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FRESHWATER ANIMAL DIVERSITY ASSESSMENT

# Global diversity of true bugs (Heteroptera; Insecta) in freshwater

**John T. Polhemus · Dan A. Polhemus**



**Abstract** The aquatic and semi-aquatic Heteroptera, consisting of the infraorders Leptopodomorpha, Gerromorpha, and Nepomorpha, comprise a significant component of the world's aquatic insect biota. Within these three infraorders as a whole there are currently 23 families, 343 genera and 4,810 species group taxa considered valid, of which 20 families, 326 genera and 4,656 species inhabit freshwater. In addition, more than 1,100 unequivocally diagnosed species remain to be described. Aquatic Heteroptera occur on all continents except Antarctica, and are most numerous in the tropical regions, although there are many distinctly cold-adapted genera. Overall species richness is highest in the Neotropical and Oriental regions, which harbor 1,289 and 1,103 species, respectively. In comparison to these core tropical regions, species richness is significantly lower in the Afrotropical (799 species), Australasian (654 species), Palearctic (496 species), Nearctic (424 species) and Pacific (37 species) regions. Aquatic Heteroptera are notable for utilizing an exceptionally broad range of habitats, from marine and intertidal to arctic and high alpine, across a global altitudinal range of 0–4,700 m. Species may be found in almost every freshwater biotope, and many exhibit striking morphological adaptations to their aquatic environment, making them excellent subjects for ecological and biogeographic studies.

**Keywords** Heteroptera · Aquatic · Diversity · Richness · Distribution · Endemism

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Freshwater Animal Diversity Assessment

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## Introduction

The aquatic and semi-aquatic Heteroptera, referred to herein subsequently as "aquatic Heteroptera", are composed of three monophyletic infraorders, the Gerromorpha, Nepomorpha, and Leptopodomorpha, with worldwide distribution. Because of their general abundance in many freshwater systems, coupled with unusual morphological specializations for exploitation of specialized microhabitats, the group has long attracted the interest of aquatic entomologists, and has a relatively mature taxonomy (Polhemus & Polhemus,

in press). The majority of species occurring in Europe, North America, and Australia have been now described, and significant recent progress has also been made in documenting the aquatic Heteroptera biotas of tropical South America, Africa, Asia and the Pacific. Although many taxa still remain to be formally named from these latter regions, the biotas have in many cases been moderately well collected and informally diagnosed to the morphospecies level.

The analysis of global patterns of taxonomic richness in aquatic Heteroptera presented herein follows the guidelines developed in a workshop entitled "A global assessment of animal diversity in freshwater" convened in Mechelen, Belgium, October 13–16, 2005. The term "freshwater" excludes species inhabiting dry terrestrial or marine habitats, but can include marine species that also inhabit essentially freshwater, e.g., several species of the typically marine gerrid genus *Halobates*. It was decided to include as freshwater species two different categories of taxa, defined as: (1) "real aquatic species" with all or part of their lifecycle in aquatic habitats (in or on the water), and (2) "water dependent species" with a close/specific dependence on aquatic habitats. Under these guidelines all Leptopodomorpha (the shorebugs) are deemed to be water dependent (WDpt), and all Gerromorpha (water striders; which live on the water, but only rarely in the water) and all Nepomorpha (water bugs; which live mostly in the water, except for two littoral families) are deemed to be real aquatic species. In order to present a balanced picture of the aquatic and semi-aquatic Heteroptera of the world, we give both the entire global fauna, and the freshwater component of the global fauna in Table 1 according to the guidelines stated above. Table 2 gives the distribution of the freshwater species, and Table 3 the genera, assigned to the biogeographical regions developed during the workshop. Table 4 gives the estimated number of species that are known to us as morphospecies but as yet undescribed, to provide a more complete picture of the total global fauna as presently known. We also discuss below the "excluded marine" species and the "Holarctic" species.

**Table 1** Global freshwater aquatic Heteroptera diversity—Fall 2005

| Family | Genera | Species |
|---|---|---|
| Leptopodomorpha | | |
| Aepophilidae | 0 (1) | 0 (1) |
| Omaniidae | 0 (2) | 0 (6) |
| Leptopodidae | 8 (10) | 32 (39) |
| Saldidae | 25 (29) | 322 (335) |
| Total | 33 (42) | 354 (381) |
| Gerromorpha | | |
| Gerridae | 62 (67) | 700 (751) |
| Hebridae | 9 (9) | 221 (221) |
| Hermatobatidae | 0 (1) | 0 (9) |
| Hydrometridae | 7 (7) | 125 (126) |
| Macroveliidae | 3 (3) | 3 (3) |
| Mesoveliidae | 12 (12) | 46 (46) |
| Paraphrynoveliidae | 1 (1) | 2 (2) |
| Veliidae | 58 (61) | 896 (962) |
| Total | 152 (161) | 1993 (2,120) |
| Nepomorpha | | |
| Aphelocheiridae | 1 (1) | 78 (78) |
| Belostomatidae | 9 (9) | 160 (160) |
| Corixidae | 35 (35) | 607 (607) |
| Gelastocoridae | 3 (3) | 111 (111) |
| Helotrephidae | 21 (21) | 180 (180) |
| Naucoridae | 37 (37) | 391 (391) |
| Nepidae | 15 (15) | 268 (268) |
| Notonectidae | 11 (11) | 400 (400) |
| Ochteridae | 3 (3) | 68 (68) |
| Pleidae | 3 (3) | 38 (38) |
| Potamocoridae | 2 (2) | 8 (8) |
| Total | 140 (140) | 2309 (2309) |
| Total | 326 (343) | 4656 (4810) |

Summary excludes fossils; (x) total genus/species number of aquatic Heteroptera including species of marine and xeric habitats

## General aspects of aquatic heteroptera

Heteroptera are hemimetabolous insects, typically developing via a series of 5 nymphal instars. The body consists of 3 distinct parts (although the head and thorax are closely adjoined in Pleidae and Helotrephidae), with mouthparts specialized for piercing and sucking (except in the Corixidae). All aquatic families are predaceous (except once again for the Corixidae, which are omnivores), with their prey consisting of any organism that can be subdued by injection of a venom consisting of toxins and proteolytic enzymes. In aquatic systems devoid of large fishes, aquatic Heteroptera may sometimes represent the top predators in the trophic chain; this

**Table 2** Global distribution of aquatic Heteroptera species diversity

| | PA | NA | NT | AT | OL | PAC | AU | WORLD |
|---|---|---|---|---|---|---|---|---|
| Leptopodomorpha (all are water dependent; WDpt 100%) | | | | | | | | |
| Leptopodidae | 7 | 1 | 1 | 13 | 6 | 0 | 4 | 32 |
| Saldidae | 147 | 70 | 41 | 28 | 22 | 13 | 23 | 344 |
| Total | 154 | 71 | 42 | 41 | 28 | 13 | 27 | 376 |
| Gerromorpha (most are water surface dwellers; WDpt 2%) | | | | | | | | |
| Gerridae | 51 | 47 | 141 | 66 | 287 | 8 | 113 | 712 |
| Hebridae | 16 | 15 | 31 | 77 | 76 | 0 | 8 | 223 |
| Hydrometridae | 6 | 6 | 37 | 31 | 30 | 4 | 15 | 129 |
| Macroveliidae | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 3 |
| Mesoveliidae | 2 | 3 | 15 | 5 | 9 | 2 | 13 | 49 |
| Paraphrynoveliidae | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 2 |
| Veliidae | 44 | 31 | 290 | 158 | 199 | 5 | 176 | 903 |
| Total | 119 | 104 | 515 | 339 | 601 | 19 | 325 | 2021 |
| Nepomorpha (most are sub-surface dwellers; WDpt 7%) | | | | | | | | |
| Aphelocheiridae | 19 | 0 | 0 | 6 | 47 | 0 | 6 | 78 |
| Belostomatidae | 4 | 17 | 111 | 23 | 9 | 0 | 5 | 169 |
| Corixidae | 140 | 136 | 152 | 111 | 77 | 0 | 46 | 662 |
| Gelastocoridae | 2 | 7 | 48 | 2 | 9 | 1 | 47 | 116 |
| Helotrephidae | 0 | 0 | 10 | 31 | 111 | 0 | 12 | 164 |
| Naucoridae | 6 | 29 | 186 | 67 | 74 | 0 | 36 | 398 |
| Nepidae | 7 | 13 | 93 | 84 | 48 | 0 | 23 | 268 |
| Notonectidae | 36 | 35 | 96 | 85 | 75 | 3 | 92 | 422 |
| Ochteridae | 3 | 6 | 16 | 6 | 15 | 0 | 29 | 75 |
| Pleidae | 6 | 6 | 12 | 4 | 9 | 1 | 6 | 44 |
| Potamocoridae | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 8 |
| Total | 223 | 249 | 732 | 419 | 474 | 5 | 302 | 2404 |
| Total species richness by region | 496 | 424 | 1289 | 799 | 1103 | 37 | 654 | 4801 |

PA, Palaearctic; NA, Nearctic; NT, Neotropical; AT, Afrotropical; OL, Oriental; AU, Australasian; PAC, Pacific Oceanic Islands; ANT, Antarctic

is particularly true for some of the larger taxa in the familes Belostomatidae and Nepidae. Members of this group also exhibit considerable variation in body size, ranging from <1 mm (the genus *Micronecta* in the Corixidae) to >110 mm (the genus *Lethocerus* in the Belostomatidae).

Across the aquatic Heteroptera as a whole the morphology of the included families and genera is extremely variable, with many demonstrating striking morphological adaptations to particular microhabitats (Fig. 1-1–1-4). The Hydrometridae, or water measurers, have extremely elongate bodies and legs, allowing them to walk in stilt-like fashion across the surfaces of ponds and stream pools. The Helotrephidae, or BB Bugs, are by contrast compact, globular bugs that swim upside down, inhabiting quiet waters of lotic and occasionally lentic ecosystems. The Nepidae, or water scorpions, have a siphon to pierce the water surface for air, and bodies that resemble sticks and leaves, allowing them to remain motionless as sit-and-wait predators along pond margins, waiting for prey to come within reach. In the Notonectidae, or backswimmers, the genus *Anisops* utilizes haemoglobin to bind or release oxygen, allowing individuals to attain neutral buoyancy and remain quietly suspended at any depth in the water column. Aphelocheiridae and some Naucoridae use a plastron of ultramicroscopic hairs to create a physical gill form of respiration, obviating the

**Table 3** Global distribution of aquatic Heteroptera generic diversity

| | PA | NA | NT | AT | OL | PAC | AU | WORLD |
|---|---|---|---|---|---|---|---|---|
| Leptopodomorpha (all are water dependent; WDpt 100%) | | | | | | | | |
| Leptopodidae | 5 | 1 | 1 | 5 | 3 | 0 | 1 | 16 |
| Saldidae | 12 | 11 | 6 | 8 | 7 | 1 | 6 | 51 |
| Total | 17 | 12 | 7 | 13 | 10 | 1 | 7 | 67 |
| Gerromorpha (most are water surface dwellers; WDpt 8%) | | | | | | | | |
| Gerridae | 6 | 8 | 20 | 17 | 31 | 3 | 20 | 104 |
| Hebridae | 2 | 3 | 3 | 2 | 6 | 0 | 3 | 19 |
| Hydrometridae | 1 | 1 | 4 | 2 | 2 | 3 | 1 | 14 |
| Macroveliidae | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 3 |
| Mesoveliidae | 1 | 1 | 4 | 3 | 5 | 2 | 4 | 20 |
| Paraphrynoveliidae | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| Veliidae | 3 | 4 | 14 | 17 | 18 | 2 | 20 | 78 |
| Total | 13 | 19 | 46 | 42 | 62 | 10 | 48 | 239 |
| Nepomorpha (most are sub-surface dwellers; WDpt 4%) | | | | | | | | |
| Aphelocheiridae | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 4 |
| Belostomatidae | 3 | 3 | 6 | 4 | 3 | 0 | 2 | 21 |
| Corixidae | 13 | 18 | 14 | 7 | 5 | 0 | 5 | 62 |
| Gelastocoridae | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 10 |
| Helotrephidae | 0 | 0 | 2 | 6 | 14 | 0 | 1 | 23 |
| Naucoridae | 3 | 4 | 13 | 9 | 13 | 0 | 8 | 50 |
| Nepidae | 2 | 3 | 4 | 6 | 6 | 0 | 5 | 26 |
| Notonectidae | 4 | 3 | 4 | 5 | 6 | 3 | 6 | 31 |
| Ochteridae | 1 | 1 | 2 | 1 | 1 | 0 | 2 | 8 |
| Pleidae | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 10 |
| Potamocoridae | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 |
| Total | 30 | 36 | 52 | 41 | 51 | 5 | 32 | 247 |
| Total genus richness by region | 60 | 67 | 105 | 96 | 123 | 16 | 87 | |

PA, Palaearctic; NA, Nearctic; NT, Neotropical; AT, Afrotropical; OL, Oriental; AU, Australasian; PAC, Pacific Oceanic Islands; ANT, Antarctic

need to surface for air and thus allowing them to hunt for prey beneath stones in swift running waters. The Belostomatidae, or giant water bugs (Fig. 1-3), are fierce predators with powerful venoms, the largest capable of killing sizable fish, and in some cases even birds. In the Veliidae, the genus *Phoreticovelia*, or Zeus Bugs, has phoretic males that are fed by secretions from the anterior thorax of the females (Arnqvist et al., 2003). The Saldidae, or shore bugs (Fig. 1-1), feed largely on sub-surface prey in littoral habitats that they locate via chemoreceptive setae on the antennae (Polhemus, 1985). The above are just a few representative examples of the great ecological and morphological plasticity exhibited by these insects.

Modern water bug lineages can be traced back by fossil evidence to the Mesozoic, with some families, such as Belostomatidae, occurring in the Triassic, 180 Mya (Polhemus, 2000). Cladistic evidence indicates that they are most likely derived from terrestrial ancestors. The age of the group is reflected by the fact that numerous sister genera and species are separated by modern oceans; examples include Japan/Mexico (*Speovelia* in the Mesoveliidae), South America/Africa (*Platyvelia*/*Angilia*, in the Veliidae), and South America/Australasia (*Metrobates*/*Metrobatoides*, in the Gerridae). Vicariance, orogeny, and tectonic fusion or fragmentation are the most likely drivers of diversification, a prime example being the geologically young, mountainous, and tectonically

**Table 4** Estimated number of undescribed aquatic Heteroptera species and global distribution

| Family | Total genera | Total species | PA | NA | NT | AT | OL | PAC | AU |
|---|---|---|---|---|---|---|---|---|---|
| Leptopodomorpha | | | | | | | | | |
| Aepophilidae | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Omaniidae | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Leptopodidae | 10 | 14 | 0 | 0 | 0 | 0 | 8 | 0 | 6 |
| Saldidae | 29 | 96 | 5 | 5 | 25 | 8 | 8 | 25 | 20 |
| Total | 42 | 110 | 5 | 5 | 25 | 8 | 16 | 25 | 26 |
| Gerromorpha | | | | | | | | | |
| Gerridae | 67 | 86 | 6 | 0 | 15 | 15 | 30 | 0 | 20 |
| Hebridae | 9 | 96 | 6 | 0 | 20 | 20 | 30 | 0 | 20 |
| Hermatobatidae (m) | 1 | (3) | 0 | 0 | 0 | 0 | (1) | (1) | (1) |
| Hydrometridae | 7 | 26 | 3 | 0 | 8 | 8 | 4 | 0 | 3 |
| Macroveliidae | 3 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| Mesoveliidae | 12 | 26 | 0 | 0 | 4 | 4 | 10 | 0 | 8 |
| Paraphrynoveliidae | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Veliidae | 61 | 316 | 0 | 0 | 66 | 70 | 40 | 15 | 125 |
| Total | 161 | 552 | 15 | 0 | 115 | 117 | 114 | 15 | 176 |
| Nepomorpha | | | | | | | | | |
| Aphelocheiridae | 1 | 31 | 3 | 0 | 0 | 15 | 10 | 0 | 3 |
| Belostomatidae | 9 | 24 | 0 | 0 | 10 | 3 | 8 | 0 | 3 |
| Corixidae | 35 | 66 | 0 | 6 | 10 | 20 | 15 | 0 | 15 |
| Gelastocoridae | 3 | 16 | 0 | 0 | 6 | 0 | 2 | 0 | 8 |
| Helotrephidae | 21 | 52 | 0 | 0 | 6 | 6 | 30 | 0 | 10 |
| Naucoridae | 37 | 81 | 0 | 0 | 26 | 20 | 20 | 0 | 15 |
| Nepidae | 15 | 50 | 0 | 0 | 10 | 10 | 20 | 0 | 10 |
| Notonectidae | 11 | 55 | 0 | 0 | 10 | 15 | 15 | 0 | 15 |
| Ochteridae | 3 | 63 | 0 | 0 | 20 | 3 | 20 | 0 | 20 |
| Pleidae | 3 | 10 | 0 | 0 | 5 | 0 | 0 | 0 | 5 |
| Potamocoridae | 2 | 4 | 0 | 0 | 4 | 0 | 0 | 0 | 0 |
| Total | 140 | 452 | 3 | 6 | 107 | 92 | 140 | 0 | 104 |
| Total | 343 | 1114 | 23 | 11 | 247 | 217 | 270 | 40 | 306 |

PA, Palaearctic; NA, Nearctic; NT, Neotropical; AT, Afrotropical; OL, Oriental; AU, Australasian; PAC, Pacific Oceanic Islands; ANT, Antarctic. (Genera given are existing genera; species are undescribed.) This summary does not include fossils, or marine (m) species

complex island of New Guinea, where nearly every major river basin displays significant local endemicity (Polhemus, 1996; Polhemus & Polhemus, 1998).

The phylogeny of the Heteroptera as a whole and of the individual infraorders within it has been presented in a series of cladograms by Schuh & Slater (1995, p. 5). These cladistic interpretations, which were based primarily on morphological characters, were derived from the works of various authors, as follows: Leptopodomorpha (Schuh & Polhemus, 1980; Polhemus, 1985; see Schuh & Slater, 1995, p. 134); Gerromorpha (Andersen, 1982; see Schuh & Slater, 1995, p. 84); Nepomorpha (Mahner, 1993; see Schuh & Slater, 1995, p. 110). Although a limited amount of molecular data contributed to the cladograms presented by Schuh & Slater (1995, p. 5), there are now a number of ongoing studies testing the current phylogenies with more extensive molecular data sets (e.g., Hebsgaard et al., 2004).

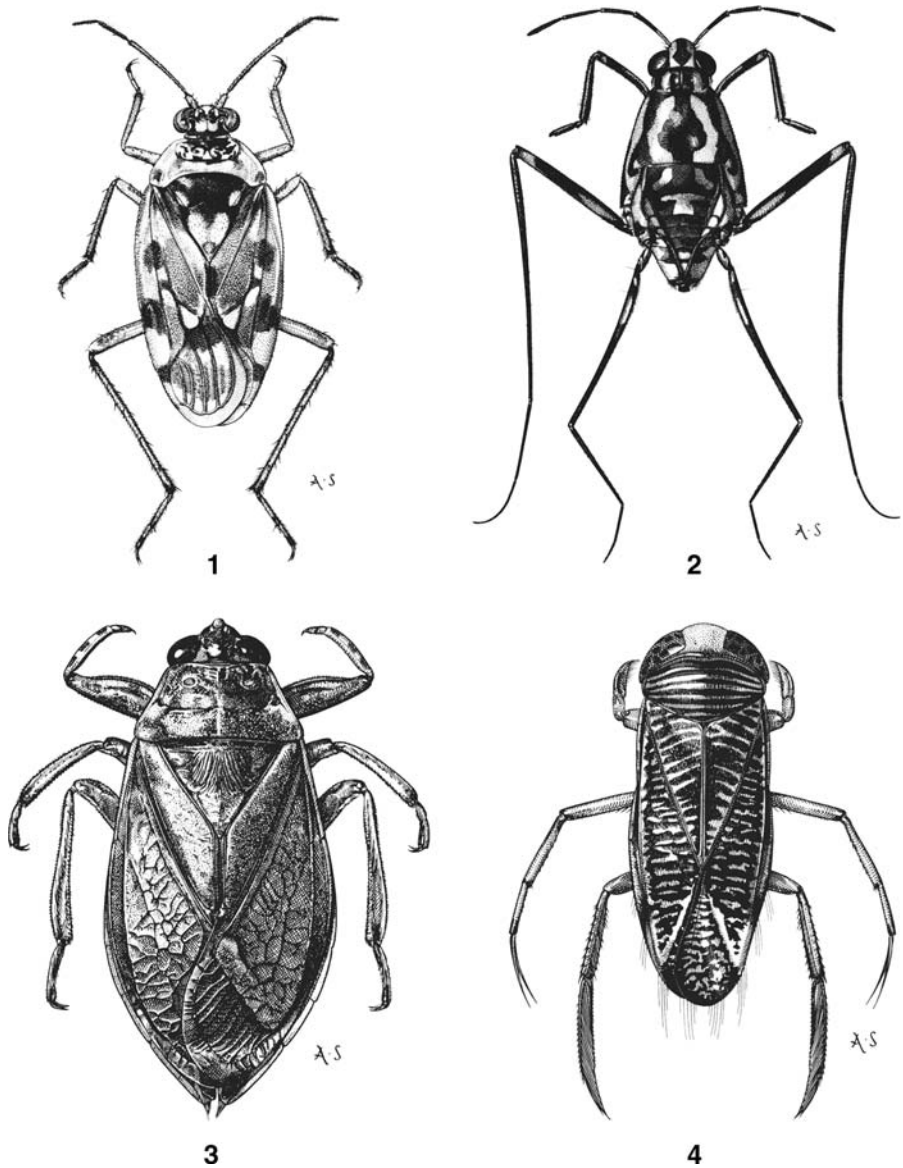


**Fig. 1** Exemplar taxa of aquatic Heteroptera in various infraorders. 1-1, *Pentacora signoreti* (Guerin) (Saldidae: Leptopodomorpha); 1-2, *Trepobates becki* Drake & Harris (Gerridae: Gerromorpha); 1-3, *Belostoma bakeri* Montandon (Belostomatidae: Nepomorpha); 1-4. *Sigrara mckinstryi* Hungerford (Corixidae: Nepomorpha)

## Species diversity

Over the past 40 years, the senior author has compiled a manuscript catalog of all taxonomic names in the aquatic Heteroptera, including synonyms, based primarily on a comprehensive library of the taxonomic literature, consisting of approximately 11,000 references containing the original descriptions of virtually all species as well as their synonyms. In the early 1990s, the junior author facilitated the entry of this manuscript catalog into a flat file database at the Smithsonian Institution, producing an electronic world checklist of all valid names in the three infraorders under study. This database was subsequently refined by additional exhaustive literature searches to detect names published in obscure journals, as well as previously overlooked synonyms and homonyms. Finally, the most recent literature

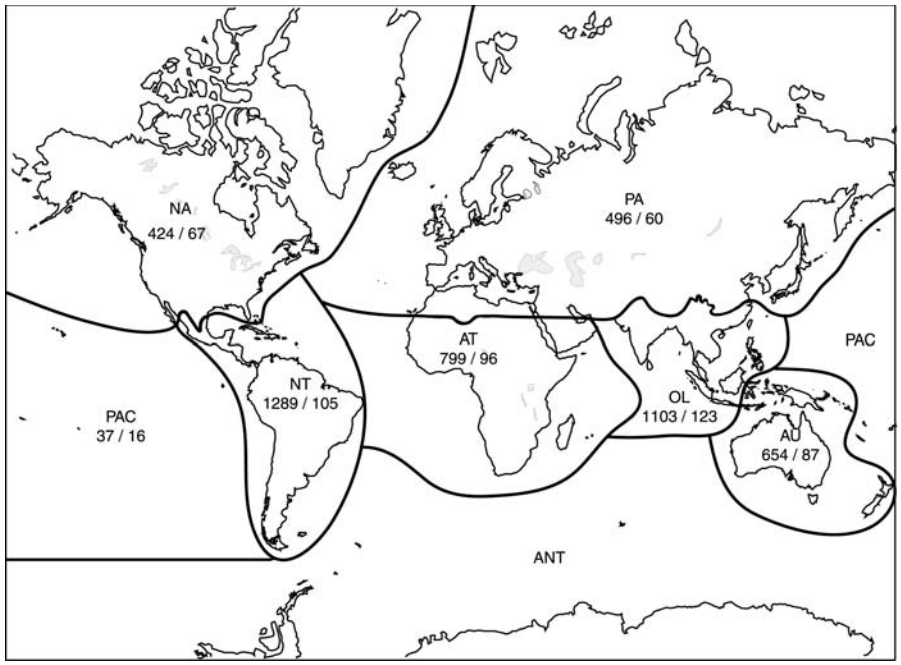


**Fig. 2** Total richness of aquatic Heteroptera species in individual biogeographic regions (see Table 2 for additional details on levels of family and genus level richness). PA, Palaearctic; NA, Nearctic; NT, Neotropical; AT, Afrotropical; OL, Oriental; AU, Australasian; PAC, Pacific Oceanic Islands; ANT, Antarctic

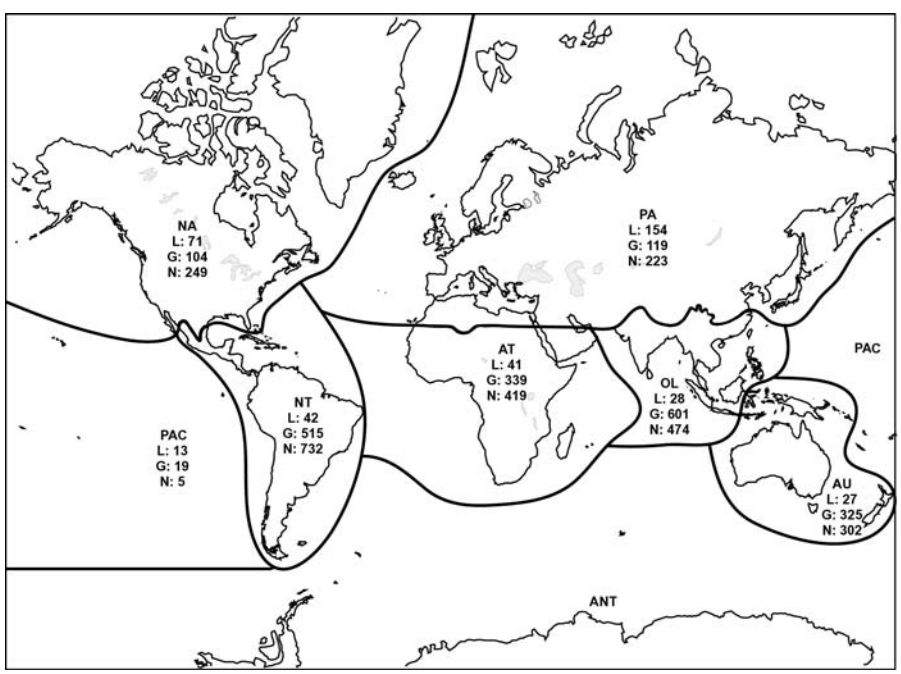


**Fig. 3** Total richness of Leptopodomorpha (L), Gerromorpha (G), Nepomorpha (N) species in individual biogeographic regions (see Table 2 for additional details on levels of family and genus level richness). PA, Palaearctic; NA, Nearctic; NT, Neotropical; AT, Afrotropical; OL, Oriental; AU, Australasian; PAC, Pacific Oceanic Islands; ANT, Antarctic

was integrated to bring the database up to date as of 15 November 2005. Parts of this work have been incorporated into regional or world faunal catalogs (Schuh et al., 1987; Henry & Froeschner, 1988; Aukema & Rieger, 1995).

Based on this data analysis, the currently described world biota of aquatic Heteroptera across all three infraorders consists of 23 families, 343 genera and 4,810 species (see Table 1, which includes all species group taxa). Of these, 20 families, 326 genera and 4,656 species are considered to inhabit freshwater (also given in Table 1). We estimate, based on known unequivocally diagnosed but still undescribed morphospecies held in major collections, that a minimum of 1,100 species still await formal taxonomic description (Table 4). Allowing for still further discoveries in remote and undersurveyed areas, and for eventual resolution of varying taxonomic interpretations regarding narrow versus broad species concepts, we would estimate that the total world biota of aquatic Heteroptera probably lies in the range of 7,000 species.

## Present distribution

Aquatic Heteroptera occur on all continents except Antarctica, and are most numerous in the tropical regions, although there are many distinctly cold-adapted genera, particularly in the Saldidae and Corixidae. Diversity is highest in first to third order streams (i.e., the smallest streams in a given drainage network), and lowest in large rivers and lakes. A high percentage of tropical endemics are found associated with rheocrenes or headwater streamlets, often in proximity to waterfalls or other habitats with high structural complexity (see Polhemus et al., 1992). As a whole, aquatic Heteroptera are notable for utilizing an exceptionally broad range of aquatic ecosystems, from marine and intertidal to arctic and high alpine, across a global altitudinal range of 0–4,700 m. As such, they are excellent subjects for comparative biogeographical and ecological studies.

Using the world checklist (Table 1), refined to include only freshwater species (also in Table 1), all included species were assigned to a biogeographic region or regions (Table 2) using the criteria specified by Royal Belgium Institute of Natural Sciences. The following biogeographic regions were recognized for the purposes of this analysis (Fig. 2): Nearctic (NA), Neotropical (NT), Afrotropical (AT), Australasian (AU), Oriental (OL), Palaearctic (PA), Pacific (PAc), and Antarctic (ANT). There are no Heteroptera known from the Antarctic region, therefore it was omitted from our tables. Based on this integration of taxonomic and distributional information, it was then possible to determine the total number of species occurring in each major biogeographic region, in terms of both raw species numbers, and representation by individual infraorders, familes and genera (see Tables 2 and 3 and Fig. 3).

Marine and xerophilous taxa have been excluded from this analysis (see Table 1). In the Leptopodomorpha, two marine families (Aepophilidae and Omaniidae), and 4 intertidal genera of Saldidae with 13 species are excluded, along with two genera and 7 species of xerophilous Leptopodidae. In the Gerromorpha, one family (Hermatobatidae) plus 8 marine genera and 126 marine species are excluded, but the estuarine genera that occupy the ecotone from mixohaline to limnetic waters are included in the freshwater totals. While the primarily marine gerrid genus *Halobates* is excluded, with a total of 46 species, three species have been added to the total of freshwater species, because two of these (*H. acherontis* J. Polhemus and *H. robinsoni* Andersen) occupy freshwater rivers in northern Australia, and one (*H. murphyi* J. & D. Polhemus) inhabits Papuan estuaries with mixohaline to limnetic waters.

It should be noted that the total numbers of species and genera from Tables 2 and 3 (distribution) will generally exceed the numbers shown in Table 1 (summary of freshwater aquatic Heteroptera global richness), because certain species and genera occur in more than one biogeographic region as defined herein.

Although aquatic Heteroptera are distributed across all of Earth's major non-polar biogeographic regions, including even the most remote islands of the Indian, Atlantic and Pacific oceans, there are obvious differences in levels of species richness in regard to both geographic regions and the distributions of individual families. Interestingly, there are only 19 Holarctic species in four families: Saldidae (12), Corixidae (5), Gerridae (1), and Veliidae (1); therefore the species totals for individual regions provide a reasonable indication of local biogeographic species richness and endemism. The following synopsis

examines these patterns on a continent-by-continent basis (see Table 2).

### Palearctic Region (PA)

The Palearctic Region has 16 families containing 496 species. There is a high richness of cold-adapted Corixidae and Saldidae, and a low richness of Veliidae (except Veliinae), and Naucoridae. The Gelastocoridae and Helotrephidae are absent.

### Nearctic Region (NA)

The Nearctic Region, with 16 families and 424 species, is nearly equivalent in species richness to the Palearctic. There is a high richness of Corixidae and Saldidae, which each have a number of cold-adapted genera restricted to this region, and a low richness of certain Veliidae (Veliinae). The Helotrephidae and Aphelocheiridae are absent.

### Afrotropical Region (AT)

There are 18 families containing 799 species in the Afrotropical Region, with a particularly high richness of Nepidae, Aphelocheiridae, and certain Veliidae (Microveliinae, Rhagoveliinae). Throughout Africa two speciose genera of Nepidae (*Laccotrephes* and *Ranatra*) dominate. The Aphelocheiridae and Veliidae (especially Rhagoveliinae) exhibit notable insular species richness and endemism in Madagascar, with many undescribed species (see Table 4). In contrast to the Neotropical and Australasian regions, there is a low richness of Gelastocoridae, with only two species, and Gerridae show only modest diversification.

### Oriental Region (OL)

The Oriental Region has 17 families represented by 1,103 species, rivaling the Neotropical Region in terms of total species richness. There is a particularly high richness of Gerridae, Naucoridae and Helotrephidae, with many undescribed species in these families. By contrast, there is a low richness of Gelastocoridae, and certain Veliidae (Rhagoveliinae). Distinctive groups confined to this region include the Eotrechinae (Gerridae) and Cheirochelini (Naucoridae).

### Neotropical Region (NT)

The Neotropical Region, with 18 families and 1,289 species, is the world's richest in terms of described species. The already high richness of Veliidae, Belostomatidae, Naucoridae and Gelastocoridae will be further amplified when the known undescribed species are published. Similarly, the known but undescribed Saldidae and Ochteridae will more than double the present numbers recorded for this region. The family Aphelocheiridae is absent, and the family Helotrephidae has limited representation.

### Australasian Region (AU)

The Australasian Region has 17 families containing 654 species, with high richness of Gerridae, Gelastocoridae, Ochteridae, Notonectidae and certain Veliidae (Microveliinae, Rhagoveliinae). The Helotrephidae are absent throughout most of this region, except for Sulawesi and the Lesser Sunda Islands. There are a large number of undescribed Veliidae in this region, most of them in the sub-families Microveliinae and Rhagoveliinae on New Guinea, which exhibits almost total endemism in regard to its water bug fauna at the species level. New Guinea also has high endemism at the generic level, with seven endemic genera of Veliidae (Polhemus & Polhemus, 2005), and six endemic genera of Naucoridae. The extensive water bug fauna of Australia, which is also highly endemic, has recently been monographed by Andersen & Weir (2004).

### Pacific Region (PAc)

The Pacific Region has 8 families containing 37 species. We would note that a distinctive eastward extension of this biotic region, not originally considered within the geographic constraints of the workshop that coordinated this analysis, consists of the Insular Pacific with its numerous high islands and

atolls (Polhemus, 1996). Although small in total land area, this sub-region spans nearly half the globe and has high endemicity and certain localized foci of high species richness. Islands included in this region include the Fiji, Tonga, Samoa, Caroline, Marshall, Gilbert, Society, Austral, Gambier, Tuamotu, Marquesas and Hawaiian archipelagoes. The faunas of these isolated island groups tend to be composed of species derived from a discrete suite of taxonomic lineages, most notably Veliidae (Microveliinae), Gerridae (Gerrinae), Mesoveliidae, Saldidae, Hydrometridae, and Notonectidae (Anisopinae), with progressive attenuation in an eastward direction from Australia and the Philippines to Hawaii. Although the Pacific Region currently appears depauperate, there are a substantial number of undescribed taxa awaiting publication.

Although held in the Pacific Region, the oldest and largest Fijian island of Viti Levu has a diverse topography and large rivers of continental magnitude, and thus might arguably be included in the Australasian region, similar to New Caledonia, under the criteria of the current analysis.

### Antarctic Region

No aquatic Heteroptera are currently recorded from Antarctica, although biogeographic evidence indicates that during the Early Tertiary this continent may have provided a biogeographic corridor for the interchange of certain groups (Gelastocoridae, trepobatine Gerridae) between Australia and South America (J. Polhemus & D. Polhemus, 2002).

## Areas of endemicity

Based on our studies and those of many colleagues worldwide, we believe that the main areas of endemicity for aquatic Heteroptera on a world basis are as follows (the following listing does not imply any form of ranking, and there may be others): (1) Madagascar; (2) New Guinea; (3) Indochina; (4) the Malay Archipelago; (5) Australia; (6) tropical central and west Africa; (7) the Guiana Shield of northern South America; (8) the Atlantic rainforests of eastern South America. These areas are largely congruent with the global biodiversity "hotspots" defined by Mittermeier et al. (1998) and are dicussed in detail further below:

(1) Madagascar has an overwhelming preponderance of endemic species, and 10 specialized endemic genera, however, most other genera are shared with mainland Africa. There are a substantial number of species awaiting description in the Veliidae (Microveliinae, *Rhagovelia*), Aphelocheiridae and Naucoridae (*Temnocoris*).

(2) New Guinea has a higher percentage of endemic genera than any other large landmass, primarily concentrated in the Gerromorpha and Nepomorpha (Naucoridae). We estimate the species endemism for this very large island at well over 90%. There are substantial numbers of Veliidae (Rhagoveliinae and Microveliinae), Gerridae (*Tenagogonus*), Notonectidae (*Enithares*) and Ochteridae (*Ochterus*) still awaiting description, all of them endemic.

(3) Indochina is extremely rich in aquatic Heteroptera, and contains a number of endemic genera, although most of its genera are shared with the Australasian and Palearctic regions. The enormous number of endemic species is due to the geological age of the region, the complex topography created by the accretion of the Indian Plate to southern Asia, and region's proximity to the western Austalasian Region and the remainder of Asia, which has resulted in high lineage diversity. A number of intensive studies are presently focused on this area, resulting in a continuing flood of new taxonomic descriptions, mostly of newly discovered endemics.

(4) The Malay Archipelago (defined as extending from the Malay Peninsula to Timor, and excluding New Guinea; see above) is rich in insular endemic species, but has few endemic genera, instead sharing most of its genera with mainland tropical Asia. Our knowledge of this area is still limited; a number of brief baseline surveys have been undertaken but a comprehensive knowledge of the aquatic Heteroptera on a region-wide basis is far from complete, and further discoveries of endemic taxa or even genera, particularly at higher elevations, are nearly certain. A recent compedium of

knowledge to date for the water bugs (excluding shore bugs) of this region is now available (Chen et al., 2005), providing a useful basis for further studies.

(5) Australia is a huge but still under-surveyed continent, especially in its tropical regions. Of the 54 genera of water bugs found on the continent, 14 are endemic, and it will be surprising to see further additions. Most of the species are endemic, and others are shared only with immediately neighboring areas, particularly New Guinea and Timor. About 25% of the Australian species are marine, and some of these latter previously thought to be endemic have been recently found on the islands bordering the northern margin of the Coral Sea, thousands of kilometers to the northeast (Polhemus & Polhemus, 2006). A comprehensive treatment of the known Australian water bugs (excluding shore bugs) is now available (Andersen & Weir, 2004), which will facilitate recognition and treatment of new discoveries.

(6) Tropical central and west Africa has been partly surveyed over time, but in a geographically haphazard fashion, thus is still poorly understood. The known fauna has a number of endemic genera, and a high proportion of endemic species. The few taxa that are known from the plateaus of Angola, which lies on the periphery of this region, are also mostly endemic. Chronic political instability and poor infrastructure make prospects for further field work in this region uncertain at best.

(7) The Guiana Shield is a very rich region for aquatic Heteroptera, due to its great geological age, equatorial location, and high topographic complexity. The region shares most of its genera with the remainder of tropical South America, but has many locally endemic species, a large number of which are yet undescribed. The eastern slopes of the Andes, extending south and west of the Guiana Plateau, also exhibit high richness and endemicity, and might logically be included as an extension of this region bounding the western limits of the Amazon basin. Further collections are badly needed throughout this entire area, but are complicated by remote and complex terrain, and social factors such as the narcotics trade.

In addition to these large-scale areas of endemism and richness, there are many other more localized areas of endemism for aquatic Heteroptera found in all major biogeographic regions (for instance, the Great Basin of the western United States; D. Polhemus & J. Polhemus, 2002). In many cases these are internal sub-divisions of the larger areas discussed above; for instance, a recent study identified 40 areas of endemism for aquatic Heteroptera in New Guinea alone (Polhemus et al., 2004).

### Under-collected areas (black holes)

The following are areas that appear to be of high importance but which lack adequate surveys, and as such represent "black holes" of aquatic Heteroptera knowledge (the following listing does not imply any form of ranking): (1) the sub-tropical plateaus of Angola and adjacent southwest Africa; (2) portions of the Malay Archipelago, notably the Lesser Sunda Islands, the Moluccas, and the southeastern mountains of Borneo; (3) portions of interior Indochina, particularly Cambodia (Cardamom Mountains) and Laos; (4) The southeastern margin of the Himalayan uplift, including northern Burma, Assam, southwest China and eastern Tibet; (5) the mountains of Ethiopia and the adjacent Horn of Africa; (6) tropical and sub-tropical West Africa; (7) central tropical Africa, particularly Lake Tanganyika and associated drainages, which are a renowned center of endemism for other freshwater groups; (8) the Atlantic coastal rainforests of Brazil from Rio de Janeiro north to the mouth of the Amazon; (9) many Pacific islands.

For most of these areas we have a few scattered samples, which are sufficient to underscore the importance of these areas and the need for additional surveys (for instance, two endemic genera of Naucoridae are known from Lake Tanganyika). Additional areas that could be added here might include inner Tibet and far western China, although much of this area is cold, dry and likely depauperate for aquatic Heteroptera.

## Summary of general biogeographic patterns

Based on the current analysis, the following general biogeographic patterns have emerged:

(1) The Corixidae and Saldidae exhibit a distinctly higher species richness in the Northern Hemisphere in comparison to tropical regions.
(2) Among the Gerromorpha, there is a disproportionate richness of Veliidae in the Neotropical region, and of Gerridae in the Oriental region. In many cases it appears that certain endemic genera are filling ecologically equivalent roles in the two regions (i.e., the gerrid genus *Metrocoris* in the Oriental region may be ecologically equivalent to the veliid genus *Rhagovelia* in the Neotropical region).
(3) The family Helotrephidae is entirely confined to land masses derived from Gondwanaland. The Gelastocoridae and Ochteridae show a nearly similar pattern, except for presumably recent dispersal into the southern section of the Nearctic region via the Mesoamerican land bridge.
(4) The family Aphelocheiridae is confined to the Eastern Hemipshere, with no representation in the Neotropical and Nearctic regions.
(5) Cosmopolitan groups with at least some representation in all non-polar biogeographic regions include Gerridae, Veliidae, Mesoveliidae, Hydrometridae, Hebridae, Pleidae, Belostomatidae, Nepidae, Notonectidae, Saldidae and Leptopodidae.

## Conservation

Aquatic Heteroptera are hardy and adaptable insects, and based on current information it appears that most species are not at risk. There are a few documented cases in Europe, North America, and Japan where taxa with particularly circumscribed ranges have become endangered through loss of habitat. This trend seems to be most pronounced in the Saldidae (*Salda morio* Zetterstedt not seen in the Netherlands since 1918, when its peat bog habitat largely disappeared; Aukema, 2003), Naucoridae (*Ambrysus amargosus* LaRivers, endemic to small springs in Ash Meadows, Nevada, threatened by habitat destruction; Polhemus, 1994) and Aphelocheiridae (*Aphelocheirus kawamurae* Matsumura now thought to be extinct because of alteration of the river system from Biwa-ko Lake, Japan; Tomokuni et al., 1995). For tropical regions, our documentation of species ranges and ecologies is so incomplete that no solid conclusions can be drawn in regard to these topics, but potential threats exist from both human alteration of landscape ecologies (such as conversion of rain forests to plantations or cattle pastures) and from ecosystem transformations driven by global climate change.

Many species of aquatic Heteroptera are also useful in terms of global or regional conservation planning for preservation of freshwater biodiversity, due to the largely non-overlapping nature of the broad regional biotas, coupled with a high degree of localized endemism within regions (Polhemus et al., 2004). Certain species are also effective biological controls of mosquitoes and other pest flies because they feed on the immatures, and other species have been documented as natural enemies of rice pests. The various families also display differing tolerances to water pollution, and as a result have potential utility as bioindicators of water quality (Jansson, 1977). In light of this, their preservation is in the best interests of human societies as a whole.

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