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FRESHWATER ANIMAL DIVERSITY ASSESSMENT

Global diversity of Isopod crustaceans (Crustacea; Isopoda) in freshwater

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Abstract The isopod crustaceans are diverse both morphologically and in described species numbers. Nearly 950 described species ($\sim$9% of all isopods) live in continental waters, and possibly 1,400 species remain undescribed. The high frequency of cryptic species suggests that these figures are underestimates. Several major freshwater taxa have ancient biogeographic patterns dating from the division of the continents into Laurasia (Asellidae, Stenasellidae) and Gondwana (Phreatoicidea, Protojaniridae and *Heterias*). The suborder Asellota has the most described freshwater species, mostly in the families Asellidae and Stenasellidae. The suborder Phreatoicidea has the largest number of endemic genera. Other primary freshwater taxa have small numbers of described species, although more species are being discovered, especially in the southern hemisphere. The Oniscidea, although primarily terrestrial, has a small number of freshwater species. A diverse group of more derived isopods, the 'Flabellifera' sensu lato has regionally important species richness, such as in the Amazon River. These taxa are transitional between marine and freshwater realms and represent multiple colonisations of continental habitats. Most species of freshwater isopods species and many genera are narrow range endemics. This endemism ensures that human demand for fresh water will place these isopods at an increasing risk of extinction, as has already happened in a few documented cases.

Keywords Isopoda · Crustacea · Gondwana · Laurasia · Diversity feeding · Reproduction · Habits · Fresh water · Classification

Introduction

The Isopoda are a diverse group of crustaceans, with more than 10,300 species found in all realms from the deepest oceans to the montane terrestrial habitats; approximately 9% of these species live in continental waters. Isopods are thought of as dorsoventrally flattened, and indeed many species fit this morphological stereotype. Diverse taxa found in the deep sea and those found in groundwater habitats depart considerably from this generalised body plan. Palaeontogical and phylogenetic evidence (Brusca & Wilson, 1991; Wilson & Edgecombe, 2003) suggests that the ancestral isopod may have had a narrow

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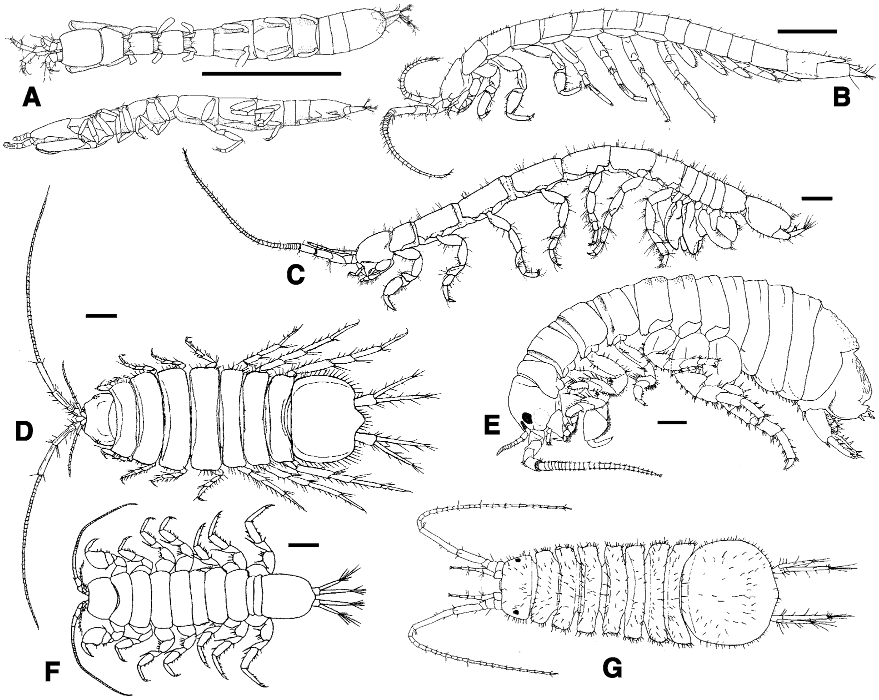

Fig. 1 Freshwater Isopoda, a selection of body forms. (**A**) Microcerberidae sp. (interstitial, Western Australia), dorsal and lateral view; (**B**) *Pygolabis* sp., Tainisopidae (hypogean, Western Australia); (**C**) *Phreatoicoides gracilis*, Hypsimetopidae (epigean, Victoria Australia); (**D**) *Asellus aquaticus*, Asellidae (epigean, Europe, from Sars 1897); (**E**) *Eophreatoicus* sp., Amphisopidae (epigean, Northern Territory Australia); (**F**), *Stenasellus chapmani*, Stenasellidae (hypogean, Indonesia, from Coineau et al. 1994; (**G**) *Heterias* sp., Janiridae (hyporheic & pholoteric, South America; from Bowman et al. 1987). Scale bars 1 mm, except for A, 0.5 mm

vaulted body with legs projecting ventrally (Fig. 1E, *Eophreatoicus*, Amphisopidae). Freshwater taxa include either typical flattened isopods (Fig. 1D, F, G) or narrow body forms (Fig. 1B, C, E), along with a few taxa that are thin and vermiform, often with legs that emerge close to the dorsal surface (Fig. 1A). Other peculiarities of isopods include respiration using their broad posterior limbs (swimming legs or pleopods) with the heart positioned in the posterior part of the body, and biphasic moulting, wherein the back part of the body is cast off before the anterior part. Limb forms are diverse in the isopods, but the first walking leg (second thoracic limb) is modified for grasping in most species.

Feeding

Isopods have a broad range of feeding types from omnivory in Sphaeromatidae to carnivory in the Cirolanidae. Oniscideans and Asellidae are well-known as leaf litter shredders and have bacterial endosymbionts to aid digestion (Zimmer, 2002, Zimmer & Bartholme, 2003). Tainisopidae may be carnivorous scavengers because they can be captured using baited traps. Most freshwater isopods (e.g. Asellota or Phreatoicidea) can be characterised as generalised detritivores-omnivores, but may facultatively choose other items. Phreatoicideans feed on decaying vegetation and roots, or perhaps the microflora and microfauna associated with these substrates (Wilson & Fenwick, 1999), but on occasion will engage in carnivory. Among the 942 described species found in continental waters, the presumptive feeding types (based on extrapolation from taxa where habits are known) are as follows: 3.2% are carnivores, 6.9% scavenger-carnivores, 9.9% ectoparasites, 0.4% herbivores, 6.1% omnivores and the remaining 73.5% are detritivores-omnivores, mostly Asellota and Phreatoicidea.

Reproduction

Isopods, like all peracarid crustaceans, have direct development with the young brooded in a ventral pouch until they are released as small adults. Isopods have internal fertilisation (Wilson, 1991) that occurs prior to the release of embryos into the marsupium, unlike other peracarid crustaceans. Brood sizes range from 4–5 young in tiny interstitial isopods to hundreds in the parasitic forms, and lifetime reproduction may be limited to one or several broods in most species (Johnson et al., 2001). Many isopods, especially the suborders Asellota and Oniscidea, have secondary sexual features for intromission in both males and females that are also useful for systematics. Brooding of the young, direct development and internal fertilisation may be major contributory factors in the high degree of endemism observed in most isopod taxa (Wilson, 1991).

Habitats

Isopods occur in epigean lotic and lentic habitats (e.g. Asellidae like the common European *Asellus aquaticus* and Phreatoicidae in Tasmania), but many live in a variety of subterranean habitats. The Microcerberidae are found interstitially in freshwater or marine sands. Many families are limited to cavernicolous or subterranean habitats, such as Stenasellidae, Microparasellidae, or Tainisopidae. North American and European members of the Asellidae can be both epigean and hypogean (e.g. Turk et al., 1996; Lewis & Bowman, 1981). Some taxa (e.g. Hypsimetopidae or *Heterias*, Janiridae) could best be described as infaunal, living in near subsurface habitats, either burrowing among submerged roots, living in submerged burrows of other animals (pholoteros) or in the subsurface water of streams (hyporheos). A few isopods occur in unusual habitats, such as *Thermosphaeroma thermophilum* in hot springs of the USA southwest. Some oniscideans, which are ordinarily terrestrial, have re-invaded the continental saline waters (e.g. *Haloniscus searlei*) or even normal freshwater (e.g. Trichoniscidae and Styloniscidae). Australian collection records suggest that some Philosciidae and Trichoniscidae may be amphibious (see also Taiti & Humphreys, 2001; Tabacaru, 1999).

Methods

(See additional information on the article webpage). The biodiversity of freshwater isopods is derived from my research on the Phreatoicidea and Asellota, and from the online "World List of Isopoda" (Kensley et al., 2005). The classification is derived from that list (*not* as in Banerescu, 1990), but includes the informal taxon 'Flabellifera' sensu lato (see Wilson, 1999). The World List uses the traditional classification of the 'Flabellifera' that is known to be paraphyletic (Brusca & Wilson, 1991; Wägele, 1989; Tabacaru & Danielopol, 1999). The Microcerberidea includes two families, Microcerberidae and Atlantasellidae (*not* Asellota as in Banarescu, 1990; Wägele, 1983; Jaume, 2001). The peculiar family Calabozidae is classified as Oniscidea owing to its possession of in-group genitalia and coxal plates incorporated into the body (Brusca & Wilson, 1991). Marine species, including those from anchialine cave and marine beach interstitial environments, were filtered out of the downloaded list, either using the type habitat from the list or by consulting the original literature. The data included species from saline continental waters, such as *Haloniscus*. Subspecies records were treated as species-level taxa. Undescribed species (e.g. *Heterias* species) known to me were added to the list where possible, although less than 100 species were added. An estimate of the unknown species was determined for the Phreatoicidea (Wilson in progress; see supplementary information), and information from Gouws et al. (2004, 2005). A diversity estimate for other isopod groups used the simple known to unknown ratio from the Phreatoicidea as applied to the other taxa (Table 1). Although the assumption of similarity between Phreatoicidea and other freshwater isopods has obvious problems, this procedure at least provides an hypothesis for further refinement.

Species diversity

Of the entirely freshwater isopods (marked with an asterisk in Table 1), the Asellota has the most of the 942 described species, with the largest number of species in the family Asellidae, followed by the Stenasellidae. The Phreatoicidea have at least four families with many undescribed species (see Table in supplementary information) that may double the number of described species. Other freshwater families have small numbers of described species, although more species are being discovered as surveys are carried out in the southern hemisphere. The Protojaniridae are tiny and fragile, and may require specialised techniques to recover them from hypogean habitats; 12 species in five genera are described, but more remain to be found. Recently,

Table 1 Species Diversity of Freshwater Isopoda. Estimation method and classification explained in text and supplementary material (see additional information)

Suborder	Family	Species, described and new	Estimated unknown species	Estimated total diversity
PHREATOICIDEA Stebbing, 1893	*Amphisopidae Nicholls, 1943	36	48	84
	*Hypsimetopidae Nicholls, 1943	11	19	30
	*Incertae sedis (*Crenisopus*)	1		1
	*Phreatoicidae Chilton, 1891	49	71	120
	*Ponderellidae Wilson & Keable, 2004	2		2
Subtotal, used for estimates other suborders		99	138	237
Unknown to Known ratio 1.39				
ASELLOTA Latreille, 1803	*Asellidae Rafinesque-Schmaltz, 1815	379	529	908
	Janiridae G. O. Sars, 1897	76	106	182
	Microparasellidae Karaman, 1933	73	102	175
	*Protojaniridae Fresi, Idato & Scipione, 1980	15	21	36
	*Stenasellidae Dudich, 1924	73	102	175
MICROCERBERIDEA Lang, 1961	Microcerberidae Karaman, 1933	21	30	51
ONISCIDEA Latreille, 1803	*Calabozoidae Van Lieshout, 1983	2	3	5
	Philosciidae Kinahan, 1857	1	2	3
	Scyphacidae Dana, 1852	5	7	12
	Trichoniscidae Sars, 1899	1	2	3
‘FLABELLIFERA’ sensu lato	Aegidae Leach, 1815	1	2	3
	Anthuridae Leach, 1814	19	27	46
	Bopyridae Rafinesque-Schmaltz, 1815	33	46	79
	Cirolanidae Dana, 1852	65	91	156
	Corallanidae Hansen, 1890	4	6	10
	Cymothoidae Leach, 1818	51	72	123
	Entoniscidae Kossmann, 1881	4	6	10
	Idoteidae Samouelle, 1819	4	6	10
	Leptanthuridae Poore, 2001	3	5	8
	Paranthuridae Menzies & Glynn, 1968	1	2	3
	Sphaeromatidae Latreille, 1825	57	80	137
	*Tainisopidae Wilson, 2003	7	10	17
	Total	994	1395	2625

(*Entirely freshwater families)

J. Pérez-Schultheiss in Chile sent specimens of a new protojanirid; another new species is known from northern Australia. The application of “known to unknown” estimates from the Phreatoicidea to the other freshwater isopods results in 62% more than those known, or approximately a total of 2,630 species (Table 1).

Evidence from molecular studies suggest that this estimate could be highly conservative. RAPD (random amplified polymorphic DNA) studies on both species of Asellidae and Stenasellidae (Baratti et al., 1999; Verovnik et al., 2003) have uncovered previously unsuspected diversity in well-known populations of *Stenasellus* and *Proasellus*. Similar results have been obtained from studies of genetic variation using enzymatic loci (*Proasellus*: Ketmaier, 2002) or the mtDNA cytochrome oxidase I gene (CO-I) (*Stenasellus*: Ketmaier et al., 2003). Cryptic species in the epigean phreatoicidean genus *Mesamphisopus* (Gouws et al., 2004, 2005) could include between 15–20 species in South Africa (G. Gouws pers. comm.). Four new Tainisopidae species of the hypogean genus *Pygolabis* (Keable & Wilson, 2006) from the Pilbara region of Western Australia are morphologically similar and difficult to identify, but their species concepts are supported by CO-I studies (C. Francis pers. comm.). These results suggest that freshwater isopods have many more species-level taxa than the current list might suggest.

Phylogeny and historical patterns

Isopods that live in freshwater may be divided into two groups based on their presumptive age and adaptation to fresh water. The first group contains exclusively freshwater higher-level taxa (i.e., families) that are named 'primary freshwater.' Several entirely freshwater families of Asellota, and the entire suborder Phreatoicidea are considered 'primary freshwater.' Both subordinal taxa are ancient, with originations in the Palaeozoic (Wilson, 1999) and both are derived basally in most phylogenies of the Isopoda, owing to their lack of specialised broad coxal plates (Brusca & Wilson, 1991) and other derived features that characterise the remainder of the Isopoda (Wägele, 1989). The 'secondary freshwater' group are those higher level taxa that have members ranging from marine to freshwater habitats. The secondary freshwater groups are in the process of evolving freshwater habits, and have marine representatives at a low taxonomic level (i.e. within the same family or genus).

The transition from marine to freshwater habitats is repeated independently in all isopod groups, and obligate freshwater adaptations appear at different phylogenetic levels. For example, the Palaeophreatoicidae, an extinct Palaeozoic family of the Phreatoicidea, were marine or possibly estuarine, while the fossil *Protamphisopus*, which is classified among the crown group phreatoicideans, appears in freshwater lacustrine Triassic facies (Wilson & Edgecombe, 2003). The Asellota have both freshwater and marine taxa but do not fossilise, so whether the ancestor was freshwater or marine is not directly determinable. Several diverse higher-level asellote taxa are strictly freshwater (Asellidae, Stenasellidae, Protojaniridae). Henry & Magniez (1995) proposed that independent clades of Asellidae evolved from separate marine ancestors. No marine asellid taxa, however, are known in the modern fauna, so this hypothesis remains untested. The Microcerberidae was argued by Wägele et al. (1995) to be primitively freshwater, but this hypothesis is unparsimonious (Wilson, 1996). Wägele (1983) highlighted similarities of Microcerberidae and Atlantasellidae (known only from insular marine caves; Jaume, 2001), such as the coxal plates or spines on the anterior pereonites. These plates, found also in marine microcerberids, are plesiomorphic at the family-level because they are present in both families. Finding interstitial microcerberids with coxal spines on continental Australia (Fig. 1A) suggests that these marine taxa have colonised freshwater independently in different parts of the world. Their freshwater distribution pattern is similar to 'Flabellifera' sensu lato and Oniscidea (Fig. 2).

The remainder of the isopods, the terrestrial isopods (Oniscidea) and the 'Flabellifera' sensu lato, are derived much later in phylogenetic estimates (Wägele, 1989; Brusca & Wilson, 1991; Tabacaru & Danielopol, 1999), and the fossil record of modern families does not begin until the middle to late Mesozoic or later, with few peculiar taxa possibly related to modern families appearing in the Triassic (e.g. Guinot et al., 2005). The Oniscidea, although terrestrial, have their least-derived taxa living on marine seashores, and have a few freshwater taxa. Among these later-derived, secondarily freshwater taxa, some genera may be found in either fresh or saline waters, or are clearly transitional, like the bopyrid genus *Probopyrus* that parasitises members of the estuarine and freshwater decapod family Palaemonidae. The peculiar aquatic family Calabozidae is exclusively freshwater, but may be derived from terrestrial ancestors (Brusca & Wilson, 1991).

The Australian family Tainisopidae, among the higher isopods, lacks known marine or estuarine representatives. All of its species are hypogean, narrow range endemics, and retain isopod plesiomorphies lost by other 'Flabellifera' *sensu lato*. Whether this family should be classified as 'secondary' or 'primary' freshwater depends on its phylogenetic relationships relative to the remainder of the Isopoda. These relationships, however, are still controversial, with two competing subordinal placements in the literature (Wilson, 2003; Brandt & Poore, 2003).

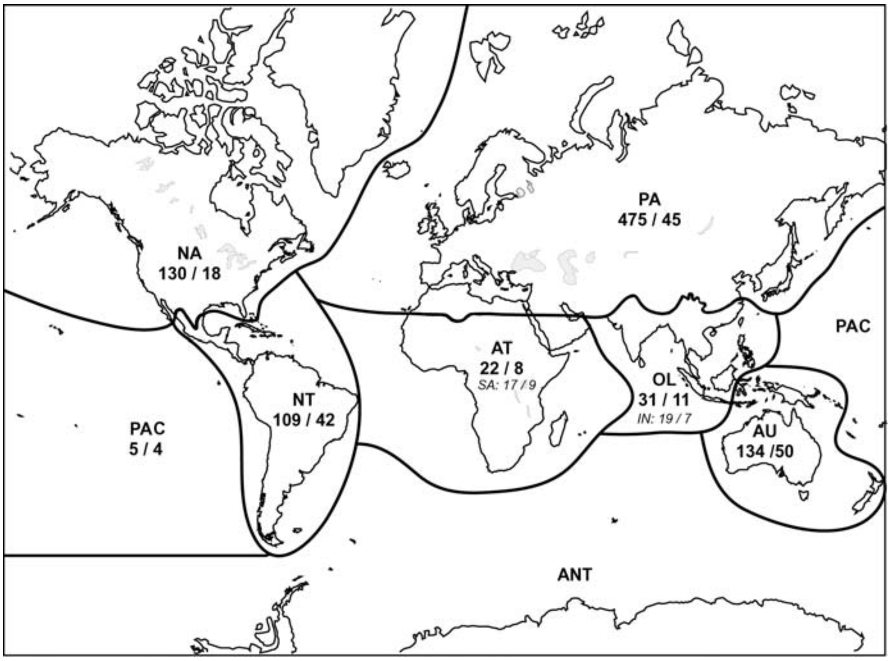

Fig. 2 Distribution of freshwater Isopoda species and genera by zoogeographical region (species number/genus number). Regional abbreviations, with Gondwanan subareas shown separately in parentheses: PA, Palaearctic; NA, Nearctic; NT, Neotropical; AT(SA), Afrotropical (South African); OL (IN), Oriental (Indian); AU, Australasia; PAC, Pacific Oceanic Islands; ANT, Antarctic. Only described species included

Several marine Asellota ancestors may have colonised freshwaters late in Pangean times, and subsequent independent evolution gave rise to two freshwater groups, the Laurasian Asellidae and Stenasellidae and the Gondwanan Protojaniridae (see next section). Where the asellotan genus *Heterias*, found on continents South America, Australia and New Zealand, fits into this picture will ultimately depend on the resolution of the phylogeny of the Janiridae. The presence of *Heterias* and the Protojaniridae on fragments of Gondwana argues for independent freshwater colonisation events, as the two taxa are distinct and not closely related (Wilson, 1987). The ancestral Asellota may have been diverse prior to the break-up of Gondwana, because at least four distinct lineages gave rise to fresh water taxa. If this is the case, then the Asellota has a minimum age of Triassic.

Endemicity and distribution

Except for a few widespread species like *Asellus aquaticus* or epiparasitic *Tachea* species, most species of freshwater isopods are narrow range endemics. Thus all areas in Table 3 are made up of species found only on one landmass, with patterns reflecting, at least partially, sampling effort. Generic endemism (Table 4) is similarly high, with only a few secondary aquatic taxa like *Probopyrus* (Bopyridae) or *Gnorimosphaeroma* (Sphaeromatidae) appearing on more than one continent. Genera counted in Table 4 are mostly unique to fresh water, even in the secondarily aquatic groups. Surprisingly, Australia has the highest number of genera even though the largest number of species is found in the Palaearctic, where more research has been done. This pattern arises because, in addition to different taxonomic styles among asellotan and phreatoicidean workers, speciose genera (such as *Asellus*) are widespread in Eurasia while Australian genera have highly restricted ranges, on scales of 10^{0-2} km. In the northern hemisphere, glaciation, which had much less impact in the south, may have had the dual role of pruning the fauna of rare unique taxa (thus decreasing generic diversity) as well as providing a rich environment for speciation, with multiple opportunities for diversification during the advance and retreat of the ice caps (Magniez, 1974). Several phreatoicidean genera are more widespread, such as the speciose *Colubotelson*, which can be found in most freshwater bodies in Tasmania and upland springs in Victoria, and the genus *Crenoicus*, which is characteristic of highland bogs and springs on the Great Dividing Range. But these taxa are the exception rather than the rule, probably attesting to

Table 2 Geographic partitioning of freshwater isopod species diversity

Suborder region	PA	NA	NT	AT(SA)	OL(IN)	AU	PAC	World
Asellota Latreille, 1803	384	120	7	19(8)	13(4)	6	2	563
'Flabellifera' sensu lato	82	9	96	3(2)	17(13)	25	2	249
Microcerberidea Lang, 1961	8	1	4	(3)	(1)	4		21
Oniscidea Latreille, 1803	1		2			5	1	9
Phreatoicidea Stebbing, 1893				(4)	(2)	94		100
Regional total	475	130	109	22(17)	31(19)	134	5	942

Regional abbreviations, with Gondwanan subareas shown separately in parentheses: PA, Palaearctic; NA, Nearctic; NT, Neotropical; AT(SA), Afrotropical (South African); OL (IN), Oriental (Indian); AU, Australasian; PAC, Pacific Oceanic Islands. Only described species included

Table 3 Geographic partitioning of freshwater species diversity in the suborder Asellota

Family region	PA	NA	NT	AT(SA)	OL(IN)	AU	PAC	World
Asellidae Rafinesque-Schmaltz, 1815	265	112	1		1			379
Janiridae G. O. Sars, 1897	19		1	1		3		24
Microparasellidae Karaman, 1933A	65		3			2	2	72
Protojaniridae Fresi, Idato & Scipione, 1980			2	(8)	(4)	1		15
Stenasellidae Dudich, 1924	35	8		18	12			73
Regional Total	384	120	7	19(8)	13(4)	6	2	563

See Table 2 for regional abbreviations

Table 4 Geographic partitioning of freshwater isopod generic diversity

Suborder region	PA	NA	NT	AT (SA)	OL (IN)	AU	PAC	World
ASELLOTA Latreille, 1803	26	11	5	6(3)	2(2)	3	1	59
'FLABELLIFERA' sensu lato	15	6	32	2(2)	8(4)	13	2	84
MICROCERBERIDEA Lang, 1961	3	1	3	(3)	1	1		12
ONISCIDEA Latreille, 1803	1		2			4	1	8
PHREATOICIDEA Stebbing, 1893				(1)	(1)	29		31
Regional Total	45	18	42	8(9)	11(7)	50	4	194

See Table 2 for regional abbreviations. Gondwanan areas in parentheses

the geological history of Australia as an arid continent, with patchy epigean sources of water and extensive marine transgressions during the Mesozoic era that transformed the continent into a series of smaller islands (Wilson & Johnson, 1999). The secondary freshwater taxa seem to be patchily spread across the continents, representing either sampling effort or pecularities of the region. The Amazon and other major rivers of South America (Neotropics) are significant hot spots for the fish-parasitic group Cymothoidae, with more than 40 species in this family alone. This result may reflect the diversity of their hosts in this region (see Chapt. 43).

The distribution of the freshwater isopods on the continental scale shows significant non-random patterns (Tables 2, 3, 4; Fig. 2) among the more ancient groups. The Asellotan families Asellidae and Stenasellidae conversely show a Laurasian pattern, with no species occurring among known terranes of Gondwana. A single species of *Caecidotea* (Asellidae) has been reported from the highlands of Guatemala (Argano, 1977), but this record may be the southern limit of a Nearctic pattern for the genus. The Stenasellidae have numerous African records, and scattered records among Oriental and southern margins of North America. This pattern appears to be

Tethyan, but more detail is needed on the phylogeny of the Stenasellidae and Asellidae before a historical biogeographical assessment can be made. The Phreatoicidea have a strictly Gondwanan pattern (Wilson & Edgecombe, 2003), and occur only in the terranes of Gondwana, including South Africa, India and Australia-New Zealand. Since the ancestors of the freshwater Asellota and the Phreatoicidea were marine and possibly cosmopolitan in the Palaeozoic, these patterns may be interpreted as the result of colonisation of freshwaters, with subsequent extinction in marine waters. Some Asellota also show a Gondwanan pattern. The family Janiridae, which is known to be non-monophyletic (Wilson, 1994), contains a diverse group of transitional freshwater and marine taxa (best exemplified by the European genus *Jaera*). Among these taxa, the southern hemisphere genus *Heterias* occurs in Australia and in South America (Wilson & Wägele, 1994). *Heterias* species are diverse in southern Australian hyporheos and pholeteros, and recently they have been found in New Zealand by Dean Olsen. The Protojaniridae are strictly freshwater and occur on terranes derived from Gondwana. These observations could be related to rareness and sampling bias, but documented effort in the northern hemisphere argues that this pattern is real. Until recently, protojanirids were only known from Sri Lanka and South Africa, but undescribed species have been found recently in Australia and in Chile Fig. 3.

Human related issues

As more human demand on water resources impacts all parts of the world, we can expect that freshwater isopods will become increasingly at risk of extinction. A point made above, that most species of freshwater isopods are short-range endemics, comes to the foreground in our consideration of human impacts. Wherever small endemic populations of isopods occur, human over-exploitation of water may be a threat to their continued survival. Almost certainly, phreatoicidean species have become extinct owing to water and land use practises in Australia. For example, the artesian spring at the type locality of

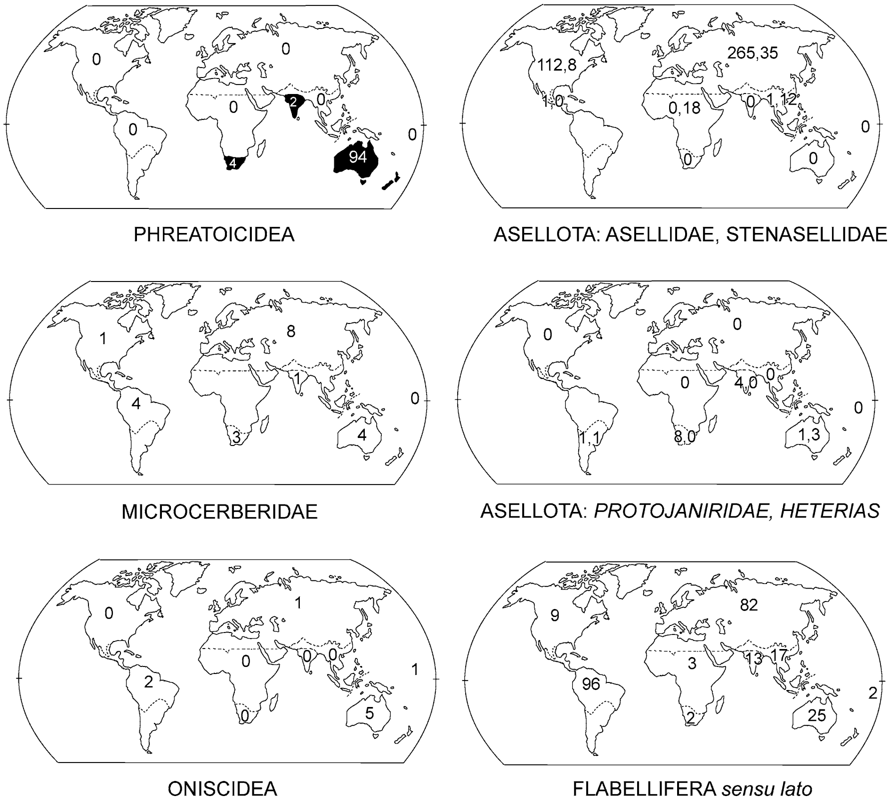

Fig. 3 Global distribution of freshwater isopod diversity. The areas are marked as in Tables 3–5. The darkened areas on the Phreatoicidean map indicate Gondwana biogeographic regions. Not all Asellota shown

Phreatomerus latipes, a bore at Hergott (Maree) in South Australia, has become extinct, presumedly along with the unique population of this isopod species (W. Ponder pers. comm.). Land clearing in the last 200 years along the Great Dividing Range in New South Wales are likely to have been responsible for the extinction of many *Crenoicus* species, by causing the disappearance of the highland springs and *Sphagnum* bogs where they occur. The genus type species, *C. mixtus* is probably extinct because the springs that supplied water to the town of Ballarat (Nicholls, 1944), where this species lived, are now occupied by a large dam and surrounded by a pine plantation. The risks for epigean species are more easily assessed than for the hypogean species, because the latter may be easily collected. Phreatobitic species are only collected from springs, wells, bores and caves, but these animals are clearly adapted to living deep underground in narrow cracks and crevices, where we have little chance to discover their true distribution. As a result, we have great difficulties for assessing the risk to these species where human activities over-exploit the subterranean aquifers. As discussed above, genetic studies show that each restricted aquifer can have an isolated and phylogenetically unique population. As a result, conservation activities for such hypogean species must understand the hydrology of the region, and assessments of their populations must continue while water is being used. To do otherwise is to risk the loss of a substantial component of the regional phylogenetic diversity.

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