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Validation of *Heterocerus heydeni* Kuwert, 1890 based on morphology and DNA barcoding, with notes on the problems of classification of the Heteroceridae (Coleoptera)

STANISLAV V. LITOVKIN[1,4], ALEXEY S. SAZHNEV[2] & FEDOR ČIAMPOR JR[3]
[1]*Russian Entomological Society, Samara, Russia. E-mail: sats.lit@gmail.com*
[2]*Papanin Institute for Biology of Inland Waters, Yaroslavl' Province, Borok, 152742 Russia. E-mail: sazh@list.ru*
[3]*Zoology Lab, Plant Science and Biodiversity Center, Slovak Academy of Sciences, Bratislava, SK-84523, Slovakia.*
E-mail: *f.ciampor@savba.sk*
[4]*Correspondent author*

Abstract

New taxonomic data on mud-loving beetles are provided based on morphological characters and DNA barcoding. *Heterocerus heydeni* Kuwert, 1890 was previously considered a junior synonym of *H. flexuosus* Stephens, 1828, but we support the validity of the species and restore the name. *H. heydeni* is redescribed, based on material from Central Asia and European part of Russia. Specimens of *H. hauseri* Kuwert, 1893 were also studied, suggesting it as a possible junior synonym of *H. heydeni*. We provide new DNA barcodes for *H. flexuosus* and *Augyles* cf. *flavidus* and comment on *Heterocerus* barcode data published in Barcode Of Life Data Systems (BOLD).

Key words: Coleoptera, Byrrhoidea, Heteroceridae, synonymy, sibling species, DNA barcoding, Central Asia, European Russia, BOLD

Introduction

Definitely, there is a little information on the taxonomy and systematics of Heteroceridae. Only few genera (around 4–5) were recognized (King *et al*. 2011), but 55 years ago Pacheco (1964) divided Heteroceridae of the New World into five tribes and 19 genera. His system was however based almost solely on the characters of male genitalia. It was likely not very stable, which was clearly shown in the phylogenetic study of King *et al*. (2011) employing molecular data. As a result, the traditional classification is prefered, which includes 5 genera: *Augyles* Schiødte, 1866; *Heterocerus* Fabricius, 1792; *Elythomerus* Waterhouse, 1874; *Micilus* Mulsant & Rey, 1872 and *Tropicus* Pacheco, 1964. However, it is important to note that the molecular analysis mentioned above is based predominantly on the New World species and does not cover the whole diversity of the family.

The situation with the DNA barcoding data available for Heteroceridae is somewhat similar with the knowledge on phylogeny and systematics of the whole family. The data available in the most important global DNA barcodes database—Barcoding of Life Data Systems (BOLD) comprise 399 records representing 43 taxa including synonyms (November 2018). However, only 28 taxa including synonyms are correctly barcoded (i.e. COI sequences are ≥500bp long), which means that less than 10% of the known species diversity is covered and thus can be identified using DNA barcodes. This is not a very encouraging situation, although not uncommon throughout Coleoptera. DNA barcodes proved to be very useful and reliable in the species determination and also in delimitation of genera (e.g. Čiampor Jr *et al*. 2017, Laššová *et al*. 2014) and improving data on Heteroceridae would for sure greatly contribute also clarifying the taxonomy of Heteroceridae.

Specimens of *Heterocerus* not belonging to any valid taxon were found when studying collection material from Kazakhstan, Turkmenistan, Uzbekistan and south of the European part of Russia. However, two synonymous taxa, *Heterocerus heydeni* Kuwert, 1890 and *H. hauseri* Kuwert, 1893 were of special interest due to similarities in morphology and type locality.

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H. heydeni was described from Uzbekistan (Dzhizak) (Kuwert 1890). Later, this species was also found in other regions of Central Asia (Zaitzev 1908; Jacobson 1913; Hebauer 1991). Locality and number of type specimens is not known. Specimens from Uzbekistan (Tashkent) and other adjacent regions identified as "*H. parallelus* Gebl. subsp. *heydeni* Kuw." by F.A. Zaitsev (= Ph.A. Zaitzev) were studied by Charpentier and, based on outer morphology and male genital structure, *H. heydeni* was synonimized with *H. flexuosus* Stephens, 1828 (Charpentier 1979).

H. hauseri was described from Turkmenistan (Kizyl-Arvat, now Serdar) (Kuwert 1893). No new record of this species was published since. The number of type specimens and the place of deposit is currently unknown. Reitter has pointed out to insolvency of taxon's features and synonymized it with *H. parallelus* Gebler, 1830 (Reitter 1907). Synonymy was supported by some authors (Zaitzev 1908; Mascagni 2006, 2016). At the same time, Breit has found *H. hauseri* cotypes he studied in the collection of the Natural History Museum in Vienna to be identical to *H. flexuosus* (Breit 1916). Synonymy was supported by Charpentier (1979).

Materials and methods

This work is based on the material from collection of the first author, museum collections and material granted by our colleagues. The majority of beetles were collected by light traps. Specimens from typical habitats were collected using trampling and flushing. Studied material is stored in the following collections:

Acronyms:

CBRB =	Plant Science and Biodiversity Centre, Slovak Academy of Sciences (Bratislava, Slovakia)
CK =	private collection of Yakov Kovalenko (Belgorod, Russia)
CL =	private collection of Stanislav Litovkin (Samara, Russia)
IBIW =	Papanin Institute for Biology of Inland Waters (Borok, Russia)
MSPU =	Moscow State Pedagogical University (Moscow, Russia)
ZIN =	Zoological Institute of the Russian Academy of Sciences (St. Petersburg, Russia)

The material was studied using stereomicroscopes LOMO MBS-200 and LOMO MBS-9 with magnification up to 120×. Photographs of habitus were taken using a Nikon D3200 DSLR camera with attached microscope objective LOMO Plan 3.5×0.10. Photographs were stacked using Helicon Focus 5.3 software and then processed in Adobe Photoshop CS3. Male genitalia were studied using LOMO Biolam R-17 + OI-35 compound microscope at magnifications up to 450×. Dissected male genitalia were cleaned in 10% KOH for 12 hours at room temperature, rinsed in a solution of ethanol and studied as temporary glycerin slides. Genitalia drawings were made using a RA-6 drawing tube attached to the microscope. Digitized drawings were edited in Adobe Photoshop CS3. All measurements were performed using ocular measuring scales. Species comparison was carried out using specimens from Central Asia and Russia. For each studied species, several tens genital preparations were observed. Map was created in SimpleMappr online service (www.simplemappr.net). Terminology is partly taken from Mascagni (2014). Coefficient k is the ratio of elytral width behind shoulders to its length. For the analysis of the DNA barcodes, 11 adults of *Heterocerus* were used for the DNA extraction. DNA was isolated from the whole specimens using innuPREP DNA Mini Kit (analytikjena) according to manufacturer's protocol. Vouchers are stored at CBRB. Fragment of the 5' end of the mitochondrial gene for cytochrome c oxidase subunit I (cox1) was amplified with primers LCO1490, HCO2198 (Folmer *et al*. 1994). Amplification products were purified by alkaline phosphatase (FastAP) and exonuclease and sequenced from both sides by Macrogen Europe Inc. (Amsterdam, Netherlands). Raw sequences were assembled and edited in Sequencher v5.1. Additionally 44 sequences of the *Heterocerus* species and two *Limnichus* samples (used as outgroups) were downloaded from the Barcode of Life Datasystems (BOLD). The measure of the genetic distance using K2P model, maximum likelihood tree, bootstrap support and the selection of the best fitted substitution model (GTR+I+G) were performed with MEGA software v7 (Kumar *et al*. 2016). Final tree was edited with FigTree v1.4.2 and Adobe Illustrator.

Results

DNA barcoding

Out of eleven samples, we successfully sequenced 6 barcoding fragments representing three species (Fig. 1). The sample of *H. flexuosus* unambiguously groups with conspecific sequences from BOLD, three sequences presumably representing *H. heydeni* form sister clade with *H. flexuosus* distanced by 6.4%, forming distinctly separated clade (species). Remaining two sequences representing *A.* cf. *flavidus* (Rossi, 1794) form a separate clade, sister to *A. hispidulus* (Kiesenwetter, 1843). Mean K2P distance between *Heterocerus* species available in BOLD database ranged from 5.4–26%, we detect genetic identity between barcodes of *H. brunneus* Melsheimer, 1844 and *H. completus* Hatch, 1965*,* which is obviously due to the erroneous determination of the *H. brunneus* sample. This species distinctly differs morphologically from *H. completus* (syn. *H. fenestratus*). The second branch of *H. fenestratus*, sister to *H. mollinus* (Kiesenwetter, 1851), also probably represents erroneously determined specimens. Moreover, the analysis of BOLD data showed significant uncertainties in the taxonomy of genera: the genus *Heterocerus* sensu lato is obviously polyphyletic in respect to *Augyles* and *Tropicus* nested within it. The taxon "*Littorimus* Gozis, 1885" was earlier shown to be a synonym of *Augyles*. Among six species of *Augyles* sensu lato (*Augyles auromicans* (Kiesenwetter, 1851)*, A. crinitus* (Kiesenwetter, 1850)*, A. intermedius* (Kiesenwetter, 1843)*, A. sericans* (Kiesenwetter, 1843), and *A.* cf. *flavidus*) the type species *A. hispidulus* of genus *Augyles* is included in the analysis. Some samples are however included in *Heterocerus* and the whole genus, as recorded by analysis of BOLD samples seems to be polyphyletic. The synonymy of *H. fenestratus*, *H. completus* and *Lapsus tristis* (Mannerheim, 1853) is also supported by maximum likelihood analysis, and for *H. completus* this was done by the molecular data for the first time.

Taxonomy

Our detailed study of *H. heydeni* specimen studied by Charpentier (male, ZIN) from Kazakhstan (Dzhulek) (Fig. 2) has shown it to represent a single valid species. Comparison has also shown its conspecificity with specimens we have collected in Central Asia and Russia. Therefore, we are reestablishing the validity of *H. heydeni*. A male with the similar genital structure of *H. heydeni* was recorded from Iran (near Ahvaz), he was listed as *H. flexuosus* with atypical aedeagus (Skalický 1998: Fig. 1). Due to insufficient material, the differences in the structure were not given any taxonomic significance.

The original description and identification keys (Kuwert 1890) give a rather detailed view of *H. heydeni* external features. Size, body and leg coloration, elytral pattern, features of dorsal pubescence, as well as male clypeus structure are in good accordance with specimens we have studied. It confirms their correct identification as *H. heydeni* with a high degree of certainty. Undoubtedly, there is some possibility of incorrect understanding of this taxon without examining the type material. However, we abstain from describing the discussed species as new for science to avoid unnecessary complication of nomenclature by an additional name.

Body and leg coloration, elytral pattern and pubescence features of *H. hauseri* given in the original description (Kuwert 1893) are in good accordance with those of specimens of *H. heydeni* with a reduced dark pattern in the main third of the elytra. Based on that we consider synonymy of *H. hauseri* with *H. flexuosus* to be doubtful. Synonymy with *H. parallelus* is also questionable, taking Breit's comments into account. The specimens from South Kazakhstan (ZIN) with identification labels "*Heterocerus parallelus* Reitter det.; *Heterocerus parallelus* pale form" and "*Heterocerus hauseri*" (see material examined) refer to *H. heydeni*. As we have not studied type specimens of *H. hauseri* we leave its synonymy with *H. heydeni* open to question.

Family Heteroceridae Macleay, 1825

Genus *Heterocerus* Fabricius, 1792

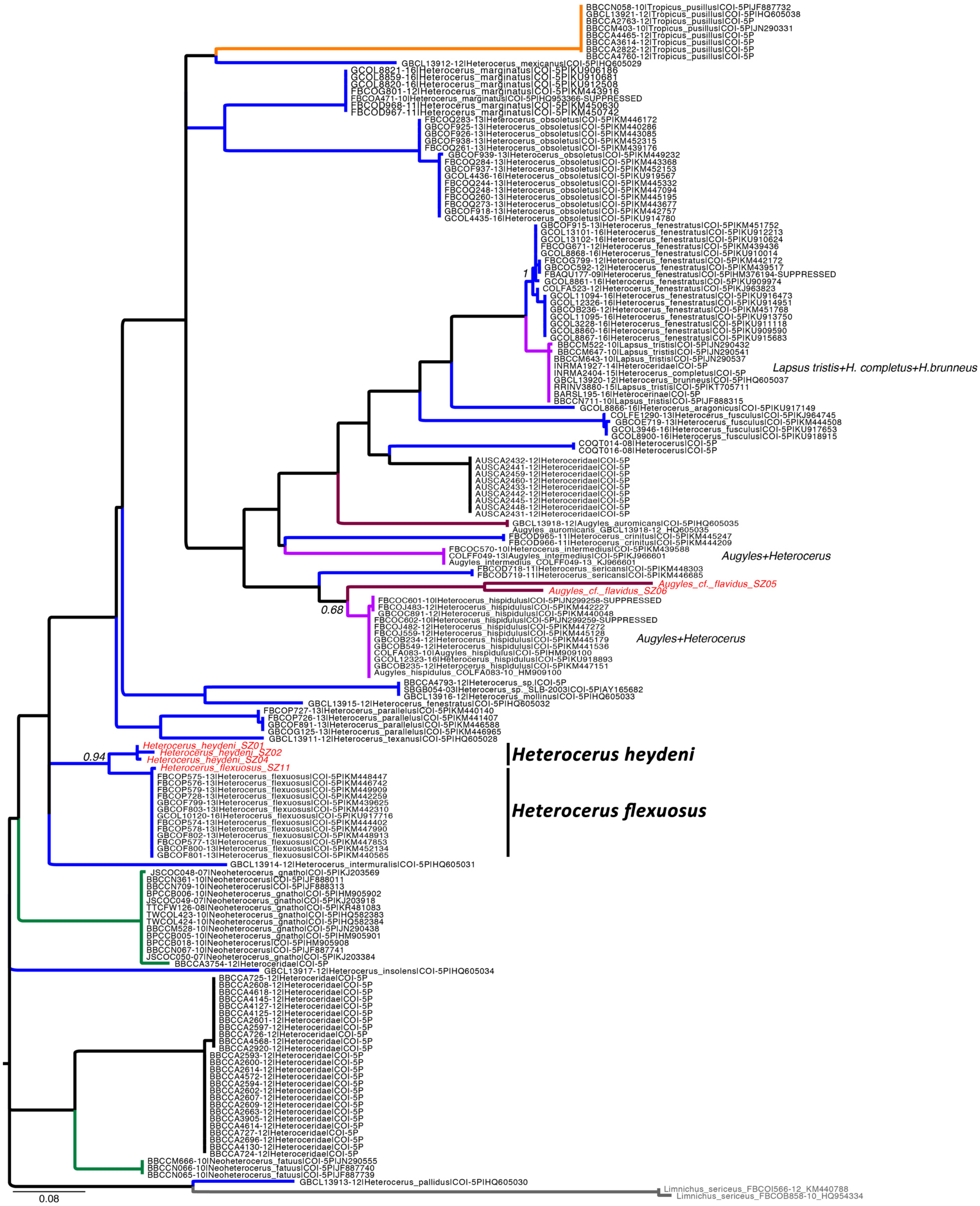


FIGURE 1. Maximum likelihood tree of Heteroceridae samples. Colour of branches: blue—*Heterocerus*, orange—*Tropicus*, green—*Augyles*, black—undetermined Heteroceridae. New samples in red, number next to nodes—bootstrap support (only if > 0.50). Samples with retained generic and species names as in BOLD data systems database.

Heterocerus heydeni **Kuwert, 1890 stat. resurr.**

(Figs. 2–4, 6–16, 18–20, 24)

Heterocerus hauseri Kuwert, 1893 **? syn.n.**

Material examined. 1583 specimens. **KAZAKHSTAN.** *Akmola Oblast*: Esil environs, near Ishim River, 51.95°N 66.32°E, at light, 25 May 2005, leg. A. Shapovalov, 1 specimen (CL); *Aktobe Oblast*: 25 km SW Emba, Peski Kumzhargan, 48.64408°N 57.91611°E, 25 Apr. 2012, leg. A. Ivanov, 4 specimens (IBIW); 3.3 km NE Khlebodarovka, 50.5340°N 56.9579°E, 207 m, hills, steppe, at light, 21–22 Apr. 2013, leg. S. Litovkin, 2 specimens (CL); 24 km WSW Yrgyz, 48.58361°N 60.90620°E, 167 m, at light, 28–29 May 2017, leg. S. Litovkin, 6 specimens (CL); *Almaty Oblast*: Sarkand Distr., 15 km N Lepsy, SE shore of Balkhash Lake, 46.359741°N 78.878415°E, sands, at light, 14 May 2014, leg. S. Kolov, 2 specimens (CL); 26 km SE Koktal, Ili Riv., 43.96364°N 79.60528°E, 506 m, 01 July 2015, leg. S. Korb, 1 specimen (IBIW); E Kazakhstan, 43.24294°N 78.88006°E, at light, 25 May 2016, leg. A. Ivanov, 1 specimen (IBIW); SE Kazakhstan, 8 km N Kanshengel, Peski Taukum, 44.41222°N 75.55675°E, 402 m, 02 June 2016, leg. A. Ivanov, 1 specimen (IBIW); *Atyrau Oblast*: Atyrau (Guryev), 02 Apr. 1911, leg. P. Shmidt, 1 specimen (ZIN); *Kostanay Oblast*: Aksuat Lake, 250 km S of Kostanay, [51.5°N 64.5°E], 19 July 1947, leg. Formozov, 1 specimen (ZIN); *Kyzylorda Oblast*: Baygekum near Dzhulek, 04 June 1907, leg. D. Glazunov, 4 specimens (ZIN); Dzhulek [44.29°N 66.43°E], Orenburg–Tashkent railway, Syrdarja, 01 July 1910, leg. I. Kozhantshikov, 1 male (ZIN) (Fig. 1); same locality data, 14 July 1910, leg. I. Kozhantshikov, 4 specimens (ZIN); near of Kyzylorda (Perovsk), 19 May 1916, leg. N. Pulikovskaya, 1 specimen (ZIN); 42 km SE Aralsk, 46.45306°N, 61.91000°E, 26 Apr. 2011, leg. A. Shapovalov, 1 specimen (CL); 15 km SE Kyzylorda, 44.71183°N 65.75561°E, 127 m, at light, 30 Apr. 2012, leg. A. Ivanov, 2 specimens (IBIW); 2.7 km NE Maylibash, 45.8409°N 62.6555°E, 79 m, desert, at light, 24–25 Apr. 2013, leg. S. Litovkin, 1 specimen (CL); Karatau Mts., 18.5 km ENE Birlik, Akuyik River valley, 43.937°N 67.680°E, 380–400 m, mountain river valley, at light, 29 Apr.–02 May 2013, leg. S. Litovkin, 76 specimens (CL, IBIW); 21 km NW Aralsk, 46.9638°N 61.4853°E, 79 m, sand-soil desert, at light, 07–08 May 2013, leg. S. Litovkin, 6 specimens (CL); same locality data, at light, 01–03 May 2015, leg. S. Litovkin, 8 specimens (CL); 67 km N Chiili, 44.77786°N 66.96811°E, 21 Apr. 2014, leg. A. Ivanov, 5 specimens (IBIW); 52 km SSE Aralsk, [46.36°N 61.95°E], at light, 20–21 Apr. 2015, leg. A. Prosvirov, 7 specimens (IBIW); 30 km SE Kazaly, [45.54°N 62.35°E], at light, 21–22 Apr. 2015, leg. A. Prosvirov, 9 specimens (IBIW); 42 km NE Kyzylorda, Tartogay, [44.4°N 66.2°E], 09–11 May 2015, leg. A. Prosvirov, 3 specimens (IBIW); 4.3 km SE Tartogay, 44.41040°N 66.27504°E, 145 m, tugay woodland, near Syrdarja River, at light, 13–14 June 2015, leg. S. Litovkin, 12 specimens (CL); same locality data, at light, 23–24 July 2017, leg. S. Litovkin, 4 specimens (CL); 42 km SSE Aralsk, 46.44609°N 61.89872°E, 56 m, sand-soil desert, at light, 25–26 July 2017, leg. S. Litovkin, 1 specimen (CBRB); *Mangystau Oblast*: Ustyurt Nature Reserve, cordon Kenderli, 42.95742°N 54.69278°E, 19 May 2011, leg. A. Ivanov, 1 specimen (IBIW); Mangystau Reg., 9 km E Shetpe, 44.15078°N 52.26886°E, 04–06 June 2017, leg. D. Potanin and A. Potanina, 2 specimens (IBIW); Karakiyansky Reg., 55 km NE Senek, 43.07639°N 53.92858°E, 07–09 June 2017, leg. D. Potanin and A. Potanina, 1 specimen (IBIW); Karakiyansky Reg., 5 km NW Senek, 43.39089°N 53.33494°E, 09–11 June 2017, leg. D. Potanin and A. Potanina, 2 specimens (IBIW); Tupkaragan Reg., Taushik, 44.40786°N 51.07508°E, 12–13 June 2017, leg. D. Potanin and A. Potanina, 1 specimen (IBIW); *Turkestan Oblast* (former *Southern Kazakhstan Oblast*): 60 km ESE Turkestan, 14 km SSW Mynbulak, [43.103°N 68.936°E], 23–24 Apr. 2015, leg. A. Prosvirov, 2 specimens (IBIW); Karatau Mts., 11 km NW Aksumbe, 44.51456°N 67.42278°E, 376 m, 16 May 2015, leg. A. Ivanov, 2 specimens (IBIW); 7.3 km NE Baltakol, 43.15872°N 67.84753°E, ~180 m, sandy shore of Syrdarja River, 08 June 2016, leg. S. Litovkin, 1 specimen (CL); 7.4 km NE Baltakol, 43.15871°N 67.85095°E, ~180 m, near Syrdarja River, at light, 08–10 June 2016, leg. S. Litovkin, 50 specimens (CL, IBIW, CBRB); 7.3 km NE Baltakol, 43.15673°N 67.84992°E, ~180 m, tugay woodland, near Syrdarja River, at light, 09–10 June 2016, leg. S. Litovkin, 5 specimens (CL); 9 km NE Baltakol, 43.17198°N 67.86345°E, ~180 m, sandy shore of Syrdarja River, 10 June 2016, leg. S. Litovkin, 1 specimen (CL); 3 km W Baltakol, N border of Kyzylkum Desert, 43.11790°N 67.71356°E, 181 m, at light, 13–14 June 2016, leg. S. Litovkin, 9 specimens (CL); 6 km NE Baltakol, 43.16040°N 67.83648°E, tugay, at light, 22–23 July 2017, leg. S. Litovkin, 55 specimens (CL); *Zhambyl Oblast*: Mujunkum [= Moiynkum], identification labels "*Heterocerus parallelus* Reitter det.", "*Heterocerus parallelus* pale form", July 1907, leg. E. Fischer, 2 specimens (ZIN); Taraz (Aulie-Ata), identification label "*Heterocerus hauseri*", leg. Willberg, 4 specimens. (ZIN); Moiynkum Distr., Aksuyek, [44.620°N 74.511°E], 07–11 Jule 1993, leg. A. Tilly, 1 specimen (CL); 42 km NE Karatau, Akkol, [43.443°N 70.787°E], 02–03 May 2015, leg. A. Prosvirov, 4 specimens (IBIW); vicinity of Kyzylkol Lake, 43.77602°N 69.51012°E, 335 m, saline soil, at light, 04–07 May 2015, leg. S. Litovkin, 882 specimens (CL, IBIW); same locality data, at light, 22–23 May 2015, leg. S. Litovkin, 48 specimens (CL); same locality data, at light, 04–06 June 2015, leg. S. Litovkin, 24 specimens (CL); same locality, but 43.77°N 69.50°E, at light, 31 May–01 June 2017, leg. S. Litovkin, 2 specimens (CL); along N bank of Kyzylkol Lake, 43.75995°N 69.50293°E, 330 m, sand, gravel, algae, 05–06 May, leg. S. Litovkin, 4 specimens (CL); same locality data, 04 June 2015, leg. S. Litovkin, 10 specimens (CL); Peski Moiynkum (= Moiynkum Desert), 44.29262°N 70.16508°E, 315 m, sandy desert, at light, 09–11 May 2015, leg. S. Litovkin, 9 specimens (CL); same locality data, but 44.29290°N 70.17608°E, 310 m, at light, 31 May–02 June 2015, leg. S. Litovkin, 35 specimens (CL); 7 km NE Kumkent, 43.81614°N 69.69615°E, 300 m, saline soil, at light, 13–14 May 2015, leg. S. Litovkin, 160 specimens (CL, IBIW); W bank of Akkol Lake, 43.40997°N 70.62446°E, 405 m, at light, 17–18 May 2015, leg. S. Litovkin, 37 specimens (CL); vicinity of Ashchykol Lake (hypersaline lake), 43.53851°N 70.63009°E, 378 m, at light, 18–19 May 2015, leg. S. Litovkin, 4 specimens (CL); same locality data, at light, 02–04 June 2015, leg. S. Litovkin, 7 specimens (CL); Karatau Mts., 13 km ENE Bayzhansay, 43.21416°N 70.06335°E, 930 m, mountain stream valley, at light, 28–30 May 2015, leg. S. Litovkin, 1 specimen (CL). **RUSSIA.** *Astrakhan Oblast*: Astrakhan Nature Reserve, to UV light, 26 June / 17 July 1956, leg. Breev, 1 specimen (ZIN); Krasnoyarsk Distr., 2 km E Dosang, at UV light, 09–12 June 2005, leg. A. Tilly, 1 specimen (CL); Krasnoyarsk Distr., Dosang environs, coast of Akhtuba River, 06 May 2009, leg. Ya. Kovalenko, 1 specimen (IBIW); Krasnoyarsk Distr., 14 km NE Dosang, dune Tuvayak, 01 May 2011, leg. A. Prosvirov, 2 specimens (IBIW); Liman Distr., Yango Asker, at light, 30 June 2010, leg. A. Prosvirov, 1 specimen (IBIW); Liman Distr., Stantsiya Basinskaya, at light, 03 July 2010, leg. A. Prosvirov, 1 specimen (IBIW); *Crimea*: Donuzlav Bay, Krasnoyarskoe, [45.50°N 33.26°E] 24 July 2016, leg. V. Shaporinsky, 4 specimens (IBIW); *Dagestan*: Kizlar Distr., vicinity of Bryansk, 44.3292°N 46.9797°E, 10 June 2009, 1 specimen (IBIW); Makhachkala, 20 June 2009, leg. E. Il'ina, 1 specimen (IBIW); Tarumovsky Distr., Staryy Biryuzak, Kuma Riv., 04 June 2015, leg. E. Il'ina, 3 specimens (IBIW); *Kalmykia*: 25 km SE from Elista, to light at night, 24 July 1986, leg. Makarova, 4 specimens (MSPU); *Orenburg Oblast*: Western part of Orenburg Oblast, 3 km N Kurlin, 10–11 June 2004, leg. A. Tilly, 1 specimen (CL); Guberlya environs, 51°16'47''N 58°09'37''E, at light, 17 May 2005, leg. A. Shapovalov, 1 specimen; Gaysky Distr., Guberlinsky sovkhoz, Khmelyovka, [51.245°N 57.868°E], at light, 07–08 May 2012, leg. A. Ukrainsky, 5 specimens (IBIW); Akbulak Distr., 18.5 km SE Akbulak, 50.93025°N 55.89042°E, near Karabutak River, at light, 15–16 June 2015, leg. S. Litovkin, 4 specimens (CL); *Saratov Oblast*: Krasnokutsky Distr., vicinity of D'yakovka, [50.731°N 46.769°E], June 2004, leg. A. Ukrainsky, 3 specimens (IBIW); *Volgograd Oblast*: Palassovsky Distr., Elton Settlm. environs, at UV light, 21–28 May 2006, leg. A.V. Matalin, 4 specimens (IBIW); same locality data, at UV light, 27–28 June 2006, leg. A.V. Matalin, 2 specimens (IBIW). **TURKMENISTAN.** *Ahal Velayat*: South Turkmenia, Tedzhen environs. 17–24 Apr. 1985, leg. A. Tilly and V. Nikulin, 1 specimen (CL); *LebapVelayat*: Farap, 01 June 1905, leg. G.G. Sumakov, 3 specimens (ZIN); Birata (Darganata), 03 July 1910, leg. E. Fisher, 1 specimen (ZIN); Repetek, 10 Mar. 1982, leg. Krivokhatsky, 1 specimen (ZIN); *Mary Velayat*: Ýolöten, 07 June 1926, leg. V. Kizeritsky, 1 specimen (ZIN); Merv, 17 May 1976, leg. G. Medvedev, 1specimen (ZIN); **UZBEKISTAN.** *Khorezm Oblast*: Khiva, 03 July 1910, leg. E. Fisher, 1 specimen (ZIN); *Qashqadaryo Oblast*: Qamashi on NO by Guzar, 12 June 1932, leg. Pogg, 1 specimen (ZIN); Qamashi, 22 July 1932, leg. V. Gussakov, 1 specimen (ZIN); Mirishkor Reg., Urta-Bulak deposit environs, at light, 14 Apr. 2014, leg. Ya. Kovalenko, 1 specimen (CK).

Additional material without detailed label data from ZIN. A several dozens specimens. **KAZAKHSTAN.** *Aktobe Oblast*: Shalkar (Chankara), [47.8°N 59.6°E]; Temir (Kok-Dzhizha), [49.1°N 57.1°E]; *Atyrau Oblast*: Inder Lake, [48.5°N 51.8°E]; *Kyzylorda Oblast*: Kazalinsk, [45.8°N 62.1°E]; Baygekum, [44.3°N 66.5°E]; *Western Kazakhstan Oblast*: Khan Ordasy (Khanskaya Stavka), [48.8°N 47.4°E]; Uralsk, [51.2°N 51.4°E]. **RUSSIA.** *Volgograd Oblast*: Sarepta, [48.5°N 44.6°E].

Redescription. Body length from the apex of labrum to the apex of elytra 3.6–5.2 mm, males and females do not differ.

Ground colour yellow; a combination of black-brown, almost black blotches on the pronotum, elytra and abdomen form a characteristic pattern. Head and mandibles black-brown. Antennae vary from completely yellow to brownish on the club. Pronotum black-brown with a more or less wide yellow edging on the sides and narrow yellow stripe along the front edge; there with often a reddish or yellow basomedial spot, its size females is usually larger than in males, additionally it can stretch into a poorly distinguishable middle line in females (Fig. 11). Scutellum black-brown. Yellow pattern of each elytron normally (Fig. 4) forms edging, S-shaped basal mark, M-shaped medial mark, apical spot and suture stripe. Basal marks close in along the suture forming a solid yellow field; with a dark space between them like in *H. flexuosus* for a few specimens. Dark pattern of elytra ranges from black-brown to brownish almost blending with the yellow background, often reduced in basal third (e.g. Figs. 6, 11); only in some specimens the dark pattern of elytra dominates over the light pattern (Figs. 9, 13). Prosternum black-brown with yellow episternae and yellowish front margin or mostly yellow. Mesepisternum and metepisternum black-brown. Abdomen black-brown with yellow pattern; only the rear corners of ventrites and part of hypopygidium are yellow in males (Fig. 15), while females possess a more or less wide yellow edge (Fig. 16). Legs, except dark metacoxae, yellow; front legs with brownish knees and margins of tibiae.

Body moderately elongated, compressed dorsoventrally.

Head possess structure typical for the family; relatively wider in large and medium males compared with females; covered with dense, whitish hairs including labrum. Clypeus transversal, with front edge widely emarginate; gently sloping towards the labrum in females and smaller males, forming a rung over it in larger males; with a pair of tubercles on the sides of the medial line in larger males (hardly visible under the hairs) (Fig. 14). Structure of mandibles of males and females slightly different; mandibles of larger males are more elongate, their dorsal arista possesses a denticle pointed upwards or inwards. Antennae 11-segmented with 7-segmented club.

Pronotum not bordered basally; slightly narrower or comparable in width with base of elytra in females and smaller males, in medium and large males slightly wider than elytral base (Figs. 6–7). Hairs on disc dense, short, pressed, long and standing on the sides; whitish and yellowish. Puncturation dense, fine and matted.

Elytra moderately wide, $k \geq 0.60$; covered with different lengths of hairs variously raised; long hair length is comparable with the length of first spines of mesotibiae; hairs slightly longer along sides and near the elytral apex; yellowish hairs alternate with more rare dark ones. Puncturation double, dense, matted; punctures slightly depressed; the diameters of large and small punctures vary in different degrees from different specimens.

Abdomen (Figs. 15–16) covered with elevated yellowish hairs of different length; punctures with rasp-like edges; microsculpture represented by transversal creases. Postmetacoxal lines absent. Stridulatory ridge (plectrum) in males with few distinct striae in the basal third, smooth or with small creases in females.

Legs of structure typical for family, covered with yellowish or whitish hairs.

Aedeagus (Figs. 18–20) vaginate, characteristic wedge-shaped with truncate top, length 0.77–0.86 mm, tegmen surface with nested penis oriented ventrally. Lateral lobes of phallobase cuneiformly narrowed, continued into narrow lateral walls in the apical part of the tegmen (Fig. 18). Apical edge of phallobase {-shaped (bow-shaped), often with very small medial notch (Figs. 19–20). Sclerotization of dorsal surface of tegmen usually uniform (Fig. 20). Penis elongate, almost parallel-sided, narrowing in the basal third. Penis apex is asymmetric, comes forward of the endophallus loop in a shape of short, rounded lobe. Endophallus rather long, carrying a dense brush of large teeth along its length.

Judging by the general structure and orientation of the aedeagus, the morphology of the male clypeus and pronotum, and the elytral pattern, *H. heydeni* belongs to the *flexuosus* group (*sensu* Charpentier 1965).

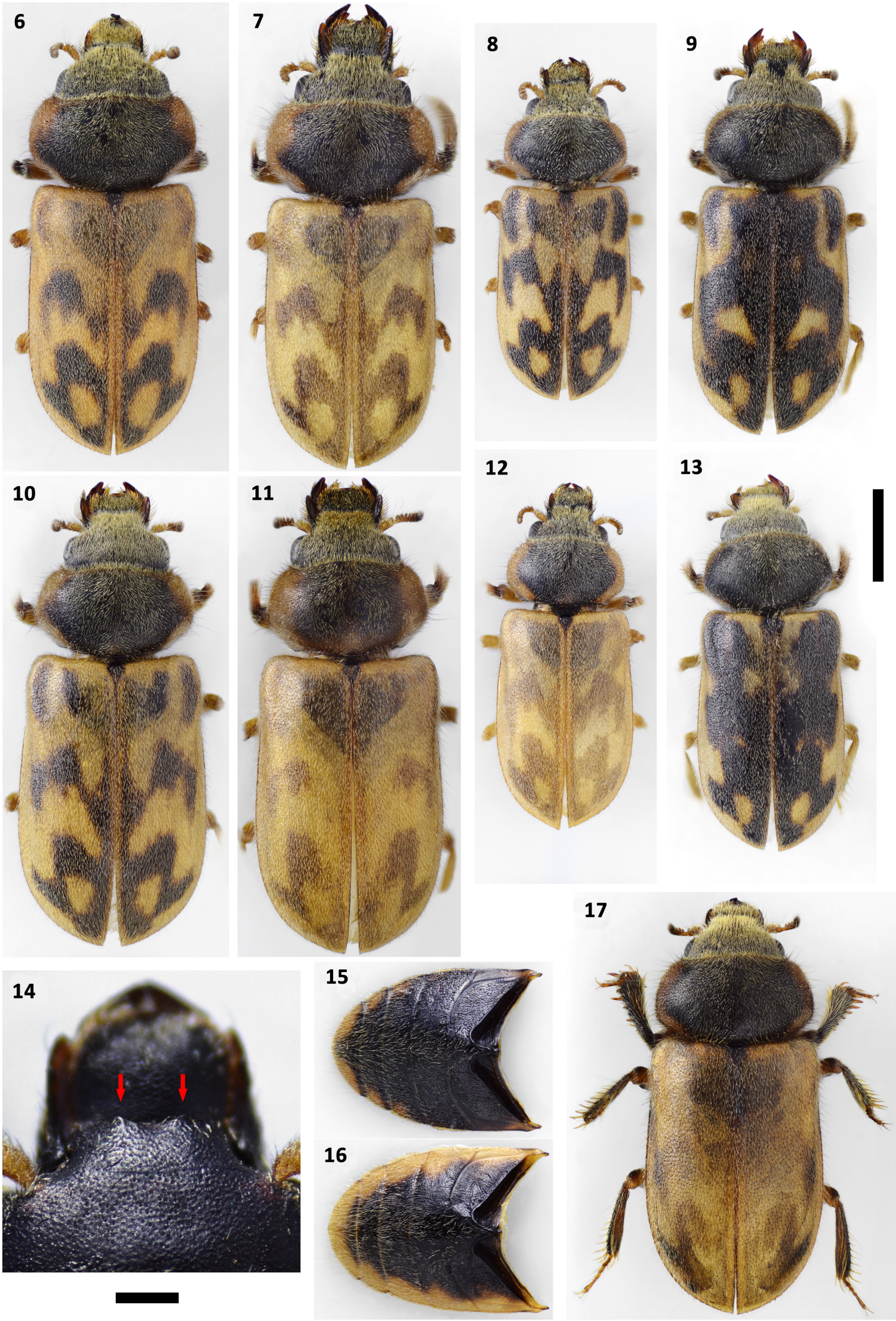
Comparison. Characteristic for *H. heydeni*: the apex of the tegmen is unsplit, characteristic bow-shaped form; legs are completely yellow, with the exception of small darkening on the front knees and tibiae; elytral pattern characteristic of *flexuosus* group of species, with yellow pattern predominant or equal in area to dark pattern.

H. heydeni and *H. flexuosus* are very similar externally (Figs. 4–5); they possess similar pattern and pubescence of elytra; they lack distinct sexual dimorphism; their aedeagi are similar in shape and structure. *H. flexuosus* is different in that it has dark body coloration; black-brown, almost black pattern predominate on the pronotum and elytra; bright pattern of elytra is either yellow or ochre, often reduced to a different degree; only some specimens (from 851) light elytron pattern prevails over dark (e.g. Fig. 17); scutellum is completely surrounded by a dark field; legs from black-brown to brownish, but not yellow; the elytral puncturing is double, large punctures usually coarser than small; aedeagus (Figs. 21–23) slightly larger; lateral walls in tegmen apical part are wide (Fig. 21); apical edge of phallobase rounded, with a medial short split (seen as a dark, elongate umbilicus at low magnification) (Figs. 22–23); sclerotization of dorsal side of tegmen uneven (Fig. 23); penis fusiform; penis apex protrudes significantly forward of the endophallus loop, looks like a tongue-like lobe; endophallus relatively short; teeth of endophallus are significantly smaller in size. Dark specimens of *H. heydeni* are similar in appearance with *H. flexuosus*; their legs remain yellow.

H. heydeni and *H. parallelus* are similar in coloration of body and legs. *H. parallelus* is larger; has elongate elytra with $k<0.60$; elytra with short and dense pubescence; bright pattern of elytra often greenish-yellow; sexual dimorphism is distinct; hypermandibular males are common; phallobase apex is two-lobed.

Biology. Poorly studied. A few specimens were collected in sandy-gravel substrate on the shore of saline lake Kyzylkol (Kazakhstan) together with mass *H. parallelus*. Two specimens were collected on sandy shore of Syrdarja River (Kazakhstan) together with *Augyles* cf. *flavidus* (Rossi, 1794) and *H. fenestratus* (Thunberg, 1784).

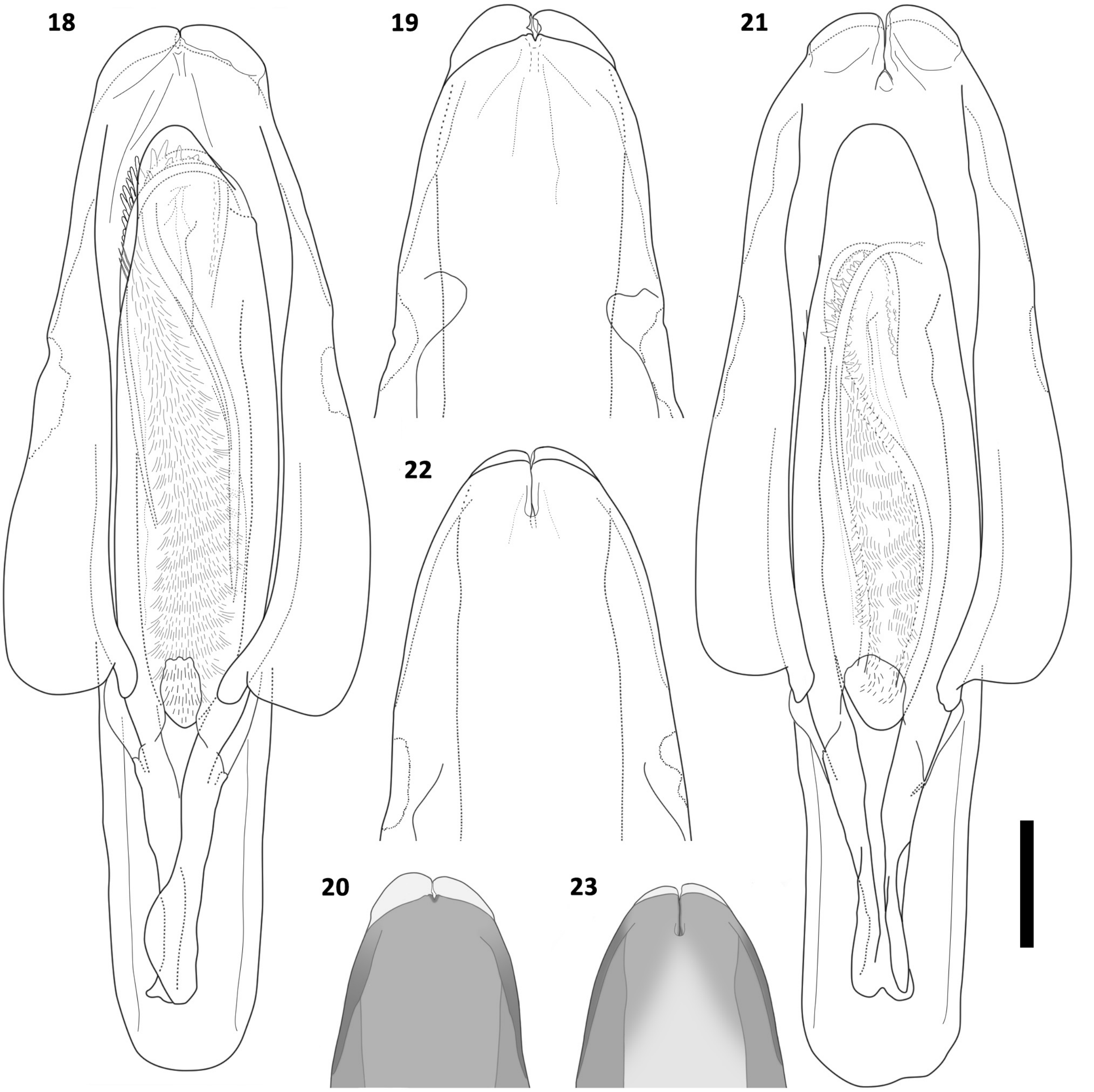
FIGURES 2–5. *Heterocerus* spp. 2—male *H. heydeni* from collection ZIN (photo by A. Kovalev); 3—labels of this specimen: handwriting by F.A. Zaitsev (ink), handwriting by R. Charpentier (pencil); 4—*H. heydeni* general view, male (South Kazakhstan); 5—*H. flexuosus* general view, male (South Kazakhstan). Scale bar = 1 mm.



FIGURES 6–17. Variability and sexual dimorphism of *Heterocerus* spp. 6–9—*H. heydeni*, males (South Kazakhstan); 10–13—*H. heydeni*, females (South Kazakhstan); 14—*H. heydeni*, tubercles on clypeus of male, hairs removed; 15—*H. heydeni*, male abdomen; 16—*H. heydeni*, female abdomen; 17—*H. flexuosus*, female with extremely light elytra (Crimea). Scale bars = 1 mm (Figs. 6–13, 15–17) and 0.2 mm (Fig. 14).

Prevalent part of material is attracted to artificial light. Attraction of beetles to light was observed in saline habitats, sandy and sand-saline deserts, riparian forests (tugay forest), in stream valleys at elevations up to 930 m a.s.l., in steppes and once in a steppe forest plantation. Beetles were observed at distances of up to 12 km from permanent large water bodies. The following species were attracted to light together with *H. heydeni*: *H. parallelus*, *H. flexuosus*, *H. fenestratus*, *H. mus* Charpentier, 1965, *H. obsoletus* Curtis, 1828, *H. fusculus* Kiesenwetter, 1843, *Augyles.* cf. *flavidus*, *A. turanicus* (Reitter, 1887), *A. dilutissimus* (Reitter, 1887). It is one of the most common species in southern Kazakhstan.

Distribution. Dzhizak and Alai (Zaitzev 1908). Former Zakaspiyskaya, Samarkand and Fergana oblasts (Jacobson 1913), presently—territories of Uzbekistan, Turkmenistan and Kyrgyzstan (catalog data need clarification), Tadzhikistan (Hebauer 1991); ? SW Iran (Skalický 1998) (material study required). South of the European part of Russia east to the Ural Mountains, Crimean Peninsula, Kazakhstan excluding the north-east, Turkmenistan, Uzbekistan (Fig. 24).



FIGURES 18–23. Male genitalia of *Heterocerus* spp. 18—aedeagus *H. heydeni*, ventrally; 19—tegmen apex *H. heydeni*, dorsally; 20—tegmen sclerotization *H. heydeni*, dorsal; 21—aedeagus *H. flexuosus*, ventrally; 22—tegmen apex *H. flexuosus*, dorsally; 23—tegmen sclerotization *H. flexuosus*, dorsal. On Figs. 18 & 21 most of the sclerites and membranes connecting the lateral lobes of tegmen and penis base are omitted. Scale bar = 0.1 mm.

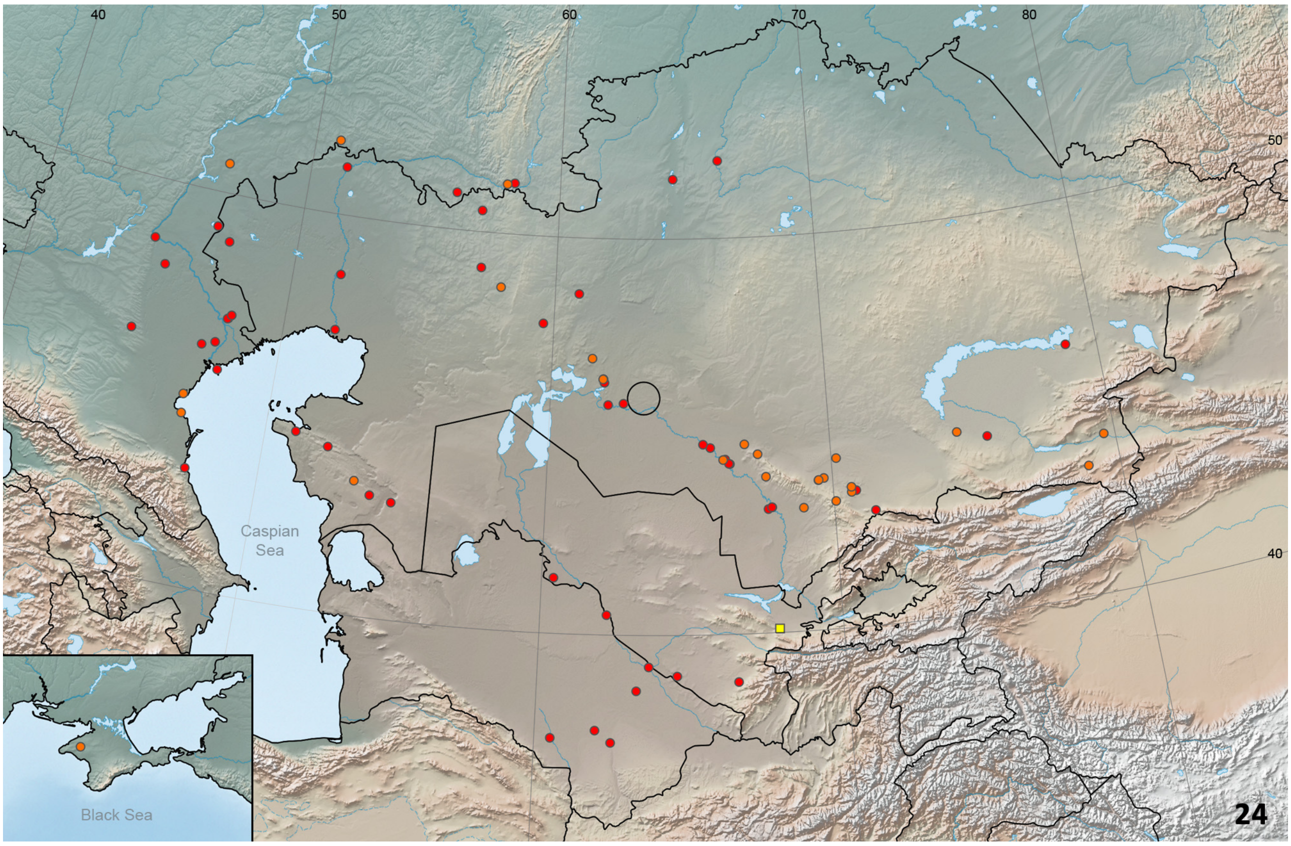


FIGURE 24. Distribution of *Heterocerus heydeni*. Circles—studied material: red circles—records only *H. heydeni*; orange circles—records *H. heydeni* and *H. flexuosus*; square—type locality (Dzhizak, Uzbekistan).

Discussion

Breit (1916) and Charpentier (1979) regard *H. heydeni*, *H. hauseri* and a number of other taxa as color forms of *H. flexuosus*. Breit points out the wide distribution of brightly colored *H. flexuosus* in Central Asia and in the south of European Russia. The form with yellow legs is prevalent in Mongolia, Central Asia, North Africa and rare in Europe according to Charpentier.

In reality *H. heydeni* and *H. flexuosus* are sympatric sibling species, which can often be collected at the same site (Fig. 24). The transitional forms between the two types of the aedeagus structure have not been observed. External morphological features of both species are fairly constant and deviations from them are quite rare. The variability of the elytral coloring does not correlate with the coloring of the legs. Along with the male genital structures, leg coloration may be considered reliable diagnostic feature for both species. The characteristics of the elytral pattern overlap partially in both species, however if bigger series are available, this feature works fairly good. Coloration of the scutellar area of elytra and of elytral puncturing may be considered auxiliary diagnostic features.

Obviously the color forms of *H. flexuosus* in Charpentier and Breit's understanding are in fact a complex of species, described or not. All synonyms of *H. flexuosus* require revision. For example, the validity of *Heterocerus fausti* Reitter, 1879 has been restored recently (Sazhnev 2018). It is likely that *H. senegalensis* Fairmaire, 1894 is a valid species. Aedeagus of Senegalese specimen of "*H. flexuosus*" (Charpentier 1965; Fig. 119) is clearly different from *H. flexuosus* in the structure of aedeagus.

The DNA barcoding already became frequently used and useful tool in the species identification (Hebert *et al*. 2003). However, barcoding data on heterocerids are still scarce and incomplete. The analysis of the available barcoding data for this family shows huge gaps and suggested samples missidentification or paraphyly of known genera. On the other hand DNA barcodes proved very useful for unambiguous species delimitation. The previous taxonomic research on Heteroceridae revealed often very contrasting hypotheses. This is likely due to the morphological uniformity of these beetles, which however does not reflect the real species (genetic) diversity. From this point of view it is clear that employing molecular techniques in the research of mud-loving variegated beetles should increase in the future to gain precise and stable image of their real diversity, taxonomy and evolution.

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