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Arthropod-associated leeches (Annelida: Hirudinida) of the World: Diversity, taxonomic reappraisal, ecological classification of host associations, and convergent evolution

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Abstract

Leeches (order Hirudinida) occur in diverse associations with invertebrate animals, mostly molluscs and arthropods. If information on mollusc-associated leeches was updated in a series of recent studies, our knowledge of leech-arthropod associations is still in its infancy. In this review, we summarize available literature and original data on the taxonomic diversity, biogeographic affinities, and ecological preferences of arthropod-associated leeches at the global scale. This assemblage accounts for 45 species, 26 genera, and three families of aquatic leeches (Piscicolidae, Glossiphoniidae, and Praobdellidae). They occur in fresh, estuarine, and marine waters and use no less than 79 species, 52 genera, 24 families, and six orders of arthropods as hosts. The majority of host species belong to crustaceans (class Malacostraca; 72 species, including amphipods, crabs, isopods, mysids, shrimps, spiny and squat lobsters), followed by sea spiders (class Pycnogonida; 4 species), and insects (class Hexapoda; 3 species). Associations of leeches with crabs and shrimps are the most widespread and common in aquatic environments globally. Leeches may act as ectosymbionts, being ectoparasites or commensals, as well as endosymbionts (dwelling in the gill chamber of crabs and a shrimp). Based on our comprehensive datasets, we have designed an ecological classification of leech-arthropod associations that takes into account the key type of biotic interaction, the level of specialization of leeches, and the degree of association with host. Several cases of parallel origins (convergent evolution) of analogous leech-arthropod associations are also described, including (1) specialized permanent ectoparasites of crustaceans (fresh and sea waters); (2) specialized crab-dwelling commensals, using frogs as primary host (fresh water); (3) specialized shrimp-dwelling commensals, feeding on fish (fresh and sea waters); (4) non-specialized crab- and sea spider-dwelling commensals, attaching cocoons to the host's surface (sea water); and (5) non-specialized temporary ectoparasites of crabs (fresh water). Based on a revision of arthropod-associated leeches and related species from the family Glossiphoniidae, we here propose two new genera, one new species, 14 new combinations, and four new synonyms. New genera are as follows:

Aotearoabdella Bolotov **gen. nov.** (type species: *Placobdella maorica* Benham, 1907) and *Palaemobdella* Bolotov **gen. nov.** (type species: *Placobdella ornata* Oka, 1929: junior secondary homonym of *Placobdella ornata* (Verrill, 1872), reinstated by us based on Art. 59.4 of ICZN; = *Placobdella okai* Soós, 1969). Revised genera with amended diagnoses, species lists, and distribution are as follows: *Batracobdelloides* Oosthuizen, 1986 **gen. rev.**; *Orientobdelloides* Bolotov, Eliseeva & Kondakov, 2022 **gen. rev.**; *Paraclepsis* Harding, 1924 **gen. rev.**; and *Placobdelloides* Sawyer, 1986 **gen. rev.** A new species is as follows: *Paraclepsis dongnaiensis* Bolotov, Eliseeva & Kondakov **sp. nov.** [= *Paraclepsis vulnifera* Moore, 1935 nec Harding, 1924]. New combinations are as follows: *Aotearoabdella bdellae* (Ingram, 1957) **comb. nov.**; *Aotearoabdella maorica* (Benham, 1907) **gen. & comb. nov.**; *Batracobdelloides fulvus* (Harding, 1924) **comb. nov.**; *Batracobdelloides gracilis* (Blanchard, 1897) **comb. nov.**; *Batracobdelloides undulatus* (Harding, 1924) **comb. nov.**; *Orientobdelloides bancrofti* (Best, 1931) **comb. nov.**; *Orientobdelloides emydae* (Harding, 1920) **comb. nov.**; *Orientobdelloides guangdongensis* (Tan & Liu, 2001) **comb. nov.**; *Orientobdelloides indicus* (Baugh, 1960) **comb. nov.**; *Orientobdelloides inleanus* (Oka, 1922) **comb. nov.**; *Orientobdelloides octostriatus* (Grube, 1867) **comb. nov.**; *Palaemobdella horai* (Baugh, 1960) **comb. nov.**; *Palaemobdella ornata* (Oka, 1929) **gen. & comb. nov.**; *Torix okadai* (Oka, 1925) **comb. nov.** New synonyms are as follows: *Hemiclepsis viridis* Chelladurai, 1934 [= *Paraclepsis gardensi* Mandal, 2004 **syn. nov.**]; *Oosthuizobdella garoui* (Harding, 1932) [= *Paraclepsis joraparensis* Mandal, 2015 **syn. nov.**]; and *Paraclepsis ceylanica* (Harding, 1909) [= *Pa. vulnifera* Harding, 1924 **syn. nov.**; = *Pa. praedatrix* Harding, 1924 **syn. nov.**].

Key words Hirudinea, biotic interations, phoresy, ectosymbiont, endosymbiont, parasite, integrative taxonomy, parallel evolution, convergence, host-driven diversification.

Introduction

Leeches (Annelida: Clitellata: Hirudinea: Hirudinida) occur abundantly in aquatic environments, being involved in a variety of biotic interactions with other organisms (Sawyer 1986; Sket and Trontelj 2008). Though these worms have parasitic or predatory life style (Lukin 1976; Sawyer 1986), there are some unusual associations of leeches with invertebrate and vertebrate animals. For instance, a diverse assemblage of mussel-associated leeches inhabit the mantle cavity of freshwater mussels (order Unionida), using these molluscs as dwelling place/shelter and secondary hosts (Bolotov et al. 2019; Bolotov et al. 2020; Bolotov et al. 2022d; Bolotov et al. 2022e). Moreover, at least one mussel-associated leech species is a hyperparasite that feeds on the eggs and embryos of bitterlings, parasitizing the same host mussel (Nishino et al. 2023; Nishino and Yoshiyama 2025). Occasionally, colonial sedentary invertebrates such as sponges and bryozoans may be used as shelter, especially by smaller immature leeches (Klass et al. 2018; Bolotov et al. 2022c).

Leeches are also involved into various relationships with arthropods (Sawyer 1986). Invertebrate-feeding leeches such as *Alboglossiphonia* spp., *Glossiphonia* spp., and *Helobdella* spp. (Glossiphoniidae) commonly prey on smaller aquatic arthropods such as insects, amphipods, isopods, copepods, and cladocerans (Davies and Everett 1975; Young 1980; Proctor and Young 1987; Young and Splelling 1989; Seaby et al. 1996). In contrast, other leech species were recorded in more complex (non-predatory) associations with arthropods, especially crustaceans (Daniels and Sawyer 1975; Sawyer et al. 1975; Zara et al. 2009; Severino-Rodrigues and De Almeida-Duarte 2020; Nazarova et al. 2024). A number of studies contain information on parasitic or commensalistic relationships of marine and freshwater leeches with amphipods (Kaygorodova and Sorokovikova 2014; Petryaeva and Kaygorodova 2015; Kaygorodova and Matveenko 2025), shrimps (Selensky 1927; Oka 1929; Baugh 1960a), mysids (Burreson and Allen 1978; Allen and Allen 1981), crabs (Moore and Meyer 1951; Yang 1986; Badets and Du Preez 2014; Kruger and Du Preez 2015; Nakano et al. 2017; Mitra and Dev Roy 2018; Schenková et al. 2021; Kudara and Kochi 2023), and other groups of arthropods. There are two comprehensive reviews, summarizing available information on symbiotic associations of leeches with crustaceans and sea spiders (Meyer and Barden 1955) and with crabs (Dev Roy et al. 2021).

This study (1) reviews the taxonomic diversity, life history, and host relationships of the global arthropod-associated leech assemblage; (2) presents a revision of arthropod-associated leeches and related taxa in the family Glossiphoniidae with description of two new genera and one new species; (3) provides an ecological classification of arthropod-leech association and a categorization of biotic interactions of leeches with arthropods; and (4) discusses new findings within a broader taxonomic and evolutionary context. Here, we consider only complex symbiotic relationships, while predator-prey interactions were not included to the present review. Our work focuses on the true leeches (order Hirudinida), whereas other groups of the subclass Hirudinea, i.e., crayfish worms (order Branchiobdellida) and leech-like salmonid parasites (order Acanthobdellida), were not considered (Tessler et al. 2018; Kambayashi and Nakano 2024).

Materials and methods

Data collection

Records of leeches on arthropod hosts were mostly compiled from the body of available literature, including some 'grey' sources (PhD and MSc theses). Published works were searched with the Google Scholar web search engine (https://scholar.google.com) using several keywords such as 'Crustacea', 'Amphipoda', 'Decapoda', 'Isopoda', 'crab', 'lobster', 'mysid', 'prawn', 'shrimp', 'Pantopoda', 'sea spider', 'Arthropoda', 'insect' in combination with 'Hirudinea', 'Hirudinida', and 'leeches'. The host-derived keywords were chosen based on earlier reviews of arthropod-leech interactions (Meyer and Barden 1955; Sawyer 1986; Dev Roy et al. 2021). From the list of references created by searching with each combination of keywords, only those containing at least one leech record on arthropod hosts were selected. The reference lists in works recovered during searching were also checked for other published sources relevant to the aims of the present review. All languages were addressed. The searching was completed on 15 March 2025. After removing references beyond the scope of this review, as well as duplicate and secondary sources, 76 works were retained in our database that is available online on *figshare* (Bolotov et al. 2025c: Dataset S1). The taxonomic names of leeches and their hosts from literature sources were updated using the World Register of Marine Species (WoRMS) online database (WoRMS Editorial Board 2025).

The final dataset contains the following fields: leech genus; leech species; leech family; leech developmental stage, associated with host (cocoon / juvenile / immature / adult); host class (Hexapoda / Malacostraca / Pycnogonida), host organism (common name of host); host genus; host species; host family; host order; localization on host; origin of host (native / non-native); key type of biotic interaction with host; six columns with binary data, showing potential types of association with host, including parasitic | commensalistic (surface dwelling) | commensalistic (phoresy) | commensalistic (cocoon substrate) | commensalistic (gill chamber dwelling); degree of association with arthropods (obligate / facultative / fortuitous; cf. Tyler and Böhlke 1972); duration of this association (permanent / temporary); primary host; region; environment (freshwater / marine / brackish); and references (Bolotov et al. 2025c: Dataset S1). All potential biotic interactions of every arthropod-associated leech species with each host were delineated to two categories: (1) key type of interaction that potentially caused the attraction of a leech to the certain host; and (2) accessory type(s) of interaction, accounting for other possible variants of biotic interactions, which are seemingly less important (supplementary) for the given leech species. For example, an ectoparasitic leech uses an arthropod species as primary host (key type of interaction) but it may also be involved in dwelling and phoretic relations, as well as may deposit cocoons on the host surface (accessory types of interaction).

To examine the spatial distribution of arthropod-leech associations, raw records of leeches on various species of the phylum Arthropoda were sampled based on literature sources and original data. This compilation is available online on *figshare* (Bolotov et al. 2025c: Dataset S2). Additionally, we collected all available geographic occurrences of leeches belonging to the crustacean-associated genera *Paraclepsis* Harding, 1924 and *Palaemobdella* **gen. nov.** (Glossiphoniidae) (Bolotov et al. 2025c: Dataset S3). The records in both datasets were thoroughly georeferenced with Google Earth (https://earth.google.com/web) using information on the collecting localities and geographic coordinates, when available. The maps of occurrences were constructed using ESRI ArcGIS 10 software (www.esri.com/arcgis).

New samples of *Paraclepsis* leeches were collected from two sites in Southern Vietnam and were fixed by 96% ethanol immediately after collection. The leeches were sampled by hand from the carapace of freshwater crabs (collector Ivan N. Marin; $n = 15$) and as free-living worms attached to the underside of stones (collector Dmitry M. Palatov; $n = 2$). Tissue snips of selected specimens from both samples were used to extract the DNA and to generate sequences of the mitochondrial *cytochrome c oxidase subunit I* (*COI*) and the nuclear *small subunit of 18S ribosomal RNA* (*18S rRNA*) gene fragments as described in our earlier works (Bolotov et al. 2019; Bolotov et al. 2022a). The new sequences were deposited in GenBank. Additional *COI* and *18S rRNA* sequences of different Glossiphoniidae species were obtained from GenBank. As outgroup, we used 37 leech species belonging to nine families (Erpobdellidae, Gastrostomobdellidae, Haemadipsidae, Haemopidae, Hirudinidae, Orobdellidae, Ozobranchidae, Piscicolidae, and Salifidae) and one species of leech-like salmonid parasites (Acanthobdellidae) (Bolotov et al. 2022a; Bolotov et al. 2022b; Bolotov and Pešić 2025). Information on the DNA sequences used for phylogenetic analyses is presented in Table S1.

Hosts of *Paraclepsis* leech specimens from Vietnam were identified through sequencing of the invertebrate-derived DNA (iDNA) that was obtained from the gut content of well-fed leeches following modern approaches (Drinkwater et al. 2021; Lynggaard et al. 2022; Fahmy et al. 2023; Eliseeva et al. 2024). The iDNA was extracted using the HiPure DNA Micro Kit (Magen Biotechnology (Guangzhou) Co., Ltd., China) according to the manufacturer’s protocol. Amplification of the *COI* gene fragment was performed using the primer pair FishF1 and FinR1 (Ward et al. 2005) under the following conditions: one cycle at 95°C (4 min), followed by 32 cycles of 95°C (50 sec), 62°C (50 sec), and 72°C (50 sec) and a final extension at 72°C (5 min). Forward and reverse sequencing was performed on an automatic sequencer (ABI PRISM3730, Applied Biosystems) using the ABI PRISM BigDye Terminator v.3.1 reagent kit. The resulting sequences were checked using a sequence alignment editor BioEdit v. 7.2.5 (Hall 1999).

Morphological examination of samples

External morphology of the glossiphoniid leeches under discussion was examined based on the body size and shape, annulation, papillation, position of genital pores, ground color, markings pattern, and the number and position of eyespots (Bolotov et al. 2022a). The images of samples and their morphological and anatomical features were taken with stereomicroscopes Leica M165C (Leica Microsystems GmbH, Germany) and Zeiss Axio Zoom.V16 (Carl Zeiss AG, Germany) and were processed using Adobe Photoshop CS v. 8.0. Body length (BL), body width (BW), width of anterior sucker (AW), and width of posterior sucker (PW) of the type specimens of the new species were measured using a stereomicroscope Leica M165C (Leica Microsystems GmbH, Germany) equipped with an ocular-micrometer.

To examine the reproductive and digestive systems of the new *Paraclepsis* species from Vietnam, we prepared a series of longitudinal slices (histological sections) of the body of one specimen (a paratype). The slices were processed using hematoxylin and eosin (H&E) stain as described in our earlier work (Bolotov et al. 2022a). The permanent slides were prepared using a mounting medium (Vitrogel, Biovitrum, Russia). Altogether 17 H&E-stained slices were mounted on two permanent slides. Histological sections were examined using a stereomicroscope Leica M165C (Leica Microsystems GmbH, Germany). Photos of histological preparations were taken using the stereomicroscope with a digital camera (FLEXACAM C1, Leica Microsystems, Wetzlar, Switzerland). Photos were processed with Adobe Photoshop CS v. 8.0.

Taxonomic verification of records from literature and online databases

Taxonomic names of leeches from older (historical) works were verified based on the body of recent literature (Sawyer et al. 1975; Sawyer 1986; Utevsky 2005; and others). Taxonomic placement of representatives of the family Glossiphoniidae was revised by means of the DNA-based (with reference sequences, if available), morphology-based, and biogeographic (range-based) approaches (Bolotov et al. 2025a).

When we were collecting raw information on records of arthropod-associated leeches for this review, several cases requiring taxonomic reappraisal were noticed (Table S2). First, *Myxobdella annandalei* Oka, 1917 (Praobdellidae), discovered on freshwater crabs in Singapore, was misidentified as Glossiphonidae indet. (Yap et al. 2023). Second, samples of the alien *Placobdella ornata* (Verrill, 1872) (Glossiphonidae) from India, deposited in NCBI GenBank, were incorrectly linked to two *Paraclepsis* nominal species (Figure S1). Third, the DNA sequences of the marine shrimp-associated leech *Crangonobdella fabricii* Malm, 1863 (Piscicolidae) appeared in the world’s leading sequence databases (NCBI GenBank and BOLD IDS) under an unpublished, unavailable name, *Crangonobdella spitzbergensis* (see Bjørdalsbakke 2011 for detail). This misidentification also occurred in the comprehensive DNA barcode reference library for Canadian invertebrates (De Waard et al. 2019). Fourth, DNA sequences of the crustacean-associated species *Crangonobdella maculosa* S. Utevsky, 2005 (Piscicolidae) from North-West Pacific (Utevsky 2005) are still listed in NCBI GenBank under a preliminary non-taxonomic name, *Crangonobdella* sp. PT-2003 (Utevsky and Trontelj 2004). Fifth, records of *Notostomum laeve* Levinsen, 1882 (Piscicolidae) on crabs off the coast of Greenland (Meyer and Barden 1955) were misidentified and belong to another species in this genus, *Notostomum cyclostomum* (Johansson, 1898) (Epshtein and Utevsky 1996).

Phylogenetic analyses

The sequences of the *COI* and *18S rRNA* gene fragments (Table S1) were aligned separately using the MUSCLE approach of MEGA11 (Tamura et al. 2021). The alignment of the *18S rRNA* gene fragment was also processed with GBlocks v. 0.91b through an online server (Castresana 2000; Dereeper et al. 2008) to exclude hypervariable positions and gaps (final length of 1697 bp; 83% of the original 2031 bp). The two alignments were joined to a two-locus combined alignment (*COI* + *18S rRNA*) with FaBox v. 1.61 (https://birc.au.dk/~palle/php/fabox) (Villesen 2007).

The maximum likelihood phylogeny was reconstructed using an online implication of IQ-TREE v. 1.6.12 software (http://iqtree.cibiv.univie.ac.at) with an automatic identification of the best evolutionary models and ultrafast bootstrapping (Nguyen et al., 2015; Trifinopoulos et al., 2016; Hoang et al., 2017; Kalyaanamoorthy et al., 2017). The best evolutionary models were selected as follows: GTR+F+I+G4 (*COI*) and SYM+G4 (*18S rRNA*). The uncorrected *COI* p-distances between haplotypes were estimated with MEGA11 (Tamura et al. 2021).

Museum abbreviations

ANSP—Academy of Natural Sciences, Philadelphia, USA
NHMUK—Natural History Museum, London, United Kingdom
RMBH—Russian Museum of Biodiversity Hotspots, N. Laverov Federal Center for Integrated Arctic Research of the Ural Branch of the Russian Academy of Sciences, Arkhangelsk, Russia
SMNH—Swedish Museum of Natural History, Stockholm, Sweden
TMAG—Tasmanian Museum and Art Gallery Invertebrate Collection, Rosny Park, Hobart, Tasmania
USNM—National Museum of Natural History, Washington, USA
ZSI—Zoological Survey of India, Kolkata, India

Results

Diversity and distribution of arthropod-associated leeches

Our review reveals that the global arthropod-associated leech assemblage contains 45 species, belonging to 26 genera and three families (Figures 1-2, Bolotov et al. 2025c: Dataset S1). The majority of arthropod-associated species belong to the family Piscicolidae (29 species, 64.4 % of the total number of species in the assemblage), followed by the Glossiphoniidae (13 species) and Praobdellidae (3 species) (Figure 1). Altogether 17 species (37.8 % of the total number of species in the assemblage) are considered obligate parasites or commensals of arthropods (exclusively crustaceans) in freshwater, estuarine, and marine environments (Figures 1-2 and Table 1). The same number and proportion of species are involved in facultative relations with arthropods (mostly crustaceans, also sea spiders and insects). Finally, no less than 11 species were recorded in accidental associations with arthropods (crustaceans, sea spiders, and aquatic insects), being considered fortuitous associates. The species richness of the latter group may largely be underestimated, because many leech species are still known from a few specimens, especially those from hard-to-access deepwater marine environments (Utevsky 2007; Utevsky and Utevsky 2018; Utevsky et al. 2019). There is no doubt that additional leech species using arthropods (e.g., crabs and sea spiders) as transport/hard substrate hosts will be discovered in the future. Moreover, some little-known fortuitous associates may actually belong to the group of facultative commensals.

Spatially, records of marine leeches being symbiotic with arthropods are largely situated in coastal waters of the Arctic and Southern oceans, as well as in the West Pacific, East Pacific, and West Atlantic (Figure 3). Records of estuarine associations exclusively occur in the New World, being concentrated along the eastern coast of the USA and in the estuaries of Colombia and Brazil. In contrast, records of freshwater associations are mostly confined to subtropical and tropical Asia, Sub-Saharan Africa, and Lake Baikal (Figure 3).

Table 1. Biotic interactions of leeches (order Hirudinida) with arthropods based on compilation of literature sources and original data (Bolotov et al. 2025c: Dataset S1)

No	Types of biotic interactions	Usage of arthropod host by leeches	Arthropod host organisms	Number of leech species	Number of host species
1.	***Ectosymbiotic***				
1.1.	*Parasitic*	Sucking the host's haemolymph (arthropods serve as primary or secondary host); may also serve as dwelling place, transport host, and cocoon substrate	Crustaceans (amphipods, crabs, isopods, mysids, shrimps, and lobsters)	16	40
1.2.	*Commensalistic*				
1.2.1.	Dwelling place (external)	Dwelling on the surface of the host's body and its parts (carapace, appendages, and so on)	Crustaceans (amphipods, crabs, isopods, mysids, shrimps, and lobsters) and sea spiders	24	59
1.2.2.	Phoresy	Transport host and hard substrate	Crustaceans (amphipods, crabs, isopods, mysids, shrimps, and lobsters), sea spiders, and aquatic insects (water bugs)	42	75
1.2.3.	Cocoon substrate	Substrate for cocoon deposition; may also serve as dwelling place and transport host	Crustaceans (crabs, isopods, mysids, shrimps, and lobsters) and sea spiders	10	24
2.	***Endosymbiotic***				
2.1.	*Commensalistic*				
2.1.1.	Dwelling place (internal)	Dwelling in the host's internal body cavities (gill chamber) that serve as closed microhabitat/shelter with specific environment	Crustaceans (crabs and shrimps)	5	9

Biotic interactions of arthropod-associated leeches with hosts

Totally, leeches use 79 species of arthropods as hosts (Figure 2 and Bolotov et al. 2025c: Dataset S1; two unidentified species of crab and shrimp are not included to this estimate). These species belong to 52 genera, 24 families, and six orders (Amphipoda, Decapoda, Isopoda, Mysida, Pantopoda, and Hemiptera). The majority of host species belong to crustaceans (class Malacostraca; 72 species, 91.1 % of the total arthropod host species richness), followed by sea spiders (class Pycnogonida; 4 species) and insects (class Hexapoda; 3 species).

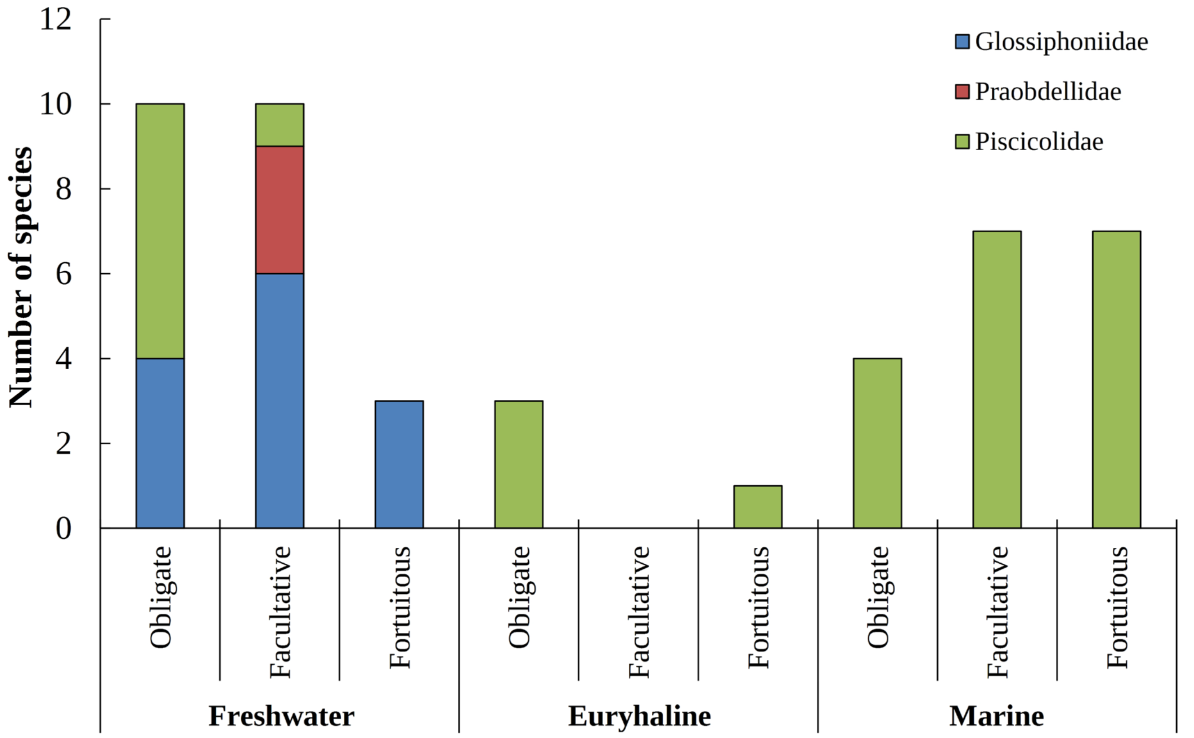
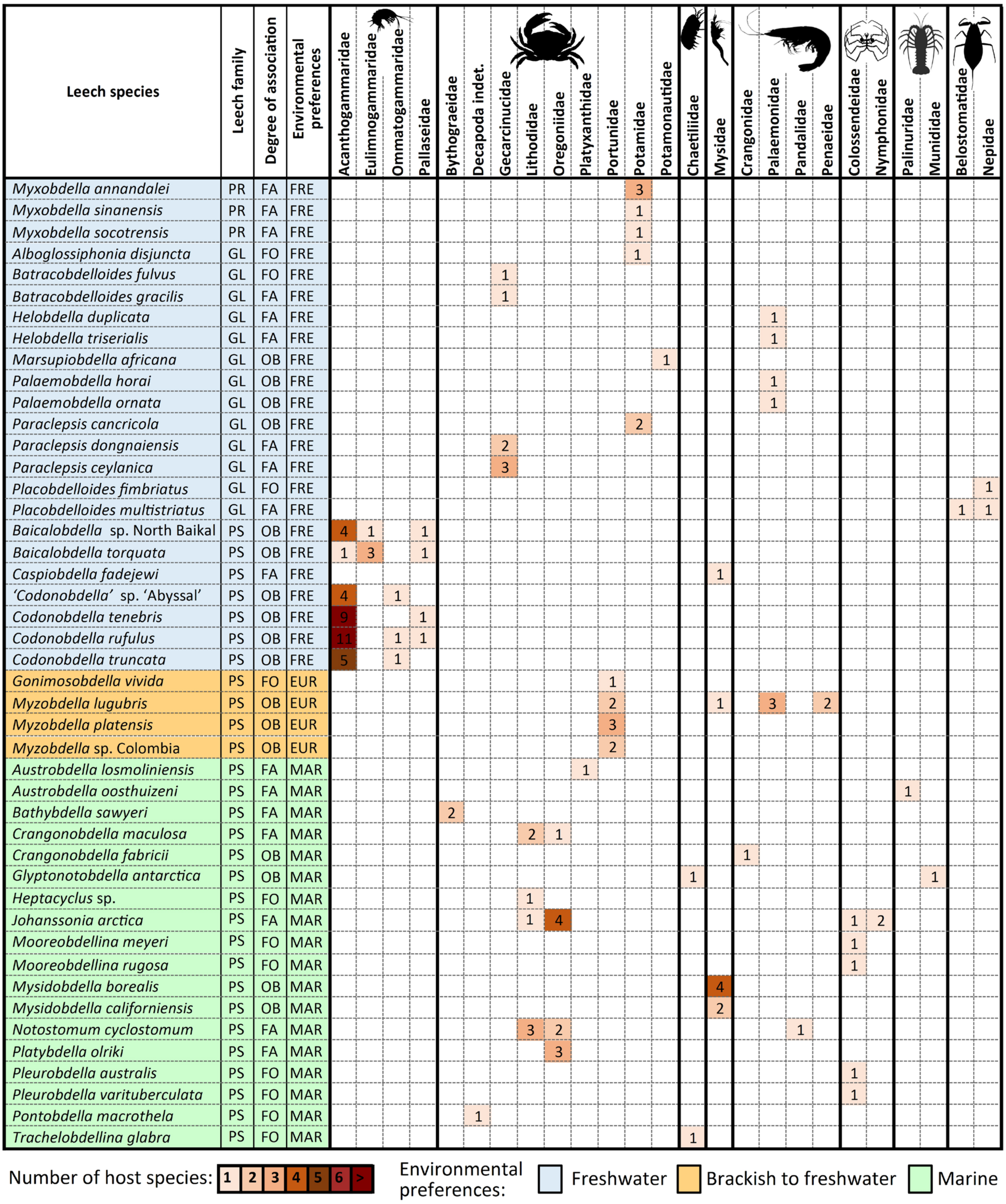


Figure 1. Taxonomic diversity of the global arthropod-associated leech assemblage (total number of species: *n* = 45) with respect to the preferred environment and degree of association with host. The raw data and references are presented in Dataset S1 on *figshare* (Bolotov et al. 2025c).

The total diversity of arthropod hosts is lower in saltwater (marine and estuarine) environments compared with that in fresh water (35 vs. 44 species, respectively) (Figure 4). However, the estimate for freshwater taxa includes 21 amphipod species endemic to Lake Baikal (Bolotov et al. 2025c: Dataset S1). One leech species may utilize from one to 13 arthropod host species (mean = 2.7 ± 0.4; *n* = 45). This value does not differ between saltwater (marine + brackish) and freshwater environments (Mann-Whitney test: $U = 248$, $P = 0.911$; $n = 22$ and 23, respectively).

Most arthropod-associated leeches may be considered ectosymbionts (Table 1 and Figure 5). A few species are ectoparasites of crustaceans, while others are commensals, using hosts as dwelling place, dispersal agents (phoresy) and/or hard substrate for cocoon deposition. Finally, no less than five species may act as endosymbionts, dwelling in the internal cavities of the host, i.e., *Paraclepsis* spp. and *Batracobdelloides gracilis* (Blanchard, 1897) **comb. nov.** in the gill cavity of freshwater crabs and *Helobdella duplicata* (Moore, 1911) in the gill chamber of a shrimp.

The associations with crabs and shrimps are the most widespread throughout the globe (Table 1, Figure 6 and Bolotov et al. 2025c: Dataset S2). They occur in marine, estuarine, and freshwater environments. A total of 27 leech species were recorded in associations with these decapods (Figure 2). The leech-mysid associations involve four species of leeches, two of which are obligate parasites of mysids, that is, *Mysidobdella borealis* (Johansson, 1898) and *My. californiensis* Burreson, Kim & Kalman Passarelli, 2012 (Figure 2). These associations were recorded from the western and eastern coast of the USA, as well as from the Bay of Biscay, White Sea, and a freshwater reservoir of Europe (Figure 6). The leech-amphipod associations exclusively occur in Lake Baikal, where several endemic species of fish leeches evolved as obligate ectoparasites of endemic lacustrine amphipods (Figure 6 and Bolotov et al. 2025c: Dataset S2). Associations of leeches with isopods are rare, with *Glyptonotobdella antarctica* (Sawyer & White, 1969) being a single obligate inhabitant of the body surface of an Antarctic isopod (Figure 6 and Bolotov et al. 2025c: Dataset S2). There are only two documented cases of leech associations with lobsters, both from lower latitudes of the Southern Hemisphere (Figure 6 and Bolotov et al. 2025c: Dataset S2). Sea spiders play a role of facultative and occasional hosts for leeches, serving as hard substrate for cocoon deposition and/or dispersal agents (Table 1). Records of this kind share a bipolar distribution and are mostly presented in the Arctic and Southern oceans (Figure 6). Finally, observations of leeches using aquatic insects (water bugs) as dispersal agents (phoresy) exclusively occurred in Africa and linked to the glossiphoniids *Placobdelloides multistriatus* (Johansson, 1909) and *Pl. fimbriatus* (Johansson, 1909) (Figure 6).



Leech species	Leech family	Degree of association	Environmental preferences	Acanthogammaridae	Eulimnogammaridae	Ommatogammaridae	Pallaseidae	Bythograeidae	Decapoda indet.	Gecarcinucidae	Lithodidae	Oregoniidae	Platyxanthidae	Portunidae	Potamidae	Potamonautidae	Chaetiliidae	Mysidae	Crangonidae	Palaemonidae	Pandalidae	Penaeidae	Colossendeidae	Nymphonidae	Palinuridae	Munididae	Belostomatidae	Nepidae
Myxobdella annandalei	PR	FA	FRE												3													
Myxobdella sinanensis	PR	FA	FRE												1													
Myxobdella socotrensis	PR	FA	FRE												1													
Alboglossiphonia disjuncta	GL	FO	FRE												1													
Batracobdelloides fulvus	GL	FO	FRE							1																		
Batracobdelloides gracilis	GL	FA	FRE							1																		
Helobdella duplicata	GL	FA	FRE																	1								
Helobdella triserialis	GL	FA	FRE																	1								
Marsupiobdella africana	GL	OB	FRE													1												
Palaemobdella horai	GL	OB	FRE																	1								
Palaemobdella ornata	GL	OB	FRE																	1								
Paraclepsis cancricola	GL	OB	FRE												2													
Paraclepsis dongnaiensis	GL	FA	FRE							2																		
Paraclepsis ceylanica	GL	FA	FRE							3																		
Placobdelloides fimbriatus	GL	FO	FRE																									1
Placobdelloides multistriatus	GL	FA	FRE																								1	1
Baicalobdella sp. North Baikal	PS	OB	FRE	4	1		1																					
Baicalobdella torquata	PS	OB	FRE	1	3		1																					
Caspiobdella fadejewi	PS	FA	FRE															1										
'Codonobdella' sp. 'Abyssal'	PS	OB	FRE	4		1																						
Codonobdella tenebris	PS	OB	FRE	9			1																					
Codonobdella rufulus	PS	OB	FRE	11		1	1																					
Codonobdella truncata	PS	OB	FRE	5		1																						
Gonimosobdella vivida	PS	FO	EUR											1														
Myzobdella lugubris	PS	OB	EUR											2				1		3		2						
Myzobdella platensis	PS	OB	EUR											3														
Myzobdella sp. Colombia	PS	OB	EUR											2														
Austrobdella losmoliniensis	PS	FA	MAR										1															
Austrobdella oosthuizeni	PS	FA	MAR																						1			
Bathybdella sawyeri	PS	FA	MAR					2																				
Crangonobdella maculosa	PS	FA	MAR								2	1																
Crangonobdella fabricii	PS	OB	MAR																1									
Glyptonotobdella antarctica	PS	OB	MAR														1									1		
Heptacyclus sp.	PS	FO	MAR								1																	
Johanssonia arctica	PS	FA	MAR								1	4											1	2				
Mooreobdellina meyeri	PS	FO	MAR																				1					
Mooreobdellina rugosa	PS	FO	MAR																				1					
Mysidobdella borealis	PS	OB	MAR															4										
Mysidobdella californiensis	PS	OB	MAR															2										
Notostomum cyclostomum	PS	FA	MAR								3	2									1							
Platybdella olriki	PS	FA	MAR									3																
Pleurobdella australis	PS	FO	MAR																				1					
Pleurobdella varituberculata	PS	FO	MAR																				1					
Pontobdella macrothela	PS	FO	MAR						1																			
Trachelobdellina glabra	PS	FO	MAR														1											

Number of host species: 1 2 3 4 5 6 >

Environmental preferences: ☐ Freshwater ☐ Brackish to freshwater ☐ Marine

Figure 2. Family-level host relations of the global arthropod-associated leech assemblage based on compilation of literature sources and original data (Bolotov et al. 2025c: Dataset S1). Leech families: GL, Glossiphoniidae; PS, Piscicolidae; and PR, Praobdellidae. Degree of association with hosts: OB, obligate; FA, facultative; and FO, fortuitous. Environmental preferences of leeches: FRE, freshwater; EUR, euryhaline (brackish to freshwater); and MAR, marine. The black silhouette images indicate host groups (left to right): amphipods, crabs, isopods, mysids, shrimps, sea spiders, lobsters, and water bugs.

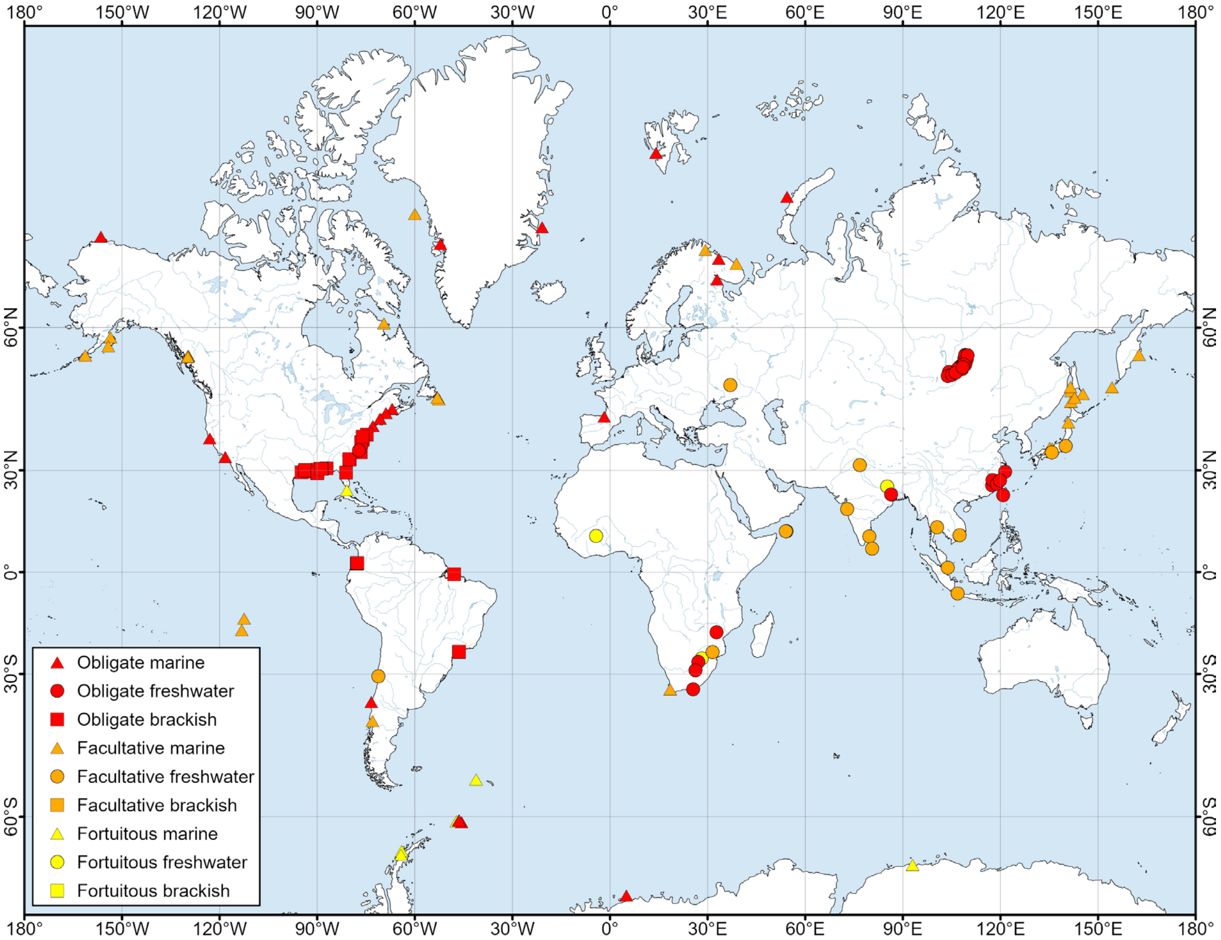


Figure 3. Records of arthropod-leech associations in the World by environment and the degree of association with hosts. The georeferenced occurrences and references are given in Dataset S2 on *figshare* (Bolotov et al. 2025c).

Here, we developed the first global ecological classification of leech-arthropod associations based on compilation of literature and original data. The associations were delineated to four types that are characterized in Table 2.

Table 2. Ecological classification of leech-arthropod associations in the World based on compilation of literature sources and original data (Bolotov et al. 2025c: Dataset S1)

Type of association with arthropods	Number of leech species (F/E/M)	List of leech species [environmental preference]	Arthropod host organisms
Type I – Obligate parasitic association; morphologically specialized leeches with narrow host range; arthropods serve as primary host, as well as dwelling place/shelter, cocoon substrate and transport host	8 (6/0/2)	*Baicalobdella torquata* (Grube, 1871) [F]; *Baicalobdella* sp. North Baikal [F]; *Codonobdella truncata* Grube, 1873 [F]; *Codonobdella tenebris* Kaygorodova, 2025 [F]; *Codonobdella rufulus* Kaygorodova, 2025 [F]; ‘*Codonobdella*’ sp. ‘Abyssal’ [F]; *Mysidobdella borealis* (Johansson, 1898) [M]; *Mysidobdella californiensis* Burreson, Kim & Kalman Passarelli, 2012 [M]	Crustaceans (amphipods, mysids)

..continued on the next page

Table 2

Type II – Obligate parasitic or commensalistic association; morphologically specialized leeches with narrow host range; arthropods may serve as secondary host, dwelling place/shelter, cocoon substrate and transport host	9 (4/3/2)	*Marsupiobdella africana* Goddard & Malan, 1912 [F]; *Palaemobdella horai* (Baugh, 1960) **comb. nov.** [F]; *Palaemobdella ornata* (Oka, 1929) **gen. & comb. nov.** [F]; *Paraclepsis cancricola* (Oka, 1928) [F]; *Myzobdella lugubris* Leidy, 1851 [E]; *Myzobdella platensis* (Cordero, 1933) [E]; *Myzobdella* sp. Colombia [E]; *Crangonobdella fabricii* Malm, 1863 [M]; *Glyptonotobdella antarctica* (Sawyer & White, 1969) [M]	Crustaceans (crabs, isopods, shrimps, mysids, squat lobsters)
Type III – Facultative parasitic or commensalistic association; morphologically unspecialized leeches, using a group of suitable hosts (e.g., crabs and sea spiders); arthropods may serve as secondary host, dwelling place/shelter, cocoon substrate and transport host	17 (10/0/7)	*Batracobdelloides gracilis* (Blanchard, 1897) **comb. nov.** [F]; *Caspiobdella fadejewi* (Epshtein, 1961) [F]; *Helobdella duplicata* (Moore, 1911) [F]; *Helobdella triserialis* (Blanchard, 1849) [F]; *Myxobdella annandalei* Oka, 1917 [F]; *Myxobdella sinanensis* Oka, 1925 [F]; *Myxobdella socotrensis* Schenkova et al., 2021 [F]; *Paraclepsis dongnaiensis* **sp. nov.** [F]; *Paraclepsis ceylanica* (Harding, 1909) [F]; *Placobdelloides multistriatus* (Johansson, 1909) [F]; *Austrobdella losmoliniensis* Williams, Urrutia & Burreson, 2007 [M]; *Austrobdella oosthuizeni* A. Utevsky, 2004 [M]; *Bathybdella sawyeri* Burreson, 1981 [M]; *Crangonobdella maculosa* S. Utevsky, 2005 [M]; *Johanssonia arctica* (Johansson, 1898) [M]; *Notostomum cyclostomum* (Johansson, 1898) [M]; *Platybdella olriki* Malm, 1865 [M]	Crustaceans (crabs, mysids, shrimps, spiny lobsters), sea spiders, and water insects
***Type IV** – Fortuitous commensalistic association; morphologically unspecialized leeches, using available hosts on occasion; arthropods may serve as transport host and hard substrate for leech attachment	11 (3/1/7)	*Alboglossiphonia disjuncta* (Moore, 1939) [F]; *Batracobdelloides fulvus* (Harding, 1924) **comb. nov.** [F]; *Placobdelloides fimbriatus* (Johansson, 1909) [F]; *Gonimosobdella vivida* (Verrill, 1872) [E]; *Heptacyclus* sp. [M]; *Mooreobdellina meyeri* A. Utevsky, 1997 [M]; *Mooreobdellina rugosa* Moore, 1938 [M]; *Pleurobdella australis* (Epstein, 1970) [M]; *Pleurobdella varituberculata* (Moore, 1938) [M]; *Pontobdella macrothela* Schmarda, 1861 [M]; *Trachelobdellina glabra* Moore, 1957 [M]	Crustaceans (crabs, isopods), sea spiders, and water insects

Abbreviations: F, freshwater species; E, euryhaline species (brackish to fresh water); and M, marine species.
*The fourth group contains little-known species, some of which may belong to facultative commensals (type III).

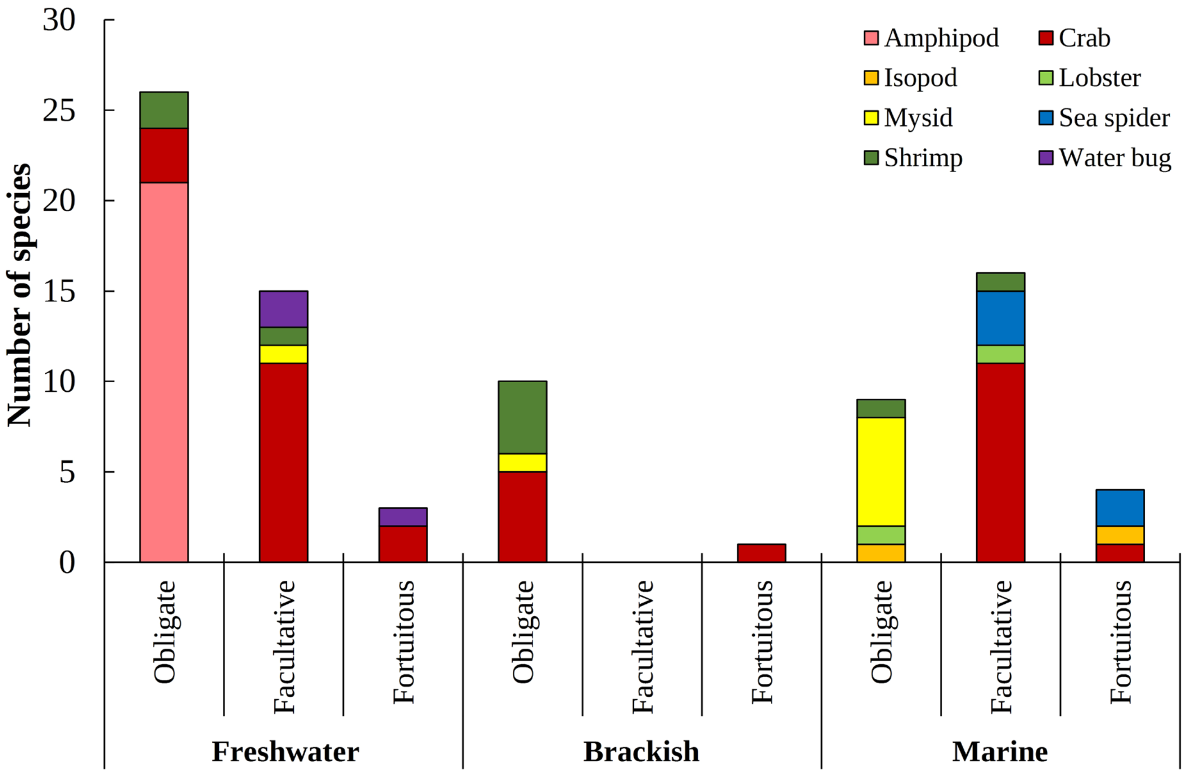


Figure 4. Global diversity of arthropod hosts of leeches (total number of species: *n* = 79) with respect to the preferred environment and degree of leech association with these organisms. The raw data and references are presented in Dataset S1 on *figshare* (Bolotov et al. 2025c).

Taxonomic richness of arthropod-associated glossiphoniid leeches

Our results show that the glossiphoniid members of the global arthropod-associated leech assemblage belong to 13 species and seven genera (Table 3). The taxonomic placement of *Alboglossiphonia disjuncta* (Moore, 1939), *Helobdella duplicata*, *He. triserialis* (Blanchard, 1849), *Marsupiobdella africana* Goddard & Malan, 1912, *Placobdelloides multistriatus*, and *Pl. fimbriatus* was already established (Sawyer 1986; Siddall and Borda 2003; Jueg 2023; Torres-Carrera et al. 2023). In this work, we propose taxonomic opinions on the systematics of other arthropod-associated nominal species and some related taxa (see Taxonomic account and Table 3 for detail). Most of these species were placed in *Placobdelloides* Sawyer, 1986, a large, composite genus of blood-sucking leeches, having one pair of eyespots, esophagial glands, seven pairs of crop caeca, and terminal mouth pore (Sawyer 1986).

A few nominal species of crab-associated and free-living leeches were assigned to the genus *Paraclepsis*, a little-known group from tropical and subtropical Asia (Table 3). Here, we revise this genus based on morphological and molecular evidence. The two-locus maximum likelihood phylogeny (*COI* + *18S rRNA*) reveals that *Paraclepsis dongnaiensis* **sp. nov.** (Vietnam) and *Pa. cancricola* (Oka, 1928) (China) are cluster together with high support value (BS = 88). Morphologically, both species possess diagnostic features, unique for this genus: (1) three pairs of eyespots on III, IV a1 and V a2 and (2) second and third pairs of eyespots are separated by two annuli. This combination of characters also occur in three nominal species from India and Sri Lanka, that is, *Paraclepsis ceylanica* (Harding, 1909), *Pa. praedatrix* Harding, 1924, and *Pa. vulnifera* Harding, 1924 (Table 3). In our opinion, these nominal taxa shall be lumped to one accepted species due to the lack of reliable distinguishing features (see Taxonomic account for detail).

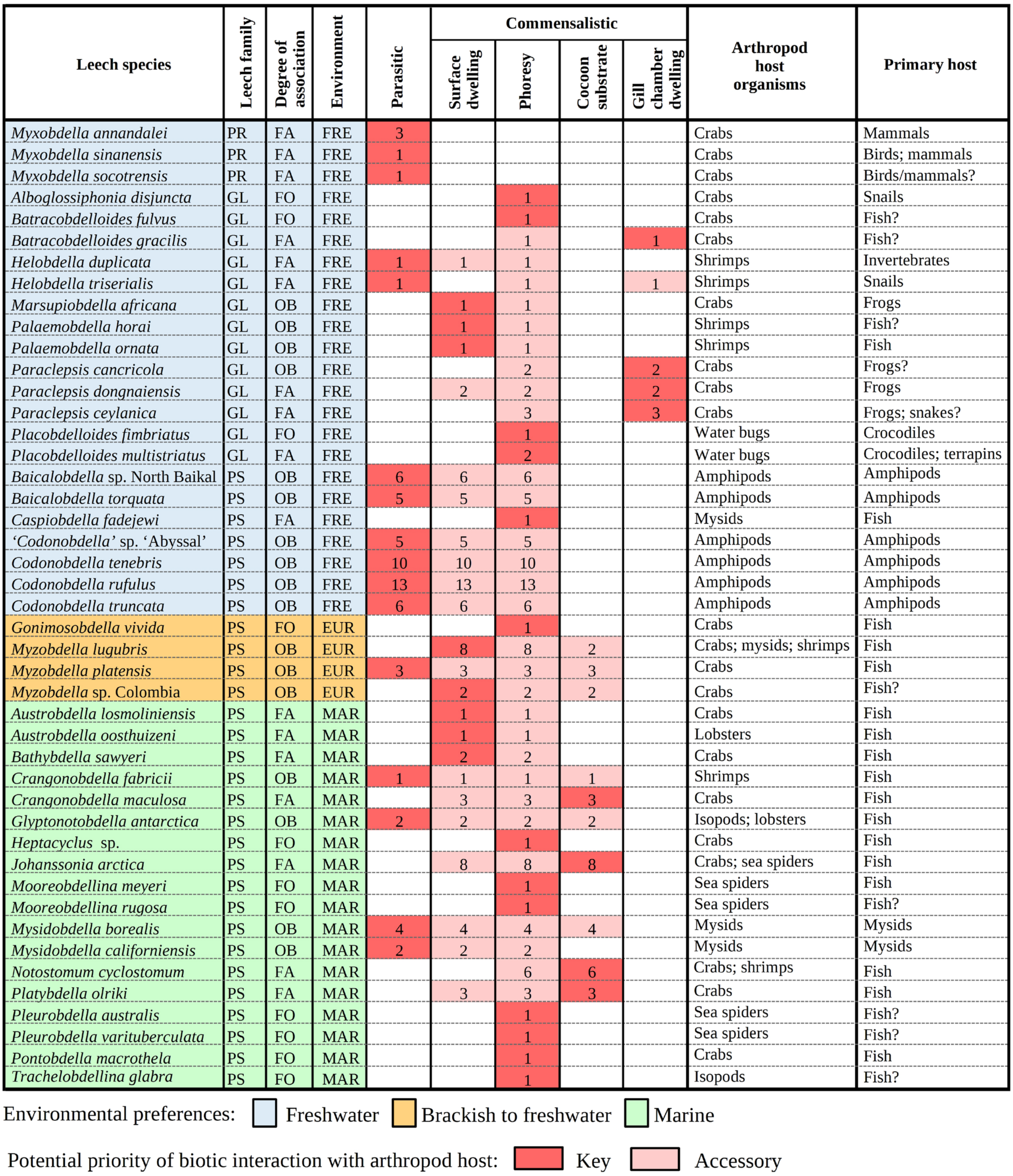
Table 3. Taxonomic review of arthropod-associated glossiphoniid leeches (Hirudinida: Glossiphoniidae).

Taxa with original combinations and synonyms	Type and reference DNA sequences	Type locality	Distribution and hosts
***Alboglossiphonia* Lukin, 1976**			
Alboglossiphonia disjuncta (Moore, 1939) = *Glossiphonia disjuncta* Moore (1939): 299, pl. 25, fig. 1 [original description] = *Batracobdella disjuncta* Oosthuizen (1978): 93 [new combination] = *Alboglossiphonia disjuncta* Sawyer (1986): 659 [new combination]	Holotype: NHMUK (coll. No. BMNH 1933.1.21.17; fide Meyer 1968) Reference DNA sequences: not available	'Bufundi on Lake Bunyoni, Uganda' [Uganda: Bufundi, Lake Bunyonyi, 1.2908°S, 29.8915°E] (Moore 1939)	Sub-Saharan Africa, including Uganda, Ethiopia, the Democratic Republic of Congo, Togo, South Africa and Namibia; phoretic/dwelling host: crab *Potamon* sp. (Decapoda: Potamidae) [fortuitous association; localization: unknown]; primary host: freshwater snails such as *Bulinus tropicus* (Krauss, 1848) [in the mantle cavity] (Oosthuizen 1978; Jueg 2023)
***Batracobdelloides* Oosthuizen, 1986**			
Batracobdelloides fulvus (Harding, 1924) **comb. nov.** = *Placobdella fulva* Harding (1924): 494, pl. 13 [original description] = *Placobdelloides fulva* Sawyer (1986): 657 [new combination]	Type: whereabouts unknown Reference DNA sequences: not available	'Purulia, Manbhum dist., Chota Nagpur div., Bengal' [India: Purulia, 23.33°N, 86.36°E, West Bengal] (Harding 1924)	India; phoretic/dwelling host: crab *Maydelliathelphusa lugubris* (Wood-Mason, 1871) (Decapoda: Gecarcinucidae) [fortuitous association; localization: carapace]; primary host: unknown (most likely fish) (Nesemann et al. 2007)
Batracobdelloides gracilis (Blanchard, 1897) **comb. nov.** = *Helobdella gracilis* Blanchard (1897): 334, fig. 2 [original description] = *Placobdella gracilis* Soós (1969): 431 [new combination] = *Batracobdella gracilis* Sawyer (1986): 656 [new combination]	Type: whereabouts unknown. Reference DNA sequences: not available	'Buitenzorg (Java)' [Indonesia: Bogor, 6.60°S, 106.80°E, Java Island] (Blanchard 1897)	Java, Indonesia; phoretic/dwelling host: crab *Parathelphusa* sp. (Decapoda: Gecarcinucidae) [facultative association; localization: gill chamber]; primary host: unknown (most likely fish) (Blanchard 1897)
***Helobdella* Blanchard, 1896**			
Helobdella duplicata (Moore, 1911) = *Glossiphonia duplicata* Moore (1911): 675, pl. 49, fig. 10, pl. 50, figs 16-22 [original description]	Two complete syntypes ANSP 570 and one sectioned syntype USNM 36301 (fide Meyer 1968) Reference DNA sequences: not available	Several localities on Rio Chico of 15, 25 and 30 miles above 'Sierra Oveja' and of 25 miles above 'Sierra Ventana' [Argentina: Chico River basin, Santa Cruz Province] (Moore 1911)	Bolivia, Brazil, Chile, Peru, and Uruguay; primary host: shrimp *Macrobrachium caementarius* (Molina, 1782) (Decapoda: Palaemonidae) [facultative association; localization: gill chamber] and, most likely, other invertebrates such as freshwater snails

Taxa with original combinations and synonyms	Type and reference DNA sequences	Type locality	Distribution and hosts
			(Ringuelet 1985; Tello et al. 2007)
Helobdella triserialis (Blanchard, 1849) = *Glossiphonia triserialis* Blanchard (1849): 50 [original description]	Type: whereabouts unknown. Reference DNA sequences: AF329054 (*COI* gene) and AY962435 (*18S rRNA* gene) (Siddall and Borda 2003; Siddall et al. 2005)	'en Carelmapu en las aguas dulces' [Chile: fresh waters, Carelmapu, approx. 41.7458°S, 73.7064°W] (Blanchard 1849)	South America; primary host: shrimp *Macrobrachium caementarius* (Molina, 1782) (Decapoda: Palaemonidae) [facultative association; localization: pleopods] and freshwater snails (Siddall and Borda 2003; Vega et al. 2006; Christoffersen 2009; De-Carli et al. 2014)
***Marsupiobdella* Goddard & Malan, 1912**			
Marsupiobdella africana Goddard & Malan, 1912 = *Marsupiobdella africana* Goddard & Malan (1912): 309 [original description]	Type: whereabouts unknown Reference DNA sequences: AF116015 (*COI* gene) and AF115979 (*18S rRNA* gene) (Apakupakul et al. 1999)	'Backen's River, Cape Colony' [South Africa: Backens River, approx. 33.9669°S, 25.5788°E, Eastern Cape Province] (Goddard and Malan 1912)	South Africa (probably more widespread but overlooked: e.g., Zimbabwe; Turnbull-Kemp 1960); phoretic/dwelling host: crab *Potamonautes perlatus* (H. Milne Edwards, 1837) (Decapoda: Potamonautidae) [obligate association; localization: carapace and appendages]; primary host: frog *Xenopus laevis* (Daudin, 1802) (Anura: Pipidae) (Badets and Du Preez 2014; Kruger and Du Preez 2015)
***Palaemobdella* Bolotov gen. nov.**			
Palaemobdella horai (Baugh, 1960) **comb. nov.** = *Placobdella horai* Baugh (1960a): 287, figs 1a-b, 2a-b [original description] = *Placobdelloides horai* Sawyer (1986): 765 [new combination]	Holotype ZSI W3760/1; paratypes W3761-3763/1(fide Baugh 1960a); topotype ZSI An4600/1 (Figure S5*b*) Reference DNA sequences: not available	'A lake popularly known as 'Sahib Bandh' in Purulia, Manbhum District (Bihar)' [India: Lake Saheb Bandh, 23.3383°N, 86.3596°E, Purulia, West Bengal] (Baugh 1960a)	India (known only from the type locality); phoretic/dwelling host: shrimp *Macrobrachium lamarrei* (H. Milne Edwards, 1837) (Decapoda: Palaemonidae) [obligate association; localization: carapace]; primary host: unknown (most likely fish) (Baugh 1960a)
Palaemobdella ornata (Oka, 1929) **gen. & comb. nov.** = *Placobdella ornata* Oka (1929): 249, figs A-B [original description; junior secondary homonym of *Placobdella ornata* (Verrill, 1872); reinstated	Type: whereabouts unknown Reference DNA sequences: not available	'le sud de la Formose' [China: Southern Taiwan] (Oka 1929)	Taiwan; phoretic/dwelling host: unidentified shrimp (Decapoda: Palaemonidae) [obligate association; localization: carapace]; primary host: fishes *Rhodeus ocellatus* (Kner, 1866) (Cyprinidae) and *Monopterus albus* (Zuiew,

Taxa with original combinations and synonyms	Type and reference DNA sequences	Type locality	Distribution and hosts
by us based on Art. 59.4 of the Code (ICZN 1999)] = *Placobdella okai* Soós (1969): 433 [new name for *Placobdella ornata* Oka, 1929] = *Placobdelloides okai* Sawyer (1986): 657 [new combination with a question mark]			1793) (Synbranchidae) (Lai and Chen 2010)
***Paraclepsis* Harding, 1924**			
Paraclepsis cancricola (Oka, 1928) = *Hemiclepsis cancricola* Oka (1928): 607, figs A-B [original description] = *Batracobdella cancricola* Soós (1967): 245 [new combination] = *Paraclepsis cancricola* Sawyer (1986): 659 [new combination]	Type: whereabouts unknown Reference DNA sequences: OR578897 (*COI* gene) and OQ076769 (*mt-genome*) (Genbank)	'Pan-chi, Feng-hua, prov. Che-chiang' [China: an unknown locality in the Fenghua District, Zhejiang Province, approx. 29.65°N, 121.42°E] (Oka 1928)	South-East China: Zhejiang and Fujian provinces; phoretic/dwelling host: crabs *Longpotamon fujianense* (Dai & Chen, 1979) and *Bottapotamon fukienense* (Dai & Lin, 1979) (Decapoda: Potamidae) [obligate association; localization: gill chamber]; primary host: unknown (most likely frog) (Yang 1986)
Paraclepsis dongnaiensis **sp. nov.** = *Paraclepsis vulnifera* Moore (1935): 68 [nec Harding, 1924; identification error]	Holotype: RMBH Hir-1190-H Reference DNA sequences: PV132090, PV132091, PV132092, PV132089 (*COI* gene) and PV130378, PV130379, PV130377 (*18S rRNA* gene) (this study)	Vietnam: temporary forest pools in Cát Tiên National Park, 11.4369°N, 107.4230°E, Đồng Nai River basin, Đồng Nai Province	Southern Vietnam and Thailand (Moore 1935); phoretic/dwelling host: crabs *Somanniathelphusa triangularis* Đăng & Đỗ, 2005 and *S. sinensis* (H. Milne Edwards, 1853) (Decapoda: Gecarcinucidae) [facultative association; localization: carapace and gill chamber]; primary host: frog *Hoplobatrachus chinensis* (Osbeck, 1765) (Anura: Dicroglossidae)
Paraclepsis ceylanica (Harding, 1909) = *Glossiphonia ceylanica* Harding (1909): 233 [original description] = *Glossosiphonia ceylanica* Kaburaki (1921): 671, fig. 5 [expanded redescription] = *Paraclepsis praedatrix* Harding (1924): 495, pl. 14 [**syn. nov.**; original description] =): 497, pl. 15 [**syn. nov.**; original description] = *Placobdella ceylanica* Moore (1924): 357, pl. 19,	Type: whereabouts unknown Reference DNA sequences: not available	*Glossiphonia ceylanica*: 'Ceylon; in fresh-water' (Harding 1909) *Paraclepsis praedatrix*: 'Various places in Northern, Southern, and Eastern India' (Harding 1924); '(a) Tanjore, Trichinopoly District, S. India [Thanjavur, approx. 10.78°N, 79.14°E, Tamil Nadu, India]; (b) Bangalore, S. India, altitude circa 3000 ft. [Bengaluru, approx. 12.98°N, 77.59°E, Karnataka, India]; (c) Kalka, at base of Simla	India and Sri Lanka; phoretic/dwelling host: crabs *Spiralothelphusa hydrodroma* (Herbst, 1794); *Barusa guerini* (Milne Edwards, 1853); *Oziotelphusa ceylonensis* (Fernando, 1960) (Decapoda: Gecarcinucidae) [facultative association; localization: gill chamber and soft parts of limb joints]; additional phoretic host: turtle *Lissemys punctata vittata* (Peters, 1854) (Testudines: Trionychidae) [facultative

Taxa with original combinations and synonyms	Type and reference DNA sequences	Type locality	Distribution and hosts
figs 5a, 5b, 6, 7, pl. 21, fig. 25 [new combination] = *Parabdella ceylanica* Soós (1969): 428 [new combination] = *Paraclepsis ceylanica* Sawyer (1986): 765 [new combination]		Hills, altitude 2400 ft. [Kalka, approx. 30.83°N, 76.94°E, Haryana, India]; (d) Purulia, Manbhum District, Chota Nagpur Div., Bengal [Purulia, approx. 23.33°N, 86.36°E, West Bengal, India]; (e) Selai Kusi, Magaldhai, Assam [Mangaldoi, approx. 26.45°N, 92.03°E, Assam, India]; (f) Igatpuri Lake, W. Ghats, Bombay Presidency [Igatpuri Reservoir, 19.70°N, 73.56°E, Maharashtra, India]' (Harding and Moore 1927) *Paraclepsis vulnifera*: 'Mauganaltur, Tanjore District, Madras' [India: Manganallur Village, 11.0210°N, 79.6365°E, the former Tanjore District, Tamil Nadu] (Harding 1924; Ramachandra Rao and Susainathan 1924)	association; localization: unknown]; primary host: frogs *Euphlyctis cyanophlyctis* (Schneider, 1799) and *Fejervarya limnocharis* (Gravenhorst, 1829) (Anura: Dicroglossidae); probably, also aquatic snake *Fowlea piscator* (Schneider, 1799) (Squamata: Colubridae) (Harding 1909; Kaburaki 1921; Harding 1924; Ramachandra Rao and Susainathan 1924; Harding and Moore 1927; McCann 1937; Fernando 1960; Chandra and Saha 1967; Chandra and Mukharjee 1973)
***Placobdelloides* Sawyer, 1986**			
Placobdelloides fimbriatus (Johansson, 1909) = *Clepsine fimbriata* Johansson (1909): 148, fig. 2 [original description] = *Placobdelloides fimbriata* Sawyer (1986): 657 [new combination]	Type: whereabouts unknown Reference DNA sequences: AY962465 (*COI* gene) (Siddall et al. 2005)	Sudan (Johansson 1909)	Sub-Saharan Africa (known from Uganda, Kenya, and Nigeria); phoretic host: water bugs *Laccotrephes* sp. (Hemiptera: Nepidae) [fortuitous association; localization: venter surface]; primary host: crocodiles (Johansson 1909; Moore 1939; Siddall et al. 2005)
Placobdelloides multistriatus (Johansson, 1909) = *Placobdella catenigera* Plotnikov (1907): 137-138 [identification error] = *Clepsine multistriata* Johansson (1909): 151 [original description] = *Placobdelloides multistriata* Sawyer (1986): 657 [new combination]	Type: SMNH (fide Oosthuizen 1979) Reference DNA sequences: DQ414338 (*COI* gene) and DQ414293 (*18S rRNA* gene) (Williams and Burreson 2006)	'North of Gebel Ahmed, Sudan' [Sudan: north of an unknown mount called 'Ahmed'] (Johansson 1909; Oosthuizen 1979)	Continental Africa, Madagascar, and Yemen; phoretic host: water bugs *Lethocerus cordofanus* Mayr, 1853 (Hemiptera: Belostomatidae) and *Nepa* sp. (Hemiptera: Nepidae) [facultative association; localization: body surface]; primary host: crocodiles and terrapins (Oosthuizen 1979; Oosthuizen 1991; Nesemann and Neubert 1999; Bolotov et al. 2023a)



Leech species	Leech family	Degree of association	Environment	Parasitic	Commensalistic				Arthropod host organisms	Primary host
					Surface dwelling	Phoresy	Cocoon substrate	Gill chamber dwelling		
Myxobdella annandalei	PR	FA	FRE	3					Crabs	Mammals
Myxobdella sinanensis	PR	FA	FRE	1					Crabs	Birds; mammals
Myxobdella socotrensis	PR	FA	FRE	1					Crabs	Birds/mammals?
Alboglossiphonia disjuncta	GL	FO	FRE			1			Crabs	Snails
Batracobdelloides fulvus	GL	FO	FRE			1			Crabs	Fish?
Batracobdelloides gracilis	GL	FA	FRE			1		1	Crabs	Fish?
Helobdella duplicata	GL	FA	FRE	1	1	1			Shrimps	Invertebrates
Helobdella triserialis	GL	FA	FRE	1		1		1	Shrimps	Snails
Marsupiobdella africana	GL	OB	FRE		1	1			Crabs	Frogs
Palaemobdella horai	GL	OB	FRE		1	1			Shrimps	Fish?
Palaemobdella ornata	GL	OB	FRE		1	1			Shrimps	Fish
Paraclepsis cancricola	GL	OB	FRE			2		2	Crabs	Frogs?
Paraclepsis dongnaiensis	GL	FA	FRE		2	2		2	Crabs	Frogs
Paraclepsis ceylanica	GL	FA	FRE			3		3	Crabs	Frogs; snakes?
Placobdelloides fimbriatus	GL	FO	FRE			1			Water bugs	Crocodiles
Placobdelloides multistriatus	GL	FA	FRE			2			Water bugs	Crocodiles; terrapins
Baicalobdella sp. North Baikal	PS	OB	FRE	6	6	6			Amphipods	Amphipods
Baicalobdella torquata	PS	OB	FRE	5	5	5			Amphipods	Amphipods
Caspiobdella fadejewi	PS	FA	FRE			1			Mysids	Fish
‘*Codonobdella*’ sp. ‘Abyssal’	PS	OB	FRE	5	5	5			Amphipods	Amphipods
Codonobdella tenebris	PS	OB	FRE	10	10	10			Amphipods	Amphipods
Codonobdella rufulus	PS	OB	FRE	13	13	13			Amphipods	Amphipods
Codonobdella truncata	PS	OB	FRE	6	6	6			Amphipods	Amphipods
Gonimosobdella vivida	PS	FO	EUR			1			Crabs	Fish
Myzobdella lugubris	PS	OB	EUR		8	8	2		Crabs; mysids; shrimps	Fish
Myzobdella platensis	PS	OB	EUR	3	3	3	3		Crabs	Fish
Myzobdella sp. Colombia	PS	OB	EUR		2	2	2		Crabs	Fish?
Austrobdella losmoliniensis	PS	FA	MAR		1	1			Crabs	Fish
Austrobdella oosthuizeni	PS	FA	MAR		1	1			Lobsters	Fish
Bathybdella sawyeri	PS	FA	MAR		2	2			Crabs	Fish
Crangonobdella fabricii	PS	OB	MAR	1	1	1	1		Shrimps	Fish
Crangonobdella maculosa	PS	FA	MAR		3	3	3		Crabs	Fish
Glyptonotobdella antarctica	PS	OB	MAR	2	2	2	2		Isopods; lobsters	Fish
Heptacyclus sp.	PS	FO	MAR			1			Crabs	Fish
Johanssonia arctica	PS	FA	MAR		8	8	8		Crabs; sea spiders	Fish
Mooreobdellina meyeri	PS	FO	MAR			1			Sea spiders	Fish
Mooreobdellina rugosa	PS	FO	MAR			1			Sea spiders	Fish?
Mysidobdella borealis	PS	OB	MAR	4	4	4	4		Mysids	Mysids
Mysidobdella californiensis	PS	OB	MAR	2	2	2			Mysids	Mysids
Notostomum cyclostomum	PS	FA	MAR			6	6		Crabs; shrimps	Fish
Platybdella olriki	PS	FA	MAR		3	3	3		Crabs	Fish
Pleurobdella australis	PS	FO	MAR			1			Sea spiders	Fish?
Pleurobdella varituberculata	PS	FO	MAR			1			Sea spiders	Fish?
Pontobdella macrothela	PS	FO	MAR			1			Crabs	Fish
Trachelobdellina glabra	PS	FO	MAR			1			Isopods	Fish?

Environmental preferences: 🟦 Freshwater 🟧 Brackish to freshwater 🟩 Marine

Potential priority of biotic interaction with arthropod host: 🟥 Key ▨ Accessory

Figure 5. Biotic interactions of arthropod-associated leeches with hosts based on compilation of literature sources and original data (Bolotov et al. 2025c: Dataset S1). Leech families: GL, Glossiphoniidae; PS, Piscicolidae; and PR, Praobdellidae. Degree of association with hosts: OB, obligate; FA, facultative; and FO, fortuitous. Environmental preferences of leeches: FRE, freshwater; EUR, euryhaline (brackish to freshwater); and MAR, marine. Numbers in the cells indicate the number of arthropod host species.

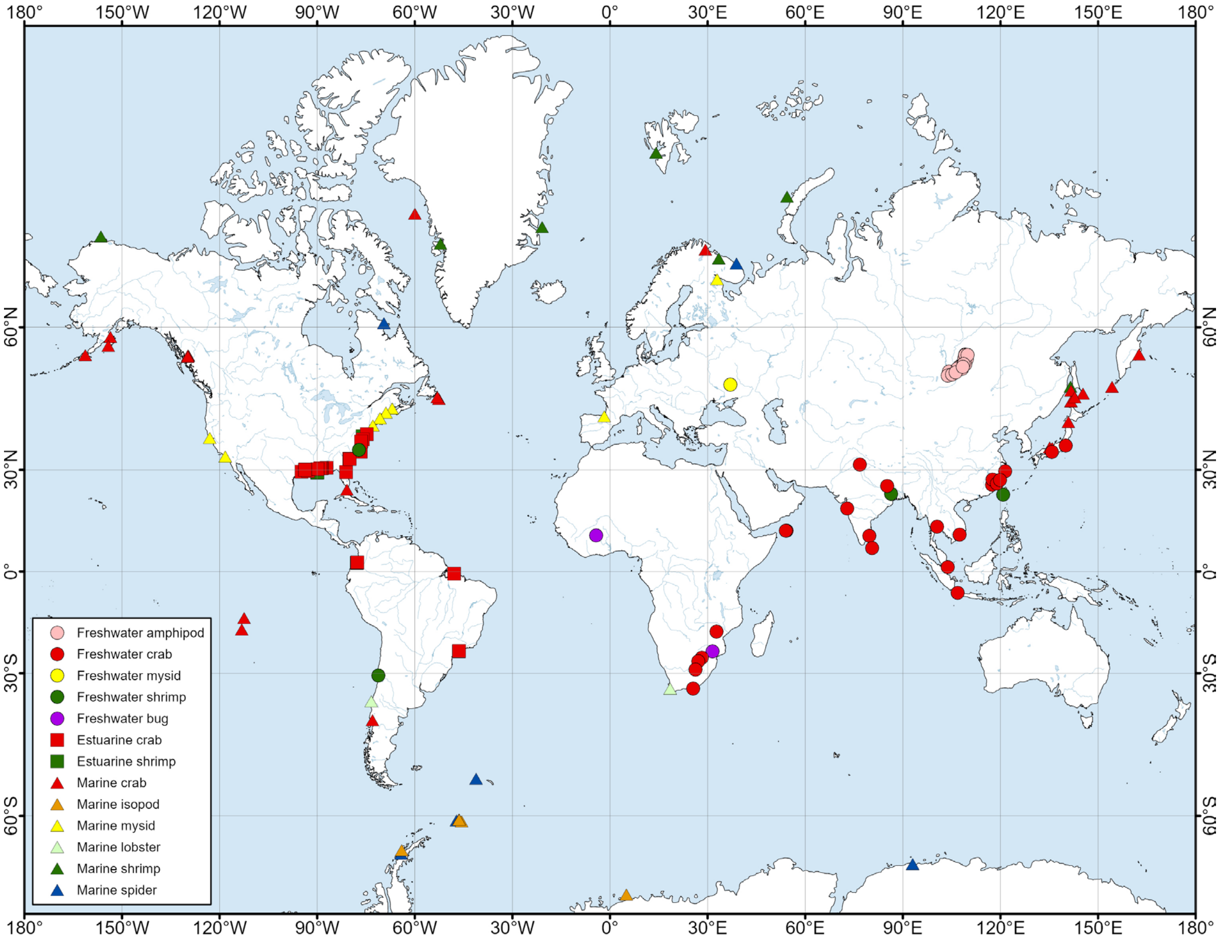


Figure 6. Records of arthropod-leech associations in the World by environment and the host organism. The georeferenced occurrences and references are given in Dataset S2 on *figshare* (Bolotov et al. 2025c).

Taxonomic account with opinions on selected arthropod-associated glossiphoniid leeches and related taxa

Class Clitellata Michaelsen, 1919
Subclass Hirudinea Lamarck, 1818
Order Hirudinida Siddall, Apakupakul, Burreson, Coates, Erséus, Gelder, Källersjö & Trapido-Rosenthal, 2001
Suborder Glossiphoniiformes Tessler & de Carle, 2018
Family Glossiphoniidae Vaillant, 1890
Subfamily Glossiphoniinae Vaillant, 1890

Genus *Paraclepsis* Harding, 1924 gen. rev.

Figure S2

Type species. *Paraclepsis praedatrix* Harding, 1924 (subsequent designation by Soós, 1969).

Differential diagnosis. Small leeches (length up to 15.5 mm; Harding 1924); three pairs of eyespots on III, IV a1 and V a2 (second and third pairs of eyespots are separated by two annuli); body with 70-73 annuli, mid-body somites triannulate; dorsum with four rows of ovate shallow papillae; mouth pore is subterminal (near the rim of the anterior sucker); two pairs of compact salivary glands; esophagus with broad, bag-like pharingeal bulb; seven pairs of crop caeca; six pairs of testisacs; gonopores separated by two annuli: male gonopore on XI a3 / XII a1, female gonopore on XII a2 /

XII a3; posterior sucker is small, circular, ventrally directed. Phylogenetically, this genus represents a separate, distant group that is sister to the clade *Orientobdelloides* + *Batracobdella*.

Distribution. India, Sri Lanka, Thailand, Vietnam, and South-East China (Table 3).

List of species. *Paraclepsis cancricola* (Oka, 1928) [South-East China]; *Pa. dongnaiensis* **sp. nov.** [Thailand and Vietnam]; *Pa. ceylanica* (Harding, 1909) [= *Pa. vulnifera* Harding, 1924 **syn. nov.**; = *Pa. praedatrix* Harding, 1924 **syn. nov.**; India and Sri Lanka] (Table 3).

Hosts. Historically, freshwater turtles (Trionychidae) and crabs (Gecarcinucidae) were considered hosts for leeches in this genus (Harding 1924; Harding and Moore 1927; Soós 1969). However, there are reliable records from frogs (Dicroglossidae) (Kaburaki 1921; Chandra and Mukharjee 1973) and from the buccal cavity of an aquatic snake (Colubridae) (Chandra and Saha 1967). In our opinion, relationships of these leeches with turtles and crabs may be regarded as phoretic/dwelling biotic interactions, whereas frogs and the snake may serve as primary hosts (Table 3). It is well known that various leech species (both parasitic and predatory taxa) may use turtles as phoretic hosts (e.g., Oosthuizen 1991; Marrone et al. 2016; Perera et al. 2019; Watermolen 2021).

Comments. Our concept of *Paraclepsis* is largely based on the morphology-based revision of Sawyer (1986), who transferred the nominal taxa *Placobdella ceylanica* and *Batracobdella cancricola* to this genus. This author also assumed that *Paraclepsis vulnifera* may represent an intraspecific form of *Pa. praedatrix* but did not formally synonymize these nominal species (Sawyer 1986: 764).

Three nominal species from India and Sri Lanka, that is, *Paraclepsis ceylanica*, *Pa. vulnifera*, and *Pa. praedatrix* cannot be delineated using the morphological and anatomical diagnostic characters presented in their original descriptions and subsequent re-descriptions (Figure S2; Harding 1909; Kaburaki 1921; Harding 1924; Harding and Moore 1927). For instance, *Pa. vulnifera* is similar to *Pa. praedatrix* but differs from it by a few minor traits as follows: (1) the head region is continuous with the body and is not separated from it by a posterior constriction; (2) smaller number of annuli (70 vs. 73); and (3) the lack of large vesiculae seminales (Harding 1924; Harding and Moore 1927). It was also noted that the condition of the type series of *Pa. vulnifera* was unfavorable for observation of the papillae and coloration (Harding 1924). In our opinion, the shape of the head region cannot be used as a reliable diagnostic trait in leeches because this feature may vary depending on the condition of specimens and the methods of their fixation (see the series of specimens on Figure 8A-F). The precise counting of the total number of annuli can be difficult in contracted specimens, while the development of vesiculae seminales may differ depending on the degree of maturity of individuals. Therefore, we agree with Sawyer's (1986) assumption that the two nominal species are conspecific. Moreover, they are morphologically indistinguishable from an older nominal species, *Paraclepsis ceylanica*, and are considered its synonyms.

Here, we also confirm the placement of *Paraclepsis cancricola*, a crab-associated leech from South-East China, in this genus based on the phylogenetic evidence (see Figure 7). Morphologically, this leech fully aligns with the generic diagnosis and has three pairs of eyespots with the two posterior pairs separated by two annuli, body with 70 annuli, seven pairs of crop caeca, esophagus with an esophagial bulb, six pairs of testisacs, and two annuli between gonopores (Yang 1986).

Two nominal species in the genus *Paraclepsis* were recently described from India:

(1) *Paraclepsis gardensi* Mandal, 2004 [holotype: ZSI An 2768/1; type locality: King Lake, 22.5598°N, 88.2879°E, Botanical Garden, Shibpur, Howrah, West Bengal, India; host: unknown] (Mandal 2004);

(2) *Paraclepsis joraparіensis* Mandal, 2015 [holotype: ZSI An 3702/1; type locality: Jorapari, 24.1°N, 86.3°E, Giridih District, Jharkhand, India; host: unknown] (Mandal 2015).

Although the DNA sequences of these nominal species are not available, they cannot be considered representatives of the original genus based on morphological criteria. In particular, *Paraclepsis gardensi* is characterized by (1) three pairs of eyespots with the two posterior pairs separated by one annulus, and (2) the position of the mouth pore in the anterior half of the oral sucker (Figure S3). There is a peculiar subgroup in the genus *Hemiclepsis* Vejdovsky, 1884, the representatives of which have three pairs of eyespots in this kind of arrangement, as well as a similar position of the mouth pore. This subgroup contains three species: *Hemiclepsis bhatiai* Baugh, 1960 [Bihar and Jammu and Kashmir, India], *Hm. erhaiensis* Yang, 1981 [Erhai, Dianchi and Chenghai lakes, Yunnan, China], and *Hm. viridis* Chelladurai, 1934 [Kerala and Tamil Nadu, India] (Chelladurai 1934; Baugh, 1960a; Yang 1996; Bolotov et al. 2019). The second pair of eyespots is the largest in *Hemiclepsis bhatiai* and *Paraclepsis*

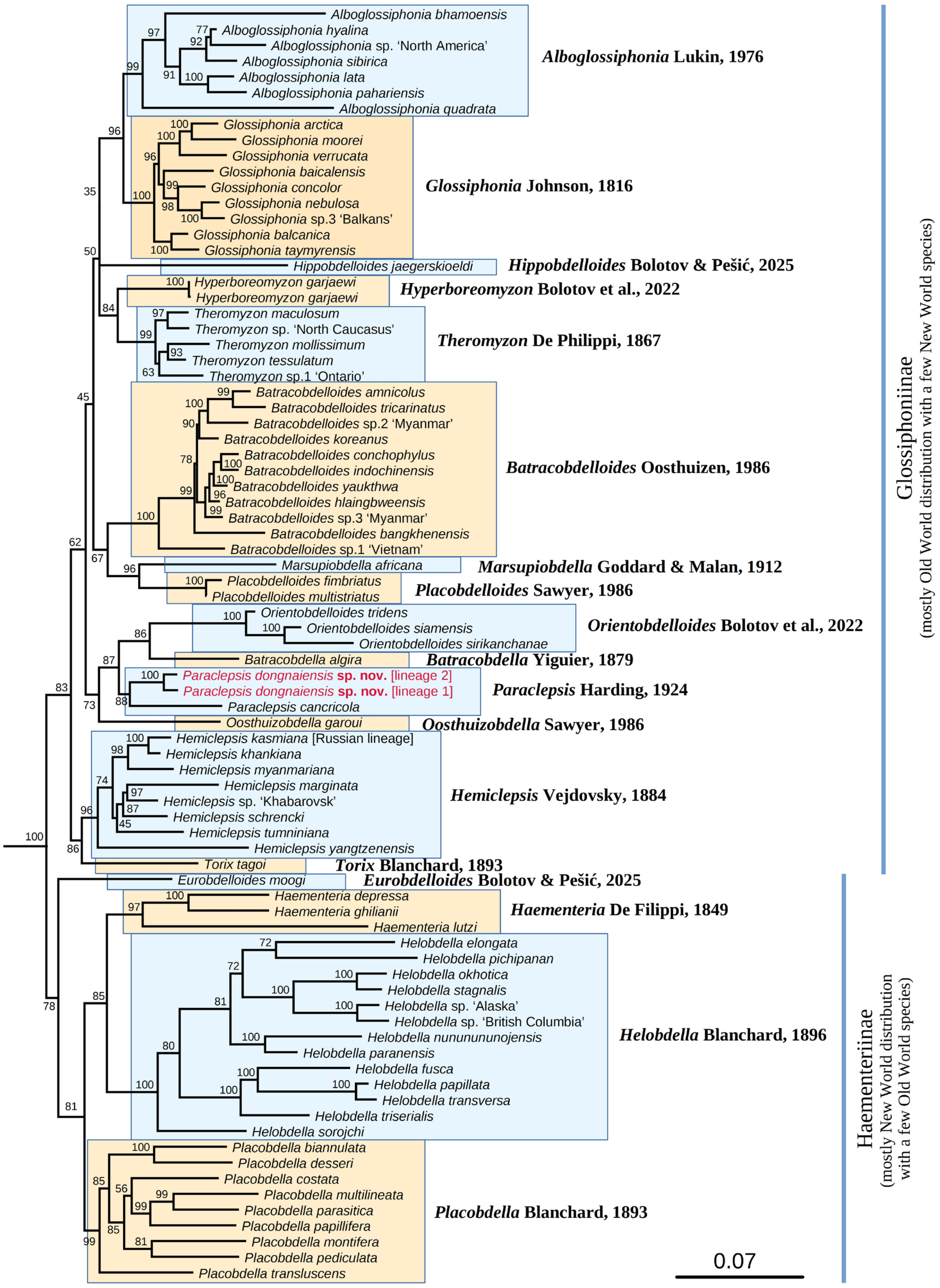


Figure 7. Maximum likelihood phylogeny of the Glossiphoniidae based on the combined *COI* and *18S rRNA* gene fragments (Table S1). The black numbers near nodes are bootstrap support values of IQ-TREE v. 1.6.12. The scale bar indicates the branch lengths (substitutions per site). Outgroup taxa are omitted.

gardensi. However, the latter species can be distinguished from *Hemiclepsis bhatiai* by having 18 longitudinal greenish stripes on the dorsum (vs. four longitudinal series of brown spots). In turn, dorsum of *Hemiclepsis viridis* bears 15 to 25 longitudinal green lines but in this nominal species the third pair of eyespots is the largest (Chelladurai 1934). It is known that the size of eyespots in the Glossiphoniidae is rather variable (Soós 1969; but see Eliseeva et al. 2024 for exception). Moreover, a paratype of *Paraclepsis gardensi* has the second and third pair of eyespots of similar size (Figure S3). Therefore, we propose the new synonymy as follows: *Hemiclepsis viridis* Chelladurai, 1934 [= *Paraclepsis gardensi* Mandal, 2004 **syn. nov.**].

Paraclepsis jorapariensis Mandal, 2015 was described based on a single specimen (the holotype). The original diagnosis of this species is as follows: length 15 mm; four pairs of eyespots: the first three pairs are in two subparallel rows, while the fourth pair is laterally arranged; dorsum with seven longitudinal greyish-yellow lines; four series of dorsal papillae; 71 annuli; the gonopores are separated by 2-3 annuli; and eight pairs of crop caeca (Mandal 2015). The four pairs of eyespots rarely occur in the Glossiphoniidae, being the diagnostic trait of only two genera: *Theromyzon* Philippi, 1867 and *Oosthuizobdella* Sawyer, 1986 (Sawyer 1986; Bolotov et al. 2022a). *Theromyzon* has four pairs of eyespots in two subparallel rows, whereas *Oosthuizobdella* is characterized by the lateral position of the fourth (buccal) pair of eyespots (Sawyer 1986; Nesemann et al. 2007). Based on this diagnostic feature, we consider that *Paraclepsis jorapariensis* belongs to the latter genus. Morphologically, the holotype of *Paraclepsis jorapariensis* largely agrees with *Oosthuizobdella garoui* (Harding, 1932) by having light greenish ground color of the body, dorsum with broken longitudinal brownish stripes, dark yellow spots at a2 in outer paramedian, outer paramarginal and marginal positions (Oosthuizen 1982; Nesemann et al. 2007; Mandal 2015: plate I). It seems to be an immature specimen of the same species. Therefore, we propose the new synonymy as follows: *Oosthuizobdella garoui* (Harding, 1932) [= *Paraclepsis jorapariensis* Mandal, 2015 **syn. nov.**].

***Paraclepsis dongnaiensis* Bolotov, Eliseeva & Kondakov sp. nov.**
= *Paraclepsis vulnifera* Moore (1935): 68 [nec Harding, 1924; identification error; locality: Bangkok, Thailand; host: *Somanniathelphusa sinensis* (H. Milne Edwards, 1853) (Decapoda: Gecarcinucidae)].
Figures 8-12, Bolotov et al. 2025c: Dataset S4; high-resolution images of the holotype and selected paratypes are deposited at *figshare* (https://doi.org/10.6084/m9.figshare.28922393; Bolotov et al. 2025b).
https://zoobank.org/urn:lsid:zoobank.org:act:E9738BC4-FA5F-413B-A3CF-EDC60324AD9D

Holotype. RMBH Hir_1190-H; VIETNAM: Cát Tiên National Park, 11.4369°N, 107.4230°E, altitude 130 m, Đồng Nai River basin, Đồng Nai Province, temporary forest pools, on the carapace of freshwater crab *Somanniathelphusa triangularis* Đăng & Đỗ, 2005 (Decapoda: Gecarcinucidae), October 2024, Ivan N. Marin leg. (Figure 8A).

Paratypes (*n* = 16). VIETNAM: the type locality, the same habitat, host, collecting date and collector – 14 specimens (lot RMBH Hir_1190) (Figure 8B-D). VIETNAM: underside large stones in spring at the entrance of a mountain massif, 3.5 km SW of Tri Tôn city, 10.3959°N, 104.9828°E, altitude 38 m, Tri Tôn Rural District, An Giang Province, Mekong Delta Region, 11 November 2023, Dmitry M. Palatov leg. – 2 specimens (lot RMBH Hir_1137) (Figure 8E-F).

Etymology. This species is named after the Đồng Nai River, in the drainage of which its type locality is situated.

Differential diagnosis. Small leech with leaf-shaped body; three pairs of eyespots in the genus-characteristic arrangement; four rows of ovate shallow dorsal papillae of moderate size (outer paramedian and outer paramarginal series); two annuli between the male (XI a3 / XII a1) and female (XII a2/a3) genital pores; esophagus with a broad, bag-like pharingeal bulb; two pairs of compact salivary glands; 7 pairs of crop caeca. The new species differs from *Paraclepsis ceylanica* and *Pa. cancricola* by having simple crop caeca (vs bilobate).

Molecular diagnosis. The mean uncorrected *COI* p-distance between the new species and *Pa. cancricola* is 11.2 ± 0.1 %. The GenBank acc. numbers of reference DNA sequences of the new species (*COI* and *18S rRNA*) are given in Table S1.

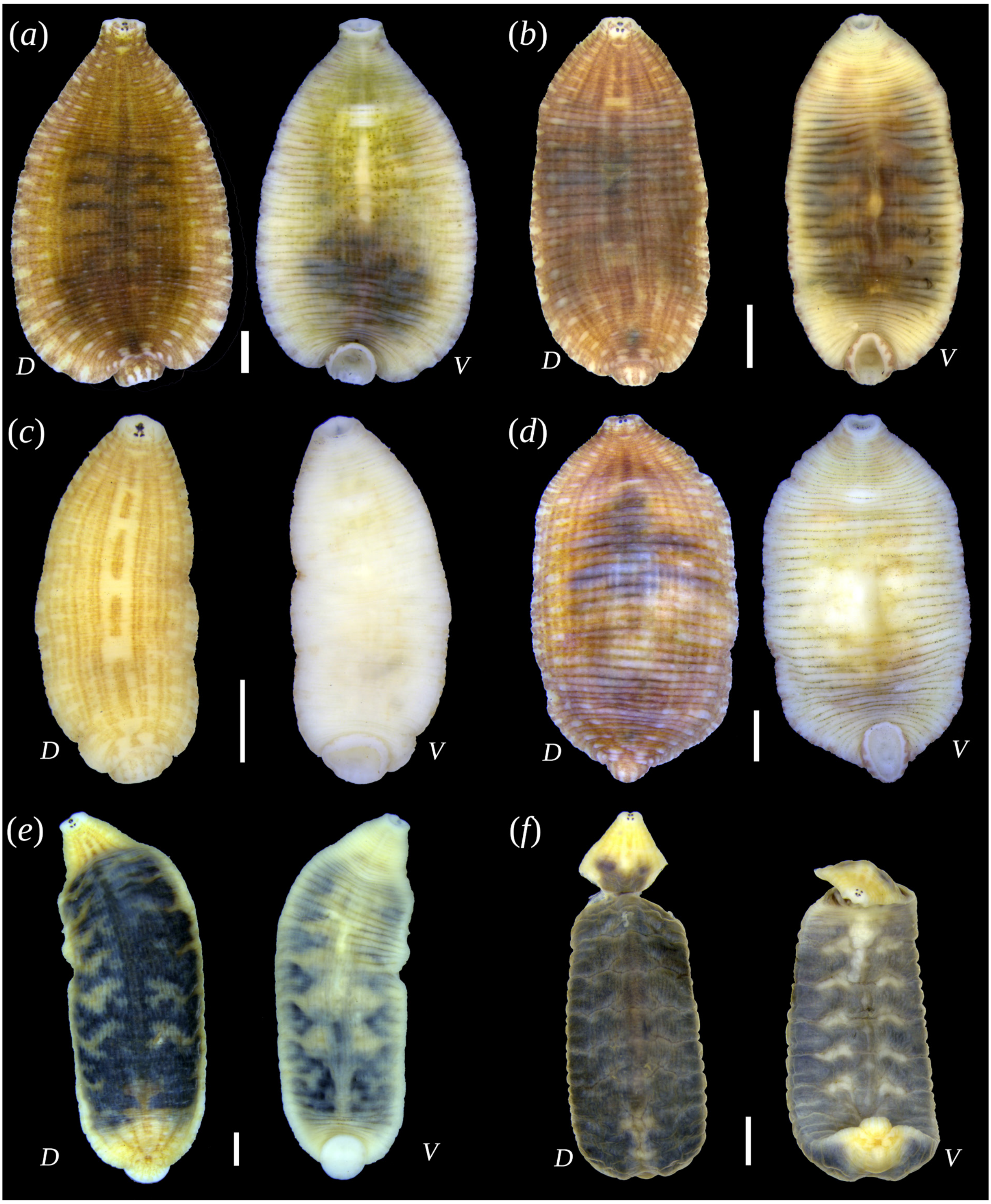


Figure 8. Dorsal (*D*) and ventral (*V*) views of the holotype and selected paratypes of *Paraclepsis dongnaiensis* **sp. nov.** from Southern Vietnam. (*a*) Holotype RMBH Hir-1190-H. (*b*) Paratype RMBH Hir-1190-2 (sequenced). (*c*) Paratype RMBH Hir-1190. (*d*) Paratype RMBH Hir-1190 (dissected). (*e*) Paratype RMBH Hir-1137-1 (sequenced). (*f*) Paratype RMBH Hir-1137-2. Scale bars = 1 mm. Photos: Tatyana A. Eliseeva.

Description. Small leech (body length up to 11.6 mm). The measurements of the holotype and paratypes are presented in Dataset S4 on *figshare* (Bolotov et al. 2025c). Body is broad, leaf-shaped, elongate-ovate (Figure 8A-F). Dorsum with four rows of ovate shallow papillae of moderate size on annulus a2 (outer paramedian and outer paramarginal series). Posterior sucker is small, circular (maximum diameter of 1.5 mm), and ventrally directed. Proboscis pore at the rim of anterior sucker.

Coloration of living animals: dorsum is translucent, light-brown, sometimes with sparse green chromatophores; a median series of 7-8 yellow spots of irregular shape, which are larger at the posterior part of the body; four additional series of small yellow round spots at the outer paramarginal and marginal positions; some specimens have dorsum with multiple brown longitudinal lines and a marginal series of light round spots; posterior sucker is brown with light radial stripes (Figures 9A-C, 10A-B). It largely agrees with that of the carapace of crab hosts and, at first glance, could be considered a camouflage (cryptic) coloration (Figures 9A-C). Coloration of ethanol-preserved animals: dorsum is dark brown, sometimes with numerous darker longitudinal stripes; three longitudinal rows of yellow spots at marginal (large ovate spots at a3), outer paramarginal (smaller ovate spots at a2) and outer paramedian (minute dots at a2) position; the anterior eyespots-bearing part with light margin and large light spot around the third pair of eyespots. Some specimens have yellow dorsum with multiple longitudinal brown lines; median line is broad and broken, consisting of several parts, separated by

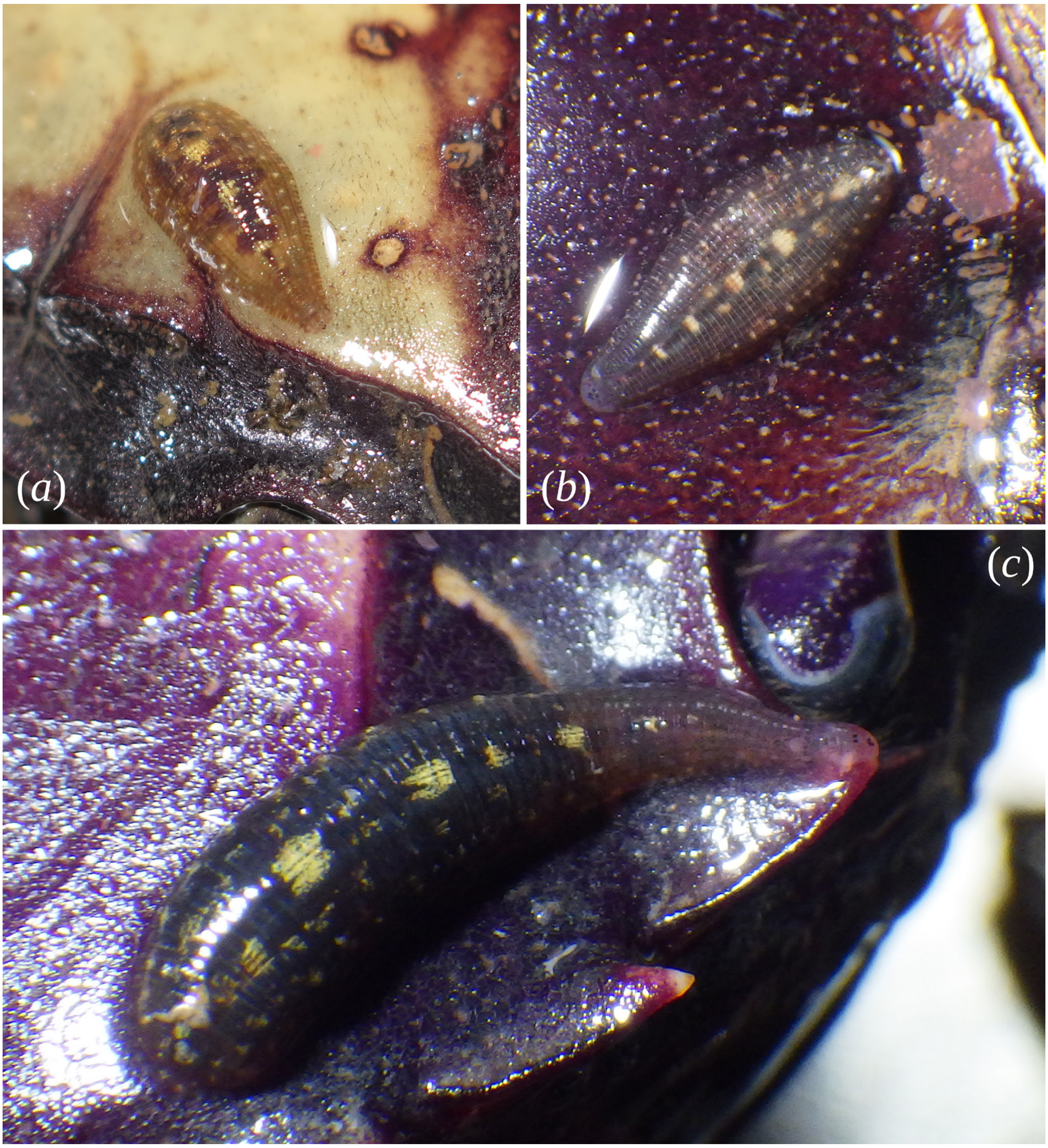


Figure 9. Cryptic coloration (camouflage) of living specimens of *Paraclepsis dongnaiensis* **sp. nov.** on the dorsal surface of the carapace of its crab host, *Somanniathelphusa triangularis* Đăng & Đỗ, 2005, in the type locality. (*a*, *b*) Leech on the anterior part of the carapace. (*c*) Leech on the lateral part of the carapace close to eye. Photos: Ivan N. Marin.

ground yellow color; other lines are narrow, continuous (Figure 8A-F). Three pairs of circular or cup-shaped eyespots are situated on III, IV a1 and V a2 (second and third pairs of eyespots are separated by two annuli) and arranged to a triangle with narrow base: eyespots of the first pair are small, joined to a single spot and usually connected with the second pair; eyespots of the second pair are circular, situated close to each other or connected; eyespots of the third pair are circular, separate (Figure 10C-F). Venter is smooth, yellowish to whitish, sometimes with sparse brown to dark green chromatophores and a white patch around the gonopores. Total number of annuli: 70. Somites I-III uniannulate, IV biannulate, V–XXIV triannulate, XXV-XXVI biannulate, XXVII uniannulate. The male and female genital pores are separated by two annuli and are located in furrows XI a3 / XII a1 and XII a2/a3, respectively (Figure 10G). Reproductive system: six pairs of large, ovate testisacs intersegmentally from XIV/XV to XIX/XX; atrium spherical, the atrial cornua massive, twisted anteriorly; paired ejaculatory ducts long, extending to XVII; paired ovisacs moderately long, arranged as loops (Figure 11A-D). Digestive system: proboscis sheath short, of moderate size; esophagus with a broad, bag-like pharingeal bulb; salivary glands compact, two pairs; crop with seven pairs of crop caeca: 1st–6th simple, elongate finger-like, 7th pair (posterior caeca) with four blind processes; intestine with four simple processes.

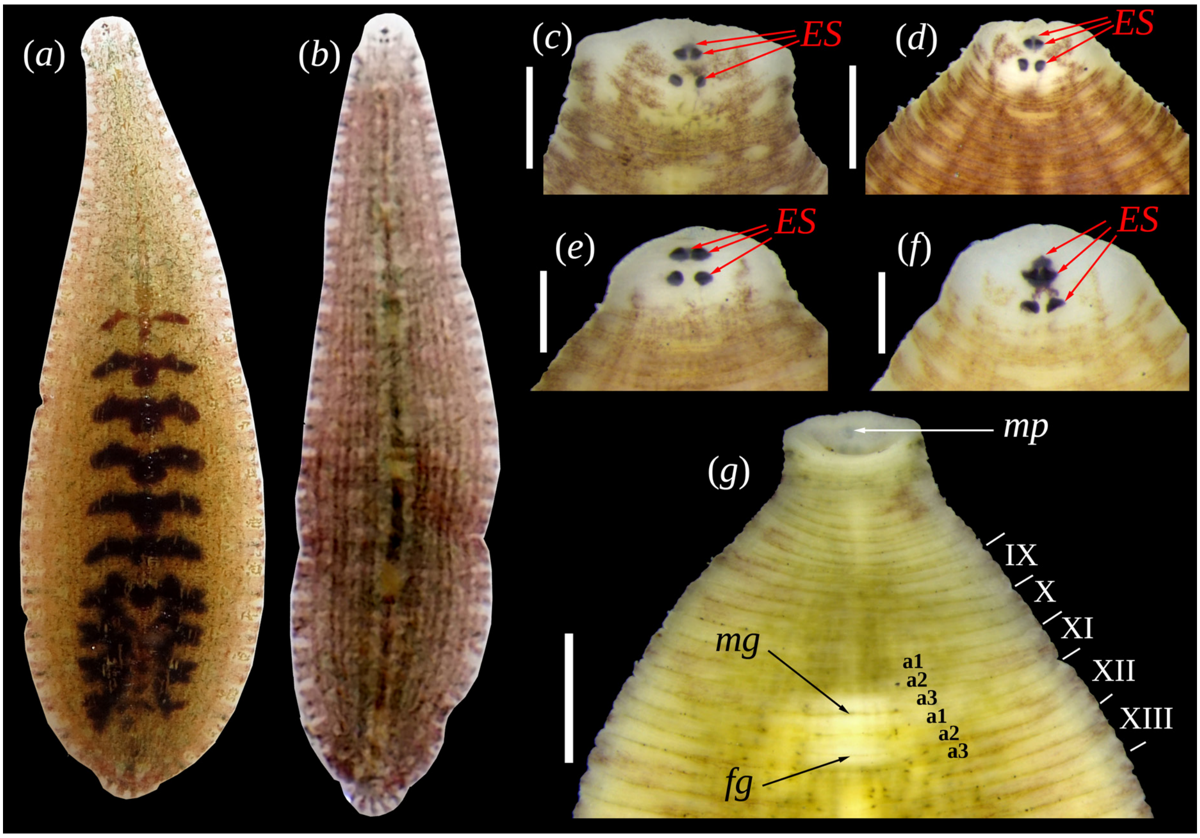


Figure 10. Morphological features of *Paraclepsis dongnaiensis* **sp. nov.** from the type locality (lot RMBH Hir-1190). (*a*) Living specimen (dorsal view) with crop filled with blood of its primary host – the frog species *Hoplobatrachus chinensis* (Osbeck, 1765) (Anura: Dicroglossidae). (*b*) Dorsal view of starved living specimen (dorsal view). (*c-f*) Anterior region with eyespots (dorsal view): holotype RMBH Hir-1190-H (*c*), paratypes RMBH Hir-1190 (*d-f*). (G) Gonopores of the holotype RMBH Hir-1190-H (ventral view). Abbreviations: *ES*, eyespots; *mg*, male gonopore; *fg*, female gonopore; and *mp*, mouth pore. Body somites are indicated by Roman numerals; bold symbols a1, a2, and a3 indicate 1st, 2nd, and 3rd annulus of a somite, respectively. Scale bars = 0.5 mm (*c-d*), 0.25 mm (*e-f*), and 1.0 mm (*g*). Photos: Ivan N. Marin (*a-b*) and Tatyana A. Eliseeva (*c-g*).

Distribution. Thailand (Moore 1935) and Southern Vietnam (Figure 12).

Phoretic/dwelling host. In the type locality, specimens of the new species were collected on the carapace of the freshwater crab *Somanniathelphusa triangularis* Đặng & Đỗ, 2005 (Gecarcinucidae). In Thailand, it was collected from the gill chamber of another crab species in this genus, *S. sinensis* (H. Milne Edwards, 1853) (Moore 1935).

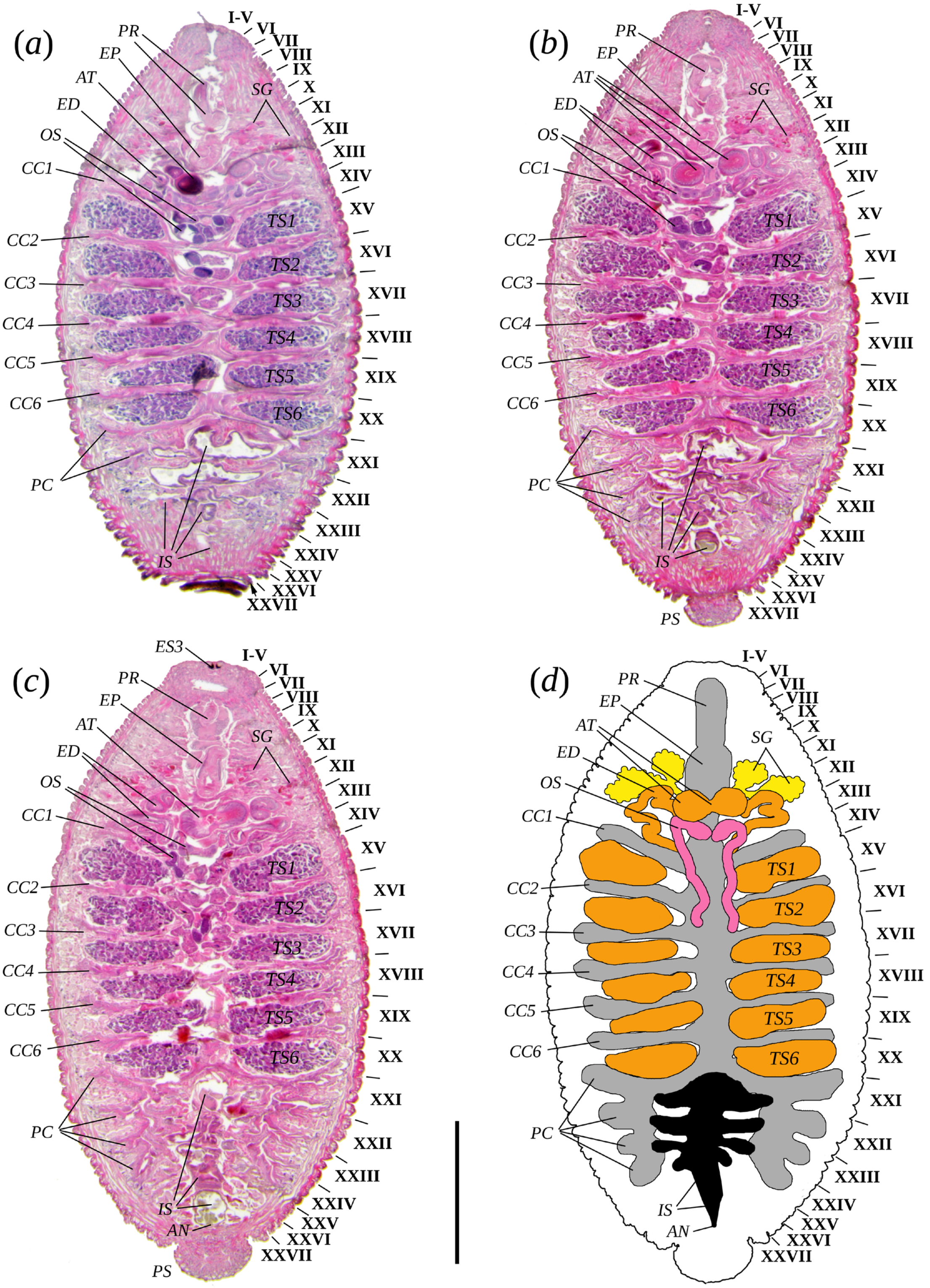


Figure 11. Anatomical features and annulation patterns of *Paraclepsis dongnaiensis* **sp. nov.** (*a-c*) H&E-stained longitudinal slices of a paratype (lot RMBH Hir_1190): closer to the dorsal side of the specimen (*a*); middle part of its body (*b*); and closer to the ventral side of the specimen (*c*). (*d*) General scheme of the digestive and generative systems based on a series of longitudinal slices (dorsal view; line contours of the body and posterior sucker are shown). Abbreviations: *PR*, proboscis sheath; *EP*, esophagus; *SG*, salivary glands; *CC*, pairs of crop caeca with their numbers; *PC*, the last pair of crop caeca (posterior caeca); *IS*, intestine; *AN*, anus; *AT*, small spherical atrium with massive atrial cornua; *ED*, ejaculatory ducts; *TS*, testisacs with their numbers; *OS*, ovisacs; *PS*, posterior sucker; and *ES*, eyespots with numbers of their pairs. Body somites are indicated by roman numerals and are delineated by black bars. Scale bar = 1.0 mm. Photos: Alexander V. Kropotin; graphics: Ivan N. Bolotov.

Primary host. The *COI* sequences of iDNA that was taken from the gut content of three paratypes reveal that they suck blood of the frog species *Hoplobatrachus chinensis* (Osbeck, 1765) (Dicroglossidae). The accession numbers of the host *COI* sequences are as follows: PV132093 (paratype RMBH Hir_1137-1); PV132094 (paratype RMBH Hir_1190 DNA-2); and PV132095 (paratype RMBH Hir_1190 DNA-3) (Bolotov et al. 2025c: Dataset S4).

Habitats. The type series was collected from temporary forest pools (on crabs) and a spring (free-living, beneath stones). The crop of two available specimens (sample RMBH Hir_1137) from a spring is completely filled with frog host blood (Figure 8E-F), while that of leeches from crabs (sample RMBH Hir_1190) is less filled with the same content (Figure 8A-D). We assume that amphibious crabs may serve as transport hosts and shelter for dispersal through land barriers between separate water bodies, especially during dry season (see Discussion for detail).

Biogeographical notes. Available samples of the new species comprises of two distant genetic lineages with an uncorrected *COI* p-distance of 3.7 %. The first lineage was discovered in the Cát Tiên National Park (the type locality of the new species) and most likely inhabits the Đồng Nai River basin. The latter basin is situated east of the Mekong Delta (see Figure 12). The second lineage was recorded from a spring in An Giang, belonging to the Mekong River basin and situated west of the Mekong Delta. We were unable to find any diagnostic differences between the two lineages by means of morphological and anatomical analyses, and these samples are here considered conspecific.

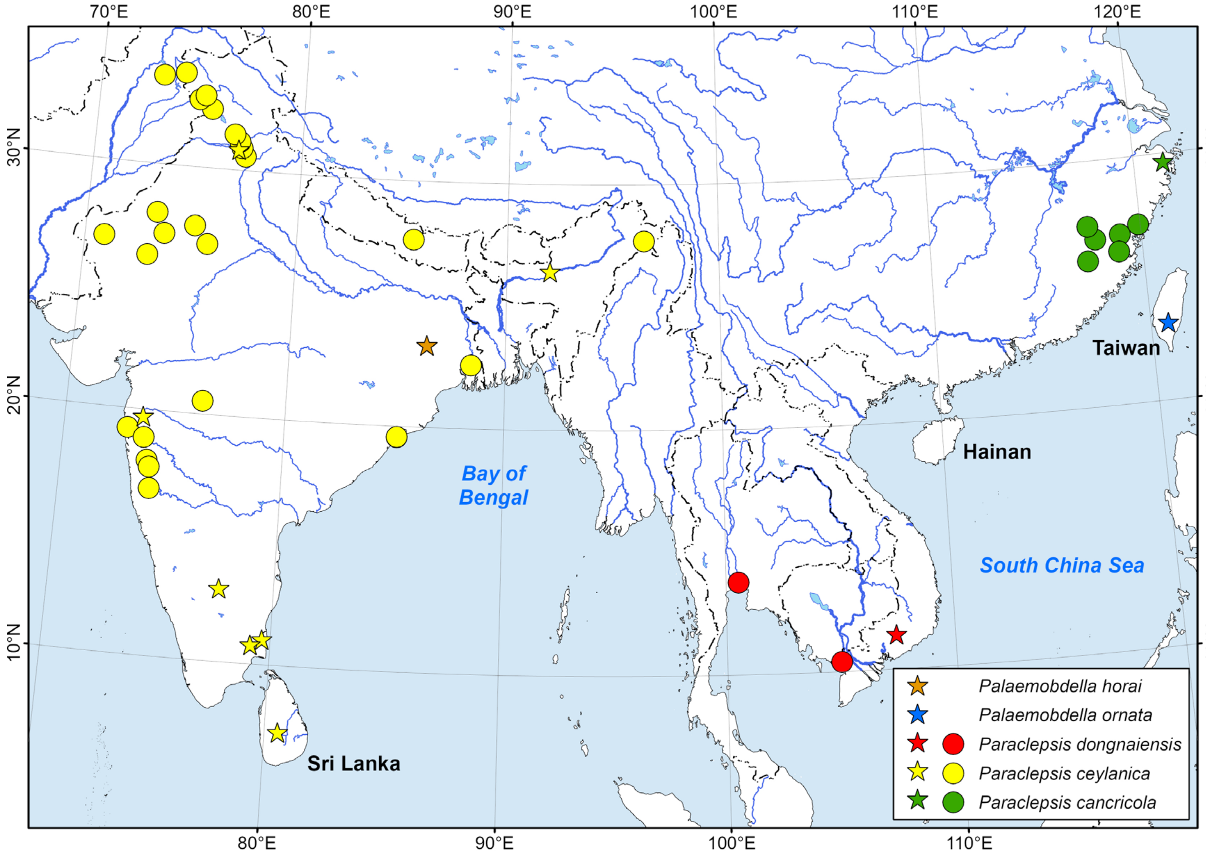


Figure 12. Map of the type localities and records of *Paraclepsis* and *Palaemobdella* leeches. The stars indicate type localities of nominal species (including synonyms) and the circles indicate records. The raw georeferenced occurrence data with references is presented in Dataset S3 on *figshare* (Bolotov et al. 2025c).

The relatively large genetic distance between these populations could be explained by several reasons. First, the deep, turbulent mainstream of the Mekong River itself may serve as an effective barrier to dispersal of the crabs and the leeches using them as transport hosts (e.g., Gascon et al. 2000; Zhang et al. 2010; Wang et al. 2015; Yuan et al. 2016; De Castro Godinho and Silva 2018; Brunke et al. 2019). It is known that the *Somanniathelphusa* host crabs (Gecarcinucidae) are rather amphibious than fully aquatic (Yeo and Nguyen 1999; Shih et al. 2007). They dwell in shallow water bodies such as forest pools, streams, and flooded paddy fields. The leeches we found were collected from crabs that lived in shallow forest pools or small streams, whereas these leeches were never recorded on crabs collected from the beds of the Đồng Nai and Mekong rivers or from paddy fields in the Mekong Delta. These patterns may explain the recent lack of gene flow between populations of leeches.

Second, paleogeographic events such as periodical marine transgressions and regressions might have influence the past connectivity of freshwater leech populations in the southern edge of the the Indochina Peninsula (Gupta 2009; Tjallingii et al. 2010). There were large fluctuations in the sea level in the Miocene, ranging between -300 and +180 m (Miller et al. 2005). Marine regressions connected the Mekong with other basins such as Đồng Nai and Chao Phraya (Morley 2012; Morley and Morley 2013; Arifin et al. 2022; Giao et al. 2023). In turn, massive marine transgressions led to the flooding of the Mekong Delta with saline waters, crossing the modern borders of Cambodia and reaching the Tonle Sap Lake (Penny 2006; Miller et al. 2005). In the Pleistocene, the eustatic sea level fluctuations reached smaller magnitudes from -120 to +50 meters (Haq et al. 1987; Woodruff 2003; Miller et al. 2005). The deglacial sea-level rise and the maximum flooding period (19–8 and 8–6 Kya, respectively) reduced the lower part of the Mekong Delta (Tjallingii et al. 2010; Thanh et al. 2021) and likely divided the basins of the Mekong and Đồng Nai rivers. The events, mentioned above, might have contributed to the isolation of freshwater animal populations in the region (De Bruyn et al. 2013; Sholihah et al. 2021; Delrieu-Trottin et al. 2025).

Genus *Batracobdelloides* Oosthuizen, 1986 gen. rev.

Figure S4

Type species. *Helobdella tricarinata* Blanchard, 1897 (by original designation).

Differential diagnosis. Small to medium-sized leeches (length up to 20 mm; Oosthuizen 1989); two pairs of eyespots on III (eyespots of the first pair are strongly reduced and usually joined with the second pair; eyespots of the second pair are larger, round or angulate, merging); body with 68-70 annuli, mid-body somites triannulate; dorsum with three or five longitudinal rows of prominent tubercles; mouth pore is shifted to the anterior part of the anterior sucker; salivary glands diffuse, extensively developed; proboscis slender; esophagus long, slender, slightly muscular; esophageal organ present; seven weakly branched pairs of crop caeca; gonopores separated by two annuli: male gonopore on furrow XI a3 / XII a1 and female gonopore on furrow XII a2 / XII a3; six pairs of testisacs; eggs carried in temporary, ventral brood chamber but not attached to the body; posterior sucker is small, circular, ventrally directed.

Distribution. Africa, South Asia (India and Sri Lanka), South-East Asia (Myanmar, Thailand, and Vietnam), East Asia (South Korea), and the Greater Sunda Islands (Java, Indonesia). The former representative of this genus from Europe was recently transferred to its own monotypic genus: *Eurobdelloides moogi* (Nesemann & Csányi, 1995) (Bolotov and Pešić 2025). The latter taxon is a relict phylogenetic lineage and does not relate to the *Batracobdelloides* clade but has some degree of convergent morphological similarity with it.

List of species. The genus contains 12 accepted species: *Batracobdelloides amnicolus* (Moore, 1958) [Republic of South Africa, Namibia, Lesotho, and Botswana]; *B. bangkhenensis* Chiangkul et al., 2021 [Thailand]; *B. conchophylus* Bolotov et al., 2019 [Myanmar]; *B. fulvus* (Harding, 1924) **comb. nov.** [India]; *B. gracilis* (Blanchard, 1897) **comb. nov.** [Java, Indonesia]; *B. hlaingbweensis* Bolotov et al., 2019 [Myanmar]; *B. indochinensis* Bolotov et al., 2019 [Myanmar]; *B. koreanus* Bolotov et al., 2019 [South Korea]; *B. reticulatus* (Kaburaki, 1921) [India]; *B. tricarinatus* (Blanchard, 1897) [Tanzania, Kenya, Uganda, Democratic Republic of the Congo, Angola, Sudan, Ghana, Zambia, Egypt, and, probably, Israel]; *B. undulatus* (Harding, 1924) **comb. nov.** [Sri Lanka, and, probably, India]; *B. yaukthwa* Bolotov et al., 2019 [Myanmar] (Oosthuizen 1989; Bolotov et al. 2019; Chiangkul et al. 2021b). Additionally, our samples contain three new mussel-associated *Batracobdelloides* species from South-East Asia (see Figure 7 and Table S1) that will be described elsewhere.

Hosts. Typically, freshwater molluscs act as shelter/dwelling place and/or secondary host and freshwater fishes serve as primary host (Bolotov et al. 2019; Chiangkul et al. 2021b). However, available observations indicate that freshwater crabs may act as phoretic/dwelling host for two species (Table 3).

Comments. Here, we transfer three nominal species from other genera to *Batracobdelloides* based on morphological features and propose new combinations as follows:

(1) *Batracobdelloides fulvus* (Harding, 1924) **comb. nov.** [= *Placobdella fulva* Harding, 1924; = *Placobdelloides fulva* (Harding, 1924); type locality: Purulia, 23.33°N, 86.36°E, West Bengal, India; phoretic/dwelling host: freshwater crab *Maydelliathelphusa lugubris* (Wood-Mason, 1871) (Gecarcinucidae); primary host: unknown (most likely fish)] (Harding 1924; Soós 1969; Sawyer 1986);

(2) *Batracobdelloides gracilis* (Blanchard, 1897) **comb. nov.** [= *Helobdella gracilis* Blanchard, 1897; = *Placobdella gracilis* (Blanchard, 1897); = *Batracobdella gracilis* (Blanchard, 1897); type locality: Bogor, 6.60°S, 106.80°E, Java Island, Indonesia; host: phoretic/dwelling host: freshwater crab *Parathelphusa* sp. (Gecarcinucidae); primary host: unknown (most likely fish)] (Blanchard 1897; Soós 1969; Sawyer 1986);

(3) *Batracobdelloides undulatus* (Harding, 1924) **comb. nov.** [= *Placobdella undulata* Harding, 1924; = *Placobdelloides undulata* (Harding, 1924); type locality: Colombo Lake [Beira Lake, 6.9294°N, 79.8542°E], Sri Lanka; host: fish *Etroplus suratensis* (Bloch, 1790) (Cichlidae)] (Harding 1924; Soós 1969; Sawyer 1986).

It should be noted that fixed samples of *Batracobdelloides* often appear as bioculate leeches, because the anterior pair of eyespots is very small and is easily disappeared under the influence of a preservative fluid (Bolotov et al. 2019). For this reason, the nominal species, listed above, were placed in *Placobdella*, *Helobdella* and/or *Placobdelloides*.

Genus *Palaemobdella* Bolotov gen. nov.

Figure S5

https://zoobank.org/urn:lsid:zoobank.org:act:D085957B-0D0A-47C4-8DCF-DE6629AA83DE

Type species. *Placobdella ornata* Oka, 1929 [= *Placobdella okai* Soós, 1969; replacement name that is rejected by us based on Art. 59.4 of the Code (ICZN 1999)].

Differential diagnosis. Small leeches (length up to 12 mm); one pair of cup-shaped (sometimes triangular or round) eyespots on II (in some cases, eyespots are invisible but can be detected histologically as aggregations of visual cells); characteristic dorsal pigmentation patterns with deep chocolate brown ground color, yellow or white longitudinal medial band and lateral yellow or white band or large spots, two or four series of yellow or white spots at a2 (outer paramarginal or outer paramarginal and outer paramedian position); posterior sucker with yellow or white edge and a series of light spots along the margin (Figure S5); body with 66-67 annuli, mid-body somites triannulate; dorsum is densely covered with small, closely set papillae; mouth pore is subterminal; one pair of compact salivary glands; seven pairs of crop caeca; six pairs of testisacs; gonopores separated by two annuli: male gonopore on furrow XI a3 / XII a1 and female gonopore on furrow XII a2 / XII a3 (*Palaemobdella horai*) or male gonopore on XI a3 and female gonopore on XII a2 (*Palaemobdella ornata*); posterior sucker is small, circular, ventrally directed. Phylogenetic data are not available.

Etymology. The name of this genus is combined from two parts: '*Palaemo*' (reference to its crustacean hosts, the family Palaemonidae) and '*bdella*' (leech in Greek).

Distribution. The new genus seems to have a disjunctive range (Baugh 1960a; Lai and Chen 2010). In particular, there are records from India (known only from a small lake in West Bengal) and Taiwan (known from a few localities in the middle and southern part of the island) (Figure 12). However, we assume that some additional species of this genus may occur within a continuous gap between India and Taiwan. These inconspicuous shrimp-associated leeches might have been overlooked by researchers, as it was the case for a diverse assemblage of mussel-associated leeches (Bolotov et al. 2019).

List of species. *Palaemobdella ornata* (Oka, 1929) **gen. & comb. nov.** [Taiwan] and *Pe. horai* (Baugh, 1960) **comb. nov.** [India] (Table 3).

Hosts. Freshwater shrimps (Palaemonidae; phoretic/dwelling host) and fishes (Cyprinidae and Synbranchidae; primary host) (Baugh 1960a; Lai and Chen 2010).

Comments. Previously, the two shrimp-associated species of the new genus were placed in *Placobdelloides* (see Sawyer 1986) but they differ from its members by the lack of esophageal glands, the smaller number of annuli (66-67 vs. 70-71), the position of eyespots on II, and a very specific dorsal pigmentation patterns.

Genus *Placobdelloides* Sawyer, 1986 gen. rev.

Type species. *Clepsine multistriata* Johansson, 1909 (by original designations)

Differential diagnosis. Medium-sized leeches (length up to 40 mm; Oosthuizen 1979); one pair of eyespots on III; body with 70 annuli, mid-body somites triannulate; dorsum with six rows of conical papillae at a2 and with multiple small, irregularly arranged papillae on each annulus; mouth pore is terminal; one or two pairs of compact salivary glands; esophageal glands present; seven pairs of crop caeca (2nd to 6th pairs of crop caeca each with three lobes); six pairs of testisacs; the gonopores separated by two annuli: male gonopore on XI a3 / XII a1, female gonopore on XII a2 / XII a3; posterior sucker of large or moderate size, circular, ventrally directed. Phylogenetically, this genus is sister to the *Marsupiobdella* lineage (Figure 7).

Distribution. Africa, Madagascar, Yemen, Malaysia, and Singapore (Oosthuizen 1979; Bolotov et al. 2022b; Bolotov et al. 2023a).

List of species. Apparently, *Placobdelloides* s. str. contains two reptilian-associated African species, that is, *Pl. multistriatus* (Johansson, 1909) [the type species of the genus; continental Africa, Madagascar, and Yemen; host: turtles, terrapins, and crocodiles] and *Pl. fimbriatus* (Johansson, 1909) [Uganda, Kenya, Nigeria; host: crocodiles] (Moore 1939; Cott 1961; Oosthuizen 1979; Oosthuizen 1991; Bolotov et al. 2022b; Bolotov et al. 2023a). Morphological features of *Pl. stellapapillosus* Govedich, Bain & Davies, 2002 [Singapore and Malaysia; host: turtles, crocodiles, and gavials] partly agree with the diagnosis of this genus (one pair of eyespots, one pair of compact salivary glands, six pairs of testisacs, two annuli between the gonopores, seven pairs of lobed crop caeca) (Sawyer 1986; Govedich et al. 2002; Neely et al. 2017). Conversely, two specific traits, that is, the position of eyespots on I or II and the presence of unique star-shaped papillae on its dorsum, indicate that the generic placement of this species needs future research based on the DNA sequence data.

Hosts. Crocodiles, gavials, turtles, and terrapins serve as primary hosts (reptilian-associated leeches). Water bugs (Hemiptera) were recorded as phoretic host for the two African species (Table 3).

Comments. This genus in its original understanding (Sawyer 1986) was a paraphyletic group (Bolotov et al. 2022b). Here, four *Placobdelloides* species transferred to *Palaemobdella* **gen. nov.** (two species) and *Batracobdelloides* (two species) (see the corresponding accounts above for detail). An African member of the genus, *Placobdelloides jaegerskioeldi* (Johansson, 1909), represents a distant phylogenetic lineage and was recently placed in the monotypic genus *Hippobdelloides* Bolotov & Pešić, 2025 (Bolotov and Pešić 2025).

Turtle-associated *Placobdelloides* leeches from tropical Asia were also found to be a separate clade that was described as the genus *Orientobdelloides* Bolotov, Eliseeva & Kondakov, 2022 (Bolotov et al. 2022b). Three former members of *Placobdelloides* were placed in the genus *Orientobdelloides* as follows: *Or. siamensis* (Oka, 1917) [the type species of the genus], *Or. sirikanchanae* (Trivalairat, Chiangkul & Purivirojkul, 2019), and *Or. tridens* (Chiangkul, Trivalairat, Kunya & Purivirojkul, 2021). Based on morphological features, six additional nominal species should be considered representatives of this group:

(1) *Orientobdelloides emydae* (Harding, 1920) **comb. nov.** [= *Placobdella emydae* Harding, 1920; = *Placobdelloides emydae* (Harding, 1920); composite type locality: ‘Station No. 52, 4-9 mi. E.1/2N. of Patsahanipur, Lake Chilka’; ‘outskirts of Calcutta’; ‘Gatiagurh, Dist. Hughly, Bengal’; ‘R. Mahanaddi, Sambalpur, Orissa’; ‘near Purulia, Chota Nagpur Div., Bihar’; ‘Nagpur, C.P.’, India; range: India; host: turtle *Lissemys punctata* (Lacépède, 1788) (Trionychidae)] (Harding 1920; Harding and Moore 1927; Sawyer 1986);

(2) *Orientobdelloides indicus* (Baugh, 1960) **comb. nov.** [= *Placobdella indica* Baugh, 1960; = *Placobdelloides indica* (Baugh, 1960); type locality: ‘a rocky pool ‘Sitkundi’ in Kalipahar about 7 miles S.W. of Monghyr Dist. (Bihar)’, approx. 25.3105°N, 86.5052°E, India; range: India; host: unknown (likely freshwater turtles)] (Baugh 1960b; Sawyer 1986);

(3) *Orientobdelloides inleanus* (Oka, 1922) **comb. nov.** [= *Glossiphonia inleana* Oka, 1922; = *Placobdella inleana* (Oka, 1922); type locality: ‘Fort Stedman, Inle Lake’, approx. 20.5773°N, 96.9436°E, Myanmar; range: Myanmar; host: turtle *Cyclemys oldhami shanensis* Annandale, 1918 (Geoemydidae)] (Oka 1922; Harding and Moore 1927);

(4) *Orientobdelloides guangdongensis* (Tan & Liu, 2001) **comb. nov.** [= *Hemiclepsis guangdongensis* Tan & Liu, 2001; type locality: Guangzhou City, approx. 23.02°N, 113.03°E,

Guangdong Province, China; range: Pearl River basin, South-East China; host: turtle *Cuora amboinensis* (Daudin, 1801) (Geoemydidae)] (Tan and Liu 2001);

(5) *Orientobdelloides bancrofti* (Best, 1931) **comb. nov.** [= *Helobdella bancrofti* Best, 1931; = *Placobdella bancrofti* (Best, 1931); = *Placobdelloides bancrofti* (Best, 1931); type locality: Burnett River, Queensland, Australia; range: Australia; host: turtles *Emydura macquarii krefftii* (Gray, 1871) and *Myuchelys latisternum* (Gray, 1867) (Chelidae)] (Best 1931; Sawyer 1986; Govedich 2001; McKenna et al. 2005);

(6) *Orientobdelloides octostriatus* (Grube, 1867) **comb. nov.** [= *Clepsine octostriata* Grube, 1867; = *Placobdelloides octostriata* (Grube, 1867); type locality: Rockhampton, approx. 23.3739°S, 150.5128°E, Queensland, Australia; range: Australia; host: turtles *Emydura australis* (Gray, 1841) and *Chelodina burrungandjii* Thomson, Kennett & Georges, 2000 (Chelidae)] (Grube 1867; Grube 1871; Govedich 2001; Tucker et al. 2005).

Two nominal species, that is, *Orientobdelloides tridens* and *Or. indicus*, are characterized as having trident-shaped (trilobate) crop caeca (Figure S6). This pattern was considered a unique diagnostic trait of the first species (Chiangkul et al. 2021a; Kambayashi et al. 2024). However, *Orientobdelloides tridens* differs from *Or. indicus* by having one pair of compact salivary glands (vs. two pairs) (Figure S6). It should be noted that *Orientobdelloides tridens* was recently discovered from Java, Indonesia (Kambayashi et al. 2024). This record reveals that the range of this turtle-associated species is broader than it was initially expected (Chiangkul et al. 2021a), although populations of this leech on Java and in Thailand are rather distant phylogenetically (the uncorrected *COI* p-distance = 5.2 %) (Kambayashi et al. 2024). The data, outlined above, indicate that there may be a species complex of leeches with trident-shaped crop caeca, containing *Or. tridens*, *Or. indicus*, and some additional species.

Next, *Placobdelloides okadai* (Oka, 1925) [= *Hemiclepsis okadai* Oka, 1925; = *Placobdella okadai* (Oka, 1925)] was described based on a composite type series that contains specimens collected from the Ryukyu Archipelago of Japan [Amami Ōshima Island and Shuri on Okinawa Island; host: frogs *Limnonectes namiyei* (Stejneger, 1901) (Dicroglossidae) and *Babina holsti* (Boulenger, 1892) (Ranidae)] and from North China (Beijing; host: unspecified turtle) (Oka 1925; Soós 1969; Sawyer 1986). The description and illustrations of the species are mostly based on the Japanese specimens (Oka 1925) and, hence, the type locality could be restricted to the two islands of the Ryukyu Archipelago. According to the protologue, this nominal species is characterized by the following combination of characters: small leeches (length up to 15 mm); live animal has uniform dark olive ground color, without bands and spots; one pair of eyespots on II (very close to each other); dorsum smooth; body with 66 annuli: somites I-IV uniannulate, V-VI biannulate, VII-VIII 'transitional from biannulate to triannulate' [calculated as biannulate by Oka], IX-XXV triannulate, XXVI biannulate, XXVII uniannulate; the mouth pore is terminal; seven pairs of branched crop caeca; six pairs of testisacs; the gonopores separated by two annuli: male gonopore on XI a3 / XII a1, female gonopore on XII a2 / XII a3; very large posterior sucker (diameter as great as the body width) (Oka 1925). The salivary glands are not described. Oka (1925) also noted that this species externally resembles the biannulate species *Oligobdella orientalis* (Oka, 1925) [synonym of *Torix tagoi* (Oka, 1925); Kambayashi and Nakano 2023] and *Oligobdella biannulata* (Moore, 1900) [now *Placobdella biannulata*; Siddall et al. 2005]. Indeed, most features of *Placobdelloides okadai* agree with the diagnosis of the genus *Torix* Blanchard, 1893, except for triannulate mid-body somites (vs. biannulate) (Kambayashi and Nakano 2023). In our opinion, *Placobdelloides okadai* could be considered a member of the latter genus, morphologically representing a transitional form from triannulate to biannulate condition. It is known that triannulate and biannulate species may occur within one genus (e.g., *Placobdella biannulata*) (Siddall et al. 2005). As a conclusion, we propose a new combination as follows: *Torix okadai* (Oka, 1925) **comb. nov.** It can be considered endemic to the Ryukyu Islands and may represent a sister lineage to *Torix tagoi*, although this preliminary hypothesis needs to be confirmed in the future by means of a DNA-based approach. The part of the type series of this nominal species collected from the mouth of a turtle in Beijing may belong to a species of the genus *Mooreotorix* Lukin, 1976. In turn, records of '*Placobdelloides okadai*' from Honshu (Yamauchi et al. 2008) most likely belong to *Torix tagoi* (see Kambayashi and Nakano 2023). A specimen of '*Placobdella okadai*' from Nanking, China described by Moore (1930) may belong to an additional species of *Torix*.

Finally, morphological features of *Placobdelloides bdellae* (Ingram, 1957) and *Placobdelloides maorica* (Benham, 1907) from Tasmania and New Zealand, respectively (Benham 1907; Ingram 1957;

Mason 1974; Sawyer 1986; Govedich 2001) do not fully consistent with the differential diagnosis of *Placobdelloides* s. str. (see above). In particular, these species can be distinguished from representatives of the latter genus by having a greatly enlarged and anteriorly directed first pair of crop caeca (vs. small, laterally or antero-laterally directed) (Figure S7). Therefore, we propose a new genus to incorporate these two species (see below).

Genus *Aotearoabdella* Bolotov gen. nov.

Figure S7
https://zoobank.org/urn:lsid:zoobank.org:act:439BA4D8-D762-4D71-B805-CC28FF06865C

Type species. *Placobdella maorica* Benham, 1907.

Differential diagnosis. Small leeches (length up to 16 mm; Mason 1974); one pair of eyespots on III; body with 69-70 annuli, mid-body somites triannulate; mouth pore is subterminal; one pair of compact salivary glands; small esophageal glands present; seven pairs of branched crop caeca; the first pair of crop caeca are anteriorly directed and are approximately 1.5-2 times longer than those of the 2nd – 6th pairs; six pairs of testisacs; gonopores separated by two annuli: male gonopore on furrow XI a3 / XII a1 and female gonopore on furrow XII a2 / XII a3; posterior sucker is small, circular, ventrally directed; phylogenetic data are not available.

Etymology. the name of this genus is combined from two parts, that is, '*Aotearoa*' (Maori name for New Zealand) and '*bdella*' (leech in Greek).

Distribution. New Zealand and Tasmania.

List of species. Two new combinations are proposed as follows:

(1) *Aotearoabdella maorica* (Benham, 1907) **gen. & comb. nov.** [=*Placobdella maorica* Benham, 1907; = *Placobdelloides maorica* (Benham, 1907); type locality: Ruapuke Island, 46.76°S, 168.52°E, New Zealand; range: New Zealand; host: Pacific black duck *Anas superciliosa* Gmelin, 1789 (Anatidae) and man] (Benham 1907; Mason 1974; Sawyer 1986; Govedich 2001);

(2) *Aotearoabdella bdellae* (Ingram, 1957) **comb. nov.** [= *Placobdella bdellae* Ingram, 1957; = *Placobdelloides bdellae* (Ingram, 1957); type locality: Salmon Ponds, 42.7557°S, 146.9682°E, Plenty River, Tasmania (based on the label of syntypes from D.M. Ingram leech collection: TMAG K0737; K0738; K0739; K0740; K0741; and K0784); range: Tasmania; host: pouched lamprey *Geotria australis* Gray, 1851 (Geotriidae)] (Ingram 1957; Mason 1974; Sawyer 1986).

Discussion

Taxonomic updates and challenges, concerning arthropod-associated leeches and related taxa

In this study, we present a global overview of arthropod-associated leeches based on a comprehensive dataset compiled from literature sources and original records (see Bolotov et al. 2025c: Datasets S1-S2). We show that 45 leech species from three families (Glossiphoniidae, Piscicolidae, and Praobdellidae) were recorded in permanent or temporary associations with arthropods globally. The order Hirudinida may comprise of approximately 700 species worldwide (Sket and Trontelj 2008; Kambayashi and Nakano 2024); therefore, 6.4 % of them occur in symbiotic relationships with arthropods. Our current estimate of the arthropod-associated leech assemblage's species richness is four times higher than that presented in a previous review on this topic, published 70 years ago (Meyer and Barden 1955: 11 species, except for synonyms and doubtful records).

The global number of arthropod-associated leech species seems to be comparable with that of mollusc-associated leeches, inhabiting the mantle cavity of Mollusca in fresh and saline waters. Available data indicate that the latter group accounts for 48 species, belonging to two families, the Glossiphoniidae and Piscicolidae (Oka 1927; Sawyer et al. 1975; Hochberg 1983; Janssen 1993; Williams et al. 2007; Bolotov et al. 2022c; Bolotov et al. 2022d; Bolotov et al. 2022e; Ruiz-Escobar et al. 2025; our unpublished data). However, the diversity of this assemblage is largely shifted to continental water bodies, with 40 leech species dwelling in the mantle cavity of freshwater bivalves and gastropods (Bolotov et al. 2019; Bolotov et al. 2022c; Bolotov et al. 2022d; Bolotov et al. 2022e). The saltwater members contain seven marine and one estuarine leech species, associated with octopuses, clams, and an oyster (Oka 1927; Sawyer et al. 1975; Hochberg 1983; Janssen 1993; Williams et al. 2007; Ruiz-Escobar et al. 2025).

Here, we propose a tentative revision of the genus *Paraclepsis* with a description of one new species from South-East Asia. We show that *Paraclepsis ceylanica*, *Pa. praedatrix*, and *Pa. vulnifera* cannot be delineated based on the original diagnoses and that these nominal species should be lumped to one biological species. Our decision agrees with an earlier assumption that *Paraclepsis praedatrix* and *Pa. vulnifera* may be conspecific due to the lack of reliable distinguishing characters (Sawyer et al. 1982; Sawyer 1986). Moreover, available DNA sequences and morphological data support Sawyer's (1986) opinion that *Batracobdella cancricola* is a member of the genus *Paraclepsis*. From this perspective, the genus seems to be a small monophyletic radiation of crab-associated leeches, using frogs as primary host, although this hypothesis needs to be checked in a future based on the DNA sequences of *Paraclepsis ceylanica*.

Additionally, we show that two nominal *Paraclepsis* species recently described from India (Mandal 2004; Mandal 2015) belong to other genera and that they are synonyms of *Oosthuizobdella garoui* [= *Paraclepsis jorapariensis* **syn. nov.**] and *Hemiclepsis viridis* [= *Paraclepsis gardensi* **syn. nov.**]. *Oosthuizobdella garoui* is a widespread African species (Oosthuizen 1982) that was also recorded from Nepal (Nesemann et al. 2007) and now from India. The origin of its population on the Indian Subcontinent is unclear but, at first glance, it could be linked to a human-mediated or bird-associated dispersal event. *Barbronia gwalagwalensis* Westergren & Siddall, 2004 (Salifidae) is another example of a freshwater leech having a disjunctive range in Africa and Asia (Westergren and Siddall 2004; Klass et al. 2021). This species was described from South Africa but later on it was found to be native to East and South-East Asia (Bolotov et al. 2023b).

Interestingly, the GenBank sequences of leeches from India labeled as '*Paraclepsis vulnifera*' and '*Paraclepsis jorapariensis*' belong to the Nearctic turtle-associated species *Placobdella ornata* (see Table S2 and Figure S1 for detail). This finding reveals an invasion of the latter species to India, probably with introduced freshwater turtles. The time of its appearance in the country can perhaps be traced through re-examination of the ZSI collection. Establishment of a non-native population of this species in Europe was genetically confirmed based on samples from Belgium (Soors et al. 2015).

In this study, we continue the dissolution of the composite genus *Placobdelloides* (Glossiphoniidae), which was started from separation of the genera *Orientobdelloides* (a clade of turtle-associated leeches) and *Hippobdelloides* (a monotypic lineage of the hippopotamus-associated leech) (Bolotov et al. 2022b; Bolotov and Pešić 2025). A new genus, *Palaemobdella*, is here described for two peculiar shrimp-associated *Placobdelloides* species from India and Taiwan. In turn, *Placobdelloides fulvus*, *Placobdelloides undulatus* and *Batracobdella gracilis* are transferred to the genus *Batracobdelloides* based on a combination of morphological characters (see Taxonomic account for detail). Several nominal species are additionally transferred to the genus *Orientobdelloides* and six new combinations and one new synonym are established. The nominal species *Placobdelloides okadai* is considered a member of the genus *Torix*, whereas two former *Placobdelloides* species from New Zealand and Tasmania are placed in a new genus, *Aotearoabdella*. Thus, representatives of the former *Placobdelloides* are currently separated to six genera: *Placobdelloides* s. str., *Orientobdelloides*, *Batracobdelloides*, *Hippobdelloides*, *Palaemobdella* **gen. nov.**, and *Aotearoabdella* **gen. nov.** The morphology-based taxonomic opinions, presented herein, need to be confirmed in a future by means of a phylogenetic approach. Generally, there is an urgent need of an integrative taxonomic revision of the Oriental and Australasian Hirudinida based on broad sampling efforts, focusing on topotypes of all nominal species, described from these regions. Currently, our knowledge of the systematics and biogeography of leeches from tropical regions of Asia and Australasia is largely relied upon historical works.

The role of arthropod hosts in the life cycles of leeches

Our global overview of biotic interactions of leeches with arthropods shows that obligate ectoparasitic leeches are involved in the closest relationships with their hosts, exclusively crustaceans (Type I; see Table 2). Some of them permanently dwell on the surface of the host during the entire life cycle from eggs to adults (*Mysidobdella* spp. on mysids; Burreson and Allen 1978; Allen and Allen 1981). The fish leeches from Lake Baikal (two *Baicalobdella* and three *Codonobdella* species) serve as permanent ectoparasites of amphipods (Epshtein 1959; Kaygorodova and Sorokovikova 2014; Matveenko 2023;

Nazarova et al. 2024; Kaygorodova and Matveenko 2025) but attach cocoons outside their host using various hard substrates such as rocks and even plastic litter on the bottom of the lake (Kondratov et al. 2021).

The second group contains leeches that are involved in obligatory parasitic or commensalistic associations with their host, also crustaceans only (Type II; see Table 2). Most of these species dwell on the host during a certain period of their life. In particular, *Marsupiobdella africana*, *Palaemobdella* spp., *Paraclepsis cancricola*, *Crangonobdella fabricii*, and *Myzobdella* spp. use crustaceans as dwelling place and/or cocoon substrate but feed on a vertebrate host (fish or frog) (see Figure 5). *Myzobdella platensis* (Cordero, 1933) sucks haemolymph of crabs but they may serve as secondary host, because this leech commonly occurs as ectoparasite on various fish species (Zara et al. 2009). *Paraclepsis cancricola* is an obligate endosymbiont of the gill chamber of crabs, whereas frogs are probably served as primary hosts (Yang 1986). *Glyptonotobdella antarctica* may move between different invertebrate hosts from isopods and lobsters to octopuses and sea urchins but deposits cocoons on crustaceans and uses fish as primary host (Janssen 1993; Enriquez-Briones and Gallardo 1994; Utevsky 2007).

The third group contains facultative parasitic or commensalistic associations of leeches with arthropods, including crustaceans, sea spiders, and aquatic insects (Type III; see Table 2). This group is an amalgam of species, having different life history and ecological traits. *Myxobdella* spp. are temporary ectoparasites of crabs, probably using them as secondary hosts (Van Damme and Segers 2004; Nakano et al. 2017; Mitra and Dev Roy 2018; Schenkova et al. 2021; Kudara and Kochi 2023), while vertebrate animals such mammals and birds seem to serve as primary hosts (Oka 1934; Phillips et al. 2010; Chatterjee et al. 2018; Ito et al. 2022). *Caspiobdella fadejewi* (Epshtein, 1961), *Austrobdella losmoliniensis* Williams, Urrutia & Burreson, 2007, *Au. oosthuizeni* A. Utevsky, 2004, and *Bathybdella sawyeri* Burreson, 1981 use host crustaceans as dwelling place/shelter. Four species, that is, *Batracobdelloides gracilis*, *Paraclepsis dongnaiensis* **sp. nov.**, *Pa. ceylanica*, and *Helobdella duplicata* may serve as endosymbionts (parasites or commensals; cf. Hertig et al. 1937; Brian and Aldridge 2019) in the gill chamber of freshwater crabs and a shrimp. Interestingly, the endosymbiotic *Helobdella duplicata* occurs in sympatry with ectosymbiotic *He. triserialis* on the same shrimp host in Chile (Tello et al. 2007). They use different microhabitats: the first species dwells in the gill chamber, whereas the second species exclusively occurs on pleopods.

Dwelling in the gill chamber of a crab host seems to be a useful behavioral trait in the light of Sawyer's (1986) concept on the leech adaptations to terrestrialism. This author stated that the importance of periodic wet and dry seasons, driven by annual rainfalls, is the dominant feature in the ecology of tropical leeches (Sawyer 1986: 631). Our data largely support this idea. The gill cavity of crabs represents a specific microhabitat with more or less stable environmental conditions, especially humidity (a 'wet camera'). The preference of leeches to this kind of microhabitats seemingly important during the dry period. In particular, McCann (1937: 539) noted that: "Leeches [*Paraclepsis ceylanica*] infest the crabs [*Barusa guerini* (H. Milne Edwards, 1853) (Gecarcinucidae)] mostly towards the end of the rains. The gill chambers seem to be the breeding ground and when the crab moves about in water the leeches, both young and old, come out of the chambers and wander about the carapace. I am of the opinion that the leeches also use the gill chambers during the dry season as a convenient harbor to tide over this period". Ramachandra Rao and Susainathan (1924) reported on records of large adult and small young leeches [*Paraclepsis ceylanica*] in the gill chamber of crabs *Spiralothelphusa hydrodroma* (Herbst, 1794) (Gecarcinucidae). Fernando (1960) showed that in dry season crabs *Oziotelphusa ceylonensis* (Fernando, 1960) (Gecarcinucidae) dig a deep burrow near the shore of a water body, the entrance of which closed by a ground plug. Thus, the leeches, commonly dwelling in the gill chamber of this crab on Sri Lanka, may survive seasonal drought in a locally suitable condition. There is some evidence that the mantle cavity of Mollusca may also serve as a seasonal 'wet camera'/shelter for leeches. In particular, numerous leeches [most likely *Batracobdelloides tricarinatus*] and other small animals were discovered in the mantle cavity of freshwater mussels, completely burrowed into emerged bottom of a stream, dried up during the dry season, near Lake Tanganyika, East Africa (Vanderplank 1941). Interestingly, a few leech species use plant-derived cavities as a kind of partly isolated microhabitat, that is, the so-called bromeliad leeches *Helobdella budgei* (Grube, 1871) and *He. buzz* Iwama, Nogueira & Gonçalves, 2017 (Ringuelet 1985; Iwama et al. 2017). These species exclusively dwell in tank waters of epiphytic and terrestrial plants of the family Bromeliaceae in South America.

Unlike slow-moving and genuinely water-dependent molluscs, freshwater crabs are mobile and largely amphibious animals (McCann 1937; Fernando 1960; Shih et al. 2007) and may also serve as transport hosts, transferring leeches inside their gill cavity between separate bodies of water even during the dry season. For example, host crabs of *Paraclepsis dongnaiensis* **sp. nov.** in Vietnam were collected from isolated temporary pools in forest. These pools were situated relatively far from the Đồng Nai River (distance of 500-600 m) but served as dwelling place for crabs and other hydrobionts. Such an adaptation may ensure a safe movement of leeches through land barriers to reach a local population of aquatic primary host, even in temporary water bodies (frogs in *Paraclepsis* spp. and fish in *Batracobdelloides gracilis*). Records of *Paraclepsis ceylanica* from *Lissemys punctata vittata* (Peters, 1854) (Testudines: Trionychidae) (Harding 1924; Harding and Moore 1927) indicate that freshwater turtles may also serve as phoretic host for these leeches (cf. Richardson et al. 2017a; Watermolen 2021). Dwelling on the external surface of an arthropod host may also provide an advantage to aquatic leeches by several ways. First, the surface dwellers are less accessible for predators, giving that the predator pressure appears to one of the most important drivers of the Hirudinida evolution (Sawyer 1986; Kutschera and Wirtz 2001). Some of the crustacean surface dwellers, e.g., *Crangonobdella fabricii*, *Palaemobdella* spp., and *Paraclepsis* spp., possess a cryptic coloration (camouflage), aligning with that of the host (Meyer and Barden 1955; Lai and Chen 2010; this study: see Figure 9).

Second, dwelling on the surface of a host at various developmental stages (from cocoon to adults) is a useful trait in inhospitable soft-bottom environments with the deficient of hard substrates such as rocks and stones. There is a specific assemblage of leeches depositing cocoons on the surface of arthropod hosts (crustaceans and sea spiders) (see Figure 5). This assemblage includes obligate parasites and commensals (e.g., *Mysidobdella* and *Myzobdella*), as well as facultative commensals (e.g., *Crangonobdella maculosa*, *Johanssonia arctica* (Johansson, 1898), and *Notostomum cyclostomum*). It is known that the facultative commensals may use other kinds of hard substrate, available in a given habitat, as sites for cocoon deposition. For example, *Notostomum cyclostomum* may also attach cocoons to gastropod shells (Epshtein and Utevsky 1996; Nagasawa and Ueda 2013). Usage of the exosceleton of crustaceans and sea spiders as cocoon substrate is a behavioral trait that likely evolved as adaptation to dwelling in aquatic habitats, the bottom of which is covered by continuous soft (silty) substrates (Epshtein and Utevsky 1996). There is some evidence that the density of arthropod hosts in a certain habitat may directly influence the abundance of associated leeches. In particular, an increase of trypanosome infection in the Atlantic cod *Gadus morhua* Linnaeus, 1758 (Gadidae) in the Barents Sea corresponds to introduction of the red king crab *Paralithodes camtschaticus* (Tilesius, 1815) (Lithodidae), supporting an increased population growth of *Johanssonia arctica*, the main vector for a trypanosome blood parasite in marine fish (Hemmingsen et al. 2005).

Third, arthropods may also serve as dispersal agents (phoretic hosts) for leeches, dwelling on their surface. For example, *Mysidobdella borealis* is involved in seasonal migrations between estuaries and open marine waters with its mysid hosts (Burreson and Allen 1978; Allen and Allen 1981). Long-distance ontogenetic movements and seasonal migrations are known to occur in marine crabs and lobsters, serving as hosts for several surface-dwelling leeches (Somerton and Otto 1986; Booth 1997; Lovrich and Thiel 2011; Mullowney et al. 2018; Van Zyl et al. 2025).

The fourth group of leeches (Type IV; see Table 2) contains fortuitous associates that were accidentally recorded on arthropods. The role of arthropod hosts for these leech species is largely unclear but in most cases can be linked to phoresy. Some of them were likely attached to a crustacean, sea spider or aquatic insect accidentally, while others may be involved into deeper symbiotic relationships with arthropods. Currently, available data are too limited for a sound decision on most of these species.

A recent global review of phoresy in animals lists only three examples of leeches, associated with transport hosts (Bartlow and Agosta 2021). Two of these leech species use amphibians as dispersal agents (Khan and Frick 1997; Maia-Carneiro et al. 2012), whereas the third one (*Marsupiobdella africana*) is said to be phoront on crabs and frogs (Badets and Du Preez 2014). Here, we show that 42 leech species use 75 arthropod species as phoretic hosts (see Table 1 and Bolotov et al. 2025c: Dataset S1 for detail). Moreover, that review (Bartlow and Agosta 2021) overlooked that a number of leech species were recorded attached to various freshwater turtles for non-nutritional (mostly phoretic) reasons in Europe, North America, and other regions (Richardson et al. 2017a; Richardson et al. 2017b; Perera et al. 2019).

Parallel origin of analogous associations with arthropods in leeches

Our review highlights several cases of parallel origin of traits (convergent evolution) in the order Hirudinida, traceable to biotic interactions with arthropods, which are characterized below.

(1) Specialized, permanent ectoparasites of crustaceans, using them as primary hosts (Piscicolidae): *Codonobdella* spp. (radiation of three freshwater species; Lake Baikal) vs. *Baicalobdella* spp. (two sister freshwater species; Lake Baikal) vs. *Mysidobdella* (two marine species, probably sister; coastal marine environments) (Burreson and Allen 1978; Allen and Allen 1981; Burreson et al. 2012; Kaygorodova and Sorokovikova 2014; Matveenko 2023; Kaygorodova and Matveenko 2025). There is a parallel diet shift from fish blood to crustacean haemolymph, occurring in crustacean-rich ecosystems. It is likely driven by an extremely high abundance of dominant organisms such as benthic amphipods in Lake Baikal (up to 90% of benthic biomass and species: Jakob et al. 2016) and pelagic mysids in coastal marine waters (Burnham 2015; Mayor et al. 2017). Morphological specialization: specific coloration (camouflage), aligning with that of the crustacean host; smaller body size. The endemic leeches of Lake Baikal are mostly associated with small and medium-sized littoral amphipods but in deepwater areas they may also parasitize larger species (body up to 40-80 mm long) (Matveenko 2023; Kaygorodova and Matveenko 2025), having massive exosceleton with multiple processes/spines and colorful pigmentation (Takhteev 2019; Drozdova et al. 2020).

(2) Specialized crab-dwelling commensals, using frogs as primary host (Glossiphoniidae): *Marsupiobdella africana* (one highly divergent freshwater species; South Africa) vs. *Paraclepsis* spp. (radiation of three freshwater species; tropical and subtropical Asia) (Badets and Du Preez 2014; Kruger and Du Preez 2015; this study). There is an independently evolved strategy to use crabs as phoretic host/dwelling place and to feed on frog blood. It occurs in warm regions with periodic wet and dry seasons, probably as an adaptation to terrestrialism (sensu Sawyer 1986). The crab host may also serve as shelter, protecting from predators. Morphological specialization: specific coloration (camouflage), aligning with that of the crustacean host.

(3) Specialized shrimp-dwelling commensals, feeding on fish (Glossiphoniidae and Piscicolidae): *Palaemobdella* spp. (two freshwater species, probably sister; India and Taiwan) vs. *Crangonobdella fabricii* (one marine species; coastal waters of the Arctic and North Pacific oceans). There is a parallel evolution of a similar strategy to use shrimps as phoretic host/dwelling place and to feed on fish blood. It is probably driven by a high abundance of shrimps in some aquatic habitats. Attachment to shrimps seems to be an effective way to avoid the predator pressure. Morphological specialization: specific coloration (camouflage), aligning with that of the crustacean host.

(4) Non-specialized crab- and sea spider-dwelling commensals, using them as substrate for cocoon attachment (Piscicolidae): a paraphyletic assemblage, containing *Myzobdella* spp. (small clade of three estuarine species; brackish waters of the Americas) and no less than four independent marine lineages (*Crangonobdella maculosa*, *Johanssonia arctica*, *Notostomum cyclostomum*, and *Platybdella olriki* Malm, 1865). The parallel evolution of this strategy is likely driven by a deficient of hard substrates (e.g., rocks and boulders) in some estuarine and marine areas (Epshtein and Utevsky 1996).

(5) Non-specialized temporary ectoparasites on crabs (Praobdellidae): the genus *Myxobdella* seems to be a paraphyletic assemblage, because each of its crab-associated representatives (*My. annandalei*, *My. sinanensis* Oka, 1925, and *My. socotrensis* Schenkova et al., 2021) takes a separate position on multi-locus phylogenies (Nakano et al. 2017; Schenková et al. 2021). This pattern may indicate that the trait to use crabs as a supplementary (or even primary?) feeding source independently evolved in no less than three separate praobdellid lineages. This trait could be driven by the deficient of available vertebrate hosts in certain habitats such as arid springs of Socotra and turbulent mountain streams of subtropical and tropical Asia (Nakano et al. 2017; Mitra and Dev Roy 2018; Schenková et al. 2021). It was shown that the freshwater crab *Geothelphusa dehaani* (White, 1847) (Potamidae) possess a strong behavioral response to the presence of *Myxobdella sinanensis* based on visual and/or physical cues (Kudara and Kochi 2023). This finding indicates that feeding of the leech on this crab species is not an accidental phenomenon (fortuitous interactions) but, instead, there was a long-term co-evolution between the crab and its ectoparasite.

The entire order Branchiobdellida represents a massive species-rich radiation of crayfish worms, all known species of which are obligate crustacean symbionts (Sawyer 1986; Gelder and Williams 2016; Tessler et al. 2018). In contrast, in the order Hirudinida crustacean-associated clades occur very rarely and are species-poor, each having no more than three species (i.e., *Codonobdella*, *Paraclepsis*, and

Myzobdella). The new genus *Palaemobdella*, described above, may represent a largely overlooked radiation of shrimp-associated leeches in tropical Asia but it is unlikely to be species-rich. Thus, the majority of arthropod-associated leeches are independent species-level lineages or pairs of sister species (Utevsky and Trontelj 2004; Bolotov et al. 2022e; Ruiz-Escobar et al. 2025; this study). Single-species lineages and small species groups also prevail in the mollusc-associated leech assemblage (Bolotov et al. 2019; Bolotov et al. 2020; Bolotov et al. 2022c; Ruiz-Escobar et al. 2025). Conversely, the genus *Batracobdelloides* represents a rather diverse radiation of facultative and obligate molluscan associates (>10 species), the diversification of which might have started since the Early Miocene (Bolotov et al. 2019).

Conclusion

In this study, we review available data on the diversity, biogeography, and ecology of the global arthropod-associated leech assemblage based on a comprehensive compilation of host records from the body of literature and original material (Bolotov et al. 2025c: Dataset S1). Our data reveal that it contains 45 species, belonging to 26 genera and three families, that is, the Piscicolidae, Glossiphoniidae, and Praobdellidae. Thus, nearly 6.4 % of all world's leech species (order Hirudinida) may occur in associations with arthropods. The assemblage contains 23 freshwater, 18 marine, and 4 euryhaline (mostly estuarine) leech species. According to the degree of association with hosts, they can be delineated to obligate, facultative, and fortuitous associates (17, 17, and 11 species, respectively).

No less than 79 species of arthropods are used by leeches as hosts, including amphipods, crabs, isopods, mysids, shrimps, spiny and squat lobsters, sea spiders, and water bugs. They belong to six orders (Amphipoda, Decapoda, Isopoda, Mysida, Pantopoda, and Hemiptera) and three classes (Hexapoda, Malacostraca, and Pycnogonida). Leeches occur in ectosymbiotic and endosymbiotic interactions with arthropod hosts. Ectosymbionts contain a few ectoparasites, feeding on the host's haemolymph, as well as commensals, using host as dwelling place/shelter, dispersal agents (phoresy) and/or substrate for cocoon deposition. In turn, endosymbionts are a small group of exclusively freshwater species, dwelling in the gill chamber of crabs and a shrimp. The gill chamber of crabs provides a stable moist microhabitat that is especially important for survival and dispersal of leeches throughout the dry season. Moreover, it is a closed shelter, effectively protecting leeches and their offspring from predators. We propose the first ecological classification of leech-arthropod associations based on the key type of biotic interaction, the level of morphological specialization of leeches, and the degree of association with host. It is shown that leech associations with crabs and shrimps are the most common and widespread around the globe and occur in fresh, brackish, and marine waters.

Cladistically, arthropod-associated leeches are mostly represented by single-species lineages and sister species pairs. Additionally, there are three small clades, which may be considered radiations from an arthropod-associated ancestor, that is, *Paraclepsis* (crabs; tropical and subtropical Asia), *Codonobdella* (amphipods; Lake Baikal), and *Myzobdella* (mostly crabs; estuaries of the Americas). It seems that arthropods as hosts may trigger a limited diversification in leeches, unlike the case of crayfish worms (Branchiobdellida), representing a global, ancient, and species-rich radiation around the crustacean hosts.

Several cases of the parallel origin (convergent evolution) of leech associations with arthropods are described. These examples include independent origins of (1) specialized permanent ectoparasites of crustaceans (fresh and sea waters); (2) specialized crab-dwelling commensals, using frogs as primary host (fresh water); (3) specialized shrimp-dwelling commensals, feeding on fish (fresh and sea waters); (4) non-specialized crab- and sea spider-dwelling commensals, attaching cocoons to the host's surface (sea water); and (5) non-specialized temporary ectoparasites of crabs (fresh water).

If the taxonomic affinities of arthropod-associated species from the families Piscicolidae and Praobdellidae are well established, those of the Glossiphoniidae representatives were not re-appraised since the classical monograph of Sawyer (1986). Therefore, we revise the taxonomic placement of the arthropod-associated species and related taxa from the latter family, using combination of (rather limited) molecular data, morphological diagnostic features, and biogeographic criteria. We think that the taxonomic opinions, presented herein, will contribute to better understanding of the systematics and biogeography of the glossiphoniid leeches, especially those from the Oriental and Australasian regions.

The taxonomic novelties in the family Glossiphoniidae, proposed by us, are summarized below (asterisk symbol shows arthropod-associated taxa). Most of these changes applied to nominal species that were placed in the composite genus *Placobdelloides*. This genus was repeatedly found as a paraphyletic assemblage from both phylogenetic and morphological perspective (Siddall et al. 2005; Bolotov et al. 2022b; Torres-Carrera et al. 2023; Bolotov and Pešić 2025).

(1) New genera (*n* = 2): *Aotearoabdella* Bolotov **gen. nov.** [type species: *Placobdella maorica* Benham, 1907; Tasmania and New Zealand] and **Palaemobdella* Bolotov **gen. nov.** [type species: *Placobdella ornata* Oka, 1929; Taiwan and India].

(2) Revised genera with amended diagnoses, lists of species, and distribution (*n* = 4): *Batracobdelloides* Oosthuizen, 1986 **gen. rev.** [12 species; Africa, South Asia, South-East Asia, East Asia, and the Greater Sunda Islands]; *Orientobdelloides* Bolotov, Eliseeva & Kondakov, 2022 **gen. rev.** [9 species; South Asia, South-East Asia, Indonesia, and Australia]; **Paraclepsis* Harding, 1924 **gen. rev.** [3 species; India, Sri Lanka, Thailand, Vietnam, and South-East China]; and *Placobdelloides* Sawyer, 1986 **gen. rev.** [3 species; Africa, Madagascar, Yemen, Malaysia, and Singapore].

(3) New species (*n* = 1): **Paraclepsis dongnaiensis* Bolotov, Eliseeva & Kondakov **sp. nov.** [= *Paraclepsis vulnifera* Moore, 1935 nec Harding, 1924, identification error; Thailand and Vietnam].

(4) New combinations (*n* = 14): *Aotearoabdella bdellae* (Ingram, 1957) **comb. nov.** [= *Placobdella bdellae* Ingram, 1957; = *Placobdelloides bdellae* (Ingram, 1957); Tasmania]; *Aotearoabdella maorica* (Benham, 1907) **gen. & comb. nov.** [= *Placobdella maorica* Benham, 1907; = *Placobdelloides maorica* (Benham, 1907); New Zealand]; **Batracobdelloides fulvus* (Harding, 1924) **comb. nov.** [= *Placobdella fulva* Harding, 1924; = *Placobdelloides fulva* (Harding, 1924); India]; **Batracobdelloides gracilis* (Blanchard, 1897) **comb. nov.** [= *Helobdella gracilis* Blanchard, 1897; = *Placobdella gracilis* (Blanchard, 1897); = *Batracobdella gracilis* (Blanchard, 1897); Java, Indonesia]; *Batracobdelloides undulatus* (Harding, 1924) **comb. nov.** [= *Placobdella undulata* Harding, 1924; = *Placobdelloides undulata* (Harding, 1924); Sri Lanka]; *Orientobdelloides bancrofti* (Best, 1931) **comb. nov.** [= *Helobdella bancrofti* Best, 1931; = *Placobdella bancrofti* (Best, 1931); = *Placobdelloides bancrofti* (Best, 1931); Australia]; *Orientobdelloides emydae* (Harding, 1920) **comb. nov.** [= *Placobdella emydae* Harding, 1920; = *Placobdelloides emydae* (Harding, 1920); India]; *Orientobdelloides guangdongensis* (Tan & Liu, 2001) **comb. nov.** [= *Hemiclepsis guangdongensis* Tan & Liu, 2001; South-East China]; *Orientobdelloides indicus* (Baugh, 1960) **comb. nov.** [= *Placobdella indica* Baugh, 1960; = *Placobdelloides indica* (Baugh, 1960); India]; *Orientobdelloides inleanus* (Oka, 1922) **comb. nov.** [= *Glossiphonia inleana* Oka, 1922; = *Placobdella inleana* (Oka, 1922); Lake Inle, Myanmar]; *Orientobdelloides octostriatus* (Grube, 1867) **comb. nov.** [= *Clepsine octostriata* Grube, 1867; = *Placobdelloides octostriata* (Grube, 1867); Australia]; **Palaemobdella horai* (Baugh, 1960) **comb. nov.** [= *Placobdella horai* Baugh, 1960; = *Placobdelloides horai* Sawyer, 1986 ; India]; **Palaemobdella ornata* (Oka, 1929) **gen. & comb. nov.** [= *Placobdella ornata* Oka, 1929: junior secondary homonym of *Placobdella ornata* (Verrill, 1872), reinstated by us based on Art. 59.4 of the Code; = *Placobdella okai* Soós, 1969: new name for *Placobdella ornata* Oka, 1929; = *Placobdelloides okai* Sawyer, 1986; Taiwan]; *Torix okadai* (Oka, 1925) **comb. nov.** [= *Hemiclepsis okadai* Oka, 1925; = *Placobdella okadai* (Oka, 1925); Ryukyu Islands of Japan].

(5) New synonyms (*n* = 4): *Hemiclepsis viridis* Chelladurai, 1934 [= *Paraclepsis gardensi* Mandal, 2004 **syn. nov.**]; *Oosthuizobdella garoui* (Harding, 1932) [= *Paraclepsis jorapariensis* Mandal, 2015 **syn. nov.**]; and **Paraclepsis ceylanica* (Harding, 1909) [= *Pa. vulnifera* Harding, 1924 **syn. nov.**; = *Pa. praedatrix* Harding, 1924 **syn. nov.**].

Data availability

The type specimens of the new *Paraclepsis* species are available in RMBH. High-resolution photographs of the holotype and selected paratypes can be downloaded from *figshare* (https://doi.org/10.6084/m9.figshare.28922393; Bolotov et al. 2025b). The datasets with available records of leech-arthropod associations, georeferenced occurrences of *Paraclepsis* and *Palaemobdella* leeches, as well as with information on the type series of *Paraclepsis dongnaiensis* **sp. nov.** are also presented online on *figshare* (https://doi.org/10.6084/m9.figshare.28925147; Bolotov et al. 2025c: Datasets S1-S4). Sequence data used in this study are available in NCBI GenBank (https://www.ncbi.nlm.nih.gov).

Conflicts of interest
The authors declare that they have no conflicts of interest.

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Author contributions
I.N.B. designed the study. I.N.M., D.M.P., and T.D.N. undertook the field sampling of *Paraclepsis* leeches in Vietnam. I.N.M. photographed living *Paraclepsis* leeches on crabs. T.A.E. and A.V.K. sequenced leech samples for both DNA and iDNA. T.A.E. took photos of fixed specimens and prepared the type series of the new species. A.V.K. prepared and photographed H&E-stained longitudinal slices of *Paraclepsis*. I.N.B. compiled Datasets S1-S4, conducted data analysis and prepared summary figures and tables. M.Y.G. created the maps. I.N.B. wrote and edited the manuscript. All authors read, revised, and approved the final version of the manuscript.

References

Allen, D. M. & Allen, W. B. (1981) Seasonal dynamics of a leech-mysid shrimp interaction in a temperate salt marsh. *Biological Bulletin*, 160(1), 1–10. https://doi.org/10.2307/1540896

Apakupakul, K., Siddall, M. E. & Burreson, E. M. (1999) Higher level relationships of leeches (Annelida: Clitellata: Euhirudinea) based on morphology and gene sequences. *Molecular Phylogenetics and Evolution*, 12(3), 350–359. https://doi.org/10.1006/mpev.1999.0639

Arifin, U., Smart, U., Husemann, M., Hertwig, S. T., Smith, E. N., Iskandar, D. T. & Haas, A. (2022) Phylogeographic inference of Sumatran ranids bearing gastromyzophorous tadpoles with regard to the Pleistocene drainage systems of Sundaland. *Scientific Reports*, 12, 12013. https://doi.org/10.1038/s41598-022-14722-9

Badets, M. & Du Preez, L. (2014) Phoretic interaction between the kangaroo leech *Marsupiobdella africana* (Hirudinea: Glossiphoniidae) and the cape river crab *Potamonautes perlatus* (Decapoda: Potamonautidae). *International Journal for Parasitology: Parasites and Wildlife*, 3(1), 6–11. https://doi.org/10.1016/j.ijppaw.2013.10.001

Bartlow, A. W. & Agosta, S. J. (2021) Phoresy in animals: review and synthesis of a common but understudied mode of dispersal. *Biological Reviews*, 96(1), 223–246.

https://doi.org/10.1111/brv.12654

Baugh, S. C. (1960a) Studies on Indian Rhynchobdellid leeches I. *Parasitology*, 50, 287–301. https://doi.org/10.1017/s0031182000025403

Baugh, S. C. (1960b) Studies on Indian Rhynchobdellid Leeches II. *Zoologischer Anzeiger*, 165, 468–477.

Benham, W. B. (1907) Art. XVI.—Two new species of leech in New Zealand. *Transactions and Proceedings of the Royal Society of New Zealand*, 39, 180–192. https://paperspast.natlib.govt.nz/periodicals/TPRSNZ1906-39.2.8.1.16

Best, E. W. (1931) The anatomy of an Australian leech, *Helobdella bancrofti*. *Transactions and Proceedings of the Royal Society of South Australia*, 55, 23–31. https://www.biodiversitylibrary.org/page/41567103

Bjørdalsbakke, L. K. (2011) *Population structure, parasitism and prey preference in Sclerocrangon boreas and S. ferox, Svalbard*. Master Thesis, Norwegian University of Science and Technology (NTNU), Trondheim, Norway, 41 pp. http://hdl.handle.net/11250/245779

Blanchard, E. (1849) Hirudineanos. *Historia fisica y politica de Chile*, 3, 43–52. https://www.biodiversitylibrary.org/item/55380#page/41 [In Spanish]

Blanchard, R. (1897) Hirundinées des Indes Néerlandaises. *Zoologische Ergebnisse einer reise in Niederländisch Ost-Indien*, 4(1), 332-356. https://www.biodiversitylibrary.org/item/101512#page/4 [In French]

Bolotov, I. N., Eliseeva, T. A., Gofarov, M. Y., Tsiplenkina, I. G. & Kondakov, A. V. (2025a) Taxonomic diversity of leeches on the world's highest mountain ranges and plateaus. *Zoological Journal of the Linnean Society*, 204(2), zlaf051. https://doi.org/10.1093/zoolinnean/zlaf051

Bolotov, I. N., Eliseeva, T. A., Marin, I. N., Palatov, D. M., Nguyen, T. D., Kropotin, A. V., Gofarov, M. Y. & Kondakov, A. V. (2025b) Image dataset: Type series of the new crab-associated leech species *Paraclepsis dongnaiensis* Bolotov, Eliseeva & Kondakov, 2025 from Vietnam (Hirudinida: Glossiphoniidae). Available at *figshare*: https://doi.org/10.6084/m9.figshare.28922393

Bolotov, I. N., Eliseeva, T. A., Marin, I. N., Palatov, D. M., Nguyen, T. D., Kropotin, A. V., Gofarov, M. Y. & Kondakov, A. V. (2025c) Data from 'Arthropod-associated leeches (Annelida: Hirudinida) of the World: Diversity, taxonomic reappraisal, ecological classification of host associations, and convergent evolution'. Available at *figshare*: https://doi.org/10.6084/m9.figshare.28925147

Bolotov, I. N., Kondakov, A. V., Eliseeva, T. A., Aksenova, O. V., Babushkin, E. S., Bespalaya, Y. V., Chertoprud, E. S., Dvoryankin, G. A., Gofarov, M. Y., Klass, A. L., Konopleva, E. S., Kropotin, A. V., Lyubas, A. A., Makhrov, A. A., Palatov, D. M., Shevchenko, A. R., Sokolova, S. E., Spitsyn, V. M., Tomilova, A. A., Vikhrev, I. V., Zubrii, N. A. & Vinarski, M. V. (2022a) Cryptic taxonomic diversity and high-latitude melanism in the glossiphoniid leech assemblage from the Eurasian Arctic. *Scientific Reports*, 12, 20630. https://doi.org/10.1038/s41598-022-24989-7

Bolotov, I. N., Eliseeva, T. A. & Kondakov, A. V. (2022b) A new freshwater leech genus from Southeast Asia (Hirudinea: Glossiphoniidae). *Ecologica Montenegrina*, 56, 1–9. https://doi.org/10.37828/em.2022.56.1

Bolotov, I. N., Eliseeva, T. A., Kondakov, A. V., Konopleva, E. S., Palatov, D. M., Sokolova, A. M., Vikhrev, I. V., Gofarov, M. Y., Bovykina, G. V., Nyein Chan, Zau Lunn & Than Win (2022c) Hidden shelter-like associations of minute *Alboglossiphonia* leeches (Hirudinea: Glossiphoniidae) with sedentary animals and molluscs. *Limnologica*, 97, 126028. https://doi.org/10.1016/j.limno.2022.126028

Bolotov, I. N., Eliseeva, T. A., Kondakov, A. V., Gofarov, M. Y., Konopleva, E. S., Lyubas, A. A. & Vikhrev, I. V. (2022d) *Helobdella stagnalis* (Hirudinea: Glossiphoniidae), the first facultative mussel-associated leech in Europe. *Ecologica Montenegrina*, 54, 32–43. https://dx.doi.org/10.37828/em.2022.54.5

Bolotov, I. N., Maryinsky, V. V., Palatov, D. M., Kondakov, A. V., Eliseeva, T. A., Konopleva, E. S., Gofarov, M. Y., Vikhrev, I. V. & Bespalaya, Y. V. (2022e) Host range and phylogenetic position of *Acipenserobdella volgensis* (Zykoff, 1904) (Hirudinea: Piscicolidae) with a global checklist of bivalve-associated fish leeches. *Water*, 14(24), 4010. https://doi.org/10.3390/w14244010

Bolotov, I. N., Eliseeva, T. A., Tsiplenkina, I. G., Gofarov, M. Y. & Kondakov, A. V. (2023a) Long forgotten record of a freshwater leech on Madagascar indicates a host-associated dispersal event from continental Africa. *Ecologica Montenegrina*, 61, 56–67. https://doi.org/10.37828/em.2023.61.7

Bolotov, I. N., Eliseeva, T. A., Kondakov, A. V., Gofarov, M. Y., Aksenova, O. V., Bespalaya, Y. V., Kropotin, A. V., Travina, O. V. & Vinarski, M. V. (2023b) *Barbronia borealis* sp. nov., the first salifid leech discovered in Russia, with a global checklist of this genus. *Ecologica Montenegrina*, 63, 24–38. https://doi.org/10.37828/em.2023.63.3

Bolotov, I. N., Klass, A. L., Kondakov, A. V., Vikhrev, I. V., Bespalaya, Y. V., Gofarov, M. Y., Filippov, B. Y., Bogan, A. E., Lopes-Lima, M., Zau Lunn, Nyein Chan, Aksenova, O. V., Dvoryankin, G. A., Chapurina, Y. E., Kim, S. K., Kolosova, Y. S., Konopleva, E. S., Lee, J. H., Makhrov, A. A., Palatov, D. M., Sayenko, E. M., Spitsyn, V. M., Sokolova, S. E., Tomilova, A. A., Than Win, Zubrii, N. A. & Vinarski, M. V. (2019) Freshwater mussels house a diverse mussel-associated leech assemblage. *Scientific Reports*, 9, 16449. https://doi.org/10.1038/s41598-019-52688-3

Bolotov, I. N., Klass, A. L., Konopleva, E. S., Bespalaya, Y. V., Gofarov, M. Y., Kondakov, A. V. & Vikhrev, I. V. (2020) First freshwater mussel-associated piscicolid leech from East Asia. *Scientific Reports*, 10, 19854. https://doi.org/10.1038/s41598-020-76854-0

Bolotov, I. N. & Pešić, V. (2025) Two new genera of freshwater leeches from Europe and Africa (Hirudinea: Glossiphoniidae). *Ecologica Montenegrina*, 82, 96–112. https://doi.org/10.37828/em.2025.82.7

Booth, J. D. (1997) Long-distance movements in *Jasus* spp. and their role in larval recruitment. *Bulletin of Marine Science*, 61(1), 111–128.

Brian, J. I. & Aldridge, D. C. (2019) Endosymbionts: An overlooked threat in the conservation of freshwater mussels? *Biological Conservation*, 237, 155–165. https://doi.org/10.1016/j.biocon.2019.06.037

Brunke, J., Radespiel, U., Russo, I. R., Bruford, M. W. & Goossens, B. (2019) Messing about on the river: the role of geographic barriers in shaping the genetic structure of Bornean small mammals in a fragmented landscape. *Conservation Genetics*, 20, 691–704. https://doi.org/10.1007/s10592-019-01159-3

Burnham, R. E. (2015) Reproductive strategies conferring species dominance in marine mysid (Peracarida, Mysida) species in coastal waters off Vancouver Island, BC. *Crustaceana*, 88(12–14), 1421–1438. https://doi.org/10.1163/15685403-00003502

Burreson, E. M. & Allen, D. M. (1978) Morphology and biology of *Mysidobdella borealis* (Johansson) comb. n. (Hirudinea: Piscicolidae), from mysids in the western North Atlantic. *Journal of Parasitology*, 64(6), 1082–1091. https://doi.org/10.2307/3279730

Burreson, E. M., Kim, B. & Passarelli, J. K. (2012) A new species of *Mysidobdella* (Hirudinida: Piscicolidae) from mysids along the California coast. *Journal of Parasitology*, 98(2), 341–343. https://doi.org/10.1645/GE-2921.1

Castresana, J. (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution*, 17, 540–552. https://doi.org/10.1093/oxfordjournals.molbev.a026334

Chandra, M. & Mukharjee, R. N. (1973) Record of *Paraclepsis praedatrix*, Harding, 1924 and *Glossiphonia weberi* Blanchard, 1897 (Annelida: Hirudinea), from a new host, *Rana limnocharis* Wiegman. *Current Science*, 42(14), 512–513. https://www.jstor.org/stable/24075604

Chandra, M. & Saha, S. S. (1967) Record of *Paraclepsis praedatrix* Harding, 1924 (Annelida: Hirudinea), from a new host, *Natrix piscator* (Schneider), the Checkered Keelback (Reptilia: Serpentes). *Journal of the Bombay Natural History Society*, 63, 448–448. https://biostor.org/reference/149208

Chatterjee, N., Dhar, B., Bhattarcharya, D., Deori, S., Doley, J., Bam, J., Das, P. J., Bera, A. K., Deb, S. M., Devi, N. N., Paul, R., Malvika, S. & Ghosh, S. K. (2018) Genetic assessment of leech species from yak (*Bos grunniens*) in the tract of Northeast India. *Mitochondrial DNA Part A*, 29(1), 73–81. https://doi.org/10.1080/24701394.2016.1238914

Chelladurai, J. E. (1934) On a new Indian leech, *Hemiclepsis viridis*, sp. nov. *Records of the Zoological Survey of India*, 36(3), 345–352. https://doi.org/10.26515/rzsi/v36/i3/1934/162940

Chiangkul, K., Trivalairat, P., Kunya, K. & Purivirojkul, W. (2021a) *Placobdelloides tridens* sp. n., a new species of glossiphoniid leech (Hirudinea: Rhynchobdellida) found feeding on captive *Orlitia borneensis* in Thailand, and an update to the host distribution of *P. siamensis*. *Systematic Parasitology*, 98, 141–154. https://doi.org/10.1007/s11230-021-09967-3

Chiangkul, K., Trivalairat, P. & Purivirojkul, W. (2021b) *Batracobdelloides bangkhenensis* sp. n. (Hirudinea: Rhynchobdellida), a new leech species parasite on freshwater snails from Thailand. *Parasitology Research*, 120, 93–107. https://doi.org/10.1007/s00436-020-06919-6

Christoffersen, M. L. (2009) A catalogue of *Helobdella* (Annelida, Clitellata, Hirudinea, Glossiphoniidae), with a summary of leech diversity, from South America. *Neotropical Biology and Conservation*, 4, 89–98. https://doi.org/10.4013/nbc.2009.42.04

Cott, H. B. (1961) Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (*Crocodilus niloticus*) in Uganda and Northern Rhodesia. *Transactions of the Zoological Society of London*, 29(4), 211–356. https://doi.org/10.1111/j.1096-3642.1961.tb00220.x

Daniels, B. A. & Sawyer, R. T. (1975) The biology of the leech *Myzobdella lugubris* infesting blue crabs and catfish. *Biological Bulletin*, 148(2), 193–198. https://doi.org/10.2307/1540542

Davies, R. W. & Everett, R. P. (1975) The feeding of four species of freshwater Hirudinoidea in Southern Alberta. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen*, 19(4), 2816–2827. https://doi.org/10.1080/03680770.1974.11896383

De Bruyn, M., Rüber, L., Nylinder, S., Stelbrink, B., Lovejoy, N. R., Lavoué, S., Tan., H. H., Nugroho, E., Wowor, D., Ng, P. K. L., Siti Azizah, M. N., Von Rintelen, T., Hall, R. & Carvalho, G. R. (2013) Paleo-drainage basin connectivity predicts evolutionary relationships across three Southeast Asian biodiversity hotspots. *Systematic Biology*, 62(3), 398–410. https://doi.org/10.1093/sysbio/syt007

De Carli, B. P., Rotundo, M. M., Paschoal, L. R., Andrade, D. P. & Cavallari, D. C. (2014) First record of the association between the leech *Helobdella triserialis* (Hirudinea, Glossiphoniidae) and two species of *Pomacea* (Gastropoda, Ampullariidae) in Brazil. *Pan-American Journal of Aquatic Sciences*, 9(2), 136–140. http://hdl.handle.net/11449/171672

De Castro Godinho, M. B. & Da Silva, F. R. (2018) The influence of riverine barriers, climate, and topography on the biogeographic regionalization of Amazonian anurans. *Scientific Reports*, 8, 3427. https://doi.org/10.1038/s41598-018-21879-9

De Waard, J. R., Ratnasingham, S., Zakharov, E. V., Borisenko, A. V., Steinke, D., Telfer, A. C., Perez, K. H. J., Sones, J. E., Young, M. R., Levesque-Beaudin, V., Sobel, C. N., Abrahamyan, A., Bessonov, K., Blagoev, G., De Waard, S. L., Ho, C., Ivanova, N. V., Layton, K. K. S., Lu, L., Manjunath, R., McKeown, J. T. A., Milton, M. A., Miskie, R., Monkhouse, N., Naik, S., Nikolova, N., Pentinsaari, M., Prosser, S. W. J., Radulovici, A. E., Steinke, C., Warne, C. P. & Hebert, P. D. (2019) A reference library for Canadian invertebrates with 1.5 million barcodes, voucher specimens, and DNA samples. *Scientific Data*, 6, 308. https://doi.org/10.1038/s41597-019-0320-2

Delrieu-Trottin, E., Ben Chehida, S., Sukmono, T., Dahruddin, H., Sholihah, A., Kustiati, K., Fitriana, Y., Muchlisin, Z. A., Elvyra, R., Wibowo, A., Utama, I. V., Nurhaman, U, Sauri, S., Risdawati, R., Arifin Zein, M. S., Pouzadoux, J., Agnèse, J. F., Tilak, M. K., Page, L. M., Von Rintelen, T., Wowor, D., Steinke, D., Mona, S., Rüber, L., Hebert, P. D. N. & Hubert, N. (2025) Aquatic biotas of Sundaland are fragmented but not refugial. *Systematic Biology*, 74, syaf005. https://doi.org/10.1093/sysbio/syaf005

Dereeper, A., Guignon, V., Blanc, G., Audic, S., Buffet, S., Chevenet, F., Dufayard, J. F., Guindon, S., Lefort, V., Lescot, M., Claverie, J. M. & Gascuel, O. (2008) Phylogeny.fr: robust phylogenetic analysis for the non-specialist. *Nucleic Acids Research*, 36, W465–W469. https://doi.org/10.1093/nar/gkn180

Dev Roy, M. K., Mitra, S. & Nandi, N. C. (2021) Host-parasite association between crabs and leeches – a review. *Journal of Environment and Sociobiology*, 18(2), 125–132.

Drinkwater, R., Jucker, T., Potter, J. H., Swinfield, T., Coomes, D. A., Slade, E. M., Gilbert, M. T. P., Lewis, O. T., Bernard, H., Struebig, M. J., Clare, E. L. & Rossiter, S. J. (2021) Leech bloodmeal invertebrate-derived DNA reveals differences in Bornean mammal diversity across habitats. *Molecular Ecology*, 30(13), 3299–3312. https://doi.org/10.1111/mec.15724

Drozdova, P., Saranchina, A., Morgunova, M., Kizenko, A., Lubyaga, Y., Baduev, B. & Timofeyev, M. (2020) The level of putative carotenoid-binding proteins determines the body color in two species of endemic Lake Baikal amphipods. *PeerJ*, 8, e9387. https://doi.org/10.7717/peerj.9387

Eliseeva, T. A., Bolotov, I. N., Gofarov, M. Y., Bovykina, G. V., Tsiplenkina, I. G. & Kondakov, A. V. (2024) A high-altitude population of *Hyperboreomyzon polaris* (Hirudinea: Glossiphoniidae) in Altai Mountains, South Siberia, Russia. *Systematic Parasitology*, 101, 66. https://doi.org/10.1007/s11230-024-10169-w

Enriquez-Briones, S. & Gallardo, V. A. (1994) *Glyptonotobdella antarctica* (Sawyer & White, 1969) (Hirudinea: Piscicolidae) epizoo occasional del langostino colorado *Pleuroncodes monodon* H. Milne-Edwards, 1837 (Anomura: Galatheidae). *Gayana Oceanologia*, 2, 1–3. https://www.biodiversitylibrary.org/item/127477#page/9/mode/1up [In Spanish]

Epshtein, V. M. (1959) On systematic position, life style and origin of the endemic Baikal leech *Trachelobdella torquata* (Grube). *Doklady Akademii nauk SSSR*, 125(4), 935–937. [In Russian]

Epshtein, V. M. & Utevsky, S. Y. (1996) The geographical distribution and hosts of the *Notostomum* leeches (Hirudinea, Piscicolidae). *Vestnik Zoologii*, 3, 26–31. [In Russian]

Fahmy, M., Andrianoely, D., Wright, P. C. & Hekkala, E. (2023) Leech-derived iDNA complements traditional surveying methods, enhancing species detections for rapid biodiversity sampling in the tropics. *Environmental DNA*, 5(6), 1557–1573. https://doi.org/10.1002/edn3.474

Fernando, C. H. (1960) The Ceylonese freshwater crabs (Potamonidae). *Ceylon Journal of Science (Biological Sciences)*, 3(2), 191–222.

Gascon, C., Malcolm, J. R., Patton, J. L., da Silva, M. N., Bogart, J. P., Lougheed, S. C., Peres, C. A., Neckel, S. & Boag, P. T. (2000) Riverine barriers and the geographic distribution of Amazonian species. *Proceedings of the National Academy of Sciences*, 97(25), 13672–13677. https://doi.org/10.1073/pnas.230136397

Gelder, S. R. & Williams, B. W. (2016) Global Overview of Branchiobdellida (Annelida: Clitellata). *In:* Kawai, T, Faulkes, Z & Scholtz, G (Eds), *Freshwater Crayfish: A Global Overview*. CRC Press, New York, USA, pp. 628–654. https://doi.org/10.1201/b18723

Giao, P. H., Thoang, T. T., Hiep, H., Hien, D. H., Van Long, P., Van Kieu, N. & Dung, N. T. (2023) Geological-geotechnical correlation of a deltaic subsoil profile and characterization of its uppermost soft marine clay deposit with reference to infrastructure development in the Saigon-Dong Nai delta, Vietnam. *Bulletin of Engineering Geology and the Environment*, 82(12), 441. https://doi.org/10.1007/s10064-023-03461-4

Goddard, E. J. & Malan, D. E. (1912) The South African Hirudinea – Part I. *Annals of the South African Museum*, 11(4), 307–319. https://www.biodiversitylibrary.org/page/1522218

Govedich, F. R. (2001) A reference guide to the ecology and taxonomy of freshwater and terrestrial leeches (Euhirudinea) of Australasia and Oceania. *Cooperative Research Centre for Freshwater Ecology Identification Guide*, 35, 1–67.

Govedich, F. R., Bain, B. A. & Davies, R. W. (2002) *Placobdelloides stellapapillosa* sp. n. (Glossiphoniidae) found feeding on crocodiles and turtles. *Hydrobiologia*, 474, 253–256. https://doi.org/10.1023/A:1016591922650

Grube, E. (1867) Über Landblutegel. *Jahres-Bericht der Schlesischen Gesellschaft für Vaterländische Cultur*, 44, 59–61. https://www.biodiversitylibrary.org/item/177083#page/65 [In German]

Grube, E. (1871) Beschreibungen einiger Egel-Arten. *Archiv für Naturgeschichte*, 37(1), 87–121. https://www.biodiversitylibrary.org/item/30468#page/103 [In German]

Gupta, A. (2009) Geology and Landforms of the Mekong Basin. In: Campbell, I. C. (Ed.), *The Mekong: Biophysical Environment of an International River Basin*. Elsevier: Amsterdam, Netherlands, pp. 251–272. https://doi.org/10.1016/B978-0-12-374026-7.00003-6

Hall, T. A. (1999) BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, 41, 95–98.

Haq, B. U., Hardenbol, J. & Vail, P. R. (1987) Chronology of fluctuating sea levels since the Triassic. *Science*, 235(4793), 1156–1167. https://doi.org/10.1126/science.235.4793.1156

Harding, W. A. (1909) Note on two new leeches from Ceylon. *Proceedings of the Cambridge Philosophical Society*, 15(3), 233–234.

https://www.biodiversitylibrary.org/item/97262#page/279

Harding, W. A. (1920) Fauna of the Chilka Lake: Hirudinea. *Memoirs of the Indian Museum*, 5(7), 509–517. https://www.biodiversitylibrary.org/item/112420

Harding, W. A. (1924) XLIX.—Descriptions of some new leeches from India, Burma, and Ceylon. *Annals and Magazine of Natural History*, 14(82), 489–499. https://doi.org/10.1080/00222932408633143

Harding, W. A. & Moore, J. P. (1927) *Hirudinea. The Fauna of British India, including Ceylon and Burma*. Taylor and Francis, London, UK, 302 pp.

Hemmingsen, W., Jansen, P. A. & MacKenzie, K. (2005) Crabs, leeches and trypanosomes: an unholy trinity? *Marine Pollution Bulletin*, 50(3), 336–339.

Hertig, M., Taliaferro, W. H. & Schwartz, B. (1937) Supplement to the Report of the Twelfth Annual Meeting of the American Society of Parasitologists: Report of the Committee on terminology. *Journal of Parasitology*, 23(3), 325–329. https://www.jstor.org/stable/3272436

Hoang, D. T., Chernomor, O., Von Haeseler, A., Minh, B. Q. & Vinh, L. S. (2018) UFBoot2: improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution*, 35(2), 518–522. https://doi.org/10.1093/molbev/msx281

Hochberg, F. G. (1983) The parasites on cephalopods: a review. *Memoirs of Museum Victoria*, 44, 109–145. https://doi.org/10.24199/j.mmv.1983.44.10

ICZN (International Commission on Zoological Nomenclature) (1999) *International Code of Zoological Nomenclature. Fourth edition*. International Trust for Zoological Nomenclature, London, UK, 306 pp.

Ingram, D. M. (1957) Some Tasmanian Hirudinea. *Papers and Proceedings of the Royal Society of Tasmania*, 91, 191–232. https://eprints.utas.edu.au/13999

Ito, Y., Nakano, T., Ohara, M., Shimizu, E., Ogawa, Y. & Negishi, K. (2022) Ocular infestation by a juvenile leech, *Myxobdella sinanensis* in Japan. *American Journal of Ophthalmology Case Reports*, 25, 101389. https://doi.org/10.1016/j.ajoc.2022.101389

Iwama, R. E., Nogueira, J. & Goncalves, A. Z. (2017) *Helobdella buzz* n. sp. (Clitellata: Hirudinida), a bromeliad leech from the Brazilian Atlantic Forest. *Zootaxa*, 4272(4), 591–595. https://doi.org/10.11646/zootaxa.4272.4.9

Jakob, L., Axenov-Gribanov, D. V., Gurkov, A. N., Ginzburg, M., Bedulina, D. S., Timofeyev, M. A., Luckenbach, T., Lucassen, M, Sartoris, F. J. & Pörtner, H. O. (2016) Lake Baikal amphipods under climate change: thermal constraints and ecological consequences. *Ecosphere*, 7(3), e01308. https://doi.org/10.1002/ecs2.1308

Janssen, H. H. (1993) Morphology, egg cocoons, and transmission paths of the Antarctic leech *Glyptonotobdella antarctica* Sawyer and White, 1969 (Hirudinea: Rhynchobdelliformes: Piscicolidae). *Polar Biology*, 13(5), 347–354. https://doi.org/10.1007/BF00238361

Johansson, L. (1909) Einige neue Arten Glossosiphoniden aus dem Sudan. *Zoologischer Anzeiger*, 35(4–5), 146–154. https://www.biodiversitylibrary.org/item/37586#page/160 [In German]

Jueg, U. (2023) *Alboglossiphonia afroalpina* sp. nov. and *Alboglossiphonia buniana* sp. nov.–two new leech species from Africa and revision of the genus *Alboglossiphonia* Lukin, 1976 in Africa. *Evolutionary Systematics*, 7(1), 1–34. https://doi.org/10.3897/evolsyst.7.94507

Kaburaki, T. (1921) Fauna of the Chilka Lake. On some leeches from the Chilka Lake. *Memoirs of the Indian Museum*, 5, 661–675. https://www.biodiversitylibrary.org/item/112420

Kalyaanamoorthy, S., Minh, B. Q., Wong, T. K., Von Haeseler, A. & Jermiin, L. S. (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods*, 14(6), 587–589. https://doi.org/10.1038/nmeth.4285

Kambayashi, C., Herlambang, A. E. N., Animalesto, G., Hamidy, A. & Nakano, T. (2024) First record of *Orientobdelloides tridens* (Hirudinea: Glossiphoniidae) from Indonesia, with remarks on its taxonomic characters. *Comparative Parasitology*, 91(2), 102–107. https://doi.org/10.1654/COPA-D-24-00012

Kambayashi, C. & Nakano, T. (2023) Lumping three nominal species into one: taxonomic revision of amphibian parasitic leeches of *Torix* in Far East Asia (Hirudinea: Glossiphoniidae). *Invertebrate Systematics*, 37(12), 819–833. https://doi.org/10.1071/IS23042

Kambayashi, C. & Nakano, T. (2024) Higher-level phylogenetic relationships and latest classification of leeches. *Proceedings of the Japanese Society of Systematic Zoology (TAXA)*, 57, 28–35.

https://doi.org/10.19004/taxa.57.0_28 [In Japanese]

Kaygorodova, I. & Matveenko, E. (2025) Whoever Seeks Will Always Find: A Revision of the Endemic Deep-Sea *Codonobdella* Cryptic Group (Hirudinea, Piscicolidae) from Lake Baikal, with Description of Two New Species. Available at SSRN: http://dx.doi.org/10.2139/ssrn.5218071

Kaygorodova, I. A. & Sorokovikova, N. V. (2014) Mass leech infestation of sculpin fish in Lake Baikal, with clarification of disease-prone species and parasite taxonomy. *Parasitology International*, 63(6), 754–757. https://doi.org/10.1016/j.parint.2014.06.009

Khan, R. N. & Frick, M. G. (1997) *Erpobdella punctata* (Hirudinea: Erpobdellidae) as phoronts on *Ambystoma maculatum* (Amphibia: Ambystomatidae). *Journal of Natural History*, 31(2), 157–161. https://doi.org/10.1080/00222939700770101

Klass, A. L., Kondakov, A. V., Vikhrev, I. V., Bespalaya, Y. V., Zau Lunn, Nyein Chan, Gofarov, M. Y. & Bolotov, I. N. (2021) Is the South African leech *Barbronia gwalagwalensis* Westergren & Siddall, 2004 (Hirudinida: Erpobdelliformes: Salifidae) a Paleotropical species? *Zootaxa*, 4974(3), 585–595. https://doi.org/10.11646/zootaxa.4974.3.7

Klass, A. L., Sokolova, S. E., Kondakov, A. V., Bespalaya, Y. V., Gofarov, M. Y., Tomilova, A. A., Vikhrev, I. V. & Bolotov, I. N. (2018) An example of a possible leech-bryozoan association in freshwater. *Zookeys*, 794, 23–30. https://doi.org/10.3897/zookeys.794.28088

Kondratov, I. G., Sitnikova, T. Y., Kaygorodova, I. A., Denikina, N. N., Annenkov, V. V., Khanaev, I. V., Kirilchik, S. V., Nebesnykh, I. A. & Dzyuba, E. V. (2021) Amazing discoveries of benthic fauna from the abyssal zone of Lake Baikal. *Biology*, 10(10), 972. https://doi.org/10.3390/biology10100972

Kruger, N. & Du Preez, L. (2015) Reproductive strategies of the kangaroo leech, *Marsupiobdella africana* (Glossiphoniidae). *International Journal for Parasitology: Parasites and Wildlife*, 4(1), 142–147. https://doi.org/10.1016/j.ijppaw.2015.01.005

Kudara, T. & Kochi, K. (2023) Behavioral responses of the Japanese freshwater crab, *Geothelphusa dehaani*, to the leech, *Myxobdella sinanensis*. *Journal of Ethology*, 41(3), 215–222. https://doi.org/10.1007/s10164-023-00789-y

Kutschera, U. & Wirtz, P. (2001) The evolution of parental care in freshwater leeches. *Theory in Biosciences*, 120(2), 115–137. https://doi.org/10.1007/s12064-001-0012-1

Lai, Y. T. & Chen, J. H. (2010) *Leech Fauna of Taiwan*. National Taiwan University Press, Taipei, 118 pp.

Lovrich, G. A. & Thiel, M. (2011) Ecology, physiology, feeding and trophic role of squat lobsters. *In:* Poore, G. C. B., Ahyong, S. T. & Taylor, J. (Eds), *The Biology of Squat Lobsters*. CSIRO Publishing, Clayton, Victoria, Australia, pp. 183–222.

Lukin, E. I. (1976) Leeches of fresh and brackish water bodies. *Fauna of the USSR*, 109, 1–484. [In Russian]

Lynggaard, C., Oceguera-Figueroa, A., Kvist, S., Gilbert, M. T. P. & Bohmann, K. (2022) The potential of aquatic bloodfeeding and nonbloodfeeding leeches as a tool for iDNA characterisation. *Molecular Ecology Resources*, 22(2), 539–553. https://doi.org/10.1111/1755-0998.13486

Maia-Carneiro, T., Dorigo, T., Wachlevski, M. & Rocha, C. (2012) Evidence of phoresy by leeches (Hirudinoidea) on *Rhinella abei* (Anura: Bufonidae) in the Atlantic Rainforest in the state of Santa Catarina, southern Brazil. *Acta Herpetologica*, 7(1), 163–169. https://doi.org/10.13128/Acta_Herpetol-10807

Mandal, C. K. (2004) *Paraclepsis gardensi* (Hirudinea: Glossiphonidae) a new species of leech from West Bengal, India. *Records of the Zoological Survey of India*, 103(1-2), 111–114. https://doi.org/10.26515/rzsi/v103/i1-2/2004/159490

Mandal, C. K. (2015) *Paraclepsis joraparienisis* sp. nov. (Hirudinea: Glossiphonidae): a new leech from Jharkhand, India. *Records of the Zoological Survey of India*, 115, 231–235. https://doi.org/10.26515/rzsi/v115/i3/2015/120707

Marrone, F., Sacco, F., Kehlmaier, C., Arizza, V. & Arculeo, M. (2016) Some like it cold: the glossiphoniid parasites of the Sicilian endemic pond turtle *Emys trinacris* (Testudines, Emydidae), an example of 'parasite inertia'? *Journal of Zoological Systematics and Evolutionary Research*, 54(1), 60–66. https://doi.org/10.1111/jzs.12117

Mason, J. (1974) Studies on the freshwater and terrestrial leeches of New Zealand—1. Family Glossiphoniidae Vaillant. *Journal of the Royal Society of New Zealand*, 4(3), 327–343.

https://doi.org/10.1080/03036758.1974.10419401

Matveenko, E. Y. (2023) *Species composition, distribution and molecular-genetic passportisation of the fauna of leeches of the family Piscicolidae Johnston, 1865 (Clitellata, Hirudinea) of the Baikal Region*. PhD Thesis, Limnological Institute of the Siberian Branch of RAS, Irkutsk, 175 pp. https://rusneb.ru/catalog/000199_000009_012376107 [In Russian]

Mayor, E., Chigbu, P., Pierson, J. & Kennedy, V. S. (2017) Composition, abundance, and life history of mysids (Crustacea: Mysida) in the coastal lagoons of MD, USA. *Estuaries and Coasts*, 40, 224–234. https://doi.org/10.1007/s12237-016-0131-z

McCann, C. (1937) Notes on the common land crab *Paratelphusa* (*Barytelphusa*) *guerini* (M.-Eds.) of Salsette Island. *Journal of the Bombay Natural History Society*, 39(3-4), 531–542. https://biostor.org/reference/150378

McKenna, S. A., Betts, D. A., Pong, W. W., Govedich, F. R. & Barton, D. P. (2005) A redescription of the Australian Leech *Placobdelloides bancrofti* with new records of its distribution. *Journal of Parasitology*, 91(1), 117–121. https://www.jstor.org/stable/3286480

Meyer, M. C. (1968) Moore and the Hirudinea with emphasis on his type-specimens. *Proceedings of the United States National Museum, Smithsonian Institution*, 125(3664), 1–32. https://doi.org/10.5479/si.00963801.125-3664.1

Meyer, M. C. & Barden, A. A. (1955) Leeches symbiotic on Arthropoda, especially Decapod Crustacea. *Wasmann Journal of Biology*, 13(2), 297–311.

Miller, K. G., Kominz, M. A., Browning, J. V., Wright, J. D., Mountain, G. S., Katz, M. E., Sugarman, P. J., Cramer, B. S., Christie-Blick, N. & Pekar, S. F. (2005) The Phanerozoic record of global sea-level change. *Science*, 310(5752), 1293–1298. https://doi.org/10.1126/science.1116412

Mitra, S. & Dev Roy, M. K. (2018) First evidence of ectoparasitism on freshwater crab by a leech. *ENVIS Newsletter*, 24(4), 10–11.

Moore, J. P. (1911) Part VII. Hirudinea of Southern Patagonia. *Reports of the Princeton University Expeditions to Patagonia, 1896-1899*, 3(7), 669–689, pls. 49–50. https://www.biodiversitylibrary.org/item/75982#page/305

Moore, J. P. (1924) Notes on Some Asiatic Leeches (Hirudinea) Principally from China, Kashmir, and British India. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 76, 343–388. https://www.jstor.org/stable/4063928

Moore, J. P. (1930) Leeches (Hirudinea) from China with Descriptions of New Species. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 82, 169–192. https://www.jstor.org/stable/4064069

Moore, J. P. (1935) Leeches from Borneo and the Malay Peninsula. *Bulletin of the Raffles Museum*, 10, 67–79.

Moore, J. P. (1939) Additions to our knowledge of African Leeches (Hirudinea). *Proceedings of the Academy of Natural Sciences of Philadelphia*, 90, 297–360. https://www.jstor.org/stable/4064254

Moore, J. P. & Meyer, M. C. (1951) Leeches (Hirudinea) from Alaskan and adjacent waters. *Wasmann Journal of Biology*, 9, 11–77.

Morley, R. J. (2012) A review of the Cenozoic palaeoclimate history of Southeast Asia. *In:* Gower, D., Johnson, K., Richardson, J., Rosen, B., Rüber, L. & Williams, S. (Eds), *Biotic evolution and environmental change in Southeast Asia.* Cambridge University Press, Cambridge, UK, pp. 79–114. https://doi.org/10.1017/CBO9780511735882.006

Morley, R. J. & Morley, H. P. (2013) Mid Cenozoic freshwater wetlands of the Sunda Region. *Journal of Limnology*, 72(2), 18–35. https://doi.org/10.4081/jlimnol.2013.s2.e2

Mullowney, D., Morris, C., Dawe, E., Zagorsky, I. & Goryanina, S. (2018) Dynamics of snow crab (*Chionoecetes opilio*) movement and migration along the Newfoundland and Labrador and Eastern Barents Sea continental shelves. *Reviews in Fish Biology and Fisheries*, 28, 435–459. https://doi.org/10.1007/s11160-017-9513-y

Nagasawa, K. & Ueda, Y. (2013) Gastropod shell as a substrate for cocoon deposition by the deep-sea fish leech *Notostomum cyclostomum* (Hirudinida: Piscicolidae). *Biogeography*, 15, 107–109. https://hiroshima.repo.nii.ac.jp/records/2006429

Nakano, T., Tomikawa, K., Sakono, T. & Yoshikawa, N. (2017) Praobdellidae (Hirudinida: Arhynchobdellida) is not specific only to the mucous-membrane after all: Discovery of a praobdellid leech feeding on the Japanese freshwater crab *Geothelphusa dehaani*. *Parasitology International*, 66(3), 210–213. https://doi.org/10.1016/j.parint.2017.01.018

Nazarova, A., Mutin, A., Skafar, D., Bolbat, N., Sedova, S., Chupalova, P., Pomazkin, V., Drozdova, P., Gurkov, A. & Timofeyev, M. (2024) Leeches *Baicalobdella torquata* feed on haemolymph but have a low effect on the cellular immune response of amphipod *Eulimnogammarus verrucosus* from Lake Baikal. *PeerJ*, 12, e17348. https://doi.org/10.7717/peerj.17348

Neely, W. J., Freeman, J. M., Greiner, E. C. & Dronen, N. O. (2017) A Sample of Endohelminths from Four Species of Malaysian Freshwater Turtles (Geoemydidae) Confiscated in 2001 by Authorities in Hong Kong, People's Republic of China. *Comparative Parasitology*, 84(2), 201–205. https://doi.org/10.1654/1525-2647-84.2.201

Nesemann, H. &Neubert, E. (1999) Süßwasserfauna von Mitteleuropa, Bd. 6/2, Annelida: Clitellata: Branchiobdellida, Acanthobdellea, Hirudinea. Spektrum Akademischer Verlag, Heidelberg, Berlin, Germany, 178 pp.

Nesemann, H., Sharma, S., Sharma, G., Khanal, S. N., Pradhan, B., Shah, D. N. & Tachamo, R. D. (2007) Aquatic Invertebrates of the Ganga River System: Volume 1 – Mollusca, Annelida, Crustacea (in part). Hasko Nesemann and Chandi Press, Kathmandu, Nepal, 263 pp.

Nguyen, L. T., Schmidt, H. A., von Haeseler, A. & Minh, B. Q. (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, 32, 268–274. https://doi.org/10.1093/molbev/msu300

Nishino, D., Nishida, T. & Yoshiyama, K. (2023) Feeding of mussel-associated leeches *Hemiclepsis kasmiana* on bitterling embryos: Novel interaction between parasites in a shared host. *Journal of Fish Biology*, 103(5), 1232–1236. https://doi.org/10.1111/jfb.15510

Nishino, D. & Yoshiyama, K. (2025) Mussel preferences of two spring-spawning bitterling species are differently affected by the presence of mussel-associated leeches. *Environmental Biology of Fishes*, 108(2), 279–289. https://doi.org/10.1007/s10641-024-01664-6

Oka, A. (1922) Hirudinea from Inle Lake, S. Shan States, Burma. *Records of the Indian Museum*, 24, 521–534. https://www.biodiversitylibrary.org/item/113505#page/605

Oka, A. (1925) Notices sur les Hirudinées d'Extreme Orient, V–VII. *Annotationes Zoologicae Japonenses*, 10, 327–335. https://dl.ndl.go.jp/pid/10853149 [In French]

Oka, A. (1927) Sur une nouvelle Ichthyobdellide parasite de l'Huître. *Proceedings of the Imperial Academy*, 3(6), 364–367. https://doi.org/10.2183/pjab1912.3.364 [In French]

Oka, A. (1928) Sur une nouvelle espèce d'*Hemiclepsis*, parasite d'un crabe fluviatile de Chine. *Proceedings of the Imperial Academy*, 4(10), 607–608. https://doi.org/10.2183/pjab1912.4.607 [In French]

Oka, A. (1929) Sur une nouvelle *Placobdella*, parasite d'une Crevette fluviatile de Formose. *Proceedings of the Imperial Academy*, 5(6), 249–251. https://doi.org/10.2183/pjab1912.5.249 [In French]

Oka, A. (1934) Note sur les moeurs de la *Myxobdella sinanensis*. *Proceedings of the Imperial Academy*, 10, 519–520. https://doi.org/10.2183/pjab1912.10.519 [In French]

Oosthuizen, J. H. (1978) Two new *Batracobdella* species from southern Africa and a redescription of *Batracobdella disjuncta* (Moore, 1939) comb. nov. (Hirudinea: Glossiphoniidae). *Madoqua*, 11(2), 89–117. https://hdl.handle.net/10520/AJA10115498_175

Oosthuizen, J. H. (1979) Redescription of *Placobdella multistriata* (Johansson, 1909) (Hirudinea: Glossiphoniidae). *Koedoe*, 22(1), 61–79. https://doi.org/10.4102/koedoe.v22i1.651

Oosthuizen, J. H. (1982) Redescriptions of *Placobdella stuhlmanni* (Blanchard, 1897) and *Placobdella garoui* (Harding, 1932) (Hirudinea: Glossiphoniidae). *Journal of the Limnological Society of Southern Africa*, 8(1), 8–20. https://doi.org/10.1080/03779688.1982.9633228

Oosthuizen, J. H. (1989) Redescription of the African fish leech *Batracobdelloides tricarinata* (Blanchard, 1897) (Hirudinea: Glossiphoniidae). *Hydrobiologia*, 184, 153–164. https://doi.org/10.1007/BF02392951

Oosthuizen, J. H. (1991) An annotated check list of the leeches (Annelida: Hirudinea) of the Kruger National Park with a key to the species. *Koedoe*, 34(2), 25–38. https://doi.org/10.4102/koedoe.v34i2.421

Penny, D. (2006) The Holocene history and development of the Tonle Sap, Cambodia. *Quaternary Science Reviews*, 25(3), 310–322. https://doi.org/10.1016/j.quascirev.2005.03.012

Perera, A., Hernandez-Sastre, P. & Ayres, C. (2019) Hitch me a ride: first report of the alien leech *Helobdella octatestisaca* in Europe associated with freshwater turtles. *Biological Invasions*, 21(12), 3467–3471. https://doi.org/10.1007/s10530-019-02076-9

Petryaeva, E. Y. & Kaygorodova, I. A. (2015) Molecular ecology of fish leeches (Hirudinea: Piscicolidae) of Lake Baikal. *In: Modern Issues of Ecological Monitoring of Aquatic and Land Ecosystems: Proceedings of Internationsl Scientific Conference*. AzNIIRKh, Rostov-on-Don, Russia, pp. 183–188. https://doi.org/10.13140/rg.2.2.15234.68809 [In Russian]

Phillips, A. J., Arauco-Brown, R., Oceguera-Figueroa, A., Gomez, G. P., Beltrán, M., Lai, Y. T. & Siddall, M. E. (2010) *Tyrannobdella* rex n. gen. n. sp. and the evolutionary origins of mucosal leech infestations. *PLoS ONE*, 5(4), e10057. https://doi.org/10.1371/journal.pone.0010057

Plotnikov, V. (1907) Glossosiphoniidae, Hirudinidae et Herpobdellidae du Musée Zoologique de l'Académie Impériale des Sciences. *Annuaire du Musée zoologique de l'Académie des sciences de St. Pétersbourg*, 10, 133–158. https://www.biodiversitylibrary.org/item/121130#page/5 [In Russian]

Proctor, R. M. & Young, J. O. (1987) The life history, diet and migration of a lake-dwelling population of the leech *Alboglossiphonia heteroclita* (L.). *Hydrobiologia*, 150, 133–139. https://doi.org/10.1007/BF00006660

Ramachandra Rao, R. S. Y. & Susainathan, P. (1924) A note on *Paratelphusa hydrodromus*, Herbst, the fresh-water crab of South India. *In:* Bainbrigge Fletcher, T. (Ed.), *Report of the Proceedings of the Fifth Entomological Meeting held at Pusa on the 5th to 10th February 1923*. Superintendent Government Printing, Calcutta, India, pp. 136–140.

Richardson, D. J., Moser, W. E., Hammond, C. I., Lazo-Wasem, E. A. & Barger, M. A. (2017a) Host associations of *Helobdella octatestisaca* (Hirudinida: Glossiphoniidae) and the first report of this leech in the United States. *Comparative Parasitology*, 84(1), 18–20. https://doi.org/10.1654/1525-2647-84.1.18

Richardson, D. J., Hammond, C. I., Moser, W. E., Heaton, A. J. & McAllister, C. T. (2017b) Leech parasitism of the Gulf Coast box turtle, *Terrapene carolina major* (Testudines: Emydidae) in Mississippi, USA. *Journal of the Arkansas Academy of Science*, 71(1), 105–108. https://doi.org/10.54119/jaas.2017.7122

Ringuelet, R. A. (1985) Annulata Hirudinea. *Fauna de agua dulce de la Republica Argentina*, 17, 1–321. [In Spanish]

Ruiz-Escobar, F., Colunga-Ramírez, G. E., Oceguera-Figueroa, A. & Castellanos-Martínez, S. (2025) *Cochimibdella mexicana* n. gen. n. sp. (Hirudinida: Piscicolidae), from *Octopus bimaculatus* Verrill (Cephalopoda: Octopodidae) in the Gulf of California, Mexico. *Systematic Parasitology*, 102(2), 23. https://doi.org/10.1007/s11230-025-10217-z

Sawyer, R. T. (1986) *Leech Biology and Behaviour. Vol. 2. Feeding Biology, Ecology, and Systematics*. Clarendon Press, Oxford, UK, pp. 419–793.

Sawyer, R. T., Lawler, A. R. & Oversrteet, R. M. (1975) Marine leeches of the eastern United States and the Gulf of Mexico with a key to the species. *Journal of Natural History*, 9(6), 633–667. https://doi.org/10.1080/00222937500770531

Sawyer, R. T., Taylor, A. & Sahat, M. J. H. (1982) The leeches of Brunei (Annelida: Hirudinea), with a checklist and key to the known and expected freshwater, terrestrial and marine leeches of Borneo. *Journal of Brunei Museum*, 5(2), 168–201.

Schenková, J., Kment, P., Malenovský, I. & Tóthová, A. (2021) *Myxobdella socotrensis* sp. nov., a new parasitic leech from Socotra Island, with comments on the phylogeny of Praobdellidae (Hirudinida: Arhynchobdellida). *Parasitology International*, 82, 102310. https://doi.org/10.1016/j.parint.2021.102310

Seaby, R. M. H., Martin, A. J. & Young, J. O (1996) Food partitioning by lake-dwelling triclads and glossiphoniid leeches: field and laboratory experiments. *Oecologia*, 106, 544–550. https://doi.org/10.1007/BF00329714

Selensky, W. D. (1927) On a new Ichthybdellidae (*Mysidobdella oculata* n.g. n.sp.), a parasite on Crustacea. *Proceedings of the Second Congress of Zoologists, Anatomists, and Histologists of the USSR*, 2, 32–33. [in Russian]

Severino-Rodrigues, E. & de Almeida-Duarte, A. (2020) Environmental conditions influencing the leech infestation by *Myzobdella platensis* (Hirudinea: Piscicolidae) on the swimming crabs

(*Callinectes* spp.) (Decapoda: Portunidae) in a Brazilian tropical estuary. *Pan-American Journal of Aquatic Sciences*, 15(2), 121–132. https://panamjas.org/pdf_artigos/PANAMJAS_15(2)_121-132.pdf

Shih, H. T., Fang, S. H. & Ng, P. K. L. (2007) Phylogeny of the freshwater crabs genus *Somanniathelphusa* Bott (Decapoda: Parathelphusidae) from Taiwan and the coastal regions of China, with notes on their biogeography. *Invertebrate Systematics*, 21(1), 29–37. https://doi.org/10.1071/IS06007

Sholihah, A., Delrieu-Trottin, E., Condamine, F. L., Wowor, D., Rüber, L., Pouyaud, L., Agnèse, J. F. & Hubert, N. (2021) Impact of Pleistocene eustatic fluctuations on evolutionary dynamics in Southeast Asian biodiversity hotspots. *Systematic Biology*, 70(5), 940–960. https://doi.org/10.1093/sysbio/syab006

Siddall, M. E. & Borda, E. (2003) Phylogeny and revision of the leech genus *Helobdella* (Glossiphoniidae) based on mitochondrial gene sequences and morphological data and a special consideration of the *triserialis* complex. *Zoologica Scripta*, 32(1), 23–33. https://doi.org/10.1046/j.1463-6409.2003.00098.x

Siddall, M. E., Budinoff, R. B. & Borda, E. (2005) Phylogenetic evaluation of systematics and biogeography of the leech family Glossiphoniidae. *Invertebrate Systematics*, 19(2), 105–112. https://doi.org/10.1071/IS04034

Sket, B. & Trontelj, P. (2008) Global diversity of leeches (Hirudinea) in freshwater. *Hydrobiologia*, 595, 129–137. https://doi.org/10.1007/s10750-007-9010-8

Somerton, D. A. & Otto, R. S. (1986) Distribution and reproductive biology of the golden king crab, *Lithodes aequispina*, in the Eastern Bering Sea. *Fishery Bulletin*, 84(3), 571–584. https://spo.nmfs.noaa.gov/node/14297

Soors, J., Mertens, J., Moser, W. E., Richardson, D. J., Hammond, C. I. & Lazo-Wasem, E. A. (2015) Molecular confirmation of the North American leech *Placobdella ornata* (Verrill, 1872) (Hirudinida: Glossiphoniidae) in Europe. *BioInvasions Records*, 4(3), 185–188. http://dx.doi.org/10.3391/bir.2015.4.3.05

Soós, A. (1967) On the genus *Batracobdella* Viguier, 1879, with a key and catalogue to the species (Hirudinoidea: Glossiphoniidae). *Annales Historico-Naturales Musei Nationales Hungarici (Pars Zoologica)*, 59, 243–257.

Soós, A. (1969) Identification key to the leech (Hirudinoidea) genera of the World, with a catalogue of the species. VI. Family: Glossiphoniidae. *Acta Zoologica Academiae Scientiarum Hungaricae*, 15(3-4), 397–454.

Takhteev, V. V. (2019) On the current state of taxonomy of the Baikal Lake amphipods (Crustacea: Amphipoda) and the typological ways of constructing their system. *Arthropoda Selecta*, 28(3), 374–402. https://doi.org/10.15298/arthsel.28.3.03

Tamura, K., Stecher, G. & Kumar, S. (2021) MEGA11: Molecular Evolutionary Genetics Analysis version 11. *Molecular Biology and Evolution*, 38, 3022–3027. https://doi.org/10.1093/molbev/msab120

Tan, E. G. & Liu, X. Q. (2001) One new species of the genus *Hemiclepsis* (Rhynchobdellida: Glossiphoniidae). *Acta Zootaxonomica Sinica*, 3, 289–291. [In Chinese]

Tello, P., Jerez, V. & Olmos, V. (2007) Sanguijuelas (Hirudinea: Glossiphoniidae) asociadas a *Cryphiops caementarius* (Decapoda: Palaemonidae) del Río Limarí, Chile. *Revista de biología tropical*, 55(1), 255–260. [In Spanish]

Tessler, M., De Carle, D., Voiklis, M. L., Gresham, O. A., Neumann, J. S., Cios, S. & Siddall, M. E. (2018) Worms that suck: Phylogenetic analysis of Hirudinea solidifies the position of Acanthobdellida and necessitates the dissolution of Rhynchobdellida. *Molecular Phylogenetics and Evolution*, 127, 129–134. https://doi.org/10.1016/j.ympev.2018.05.001

Thanh, N. T., Stattegger, K., Dung, B. V., Yang, S., Chi, N. T. K., Tung, N. X., Tinh, N. V. & Nga, N. T. (2021) Depositional sequences of the Mekong River Delta and adjacent shelf over the past 140 Kyr, Southern Vietnam. *Journal of Asian Earth Sciences*, 206, 104634. https://doi.org/10.1016/j.jseaes.2020.104634

Tjallingii, R., Stattegger, K., Wetzel, A. & Phach, P. V. (2010) Infilling and flooding of the Mekong River incised valley during deglacial sea-level rise. *Quaternary Science Reviews*, 29(11-12), 1432–1444. https://doi.org/10.1016/j.quascirev.2010.02.022

Torres-Carrera, G., Muñiz-Pareja, F. C., Maza-Acuña, A. N. & Oceguera-Figueroa, A. (2023) Broad phylogenetic analyses of the leech family Glossiphoniidae (Annelida: Clitellata) reveals two independent origins of kangaroo leeches. *Biological Journal of the Linnean Society*, 139(2), 192–201. https://doi.org/10.1093/biolinnean/blad024

Trifinopoulos, J., Nguyen, L. T., von Haeseler, A. & Minh, B. Q. (2016) W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research*, 44, W232–W235. https://doi.org/10.1093/nar/gkw256

Tucker, A. D., Fitzsimmons, N. N. & Govedich, F. R. (2005) Euhirudinea from Australian turtles (*Chelodina burrungandjii* and *Emydura australis*) of the Kimberley Plateau, Western Australia, Australia. *Comparative Parasitology*, 72(2), 241–244. https://doi.org/10.1654/4175

Turnbull-Kemp, P. S. J. (1960) Quantitative estimations of populations of the river crab, *Potamon* (*Potamonautes*) *perlatus* (M. Edw.), in Rhodesian trout streams. *Nature*, 185(4711), 481–481. https://doi.org/10.1038/185481a0

Tyler, J. C. & Böhlke, J. E. (1972) Records of sponge-dwelling fishes, primarily of the Caribbean. *Bulletin of Marine Science*, 22(3), 601–642.

Utevsky, A. & Utevsky, S. (2018) New Antarctic deep-sea weird leech (Hirudinida: Piscicolidae): morphological features and phylogenetic relationships. *Systematic Parasitology*, 95(8), 849–861. https://doi.org/10.1007/s11230-018-9816-y

Utevsky, A. Y. (2007) Antarctic Piscicolid Leeches. *Bonner Zoologische Monographien*, 54, 1–80.

Utevsky, S., Kovalchuk, A., Kovalchuk, N., Utevsky, A. & Chernyshev, A. V. (2019) A new species of the genus *Johanssonia* Selensky, 1914 (Hirudinea: Piscicolidae) collected in the Kuril-Kamchatka Trench at the greatest depth ever recorded for fish leeches. *Progress in Oceanography*, 176, 102133. https://doi.org/10.1016/j.pocean.2019.102133

Utevsky, S. Y. (2005) A new species of marine fish leech *Crangonobdella maculosa* sp. n. (Hirudinea, Piscicolidae) from the Tatar Strait and coastal waters of the Kuril Islands. *Vestnik zoologii*, 39(2), 15–22. [In Russian]

Utevsky, S. Y. & Trontelj, P. (2004) Phylogenetic relationships of fish leeches (Hirudinea, Piscicolidae) based on mitochondrial DNA sequences and morphological data. *Zoologica Scripta*, 33(4), 375–385. https://doi.org/10.1111/j.0300-3256.2004.00156.x

Van Damme, K. & Segers, H. (2004) *Anomopus telphusae* Piovanelli, 1903, an epizoic bdelloid (Rotifera: Bdelloidea) on the Socotran endemic crab *Socotrapotamon socotrensis* (Hilgendorf, 1883). *Fauna of Arabia*, 20, 169–176.

Van Zyl, D., Van der Heever, G., Cockcroft, A. & Auerswald, L. (2025) Seasonal migration of a male *Jasus lalandii* sub-population. *Fisheries Research*, 281, 107201. https://doi.org/10.1016/j.fishres.2024.107201

Vanderplank, F. L. (1941) *Nothobranchius* and *Barbus* species: indigenous anti-malarial fish in East Africa. *East African Medical Journal*, 17(10), 431–436.

Vega, I. A., Damborenea, M. C., Gamarra-Luques, C., Koch, E., Cueto, J. A. & Castro-Vazquez, A. (2006) Facultative and obligate symbiotic associations of *Pomacea canaliculata* (Caenogastropoda, Ampullariidae). *Biocell*, 30(2), 367–375.

Villesen, P. (2007) FaBox: an online toolbox for fasta sequences. *Molecular Ecology Notes*, 7, 965–968. https://doi.org/10.1111/j.1471-8286.2007.01821.x

Wang, H., Luo, X., Meng, S., Bei, Y., Song, T., Meng, T., Li, G. & Zhang, B. (2015) The phylogeography and population demography of the Yunnan Caecilian (*Ichthyophis bannanicus*): Massive rivers as barriers to gene flow. *PLoS ONE*, 10(4), e0125770. https://doi.org/10.1371/journal.pone.0125770

Ward, R. D., Zemlak, T. S., Innes, B. H., Last, P. R. & Hebert, P. D. (2005) DNA barcoding Australia's fish species. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 360(1462), 1847–1857. https://doi.org/10.1098/rstb.2005.1716

Watermolen, D. J. (2021) Possible Cases of Phoresy Involving Leeches and Painted Turtles. *Chicago Herpetological Society*, 56(1), 1–2.

Westergren, S. & Siddall, M. E. (2004) Two new species of salifid leeches (Arhynchobdellida: Erpobdelliformes: Salifidae) from South Africa and Madagascar. *American Museum Novitates*, 2004(3456), 1–6. https://doi.org/10.1206/0003-0082(2004)456<0001:TNSOSL>2.0.CO;2

Williams, J. I. & Burreson, E. M. (2006) Phylogeny of the fish leeches (Oligochaeta, Hirudinida, Piscicolidae) based on nuclear and mitochondrial genes and morphology. *Zoologica Scripta*, 35(6), 627–639. https://doi.org/10.1111/j.1463-6409.2006.00246.x

Williams, J. I., Urrutia, P. M. & Burreson, E. M. (2007) Two new species of *Austrobdella* (Hirudinida: Piscicolidae) from Chile. *Journal of Parasitology*, 93, 184–189. https://doi.org/10.1645/GE-891R.1Woodruff, D. S. (2003) Neogene marine transgressions, palaeogeography and biogeographic transitions on the Thai–Malay Peninsula. *Journal of Biogeography*, 30(4), 551–567. https://doi.org/10.1046/j.1365-2699.2003.00846.x

WoRMS Editorial Board (2025) *World Register of Marine Species*. Available from https://www.marinespecies.org. Accessed 23 April 2025. https://doi.org/10.14284/170

Yamauchi, T., Itoh, T., Yamaguchi, K. & Nagasawa, K. (2008) Some leeches (Annelida: Hirudinida: Piscicolidae, Glossiphoniidae) in the Hii River system, Shimane Prefecture, Japan. *Laguna*, 15, 19–23.

Yang, T. (1986) On *Batracobdella cancricola* Oka, 1928 (Hirudinoidea: Glossiphoniidae). *Acta Hydrobiologica Sinica*, 10(2), 194–196. [In Chinese]

Yang, T. (1996) Fauna Sinica. Annelida Hirudinea. Science Press, Beijing, China, 261 pp. [In Chinese]

Yap, A., Lee, C., Seah, M. & Ng, D. (2023) Biodiversity Record: Glossiphonid leech on lowland freshwater crab. *Nature in Singapore*, 16, e2023068. https://doi.org/10.26107/NIS-2023-0068

Yeo, D. & Quynh, N. X. (1999) Description of a new species of *Somanniathelphusa* (Decapoda, Brachyura, Parathelphusidae) from Vietnam. *Crustaceana*, 72(3), 339–349. https://doi.org/10.1163/156854099503410

Young, J. O. (1980) A serological investigation of the diet of *Helobdella stagnalis* (Hirudinea: Glossiphoniidae) in British lakes. *Journal of Zoology*, 192(4), 467–488. https://doi.org/10.1111/j.1469-7998.1980.tb04244.x

Young, J. O. & Splelling, S. M. (1989) Food utilization and niche overlap in three species of lake-dwelling leeches (Hirudinea). *Journal of Zoology*, 219(2), 231–243. https://doi.org/10.1111/j.1469-7998.1989.tb02579.x

Yuan, Z. Y., Suwannapoom, C., Yan, F., Poyarkov, N. A., Nguyen, S. N., Chen, H. M., Chomdej, S., Murphy, R. W. & Che, J. (2016) Red River barrier and Pleistocene climatic fluctuations shaped the genetic structure of *Microhyla fissipes* complex (Anura: Microhylidae) in southern China and Indochina. *Current Zoology*, 62(6), 531–543. https://doi.org/10.1093/cz/zow042

Zara, F. J., Diogo Reigada, A. L., Domingues Passero, L. F. & Toyama, M. H. (2009) *Myzobdella platensis* (Hirundinida: Piscicolidae) is true parasite of blue crabs (Crustacea: Portunidae). *Journal of Parasitology*, 95(1), 124–128. https://doi.org/10.1645/GE-1616.1

Zhang, D. R., Chen, M. Y., Murphy, R. W., Che, J., Pang, J. F., Hu, J. S., Luo, J., Wu, S. J., Ye, H. & Zhang, Y. P. (2010) Genealogy and palaeodrainage basins in Yunnan Province: phylogeography of the Yunnan spiny frog, *Nanorana yunnanensis* (Dicroglossidae). *Molecular Ecology*, 19(16), 3406–3420. https://doi.org/10.1111/j.1365-294X.2010.04747.x

Supplementary Material

Arthropod-associated leeches (Annelida: Hirudinida) of the World: Diversity, taxonomic reappraisal, ecological classification of host associations, and convergent evolution

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