Beetles of the family Heteroceridae (Insecta: Coleoptera) in extreme environments

Alexey S. Sazhnev

I.D. Papanin Institute for Biology of Inland Waters, Russian Academy of Sciences, Borok 109, Nekouz District, Yaroslavl Region, 152742 Russia

sazh@list.ru

Received: 23.03.2020

Accepted: 09.04.2020

Published online: 06.05.2020

DOI: 10.23859/estr-200323a

UDC 574.43; 574.38

ISSN 2619-094X Print

ISSN 2619-0931 Online

Translated by S.V. Nikolaeva

Heterocerid beetles (Heteroceridae) are morphologically and ecologically uniform (all members of the family are burrowing stratobionts). Nevertheless, some groups are obviously in an active and dynamic stage of evolution, and some species have a high ecological valency. This has allowed Heteroceridae to colonize semiaquatic environments almost globally and to inhabit some extreme and adverse biotopes.

Keywords: ecology, life form, Heteroceridae, variegated mud-loving beetles, ecotone, ecological niche, distribution.

Sazhnev, A.S., 2020. Beetles of the family Heteroceridae (Insecta: Coleoptera) in extreme environments. *Ecosystem Transformation* 3 (2), 22–31.

Introduction

The natural and anthropogenic transformation of semiaquatic ecosystems is extremely rapid, due to a range of hydrological environmental factors and natural and climatic conditions, as well as increasing human impact. Terrestrial semiaquatic ecosystems have an intrazonal character, directly dependent on channel and hydrological processes of basins, resulting in their natural volatility and instability. Such semiaquatic ecosystems can be considered as ecotonic, located in the contact zone of two and/or more ecosystems (aquatic, terrestrial, air), the communities of which under such conditions are not fully complete and thus not quite stable. Semiaquatic ecosystems are characterized by external disturbances (floods, surges, changes in water level), which counteract the internal direction of succession, returning formed communities to earlier stages, which leads to successional process cycling. Therefore, unique heterotrophic communities are formed in the water-land ecotones, in which coleopteran insects (Coleoptera) play a significant role. Among the coleopterans in semiaquatic communities, the stenotopic ecomorphological group of semi-aquatic beetles plays an important role (Jäch, 1998). The

family Heteroceridae MacLeay, 1825 is among the most successful members of this group; heterocerids have evolved in the unstable habitats of water-land ecotones and show high taxonomic diversity and abundance in semiaquatic communities.

The world fauna of variegated mud-loving beetles (Heteroceridae), totals 349 extant and four extinct species (pers. data); previous estimates ranged from 320–370 species (Mascagni, 2014; Skalický and Ezer, 2014), because the fauna has not been revised. Moreover, new taxa are being described annually.

Adults and larva of burrowing stratobionts (including Heteroceridae) construct branched networks of tunnels and chambers in a moist soft substrate, which are used for feeding, egg laying and pupation. A similar lifestyle is characteristic of many inhabitants of water – land structures (supralittoral, aeropelal zone – a community characteristic of silted sand saturated with water just above the water edge (Chertoprud, 2011)). At high densities, Heteroceridae, together with similar burrowing stratobionts, give the substrate a specific microrelief that forms accessible microniches for other burrowing stratobionts and other organisms. Many types of heterocerids live syntopically (up to four species), populating a single

biotope (Sazhnev, 2016). Heteroceridae use acoustic communication by stridulation. Adults and larvae of Heteroceridae obtain nutrition as indiscriminate detritophages and/or microphytophages (algodetritophages), collectors that absorb organic detritus, microorganisms, diatoms, and other types of algae together with the substrate (Sazhnev, 2018a). Being detritophages, Heteroceridae are involved in the processing of organics included in detrital food webs, and therefore in the transfer of matter and energy in the transition zone between the two media.

Despite their relative stenotopicity, Heteroceridae are distributed around the world (except for Antarctica) and populate the marginal zone of diverse water bodies in a wide range of environmental conditions, including extreme ones. The purpose of this work is to give an overview of Heteroceridae living in conditions generally atypical for the group.

Materials and methods

This review is based on analysis of the available literature on the fauna, biology, and ecology of the family Heteroceridae, as well as my own observations and studied collection material from different climatic zones and subzones of the Palearctic and Oriental region.

The map was created using the online project Simplemapp (http://www.simplemapp.net). The dendrogram (Jaccard coefficient, single linkage based on qualitative data) was created using the STATISTICA 6.1 software package. The classification of habitats and the division of the Palearctic is given according to Emelyanov (1974).

Results

Main Trends for Habitat Selection in Heteroceridae

In general, species of the family Heteroceridae occur in temperate, subtropical, and tropical latitudes, but due to their high plasticity and vagility, some of them have colonized areas remote from their main range. The following factors are of decisive importance for Heteroceridae habitat choice: the hydrological regime of the water body, the humidity of the substrate, the nature of the soil, the presence of a food supply and the type of waterline zone (Sazhnev, 2016).

The properties of individual populations in specific local conditions are usually considered as a realized niche (the ecological equivalent of a population) (Hutchinson, 1957). The number of niche dimensions ("licenses" (Levchenko, 1993)) can be reduced to three generalized ones: 1) resources; 2) non-resource limiting factors; 3) organization of the niche carrier. The term "niche" is equally applicable to both the organism and the population or species (Pianka, 1981).

The forage base and a certain substrate structure are used as a resource measurement of a niche for

Heteroceridae species. As mentioned above, Heteroceridae are indiscriminate algo-detritophages. When choosing a habitat, they avoid frequently flushed areas of the margin of the water body, where detritus does not accumulate, as well as steep edges, preferring the second type of waterline zone (Przhiboro, 2001), a meter-wide coastal zone, usually with sediments of plant debris and away from the influence of waves. In addition to the trophic component of the ecological niche, organisms (in particular, Coleoptera) that are associated with substrates are no less important than the method of using the medium as a resource (Kashcheev, 1999); this is manifested morphologically. At all stages of ontogenesis, Heteroceridae are closely associated with the substrate, and imagoes are the most distinctive of semiaquatic burrowing stratobiont Coleoptera. Specialization for digging includes a cylindrical body shape with a well-defined shape, tapering at the prothorax and mesothorax boundary, which gives mobility to the front of the body when digging, a spatulate head with mandibles, and the presence of teeth on the tibiae, especially the front tibiae (fossorial legs). Some psammophilic species, for example, *Heterocerus fausti* Reitter, 1879, show ecomorphological adaptations to sandy substrate conditions (psammophilia) in the form of an increase in the length of the tarsal claws (Sazhnev, 2018b). Individual species of Heteroceridae, in some cases, can fit the role of niche carriers, due to their life form and morphological adaptations.

Species of the family Heteroceridae prefer finely dispersed clay and sand types of soil with sufficient moisture, on which colonies are often formed with pronounced biotopic sympatry (cohabitation of species). They less frequently inhabit pebble beaches, choosing microstations between the stones when they do. In these environments, heterocerid occurrences are irregular. Heteroceridae are not recorded in wetlands and semiaquatic areas with dense vegetation that forms sod.

The highest population density of Heteroceridae was recorded in southern Brazil, on the sandy beaches of the Atlantic Ocean (*Heterocerus freudei* (Pacheco, 1973) – 162 spec./m² (Vanin et al., 1995)). In southern Siberia, in the salt marshes, the population density of *Heterocerus parallelus* Gebler, 1830 reaches 110 spec./m² (Mordkovich and Lyubchanskii, 2017). In our studies (May–June), the average population density of heterocerids on sandy substrates, the most populated ones, was 72.0 ± 5.2 spec./m² for adults, 27.5 ± 2.6 spec./m² for adults (Sazhnev, 2018a). It should be noted that the density of colonies is also related to the strategy of sexual behavior of different species, which was shown for the North American *Heterocerus pallidus* Say, 1823 and *Augyles auromicans* Kiesenwetter, 1851 (Kaufmann, 1987).

The main non-resource limiting environmental factors that affect Heteroceridae are temperature, humidity, predators and parasites.

In poikilothermic animals, the external temperature directly affects the biochemical and physiological reactions in the body (Poole and Berman, 2001), determining the choice of specific habitats, and also forming the boundaries of the distribution range of species and populations (Sunday et al., 2011). For Heteroceridae, data on the influence on them of the environmental temperature factor are known from a study of the heat resistance of invertebrates of different trophic levels in semiaquatic soil communities (Franken et al., 2017). The obtained values of the critical thermal maximum for *Heterocerus* sp. turned out to be in the range of mean $CT_{max} = 48.6\text{--}51.7\text{ }^{\circ}\text{C}$ with an average value of $CT_{max} = 50\text{ }^{\circ}\text{C}$ (Franken et al., 2017). An inverse correlation was found between the critical thermal maximum and the size of the body of adult specimens, which is also consistent with our data on *Heterocerus fenestratus* (Thunberg, 1784), when studying individual populations which exhibit a decrease in mean body sizes from north to south within their range (pers. data). The high values of the critical thermal maximum of CT_{max} for heterocerids can be explained by the southern origin of Heteroceridae. In general, the greatest species diversity of heterocerids occurs in subtropical and tropical regions; the possible main centers of speciation of the family are in Southeast Asia (*Augyles*, *Heterocerus*) and in the north of South America (*Tropicus*). In the Palearctic, the highest percentage of endemism (33%) was noted for the Orthrian region.

The optimal humidity content of populated substrates for adults and Heteroceridae larvae ranges from 30 to 70% (Kaufmann and Stansly, 1979). According to published data, the minimum substrate moisture content for the Mediterranean *Heterocerus aragonicus* Kiesenwetter, 1850 is 23% (Pierre, 1946), and the American species *Heterocerus pallidus* Say, 1823 leaves its burrows when the humidity drops below 25% (Kaufmann and Stansly, 1979). It was noted that larvae inhabit more humid microstations close to the waterline; this is a form of coadaptation expressed in the microzonal distribution in the biotope of the developmental stages of the species, nutrition at different times of appearance in the substrate, and different duration of contact with the substrate (Sazhnev, 2018a).

During inundation, Heteroceridae leave their habitats. The beetles are covered with hydrophobic pubescence that prevent wetting, so that the adult heterocerids can stay on the surface of the water and take off from it and can also wait on the stems of herbaceous plants for short-term floods. Adult beetles have been reported under water at a considerable distance from the water's edge and in the benthos, probably associated with seasonal floods or wind-driven oscillations (Heteroceridae can trap air in the subelytral cavity, into which spiracles open).

Influence of predators and parasites is a biotic factor limiting the populations of Heteroceridae species. Different groups of zoophages, both invertebrates and vertebrates, feed on heterocerids. Members of the family Carabidae, such as the closely related genera *Dyschirius* and *Dyschiriodes*, and possibly *Clivina*, prey on the preimaginal stages of Heteroceridae (Sazhnev, 2018b) and stand out as specialized predators in the Palearctic. Additionally, there are parasitic organisms and symbionts which at present have unclear relationships with Heteroceridae, and the study of which is at an initial stage and needs to be continued (Sazhnev, 2018c). Competitive trophic relations with heterocerids include cohabiting species of the family, as well as other algodetritophages (*Bledius*, *Carpelimus*, etc.) and, to some extent, indiscriminate polyphages such as Tridactylidae.

Extreme environments

Historically (Li et al., 2020; Prokin and Ren, 2011), heterocerids are characterized by morphological and ecotopic uniformism, conservatism in the formation of morphotypes and life forms, which is primarily due to their lifestyle. Despite this, the family shows high adaptive abilities, which have allowed individual Heteroceridae taxa to colonize some adverse, and often extreme biotopes, such as seacoasts, islands, zonal tundra, highlands, deserts, and salt flats.

Heterocerids are able to withstand high environmental acidity and can withstand the presence of sulfates and heavy metals in the soil of habitats (Vinikour, 1979), while almost not accumulating them (Sazhnev and Udodenko, 2018).

Northern and southern boundaries of the range of the family

The range is a combined effect of both modern and historic conditions that determine the distribution of the taxon. The actual boundaries of the range are limited by environmental parameters (climatic, edaphic, competitive), suitable for the organism, as well as by its dispersal ability. As a rule, the most widespread ranges are characterized by low-specialized flexible species with high adaptive ability, which can also colonize extreme types of habitats.

The southern border of the Arctic is considered to be the limit of the distribution of tundra and forest-tundra at high latitudes of the Northern Hemisphere, formed at the beginning of the Oligocene. Coleoptera, as a macrotaxon, comprise 13% of the species diversity of insects in the Arctic (Chernov et al., 2014). Most species, including Heteroceridae, demonstrate adaptive capabilities in the Arctic to pessimal temperature conditions at the edge of their range. The fauna of Heteroceridae of the north is allochthonous, and faunogenesis is determined by the retreat of the last Holocene glacier and the invasion of species from more southern territories.

Quaternary records of Heteroceridae in the Northern Hemisphere (~ 42000–18000 years), which include mainly modern species, are known from the UK, Russia, Canada, and the USA (Fossilworks, 2019).

Although Heteroceridae records are rare in the Russian Arctic, four species of the family are known from this territory. The most northern finds come from the Bolshezemelskaya tundra, N 68.3° and belong to the boreal Holarctic *Augyles intermedius* (Kiesenwetter, 1843) (Kolesnikova et al., 2016; Sazhnev, 2018e). In addition, three further species have been found above the line of the Arctic Circle. The first is *Heterocerus fuscus* Kiesenwetter, 1843, reported from Agrafena Island near Zhigansk at latitude N 66.8° (Poppius, 1907); probably, this record in fact refers to the close polyzonal species *Heterocerus fenestratus* (Thunberg, 1784), known from the adjacent subarctic territories and the north of the Arctic (Mannerheim, 1853). The other two, *Heterocerus obsoletus* Curtis, 1828 and *Heterocerus flexuosus* Stephens, 1828, were found in the Poyakonda region (N 66.5°) (Sazhnev, 2018e).

In the zonal tundra, members of the family Heteroceridae are located on the edge of their range and are found locally on protected coasts (including coastal meadows), estuaries and along the banks of large rivers. The latter probably serve as resettlement channels, because for the most part they have a northern direction of flow, and their valleys are historically quite ancient and devoid of permafrost. On the other hand, the milder seaside climate of Europe, located in the zone of influence of the warm Gulf Stream, allows some species of Heteroceridae to more actively penetrate to the north. For example, it is here that *Augyles maritimus* (Guérin-Ménéville, 1844) can be found.

In the inner tundra and areas with a surface horizon of permafrost, Heteroceridae probably do not occur. The northern edge, as presently known, of the distribution of the family in the European part is determined by the coastline of the Arctic Ocean and is located on the line of the 68th parallel (Fig. 1). In the Asian part of Eurasia and in North America, the range of the family correlates with the distribution of permafrost.

One of the limiting factors in the Arctic is the high waterlogging of wetland areas. The increased humidity of the substrate combined with low temperatures is unfavorable for the development of larvae and does not allow them to complete their life cycle. A similar situation is observed in the central regions of Western Siberia, where the fauna of Heteroceridae is depleted and represented by 2–3 species. This can be explained by the relatively young age of the region's ecosystems (virtually destroyed by Pleistocene glaciations), its inundation in the Pleistocene interglacials (Arkhipov, 1971), as well as modern hydrographic conditions and waterlogging processes.

The southern border of the distribution of Heteroceridae is reported in Patagonia (S 53.1°), it was from there (from the port of Punta Arenas) that *Heterocerus subantarcticus* Trémouilles, 1999, previously considered a separate species, but subsequently synonymized (Sazhnev, 2019) under the Holarctic *Heterocerus fenestratus*. The question of the origin of populations of *Heterocerus fenestratus* in the southern hemisphere remains open. In 2015, *Heterocerus fenestratus* was discovered in Chile much to the north, 36 km from the city of Santiago (Sazhnev, 2019). Probably the disjunction of the range of the species in the New World could indicate an invasive population, but phylogeographic studies are required.

Sea coasts and islands

In general, marine spaces represent natural ecological and geographical barriers for most Heteroceridae, but some species can be attributed to typical littoral forms. The sandy beaches of the Atlantic are inhabited by the South American *Heterocerus freudei*, and in the Palearctic, species on the northern periphery of their ranges, *Augyles maritimus*, *Heterocerus flexuosus*, and *H. obsoletus* are confined to the sea coasts; probably similar species originated as littoral. Many island species have colonized marine littoral as a biotope.

It is known that island faunas have a very specific appearance: they are depleted due to the peculiarities of faunogenesis, temporary and geographical isolation, limited living space, and extreme climatic conditions. Geographical isolation is probably not a significant barrier to distribution for some Heteroceridae, because they are known for some of oceanic islands far remote from the continents. Endemic species of heterocerids are described from the south of New Zealand (*Heterocerus novaeselandiae* Charpentier, 1968) and Fiji (*Heterocerus fijiensis* Charpentier, 1968) (Charpentier, 1968), *Tropicus* sp. is known from the Galapagos Islands (Peck, 2006) and *Heterocerus* sp. from St. Helena (pers. data). At present endemic species of Heteroceridae are known for the islands of Oceania, Southeast Asia, the West Indies, Madagascar (Charpentier, 1965, 1968; Grouvelle, 1896; Mascagni, 1993; Mascagni and Monte, 2001; Mascagni and Skalický, 2007; Peck, 2005; Skalický, 2005, 2010), some of them, when examined in detail, are likely to be regional subendemics. Migration processes play a significant role in the formation of the Heteroceridae fauna of many islands: for example, *Heterocerus elongatus* Grouvelle, 1896, known from Mauritius, originates from the East Coast of South Africa and Madagascar (Charpentier, 1965). The species composition of the Heteroceridae of the mainland islands largely repeats the continental fauna; for example, endemic species are absent from Japan, Sakhalin, and the Kuril Islands (Sazhnev, 2018; Ska-

Fig. 1. Extreme points of the distribution range of Heteroceridae.

lický, 2008), and the fauna of these islands is represented mainly by stenopean nemoral species.

According to modern data, heterocerids are absent from the fauna of Greenland, Antarctic, the Arctic and most Pacific islands, including Hawaii.

Deserts and salt flats

Despite their semiaquatic way of life, Heteroceridae inhabit territories with arid climates on almost all continents: they are known from the deserts of Africa, Australia, Asia and America. Probably, one of the leading factors ensuring the survival of heterocerids in arid conditions is the presence of wet mud, which is preserved in riverbeds and at the bottom of drying basins, as well as under the crusts of large salt flats.

In the Palearctic, several faunal centers of heterocerids can be distinguished, occupying certain biogeographic regions. The most specific of them (Fig. 2) are found in the evergreen subtropical regions of the Palearctic – in the Ortrian (33 endemic and subendemic species) and the Hesperian (Mediterranean-Macaronesian) (10 endemic). In third place in terms of the number of species (28) and the percentage of endemism among the Heteroceridae of the Palearctic (about 18.5%) is the Sethian desert region.

In another interpretation scheme of biogeographical zoning, the recently described (Abdurakhmanov et al., 2017) Tethyan desert-steppe region (belt) is recognized. In it, one can distinguish (following the example of other systematic groups) two associations of taxonomic diversity of heterocerids: East Tethyan (Middle and Asia Minor, Middle East, Iran, Transcaucasia, Afghanistan) and West Tethyan (North Africa and Southern Europe). It must be remembered that

the borders of this division are rather blurred and have transitional zones (bridges), such as the south of the European part of Russia, the Sinai Peninsula, and the Greater Caucasus, through which fauna is exchanged. Probably, the Tethyan region (at least 3 elementary faunas of Heteroceridae related to the centers of diversity and speciation) is the main donor in the formation of the allochthonous fauna of Heteroceridae in Russia (and the north of the Palearctic as a whole), with the exception of some stenopean species of the Far East.

Presumably, the ancient foci of the formation of the fauna of the heterocerids of Central Asia, and in many ways the modern arid zone of the Palearctic, were located on the shores of the Tethys-descendant seas, and probably had an island type of faunogenesis (as a supralittoral group); starting from the Oligocene, they were formed as the Tethys was shrinking and the region was become more arid, while orogeny intensified. This resulted in species being restricted to salt marshes and haline basins, well as in their distribution exclusively along the coastline in the border areas of their range. This can explain the disjunctions observed in the range of some groups (genus *Micilus*), which are likely to be ecological rather than geographical in nature.

The range of *Micilus minutissimus* J.R. Sahlberg, 1900, a poorly studied assemblage of the closely related species *Augyles euphraticus* Kiesenwetter, 1843, *A. kulabensis* Reitter, 1900, *A. nebulosus* Kuwert, 1890, and *A. turanicus* Reitter, 1887 (some taxa may be synonymous with the latter), and desert-steppe species of the “*flexuosus*” group (*Heterocerus persicus* Mascagni, 1989, *H. fausti* Reitter, 1879, and

H. heydeni Kuwert, 1890 (Litovkin et al., 2019)) do not occur outside the Tethyan region. At the same time, some species of the “*flexuosus*” group immigrated to Europe. For example, the psammophilic species *Heterocerus parallelus*, reaching the south of the Czech Republic and Germany, as well as *H. flexuosus*, which reaches far to the north along the sea coasts of Europe, but which is found locally along intrazonal saline biotopes along the mainland of its European range. The range of Asian species in Europe can be regarded as an “area of penetration,” which is distinguished from their “area of dominance”, i.e. their main range, by their more sporadic occurrence (Bobrinsky et al., 1946; Prokin et al., 2019).

Of the characters in Heteroceridae adaptive to arid climates, one can distinguish the prevailing light color of desert-steppe species, which is most likely cryptic when the species inhabits the sand. In the psammophilic *Heterocerus fausti*, living in the Caspian sands, elongated tarsal claws also indicate adaptability to loose substrates. It is likely that species living in an arid climate are capable of hibernation under drought conditions: adults of Heteroceridae are often found at the bottom of dry basins.

Highlands

In the mountains, Heteroceridae are generally riparian and are quite rare. The potential for vertical distribution of Heteroceridae is realized in different regions in different ways, but there are probably no alpine (in the broad sense) species among them, and all of them are only conditionally montane.

The altitudinal distribution is heterogeneous, which is associated with the features of water bodies and the microstations of their shores. In the mountains, there is a shortage of habitats for heterocerids; most of the edges of water bodies are not suitable for adults or preimaginal stages, because they are often composed of stones and pebbles, and mountain rivers have an irregular regime associated with rain floods (Sazhnev, 2017). In the middle and high mountains, heterocerids inhabit landscapes in river valleys and on plateaus; this is especially pronounced in Transcaucasia (Zaitsev, 1946). In general, heterocerids in mountainous regions, as well as on plains, are more confined to steppe and steppe landscapes, where streams with a weak current and standing water bodies are found.

Probably, heterocerids do not penetrate above the border of the subalpine zone. It must be remem-

Fig. 2. Dendrogram of similarity of Heteroceridae faunas of the Palearctic. The numbering of regions and subregions of the Palearctic is given by: Emelyanov, 1974. Explanation: I – Circumpolar tundra Region: IA – Hyperborean tundra Subregion, IB – Northern Atlantic Subregion, IC – Northern Pacific Subregion; II – Euro-Siberian taiga (boreal) Region: IIA – Western Siberian Subregion, IIB – Eastern Siberian Subregion; III – European Nemoral Region; IV – Stenopean (Manchurian-Northern Chinese-North-Japanese Region); V – Hesperian (Mediterranean-Macaronesian) evergreen forest (subtropical) Region: VA – Macaronesian Subregion, VB – Mediterranean Subregion; VI – Orthrian (Himalayan-South Chinese-South Japanese) evergreen forest subtropical Region: VIA – West Himalayan Subregion, VIB – Eastern Orthrian Subregion; VII – Scythian steppe Region: VIIA – West Scythian Subregion, VIIB – East Scythian Subregion; VIII – Sethian (Sahara-Gobi desert) Region: VIIIA – Sahar-Arabian Subregion, VIIIB – Irano-Turanian Subregion, VIIIC – Central Asiatic Subregion.

bered that the height of the subalpine zone is different at different latitudes. For example, in the Caucasus, the subalpine zone is located at an altitude of 1800–2300 m above sea level, and on the southern slopes of the Himalayas its height ranges from 3200 to 4000 m above sea level.

The altitude record for Heteroceridae was registered in Kyrgyzstan (Tengizbai Pass), where *Augyles flavidus* (P. Rossi, 1794) was found at an altitude of 3300–3800 m above sea level. (Mascagni, 2003), probably at the upper limit of altitude. *Augyles hartmanni* Mascagni, 2003 (2600 m above sea level) was described from the highlands of Nepal, at altitudes of 2000–2100 m above sea level. *Heterocerus jujuyensis* Trémouilles, 1999 and *H. catamarcensis* Skalický, 2003 (Skalický, 2003; Trémouilles, 1999) were found in Argentina. In the Caucasus, *Heterocerus fenestratus* and *H. obsoletus* (pers. data) rise into the subalpine zone (1900–2200 m above sea level). *Heterocerus fenestratus*, the most successful and ecologically adaptable species of Heteroceridae, was found in China at heights of 2600–2900 m above sea level in the Tsaidam “salt marshes” (Zaitzev, 1910).

Conclusions

Contrary to the initial conservatism in the morphology and ecology of the family Heteroceridae, they have managed to spread over almost all regions of the planet, populate the contour biotopes of all continents (except Antarctica) and remote oceanic islands, including extreme biotopes, to penetrate high latitudes, zonal tundra, deserts and highlands. Based on the example of one species, *Heterocerus fenestratus*, which is known from the northern and southern hemispheres, capable of dwelling in the calderas of volcanoes, at altitudes > 2000 m above sea level, on the banks of high salinity water bodies, and has colonized environments toxic to other organisms, we can conclude that this is a group of organisms with a very high environmental valency.

Acknowledgments

The work was performed as part of the state assignment of the Ministry of Science and Higher Education No. AAAA-A18-118012690105-0.

References

- Abdurakhmanov, G.M., Nabozhenko, M.V., Abdurakhmanov, A.G., Teymurov, A.A., Daudova, M.G., Magomedova, M.Z., Gasangadzhieva, A.G., Gadzhiev, A.A., Ivanushenko, Yu.Yu., Klycheva, S.M., 2017. Sravnitelny analiz sostava nazemnoy fauny i flory Tetiyskoy pustynno-stepnoy oblasti Palearktiki i biogeograficheskie granitsy Kavkaza. Soobshchenie 1. Nazemnaya fauna II [Comparative analysis of the composition of the terrestrial fauna and flora of the Tethys desert-steppe region of Palearctica, biogeographic boundaries of the Caucasus. Communication 1. Terrestrial fauna II]. *Yug Rossii: ekologiya, razvitie [South of Russia: ecology, development]* 12 (2): 9–45. (In Russian). <https://doi.org/10.18470/1992-1098-2017-2-9-45>
- Arkhipov, S.A., 1971. Chetvertichnyi period v Zapadnoy Sibiri [Quaternary Period of Western Siberia]. Nauka, Novosibirsk, USSR, 331 p. (In Russian).
- Bobrinsky, N.A., Zenkevich, L.A., Birshstein, Ya.A., 1946. Geografiya zhivotnykh [Animal Geography]. Sovetskaya nauka, Moscow, USSR, 453 p. (In Russian).
- Charpentier, R., 1965. A monograph of the family Heteroceridae of the Ethiopian Region. In: Bertil Hanström (ed.), *South African Animal Life. II. Result of the Lund University expedition in 1950–1951. Vol. XI*. Swedish Natural Science Research Council, Stockholm – VA, Sweden, 215–343.
- Charpentier, R., 1968. A monograph of the family Heteroceridae (Coleoptera) of the Notogean Region. *Arkiv für Zoologie* 20, 205–241.
- Chernov, Yu.I., Makarova, O.L., Penev, L.D., Khruleva, O.A., 2014. Otryad zhestokrylykh (Insecta, Coleoptera) v faune Arktiki. Soobshchenie 1. Sostav fauny [The beetles (Insecta, Coleoptera) in the Arctic fauna. Communication 1. Faunal composition]. *Zoologicheskii zhurnal [Russian Journal of Zoology]* 93 (1), 7–44. (In Russian). <https://doi.org/10.7868/S004451341401005X>
- Chertoprud, M.V., 2011. Raznoobrazie i klassifikatsiya reofilnykh soobshchestv makrobentosa sredney polosy Evropeyskoy Rossii [Diversity and classification of rheophilic communities of macrobenthos in middle latitudes of European Russia]. *Zhurnal Obshchey biologii [Journal of General Biology]* 72 (1), 51–73. (In Russian).
- Emeljanov, A.F., 1974. Predlozheniya po klassifikatsii i nomenclature arealov [Proposals on the classification and nomenclature of ranges]. *Entomologicheskoe obozrenie [Revue d'Entomologie de l'URSS]* 53 (3), 497–522. (In Russian).
- Fossilworks, 2019. Web page. URL: <http://fossilworks.org> (accessed: 03.12.2019).
- Franken, O., Huizinga, M., Ellers, J., Berg, M.P., 2017. Heated communities: large inter- and intraspecific variation in heat tolerance across trophic levels of a soil arthropod community. *Oecologia* 186, 311–322. <https://doi.org/10.1007/s00442-017-4032-z>

- Grouvelle, M.A., 1896. Descriptions de clavicornes d'Afrique et de Madagascar. *Annales de la Société entomologique de France* **65**, 93–94. (In French).
- Hutchinson, G.E., 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* **22**, 415–427.
- Jäch, M.A., 1998. Annotated check-list of aquatic and riparian/littoral beetle families of the world (Coleoptera). *Water Beetles of China* **2**, 25–42.
- Kashcheev, V.A., 1999. Klassifikatsia morfologicheskikh tipov imago stafilinid [Classification of eco-morphological types of adult staphylinids]. *Tethys Entomological Research* **1**, 157–170. (In Russian).
- Kaufmann, T., 1987. Factors contributing to priority or nonpriority of males of two heterocerids (Coleoptera) sharing the same habitat. *Annals of the Entomological Society of America* **81**, 71–75.
- Kaufmann, T., Stansly, P., 1979. Bionomics of *Neoheterocererus pallidus* Say (Coleoptera: Heteroceridae) in Oklahoma. *Journal of the Kansas Entomological Society* **52**, 565–577.
- Kolesnikova, A.A., Makarov, K.V., Prokin, A.A., Makarova, O.L., 2016. Zhestkokrylye (Coleoptera) pribrezhnykh raionov Nenetskogo Avtonomnogo okruga [Coleoptera of coastal districts in the Nenets Autonomous Region]. Tezisy dokladov II Mezhdunarodnoy nauchnoy konferentsii “Prorodnye resursy i kompleksnoe osvoenie pribrezhnykh raionov Arkticheskoy zony [Abstracts of the 2nd International scientific conference “Natural resources and integrated development of coastal areas of the Arctic zone”]. Arkhangelsk, Russia, 226–227. (In Russian).
- Levchenko, V.F., 1993. Modeli v teorii biologicheskoy evolutsii [Models in the theory of biological evolution]. Nauka, Saint-Petersburg, Russia, 383 p. (In Russian).
- Li, Ya., Tihelka, E., Huang, D., Cai, Ch., 2020. Specialized variegated mud-loving beetles from mid-Cretaceous Burmese amber (Coleoptera: Heteroceridae). *Palaeoentomology* **3** (1), 59–67. <https://doi.org/10.11646/palaeoentomology.3.1.9>
- Litovkin, S.V., Sazhnev, A.S., Čiampor, F. Jr., 2019. Validation of *Heterocererus heydeni* Kuwert, 1890 based on morphology and DNA barcoding, with notes on the problems of classification of the Heteroceridae (Coleoptera). *Zootaxa* **4614** (1), 160–172. <https://doi.org/10.11646/zootaxa.4614.1.7>
- Mannerheim, C.G. von, 1853. Dritter Nachtrag zur Käferfauna der Nord-Amerikanischen Länder des Russischen Reiches. *Bulletin de la Société Impériale des Naturalistes de Moscou* **26** (3), 95–273. (In German).
- Mascagni, A., 1993. Quattro nuove specie ed una nuova sottospecie di Heteroceridae dell'Asia (Coleoptera). *Opuscula zoologica fluminensia, Flums (SG)* **112**, 1–11. (In Italian).
- Mascagni, A., 2003. Descriptions of three new species, and updated checklist of the Heteroceridae of China and neighbouring countries (Coleoptera: Heteroceridae). *Koleopterologische Rundschau* **73**, 285–296.
- Mascagni, A., 2014. The Variegated Mud-Loving Beetles of Europe (first part) (Coleoptera: Heteroceridae). *Onychium* **10**, 78–118.
- Mascagni, A., Monte, C., 2001. Contributo alla conoscenza degli Heteroceridae del Sudafrica e del Madagascar con descrizione di *Heterocererus uhligi* spec. nov. (Coleoptera). *Opuscula zoologica fluminensia* **197**, 1–9. (In Italian).
- Mascagni, A., Skalický, S., 2007. New species and new statuses of Heteroceridae from the Oriental region. *Folia Heyrovskyana* **14** (3), 87–94.
- Mordkovich, V.G., Lyubechanskii, I.I., 2017. The Role of Large Arthropods in the Development of Halomorphic Soils in the South of Siberia. *Eurasian Soil Science* **50** (6), 688–700. <https://doi.org/10.1134/S1064229317040068>
- Peck, S.B., 2005. A Checklist of the Beetles of Cuba with Data on Distributions and Bionomics (Insecta: Coleoptera). *Arthropods of Florida and Neighboring Land Areas* **18**, 241.
- Peck, S.B., 2006. The Beetles of the Galápagos Islands, Ecuador: Evolution, ecology and diversity (Insecta: Coleoptera). National Research Council of Canada Research Press, Ottawa, Canada, 313 p.
- Pianka, E.R., 1981. Evolutsionnaya ekologiya [Evolutionary Ecology]. Mir, Moscow, USSR, 400 p. (In Russian).
- Pierre, F., 1946. La larve d'*Heterocererus aragonicus* Kiesw. et son milieu biologique (Col. Heteroceridae). Considération sur la morphologie et la biologie des premiers stades de cette famille. *Revue Française d'Entomologie* **13**, 166–174. (In French).

- Poole, G.C., Berman, C.H., 2001. An ecological perspective on in-stream temperature: natural heat dynamics and mechanisms of human caused degradation. *Environmental Management* **27**, 787–802.
- Poppius, B., 1907. Beiträge zur Kenntnis der Coleopteren-Fauna des Lena-Thales in Ost-Sibirien. III. *Öfversigt af Finska Vetenskaps-Societetens Förhandlingar* **49** (2), 1–17. (In German).
- Prokin, A.A., Ren, D., 2011. New Species of Variegated Mud Loving Beetles (Coleoptera: Heteroceridae) from Mesozoic Deposits of China. *Paleontological Journal* **45** (3), 284–286.
- Prokin, A.A., Stolbov, V.A., Petrov, P.N., Filimonova, M.O., 2019. Zhestkokrylye (Coleoptera) stoyachikh vodoemov sredney chasti Gydanskiego poluostrova [Beetles (Coleoptera) in stagnant water bodies of the middle part of Gydan peninsula]. *Zoologicheskii Zhurnal [Russian Journal of Zoology]* **98** (7), 778–784. (In Russian).
- Przhiboro, A.A., 2001. Ekologiya i rol' bentosnykh dvukrylykh (Insecta: Diptera) v pribrezhnykh soobshchestvakh malykh ozer Severo-Zapada Rossii [Ecology and role of benthic dipterans (Insecta: Diptera) in shallow water communities of small lakes in the Northwestern Russia]. *Candidate of sciences (biology) dissertation abstract*. St Petersburg, Russia, 25 p. (In Russian).
- Sazhnev, A.S., 2016. Sostav i struktura naseleniya Heteroceridae (Coleoptera) v usloviyakh pribrezhnoy zony vodnykh obyektov Saratovskoy oblasti [Composition and structure of the Heteroceridae (Coleoptera) population in the shore zone of water objects in the Saratov region]. *Povolzhskiy ekologicheskii zhurnal [Povolzhskiy Journal of Ecology]* **1**, 85–93. (In Russian). <https://doi.org/10.18500/1684-7318-2016-1-85-93>
- Sazhnev, A.S., 2017. Materialy k rasprostraneniyu zhestkokrylykh semeystva Heteroceridae (Coleoptera) na Severnom Kavkaze [Materials for the distribution of beetles of the family Heteroceridae (Coleoptera) in the North Caucasus]. *Eversmannia* **50**, 8–10. (In Russian).
- Sazhnev, A.S., 2018a. On the position of Heteroceridae (Insecta: Coleoptera) in food webs in riparian communities. *Ecosystem Transformation* **1**, 49–56. <https://doi.org/10.23859/estr-180121>
- Sazhnev, A.S., 2018b. Redescription of *Heterocerus fausti* Reitter, 1879, bona species (Coleoptera, Heteroceridae). *Zootaxa* **4441** (3), 597–600. <https://doi.org/10.11646/zootaxa.4441.3.12>
- Sazhnev, A.S., 2018c. Symbiotic Associations between Beetles of Family Heteroceridae (Insecta: Coleoptera) and Other Organisms. *Inland Water Biology* **11** (1), 108–110. <https://doi.org/10.1134/S1995082918010169>
- Sazhnev, A.S., 2018d. Materialy k faune Zhukovpilousov (Coleoptera: Heteroceridae) Dalnego Vostoka Rossii [Materials to the variegated mud-loving beetle fauna (Coleoptera: Heteroceridae) of the Russian Far East]. *Kavkazskiy entomologicheskii bulletin [Caucasian Entomological Bulletin]* **14** (2), 153–155. (In Russian).
- Sazhnev, A.S., 2018e. Fauna zhestkokrylykh semeystva Heteroceridae (Insecta: Coleoptera) severa Evropeiskoi chasti Rossii [The fauna of beetles of the family Heteroceridae (Insecta: Coleoptera) in the north of the European part of Russia]. *Trudy Kazanskogo otdeleniya Russkogo entomologicheskogo obschestva [Proceedings of the Kazan branch of the Russian Entomological society]* **5**, 43–47. (In Russian).
- Sazhnev, A.S., 2019. A new synonymy of the species *Heterocerus fenestratus* (Thunberg, 1784) (Coleoptera: Heteroceridae) and his first records for South Hemisphere. *Zootaxa* **4624** (4), 589–592. <https://doi.org/10.11646/zootaxa.4624.4.10>
- Sazhnev, A.S., Udodenko, Yu.G., 2018. Soderzhanie rtuti v zhukakh semeystva Heteroceridae (Insecta: Coleoptera) Evropeyskoy chasti Rossii [Mercury content in beetles of the family Heteroceridae (Insecta: Coleoptera) of the European part of Russia]. *Tezisy Vserossiyskoy nauchnoy konferentsii i shkoly-seminara dlya molodykh uchenykh, aspirantov i studentov "Rtut i drugie tyazhelye metally v ekosistemakh. Sovremennyye metody issledovaniya soderzhaniya tiazhelykh metallov v okruzhayushchey srede" [Abstracts of the all-Russian conference and school-seminar for young scientists, postgraduates and students "Mercury and other heavy metals in ecosystems. Modern methods of studying the content of heavy metals in the environment"]*, Cherepovets. Cherepovets State University, Cherepovets, Russia, 57–58. (In Russian).
- Skalický, S., 2003. New species of Heteroceridae from Argentina, Brazil and Chile. *Mitteilungen des Internationalen Entomologischen Vereins* **28** (1–2), 1–12.

- Skalický, S., 2005. New and little known species of Heteroceridae from Java (Coleoptera: Heteroceridae). *Koleopterologische Rundschau* **75**, 349–358.
- Skalický, S., 2008. A review of Japanese Heteroceridae (Coleoptera). *Acta Musei Moraviae, Scientiae biologicae (Brno)* **93**, 47–52.
- Skalický, S., 2010. Heteroceridae: Checklist of the taxa recorded from Indonesia and the Southwest Pacific (Coleoptera). *Monographs on Coleoptera* **3**, 395–400.
- Skalický, S., Ezer, E., 2014. Coleoptera: Heteroceridae. *Folia Heyrovskyana. Icones Insectorum Europae Centralis. Series B* **18**, 1–13.
- Sunday, J., Bates, A.E., Dulvy, N., 2011. Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society. Series B* **278**, 1823–1830.
- Trémouilles, E., 1999. Descripción de tres nuevas especies de *Heterocerus* Fabricius, de América del Sur (Coleoptera, Heteroceridae). *Revista del Museo Argentino de Ciencias Naturales nueva serie* **1** (1), 103–108. (In Spanish).
- Vanin, S.A., Costa, C., Gianuca, N.M., 1995. Larvae of neotropical Coleoptera XXI: Description of immatures and Ecology of *Efflagitatus freudei* Pacheco, 1973 (Dryopoidea, Heteroceridae). *Iheringia, Série Zoologia* **78**, 99–112.
- Vinikour, W.S., 1979. Coal slurry observed as habitat for semiaquatic beetle *Lanternarius brunneus* (Coleoptera: Heteroceridae), with notes on water quality conditions. *Entomological News* **90** (4), 203–204.
- Zaitzev, Ph.A., 1910. Beiträge zur Kenntnis der Wasserkäfer des Osten von Nordsibiren. Haliplidae, Dytiscidae, Gyrinidae, Hydrophilidae, Georyssidae, Dryopidae und Heteroceridae. *Mémoires de l'Académie impériale des sciences de St. Pétersbourg. Ser. 8. Classe physico-mathématique* **8** (9), 11–52. (In German).
- Zaitsev, Ph.A., 1946. Rasprostranenie v Zakavkazie vidov sem. Pilousov (Coleoptera, Heteroceridae) [Distribution in Transcaucasia species of the variegated mud-loving beetles (Coleoptera, Heteroceridae)]. *Trudy Zoologicheskogo instituta AN Gruzinskoy SSR [Proceedings of Zoological Institute AS GruzSSR]* **6**, 213–220. (In Russian).