

Global diversity of shrimps (Crustacea: Decapoda: Caridea) in freshwater

S. De Grave · Y. Cai · A. Anker

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Abstract Freshwater caridean shrimps account for approximately a quarter of all described Caridea, numerically dominated by the Atyidae and Palaemonidae. With the exception of Antarctica, freshwater shrimp are present in all biogeographical regions. However, the Oriental region harbours the majority of species, whilst the Nearctic and western Palaearctic are very species-poor. Many species are important components of subsistence fisheries, whilst the Giant River Prawn forms the basis of an extensive aquaculture industry. A total of 13 species are threatened or endangered, with one species formally extinct.

Keywords Caridea · Decapoda · Freshwater · Biodiversity

Introduction

The suborder Caridea presently consists of approximately 2,500 described species in 31 families. They occur in all aquatic habitats on the planet, from pelagic marine species and those dwelling in anchialine caves through to freshwater species. A total of 655 freshwater species (just over a quarter of all described carideans) are presently known. Amongst the freshwater families, the two most speciose are the near exclusively freshwater Atyidae and the Palaemonidae (Subfamily Palaemoninae), which also have brackish water and marine representatives. Freshwater shrimps occur in a vast range of habitats, from torrential mountain streams down to sluggish, oligohaline waters. Freshwater stygobiont taxa are well represented, with many more taxa occasionally found in subterranean habitats (see Holthuis, 1986). Atyidae are characterised by unique feeding chelipeds, with the complex brushes on the first and second pereopods (Fig. 1A) filtering out suspended matter or sweeping up microbial films (Fryer, 1977). Members of the Palaemonidae exhibit a wide variety in habitus, from the unspecialised habitus of *Palaemonetes* species through to the males of *Macrobrachium*, which have unusually enlarged second chelae (Fig. 1B), used in agonistic interactions and

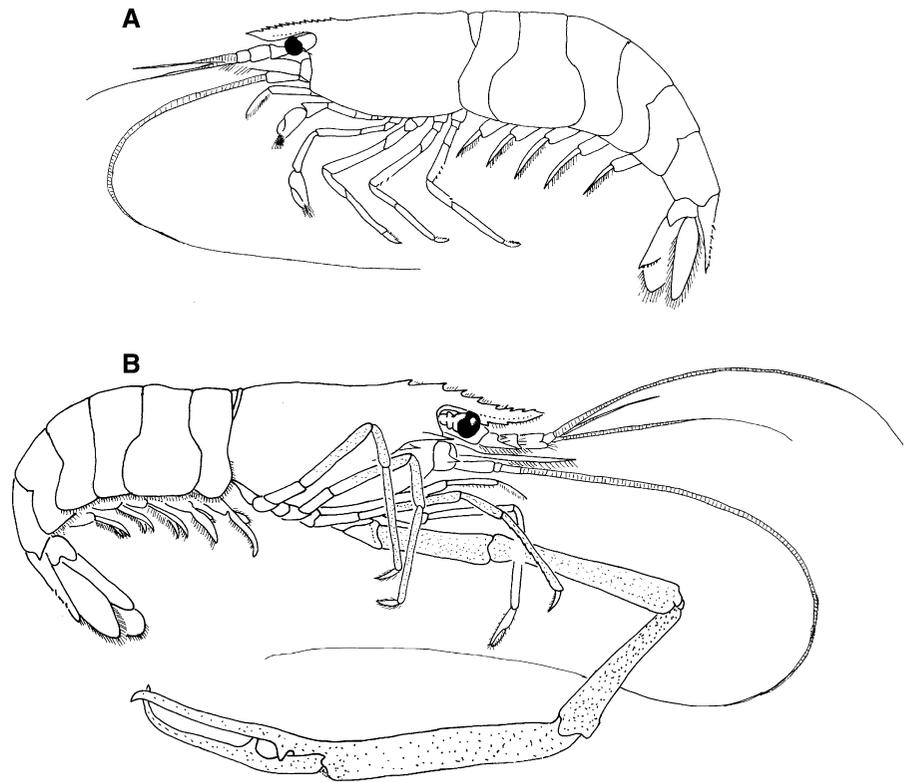
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Freshwater Animal Diversity Assessment

S. De Grave (✉)
Oxford University Museum of Natural History,
Parks Road, Oxford OX1 3PW, UK
e-mail: sammy.degrave@oum.ox.ac.uk

Y. Cai
Biodiversity Centre, National Parks Board,
1 Cluny Road, Singapore 259569,
Republic of Singapore
e-mail: caiyixiong@yahoo.com

A. Anker
Smithsonian Tropical Research Institute, Naos Unit 0948,
APO AA, Miami, FL 34002-0948, USA
e-mail: anker@si.edu

Fig. 1 Habitus of (A) *Caridina weberi* De Man, and (B) *Macrobrachium lar* (Fabricius)



predation. Many freshwater taxa are important as sources for artisanal fisheries (Holthuis, 1980), with one species, *Macrobrachium rosenbergii* (De Man), being an important aquaculture species. Freshwater species are also becoming increasingly popular in the aquarium trade. Abbreviated larval development occurs in many species of Atyidae and freshwater Palaemoninae, with members of *Neocaridina* having completely lost larval development, hatching as post larvae. Although abbreviated larval development allows these species to complete their life cycle in freshwater, many other species of both families complete part of their larval cycle in brackish water or even in fully marine conditions.

Species diversity

Freshwater species of carideans belong to eight families/subfamilies, numerically dominated by the Atyidae, with 359 species/subspecies (Table 1). Although this family is considered in many textbooks as restricted to freshwater habitats, some anchialine genera are known (e.g. *Antecaridina*, *Halocaridina*,

Typhlatya), whilst juveniles of *Atya* have been found under fully marine conditions in Atlantic waters. Although the most speciose genus *Caridina* occurs in six biogeographic regions, many genera and species are either only known from their type locality or have a narrow geographical distribution (e.g. *Lancaris* is restricted to Sri Lanka, see Cai & Bahir, 2005). Some species are morphologically adapted to live in fast-flowing water, such as the Caribbean *Atya scabra* (Leach), which lives beneath rocks under waterfalls and in rapids, whilst other species, such as many *Caridina* species are adapted to lakeshore weed beds, usually displaying a more gracile habitus. Cave dwelling taxa are well represented with many exclusively stygobiont genera. Of particular ecological interest are the only two freshwater commensal species (a widespread mode of life in marine shrimp species): *Limnocaridina iridinae* Roth-Woltereck from the mantle cavity of a unionid clam from Lake Tanganyika (Roth-Woltereck, 1958) and a *Caridina* species from Lake Towuti in Sulawesi living with freshwater sponges (Cai, pers. obs.).

The second most speciose family is the Palaemonidae (Table 1), with many more marine and brackish

Table 1 Geographical distribution of freshwater Caridea described up to December 2005

Family/Subfamily	PA	NA	NT	AT	OL	AU	PAC	ANT	World
<i>Species + subspecies</i>									
Alpheidae	–	–	1	1	2	–	–	–	4
Atyidae	31	4	19	59	209	55	13	–	359
Desmocarididae	–	–	–	2	–	–	–	–	2
Kakudicarididae	–	1	–	–	–	2	–	–	3
Palaemonidae	13	12	83	28	138	30	12	–	276
Euryrhynchinae	–	–	4	2	–	–	–	–	6
Typhlocaridinae	3	–	–	–	–	–	–	–	3
Xiphocarididae	–	–	2	–	–	–	–	–	2
Total	47	17	109	92	349	87	25	–	655
<i>Genera</i>									
Alpheidae	–	–	1	1	1	–	–	–	2
Atyidae	9	2	5	11	13	11	4	–	35
Desmocarididae	–	–	–	1	–	–	–	–	1
Kakudicarididae	–	1	–	–	–	2	–	–	3
Palaemonidae	4	2	9	2	7	2	2	–	13
Euryrhynchinae	–	–	1	2	–	–	–	–	3
Typhlocaridinae	1	–	–	–	–	–	–	–	1
Xiphocarididae	–	–	1	–	–	–	–	–	1
Total	14	5	17	17	21	15	6	–	59

Note that the family Typhlocarididae is divided into two subfamilies: Typhlocaridinae and Euryrhynchinae. PA: Palaearctic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, OL: Oriental, AU: Australasian, PAC: Pacific Oceanic Islands, ANT: Antarctic

water species known than there are freshwater taxa, all of the latter being restricted to the subfamily Palaemoninae. The numerically dominant genus is *Macrobrachium*, restricted to fresh and brackish water except for the enigmatic, single record of an undescribed species from Canadian waters. Other species-rich genera are *Palaemonetes*, a taxonomically poorly defined world-wide genus, and *Palaemon*. Some species of *Palaemonetes* are exclusively freshwater, such as the North American *Palaemonetes kadakiensis* Rathbun, but several estuarine species can tolerate fully freshwater conditions. Several species of *Palaemon* have also been recorded from marine, brackish and freshwater environments, e.g. *Palaemon concinnus* Dana (see Marquet, 1991).

Fewer species are known in the near exclusively freshwater Typhlocarididae (one species being anchialine). The Typhlocarididae comprises two subfamilies, the monogeneric stygobiont Typhlocaridinae, and the Euryrhynchinae with representatives in South America and West Africa. Although the Alpheidae are

one of the most species-rich shrimp families, a few freshwater species are known. Some members of the genus *Potamalpheops* and *Alpheus cyanoteles* Yeo & Ng occur in freshwater, with several other species either tolerating seasonally fresh water or occurring in oligohaline waters.

It is difficult to estimate the true species richness of freshwater shrimps, as every year new taxa continue to be described, mainly in the two most numerically dominant genera, *Caridina* and *Macrobrachium*. As a result, species discovery curves are not flattening out (Fig. 2), and it can be expected that many more species await discovery. New genera also continue to be erected, for instance for morphologically disparate species previously placed in *Caridina* (e.g. the genera *Lancaris*, *Sinodina*, *Paracaridina*). Genetic studies have only recently started in freshwater shrimps, with for instance the work of Baker et al. (2004) highlighting the presence of several cryptic lineages in Australian *Paratya*, some of which may well represent true species.

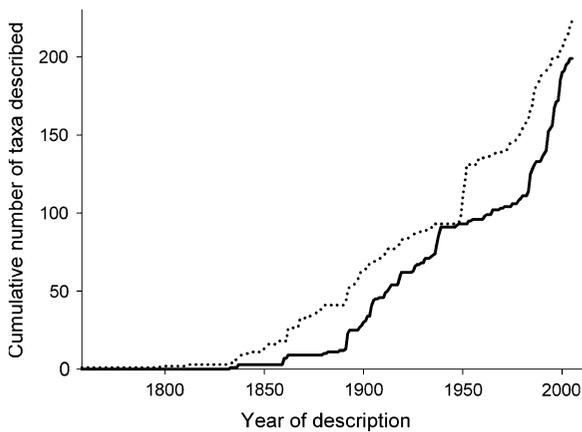


Fig. 2 Rates of discovery for the two most species-rich genera of freshwater shrimp, *Caridina* (full line) and *Macrobrachium* (dotted line)

Phylogeny and historical processes

In common with the remainder of the Caridea, very little can be said on the phylogeny of freshwater shrimps, mainly due to the paucity of higher level cladistic and genetic studies, with the study of Pereira (1997) being the sole exception for freshwater taxa. This study clearly highlighted the non-monophyletic status of many of the palaemonid genera, recently

also suggested by genetic work (Murphy & Austin, 2005).

It is however evident that, at a minimum, three invasions of freshwater must have taken place, as palaemonoid, atyoid and alpheoid shrimps are not closely related. Several lines of evidence, including the occurrence of freshwater fossils of Cretaceous age (Beurlen, 1950) testify that Atyidae are ancient inhabitants of freshwater, having diverged early from an ancestral marine stock (Fryer, 1977). The origin of *Macrobrachium* has been suggested to be in the late Oligocene or early Miocene (Short, 2004; Murphy & Austin, 2005), although there are evidence that multiple invasions of freshwater are involved (Pereira, 1997; Murphy & Austin, 2005).

Present distribution and main areas of endemism

With the exception of Antarctica, freshwater carideans shrimps are present in all the main biogeographical regions (Fig. 3). The Oriental region harbours three times as many species as the next most species-rich provinces: Neotropical, Afrotropical and Australasian. The Nearctic region harbours the lowest number of taxa, primarily due to the absence of

Fig. 3 Geographical distribution of species/subspecies and genera described up to December 2005 (Species number/Genus number), coded according to the main zoogeographic regions. PA: Palearctic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, OL: Oriental, AU: Australasian, PAC: Pacific Oceanic Islands, ANT: Antarctic

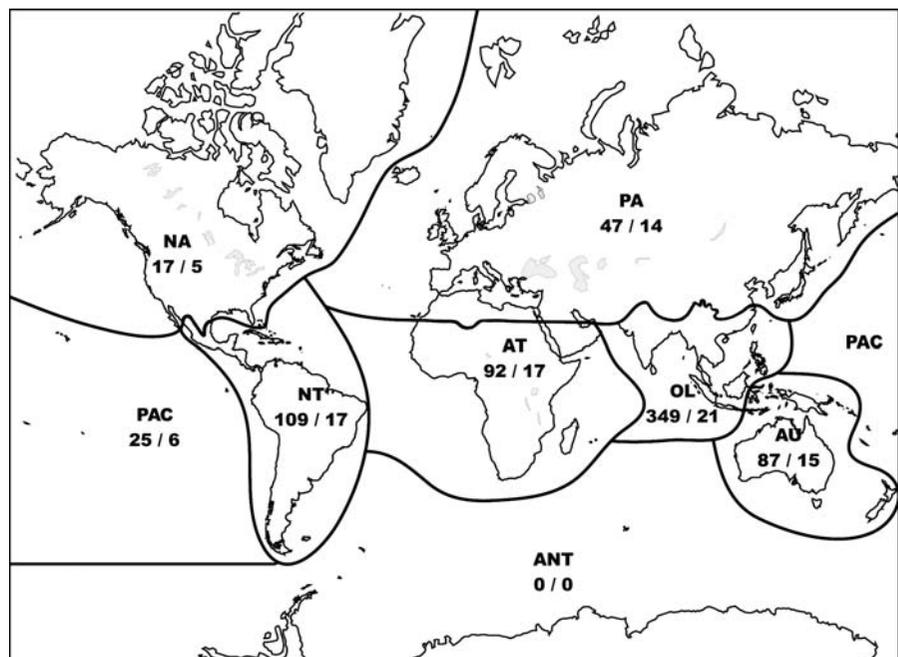


Table 2 Geographical distribution of troglobitic freshwater species of Caridea described up to December 2005

Family/Subfamily	PA	NA	NT	AT	OL	AU	PAC	ANT	World
Atyidae	13	2	–	10	6	11	1	–	43
Kakudicarididae	–	1	–	–	–	–	–	–	1
Palaemonidae	–	2	15	–	4	1	–	–	22
Typhlocaridinae	3	–	–	–	–	–	–	–	3
Total	16	5	15	10	10	12	1	–	69

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

Caridina and the low number of *Macrobrachium* present. Although the Palaearctic region harbours 47 taxa, there is a marked discrepancy in species composition between the western and eastern Palaearctic, with no overlapping species distributions.

Interestingly, the number of troglobitic taxa is roughly similar across several of the main biogeographic regions (Table 2), although within each region they are not uniformly distributed. Within the Afrotropical region for instance, all except two species (*Caridina lovoensis* Roth-Woltereck from Zaire and *Caridina lanzana* Holthuis from Somalia) occur in Madagascar (Holthuis, 1986).

On a family level, the Atyidae are present in five biogeographic regions, but with very few representatives in the western Palaearctic, Neotropical or Nearctic regions. The only representatives of this family in the western Palaearctic are the genera *Atyaephyra*, *Typhlatya*, *Troglocaris* and *Dugastella*, with in addition *Caridina nilotica* occurring in Egypt. The atyid fauna of the Nearctic is very impoverished, with only four species in two genera (*Palaemonias*, *Syncaresis*), whilst the Neotropical fauna consists of 19 species, primarily of the genus *Atya*.

The family Palaemonidae also occurs in all six biogeographic regions, but with distinct generic level differences (Table 1). *Macrobrachium* exhibits its highest diversity in the Oriental region (123 species), with far fewer species occurring in the Neotropical (53 species) and the Australasian regions (28 species). Only three species occur in the Nearctic region, whilst the eastern Palaearctic only harbours four species and the Pacific region 10.

The Desmocarididae are restricted to West Africa (Powell, 1977), in contrast the Euryrhynchinae occur in Brazil (*Euryrhynchus*) and west Africa (*Euryrhynchina*, *Euryrhynchoides*) (Powell, 1976). The Xiphocarididae are restricted to the northern part of

the Neotropical region, chiefly being distributed in the Caribbean islands; whilst the Typhlocaridinae only occur in the western Palaearctic. Perhaps the most disjunct distribution on a family level is exhibited by the Kakaducarididae, with one troglobitic species, *Calathaemon holthuisi* (Streth), from Texas, and two epigeal species in Australia (*Kakaducaris glabra* Bruce, *Leptopalaemon gagudju* Bruce & Short) (see Bruce, 1993).

The majority of genera are restricted to a single biogeographical region, with some notable exceptions, primarily those genera with marine or anchialine representatives. For instance, *Potamalpheops* occurs worldwide, but the only freshwater representatives are found in Mexico, West Africa and Singapore (Anker, 2005). Similarly, *Typhlatya* is distributed on both sides of the Atlantic, although freshwater species are only found in Europe (Jaume & Bréhier, 2005). *Caridina*, *Macrobrachium*, *Neocaridina* and *Paratya* have representatives in adjacent parts of the Afrotropical/Oriental and/or Australasian/Pacific regions. The genus *Atya* has representatives on either side of the Atlantic (Hobbs & Hart, 1982), whilst the troglobitic genus *Parisia* occurs in Madagascar, Australia and the Philippines.

On a species level, few taxa are present in more than one biogeographical region. A suite of nine species is distributed from East Africa (Afrotropical) across the Oriental region through to the Australasian/Pacific regions. However, the taxonomic status of many of these populations may be in doubt. In addition, this includes species such as *Palaemon debilis* Dana and *P. concinnus*, both also recorded from marine and estuarine habitats (Chace & Bruce, 1993), and it remains unclear if these taxa are present in freshwater throughout their range. In addition, two species of *Atya* (*Atya gabonensis* Giebel, *Atya scabra*) are known from both sides of the Atlantic;

whilst there is some species overlap between the eastern Palaearctic and the north-eastern Oriental region.

On a more regional scale, several biodiversity hotspots emerge. Madagascar harbours 26 species of Atyidae, many of which are troglobitic; with just over three quarters of all species being endemic to the island. Of the 28 species of atyids reported from Sulawesi, half of them are endemic to the island group, with a further 14 undescribed species recently discovered from either cave habitats or in the ancient lakes of the Malii group. Although the Chinese fauna can still be considered imperfectly known, 136 taxa are known to occur, many of which are endemic to Hunan province (Liang, 2004). As the majority of newly described Atyidae are from China, many more species may await discovery. Although the total species richness of Lake Tanganyika and the Amazon region is relatively low, both areas are rich in endemic genera (*Limnocaridina*, *Caridella* and

Atyella in Lake Tanganyika, *Pseudopalaemon* and *Euryrhynchus* in the Amazon).

Human related issues

Holthuis (1980) listed 16 species of Atyidae and 61 species of freshwater Palaemonidae as either of commercial interest or forming an important component of subsistence fishing, especially in South America, Africa, the Far East and many Pacific islands. In addition, he noted that many, unidentified and probably mixed populations of small species of *Caridina* are heavily fished in the Philippines, China, Sulawesi, Madagascar and parts of the Ganges Delta. In the Philippines, these are eaten fresh or salted and made into a fermented product, called alamang.

The Giant River Prawn, *Macrobrachium rosenbergii*, is not only commercially fished within its native range (India to northern Australia), but also

Table 3 Species afforded special protection by IUCN or state legislation

Species	Distribution	IUCN status	Other
<i>Creaseria morleyi</i> (Creaser)	Mexico	–	Threatened
<i>Macrobrachium acherontium</i> Holthuis	Mexico	–	Special protection afforded
<i>Macrobrachium villalobosi</i> Hobbs	Mexico	–	Special protection afforded
<i>Neopalaemon nahuatlus</i> Hobbs	Mexico	–	In danger of extinction
<i>Palaemonias alabamae</i> Smalley	USA	Endangered	Listed as endangered in the Endangered Species Act, 1975
<i>Palaemonias ganteri</i> Hay	USA	Endangered	Listed as endangered in the Endangered Species Act, 1975
<i>Palaemonetes antrorum</i> Benedict	USA	Endangered	–
<i>Palaemonetes cummingsi</i> Chace	USA	Vulnerable	listed as threatened in the Endangered Species Act, 1975
<i>Stygiocaris lancifera</i> Holthuis	Australia	–	Likely to become extinct. Listed in the Wildlife Conservation (specially protected fauna) Notice 2003
<i>Syncaris pasadenae</i> (Kingsley)	USA	Extinct	–
<i>Syncaris pacifica</i> (Holmes)	USA	Endangered	listed as endangered in the US Endangered Species Act, 1975
<i>Troglocaris anophthalmus</i> (Kollar)	Former Yugoslavia and Italy	Vulnerable	–
<i>Troglomexicanus perezfarfanteae</i> (Villalobos)	Mexico	–	In danger of extinction

Three subspecies of *T. anophthalmus* are known, which are not distinguished in the IUCN list. The other category refers to local or state protection categories

forms the basis of intensive prawn farming since the 1960s, both in its native range and outside (e.g. Alaska, USA, Nicaragua). The annual production is estimated to be around 200,000 tonnes, worth about a billion dollars. Recently Chinese prawn farms have also begun culturing *Macrobrachium nipponense* (De Haan), whilst minor quantities of *Macrobrachium malcomsoni* (H. Milne Edwards) are commercially farmed in India.

Several species are now available in the freshwater aquarium trade, some of which are being specifically cultured for this purpose (Werner, 2003). At least 18 species of *Caridina*, *Neocaridina*, *Atya*, *Atyopsis*, *Atyoida* and *Macrobrachium* are now regularly offered for sale, mainly Asiatic species.

A total of 13 species have been either listed in the IUCN Red Data Book (2004 edition) or are otherwise afforded local or state protection (Table 3). With the exception of *Syncaris pasadenae* (Kingsley), all these taxa are stygobionts, many only known from a single cave or cave system, with these systems being under threat of human encroachment and ground water pollution. *Syncaris pasadenae* is the only shrimp species presently considered as extinct. Formally it occurred in a few streams in the Los Angeles area, but the species has not been found since 1933, despite extensive searches (Martin & Wicksten, 2004).

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