



On the position of Heteroceridae (Insecta: Coleoptera) in food webs in riparian communities

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The position of the beetle family Heteroceridae in food webs of riparian communities in European Russia and Mongolia is discussed, and the main trophic links within the Heteroceridae-related communities are recorded. The feeding spectrum of heterocerids, and the main predators of preadult and adult Heteroceridae, are identified and reported. Symbionts of heterocerids are also discussed.

Keywords: trophic webs, heterocerids, ecotone, beetles, supralittoral, organism associations, feeding.

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Introduction

Land-riparian intrazonal ecosystems are extremely dynamic, because of their highly variable hydrological environment. Changes in the climate (aridization) and anthropogenic factors (including construction, hydrotechnical works, building and exploitation of water reservoirs etc.) lead to changes in humidization and result in extremely fast transformation of riparian ecosystems (Kuzmina and Treshkin, 2017).

Aquatic-land ecotone habitats are inhabited by unique heterotrophic invertebrate communities, which include many taxa of Coleoptera. The supralittoral zone contains a mixed community of true aquatic species, littoral and land riparian Coleoptera, showing the 'marginal effect' (Burke and Nol, 1998). These include a stenotopic ecomorphological group of "riparian" Coleoptera (in Jäch's (1998) classification modified by Prokin (2008)), which serves as a marker of marginal water-land systems. Heteroceridae MacLeay, 1825 (heterocerids or variegated mud-loving beetles) are among the Coleoptera taxa that have most successfully colonized these habitats.

A trophic web is one of the systemic factors of riparian communities, and includes a large and taxonomically heterogeneous group of invertebrates including decomposers, predators, parasites, symbionts, etc. This paper considers the trophic connections of the Coleoptera of riparian communities that include Heteroceridae.

Material and methods

The material studied was collected in different climatic zones and subzones of European Russia (2007–2016) and Mongolia (2016–2017), the most detailed studies having been conducted in 2011–2015 in the Saratov region. Various natural zones were researched, including: the taiga zone (southern taiga spruce forest subzone, Yaroslavl Region), the forest-steppe, steppe and semi-steppe zones of European Russia (Saratov Region), which included intrazonal landscapes in the valley of the Volga River, and steppe and deserts of Mongolia. The shorelines of various basins (reservoirs, temporary basins and streams, small rivers, lakes, and ponds) were examined. Pzhiboro's (2001)

classification of morphological types of shoreline is followed. Altogether, 20 water bodies were studied in the Saratov and Yaroslavl regions of Russia, and also in the Gov-Altai and Zavkhan aimags of Mongolia. 65 samples were collected, which contained 2135 specimens of adults and larvae of riparian Coleoptera (of these 963 were Heteroceridae). This collection was supplemented by material from other collectors from Ukraine and Kazakhstan.

Usually, riparian stratobionts inhabit a narrow transitional zone (Prokin, 2008; Sazhnev, 2016), except in cases of unstable water levels or strong waves, when this zone may move 3–5 meters onshore from the water margin, or in humid salt marshes, where the margins of this zone are blurred. Taking this into account, the samples were collected within a zone 1-meter from the water's edge. Three replicates were taken in each case, using the splashing and stirring method, a 25×25 cm quadrat and an aspirator (Golub et al., 2012). Adults and larvae were collected in Eppendorf tubes containing 70% alcohol solution as a fixing agent. The material is housed in the author's collection and in the collection of aquatic invertebrates of the Papanin Institute for Biology of Inland Waters Russian Academy of Sciences (IBIW RAS).

In addition to an analysis of the literature, direct observations of the behavior and feeding habits of the riparian Coleoptera and Heteroceridae were performed and some species were studied in captivity. In addition I studied the stomach contents of amphibians and birds donated by colleagues.

The material was studied using an MBS-9 light stereomicroscope and an XSP-101 microscope. To study the feeding habits of the Heteroceridae, adults and larvae were dissected. Over 1000 specimens of adult Heteroceridae from various regions of Russia and adjacent countries were also examined for phoretic mites and parasitic fungi. In some cases it was necessary to remove the elytra from the specimens, e.g., when searching for mites of the family Laelapidae.

Results

All life stages of heterocerids are restricted to the shores of various basins with varying degrees of salinity, from fresh-water basins and streams to seas and salt marshes. Adults and larvae are characteristic inhabitants of water margins, including the supralittoral of basins, and in reophilic communities – the aeropelal zone (Chertoprud, 2014). They construct branched tubular networks of tunnels in the substrate, which are used for feeding, laying eggs, and pupation. The community does not inhabit the wave-washed sands of beaches because of their nutrient impoverishment.

Heterocerids often occur syntopically; I have

recorded up to four species in a single biotope (Sazhnev, 2016). The densest known Heteroceridae populations were observed in southern Brazil – 162 specimens/m² (Vanin et al., 2016), and in marshes in Siberia, up to 110 specimens/m² (Mordkovich and Lyubchanskii, 2017). In our studies, the average density of the heterocerid populations was 72.0±5.2 specimens/m² for adults, 27.5±2.6 specimens/m² for larvae. In the case of dense populations, Heteroceridae together with similar burrowing stratobionts (*Dyschirius*, *Dyschiriodes*, *Bledius*) create a substrate microrelief that makes microniches available for stratobiont borer-dwellers and other organisms. After occupying a vacant plot, heterocerids eject approximately 935 g/m² of dry substrate in 24 hours, where a mean air-dried weight is ca. 8.5 g of one ejection of soil (Mordkovich and Lyubchanskii, 2017).

The humidity of the substrates colonized by the Heteroceridae adults and larvae ranges from 30 to 70% (Kaufmann and Stansly, 1979), and the density of colonies is also connected with strategies of sexual behavior, as has been shown for North American species (Kaufmann, 1987). It has been noted that larvae inhabit microstates nearer to the water level, and more humid habitats. This is likely to be related to their less prominent burrowing activities relative to adults. This phenomenon can be considered as a form of co-adaptation, which in this case includes microzonal distribution in the biotopes of the species' growth stages, feeding at different times of appearance in the substrate and different durations of connection with the substrate.

Basins with flooded banks (large water reservoirs, washed-over islands in river channels), and those with a migrating coastline, in years with consistent lowstands, at the early stages of the succession development Heteroceridae and other stratobiont taxa dominate pioneering riparian communities, while species of *Bembidion* and other Carabidae (e.g. Holeski, 1984) and Staphylinidae play a similar role as more mobile herpetobionts.

Heterocerids participate in matter and energy transfer in the transitional zone between two habitats and serve as a biogenic component in transformation of hydromorphic soils (Mordkovich and Lyubchanskii, 2017). The soil burrowing activity of heterocerids facilitates germination of seeds in sandy soils (Bernhardt, 1995) and this beetle group is certainly interlinked with other organisms in these communities (Sazhnev, 2018).

Feeding of Heteroceridae

The published record of Heteroceridae feeding is incomplete and sometimes contradictory. For example, adults of the North American *Augyles auromicans* (Kiesenwetter, 1851) have been recorded as feeding exclusively on phytoplankton

(Gwynn-Silvey, 1935). Green (1968) suggested detritus and algae as the nutrient basis for *Heterocer* adults and larvae in estuarine ecosystems of European rivers. Pacheco (1964) suggested that the adults and larvae are predators, but later (Pacheco, 1978) it emerged that most adults of North American Heteroceridae fed on zooplankton, while some of these are omnivores. Observations of live larvae of *Neoheterocer* *pallidus* (Say, 1823) showed that they consume substrate while burrowing, and are essentially selective detritivores (Kaufmann and Stansly, 1979). This agrees well with Lawrence (1991), who reported that heterocerids consumed some substrate, from which they later extract nutrients such as diatoms and other algae and other organic material.

The bionomic study of the South American species *Heterocer* *freudei* (Pacheco, 1973) found that the species feeds mostly on organic detritus, microscopic precipitated psammophiles and phytoplanktonic diatoms, and also on free-living protists, while diatoms dominated in its diet (*Navicula capitata*, *Navicula* spp., *Caloneis brevis*, *Mastogloia exigua* etc.) (Vanin et al., 1995).

There are published records of agricultural damage by heterocerids: damage to winter cereals in the vicinity of Bairamali in Turkmenistan (Bogush, 1951) and greenhouse tomatoes in Armenia (Zaitsev, 1946). Apparently, these phenomena are occasional and are related to environments, e.g., irrigation, and to attraction of adult Heteroceridae to artificial light in greenhouses – Heteroceridae are obligate photoxenes (Gornostaev, 1984).

In this study, the intestines of adults and larvae of species of the genera *Heterocer* and *Augyles* in European Russia and several neighboring countries (Kazakhstan, Mongolia, Ukraine) were found to contain organic detritus, partly digested plant remains, diatom valves and destroyed cells of filamentous algae. Particles of substrate (small grains) show little selectivity in feeding. It is possible that sand grains are used as analogs of gastroliths to assist in the breakdown of the hard skeletons of diatoms.

Thus, adults and larvae of Heteroceridae are non-selective detritivores and/or micro-phytophages (alga-detritivores), consuming organic detritus together with the substrate depending on the inhabited substrates, type, and location of water basins: microorganisms, diatoms, and other groups of algae, possibly, small soil invertebrates, and occasionally zooplankton (in case of floods, wash-up/wash-off processes, or other special aspects of flow regime). Detritivory was evidently the original feeding strategy of Coleoptera larvae (Striganova, 1980). Detritivores re-work the organics included in detrital food chains, through which over half of the

energy and matter in ecosystems pass (Begon et al., 1989).

Trophic webs in communities containing Heteroceridae

In Coleoptera, feeding habits are considered to be a major factor in the formation of different living forms (Sharova, 1981); this is true for herpetobionts, whereas for substrate-linked Coleoptera, feeding type is less important as an ecomorphological factor, since the soil environment and how it is utilized is the defining feature (Kastcheev, 1999).

In terms of evolution, it is important that certain morphoecological types appear at similar stages in a group's phylogeny when organisms, after having developed major general adaptations begin using more specific features of the environment (Krivolutsky, 1971). Among riparian Coleoptera forming a specialized stenotopic assemblage of the marginal water edge zone, Heteroceridae, the carabids *Dyschiriini* and *Clivinini*, and staphylinids of the genus *Bledius* are assigned to a group of burrowing stratobionts (the most specialized beetles, adapted to burrowing). This group is characterized by a cylindrical body with a pronounced narrowing ('waist') at the base of the pronotum, which facilitates the mobility of the anterior part of the body while burrowing, spatulate head with mandibles, and anterior tibiae with teeth.

These taxa are also closely connected by their position in trophic chains. For instance, species of the genera *Dyschirius* and *Dyschiriodes* are specialized predators on the larvae of the alga-detritivores *Bledius* and Heteroceridae. Some species of *Bledius* are also typical carnivores, e.g., *Bledius* (*Pucerus*) *verres* Erichson, 1840.

Based on published records (Deville, 1924) and my own observations, feeding on larvae and adults of Heteroceridae has been reported for members of the families Carabidae and Staphylinidae – burrowing stratobionts of the genera *Dyschirius*, *Dyschiriodes* and epigeobionts of the genus *Lesteva*. Other predators, such as the epigeobionts *Paederus*, *Stenus*, burrowing stratobionts *Bembidion*, *Philonthus*, *Xantholinus*, *Lathrobium* and others are also likely to feed on heterocerids (egg clutches and larvae) when encountering their tunnels (Gwynn-Silvey, 1935). Larger carnivores, such as members of the genera *Elaphrus*, *Agonum*, *Badister*, *Cicindela*, *Chlaenius*, some *Pterostichus* and others can also hunt adults.

The examination of the Heteroceridae-containing communities showed the presence of 195 species of Coleoptera of 20 families. The most characteristic Coleoptera taxa in the Heteroceridae-containing communities on the clay and mud substrates in the Saratov Region were epigeobionts

and burrowing stratobionts of the genera *Acupalpus*, *Bembidion*, *Badister*, *Stenus*, *Philonthus*, and *Lathrobium*, some Aleocharinae, and staphylinids of the genus *Carpelimus*, which are present in all samples, as well as some Hydrophilidae. Most communities (7 of 14) were dominated by a widespread eurytopic species *Heterocerus fenestratus* (Thunberg, 1784); in other communities various species of the families Carabidae and Hydrophilidae were dominant.

Sandy substrates almost invariably contain burrowing stratobionts of the genera *Dyschirius*, *Bledius*, and epigeobionts of the genus *Stenus*. The predatory psammocole *Omopron limbatum* (Fabricius, 1777) and algo-detritivores of the family Georissidae are not infrequent. The studied psammophilic communities of the Saratov Region are dominated and subdominated by *Dyschirius thoracicus* (P. Rossi, 1790) and *Augyles hispidulus* (Kiesenwetter, 1843), trophically connected in the predator-prey system.

The examined communities containing Heteroceridae in Mongolia have similar supraspecific taxa – members of the genera *Bembidion*, *Bledius*, *Cercyon*, *Dyschirius*, *Elaphrus*, *Georissus*, *Philonthus*, *Stenus* (Sazhnev and Prokin, 2017).

It should be noted that the taxonomic assemblage in the Heteroceridae-containing communities is relatively similar over large geographic areas (Howden, 1977; Sazhnev, 2014; Schreiner and Ozorio, 2003); apart from Coleoptera, the communities contain Saldidae (Heteroptera), larvae of Diptera, and members of the family Tridactylidae (Orthoptera); the latter may feed on egg clutches of Heteroceridae (Folkerts, 1989). In response, females of some species defend their clutch from predators and clean the eggs against contamination by fungi and microorganisms, a manifestation of parental care, which has been recorded in various families of Coleoptera (Crowson, 1981).

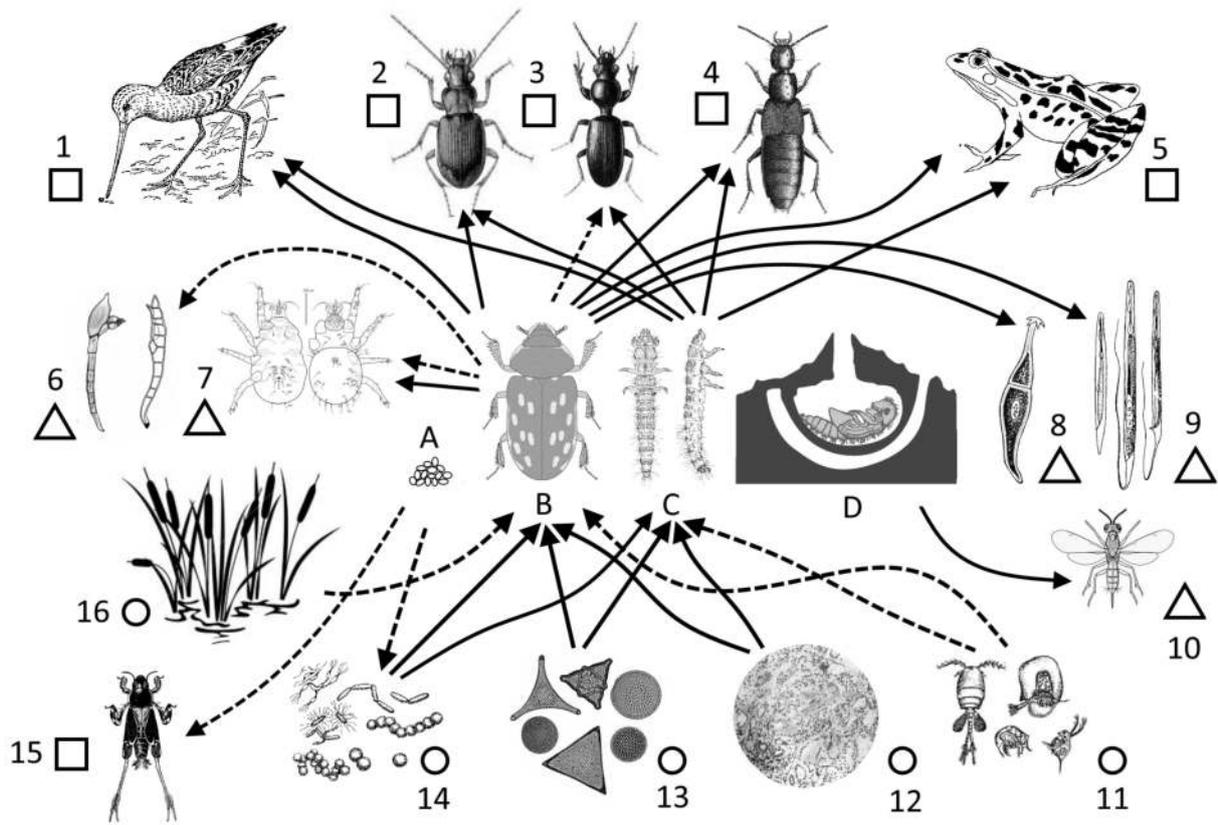


Fig. 1. Generalized scheme of the position of Heteroceridae in food webs (arrows show directions of flow of energy and matter through the web): solid line – direct trophic links; dashed lines – indirect links; circle – obligate and facultative elements of the feeding basis of heterocerids; square – consumers, positioned above in the food chain, preying on various life stages of heterocerids; triangle – parasitic organisms and symbionts with resolved relationships with Heteroceridae. Letters denote life stages of Heteroceridae: A – egg, B – adult, C – larva, D – pupa. Numbers indicate organisms which participate in considered trophic links. 1 – Scolopacidae and other birds, 2 – Carabidae of different groups, 3 – carabids of the genera *Dyschirius* and *Dyschiriodes*, 4 – Staphylinidae, 5 – amphibians, 6 – Laboulbeniales ascomycetes, 7 – phoretic and other mites, 8 – Gregarinida, 9 – nematodes, 10 – Chalcidoidea, 11 – zooplankton, 12 – detritus, 13 – phytoplankton, 14 – soil microorganisms, 15 – Tridactylidae, 16 – higher plants.

The present study revealed new results on consumption of Heteroceridae by vertebrates. The study of the food lumps and stomach contents showed that heterocerids are preyed on by the marsh frog – *Pelophylax ridibundus* (Pallas, 1771), and birds of the families Passeridae, Motacillidae, Muscicapidae and Scolopacidae, which agrees with previously published data (Schmidt et al., 2004; Turner, 1959). It is likely that in the coastal zone, heterocerids are hunted by Amphibia, waders and wagtails, whereas flycatchers and other passerines catch the adults during their twilight dispersal flights.

Symbionts of Heteroceridae

Associations formed in the habitats between species and assemblages are mostly of trophic orientation. Symbiosis is one such association. In this paper I interpret symbiosis in the broad sense – as all possible forms of co-existence between different species. As details of relationships between organisms are not always known, and never entirely known, the use of the term “parasitism” is sometimes conventional for relationships between Heteroceridae and their symbionts.

A close connection with heterocerids is known for 12 symbiotic species: 4 – Nematoda, 5 – Acari, 1 – Gregarinida, 1 – Chalcidoidea, and 1 – Ascomycota (Sazhnev, 2018). Some phoretic nematodes were reported to be symbionts of heterocerids (Hirschmann, 1952; Wachek, 1955). In particular, species of the genus *Heterocerus* “are parasitized” by larvae and adults of round worms of the subclass Spiruria, for instance, *Goffartia heteroceri* Hirschmann, 1952 and *Goffartia variabilis* (Micoletzky, 1922). Among other nematodes (family Diplogastridae), *Pristionchus Iheritieri* (Maupas, 1919) and *Protylechus heteroceri* Wachek, 1955 have been associated with heterocerids (Crowson, 1981; Wachek, 1955).

The phoretic mites associated with heterocerids include *Allopygmephorus matthesi* (Krczal, 1959), *A. persicus* Khaustov et Hajiqanbar, 2005 (Katlav et al., 2015; Khaustov and Hajiqanbar, 2006), *A. spinisetus* Khaustov et Sazhnev, 2016, and *A. punctatus* Khaustov et Sazhnev, 2016 (Khaustov and Sazhnev, 2016), and *Scutacarus sphaeroideus* Karafiat, 1959 (Khaustov and Sazhnev, 2016) is also recorded – these are species that use heterocerids for dispersal, while their feeding on heterocerids is of a supplementary nature.

Mites of the family Laelapidae – *Gaeolaelaps heteroceri* Trach, 2016 and *G. sevastianovi* Trach, 2016 (Trach, 2016) parasitize adults of the family Heteroceridae, beneath the elytra.

The mite *Histiostoma maritimum* (Oudemans, 1914), family Histiostomatidae, develops on adult heterocerids. This symbiosis is referred to as

necromeny (Wirth, 2004), when the nymphal stage stays on the animal carrier until its death, and then further development resumes on the dead animal.

The sporozoan *Gregarina heteroceri* Rauchalles, 1969 (Geus, 1969) (Gregarinida) is known to be a true endoparasite of Heteroceridae.

Wasps of the supfamily Chalcidoidea (Hymenoptera) are parasitoids of heterocerid pupae. Adult wasps have been reported in the closed pupal chambers of *Heterocerus fenestratus* (Mascagni, 2015).

Beetles are also parasitized by ascomycete fungi of the order Laboulbeniales, in particular *Botryandromyces heteroceri* (Maire), specializing on species of Heteroceridae. The ‘foot cells’ of these fungi penetrate the cuticle (Koval, 1974) giving the appearance of a surface encrustation.

Conclusions

In general, Heteroceridae are primary consumers in the trophic chains studied. The structure of communities in various natural zones at both taxonomic and trophic levels is relatively similar and can be represented by a general scheme (Fig. 1). Sandy substrates are inhabited by a psammophilic complex of species (some representative of the genera *Augyles*, *Omophron*, *Bledius*), while some groups specialize on hypersaline biotopes (some *Heterocerus*, *Bledius*, *Dyschirius*). Communities of riparian Coleoptera are taxonomically more diverse and better structured on the coastline zone according to Pzhiboro’s (2001) classification.

Syntopic species of the family, stratobiontic algal detritivores (*Bledius*, *Carpelimus*), and to some extent non-selective polyphages (Tridactylidae), compete with heterocerids. Specialized predators include members of the closely related genera *Dyschirius* and *Dyschiriodes*, perhaps also *Clivina* (all Carabidae: Scaritinae) which hunt pre-adult stages of Heteroceridae. Heterocerids are preyed on by various groups of vertebrate and invertebrate carnivores. Parasitic organisms and symbionts with an unresolved range of relationships with Heteroceridae require further study.

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