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FRESHWATER ANIMAL DIVERSITY ASSESSMENT

Global diversity of amphipods (Amphipoda; Crustacea) in freshwater

R. Väinölä · J. D. S. Witt · M. Grabowski · J. H. Bradbury · K. Jazdzewski · B. Sket

Abstract Amphipods are brooding peracaridan crustaceans whose young undergo direct development, with no independent larval dispersal stage. Most species are epibenthic, benthic, or subterranean. There are some 1,870 amphipod species and subspecies recognized from fresh or inland waters worldwide at the end of 2005. This accounts for 20% of the total known amphipod diversity. The actual diversity may still be several-fold. Amphipods are most abundant in cool and temperate environments; they are particularly diversified in subterranean environments and in running waters (fragmented habitats), and in temperate ancient lakes, but are notably rare in the tropics. Of the described freshwater taxa 70% are Palearctic, 13% Nearctic, 7% Neotropical, 6% Australasian and 3% Afrotropical. Approximately 45% of the taxa are subterranean; subterranean diversity is highest in the karst landscapes of Central and Southern Europe (e.g., Niphargidae), North America (Crangonyctidae), and Australia (Paramelitidae). The majority of Palearctic epigean amphipods are in the superfamily Gammaroidea, whereas talitroid amphipods (*Hyalella*) account for all Neotropic and much of the Nearctic epigean fauna. Major concentrations of endemic species diversity occur in Southern Europe, Lake Baikal, the Ponto-Caspian basin, Southern Australia (including Tasmania), and the south-eastern USA. Endemic family diversity is similarly centered in the Western Palearctic and Lake Baikal. Freshwater amphipods are greatly polyphyletic, continental invasions have taken place repeatedly in different time frames and regions of the world. In the recent decades, human mediated invasions of Ponto-Caspian amphipods have had great impacts on European fluvial ecosystems.

Keywords Biogeography · Continental invasions · Endemism · Gammaridea · Malacostraca · Species diversity

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Freshwater Animal Diversity Assessment

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Introduction

Amphipods are an order of macroscopic crustaceans of the class Malacostraca. Along with the isopods, cumaceans, mysids, and tanaidaceans they belong to the superorder Peracarida, whose life cycle is characterized by direct development and no independent larval stage. Amphipod females carry their embryos in a brood chamber between the thoracic legs (pereiopods). When released, the juveniles reach maturity after several molts, without any metamorphosis.

The amphipod body is segmented throughout and usually laterally compressed, with a more or less curved or hook-like profile (Fig. 1). Amphipods generally have a pair of sessile lateral compound eyes, but most subterranean species and some that inhabit deep waters are eyeless. Adult body lengths of freshwater species range 2–40 mm, most commonly between 5 and 15 mm.

Most amphipods are marine, but they also inhabit a wide spectrum of freshwater habitats. Freshwater taxa are particularly diversified in relatively cool running waters and subterranean habitats. The number of benthic burrowing (fossorial) species is relatively low, but they may be abundant in large lakes and estuaries. Epibenthic taxa are more diverse, and are usually associated with the littoral vegetation of lakes and rivers and bottom matrix of small streams and springs. Some taxa are nektobenthic, whereas pelagic and parasitic or commensal species are rare in freshwaters, unlike in the seas. There is also a widespread family of terrestrial amphipods (talitrids).

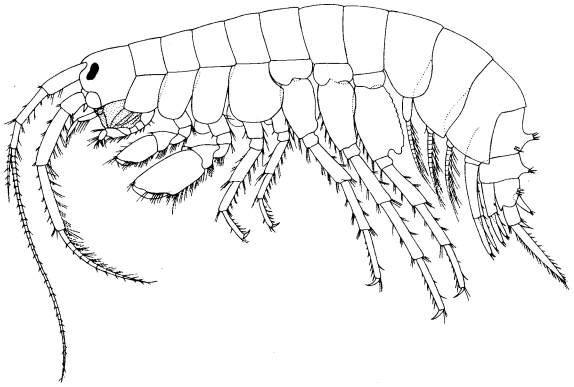

Fig. 1 Outline of an amphipod, *Dikerogammarus oskari* Birstein (size ca. 20 mm; from Barnard & Barnard, 1983). The head is followed by 7 + 3+ 3 pereional + pleonal + urosomal segments. The appendages shown include antennae 1 and 2, mandibular palp, maxillipede, gnathopods 1 and 2 (=pereiopods 1,2), pereiopods 3–7, of which two are directed backwards, three forwards (hence, *amphi podos*, or both legs), three pleopods, and finally three uropods and a terminal telson

Amphipods are among the most diverse hypogean animal groups overall (Sket, 1999), and hypogean taxa account for approximately 45% of freshwater amphipod species. These troglobiotic (stygobiotic) species and races are generally characterized by the loss of eyes and pigmentation, and by elongation of the trunk and/or appendages (troglomorphy). In karst environments or lava fields they inhabit systems of flooded fissures and caverns. Interstitial groundwater taxa are also included in the hypogean component; they are generally slender and small in size. In many areas hypogean taxa can only be accessed through wells and surface springs.

Amphipod feeding habits are diverse; they can be herbivores, detritivores, carnivores, or omnivores. Most subterranean species are supposedly omnivorous, and even when predatory, they indirectly depend on organic debris derived from surface environments. Amphipods can be important in the diets of fish, and frequently serve as intermediate hosts of their parasites. They often play a critical role in aquatic food webs, acting as conduits of nutrients and energy to higher trophic levels.

Species diversity

Data composition

This survey of world amphipod species diversity covers taxa that can complete their life cycles in true fresh waters, and also taxa native to brackish or saline inland water bodies permanently disconnected from the ocean (e.g., the Caspian Sea). We do not include taxa from anchihaline habitats directly connected to the sea, such as marginal marine caves, or those in beach interstitial waters, whereas taxa noted from slightly brackish wells (inland) have been included. Estuarine taxa are also excluded if they do not have landlocked freshwater populations. The interpretation in several cases was necessarily subjective or arbitrary due to incomplete environmental data available. Only taxa properly described by the end of 2005 are counted; no distinction is made between species and subspecies.

The data were compiled in geographical sections by the individual authors (see electronic appendix).

Where available, recent published reviews or web resources covering geographical regions (e.g., Griffiths & Stewart, 2001; Fenwick, 2001; Kamaltynov, 2002; Lowry & Stoddart, 2003) or family or genus level taxa were used in the first place (e.g., Koenemann & Holsinger, 1999; Zhang & Holsinger, 2003; Vonk & Schram, 2005; Fišer et al., 2005). For the remaining hypogean groups, *Stygofauna Mundi* (Botosaneanu, 1986) was taken as an authoritative baseline; Barnard & Barnard's (1983) comprehensive account of freshwater amphipod diversity described prior to 1980 was used as the starting point for others. A listing of new amphipod taxa described in 1974–2004, compiled by Vader (2005a) and based on his continued bibliographical monitoring in *Amphipod Newsletter* vol. 11–30, was used as a principal pointer to newer data.

Numbers of taxa: systematic account

Our total count of continental amphipod species in this inventory is 1,870, of which 145 are listed as non-nominate subspecies (Table 1). This accounts for 20% of the ca. 9,100 amphipods known worldwide according to Vader (2005a, b). The continental taxa are distributed in 53 families and 293 genera (Tables 2, 3), but only 27 families are strictly limited to continental waters. Given some 180 amphipod families recognized globally, the continental and strictly continental families respectively represent 29% and 15% of overall family diversity. The family concepts applied here are in some cases narrower than those in Martin and Davis (2001), including e.g., the new families in Kamaltynov (2002).

Barnard & Barnard (1983) enumerated 1,088 freshwater amphipod species that had been described by June 1979; a decade later the count was at 1,195 (Barnard & Karaman, 1991). Our total continental number represents an increase of 70% over the past 26.5 years, which is somewhat more than that from 6,200 to 9,100 over a similar period for all amphipods (Vader 2005b).

The higher-level systematics of amphipods remains confused, and no convincing phylogenetic hypothesis has been presented (e.g., Barnard & Karaman, 1991; Bousfield & Shih, 1994; Martin & Davis, 2001; Myers & Lowry, 2003). Yet, freshwater amphipods can be broadly discussed in terms of superfamily groups (Table 1; modified from Bousfield, 1983, Bousfield & Shih, 1994), each with a characteristic biogeography and freshwater history. Note however that the superfamily or even family concepts used are not always unequivocal; the divisions are here adopted for pragmatic reasons and are not meant as a taxonomic statement.

Gammaroids (ca. 800 spp. in continental waters) are widespread across the Holarctic, and account for most of the Palearctic epigean diversity. The distribution of the Gammaridae (304) and the genus *Gammarus* itself (204) are similarly broad, centered in Europe but extending to China and North America; they also include taxa in coastal marine waters. Other families and genera are regional, e.g., endemic to the Ponto-Caspian basin (Pontogammaridae etc.), Lake Baikal, or as with Anisogammaridae, to the North Pacific involving both marine, coastal, and inland waters.

Crangonyctoids (341) are a widespread, exclusively freshwater group largely characteristic of subterranean habitats. Different families occupy the Northern and Southern Hemispheres. The Crangonyctidae (209) comprise the majority of North American freshwater amphipod diversity, but some species in the genera *Stygobromus, Synurella and Crangonyx* also occur in Eurasia. About 80% of species are hypogean, while others inhabit small epigean water bodies. Their sister family, the Pseudocrangonyctidae (16), inhabit East Asia (Holsinger, 1994). In the south, the Paramelitidae (69) is shared by Australia and South Africa, and a number of smaller families are endemic to New Zealand, Australia, Madagascar, and South Africa (Fig. 3). Species diversity is lower in the Southern Hemisphere, but much of the Australian diversity remains undescribed (Bradbury, unpubl.).

Niphargoids (319) are the most diverse Palearctic hypogean amphipods, and also include a few epigean taxa. They are distributed through central and particularly southeastern Europe, where they exhibit high levels of endemism in karst systems. *Niphargus* (305) is currently the largest freshwater amphipod genus (Fišer et al., 2005).

Talitroids of the genus *Hyalella* (58) are the only epigean freshwater amphipods in the Neotropics and important in the Nearctic. Talitroids (chiltoniins) are also present in Australasia. The majority of world terrestrial amphipods (about 250) are in the family Talitridae; few of them have entered fresh water.

Table 1 Numbers of described continental amphipod species (and subspecies) native in the major biogeographical regions, listed by family

Superfamily Family	Region							TOT	sspp	Ecology
	PA	NA	NT	AT	OL[e]	AU	PAC			
Crangonyctoidea										
Allocrangonyctidae*		2						2		H
Austroniphargidae*				3				3		E
Crangonyctidae*	25	184						209	6	H(e)
Crymostygiidae*	1							1		H
Neoniphargidae*[a]			2			23		25		H/E
Paracrangonyctidae*						2		2		H
Paramelitidae*				26		43		69		E/H
Perthiidae*						2		2		E
Phreatogammaridae*						4		4		E(h)
Pseudocrangonyctidae*	16							16		H(e)
Sternophysingidae*				8				8		H(e)
Gammaroidea										
Acanthogammaridae*[b]	159							159	10	E
Baikalogammaridae*[b]	1							1		E
Eulimnogammaridae*[b]	122							122	8	E
Macrohectopidae*[b]	1							1		E(pelagic)
Micruropodidae*[b]	55							55	2	E
Pachyschesidae*[b]	16							16		E:p
Pallaseidae*[b]	22							22	1	E
Anisogammaridae	21	9						30		E
Behningiellidae*	4							4		E:p
Caspicolidae*	1							1		E:p
Gammaracanthidae	3	1						3		E
Gammaridae[c]	292	13						304	27	E(h)
Iphigenellidae*	1							1		E:p
Pontogammaridae*	66							66		E
Typhlogammaridae*	8							8		H
Niphargoidea										
Niphargidae*	319							319	80	H(e)
Bogidielloidea										
Artesiidae*		2						2		H
Bogidiellidae s.l.	38	1	34	6	6	1	1[d]	87	3	H
Corophioidea										
Aoridae	2				1			3		E
Corophiidae	10					1	2	13		E
Kamakidae	4							4		E
Photidae					1			1		E
Eusiroidea										
Calliopiidae	3							3		E
Eusiridae	5					4		9		E(h)

Table 1 continued

Superfamily Family	Region							TOT	sspp	Ecology
	PA	NA	NT	AT	OL[e]	AU	PAC			
Hadzioidea										
Hadziidae	14	12	33	3			1	63	4	H
Melitidae	2		1	1	6	15	4	29		H
Metacrangonyctidae	16		2					18		H
Pseudoniphargidae	50							50	1	H
Eoniphargids	2				1			3		H
Liljeborgioidea										
Sebidae		2						2		H
Salentinellidae	16							16	3	H
Lysianassoidea										
Lysianassidae			1					1		H
Uristidae	2							2		E
Oedicerotoidea										
Oedicerotidae	1				1			2	1	E
Paracalliopiidae						4		4		E
Pontoporeioidea										
Pontoporeiidae	2	1						3		E
Talitroidea										
Ceinidae						7		7		E/H
Hyalellidae* (Dogielinotidae)		8	51					58		E
Hyalidae				3				3		E/H
Talitridae	4	1			1	1	2	9		E(h)
Ingolfielloidea										
Ingolfiellidae	9		4	6				19		H
Metaingolfiellidae*	1							1		H
Total	1,319	236	128	56	17[e]	107	9 + 1[d]	1870	145	
	PA	NA	NT	AT	OL	AU	PAC	TOT	sspp	

PA—Palearctic, NA—Nearctic, NT—Neotropical, AT—Afrotropical, OL—Oriental, AU—Australasian, PAC—Pacific Islands: TOT—World). sspp: number of taxa listed as non-nominate subspecies, included in the total count. Ecology: E—epigean, H—hypogean, H(e)—predominantly hypogean (75–95% of described species hypogean), H/E—50–74% of species hypogean, E/H and E(h) correspondingly; p—parasitic or commensal. Asterisks (*) indicate families that live exclusively in fresh/continental waters (including the Ponto-Caspian basin)

[a] Includes falklandiellids (2 spp) of Falkland Islands. [b] Endemic Baikal families [c] Count includes *Sensonator valentiensis* (incertae sedis). [d] Includes the single species recorded from the Antarctic zone (Kerguelen). [e] The OL count excludes southern China, here included in PA instead

A number of additional superfamilies are present on several continents and distributed both in fresh, marine and interface habitats.

Most *bogidielloids* live in hypogean continental waters (89), fewer are marine. The distribution is almost worldwide, but diversity is centered around the Mediterranean and in continental South America, Mexico, and the West Indies. Notably the generic diversity is highest in the Neotropics while species diversity is highest in the Mediterranean area (Koenemann & Holsinger, 1999).

Hadzioids are primarily marine amphipods that have colonized fresh waters in several regions of the world. They are characteristic for the Caribbean region, the coastal Western Palearctic (Hadziidae, Pseudoniphargidae, Metacrangonyctidae), and Wes-

Table 2 Numbers of continental amphipod genera recorded in the major biogeographical regions

Superfamily Family	Region							TOT	sh	Endemism/distribution
	PA	NA	NT	AT	OL[d]	AU	PAC			
Crangonyctoidea										
Allocrangonyctidae*		1						1		
Austroniphargidae*				2				2		Madagascar
Crangonyctidae*	3	5						5	3	
Crymostygiidae*	1							1		Iceland
Neoniphargidae*[a]			2			8		10		Australia[a]
Paracrangonyctidae*						1		1		New Zealand
Paramelitidae*				3		13		16		
Perthiidae*						1		1		Australia
Phreatogammaridae*						1		1		New Zealand
Pseudocrangonyctidae*	2							2		East Asia
Sternophysingidae*				1				1		South Africa
Gammaroidea										
Acanthogammaridae*	39							39		Baikal
Baikalogammaridae*	1							1		Baikal
Eulimnogammaridae*	17							17		Baikal
Macrohectopidae*	1							1		Baikal
Micruropodidae*	5							5		Baikal
Pachyschesidae*	1							1		Baikal
Pallaseidae*	8							8		Baikal
Anisogammaridae	5	1						6		
Behningiellidae*	4							4		Ponto-Caspian
Caspicolidae*	1							1		Ponto-Caspian
Gammaracanthidae	1	1						1	1	“Glacial relict”
Gammaridae[b]	21	1						21	1	
Iphigenellidae*	1							1		Ponto-Caspian
Pontogammaridae*	22							22		Ponto-Caspian
Typhlogammaridae*	5							5		SE Europe
Niphargoidea										
Niphargidae*	9							9		West Palearctic
Bogidielloidea										
Artesiidae*		1						1		Texas
Bogidiellidae s.l.	6	1	16	3	3		1[c]	27	2	
Corophioidea										
Aoridae	1				1			1	1	
Corophiidae	2					1	2	4	1	
Kamakidae	1							1		
Photidae					1			1		
Eusiroidea										
Calliopiidae	2							2		
Eusiridae	2							2		

Table 2 continued

Superfamily Family	Region							TOT	sh	Endemism/distribution
	PA	NA	NT	AT	OL[d]	AU	PAC			
Hadzioidea										
Hadziidae	6	8	12	2			1	28	1	
Melitidae	2		1	1	3	5	4	11	2	
Metacrangonyctidae	3		1					3	1	
Pseudoniphargidae	2							2		
Eoniphargids	1				1			2		
Liljeborgioidea										
Sebidae		1						1		
Salentinellidae	2							2		SW Europe
Lysianassoidea										
Lysianassidae			1					1		
Uristidae	1							1		"Glacial relict"
Oedicrotoidea										
Oedicerotidae	1				1			2		
Paracalliopiidae						1		1		
Pontoporeioidea										
Pontoporeiidae	1	1						2		"Glacial relict"
Talitroidea										
Ceinidae						3		3		
Hyalellidae* (Dogielinotidae)		1	1					1	1	
Hyalidae				1				1		
Talitridae	2	1			[1]	[1]	1	3	1	
Ingolfielloidea										
Ingolfiellidae	1		1	4				5	1	
Metaingolfiellidae*	1							1		Italy
Total	185	23	35	17	10[d]	34	8 + 1[c]	293	16	
	PA	NA	NT	AT	OL	AU	PAC			

See Table 1 legend for general explanation. Sh: shared genera, i.e., those distributed in more than one region. Last column indicates regional endemism or distributional features; "glacial relicts"—Arctic marine genera present in boreal and Arctic lakes and/or the Caspian Sea

[a] Includes falklandiellids (2 spp. on Falkland Islands). [b] Count includes *Sensonator* (incertae sedis). [c] Includes the single species recorded from the Antarctic zone (Kerguelen). [d] The OL count excludes southern China, here attributed to PA (with mainly shared genera)

tern Australia (Melitidae). There are also significant numbers of taxa in subterranean marginal brackish or marine habitats, particularly in anchihaline caves on both coasts of the northern Atlantic and on oceanic islands.

Corophioids are primarily marine, burrowing and tube-building amphipods, which have penetrated epigean brackish (estuaries, lagoons) and freshwater environments repeatedly along continental margins (Kamakidae, Aoridae), and diversified in the Ponto-Caspian waters (Corophiidae).

Ingolfielloids comprise a few species overall (40 in total), but have an exceptional diversity of habitat preferences from the deep sea to high mountain riverine interstitial habitats, as well as other subterranean waters of fresh, brackish and marine continental habitats (Vonk & Schram, 2003, 2005). Ingolfielloids have a specialized vermiform morphology, and most of the 21 freshwater species are small (ca. 2 mm), except for a group of taxa in sub-Saharan Africa (10–20 mm). The distribution is generally spotty, with continental taxa in sub-equatorial Africa,

Table 3 Summary of described systematic diversity of continental amphipods, by major biogeographical regions

	Region								TOT
	PA	NA	AT	NT	OL	AU	PAC	ANT	
Number of species + subspecies	1319	236	56	128	17	107	9	1	1870
(including non-nominate sspp)	(138)	(5)		(2)					(145)
Proportion of world spp. + sspp.	70%	13%	3%	7%	1%	6%	0.5%		100%
Number of genera	185	23	17	35	10	34	8	1	293
Number of families	38	12	8	8	7	12	4	1	53
No. endemic (continental) families	16	2	2	–	–	4	–	–	24
No. species per genus	7	10	3	4	2	3	1	1	6.4
No. freshwater species per family	35	20	7	16	2	9	2	1	35.2
No. genera per family	5	2	2	4	1	3	2	1	5.5
Proportion of hypogean species	39%	70%	46%	61%	77%	53%	55%		46%
No. additional introduced species	3	1							

the Canaries, southern Europe, South America, and the Caribbean.

Several other families are typically marine and occasionally represented in fresh or continental waters by a few species, contributing much to family level diversity, but little to species diversity. These include the families Eusiridae, Hyalidae, Lysianassidae, Oedicerotidae, Pontoporeiidae, Sebidae, Uristidae etc. (see Table 1).

Phylogeny and historical processes

The higher-level classification and phylogenetic relationships among amphipods are in flux and not agreed upon (e.g., Martin & Davis, 2001). At the highest levels, amphipods are variously divided into three or four suborders. All freshwater amphipods are sometimes included in the suborder Gammaridea, which overall comprises the majority amphipod diversity (90–93%). Alternatively, either the ingolfielloids or corophioids are attributed different suborders (Ingolfiellidea, Corophiidea) (Barnard & Karaman, 1991; Myers & Lowry, 2003; Vonk & Schram, 2003). A robust hierarchical classification has been impeded by greatly mosaic (homoplastic) character distributions. Comprehensive phylogenetic analyses do not exist at this time, and the results from preliminary molecular work have been generally inconsistent with the previously proposed schemes (e.g., Englisch et al., 2003, Myers & Lowry, 2003; Macdonald et al., 2005). Amphipod fossils are rare and date no earlier than the Eocene, however the order is considered to be at least 250 Myr old, and on the basis of current biogeographic patterns, had diversified in fresh waters by the time Pangaea broke up 180 Myr ago (e.g., Bousfield, 1983).

Continental invasions

Freshwater amphipods are clearly polyphyletic; their evolution has involved repeated colonizations of continental habitats at different times and in different regions. Three salient historical freshwater patterns are recognizable in view of the continental paleogeographical evolution.

An ancient continental ancestry

An early widespread distribution on ancient landmasses is suggested particularly by the distribution of the Crangonyctoidea (Fig. 3). The nearly pancontinental, exclusively freshwater range suggests a Pangaean continental ancestry. Even the Holarctic family Crangonyctidae (and its individual genera) seem to have occupied Laurasia prior to the separation of Eurasia and North America in the late Mesozoic (Holsinger, 1994). The presence of the Paramelitidae in both Australia and South Africa suggests their ancestors occurred on Gondwanaland before its fragmentation in the Jurassic. The other major superfamily Gammaroidea is also typically continental, but only on land masses formerly part

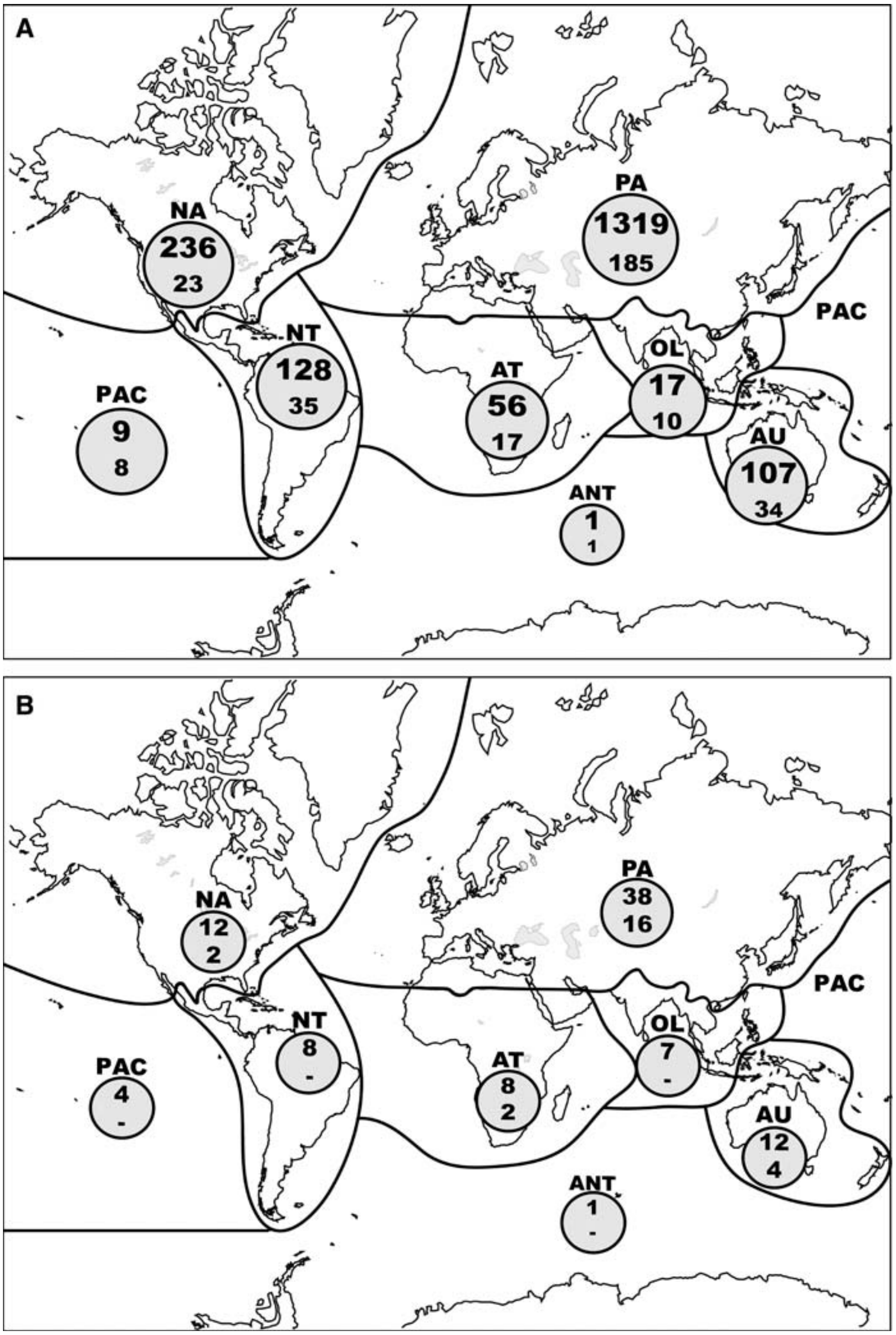

Fig. 2 Distribution of amphipod species, genera, families, and endemic families in inland waters of major biogeographical regions. (**a**) The total number of continental species and subspecies (upper number) and the number of genera (lower number); (**b**) Number of families encountered in continental waters (upper) and the number of continental families endemic to a given region. PA—Palearctic, NA—Nearctic, NT—Neotropical, AT—Afrotropical, OL—Oriental, AU—Australasian, PAC—Pacific Oceanic Islands, ANT—Antarctic

of Laurasia. However, they occur in both marine and inland waters, and continental invasions have taken place repeatedly. Yet the main gammaroid diversity throughout Eurasian continent, including the Gammaridae and the closely associated Baikalian and Ponto-Caspian family complexes, are thought to be of common continental origin and probably secondarily entered coastal seas (Barnard & Barnard, 1983; Macdonald et al., 2005).

Marine relict distributions

Hadzioids have a characteristic 'Tethyan belt' circum-temperate distribution, from Central America to

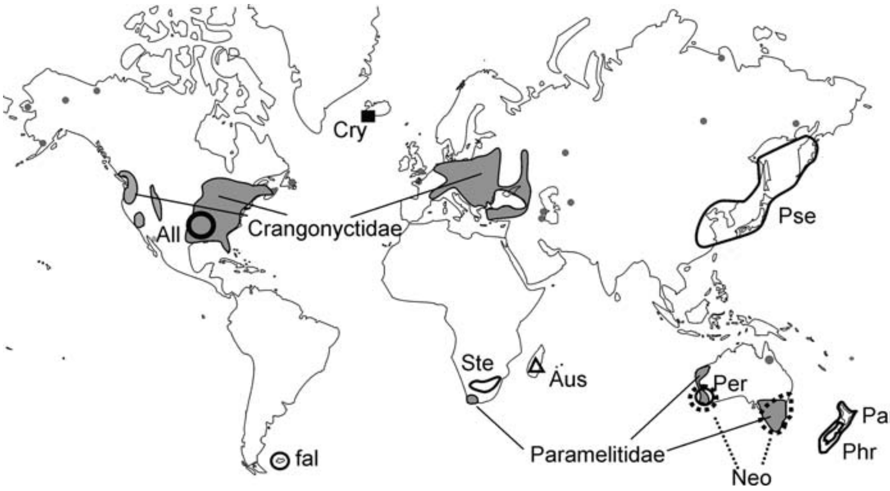

Fig. 3 Family level distributions of crangonyctoid amphipods (schematic). The exclusively freshwater superfamily Crangonyctoidea is thought to have a continental ancestry predating the break-up of Pangaea. The two families Crangonyctidae and Paramelitidae are still present on two continents, other families are endemic to single landmasses: All—Allocrangonyctidae, Aus—Austrocrangonyctidae, Cry—Crymostygiidae, fal—"falklandiellids", Neo—Neoniphargidae, Par—Paracrangonyctidae, Per—Perthiidae, Phr—Phreatogammaridae, Pse—Pseudocrangonyctidae, Ste—Sternophysingidae

the Mediterranean and SE Asia, and occur in both marine and freshwater environments. Their continental distribution in areas covered by shallow marine embayments of the Tethys in the Late Cretaceaous or Tertiary, and on oceanic islands uplifted during the same time frame, provides evidence for independent and old origins in different regions. The numerous hadzioids in marginal marine habitats, particularly anchialine caves, indicate that continental invasion is still an ongoing process (Holsinger, 1994). The bogidielloids have a similar overall distribution, but the question of primary versus secondary invasions is confused by their deep inland penetration of South America (Koenemann & Holsinger, 1999).

Distributional correlations with regional marine regressions suggest similar invasion histories in other, regional groups e.g., in the West Palearctic, but the ancestral relationships mostly remain unclear. Particularly enigmatic are the origins of the almost exclusively freshwater (only secondarily brackish) Niphargidae, diversified in the SE European karst areas that were still submerged in the Eocene, and that of Pseudoniphargidae in the Mediterranean and Central Atlantic islands. The continental vs. marine ancestry of the Ingolfiellidae also remains controversial (Vonk & Schram, 2003).

Recent continental invasions

Several epigean families that ordinarily occur in estuaries and lagoons have occasionally invaded continental waters, including the corophioideans, eusiroids, "glacial relict" pontoporeiids and gammaracanthids. These relatively recent (Neogene) invaders have not yet diversified in fresh waters, but in some cases their ranges are broad (Barnard & Barnard, 1983).

Present distribution and areas of endemism

Inter-continental patterns

Continental amphipods are typical of cool-temperate climates and are notably rare in the tropics. In warmer climates freshwater taxa still occur in subterranean environments where temperatures remain relatively cool. Diversity is also low in high northern latitudes that were directly affected by the Pleistocene glaciations, and have only recently been recolonized. Highest diversities are in the middle latitudes, e.g., the Mediterranean Europe, southern North America, or southern Australia.

The inter-continental distribution of amphipods is remarkably uneven. The Palearctic harbors 70% of described freshwater species, the Nearctic 13%, Neotropics 7%, Australasia 6%, Afrotropics 3% (Table 2, Fig. 2a). Further exploration of the Australian, Nearctic and Neotropic faunas is expected to increase their share substantially. At the family level, the Palearctic harbors 38 families (72% of 53), while the Nearctic and Australasia possess 12 each (22%), and the remaining regions 4–8 (8–15%) (Table 3, Fig. 2b).

Family level endemism is also centered in the Palearctic, with 16 endemic freshwater families (mostly in the ancient lakes), whereas Australasia has 4, and the Nearctic and Afrotropics have each 2 (Table 3, Fig. 2b). Many of these families are local and contain only one or a few species, while others have undergone remarkable regional radiations (e.g., Niphargidae, Pontogammaridae, four Baikalian families). Only 3 of the 27 exclusively freshwater families are distributed on more than one continent (Crangonyctidae, Hyalellidae, Paramelitidae). Genus level inter-continental distributions are rare even in the less strictly continental groups (Table 2). The most widespread single freshwater species is *Gammarus lacustris*, which has a nearly circum-boreal range that also extends into southern Europe and central Asia.

Hotspots

The major centers of regionally endemic species diversity (speciation hotspots) are in Southern Europe, Lake Baikal, and the Ponto-Caspian region, all also rich in endemic families. Additional concentrations occur in Southern Australia (including Tasmania), and in karst regions of the eastern United States. These are treated under the major biogeographical subdivisions themselves below.

Afrotropics (AT)

There are almost no epigean freshwater amphipods in tropical Africa, including the rift valley lakes. However, South Africa harbors two important crangonyctoid families, the epigean Paramelitidae and the hypogean Sternophysingidae (Griffiths & Stewart, 2001), in addition to a peculiar group of large-bodied Ingofiellidae (Vonk & Schram, 2003). Some Bogidiellidae are recorded from NE Africa. Madagascar has an endemic epigean family, the Austroniphargidae, and single representatives of marine families have colonized inland waters of oceanic islands (Table 1).

The Palearctic (PA)

The large fauna of the Palearctic is treated in five (zoo)geographically distinct sections: the hotspots in the ancient Lake Baikal and the Ponto-Caspian, the remaining West and East Palearctic, and northern previously glaciated areas, which may be considered part of a Northen Holarctic province extending to North America.

West Palearctic

This area alone (Europe, Northern Africa, and the Near East) contains nearly half of the world's continental described amphipods (ca. 800 in all if the Ponto-Caspian is included). Hypogean species are in majority (ca. 500), and they also represent a notable number of families. Apart from the most diverse niphargids and pseudoniphargids, these include the similarly endemic salentinellids and typhlogammarids, as well as bogidiellids, hadziids, metacrangonyctids, melitids, gammarids, and crangonyctids. The diversity is concentrated in areas around the Mediterranean and West Atlantic, and in many cases related to the ancient marine regressions of the area. The epigean diversity is dominated by *Gammarus* (ca. 100) and *Echinogammarus* s.l. (60), the latter mainly consisting of localized species in the Mediterranean region.

East Palearctic

This fauna (ca. 150 spp.) is still incompletely characterized. *Gammarus* is the most diverse epigean genus along with the anisogammarid *Jesogammarus* in the east, and accompanied by some recent marginal marine crawl-outs such as kamakids (Barnard & Barnard, 1983). The hypogean fauna includes the endemic Pseudocrangonyctidae along with some bogidiellids along the Pacific margin, and gammarids in the continental interior. Note that the Palearctic species count here encompasses whole China, including some 30 spp. from its southern provinces (particularly Yunnan highland), which more generally would be included in the Oriental region, but in fresh waters are clearly associated with East Asia to the north (Banarescu, 1990).

Lake Baikal

Lake Baikal is the largest and oldest freshwater lake on earth and has an extremely rich endemic fauna; the documented diversity and endemicity are highest in the amphipods (Kozhova & Izmesteva, 1998). There are 363 endemic species and subspecies recorded within the lake itself and further 12 in the downstream watershed, representing 72 genera and 7 endemic families (Kamaltynov, 2002). From molecular data, the true species diversity appears still much higher (Väinölä & Kamaltynov, 1999). The spectacular diversity in size, shape, body armament, color, ecology, habitat, and life style involves many patterns that have parallels in marine systems but not in other fresh waters (e.g., Takhteev, 2000). Still the fauna has no evident recent marine affinities. The whole Baikalian diversity appears to be most closely related to, and derived from the Holarctic continental gammarids, particularly *Gammarus* (Englisch et al., 2003; Macdonald et al., 2005). At any rate the diversity appears relatively old and did not evolve in the current, Pleistocene type of environment (Väinölä & Kamaltynov, 1999). Some of the peculiarities include gigantism, extreme sexual dimorphism, a mysidiform morphology and life-style of a single dominant pelagic species, and a family specialized as brood parasites of other amphipods. A single Baikalian pallaseid species has naturally dispersed to boreal lakes in Northern Europe.

The Ponto-Caspian

The Caspian Sea in fact is the world's largest lake, though brackish (no outlet; salinity <13 ppt). The Ponto-Caspian basin also encompasses the Azov and Black seas (currently connected to the Mediterranean), and was derived from the Neogene epicontinental seas in the area (Paratethys; Dumont, 1998). The indigenous non-marine amphipod fauna comprises some 95 species from several lineages, 40 of them found in the Caspian alone (Mordukhai-Boltovskoi, 1969). Apart from the rich endemic radiation of Pontogammaridae there are three peculiar small families, with, e.g., commensal and parasitic species, and a flock of corophiids. The Caspian is also inhabited by a deepwater community of recent (Pliocene) Arctic marine immigrants. Only a few Ponto-Caspian species naturally occur outside of the region, but many have recently spread with man (see below).

The Holarctic North

The most salient geographical pattern in the diversity of both northern continents is that of a few widespread species in the north, and increasing diversity with narrower ranges toward the south. The previously glaciated, and hence recently (re)colonized regions are dominated by taxa with strong dispersal abilities, such as *Gammarus lacustris* and some North American *Hyalella* taxa, that can be dispersed short distances via waterfowl, and others that dispersed through the periglacial lakes that formed as the ice sheets retreated (*Monoporeia affinis, Gammaracanthus lacustris* and *Pallaseopsis quadrispinosa* in Europe, *Diporeia hoyi* in North America). Remarkably, a few taxa survived the glaciations in subterranean refugia (three *Stygobromus* spp. in North America, *Crymostygius thingvallensis* in Iceland and *Niphargus* spp. on the British Isles.

The Nearctic (NA)

The Nearctic fauna comprises 236 freshwater taxa, of which only 10% occur in regions affected by glaciations. Diversity in non-glaciated regions consists mainly of narrow endemics, often known only from a single locality. Two-thirds of the described Nearctic diversity is subterranean (Table 3).

The majority of described species are crangonyctoids, which have an ancient freshwater ancestry (see above). These are mainly troglobiotic, and even when epigean, they are often troglophilic (Holsinger, 1994; Zhang and Holsinger, 2003). Their diversity is highest in the karst landscapes of Eastern North America, and crangonyctoid taxa west of the Great Plains probably represent a more recent radiation (Holsinger, 1993). The talitroid genus *Hyalella* is also exclusively continental, but of South American origin. In addition to eight formally described North

American *Hyalella* taxa, molecular data have revealed tens of undescribed species. Several of these even occur in formerly glaciated areas (Witt & Hebert 2000), but the most extreme levels of local endemism were found in desert springs in California and Nevada, where most spring populations contain highly divergent lineages (Witt et al., 2006). Extrapolating to similar but unexplored regions, *Hyalella* may indeed be the most diverse North American*Hyalella* amphipod genus, with 500 or more taxa.

Gammaroids exhibit several independent patterns of freshwater colonization. Anisogammarids (*Ramellogammarus*) native to Pacific coastal watersheds may be relatively recent marine crawl-outs. A group of six relatively widespread *Gammarus* species in eastern North America (e.g., *G. fasciatus)* appear to be more ancient. Since *Gammarus* has a Palearctic center of diversity, this trans-Atlantic pattern suggests a secondary colonization of North America from Atlantic marine ancestors. A largely estuarine species, *G. tigrinus*, may represent the most recent example of this crawl-out process. Finally, *G. lacustris* appears to be a recent trans-Beringian colonizer from Eurasia, and *Chaetogammarus ischnus* is a recent human mediated trans-Atlantic invader.

A diverse group of narrowly endemic taxa in areas surrounding the northwest Gulf of Mexico (Texas to NE Mexico) show a true marine relict distribution, resulting from ancient marine regressions (Holsinger, 1994). These include the weckeliid group of the hadziids, along with sebids, bogidiellids, and the *Gammarus pecos* group.

Neotropics (NT)

Associated with the last mentioned element, many hadzioid 'relict' species also occur in fresh or weakly brackish caves and wells of the Caribbean, and many more inhabit coastal and anchihaline (subterranean) environments (Holsinger, 1993). Numerous bogidielloid and a few ingolfielloid species also occur in this region.

The documented South American amphipod diversity is relatively low at the family, genus and species levels. The 13 subterranean bogidiellid species are in 9 genera, but epigean diversity is restricted to the single genus *Hyalella*, widespread across the New World. The 51 described *Hyalella* species undoubtedly underrepresent the actual diversity, particularly in Lake Titicaca, where the genus has undergone an endemic radiation with parallels to other ancient lakes (Dejoux, 1994).

Australasia (AU)

Most Australian species are crangonyctoids, which occur from alpine regions to hypogean habitats in tropical and subtropical areas (Lowry & Stoddart, 2003). Although these are the best studied group in Australasia, the majority of taxa remain undescribed. For example, molecular data have indicated that subterranean aquifers in Western Australia are each inhabited by a unique cryptic lineage, and 200 of these aquifers have yet to be surveyed (Bradbury et al., unpubl. data).

In addition to the paramelitids (shared with Southern Africa) that are relicts of Gondwanaland, two additional crangonyctoid families are endemic to Australia, and another two to New Zealand. The most important factor that has provoked diversification in these groups was the onset of drier conditions beginning in the Eocene. Where marine incursions have occurred, or salinities are relatively high, the crangonyctoids have however been replaced, principally by the Hyalidae.

The remarkable diversity of the Tasmanian genus *Antipodeus* may represent a Pleistocene radiation. This genus dominates the cave faunas of Tasmania, as well as sub-alpine and alpine streams. The Tasmanian neoniphargids, and most of those in mainland Australia are also restricted to previously glaciated alpine regions. The documented New Zealand fauna comprises some 20 freshwater species, but again most of the diversity remains undescribed (Fenwick, 2001, and pers. comm.).

Other regions (PAC, OL, AN)

Freshwater amphipods in the Pacific, Oriental (excluding China, see above) and Antarctic (Kerguelen) regions are typically marine crawl-outs and comprise notably few species but relatively many families (Table 1, Fig. 2). There is however significant diversity in marginal marine habitats (brackish lagoons, anchihaline caves) of these areas.

Human related issues

Threats

The narrow endemism in caves and comparable restricted habitats is a special feature of amphipods by which individual species (and even some genera or families) are extremely vulnerable to extinction through habitat destruction and degradation (e.g., groundwater depletion or pollution) in several regions of the world (e.g., Sket, 1999; Witt et al., 2006).

Recent biotic invasions

Another main human effect on amphipod diversity is through facilitating range expansion across biogeographical boundaries. Inter-continental exchanges of non-marine species are still few (four cases only), but intra-continental invasions enabled by break-up of natural geographical barriers have thoroughly changed freshwater faunas, particularly in Europe. Notably, most of the recent invasions, even intra-continental, have been by taxa tolerant of brackish water also. Particularly, the Ponto-Caspian fauna has long evolved in isolation at a changeable interface of fresh and brackish environments, and thus preadapted to use emerging new dispersal opportunities. The colonizing success of species from the estuaries of major Ponto-Caspian rivers may be partly related to environmental disturbances and pollution in their new territories, creating conditions with high ionic concentrations, and to their natural ability to survive in brackish estuaries and harbors (Bij de Vaate et al., 2002).

The initial invasions by Ponto-Caspian taxa were enabled by the creation of canal networks interconnecting the major eastern and western European river systems since the late 1700s. The process was later enhanced by intentional transfers of potential fish food organisms to hydropower reservoirs, particularly from the Black Sea to the Baltic drainages. In the Soviet Union, 17 amphipod species were used in the transplantations during 1940–1970, among them Ponto-Caspian *Chelicorophium curvispinum*, *Dikerogammarus haemobaphes*, *Pontogammarus robustoides*, *Obesogammarus crassus*, *Chaetogammarus ischnus*, and *C. warpachowskyi* (Jazdzewski, 1980). Still the rate and range of the invasions have dramatically increased since the late 1980s, and in the 2000s many North and Central European river communities are undergoing major change with the aggressive expansion of *D. villosus* (Bij de Vaate et al., 2002). Even a Baikalian littoral species *Gmelinoides fasciatus* (the most eurytopic member of the endemic complex) has recently been established in NE Europe (Panov & Berezina, 2003).

Chaetogammarus ischnus is the single amphipod recently spread to North America along with a more general trans-Atlantic wave of Ponto-Caspian invaders (Vanderploeg et al., 2002). The North American euryhaline *Gammarus tigrinus* in turn was introduced to Britain and then intentionally to Germany in 1957 to replace locally extinct native species (Jazdzewski, 1980), and has since then broadly occupied river, lake, and estuarine habitats in Europe.

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