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Global diversity of crayfish (Astacidae, Cambaridae, and Parastacidae—Decapoda) in freshwater

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Abstract The freshwater crayfishes are distributed across all but the Indian and Antarctic continents with centers of diversity in the southeastern Appalachian Mountains in the Northern Hemisphere and in south–east Australia in the Southern Hemisphere. There are currently over 640 described species of freshwater crayfishes with an average of 5–10 species still being described each year. Freshwater crayfishes can serve as keystone species in aquatic habitats, but a few species are also significantly invasive and can cause impressive damage to the fragile freshwater habitat. Crayfishes inhabit caves, burrows, streams, lakes and strong burrowers can even be found in terrestrial habitats where they have burrowed to the water table or where rainfall is sufficiently abundant to provide the needed moisture. The freshwater crayfishes, like the habitats in which they are encountered, are generally endangered to some degree and conservation efforts would do well to focus on them as key elements of the freshwater ecosystem.

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Freshwater Animal Diversity Assessment

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Introduction

Freshwater crayfishes are a highly diverse group of decapod crustaceans (over 640 species) with two centers of diversity, one in the Southern Appalachian Mountains of the southeastern United States (Northern Hemisphere center) and one in south–east Australia (Southern Hemisphere center). Crayfishes occupy four main habitat types; primary burrowers (those crayfish who spend their entire life cycle in borrows – indeed, primary burrowers can burrow down to the water table and are not restricted to freshwater but are essentially terrestrial), stream-dwellers, pond/lake/large river dwellers (including secondary burrowers who do require connectivity of burrows with freshwater), and stygobitic species (obligate cave-dwellers). Each habitat type has distinctive morphological adaptations for those ecosystems (Fig. 1). For example, primary burrowers typically have a vaulted carapace to accommodate larger gill surface area and robust pinchers for digging and burrow protection. Stream specialists typically have large abdomens for swimming and are highly intolerant of low oxygen content in the water. Cave species have the typical suite of cave-adapted morphologies including loss of pigmentation, loss of eyes, elongated antennae, and elongated limbs. Most

Fig. 1 *Orconectes incomptus* (Hobbs & Barr 1972), a cave adapted freshwater crayfish from the Cumberland Plateau escarpment in northern Tennessee, USA (photo by Jennifer E. Buhay©)

crayfish typically has a life span of about 2 years (although some surface and cave species can live beyond 20 years). They reproduce sexually, although hermaphroditic specimens and even parthenogenetic specimens are known to occur (Scholtz et al. 2003). Freshwater crayfishes are omnivorous and typically nocturnal. They are voracious eaters and can be extremely destructive when introduced to non-native habitats. A few freshwater crayfish are particularly invasive (e.g., *Orconectes rusticus*) and/or were distributed in the aquaculture trade (e.g., *Procambarus clarkii*). These introduced species wreak havoc on natural ecosystems to which they are not native, but the vast majority of freshwater crayfishes are extremely narrowly distributed and hence are endangered due mainly to the destruction of the freshwater ecosystems in general. In this article, we review the freshwater crayfish diversity as it is currently understood and emphasize both the phylogenetic diversity and conservation status of this interesting group of freshwater crustaceans.

Species diversity

There are over 640 described species of freshwater crayfish worldwide (Fig. 2; Table 1). Taxonomically, they are organized into two superfamilies, the Northern Hemisphere Astacoidea and the Southern Hemisphere Parastacoidea. The Astacoidea contain two families, the Cambaridae (with by far the most species diversity, containing over 420 species contained within 12 genera) and the Astacidae with six genera and 39 species (Hobbs 1989). The Parastacoidea are composed of a single family, Parastacidae, consisting of 15 genera and over 170 species (Table 1).

Phylogeny and historical processes

The freshwater crayfish are a monophyletic group and a sister taxon to the clawed lobsters from the superfamily Nephropoidea (Crandall et al. 2000) and together the Nephropoidea, Astacoidea, and Parastacoidea make up the Astacidea (Fig. 3). While much work has been done in terms of testing the monophyly and sister relationships among the crayfish and their allies, relatively little work has been published on the phylogenetic relationships among the genera of freshwater crayfish. To a large extent, this is reflective of the fact that initial studies have shown that many of the genera (especially in the family Cambaridae) do not form monophyletic groups, thereby requiring relatively complete taxonomic sampling to perform reasonable phylogenetic analyses (Sinclair et al. 2004). This is a difficult task given the large number of species of freshwater crayfish.

Given the geographic distribution of this group (Fig. 2) and the strong support for a monophyletic origin, the crayfishes must have originated in Pangaea by the Triassic period (185–225 mya). The separation of the two crayfish superfamilies represents the splitting of Pangaea into northern (Laurasia) and southern (Gondwana) land-masses around 185 mya. This separation is clearly seen in the estimates of crayfish phylogenetic relationships (Fig. 3). The antiquity of the crayfishes is supported by recent fossil evidence from Colorado and Utah with fossil crayfish and burrows associated with Permian and Early Triassic (265 mya) deposits (Hasiotis and Mitchell 1993). Furthermore, the phylogenic connection of the Southern Hemisphere crayfishes represented in southern South America, Madagascar, New Zealand, and Australia corresponds to the distribution patterns of the predatory dinosaur group Abelisauridae (Sampson et al. 1998). Thus the crayfishes offer further support for the hypothesis suggesting extended contact between these land-masses and the antiquity of the freshwater crayfish lineage (Crandall et al. 2000; Hobbs 1988; Scholtz and Richter 1995).

Table 1 Total number of described freshwater crayfish species by taxon and distribution in the geographic regions of focus. PA: Palaearctic; NA: Nearctic; NT: Neotropical; AT: Afrotropical; OL: Oriental; AU: Australasian; PAC: Pacific Oceanic Islands; ANT: Antarctic

Family	Genus	PA	NA	AT	NT	OL	AU	World
Astacidae		*31*	*8*	*0*	*0*		*0*	*39*
	Astacus	5	0	0	0		0	5
	Atlantoastacus	8	0	0	0		0	8
39 species	Austropotamobius	7	0	0	0		0	7
	Caspiastacus	2	0	0	0		0	2
	Pacifastacus	0	8	0	0		0	8
	Pontastacus	9	0	0	0		0	9
Cambaridae		*7*	*374*	*0*	*48*		*0*	*423*
	Barbicambarus	0	1	0	0		0	1
	Bouchardina	0	1	0	0		0	1
445 species	Cambarellus	0	8	0	9		0	17
	Cambaroides	7	0	0	0		0	7
	Cambarus	0	97	0	0		0	95
	Distocambarus	0	5	0	0		0	5
	Fallicambarus	0	18	0	0		0	18
	Faxonella	0	4	0	0		0	4
	Hobbseus	0	7	0	0		0	7
	Orconectes	0	91	0	0		0	89
	Procambarus	0	140	0	39		0	177
	Troglocambarus	0	2	0	0		0	2
Parastacidae		*0*	*0*	*9*	*16*		*151*	*176*
	Astacoides	0	0	9	0		0	9
	Astacopsis	0	0	0	0		3	3
175 species	Cherax	0	0	0	0		45	45
	Engaeus	0	0	0	0		39	39
	Engaewa	0	0	0	0		5	5
	Euastacus	0	0	0	0		43	43
	Geocharax	0	0	0	0		2	2
	Gramastacus	0	0	0	0		1	1
	Ombrastacoides	0	0	0	0		11	11
	Paranephrops	0	0	0	0		2	2
	Parastacus	0	0	0	8		0	8
	Samastacus	0	0	0	1		0	1
	Spinastacoides	0	0	0	3		0	3
	Tenuibranchiurus	0	0	0	1		0	1
	Virilastacus	0	0	0	3		0	3
Total		*38*	*382*	*9*	*64*		*151*	*638*

Present distribution and areas of endemicity

The most species rich family of freshwater crayfish, the Cambaridae, are distributed in North America east of the Rocky Mountains, north into southern Canada and south through Mexico and, surprisingly, in Asia (Table 1). The Asian endemic genus *Cambaroides* is a bit of an enigma both biogeographically

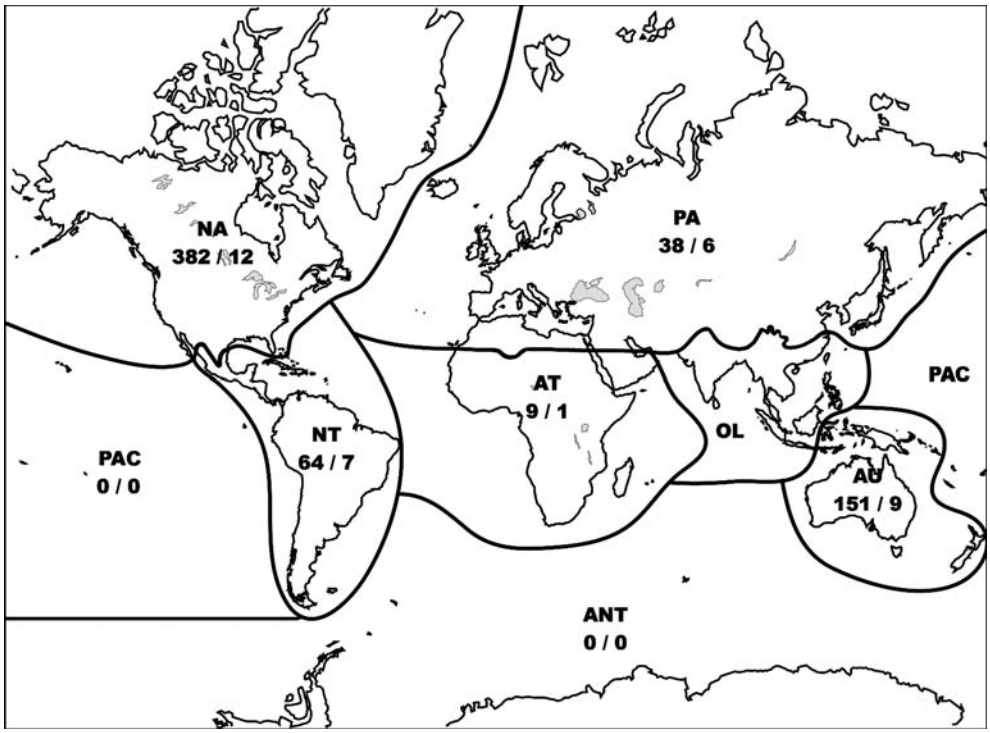

Fig. 2 Geographic distribution of the global freshwater crayfish diversity (species number/genus number). PA—Palaearctic; NA—Nearctic; NT—Neotropical; AT—Afrotropical; OL—Oriental; AU—Australasian; PAC—Pacific Oceanic Islands; ANT—Antarctic

as well as phylogenetically. Some phylogenetic analyses place it weakly with the European species (which makes more biogeographic sense), but a good sampling of *Cambaroides* to place into a robust phylogenetic analysis has yet to occur. The Astacidae are distributed west of the Rocky Mountains (mainly in the Pacific Northwest) and in Europe (Table 1). In the superfamily Parastacoidea, 10 of the 15 genera are found in Australia. The remaining genera are distributed in southern South America (three endemic genera with 12 species distributed in southern Chile, Uruguay, and southern Brazil), New Zealand (with one endemic genus and two described species), and Madagascar (with one endemic genus and nine described species).

The greatest species diversity in the freshwater crayfishes occurs in the southern Appalachian Mountains of the southeastern United States (Table 1). This region is also home to a number of other highly endemic and highly endangered stream species including freshwater fishes, salamanders, snails, and mussels. Based on phylogenetic results and biogeographic analyses, much of the species diversity in the Cambaridae is of relatively recent origin (compared to the Parastacidae) and seems to have been driven by isolating effects of pre- and post-Pleistocene river drainage changes (Crandall and Templeton 1999). Population genetic studies of species groups are beginning to unravel the evolutionary mechanisms associated with driving this amazing diversity (Buhay and Crandall 2005; Fetzner and Crandall 2003).

The Southern Hemisphere crayfishes have a center of diversity in south–east Australia. These taxa (at least the genus-level divisions) appear to be much older in origin relative to the Northern Hemisphere taxa. These genera appear to form well-defined monophyletic groups (e.g., Schull et al. 2005) as a result. The species richness of many of these genera appears to be the result of vicariance and dispersal with isolation events (e.g., Ponniah and Hughes 2004; Schull et al. 2005).

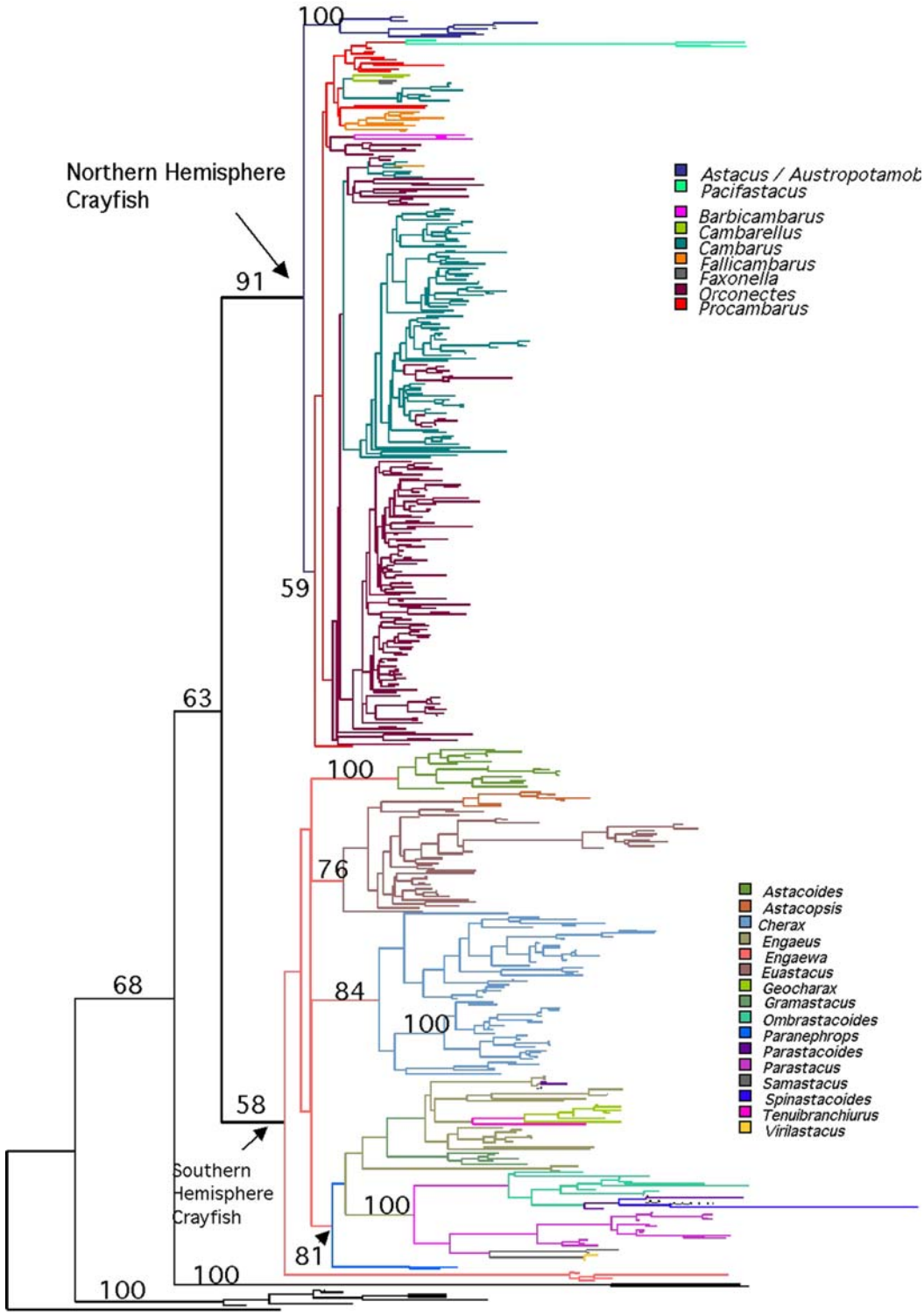

Fig. 3 Phylogenetic relationships among the global freshwater crayfish showing the strongly supported division between the two superfamilies of the Northern Hemisphere (Astacoidea) and the Southern Hemisphere (Parastacoidea). (Sinclair et al. 2004)

Human related issues

Freshwater crayfish are a much sought after food item in many cultures (Fig. 4) and a significant aquacultural commodity. Unfortunately for many of the charismatic species (e.g., the Tasmanian Giant Lobster, *Astacopsis gouldi*), over-harvesting coupled with degradation of habitat has resulted in the endangerment of many crayfish species (e.g., Horwitz 1994). Other areas, such as Madagascar, support a sustainable harvest of crayfish, yet these populations are typically imperiled by stream degradation (Jones et al. 2005). While all 640+ species of freshwater crayfish have yet to be categorized for conservation status relative to the IUCN Red List Criteria (IUCN 2001), a large number of species already occur on that list. Taylor et al. (1996) found that over 50% of the United States species of freshwater crayfish are endangered or threatened to some degree. Yet, surprising, very few of these species are under national protection with a few more under local (state, provincial) protection. For example, in the United States, 20 species are known from less than five localities (with 15 known only from a single locality) and well over 210 species are considered endangered or threatened, but only four species are listed by the federal government on the Endangered Species List. Native crayfish play an essential role in their native habitat and may act as keystone species for the freshwater ecosystems where they occur. Yet this biodiversity is at great risk of loss if national governments (especially in the US and Australia where the bulk of the species diversity occurs) do not take appropriate measures to protect the highly endangered freshwater ecosystems that house these and many other amazing species.

Fig. 4 Crayfish are staple in many cultures both as a food source and source of income; this example is from a roadside crayfish stand in Madagascar with both *Astacoides madagascarensis* and *Astacoides betsiloensis* for sale (Photo by Julia Jones© 1999 used with permission)

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