KUWERT, 1886, and revised keys to the subgenera of *Helophorus* and to the species of *Helophorus* s.str. (Coleoptera: Helophoridae)

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Abstract

The aedeagus of *Helophorus* (s.str.) *kozlovi* ZAITZEV, 1908 (Coleoptera: Helophoridae) is described and figured for the first time, based on a specimen from Qinghai (China). *Helophorus* (s.str.) *vereschaginae* sp.n. from Uzbekistan and *H.* (s.str.) *robustus* sp.n. from Kazakhstan are described. The latter resembles a large *H. oscillator* SHARP, 1915, which is here transferred from the subgenus *Trichohelophorus* KUWERT, 1886 to *Helophorus* s.str. FABRICIUS, 1775. The aedeagus of *H.* (s.str.) *dracomontanus* ANGUS, 1970 is described and illustrated for the first time. *Helophorus syriacus* KUWERT, 1885 is recorded from Kyrgyzstan for the first time. Revised keys to the subgenera of *Helophorus* and to the species of *Helophorus* s.str. are provided. The occurrence of *H.* (s.str.) *khnzoriani* ANGUS, 1970 as a Pleistocene fossil in Sweden and Greenland is briefly discussed.

Key words: Coleoptera, Helophoridae, *Helophorus*, *Trichohelophorus*, new species, China, Qinghai, Kazakhstan, Uzbekistan, subgenera, keys, karyotypes, Pleistocene fossil.

Introduction

Helophorus (s.str.) *kozlovi* ZAITZEV, 1908 remains one of the least well-known species of the genus. It was described from material of the Kozlov-Roborovsky expedition to the northern part of the Tibetan Plateau, with the type locality given as “Gory Amnen Kor” (Mount Amne Maqen, Qinghai Province, China). ANGUS (1970) gave a redescription of the species and designated a lectotype, noting that all type specimens (three specimens in Zaitzev’s collection and three in Semenov-Tian-Shansky’s collection) were all female as were a further four specimens from the same series, in Semenov’s collection, which Zaitzev had not seen and are thus not part of the type series.

Then, in 1986, Tatiana N. Vereschagina (St. Petersburg, Russia) gifted a male from Uzbekistan to R.B. Angus. This specimen closely resembles the type material of *H. kozlovi* and was erroneously identified as such by Angus, and a photograph of its aedeagus was published by ANGUS (1995: fig. 14).

Then, in the course of a visit to the Sun Yat-sen University Museum of Biology (Guangzhou, China) in 2013, Angus was shown a male *H. kozlovi* collected in the southern part of Qinghai Province (China). The aedeagus of this specimen is somewhat different from the Uzbek specimen (Figs. 15–16) but at the time Angus thought this might just be variation.

In the course of work on the description of two new species collected by S.V. Litovkin in Kazakhstan (ANGUS & LITOVKIN 2018), Litovkin mentioned that “*H. kozlovi*” was fairly common there. It transpired that this identification was based on the illustration of the aedeagus of a specimen from Uzbekistan (ANGUS 1995: fig. 14).

In fact, the specimens from Qinghai are to be regarded as the “true” *H. kozlovi*, while the specimens from Kazakhstan and Uzbekistan represent two new species, which are described below.

In addition, in the light of the material now available, one species of the subgenus *Trichohelephorus* KUWERT, 1886 is transferred to *Helophorus* s.str. FABRICIUS, 1775. Furthermore, revised keys to the subgenera of *Helophorus* and to the species of *Helophorus* s.str. are presented, and the occurrence of *H.* (s.str.) *khnzoriani* ANGUS, 1970 as a Pleistocene fossil in Sweden and Greenland is briefly discussed.

Material

The material studied is housed in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia (ZIN), the Natural History Museum, London, UK (BMNH), the Museum of Biology of Sun Yat-sen University, Guangzhou, China (SYSU) and the private collection of Stanislav V. Litovkin, Samara, Russia (PCL).

Helophorus (s.str.) *kozlovi* ZAITZEV, 1908

MATERIAL EXAMINED:

CHINA (Qinghai): Lectotype ♀, 5 paralectotypes, 4 additional specimens (BMNH, ZIN): Mount Amne Maqen; 1 ♂, 9 ♀♀ (SYSU): “Yushu, Qinghai, VI 1975”.

The general appearance of one of the non-type females from Semenov’s collection (now in the BMNH) is shown in Fig. 1, and the head and pronotum are shown in Fig. 5. The aedeagus of *H. kozlovi*, here illustrated for the first time (Fig. 15), differs from that of *H. vereschaginae* (Fig. 16) not only in being wider and with the outer margins of the parameres strongly curved, but also in its median lobe (tube and struts) being clearly longer. The difference in paramere shape is to some extent comparable with the variation in *H. aquaticus* (ANGUS 1982), but the difference in size of the median lobe is not, and demonstrates that *H. kozlovi* and *H. vereschaginae* can be regarded as different species. The aedeagus of *H. kozlovi* also appears to be genuinely wider than that of *H. vereschaginae*.

The occurrence of *H. kozlovi* is so far confirmed for Qinghai (China) only.

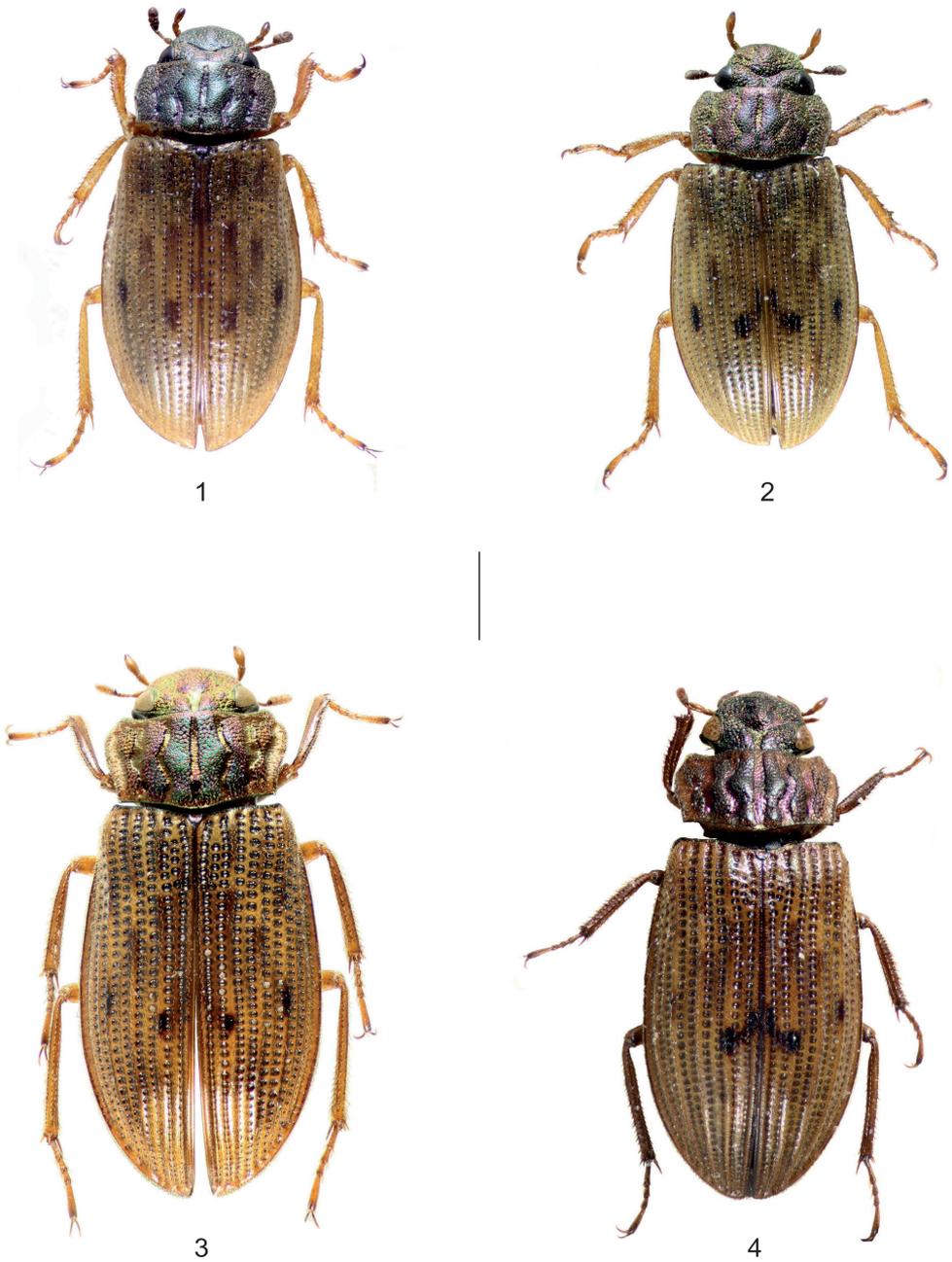
Helophorus (s.str.) *vereschaginae* sp.n.

TYPE MATERIAL: **Holotype** ♂ (BMNH): Uzbekistan, 2500 m a.s.l., West Tian Shan, Jurasaj River, 20.V.1986, T.N. Vereschagina leg.

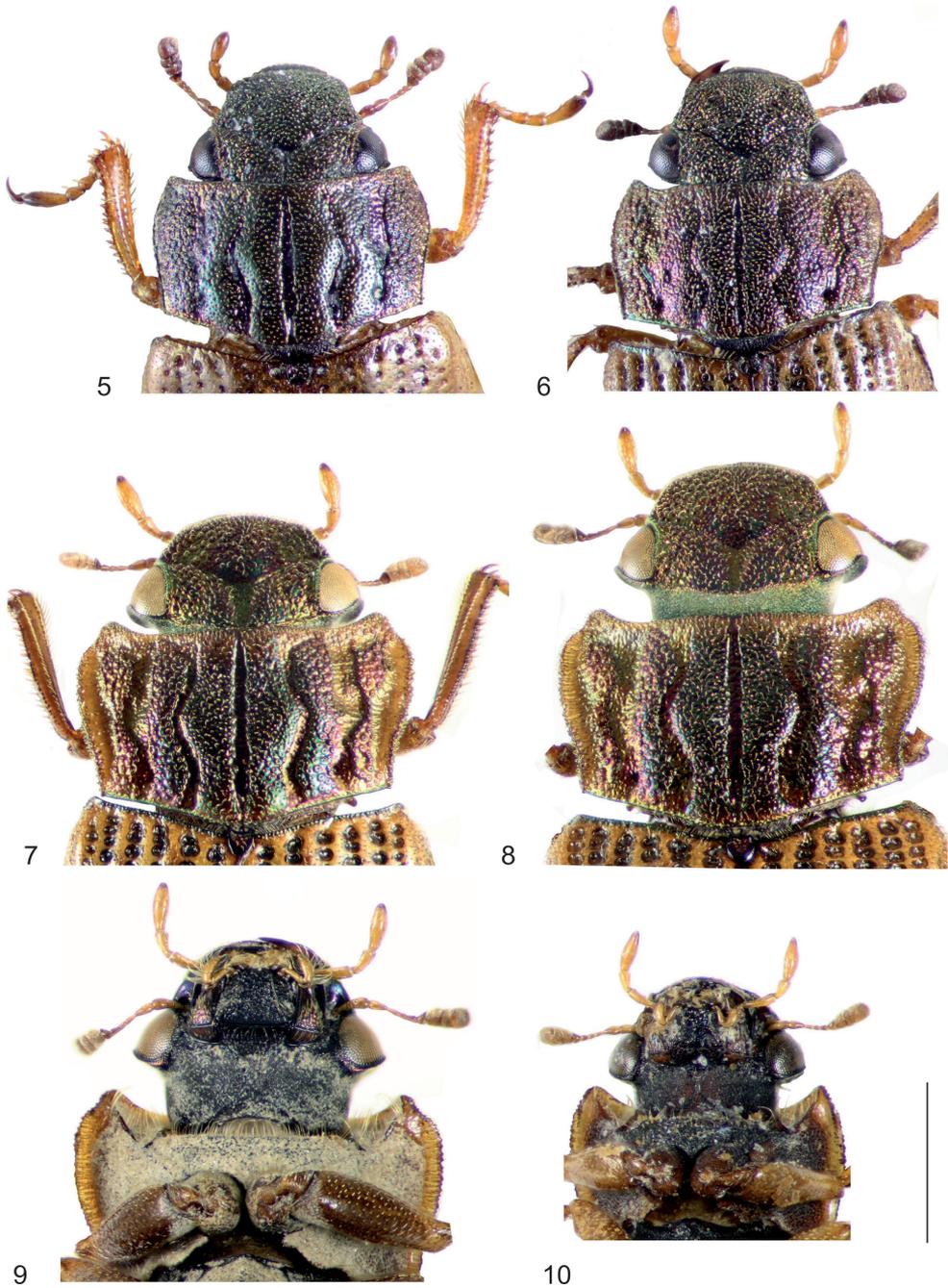
DESCRIPTION: Length: 4.5 mm, breadth: 2.5 mm. General appearance: Fig. 2. Head and pronotum: Fig. 6.

Head: Dark greenish bronze, surface with more or less flattened granulation. Stem of Y-groove parallel-sided, three times the width of its arms, floor shining with rugose punctures. Maxillary palpi pale brown, apical segment almost symmetrically oval, bluntly pointed, darkened at tip. Antennae 9-segmented, mid brown, clubs darker.

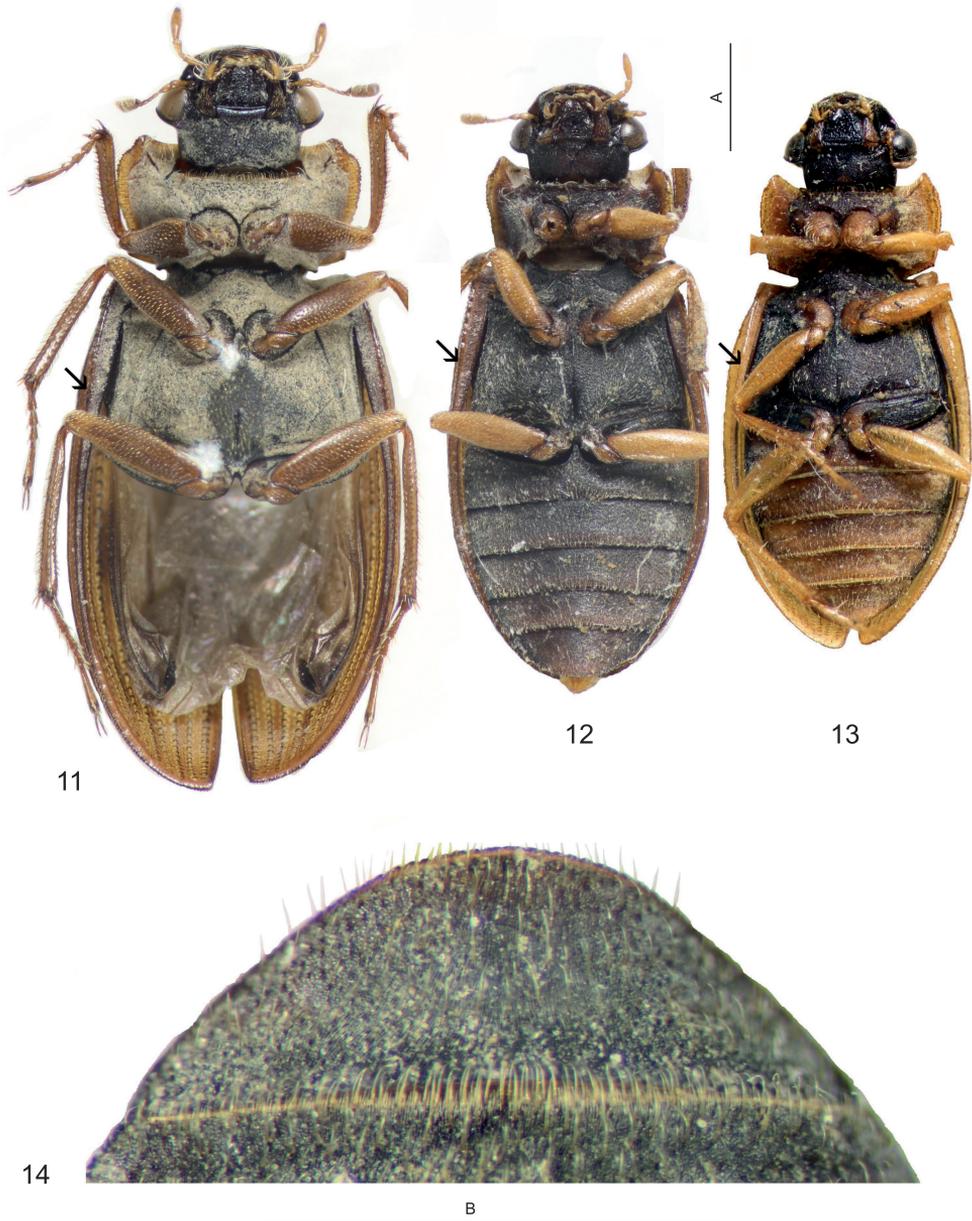
Pronotum: Moderately and evenly arched, widest at base of anterior third, sides slightly straightened posteriorly. Ground colour of intervals as head. Internal intervals punctate with impressed rings encircling some of the punctures. Middle intervals more distinctly granulate, externals coarsely so. Grooves narrow and shallow, their floors dull golden bronze with sparse ridges and punctures. Submarginal grooves wider than medians and submedians, marginals dull yellowish brown, obsolete over anterior sixth, continuous to base. Raised lateral margins narrow, crinkled.



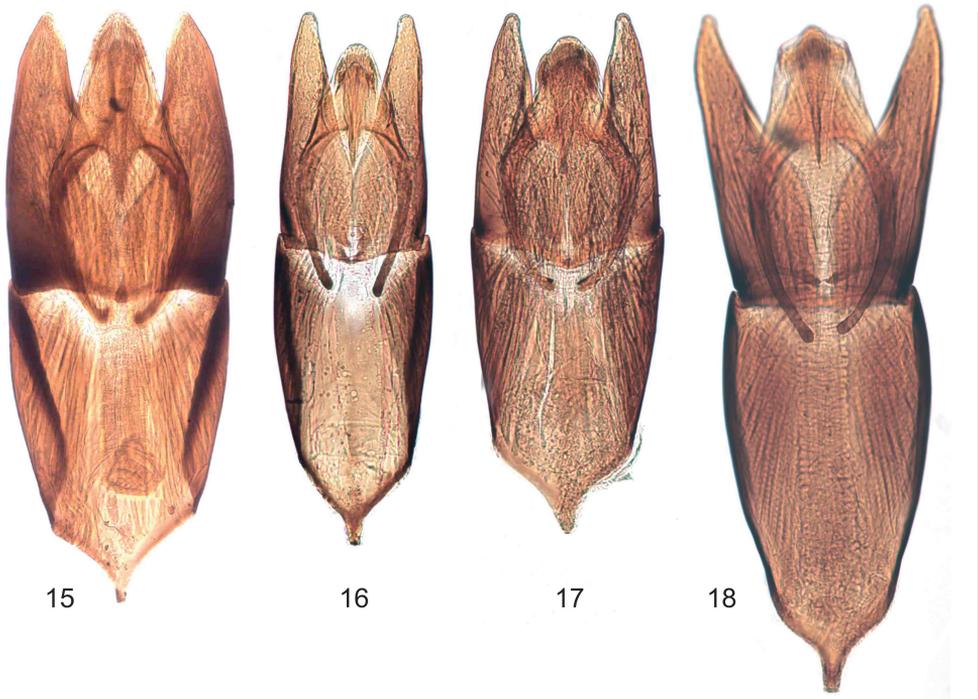
Figs. 1–4: Habitus, dorsal. 1) *Helophorus kozlovi*, China, Qinghai, Amne Maqen, female; 2) *H. vereshaginae* sp.n., holotype; 3) *H. robustus*, holotype; 4) *H. oscillator*, holotype. Scale = 1 mm.



Figs. 5–10: Heads and prothoraxes, 5–8 in dorsal view, 9–10 in ventral view. 5) *Helophorus kozlovi*, China, Qinghai, Amne Maqen; 6) *H. vereschaginae* sp.n., holotype; 7) *H. robustus*, holotype; 8–9) *H. robustus*, ♀ paratype with basal third of lateral pronotal margin more sinuate; 10) *H. oscillator*, Israel, Mt. Hermon. Scale = 1 mm.



Figs. 11–14: 11–13) Habitus, ventral, 14) abdominal apex, ventral. 11) *Helophorus robustus*, holotype; 12) *H. oscillator*, Israel, Mt. Hermon; 13) *H. alternans*, Spain; 14) *H. robustus*, holotype. Scale A = 1 mm for Figs. 11 – 13, scale B = 1 mm for Fig. 14.



Figs. 15–18: Aedeagi. 15) *Helophorus kozlovi*, China, Qinghai, Yushu; 16) *H. vereschaginae* sp.n., holotype; 17) *H. oscillator*, Israel, Golan Heights; 18) *H. robustus*, holotype. Scale = 1 mm.

Elytra: Dull mottled yellowish brown with darker and paler flecks and a prominent dark Λ -mark (inverted V-mark) in middle, extending laterally to interstice 3, and interstice 8 with elongate dark streaks opposite the Λ -mark. Flanks narrowly visible from below, outside the epipleura.

Legs: Dull yellow-brown, fairly short, tarsal claws long.

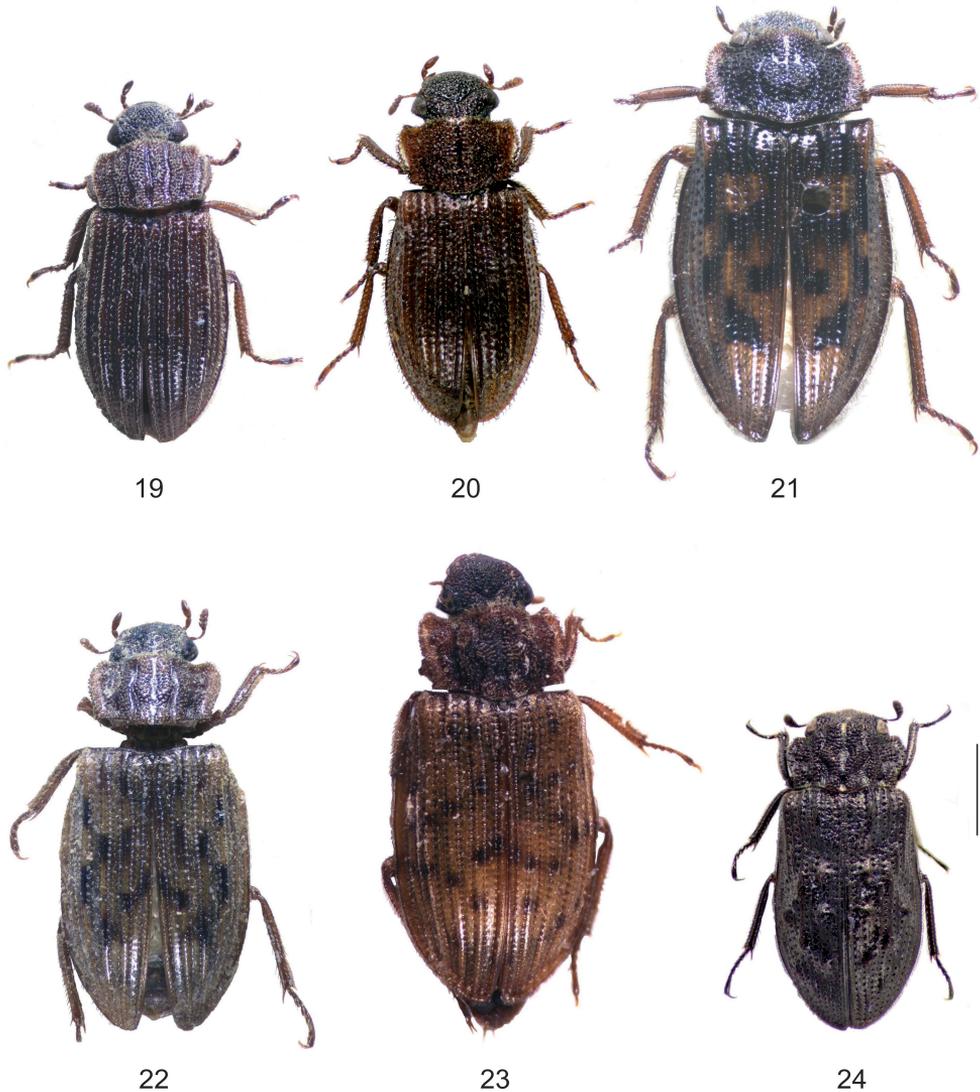
Abdomen: Black, covered in close pubescence, segment 7 with its apical margin slightly crinkled but without distinct square-ended teeth.

Aedeagus (Fig. 16; see also ANGUS 1995: fig. 14): About 0.8 mm long, parameres about three quarters the length of the basal piece, outer margins of parameres almost straight, weakly angled over apical fifths. Tube broadly triangular, slightly shorter than struts.

DIAGNOSIS: *Helophorus vereschaginae* resembles *H. kozlovi* in its size and shape, abdominal segment 7 with its apical margin crinkled but without distinct square-ended teeth, and in the brown elytra with extensive darker and paler mottling. It differs from *kozlovi*, in addition to the aedeagal differences (see above, under *H. kozlovi*), in the apical segment of the maxillary palpi being more elongate pointed oval, and in the head and pronotum being less polished and shining.

DISTRIBUTION: Known only from the type locality in Uzbekistan.

ETYMOLOGY: The species is named after Tatiana N. Vereschagina, who collected the holotype.



Figs. 19–24: Habitus, dorsal. 19) *Helophorus* (*Orphelophorus*) *obscurellus* POPPIUS, 1907, Russia, Tuva; 20) *H.* (*O.*) *arcticus* BROWN, 1937, Canada, Manitoba, Churchill; 21) *H.* (*Transithelophorus*) *crinitus* GANGLBAUER, 1901, Russia, Khabarovsk; 22) *H.* (*T.*) *beibienkoi* ANGUS, 1984, paratype; 23) *H.* (*T.*) *terminassianae* ANGUS, 1984, Turkey, İzmir; 24) *H.* (*Kyphohelophorus*) *tuberculatus* GYLLENHAL, 1808, China, Sichuan. Scale = 1 mm.

***Helophorus* (s.str.) *robustus* sp.n.**

TYPE MATERIAL: **Holotype** ♂ (ZIN): Kazakhstan, Boraldaytau Mts., 7.3 km ENE Terekty, 42.86371°N 69.86758°E, 540 m a.s.l., backwater of Boralday Riv., 8.–10.VI.2015, S.V. Litovkin leg. **Paratypes** (all from Kazakhstan, S.V. Litovkin leg.): Data as holotype, 1 ♂ (BMNH), 2 ♂♂, 2 ♀♀ (PCL). **Boraldaytau Mts.**: ~7 km ENE Terekty, 42.8636°N 69.8664°E 540 m a.s.l., Boralday River valley, water bodies, 23.–26.V.2015, 1 ♀ (PCL).

7.6 km ENE Terekty, 42.86794°N 69.86875°E, 540 m a.s.l., river valley, pool, 24.–27.V.2015, 1 ♂ (PCL). 7.3 km ENE Terekty, 42.86090°N 69.86990°E, 550 m a.s.l., mountain stream, 25.–26.V.2015, 1 ♀ (PCL). Karatau Mts.: 7.6 km SW Abay, 43.77274°N 68.81001°E, ~940 m a.s.l., stream, in gravel and under stones, 15.–16.V.2015, 1 ♂ (PCL). 13 km ENE Bayzhansay, 43.21439°N 70.06358°E, 930 m a.s.l., small pool, 29.V.2015, 2 ♂♂ (BMNH), 1 ♂, 4 ♀♀ (PCL). 13 km ENE Bayzhansay, 43.21311°N 70.06798°E, 915 m a.s.l., slow stream, silt and gravel, 29.–30.V.2015, 3 ♂♂ (PCL). 13 km NE Bayzhansay, 43.21459°N 70.06362°E, 930 m a.s.l., stream, in gravel, 29.–30.V.2015, 2 ♀♀ (BMNH), 3 ♂♂, 3 ♀♀ (PCL). 13 km NE Bayzhansay, 43.21459°N 70.06363°E, 930 m a.s.l., stream, in gravel, 18.VI.2016, 2 ♂♂, 2 ♀♀ (PCL). 9 km ENE Bayzhansay, 43.19324°N 70.03643°E, 1160 m a.s.l., temporary pool, 30.V.2015, 1 ♂ (PCL). ~9 km ENE Bayzhansay, 43.19246°N 70.02738°E, 1170 m a.s.l., temporary pools, 18.VI.2016, 3 ♂♂, 3 ♀♀ (PCL). 3 km S Achisay, 43.52078°N 68.89820°E, 685 m a.s.l., edge of stream, gravel and silt, 31.V.2017, 1 ♂ (PCL).

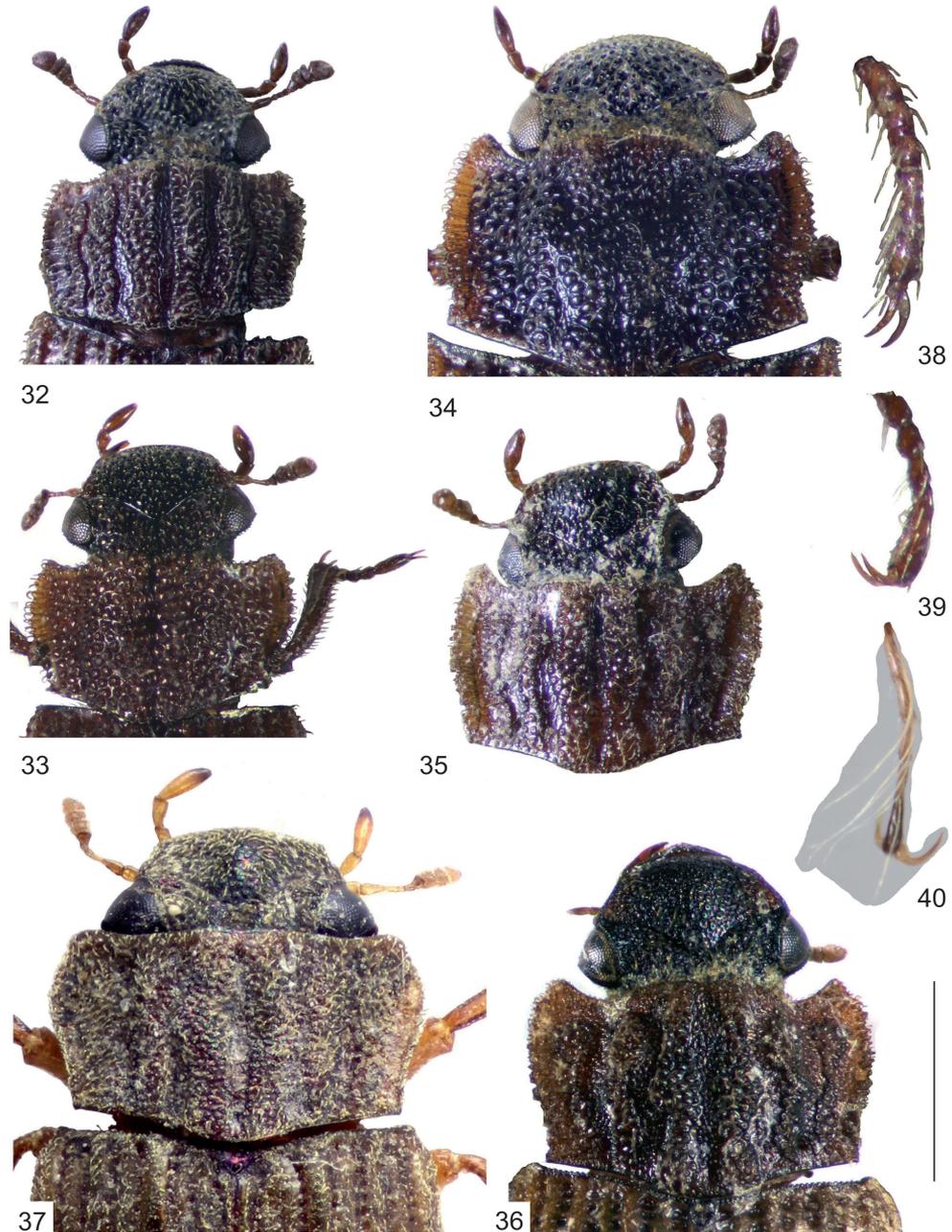


Figs. 25–31: Undersides to show the elytral epipleura and flanks. 25) *Helophorus* (*Gephelophorus*) *sibiricus* MOTSCHULSKY, 1860, Russia, Irkutsk Oblast, Tibelti; 26) *H.* (*Eutrichelophorus*) *micans* FALDERMANN, 1835, Georgia, Tbilisi, (also showing lateral excision of pronotum); 27) *H.* (*Transithelophorus*) *terminassianae*, Turkey, İzmir; 28) *H.* (*Orphelophorus*) *arcticus*, Russia, Magadan Oblast; 29) *H.* (*Empleurus*) *nubilus* FABRICIUS, 1777, France, Paris; 30) *H.* (*E.*) *schmidti* VILLA & VILLA, 1838, Spain, Puerto de Pajares; 31) *H.* (*Kyphohelophorus*) *tuberculatus*, Finland. Scale = 1 mm (25–27), 0.5 mm (28–31).

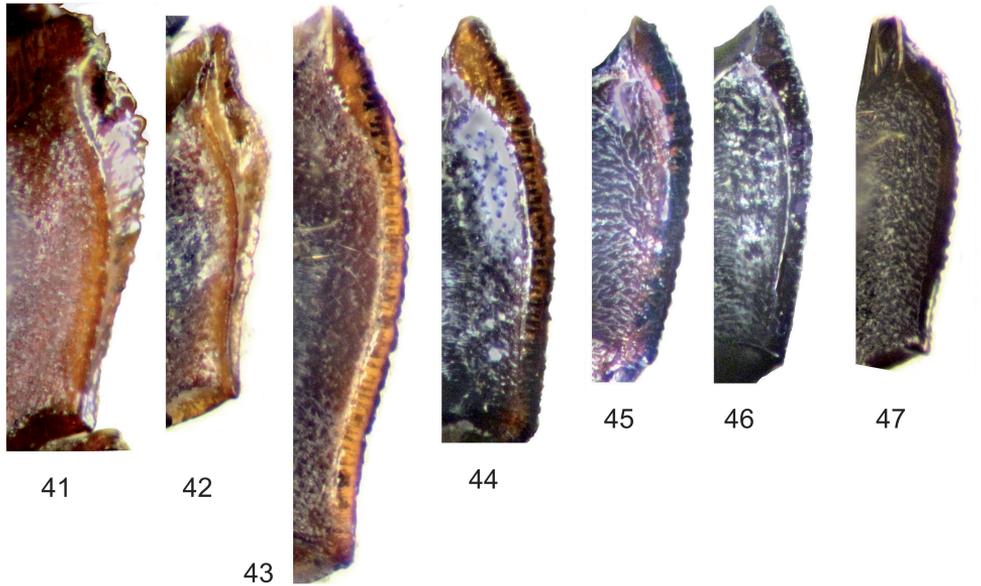
DESCRIPTION: Length: 5.9–6.8 mm, breadth: 3.6–4.2 mm. General appearance: Fig. 3. Head and pronotum: Figs. 7–8.

Head: Granulate, dull greenish bronze to shining golden, granulation reduced either side of the base of the Y-groove. Stem of Y-groove deep, broadly expanded anteriorly, its floor shining golden, rugose. Arms of Y-groove very narrow. Maxillary palpi dull yellow, apical segment almost symmetrical oval, sometimes more elongate, tip blunt, darkened. Antennae 9-segmented, mid brown, clubs darker.

Prothorax: Pronotum rather transverse, moderately arched between the external intervals, marginal grooves wide, their floors rugose, flared upwards to narrow crinkled raised margins, but absent in anterior sixth of pronotum. Widest at base of anterior third, sides curved but straighter (Fig. 7) or more distinctly recurved (Fig. 8) in basal quarter. Intervals granulate, the granulation weakest on internal intervals, strongest on externals. Grooves deep, quite wide, the submarginals and marginals twice the width of the median and submedians. Submedians angled outwards medially, recurved a quarter of the way from each end. Floors shining reddish to golden bronze, smooth in median and submedians, but with transverse ridges and furrows in the submarginals and marginals. Suprapleural area (sensu ANGUS 1992: fig. 2) fairly wide, bent inwards and further widened anteriorly, outside antennal cavity (Fig. 9).



Figs. 32–40: 32–37) Heads and pronota, 38–40) tarsi. 32) *Helophorus* (*Orphelophorus*) *obscurellus*, Russia, Tuva; 33) *H.* (*O.*) *arcticus*, Canada, Manitoba, Churchill; 34) *H.* (*Transithelophorus*) *crinitus*, Russia, Khabarovsk; 35) *H.* (*T.*) *beibienkoi*, paratype; 36) *H.* (*T.*) *terminassianae*, Turkey, İzmir; 37) *H.* (*Gephelophorus*) *sibiricus*, Russia, Tibelti, Irkutsk Oblast; 38) *H.* (*Empleurus*) *rufipes* BOSC, 1791, no locality data, midtarsus; 39) *H.* (*T.*) *beibienkoi*, paratype, foretarsus; 40) *H.* (*Rhopalohelophorus*) *salinus* ANGUS & LITOVKIN, 2018, holotype, midtarsus. Scale = 1 mm (32–37), 0.5 mm (38–39), 0.25 mm (40).



Figs. 41–47: Lateral portions of prothorax from below, to show the suprapleural areas. 41) *Helophorus* (*Gephelophorus*) *sibiricus*, Russia, Irkutsk Oblast; 42) *H. (G.) auriculatus* SHARP, 1884, Japan; 43) *H. (s.str.) grandis*, France; 44) *H. (s.str.) aquaticus*, Spain; 45) *H. (s.str.) niger*, Russia, Polyarniy Ural; 46) *H. (s.str.) khnzoriani*, Russia, Altai; 47) *H. (s.str.) dracomontanus*, holotype, China, Sichuan. Scale = 1 mm.

Elytra: Suture and alternate interstices raised, the raised interstices with bands of setigerous micropunctures, the others with these in single rows. Interstice 3 with two distinct dark spots just behind the middle and similar spots on interstice 8 just anterior to those on interstice 3. Antero-medial part of sutural Λ -mark mid brown, paler than the spots on interstice 3 and merging into a large blotch. Surface with paler and darker mottling. Flanks distinctly visible from below, opposite posterior part of metaventrite almost as wide as epipleura (Fig. 11).

Legs: Yellowish brown, moderately elongate, tarsal claws long. Tarsal natatorial setae rather weak.

Abdomen: Blackish with fine pubescence, segment 7 with apical margin clearly crinkled but without distinct square-ended teeth (Fig. 14).

Aedeagus (Fig. 18): About 1.0 mm long, parameres about two thirds the length of the basal piece, their outer margins almost straight, weakly incurved over apical fifth. Median lobe with tube broadly triangular, about two thirds the length of the struts.

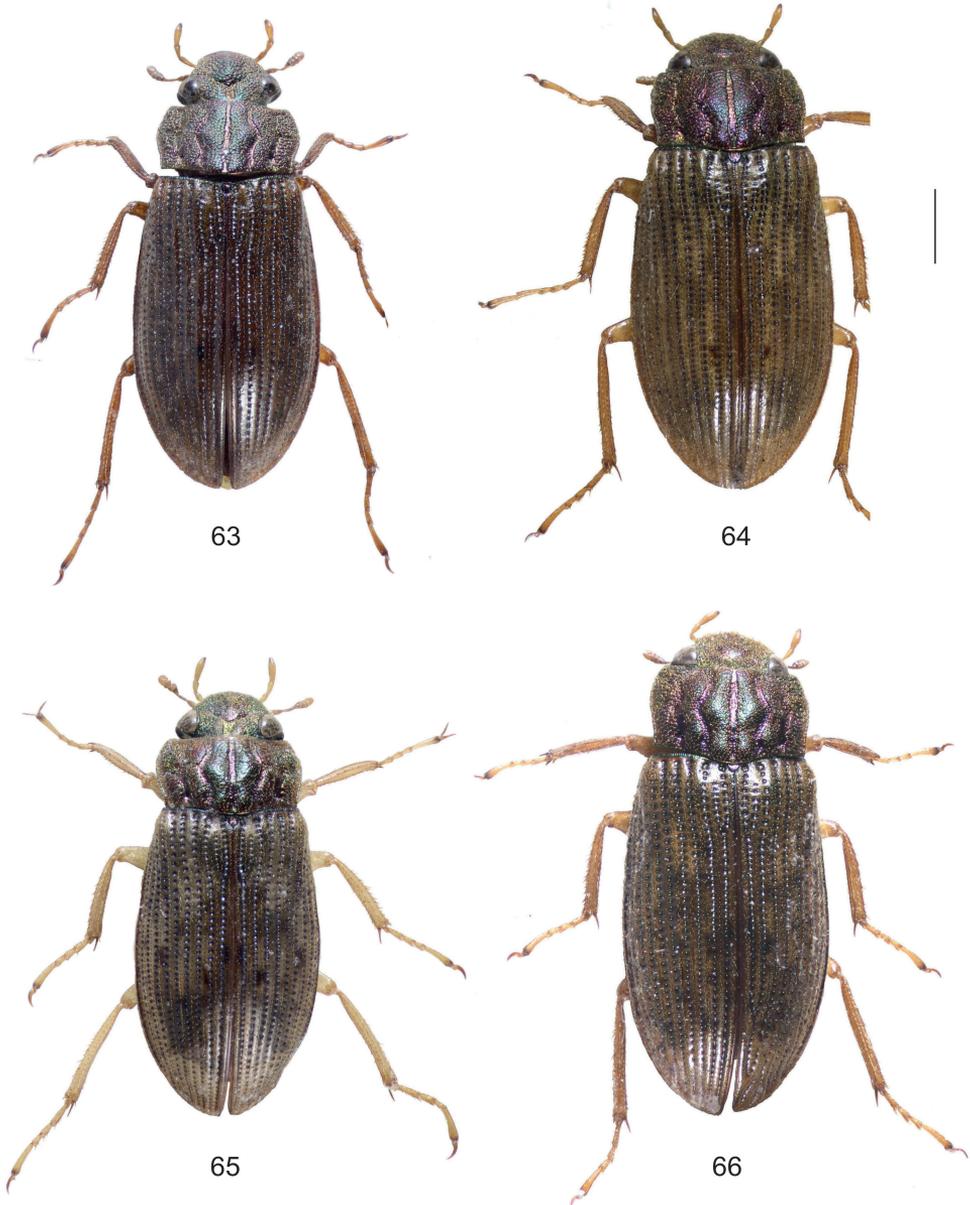
DIAGNOSIS: Closely resembling *H. oscillator* SHARP, 1915, but distinguished by the much larger aedeagus.

DISTRIBUTION: Kazakhstan (Boraldytau Mts., Karatau Mts.).

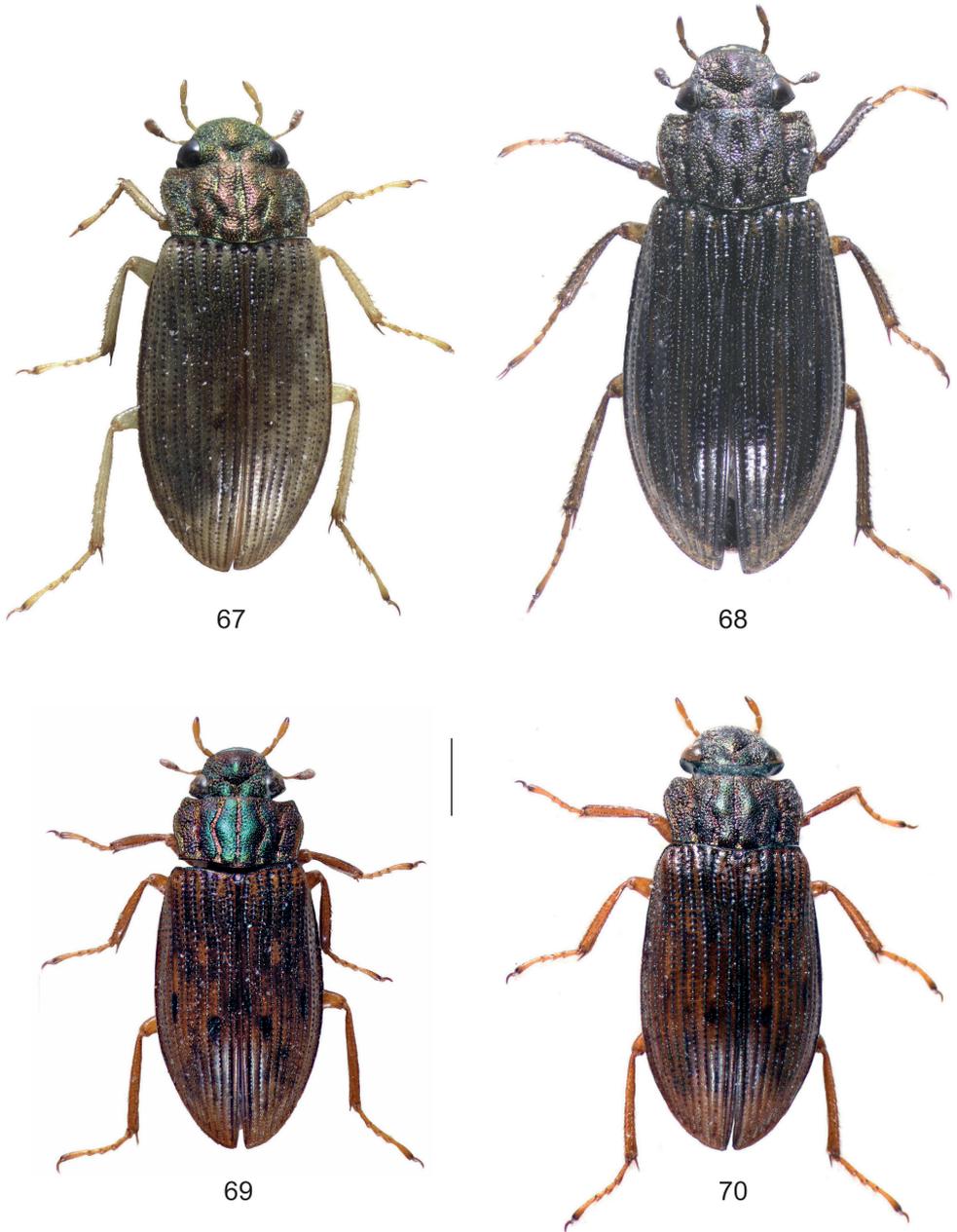
ETYMOLOGY: The name *robustus*, Latin adjective meaning large and solid, refers to the size of the aedeagus.



Figs. 48–62: Abdominal sternite 7 (last fixed). 48) *Helophorus grandis*, Russia, St. Petersburg; 49) *H. syriacus*, Israel, Golan Heights; 50) *H. maritimus*, Spain, León, Algadefe; 51) *H. milleri*, Greece, Corfu; 52) *H. occidentalis*, holotype, Spain, Cáceres, Abadía; 53) *H. liguricus*, Ukraine, Odessa; 54) *H. manchuricus*, holotype, China, “Manchuria”; 55) *H. aquaticus*, France, Tours; 56–57) *H. aequalis*, France, Tours; 58) *H. bergrothi*, Russia, Irkutsk Oblast; 59–60) *H. thauma*, Italy, Parma, 59 holotype, 60 paratype; 61) *H. hammondi* paratype, China, Heilongjiang, Harbin; 62) *H. jaechi*, China, Sichuan, Xinduqiao. Scale = 0.5 mm.



Figs. 63–66: Habitus, dorsal. 63) *Helophorus grandis*, Russia, St. Petersburg; 64) *H. maritimus*, Spain, León, Algadefe; 65) *H. milleri*, Greece, Corfu; 66) *H. occidentalis*, holotype, Spain, Abadía. Scale = 1 mm.



Figs. 67–70: Habitus, dorsal. 67) *Helophorus syriacus*, Israel, Golan Heights; 68) *H. liguricus*, Hungary, Borsod, Tiszabábolna; 69) *H. aequalis*, France, Tours; 70) *H. thauma*, holotype, Italy, Parma. Scale = 1 mm.



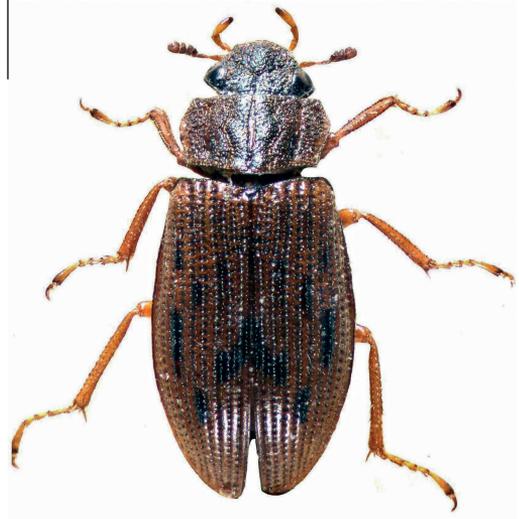
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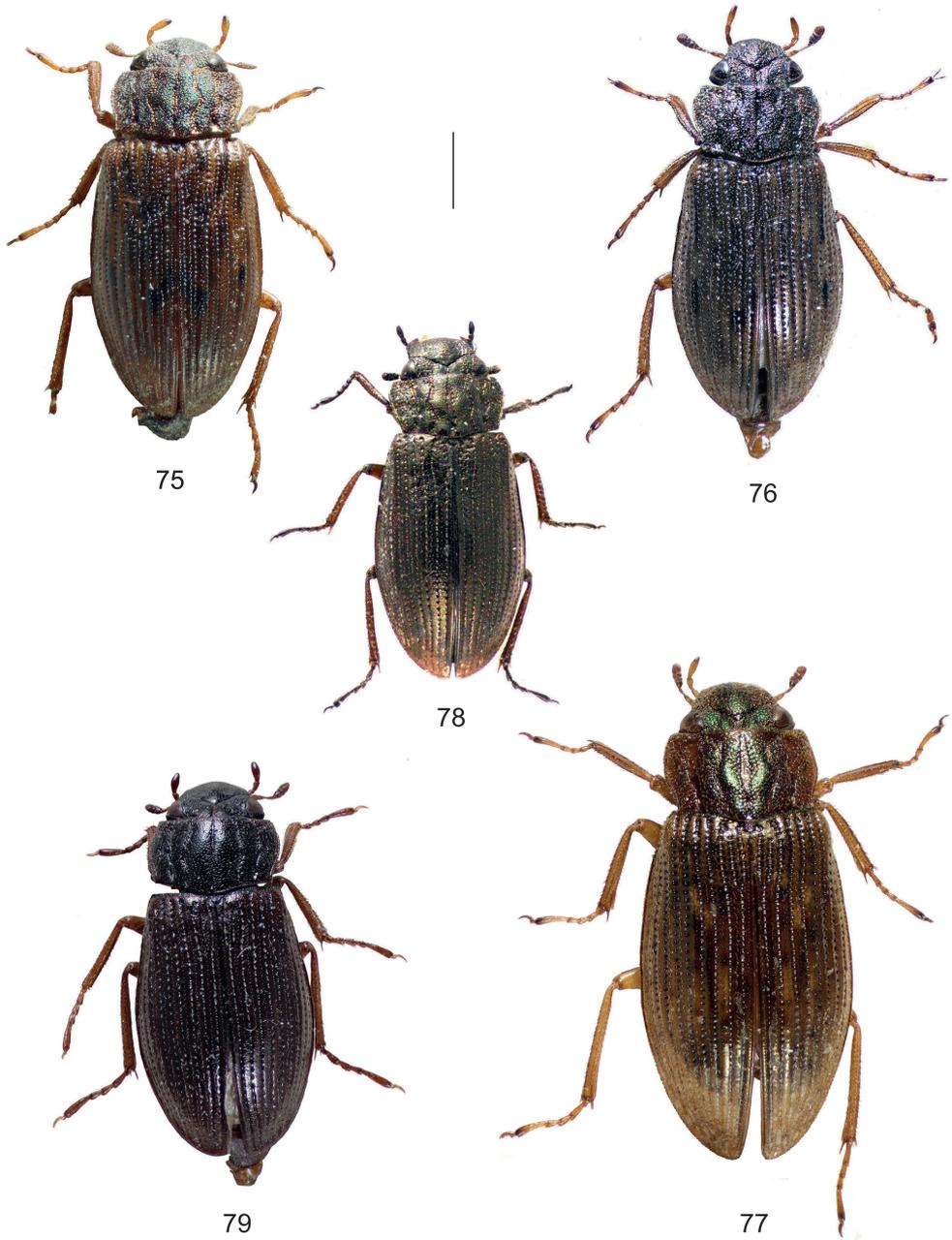


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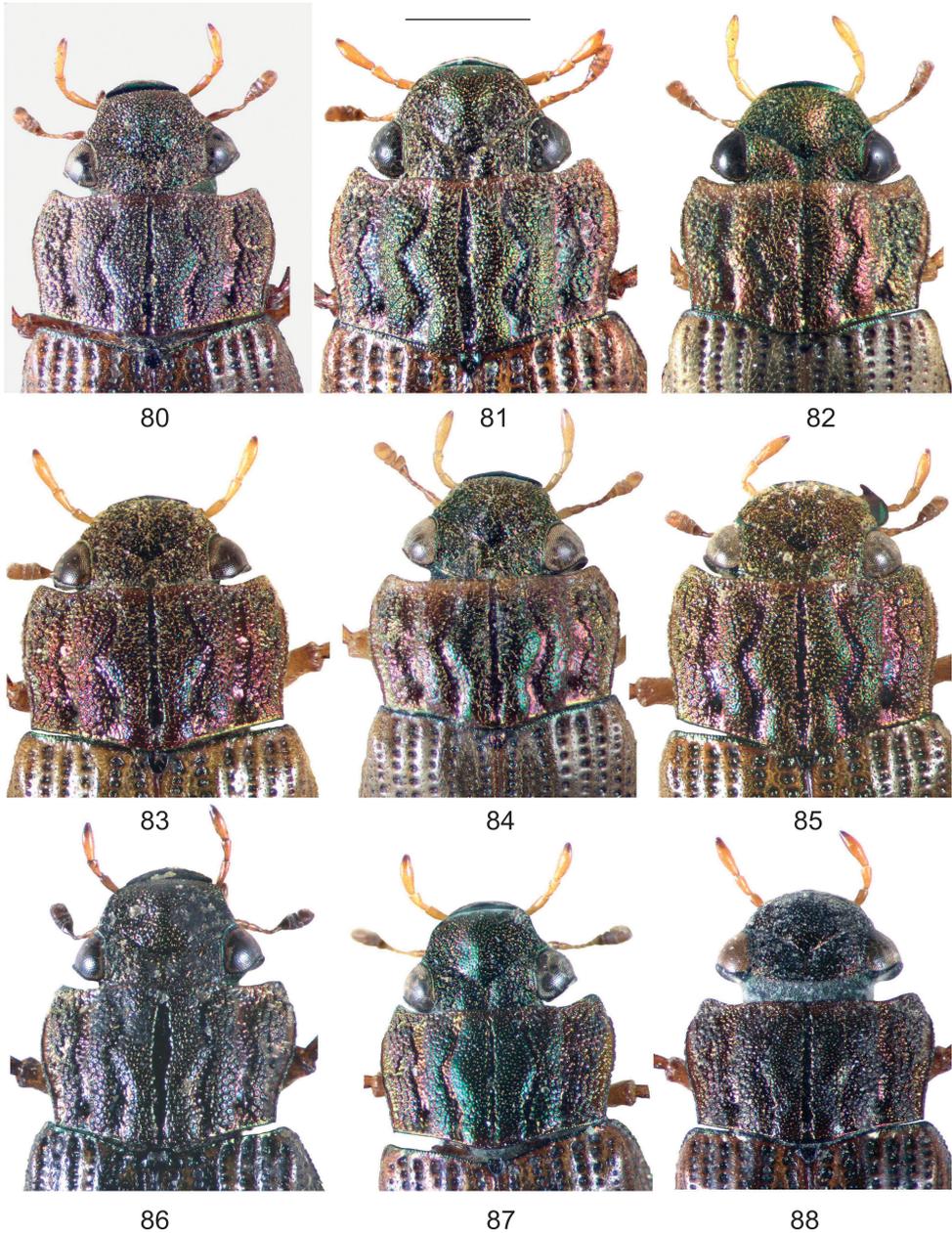


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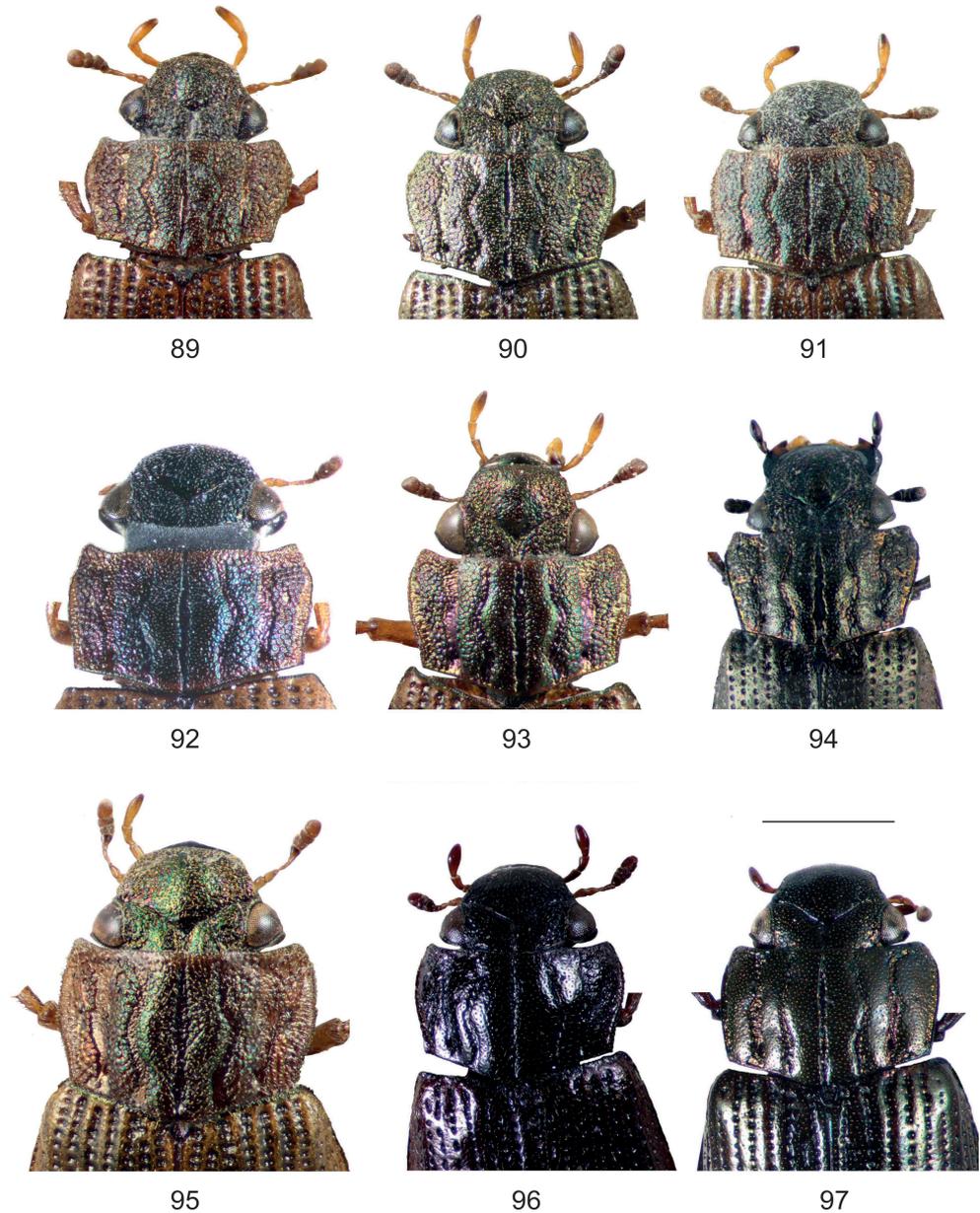
Figs. 71–74: Habitus, dorsal. 71) *Helophorus manchuricus*, holotype, China, “Manchuria”; 72) *H. aquaticus*, France, Tours; 73) *H. khnzoriani*, Russia, Altai; 74) *H. bergrothi*, Russia, Irkutsk Oblast. Scale = 1 mm.



Figs. 75–79: Habitus, dorsal. 75) *Helophorus hammondi*, China, Qinghai; 76) *H. strandi*, holotype, Finland, Inari; 77) *H. jaechi*, China, Sichuan, Xinduqiao; 78) *H. dracomontanus*, holotype, China, Sichuan; 79) *H. niger*, Russia, Polyarniy Ural. Scale = 1 mm.



Figs. 80–88: Heads and pronota. 80) *Helophorus grandis*, Russia, St. Petersburg; 81) same, Spain, Sierra Nevada; 82) *H. syriacus*, Israel, Golan Heights; 83) *H. maritimus*, Spain, León, Algadefe; 84) *H. milleri*, Greece, Corfu; 85) *H. occidentalis*, holotype, Spain, Cáceres, Abadía; 86) *H. liguricus*, Hungary, Borsod, Tiszabábolna; 87) *H. aequalis*, France, Tours; 88) *H. thauma*, holotype, Italy, Parma. Scale = 1 mm.



Figs. 89–97: Heads and pronota. 89) *Helophorus bergrothi*, Russia, Irkutsk Oblast; 90) *H. strandi*, holotype, Finland, Inari; 91) *H. hammondi*, China, Qinghai; 92) *H. manchuricus*, holotype, China, “Manchuria”; 93) *H. aquaticus*, France, Tours; 94) *H. dracomontanus*, holotype, China, Sichuan; 95) *H. jaechi*, China, Sichuan, Xinduqiao; 96) *H. niger*, Russia, Polyarniy Ural; 97) *H. khnzoriani*, Russia, Altai. Scale = 1 mm.



Figs. 98–121: Aedeagi. 98) *Helophorus grandis*, England, Surrey; 99) *H. syriacus*, Israel, Golan Heights; 100) same, Iran, South Khorasan; 101) *H. maritimus*, Spain, León, Algadefe; 102) *H. milleri*, Greece, Corfu; 103) *H. occidentalis*, holotype, Spain, Cáceres, Abadía; 104) *H. liguricus*, Ukraine, Odessa; 105–110) *H. aquaticus*, France, Tours; 111) *H. aequalis*, France, Tours; 112–113) *H. thauma*, Italy, Parma, 112) holotype, 113) paratype; 114) *H. bergrothi*, Russia, Irkutsk Oblast; 115–116) *H. hammondi* paratypes, China, Heilongjiang, Harbin; 117) *H. strandi*, holotype, Finland, Inari; 118) *H. jaechi*, China, Sichuan, Xinduqiao; 119) *H. niger*, Russia, Polyarniy Ural; 120) *H. khnzoriani*, Russia, Altai; 121) *H. dracomontanus*, China, Sichuan, Kangding. Scale = 1 mm.

Discussion

Helophorus robustus is clearly very different from both *H. kozlovi* and *H. vereschaginae*. The pronotum, especially with its wide flared marginal grooves, resembles *H. alternans* GENÉ, 1836 and *H. oscillator*, both species currently placed in the subgenus *Trichohelophorus* KUWERT,

1886. All these species are characterised by symmetrically oval apical segments of the maxillary palpi, raised alternate elytral interstices and broad elytral flanks (pseudepipleura). However, the development of these flanks is not uniform in the subgenus. In *H. alternans*, the flanks, opposite the posterior edge of the metaventricle, are clearly wider than the epipleura (Fig. 13), while in *H. oscillator* (Fig. 12) they are much narrower than the epipleura, and in *H. robustus* (Fig. 11) they are slightly but distinctly narrower. There is also an important difference in the chromosome numbers. In *H. alternans* the karyotype has $2n = 20$ autosomes plus Xy sex chromosomes, as in the subgenera *Empleurus* HOPE, 1838, *Rhopalohelophorus* KUWERT, 1886 (ANGUS 1989), *Lihelephorus* ZAITZEV, 1908 (ANGUS et al. 2016), and in the family Hydrochidae (SHAARAWI & ANGUS 1992), but in *H. oscillator* and *Helophorus* s.str. the karyotype has $2n = 16$ autosomes plus Xy sex chromosomes, as in the subgenera *Gephelephorus* SHARP, 1915 and *Eutrichelophorus* SHARP, 1915 (ANGUS 1989) as well as in most of the small and medium-sized aquatic species of Hydrophilidae. Helophoridae and Hydrochidae are families which branched off from the basal stem of Hydrophiloidea and it is thus possible that a karyotype of 22 chromosomes is a symplesiomorphy in *Helophorus*, with the reduction of the chromosome number to 18 a synapomorphy of the subgenera in which it occurs. It seems very unlikely that both these chromosome numbers should occur in one subgenus, and transferring *H. oscillator* to *Helophorus* s.str. seems a tidier arrangement. It would be very good to know the chromosome number for *H. robustus*, and to have DNA data on both *H. oscillator* and *H. robustus*. DNA data on *H. alternans* are available (Martin Fikáček, pers. comm.).

Revised key to the subgenera of *Helophorus* FABRICIUS, 1775

The numbering of the elytral interstices used in the key given by ANGUS (1992) follows SHARP (1915) in starting with interstice 1 between striae 1 and 2. Here the widely accepted current system (LAWRENCE & ŚLIPPIŃSKI 2013), which places interstice 1 between the suture and stria 1, is used.

- 1 Elytra without intercalary striae, or intercalary striae of at most three punctures, upper surface with conspicuous erect recurved setae (Figs. 19–20). Head and pronotum with large rounded granules (Figs. 32–33). Alternate interstices of elytra sharply ridged. Tarsi with stiff setae on their dorsal faces (Figs. 38–39) *Orphelophorus* ORCHYMONT, 1927
- Either elytra with well-developed intercalary striae or, if not, upper surface lacks stiff erect setae, head and pronotum do not have large rounded granules and dorsal surface of tarsi with fine hairs instead of stiff setae (Fig. 40) 2
- 2 Elytra with intercalary striae 3
- Elytra without intercalary striae *Rhopalohelophorus* KUWERT, 1886
- 3 Elytral flanks at least as wide as the epipleura opposite the posterior margin of the metaventricle (Figs. 25–31). Apical segment of maxillary palpi symmetrical oval, pointed 4
- If elytral flanks opposite base of metaventricle are as wide as, or wider than the epipleura, apical segment of maxillary palpi clearly asymmetrical (Fig. 25) 8
- 4 Elytral flanks opposite the middle of the metaventricle clearly twice as wide as epipleura (Figs. 29–31) 5
- Elytra opposite the middle of the metaventricle as wide as, or slightly wider than epipleura (Figs. 25–28) 6
- 5 Elytra black, with raised tubercles on interstices 3, 5 and 7 (Fig. 24)
..... *Kyphohelophorus* KUWERT, 1884
- Elytra brown or yellow, without raised tubercles *Empleurus* HOPE, 1838

- 6 Lateral margins of pronotum distinctly serrate, and not strongly excised before hind angles, except in *H. (Transithelophorus) crinitus* GANGLBAUER, 1901, which has the lateral serration very strong (Figs. 21–23)..... *Transithelophorus* ANGUS, 1970
- Lateral margins of pronotum not obviously serrate, or lateral margins strongly excised before hind angles..... 7
- 7 Tarsi with stiff setae on the dorsal surface (Figs. 38–39). Lateral margins of pronotum strongly excised before hind angles (Fig. 26). Serration of lateral margins moderate or weak...
..... *Eutrichelophorus* SHARP, 1915
- Tarsi without stiff setae dorsally, but instead with fine hairs (Fig. 40). Lateral margins of pronotum not excised basally and not serrate. General appearance as in *H. (s.str.) oscillator* (Fig. 4)..... *Trichohelophorus* KUWERT, 1886
- 8 Suprapleural area wide anteriorly, distinctly narrowed posteriorly (Figs. 41–42). Elytral flanks opposite base of metaventrite as wide as epipleura (Fig. 25)..... *Gephelophorus* SHARP, 1915
- Suprapleural area fairly evenly narrow throughout, only weakly narrowed posteriorly (Figs. 43–47). Elytral flanks generally at most narrowly visible from below, but sometimes nearly as wide as epipleura opposite the posterior margin of the metaventrite 9
- 9 Elytra with interstice 11 distinctly keeled *Helophorus* s.str. FABRICIUS, 1775
- Elytra with no trace of a keel on interstice 11 *Lihelophorus* ZAITZEV, 1908

Revised key to the species of *Helophorus* s.str. FABRICIUS, 1775

A key to the species of *Helophorus* s.str. was published by ANGUS (2017), but with the inclusion of three further species, one of which had hitherto been confounded with *H. kozlovi*, it seems appropriate to produce an up to date version of this key.

- 1 Seventh (last fixed) abdominal sternite with distinct square-ended teeth on apical margin (Figs. 48–57, 59–60)..... 2
- Seventh sternite without distinct teeth, apical margin crinkled (Figs. 14, 58, 61–62)..... 10
- 2 Teeth of abdominal sternite 7 large (Figs. 48–52)..... 3
- Teeth of abdominal sternite 7 clearly smaller (Figs. 53–57, 59–60)..... 7
- 3 Pronotum relatively wide, strongly and coarsely granulate over all the intervals, these normally dull (Fig. 80) but tending to be more shining in southern specimens (Fig. 81). Pronotal grooves with their sides vertical, not appearing “scooped out”. External intervals seldom interrupted by a transverse groove at the base of the anterior third. Abdomen generally black or very dark brown, teeth including some which are as wide as tall. Aedeagus characteristic (Fig. 98), length about 1.2 mm, parameres not particularly elongate..... *H. grandis* ILLIGER, 1798
- Pronotum normally more shining and less strongly granulate medially (Figs. 81–84). Grooves with their sides curved to the floors so the grooves appear “scooped out”. If not, pronotal surface is flatter, pronotum appears relatively smaller and the interruption of the external intervals is often well developed. Abdomen generally red or with red markings, and teeth normally taller, not as wide as tall. Aedeagus length 0.9–1.1 mm 4
- 4 Pronotum (Fig. 82) narrower and relatively smaller than in the other Mediterranean species of this group, its sculpture less well-developed than in these species, more as in *H. grandis*, and with the external intervals often clearly interrupted medially. Aedeagus (Figs. 99–100) shaped as in *H. grandis*, but conspicuously smaller, clearly less than 1.0 mm long. Crimea, Azerbaijan, Turkey, Cyprus, Israel, ? Iraq (“Mesopotamia”, 1 ex. BMNH), Iran, Arabian Peninsula, east to Tajikistan, Turkmenistan, Kazakhstan: Aksu-Zhabagly Nature Reserve; Kyrgyzstan (first record): Fergana Valley *H. syriacus* KUWERT, 1885
- Pronotum normally as broad as in *H. grandis*, rather strongly arched, the sculpture of the internal and middle intervals rather reduced, these intervals shining, as are the grooves, which have the sides curved to their floors, giving a characteristic “scooped out” appearance (Figs.

- 83–85). Head and pronotum with the setae arising from their granules conspicuous and those of the elytral interstices normally well developed. Aedeagus with parameres more elongate than those of *H. grandis*. The *H. maritimus* species group. Central and western Mediterranean as far east as the western coast of Anatolia 5
- 5 Specimens from the Iberian Peninsula and Morocco. Pronotum (Fig. 85) robust, its sculpture well developed. Aedeagus (Fig. 103) with the parameres generally narrower than those of *H. grandis* *H. occidentalis* ANGUS, 1983
- Specimens from Corsica and Sardinia to Crete and Greece, western Anatolia, from France (Provence) and lowland areas of central Spain..... 6
- 6 Specimens from France (Provence) and the plain of central Spain. Aedeagus (Fig. 101) with parameres noticeably elongate, slightly incurved subapically, and pronotal sculpture (Fig. 83) less pronounced than in the other species of this group *H. maritimus* REY, 1885
- Specimens from the central and eastern Mediterranean. Pronotum (Fig. 84) more or less as in *H. occidentalis*, though sometimes a bit less robust. Aedeagus (Fig. 102) with parameres generally slightly more slender apically than those of *H. occidentalis* *H. milleri* KUWERT, 1886
- At present, *Helophorus maritimus*, *H. milleri* and *H. occidentalis* can be reliably separated only by details of their chromosomes.
- 7 Pronotum not appearing conspicuously small in relation to the body size (Figs. 69–70, 72). Abdominal teeth fine, seldom including any fully twice as wide as long (Figs. 55–57, 59–60)..... 8
- Pronotum generally appearing conspicuously narrow in proportion to body size (Figs. 68, 71). Abdominal teeth generally including some fully twice as wide as long (Figs. 53–54)..... 9
- 8 Aedeagus (Figs. 105–110) variable, with the basal piece clearly longer than the parameres, though sometimes only slightly so (Fig. 110). Outer margin of parameres generally either strongly curved or angled inwards at base of apical quarter, but sometimes straight (Fig. 110).. *H. aquaticus* (L., 1758)
- Aedeagus with basal piece scarcely longer than parameres. Parameres with their outer margins either straight or bulging outwards in basal half and weakly recurved in apical half (Figs. 111–113)..... *H. aequalis* THOMSON, 1868 and *H. thauma* ANGUS & TOLEDO, 2010
- At present, these two species can be separated only by study of their chromosomes. However, it seems that some specimens of *H. thauma* have the abdominal teeth slightly taller than those of *H. aequalis* (Figs. 56, 59). *Helophorus aequalis* is widely distributed over Central and Western Europe, from Fennoscandia in the north to the Pyrenees and Bavaria in the south. It is less frequent in the mountains; records from further east require confirmation. The discovery of *H. thauma*, so far known only from the vicinity of Parma in northern Italy means that all records from E and SE Europe, Turkey and the Caucasus require confirmation.
- 9 Elytra normally with the alternate interstices raised above the others (Fig. 68). Pronotum with strong granulation over all the intervals (Fig. 86). Aedeagus (Fig. 104) characteristic, elongate, length 1.0–1.3 mm. France, Italy, Czechia, Slovakia, Austria, Croatia, Hungary, Poland, Greece, southern Russia, Ukraine, Turkey, Iran..... *H. liguricus* ANGUS, 1970
- Elytra with the interstices uniformly raised (Fig. 71). Pronotum shining, the granulation reduced on the internal intervals (Fig. 92). Known only from the female holotype. “Manchuria”. *H. manchuricus* SHARP, 1915
- 10 Head with distinct granules, including some on the clypeus (Figs. 89–95). Pronotum less evenly arched and with the middle intervals distinctly granulate. Elytra normally brown with a darker inverted V-shaped mark across the suture and/or an elongate dark spot on interstice 7 11
- Granulation of head confined to the area adjacent to the eyes and occasionally impressed rings round the punctures along the posterior margin (Figs. 96–97). Pronotum evenly arched, with reduced granulation. Elytra blackish brown without darker markings (Figs. 73, 79)..... 19
- 11 Maxillary palpi short, metallic black, apical segment almost symmetrical oval (Fig. 94). Body small, very dark, length about 4 mm (Fig. 78). Aedeagus (Fig. 121); this species was de-

- scribed from two females, but a male, collected together with the type specimens, has now been found in the SYSU *H. dracomontanus* ANGUS, 2017
- Maxillary palpi at least in part brownish or yellow, apical segment either symmetrical oval or clearly asymmetrical..... 12
- 12 Pronotum with the marginal grooves wide, as wide as middle and external intervals, flared laterally (Fig. 7). The shining suprapleural area wide after anterior quarter (Figs. 9–10)..... 13
- Pronotum with marginal grooves narrower, clearly narrower than middle and external intervals (as in Figs. 89–95). Suprapleural area not wide to base (Figs. 43–47)..... 14
- 13 Aedeagus elongate and larger, length about 1.00 mm (Fig. 18)..... *H. robustus* sp.n.
- Aedeagus less elongate and smaller, length about 0.75 mm (Fig. 17)..... *H. oscillator* SHARP, 1915
- 14 Internal intervals of pronotum without granules (Figs. 5–6). Elytra brown with extensive darker and paler mottling as well as dark marks representing the sutural Λ -mark (Figs. 1–2)..... 15
- Internal intervals of the pronotum extensively granulate. Elytra less extensively mottled (Figs. 74–77)..... 16
- 15 Aedeagus broad, outer margin of parameres curved (Fig. 15). Apical segment of maxillary palpi broad, suboval, blunt apically. Central area of pronotum polished, shining (Fig. 5). China (Qinghai)..... *H. kozlovi* ZAITZEV, 1908
- Aedeagus narrower, outer margin of parameres straighter (Fig. 16). Apical segment of maxillary palpi more symmetrical oval, pointed. Central area of pronotum with reduced granulation but not so shining (Fig. 6). Uzbekistan..... *H. vereschaginae* sp.n.
- 16 Conspicuously elongate with relatively small pronotum (Fig. 77). Head with stem of Y-groove weakly expanded apically (Fig. 95). Aedeagus with parameres narrow, slightly incurved apically (Fig. 118)..... *H. jaechi* ANGUS, 1995
- Less elongate, pronotum relatively slightly larger. Head with stem of Y-groove narrow, parallel-sided (Figs. 89–91)..... 17
- 17 Ground colour rufous brown, elytra normally with the black Λ -mark very distinct, and bold elongate dark marks on interstices 5 and 7 (Fig. 74). Aedeagus (Fig. 114) characteristic, parameres pointed apically, their sides not parallel in apical portion, and struts elongate. Siberia, Primorsky Krai *H. bergrothi* SAHLBERG, 1880
- Ground colour normally darker, greyish brown; if pale, rufous elytra either without the dark marks, or with them very reduced. Aedeagus with parameres parallel-sided or incurved in apical portion and, if the struts long, paramere apices very attenuated 18
- 18 Maxillary palpi not abruptly darkened apically, either dark brown or mid brown. Apical tarsal segments normally gradually darkened apically, and the claws normally as dark as the tips of the claw segments. Aedeagus (Fig. 117) characteristic, about 1.0 mm long, the apical part of the parameres attenuate, their outer margins almost parallel-sided. Norway, Sweden, Finland, N Russia (Murmansk); a recent record from Dolgiy Island in the Pechora Sea (PROKIN et al. 2017) requires confirmation *H. strandi* ANGUS, 1970
- Maxillary palpi normally pale dull yellow with the apical quarter abruptly darkened. Apical tarsal segments normally abruptly darkened distally, the claws generally paler. Aedeagus (Figs. 115–116) characteristic, clearly less than 1.0 mm long, the struts a little shorter than in *H. strandi*, and the apical sections of the parameres less attenuate, incurved. China (Heilongjiang, Qinghai), Mongolia, E Siberia, Primorsky Krai, Ladakh, Kazakhstan, European Russia (Kalmykia)..... *H. hammondi* ANGUS, 1970
- 19 Elytral flanks opposite base of metaventrite at most half the width of the epipleura. Pronotal marginal grooves dark reddish brown (Fig. 96). Aedeagus (Fig. 119) characteristic, the parameres attenuate, their outer margins straight. Struts short, widely separated when they leave the tube. Basal piece short. Northern Siberia from the Ural and the Ob Gulf in the west to Magadan in the east, with pockets in cold areas further south (Tibelti, Irkutsk Oblast)..... *H. niger* SAHLBERG, 1880

- Elytral flanks opposite base of metaventrite wider, about $0.75 \times$ the width of the epipleura. Pronotal marginal grooves blackish or dark maroon (Fig. 97), concolourous with the rest of the pronotum. Aedeagus (Fig. 120) more elongate than in *H. niger*, the struts closer together and the basal piece much longer. Alpine zone of the Altai and Tuva *H. khnzoriani* ANGUS, 1970

Fossil *Helophorus* (s.str.) *khnzoriani* ANGUS, 1970

This species is known as a Pleistocene fossil from an interstadial in the early part of the Last Glacial Period in northern Sweden (LUNDQVIST 1978) and from the very beginning of the Pleistocene of Cape Copenhagen in northern Greenland (BÖCHER 1995). Both Böcher's and Lundqvist's papers note the lightly sculptured heads and pronota and the reduced intercalary striae of the elytra, characters typical of *H. khnzoriani*, as is the uniformly maroon pronotum noted in Lundqvist's paper. Böcher took Angus's caution about the difficulty of identification without the aedeagus to heart and placed the beetles as "cf. *khnzoriani*", but, having reviewed the notes we are now satisfied that these are most probably true *H. khnzoriani*. A remarkable occurrence of a species which is at present known only from the Altai and Tuva.

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