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FRESHWATER ANIMAL DIVERSITY ASSESSMENT

# Global diversity of mysids (Crustacea-Mysida) in freshwater

**Megan L. Porter · Kenneth Meland · Wayne Price**



**Abstract** In this article we present a biogeographical assessment of species diversity within the Mysida (Crustacea: Malacostraca: Peracarida) from inland waters. Inland species represent 6.7% (72 species) of mysid diversity. These species represent three of the four families within the Mysida (Lepidomysidae, Stygiomysidae, and Mysidae) and are concentrated in the Palaearctic and Neotropical regions. The inland mysid species distributional patterns can be explained by four main groups representing different freshwater invasion routes: (1) Subterranean Tethyan relicts (24 spp.); (2) Autochthonous Ponto-Caspian endemics (20 spp.); (3) *Mysis* spp. 'Glacial Relicts' (8 spp.); and (4) Euryhaline estuarine species (20 spp.). The center of inland mysid species diversity is the Ponto-Caspian region, containing 24 species, a large portion of which are the results of a radiation in the genus *Paramysis*.

**Keywords** Inland fauna · Freshwater biology · Mysid · Diversity

## Introduction

The order Mysida (Crustacea: Malacostraca: Peracarida), first described in 1776 by Müller, contains over 1,000 described species distributed throughout the waters of the world (Wittmann, 1999). Although >90% of mysid species are exclusively marine, the remaining species represent either species from coastal habitats with direct marine connections (e.g., estuaries, coastal rivers, marine caves) or from true invasions of inland freshwaters (Audzijonytë, 2006; Mauchline, 1980). This review deals with the zoogeography and historical processes leading to the current diversity of freshwater mysid species. While most of the true freshwater mysids occur in 'continental' lacustrine and riverine habitats, many of the subterranean mysids occur only from island habitats; for our purposes we have, therefore, chosen to define 'inland' species, as any species with documented populations occurring in freshwaters (salinity <3 g/l). Inland mysids range in size from 3 to 22 mm, and due to the brood pouch present in mature females are

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Freshwater Animal Diversity Assessment

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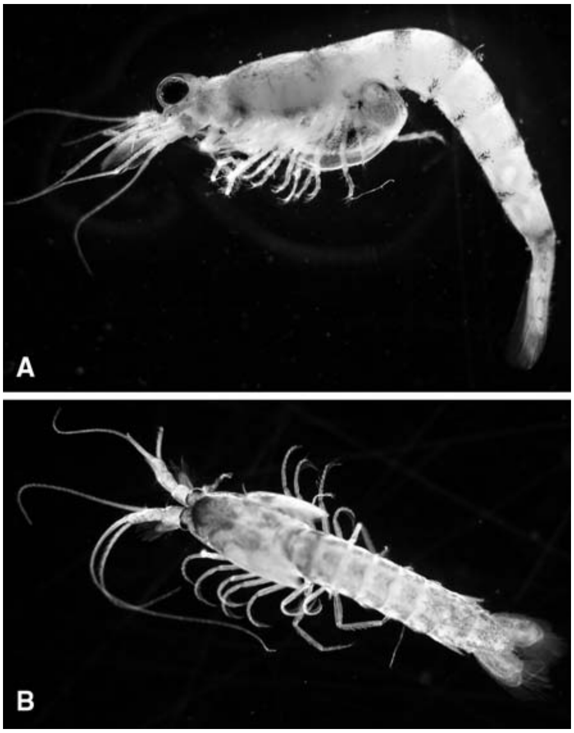

**Fig. 1** A—*Taphromysis bowmani*; B—*Spelaeomysis* sp. (Photos by E. Peebles, courtesy of the American Fisheries Society)

often called ‘opossum shrimp’ (Fig. 1). Most inland species are nektobenthic (although a few species are pelagic), omnivorous suspension-feeders, or scavengers. Some species can be found in large numbers, serving as an important food source for many other organisms.

## Species diversity

The Mysida contain ~1,073 species, only 72 of which are documented from inland waters (See supplemental material). Out of the four families within the Mysida *sensu* Martin & Davis (2001), three contain species from inland systems (Tables 1, 2). Two of these families, the Lepidomysidae and the Stygiomysidae, are monogeneric taxa (*Spelaeomysis* and *Stygiomysis*, respectively) containing species adapted to subterranean habitats (e.g., caves, groundwater, wells, and crab burrows). While all of the species in these two families (9 and 7, respectively) are from inland habitats, many are from island or coastal systems with direct connections to marine environments. Nonetheless, 7 Lepidomysidae and 5 Stygiomysidae have made the transition to what can be considered freshwater environments. In comparison, the family Mysidae contains the largest diversity of inland taxa (60 species, 23 genera), with most of this diversity found within the subfamily Mysinae, tribe Mysini (Tables 1, 2).

## Zoogeography

The inland mysid fauna are located mainly in the Palaearctic (39 species, 15 genera) and Neotropical (20 species, 6 genera) biogeographical regions (Tables 1, 2; supplementary tables; Fig. 2). Within freshwater habitats, primarily from these two broad regions, four historical diversification patterns can

**Table 1** Total number of inland mysid species found in the major geographical regions from each family (**), subfamily (*), and tribe (°) containing at least one inland species. Only species numbers from each family are used to calculate the final totals for each region. See supplementary tables for detailed information. PA: Palaearctic; NA: Nearctic; NT: Neotropical; AT: Afrotropical ; OL: Oriental; AU: Australasian; PAC: Pacific & Oceanic Islands; ANT: Antarctic

| | PA | NA | NT | AT | OL | AU | PAC | ANT | Total inland species |
|---|---|---|---|---|---|---|---|---|---|
| **Lepidomysidae | 1 | 1 | 4 | 0 | 2 | 0 | 0 | 0 | 7 |
| **Stygiomysidae | 1 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 5 |
| **Mysidae | 37 | 10 | 12 | 1 | 5 | 1 | 0 | 0 | 60 |
| *Rhopalophthalminae | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| *Mysinae | 37 | 10 | 12 | 1 | 4 | 1 | 0 | 0 | 59 |
| °Heteromysini | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| °Leptomysini | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 2 |
| °Mysini | 37 | 8 | 11 | 1 | 4 | 0 | 0 | 0 | 56 |
| Total | 39 | 11 | 20 | 1 | 7 | 1 | 0 | 0 | 72 |

*Note*: Several species occur in more than one geographical region, resulting in higher numbers of occurrences (79) than species (72)

**Table 2** Total number of inland mysid genera from the major geographical regions from each family (**), subfamily (*), and tribe (°) containing at least one inland genus. Only genera from each family are used to calculate the final totals for each region. See supplementary tables for detailed information. PA: Palaearctic; NA: Nearctic; NT: Neotropical; AT: Afrotropical; OL: Oriental; AU: Australasian; PAC: Pacific & Oceanic Islands; ANT: Antarctic

| | PA | NA | NT | AT | OL | AU | PAC | ANT | Total inland genera |
|---|---|---|---|---|---|---|---|---|---|
| **Lepidomysidae | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| **Stygiomysidae | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| **Mysidae | 13 | 6 | 4 | 1 | 5 | 1 | 0 | 0 | 23 |
| *Rhopalophthalminae | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| *Mysinae | 13 | 6 | 4 | 1 | 4 | 1 | 0 | 0 | 22 |
| °Heteromysini | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| °Leptomysini | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 2 |
| °Mysini | 13 | 4 | 3 | 1 | 4 | 0 | 0 | 0 | 19 |
| Total | 15 | 7 | 6 | 1 | 6 | 1 | 0 | 0 | 25 |

*Note*: Several genera occur in more than one geographical region, resulting in higher numbers of occurrences (36) than inland genera (25)

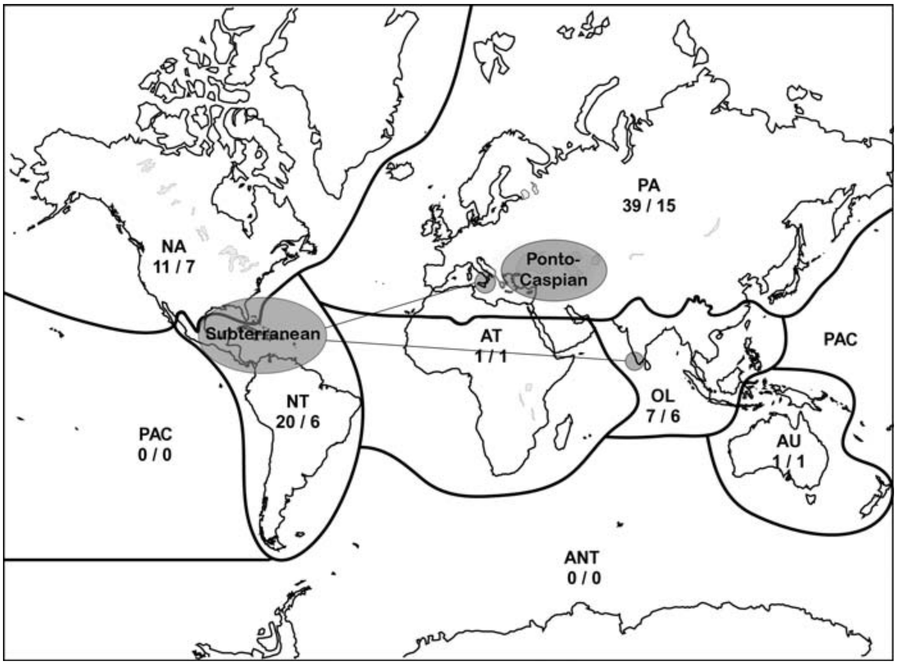


**Fig. 2** Biogeographic regions indicating the numbers of inland mysid species and genera (SP/GN) found in each: PA—Palaearctic; NA—Nearctic; NT—Neotropical; AT—Afrotropical; OL—Oriental; AU—Australasian; PAC—Pacific; ANT—Antarctica; Grey circles indicate areas of high biodiversity, i.e., the Ponto-Caspian region and the distribution of Lepidopmysidae and Stygiomysidae continental subterranean species (lines connect disjunct regions of occurrence)

account for a large percentage of mysid species diversity.

## Tethyan subterranean relicts

All of the subterranean/groundwater mysid genera considered here (*Antromysis* —6 spp., *Spelaeomysis*—7 spp., *Stygiomysis*—5 spp., and the monotypic *Troglomysis vjetrenicensis*) are found in a distributional pattern suggesting a Tethyan origin, likely colonizing groundwater habitats due to the uplift and stranding of marine ancestors during Miocene regressions of the Tethys and Mediterranean seas (Boxshall & Jaume, 2000). These hypothesized Tethyian dispersal events resulted in ancient mysid genera successfully colonizing early regions of Central America, the Caribbean, and Indian and Mediterranean basins, resulting in widespread genera that were later isolated, and presently represented by species often endemic to a single groundwater system. Additionally, the surface genera *Parvimysis* (2 spp.) and *Surinamysis* (3 spp.), distributed in the Caribbean and South America, are closely related to the genus *Antromysis* and may also be a part of this Tethyan distribution.

## Autochthonous Ponto-Caspian endemics

The Ponto-Caspian basin, consisting of the Black, Azov, and Caspian Seas, is composed of inland seas with complex geological histories dating back to the Paratethys Sea (20 Mya), including periods as lacustrine environments (Banarescu, 1991). The Ponto-Caspian mysid fauna (autochthonous + 'glacial relicts', see below) are generally considered the center of inland mysid species diversity. The autochthonous mysids that evolved in these enclosed continental basins, occur in fresh and brackish water portions of the basins including rivers, lakes, and estuaries, and are endemic to one basin or are found in parts of all three (Table 3). Although this fauna consists of seven genera and 20 species, a large portion of the endemic mysid diversity in these basins is the result of a radiation in the genus *Paramysis* (Table 3).

In a phylogeographic study of *Limnomysis benedeni* and six *Paramysis* species across the Ponto-caspian region (Audzijonytë et al., 2006), three main patterns were identified: (1) no deep subdivisions across the entire region, (2) genealogical splits matching geographical borders among basins, and (3) divergent lineages occurring only within the Caspian. The discordant molecular subdivisions among these co-distributed mysid species suggest that the similar zoogeographic patterns were formed at different times (Audzijonytë et al., 2006).

**Table 3** List of species endemic to the Black, Azov, and Caspian Seas, including the occurrence in each basin (data from Audzijonytë, 2006). In addition to the species counted here, there are at least four additional endemic Ponto-Caspian mysids (*Diamysis mecznikovi, Hemimysis serrata*, *Paramysis agigensis*, *Paramysis pontica*) whose distributions are unclear or do not occur in freshwaters and therefore have not been included in the species list

| | Black Sea | Azov Sea | Caspian Sea |
|---|---|---|---|
| 'Glacial-relict' | | | |
| *Mysis amblyops* | | | × |
| *Mysis caspia* | | | × |
| *Mysis macrolepis* | | | × |
| *Mysis microphthalma* | | | × |
| Autochtonous Ponto-Caspian | | | |
| *Caspiomysis knipowitschi* | | | × |
| *Diamysis pengoi* | × | | |
| *Diamysis pusilla* | | | × |
| *Hemimysis anomala* | × | × | × |
| *Katamysis warpachowsky* | × | × | × |
| *Limnomysis benedeni* | × | × | × |
| *Paramysis baeri* | × | × | × |
| *Paramysis eurylepis* | | | × |
| *Paramysis grimmi* | | | × |
| *Paramysis incerta* | | | × |
| *Paramysis inflata* | | | × |
| *Paramysis intermedia* | × | × | × |
| *Paramysis kessleri* | × | | × |
| *Paramysis kosswigi* | × | | |
| *Paramysis kroyeri* | × | | |
| *Paramysis lacustris* | × | × | × |
| *Paramysis loxolepis* | | | × |
| *Paramysis sowinskii* | | × | × |
| *Paramysis ullskyi* | × | × | × |
| *Schistomysis elegans* | | | × |

## *Mysis* 'glacial relicts'

The genus *Mysis* comprises 14 species, of which eight have inland freshwater distributions and can be divided into two groups: (1) The *M. relicta* group (*M. relicta, M. diluviana, M. salemaai, M. segerstralei*) with a circumpolar distribution from boreal and subarctic lakes of the previously glaciated areas of Europe and North America (Audzijonytë & Väinölä, 2005), and (2) four Caspian Sea endemics (Table 3). Phylogenetic analyses indicate that the inland *Mysis* species are a monophyletic assemblage, sister to circumarctic marine species (Audzijonytë et al., 2005). The separation of freshwater/continental *Mysis* spp. and circumarctic marine species is estimated to have taken place 3–7 Mya (Audzijonytë et al., 2005), and does not correspond to the timing in general hypotheses of continental invasions, such as mid-Pleistocene glaciation events or mid-Tertiary separation of the Arctic and Caspian basins (see Väinölä, 1995). Furthermore, molecular divergences among the boreal Nearctic (*M. diluviana*) and Palearctic (*M. relicta, M. salemaai*, *M. segerstralei*) species and the Caspian endemics indicate inland colonizations occurring at different times (Audzijonytë & Väinölä, 2006). *M. relicta* and *M. diluviana* are considered the oldest of *Mysis* freshwater species that independently colonized their respective European and American ranges during early Pleistocene (Väinölä et al., 1994). In contrast, *M. salemaai* and *M. segerstralei* are younger closely related species that have penetrated freshwaters more recently (Audzijonytë & Väinölä, 2006). As for the four endemic Caspian *Mysis* species, small molecular divergences suggest a recent, possibly late Pleistocene, sympatric radiation, possibly driven by adaptation to a deep pelagic habitat by *M. amblyops* and *M. microphthalma* (Väinölä, 1995; Audzijonytë et al., 2005).

### Euryhaline estuarine fauna

Most of the remaining mysids (20 spp., 14 genera) are euryhaline species with at least one population occurring in marginal freshwaters. These species have only very recently invaded freshwaters in portions of their distributions.

## Phylogeny

The taxonomic position and phylogenetic affiliations within the Mysida are currently under debate. Historically, the Mysida were considered members of the crustacean superorder Peracarida, placed as a sister taxon to the Lophogastrida in the order Mysidacea. More recently, molecular studies have led to raising the Mysida (and Lophogastrida) to ordinal rank (Spears et al., 2005). With respect to those families containing inland fauna, there is also taxonomic and phylogenetic uncertainty. For example, molecular and morphological data show that the subterranean family Stygiomysidae is more closely related to the order Mictacea than to other Mysida families, suggesting that they be removed from the order Mysida and placed within a separate order, Stygiomysida, comprising the families Stygiomysidae and Lepidomysidae (Meland & Willassen, 2007).

## Conservation issues

At least 19 inland mysid species are associated with groundwater habitats (caves, wells, and crab burrows) having very limited areas of distribution that are highly susceptible to pollution from the surface. These species in particular are in need of assessment for conservation ranking, as they are often found in aquifers important to local communities as a source of freshwater and may serve as indicators of water quality. Many freshwater mysid species have also served an important role in both US and European fisheries, where they have been introduced into lakes and reservoirs to serve as food for commercially important fish species (Mordukhai-Boltovskoi, 1979; Northcote, 1991).

In contrast, the autochthonous Ponto-Caspian mysids are currently invading aquatic ecosystems of Northern Europe as a result of human activities (De Vaate et al., 2002; Leppakoski et al., 2002). The impact of invasive mysid species on native lacustrine and riverine ecosystems can be large, including a severe reduction in zooplankton abundance, with concomitant negative effects on higher consumers (Spencer et al., 1991; Ketelaars et al., 1999).

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