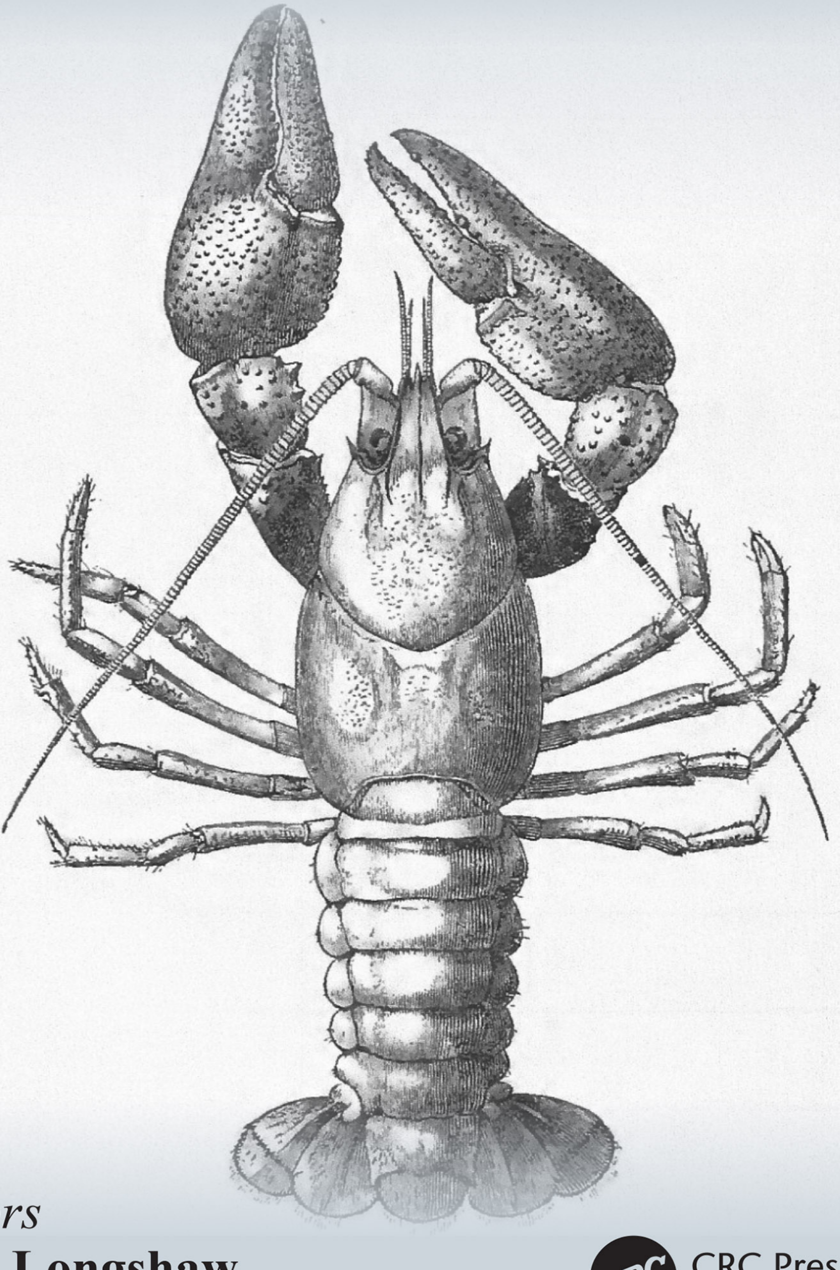
Biology and Ecology of Crayfish



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Dedication

This book is dedicated to the memory of Dr. Francesca Gherardi. Her influence on our collective understanding of the biology and ecology of crayfish is outstanding; without her collaborations and her publications we would know much less about the subject. Her impact on the subject as both an outstanding scientist and an enthusiastic individual will be sorely missed. The world is a quieter place without her.

Preface

It would be fair to say that anybody that has worked with, or written about crayfish, has probably read the seminal work of Huxley (1880) "The crayfish. An introduction to the study of zoology". His preface ably sums up why many of us work with these animals when he states "…how the careful study of one of the commonest and most insignificant animals, leads us, step by step, from every-day knowledge to the widest generalizations and the most difficult problems of zoology; and, indeed, of biological science in general…". Whilst at the time that Huxley wrote his book in 1880 crayfish may have been viewed as "insignificant animals", they are now seen in a much different light, with the importance of crayfish now being seen on a global scale. Crayfish are now extensively used in aquaculture and wild harvest for human consumption, in the aquarium trade as pets, in scientific studies as model organisms, recognised as key components of freshwater ecosystems, and are some of the most widely spread and damaging invasive species. We wonder if Huxley would have been surprised at how important his "insignificant animals" have now become.

Huxley eludes to the point that crayfish are an ideal model organism for study. As this book will hopefully demonstrate, we agree that crayfish are an excellent model as some species are readily available and are identifiable through morphological and molecular methods (Chapters 1 and 2), methods for their capture and holding are established or can be adapted from known methods (Chapter 8), they can be maintained in the lab (Chapter 9), and their inter- and intra-specific interactions as well as their drivers for individual and population success are beginning to be known to us (Chapters 3, 4, 5 and 7).

Of course, we recognise that subsequent to Huxley's book there have been a number of books on the subject of crayfish biology, culture and ecology; for example, those published by David Holdich, and the excellent works published by some of our co-authors and others. We don't expect to compete with these, rather we consider our book as complimentary to them. When we set out to edit this book, it was our intention to have a combination of reviews of the current state of knowledge in the respective disciplines that was balanced with providing some practical hints and tips that could be used on a daily basis when working with crayfish. We each recognise our own inherent biases and interests; as editors, we allowed those biases to come through in each chapter. This has meant that there is some overlap in the topics in some chapter, albeit with a different viewpoint, depending on the overall subject being discussed. However, we feel that this minor repetition helps to reinforce some key concepts throughout the book. Simply put, crayfish biology is an amalgam of a number of disciplines; none of them should be seen as isolated from any other and the use of integrated studies to fully understand crayfish in totality is of paramount importance to us. In pulling together the list of authors, we tried to find like-minded individuals—those who reflect our views of taking a holistic view of the world, those who are active in the field of crustacean biology and, to misquote Huxley, to avoid a book that was "a treatise upon our English crayfish", hence our international authorship.

The first chapter of this book covers the latest information on the taxonomy, phylogeny and global distribution of crayfish by Catherine Souty-Grosset and James Fetzner Jr. from France and the USA respectively, which is followed by a detailed chapter on the population genetics of a range of species by Catherine, emphasising the importance of understanding genetics for protection of crayfish species. The next chapter by Colin McLay from New Zealand and Anneke van den Brink from The Netherlands looks at perhaps the two most important facets of any animals' biology—growth and reproduction (Chapter 3). Without these, there would be no progeny and no more crayfish. Linked with this chapter is

Chapter 4 on behavioural aspects of crayfish biology by Ana M. Jurcak, Sara E. Lahman, Sarah J. Wofford, and Paul A. Moore from the USA. Behaviour is covered from the perspective of crayfish as predators and as prey and how they compete for space and mates, covering the range of mating behaviours that allow them to successfully grow and breed. Explanations for some of the observed behaviours are further explored in the chapter on chemical ecology (Chapter 5) by Thomas Breithaupt from the UK, Francesca Gherardi (deceased) and Laura Aquiloni and Elena Tricarico from Italy. The pivotal role of these chemicals in how crayfish make sense of their world is explored through descriptions of the morphology of the various sensory systems and the role of "infochemicals" in predator/prey interactions, social interactions, reproduction and progeny interactions, and considers the role of pollutants as "info-disrupters". In a shift towards factors affecting individuals and populations of crayfish, Matt Longshaw from the UK, provides an up to date review and listing of the estimated 900 disease agents, parasites and commensals of crayfish across their global range (Chapter 6). Touching briefly on disease as a driver for population success, Ed Willis Jones from the UK, Michelle Jackson from South Africa and Jonathan Grey from the UK, begin to tie together the various environmental drivers for population success by examining population biology and community dynamics. They consider factors such as hydrography and habitat quality as well as abiotic factors (broadly termed by us as water quality). Recruitment, a population biology measure of successful reproduction is explored in relation to those environmental factors that impact reproduction, successful dispersal and survival. Community dynamics and species interactions, again from a population driver perspective, are further explored along with the ecosystem function of crayfish in food webs and in their wider, non-trophic, interactions. Eric Larson and Julian Olden from the USA, ask the question "why do we study crayfish?" at the start of their chapter on field sampling (Chapter 8) which they use to springboard into a review of the diverse methods available for assessing population numbers. The potential biases and limitations with different methods are highlighted, including the impact of trap choice on population estimates. Suggestions for addressing the variations in population estimates through a variety of methods including tagging studies as well as statistical approaches are covered. The next chapter on laboratory methods by both of us emphasises the need for integrated studies to better understand crayfish in natural and artificial habitats. We consider methods for transporting and holding crayfish followed by a proposed methodology for tissue sampling—whether that be for disease screening, assessing reproductive state, for collection of material for molecular/genetic studies or to describe new species. The final chapter by Paul Stebbing addresses how crayfish as invasive species can be managed, a subject close to the heart of Francesca Gherardi, to whom this book is dedicated, and who contributed so much to this specific subject area.

So, here it is. Our book. We entrust it to you to use as you see fit. Delve into it for the bits that you work on or take a risk and read a chapter on an area outside your comfort zone. Either way, we hope it's useful. One of us (Paul) has been actively involved in crayfish research for a number of years with a particular interest in their management and control. The other, Matt, has been involved in the periphery of crayfish research, focusing on the parasites and diseases of indigenous and non-native crayfish in the United Kingdom. For both of us we have found the exercise of editing the book exhilarating, debilitating, frightening, frustrating, educational, enlightening and, above all fun.

Finally, we wish to extend our thanks to all the authors involved in writing this book—every editor says the same… without the support of the authors, etc… but in this case, that is true. Halfway through the process of developing the book, one of us (Matt) changed jobs, moving from a research position in the British Government to a commercially focused role in the pharmaceutical industry. The hiatus caused by the need to focus on a whole new set of skills was partly responsible for a delay in getting the book to press. In addition, during the production of the book Paul's wife gave birth to two children, also resulting in the learning of and the need to focus on a whole new set of skills, causing further delay. We are pleased to say that each and every author was understanding, for which we are eternally grateful! We thank them for their patience in getting their book out there for you all to see. We hope you appreciate their hard work and patience as much as we do; this book is a testament to their skill and knowledge.

December 15th 2015

Matt Longshaw, Edinburgh
Paul Stebbing, Weymouth

Contents

CHAPTER

1

Taxonomy and Identification

Catherine Souty-Grosset[1,*] and *James W. Fetzner Jr.*[2]

> *"My purpose is to exemplify the general truths respecting the development of zoological science which have just been stated by the study of a special case; and, to this end, I have selected an animal, the Common Crayfish, which, taking it altogether, is better fitted for my purpose than any other".*
>
> (T.H. Huxley 1880)

Introduction

According to Huxley (1880), the origin of the common name, "crayfish" involves some interesting questions of etymology, and indeed, of history. It might readily be supposed that the word "cray" had a meaning of its own, and qualified with the substantive "fish", but this is not certain. The old English method of writing the word was "crevis" or "crevice", and "cray" was simply a phonetic spelling, with the word "fish" added to reinforce our perception of it as an aquatic animal. The term "crevis" has two distinct meanings. Swahn (2004) suggests that, according to the French, that the English were the first *Astacus* eaters (there is a historical reference to people eating crayfish in England from the tenth century onwards), and as in many other cases, they accepted not only the food but also the old French name for it. The French word "(é)crevisse" was modified and the new word "cray-fish" created. In the United States, crayfish are commonly known as crawfish, crawdads, or mudbugs and constitute a diverse and important component of freshwater aquatic and semi-aquatic ecosystems around the world (Taylor and Schuster 2004). The etymology of these terms is less clear.

Similar to crabs, shrimps and lobsters, the freshwater crayfish belong to the phylum Arthropoda, subphylum Crustacea, class Malacostraca, which contains about 25,000 species with a standard segmented body plan of 20 segments within the Subclass Eumalacostraca and the Superorder Eucarida. They are decapods (the Order Decapoda contains about 14,335 species, De Grave et al. 2009) because they have ten legs, including 8 pairs of thoracic limbs, but only 5 pairs are ambulatory (pereiopods), giving the group its name. The head has a compound eye, usually stalked, two pairs of sensory antennae and three pairs of

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mouthparts. A further three pairs of thoracic limbs (the maxillipeds) are incorporated into the mouthparts. The six abdominal segments each have a pair of swimming limbs, the last pair (the uropods) expanded into a tail fan in crawling and swimming forms. They are most closely related to marine lobsters (Crandall et al. 2000) and differ from those organisms by possessing a direct juvenile development rather than a dimorphic larval stage.

Among decapods, freshwater crayfish are represented by over 640 species (Crandall and Buhay 2008), with the southeastern United States being one of the epicenters of diversity. Three hundred sixty-three species are represented in the United States (Taylor et al. 2007) and according to De Grave et al. (2009), freshwater crayfish are widely distributed across the globe, mainly in temperate and subtropical water bodies and wetlands.

Systematics of the freshwater crayfish: Infraorder Astacidea Latreille 1802

The basic taxonomy of the Infraorder Astacidea has been summarized by C. Souty-Grosset in the Treatise on Zoology - Anatomy, Taxonomy, Biology (cf. Gherardi et al. 2010: Chapter Infraorder Astacidea Latreille, 1802 Volume 9). The infraorder is further subdivided into two superfamilies, the Astacoidea and Parastacoidea. The taxonomy of crayfish was extensively studied by Hobbs between 1974 and 1994. According to Hobbs "The nephropoids, ancestors to the modern lobsters, initiated a line that was the most conservative. Not only have the descendants remained in the sea, basically an environment in which their ancestors came into existence, but also many of the characteristics that constitute the lobster facies, and the release of young as larvae by modern descendants, suggest a more generalized condition than that which exists in current derivatives of the early astacoid and parastacoid stocks". Hobbs (1988), goes on to say that "the generally more morphologically divergent and venturesome astacoids and parastacoids, forebearers of modern crayfish, were destined to invade and, for the most part, to become restricted to the freshwaters of the Northern and Southern Hemispheres, respectively, having successfully negotiated the transition from the sea to freshwater, an environment which, in the late Jurassic, seems to have been discovered by few, if any, other decapods". The diagnosis of the two superfamilies of Astacoidea and Parastacoidea is based on the description of the carapace, the form of sternal plates and podobranchia, the branchial formula, and the differences between the first pleopods of males and females. Both superfamilies lack a dorsomedian longitudinal suture or a ridge in the cardiac and posterior gastric regions of the carapace and the sternal plate between the fifth pereiopods is not fused with the sternal complex anteriorly.

Throughout his career, Horton Hobbs, Jr. described many new taxa, including one new family (Cambaridae), 38 new genera and subgenera and 286 species, all of which were based on morphological characteristics alone. His most recent taxonomic summary of species was published in 1989 and was entitled *An Illustrated Checklist of the American Crayfishes (Decapoda: Astacidae, Cambaridae and Parastacidae).*

A detailed treatise of the taxonomy is given below.

Superfamily ASTACOIDEA Latreille, 1802

Articles of the lateral ramus of antennules bear two clusters of aesthetascs (except in Cambaroidinae Villalobos, 1955, in which there is only one); branchial formula is 16 + ep; 17 + ep; 18 + 2r + ep; or 18 + 3r + ep (ep: epipod; r: rudimentary), podobranchiae of the first three pereiopods not differentiated into branchial and epipodite portions; males have first pleopods with a single sperm groove, groove may be present or absent in females, second pleopods of males show a spiral element frequently borne on a subtriangular lobe; telson divided by a transverse suture almost always, and usually completely. Species live in fresh waters but some migrate into salt waters for part of their life cycle.

Family Astacidae Latreille, 1802

Some articles of the lateral rami of antennules bear 2 clusters of aesthetascs; branchial formula 18 + 2r + ep or 18 + 3r + ep; ischia of male pereiopods lack hooks; females lack first pleopods and *annulus ventralis* (sclerites present but lack sinus and fossa); males never exhibit cyclic dimorphism, distal portion of the male first pleopods rolled to form a cylinder, distal most part contracted to form either a tube or produced into 2 simple spoon-like lobes.

Family Cambaridae Hobbs, 1942

Some articles of lateral rami of antennules bear 1 or 2 clusters of aesthetascs; branchial formula 18 + 3r + ep; 17 + ep or 16 + ep; ischia of one or more of second-fourth pereiopods with hooks; first pleopods and *annulus ventralis* may be present or absent; males exhibit cyclic dimorphism, male first pleopods either medially bear shallow sperm grooves or distal portions tightly folded with distal end of sperm groove opening on one of 2–4 terminal elements.

Family †Cricoidoscelosidae Taylor, Schram and Shen, 1999

Rostrum with rounded base and lateral spines; blade-like scaphocerite; no ischial hooks on pereiopods; rounded pleomeral pleua; first pleopod styliform, remaining pleopods annulate; telson not divided by a transverse suture.

A single extinct species, *Cricoidoscelosus aethus*, originated from the Jurassic, Jehol Group of northeastern China.

Superfamily PARASTACOIDEA Huxley, 1880

Articles of the lateral ramus of antennules never bear more than one cluster of aesthetascs; Branchial formula ranges between 12 + epr + 5r and 21 + ep (epr: rudimentary epipod), epipodite of the first maxillipeds usually have branchial filaments, podobranchiae of the first three pereiopods differentiated into branchial and epipodite portions; first pleopods absent, second pleopods of males similar to third; telson never completely divided by a transverse suture.

Family Parastacidae Huxley, 1880

Diagnosis is the same as in the superfamily.

After Hobbs, crayfish taxonomy has mainly been updated at the generic level (e.g., Fitzpatrick 1983, Fetzner and Crandall 2002, Taylor 2002). Initial efforts examined allozyme variation (Fetzner 1996, Horwitz and Adams 2000), and 16S DNA sequences from the mitochondrial genome (Pedraza-Olvera et al. 2004, Sinclair et al. 2004). In particular, Crandall and Fitzpatrick (1996) gave new insights into the molecular systematics of crayfish by using a combination of procedures. Molecular studies have also elucidated a wealth of cryptic species that likely represent units of evolution. Their identification is thus highly relevant for conservation purposes (Crandall et al. 2000, Fetzner and Crandall 2003).

Origin of crayfish and fossil taxa

Hobbs (1988) provided insightful discussions of the known fossil crayfish taxa and discussed in detail their presumed evolutionary history. There are several fossil representatives included within the Astacidea, and a few are closely related to extant crayfish species (based on morphological evidence). However, several recent discoveries may suggest an alternative evolutionary history involving crayfish. Crayfish fossils and burrows have been found in the Triassic formations of North Carolina (Olsen 1977), of Arizona (Miller and Ash 1988) and of Utah (Hasiotis 1999) dating back 225 million years (Early Carboniferous during the formation of the Pangean supercontinent). These trace and body fossils confirm that crayfish were established across a variety of ecological settings ranging from fully terrestrial to fully aquatic. The Erymidae were marine representatives and were most likely the progenitors to the clawed lobster and freshwater crayfish lines. Members of this group first appear in the fossil record some 245 million years ago and disappear around 75 million years ago.

After the break-up of Pangaea into a northern and a southern continent, Laurasia and Gondwana respectively, the differences are believed to have evolved between the northern hemisphere Astacoidea and the southern hemisphere Parastacoidea. The monophyly of the two crayfish superfamilies Parastacoidea (southern hemisphere) and Astacoidea (northern hemisphere) (Crandall et al. 2000) is consistent with the break-up of Pangaea. Subsequently, the Parastacidae have radiated in Australasia, New Zealand, South America and Madagascar. Molecular genetic studies support the monophyly of the continental subgroups (Sinclair et al. 2004), but the relationships between them remain unresolved. However, Riek (1972) suggested that members of *Astacoides* from Madagascar appear closer to *Astacopsis* from Tasmania than they are to the South American species.

The fossil record appears older for Astacoidea than for Parastacoidea (Scholtz 2002) and is supported by fossil evidence of burrows. The centre of origin of the Astacoidea is suggested to be eastern Asia, from where the cambarid ancestors could have migrated via the Bering land bridge to their current position in eastern modern day North America, while most of the Astacidae dispersed westwards into Europe, with the oldest known *Austropotamobius* appearing there in the early Cretaceous (Souty-Grosset et al. 2006: Box 1). In Europe, a petrified specimen found in the Jurassic limestone of Solnhofen, Bavaria, from the same place where *Archaeopteryx* was found, is dated to 135–145 million years ago (MYA) and has been assigned to either *Aeger tippularius* (Schlothuis, 1822), *A. bronni* (Oppel, 1862) or *A. antumpsos speciosus* (Münster, 1839). A specimen of this fossil is currently used as the insignia for the President of the International Association of Astacology (IAA) (Picture 1).

Box 1. Summary of "Geological times" and "crayfish events" (Souty-Grosset et al. 2006).

ERA	System	Epoch (Million yrs)	Major crayfish events
"Quaternary"		(ca 3.000-1000 yrs BC) = *Littorina* period	
		Holocene (0.01)	post-glacial colonizations
		Pleistocene (1.8)	actual sub-sp differentiations?
	Neogene	Pliocene (5)	actual species differentiations?
CENOZOIC		Miocene (23)	Messinian crisis (ca 5.5 MY)
"Tertiary"			
		Oligocene (33.9)	
	Paleogene	Eocene (55.8)	
		Paleocene	
		(65.5)	
	Cretaceous		oldest known *Austropotamobius*
		(145)	
MESOZOIC	Jurassic		oldest known Astacidae
"Secondary"		(200)	
	Triasic		differentiation Astacoids/Parastacoids
		(251)	
PALEOZOIC	Permian		from seawater to freshwater
			"crayfish" in Antarctica
"Primary"			Nephropoid ancestors
		(299)	

American astacids of the genus *Pacifastacus* must have dispersed eastward after the cambarids; they are considered to be the most primitive of this family (Scholtz 2002). Ice ages following the break-up of Pangaea would have extinguished crayfish from Siberia and central Asia, although this does not explain their absence from Africa and India. Either they never got there, or were eliminated by some process, with competitive exclusion by freshwater crabs being one postulated scenario. However, elsewhere, representatives of these two groups coexist today in southern Europe, Turkey, Madagascar, Australia and New Guinea (Scholtz 2002).

Breinholt et al. (2009) presented a recent analysis of the timing of the diversification of the freshwater crayfishes by calibrating the times with multiple fossils, including a newly discovered Parastacoid fossil from Australia. With such a narrow taxonomic focus, they were able to increase accuracy and provide divergence estimates that were more specific to freshwater crayfish. Their molecular time estimates support a late Permian to early Triasic divergence from Nephropoidea, with a subsequent radiation and dispersal before the breakup of Pangaea, as well as later speciation and radiation prior to, or directly associated with, the breakup of Gondwana and Laurasia. The breakup of Gondwana and Laurasia resulted in the separation of the Parastacoidea and Astacoidea during the Jurassic period. The hypothesized divergence and radiation of these two superfamilies is also supported by their molecular time estimates. For the three

Picture 1. Fossil of IAA insignia.

families of crayfish, they estimate the Astacidae radiated at 153 MYA, the Cambaridae at 90 MYA, and the diversification of the Parastacidae at 161 MYA.

Phylogeny and genera

The freshwater crayfish are a well-established monophyletic group (Scholtz and Richter 1995, Crandall et al. 2000). Recent analyses support the sister relationship between clawed lobsters and freshwater crayfishes (Crandall et al. 2000, Dixon et al. 2003, Ahyong and O'Meally 2004, Porter et al. 2005, Bracken et al. 2009, Breinholt et al. 2009), lending support to the continued recognition of Astacidea. Within the freshwater crayfish, both of the superfamilies, Parastacoidea and Astacoidea, are monophyletic groups. The generic level taxonomy of parastacoids was recently revised with the splitting of the genus *Parastacoides* Clark 1936, into two new genera, *Spinastacoides* and *Ombrastacoides* (Hansen and Richardson 2006). De Grave et al. (2009) followed the conventional higher level taxonomy outlined by Hobbs (1974), with the adjustments proposed by Hansen and Richardson (2006). There is some debate about the monophyletic status of several genera in the family Cambaridae (Fetzner 1996; Crandall and Fitzpatrick 1996, Breinholt et al. 2009). Moreover, there have also been recent additions at both the family (Taylor et al. 1999) and generic levels (Martin et al. 2008, Feldmann et al. 2011) for fossil crayfish. Breinholt et al. (2012) suggest that convergent evolution has impacted the morphological features used to delimit the subgenera of *Cambarus*, as relationships based on chelae and carapace morphology are incongruent with estimated phylogenetic relationships. Many of the current systematic relationships within the Cambaridae are based on first form male gonopod morphology. Several features suggest that subgeneric morphological diagnoses used in traditional cambarid crayfish taxonomy (form one male gonopods in combination with chela and carapace characters) might be confounded by convergent evolution across all cambarids. The use of molecular-based phylogenies may be useful in evaluating synapomorphic morphological characters that reflect evolutionary relationships that are less affected by convergent evolution. While one goal of systematic studies is to revise taxonomy to reflect evolutionary history, for *Cambarus*, this task seems unwise without complete taxon sampling. Future work in this genus specifically needs to obtain complete taxon sampling as well as increased sampling throughout the geographic range of each species. Additional studies have used extensive sampling of species from the genera *Orconectes*, *Procambarus* and *Cambarus* and have found significant population structure and cryptic diversity (Buhay and Crandall 2008, 2009). Breinholt et al. (2012) concluded that extensive sampling within species is critically important for all cambarid crayfish before inferring meaningful evolutionary hypotheses or when making taxonomic changes.

Present distribution of the families of crayfish

As explained above, freshwater crayfishes are taxonomically distributed among three families; two Northern Hemisphere families, Astacidae and Cambaridae, and one Southern Hemisphere family, Parastacidae. There are two centres of species diversity for freshwater crayfishes. The first is located in the Southeastern United States where some 80% of the cambarid species can be found. The second centre of diversity is in Victoria, Australia; which contains a large proportion of the parastacid species. Freshwater crayfishes naturally occur on all of the continents except Africa and Antarctica (Fig. 1). The Astacidae are distributed in Europe and also west of the Rocky Mountains in the Northwestern United States and extending into southern British Columbia, Canada. The Cambaridae are found in the Eastern United States and south through Mexico, with members of the genus *Cambaroides* having a disjunct distribution in Southeastern Russia, Japan and the Korean Peninsula. The Parastacidae are distributed in Australia, New Guinea, New Zealand, South America, and Madagascar. Crayfish are naturally absent from the Antarctic continent, continental Africa, the Indian subcontinent, and much of Asia.

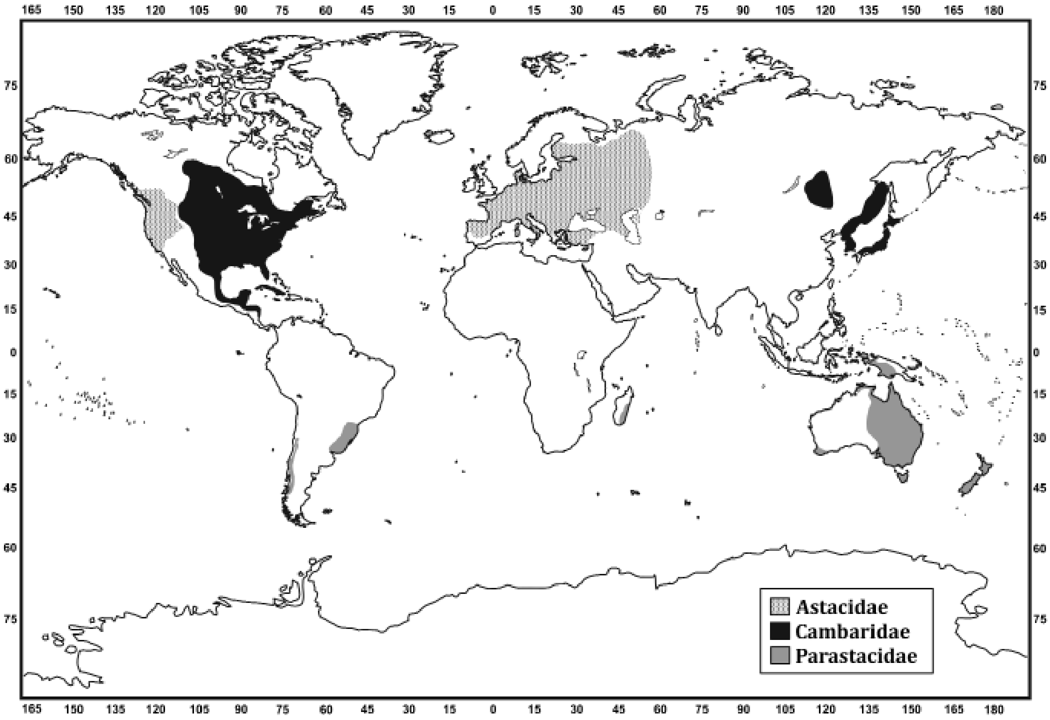


Figure 1. Distribution of crayfish around the world, exhibiting two centers of diversity in North America and Australia, respectively [Figure adapted from the Freshwater Crayfish and Lobster Taxonomy Browser: http://iz.carnegiemnh.org/crayfish/NewAstacidea/].

De Grave et al. (2009) listed below a recent classification that included both living and fossil genera of the Astacidea, in which they gave a comprehensive catalogue of crustaceans, including an examination of over 400 papers on decapod fossils. This compendium listed the current state of knowledge of the number of species of Decapoda in the Infraorder Astacidea Latreille, 1802, including 653 extant species, 5 extant species also known as fossils, and 124 exclusively fossil species (Table 1 below), although subsequent new species descriptions over the last five years have modified these numbers somewhat.

Table 1. According to De Grave et al. 2009: Taxa that are either exclusively living (extant) or exclusively fossil (the latter indicated by ††), have only one tally associated with them. In contrast, taxa that are known to include both extant and fossil species (indicated by †) are provided with three counts, e.g., "Family Parastacidae † Huxley, 1880 (164, 1, 3)". The first number represents exclusively extant species, the second number indicates extant species also represented in the fossil record, and the third is the number of exclusively fossil species. The total number of extant species is the sum of the first two numbers; in this case there are 165 known species of living Parastacidae. The total number of fossil species is the sum of the second and third numbers: there are 4 known species of fossil Parastacidae. The total number of known species (extant, fossil, or both) is the sum of all three numbers: there are 168 known species in Parastacidae.

+ indicates the number of new species described since De Grave et al. (2009).

SUPERFAMILY ASTACOIDEA † Latreille, 1802 (428, 0, 9) + 34

Family Astacidae † Latreille, 1802 (11, 0, 6)
Astacus † Fabricius, 1775 (3, 0, 4)
Austropotamobius † Skorikow, 1907 (3, 0, 1)
Pacifastacus † Bott, 1950 (5, 0, 1)

Family Cambaridae † Hobbs, 1942 (417, 0, 1) + 34
Barbicambarus Hobbs, 1969 (1) +1
Bouchardina Hobbs, 1977 (1)
Cambarellus Ortmann, 1905b (17) +1
Cambaroides Faxon, 1884 (7)
Cambarus Erichson, 1846 (100) +10
Distocambarus Hobbs, 1981 (5)
Fallicambarus Hobbs, 1969 (18) +1
Faxonella Creaser, 1933 (4)
Hobbseus Fitzpatrick and Payne, 1968 (7)
Orconectes Cope, 1872 (91) + 8
Palaeocambarus †† Taylor, Schram and Shen, 1999 (1)
Procambarus † Ortmann, 1905a (165, 0, 1) + 13
Troglocambarus Hobbs, 1942 (1)

Family Cricoidoscelosidae †† Taylor, Schram and Shen, 1999 (1)
Cricoidoscelosus †† Taylor, Schram and Shen, 1999 (1)

SUPERFAMILY PARASTACOIDEA † Huxley, 1880 (164, 1, 3) + 22

Family Parastacidae † Huxley, 1880 (164, 1, 3) + 22
Aenigmastacus †† Feldmann, Schweitzer and Leahy, 2011 (1) +1
Astacopsis † Huxley, 1880 (2, 1, 0) + 1
Astacoides Guérin-Méneville, 1839 (7)
Cherax Erichson, 1846 (34) + 15
Engaeus Erichson, 1846 (35)
Engaewa Riek, 1967 (5)
Euastacus E.M. Clark, 1936 (49) + 3
Geocharax E.M. Clark, 1936 (2)
Gramastacus Riek, 1972 (1) + 1
Lammuastacus †† Aguirre-Urreta, 1992 (1)
Ombrastacoides Hansen and Richardson, 2006 (11)
Palaeoechinastacus †† Martin, Rich, Poore, Schultz, Austin, Kool and Vickers-Rich, 2008 (1)
Paranephrops † White, 1842 (2, 0, 1) + 1
Parastacus Huxley, 1880 (8)
Samastacus Riek, 1971 (1)
Spinastacoides Hansen and Richardson, 2006 (3)
Tenuibranchiurus Riek, 1951 (1)
Virilastacus Hobbs, 1991 (3) + 1

The authors specified that subspecies were not counted, which is understandable given the fact that some may be species complexes or represent cryptic species. For example, among the Astacidae, the taxon *Austropotamobius pallipes* (Leboullet 1858) is a species complex (see Chapter 2 on Genetics) and *Pacifastacus leniusculus* (Dana 1852) currently contains three subspecies recognised in North America: *Pacifastacus l. leniusculus*, *P. l. trowbridgii* and *P. l. klamathensis* (Miller 1960). Among the Cambaridae, *Orconectes virilis* also corresponds to a cryptic species complex with several species known from North America (Mathews et al. 2008, Mathews and Warren 2008, Filipova et al. 2009); another example includes the White River Crayfish, *Procambarus zonangulus* (Hobbs and Hobbs 1990), which was part of a species complex formerly known as *P. acutus acutus* (Girard 1852), which still includes at least 3 species of crayfishes in the eastern United States (Hobbs and Hobbs 1990, Huner and Barr 1991, Huner 2002, Taylor et al. 1996).

The number of described crayfish species is subject to change, and since De Grave et al. (2009), numerous new species have been described every year. Feldmann et al. (2011) added a new monotypic fossil genus *Aenigmastacus* with *A. crandalli* designated as the type species. The most recent estimates suggest there are currently 180 extant described Parastacid species (Fetzner, personal communication). Some examples of the species described since 2007 include:

- 2007: *Procambarus maya* was described from a salt marsh 1 km from the coast, within Sian Ka'an Nature Reserve, Municipio de Felipe Carrillo Puerto, Quintana Roo, Mexico by Alvarez et al. (2007).
- 2008: Lukhaup and Herbert (2008) described a new species of crayfish, *Cherax* (*Cherax*) *peknyi,* from the Fly River drainage, in the western province region of Papua New Guinea. This species differs from all others in its subgenus by the shape of the rostrum, and chelae, and in coloration.
- 2008: In the United States, a new species, *Orconectes taylori* (common name: Crescent Crayfish), was described by Schuster (2008) from tributaries of the North Fork Obion River in western Tennessee. It occurs in small to medium size sandy bottom streams, and is found in leaf litter and woody debris along the banks. It belongs to the subgenus *Trisellescens* Bouchard and Bouchard, 1995 and can be distinguished from other species in the group by a combination of the length and curvature of the central projection of the form I gonopod, carina on the rostrum, appressed tubercles on the margin of the palm of the chela, and width of the areola.
- from 2008 to 2011, Johnson described two new crayfishes from southeastern Texas, in the United States, within the genus *Fallicambarus*, four new crayfishes from the genus *Orconectes*, a new burrowing crayfish from eastern Texas, *Fallicambarus* (*F.*) *wallsi*, and *Procambarus* (*Ortmannicus*) *luxus* from the southern part of the state (Johnson 2008, 2010, 2011a, 2011b).
- 2009: Thoma and Stocker discovered a new species of crayfish named *Orconectes* (*Procericambarus*) *raymondi* from south-central Ohio, North America. Of the recognized members of the subgenus, it is morphologically most similar to *Orconectes* (*P.*) *putnami*, found in Kentucky and Tennessee and is easily separated from it by the presence of a strong rostral carina. It is distinguished from other recognized members of the subgenus by the rostral carina, mandible structure, and a first form male gonopod having a central projection approximately 50% of total gonopod length.
- 2010: Cooper and Price described *Cambarus* (*Puncticambarus*) *aldermanorum*, a new species of crayfish that appears to be endemic to the lower Catawba and Saluda river basins in the Piedmont Plateau of South Carolinain the United States. Morphologically, it is most similar to *C.* (*P.*) *hobbsorum* and *C.* (*P.*) *hystricosus*. It differs from both species in having a long, narrow, lanceolate rostrum, and in lacking a proximomesial tubercle or spine on the ventral surface of the carpus. It further differs from *C.* (*P.*) *hobbsorum* in having hepatic spines, in other aspects of spination, and in having a broader areola. *Cambarus* (*P.*) *spicatus* of the Broad River basin is another very spinose crayfish that bears some resemblances to *C.* (*P.*) *aldermanorum*, from which it differs in having a broader rostrum with a very short acumen that is delineated at its base by marginal spines or tubercles, and a much broader, more punctate areola. Adams et al. (2010) also gave the description of three new crayfish species in the Tennessee River basin in Mississippi, and the first drainage-specific distributional information in the state for a fourth. The species—*Cambarus girardianus*, *Cambarus rusticiformis*, *Orconectes spinosus* and *Orconectes wrighti*—are also known from Alabama. They discussed taxonomic issues involving *C. girardianus*

Table 2. MS Crayfish Database (Adams and Henderson 2009). Species in bold are new state records and those with asterisks have new distributional information; ^{A}Undescribed species.

Species	Subgenus	Authority	Common name
Cambarus diogenes	*Lacunicambarus*	Girard	Devil Crawfish
C. girardianus	***Hiaticambarus***	Faxon	Tanback Crayfish
C. ludovicianus	*Lacunicambarus*	Faxon	Painted Devil Crayfish
C. rusticiformis	***Erebicambarus***	Rhoades	Depression Crayfish
C. striatus	*Depressicambarus*	Hay	Ambiguous Crayfish
Orconectes compressus	*Gremicambarus*	(Faxon)	Slender Crayfish
O. etnieri	*Trisellescens*	Bouchard and Bouchard	Ets Crayfish
Orconectes sp. *A*	*Trisellescens*		
O. spinosus	***Procericambarus***	Bundy	Coosa River Spiny Crayfish
*O. wrighti**	*Faxonius*	Hobbs	Hardin Crayfish
Procambarus ablusus	*Pennides*	Penn	Hatchie River Crayfish
P. acutus	*Ortmannicus*	(Girard)	White River Crawfish
*P. viaeviridis**	*Ortmannicus*	(Faxon)	Vernal Crayfish

and *O. spinosus*. Based on their distributions in neighboring states, they think that several other species may occur in the Mississippi portion of the basin. According to Adams et al. (2010), the Table 2 below summarizes the crayfish species known from the Tennessee River basin in Mississippi.

- 2011. Taylor and Schuster gave a description of a new crayfish of the genus *Barbicambarus* Hobbs, 1969 discovered in only two locations of the Tennessee River drainage using both morphological characters and molecular data. The new species differs from the type species in possessing a median carina, less dense setae on the antennae, a less angular central projection, a spine at the dorsodistal margin of the merus of the cheliped, and a high level of divergence in the COI gene region. They gave the name *Barbicambarus simmonsi* for this giant crayfish, which is considered native to Tennessee.
- 2011 *Cambarus* (*Puncticambarus*) *smilax*, a new species of crayfish (Cambaridae), was discovered by Loughman et al. (2011) in the Greenbrier River of West Virginia. The authors estimated there are approximately 20 to 30 undescribed species of crayfish in the state. The new species is morphologically most similar to *C.* (*P.*) *robustus*, from which it can be distinguished by a combination of the following characters: adult palm length comprising 73–76% of palm width as opposed to 63–70% in *C.* (*P.*) *robustus*; ventral surface of chela of cheliped with 0–2 subpalmar tubercles compared to 3–6 subpalmar tubercles in *C.* (*P.*) *robustus*; lack of tubercles on the dorsal surface of chela; longer, more tapering, less rectangular rostrum (47–52% rostrum width/length ratio) compared to *C.* (*P.*) *robustus* shorter, less tapering rectangular rostrum (54–63% rostrum width/length ratio); and the central projection of the form-I male gonopod curved ≤ 90 degrees to the shaft.
- 2011 In Australia, *Euastacus morgani* sp. n. was described by Coughran and McCormack (2011) from a highland, rainforest site in Bindarri National Park, in eastern New South Wales. *Euastacus morgani* is found living sympatrically with two more common species, *Euastacus dangadi* Morgan, 1997 and *Euastacus neohirsutus* Riek, 1956. Systematically, the species belongs in the '*simplex*' complex of the genus that includes *Euastacus simplex* Riek, 1956, *Euastacus clarkae* Morgan, 1997, *Euastacus maccai* McCormack and Coughran 2008 and *E. morgani* Coughran and McCormack 2011. This new species differs from its nearest congenor, *Euastacus simplex* Riek 1956, in having three mesial carpal spines. We give here the example of one type of the keys the authors give each time they discover a new species in order to specify morphological and relevant characters. Coughran and McCormack (2011) gave a key to the 'simplex' complex of the genus *Euastacus* detailed in Box 2.

Box 2. Example identification key to the *Euastacus simplex* complex.

1	Chelae with elongate, tapered fingers. Apart from one or two large molars, development of teeth on cutting edges of chelae distinctly reduced. Gape between fingers distinctly broad and lanceolate in shape	*Euastacus maccai* McCormack and Coughran, 2008
1’	Chelae with stout fingers, without distinctive gape between fingers. Lesser cutting edge teeth of moderate size	2
2	Cheliped with 3 mesial carpal spines	*Euastacus morgani* sp. n.
2’	Cheliped with 2 mesial carpal spines	3
3	Dorsal apical propodal spines present. Suborbital spine medium to large	*Euastacus clarkae* Morgan, 1997
3’	Dorsal apical propodal spines absent. Suborbital spine barely discernible to small	*Euastacus simplex* Riek, 1956

- 2012 Rudolph and Crandall discovered a new species of burrowing crayfish, *Virilastacus jarai* (Parastacidae) in the south central part of Chile. This is the fourth species of *Virilastacus*, a genus endemic to Chile, to be described to date. Features that distinguish *V. jarai* from its congeneric species are: (1) rostral carina, short, slightly prominent and widely separated from the orbital margin; (2) pilous dorsal side of the opposable margin of the P1 propodus, as is the basal zone of the ventral side, 11 to 22 teeth on its opposable margin; (3) dorsal surface of the P1 dactylus close to the opposable border, hirsute; external distal border of the ischiopodite of the third maxilliped with a large extension that ends in the form of a right angle; (4) precervical cephalothorax with dorsal ridges absent, or with two or four; (5) areola, wide and extended; (6) telson with small, but sharp, lateral spines. Morphologically, this new species is similar to *Virilastacus araucanius* and *V. retamali*, with whom it shares 14 of the 27 morphological attributes analyzed, nine of which are common to these three species. These same attributes (13 of 14) differentiate *V. jarai* from *V. rucapihuelensis*, with whom it only shares seven morphological traits. The morphological similarity of *V. jarai* with *V. araucanius* and *V. retamali* contrasts with the degree of genetic divergence that exists between these species.
- 2013 Furse et al. discovered two new species of the crayfish genus *Euastacus*, described from the Gondwana Rainforests on the Queensland—New South Wales border region of Australia—*Euastacus binzayedi* and *Euastacus angustus.* Both are small, poorly spinose species that are broadly similar in appearance and coloration to *Euastacus dalagarbe* Coughran, from the same region. Both species can be readily distinguished from *E. dalagarbe*; *Euastacus binzayedi* by the numerous bumps and protrusions on the dorsal and ventral surfaces of its chelae, and *Euastacus angustus* by its unusual, laterally compressed body shape, and the large ventromesial carpal spine. Cytochrome oxidase I divergence estimates from the most closely related species were high for both *Euastacus binzayedi* (4.8%), and *Euastacus angustus* (8.7%). Morphologically, both of these new species belong in a clearly defined, poorly spinose group, and both appear to be exceptionally rare, each known from a single locality. That same year, Loughman et al. (2013a) discovered *Cambarus* (*Puncticambarus*) *theepiensis*, a stream-dwelling crayfish that appears to be endemic to the junction of the Cumberland Mountains with the Appalachian Plateau in West Virginia and Kentucky. The new species is morphologically most similar to *Cambarus robustus* and *Cambarus sciotensis.* Moreover, Loughman et al. (2013b) described the new species *Cambarus* (*Cambarus*) *hatfieldi*, a stream-dwelling crayfish that appears to be endemic to the Tug Fork River system of West Virginia, Virginia, and Kentucky. The new species is morphologically most similar to *Cambarus sciotensis* and *Cambarus angularis.*
- 2014 Simon and McMurray (2014a) described *Orconectes alluvius* (detrital crayfish) from southwestern Indiana while Simon and Morris (2014b) described *Cambarus erythrodactylus* (warpaint mudbug) from Alabama and Mississippi, which was formerly part of the *Cambarus diogenes* complex. In addition, Thoma et al. (2014) described *Cambarus callainus* (Big Sandy crayfish), from the Big Sandy River drainage system in Kentucky, Virginia and West Virginia. These populations were previously considered to be *Cambarus veteranus* (now restricted to the Guyandotte River drainage), but both morphological and genetic data suggests these are separate taxa, both of which are being considered for listing under the U.S. Endangered Species Act.

- 2015 Several new *Cherax* species have been described from West Papua, Indonesia, including *Cherax pulcher* (Lukhaup 2015) and *Cherax gherardii* (Patoka et al. 2015), both with very restricted distributions. In the United States, Thoma and Fetzner (2015) described *Cambarus magerae* from Big Stone Gap in Virginia while Loughman et al. (2015) described *Cambarus pauleyi* from two adjacent counties in West Virginia. And finally, Pedraza-Lara and Doadrio (2015) have described Cambarellus zacapuensis, which is known from only a single locality in central México.

Insights on the families and genera

Taylor et al. (2007) provided a list of all crayfish (families Astacidae and Cambaridae) in the United States and Canada. The two families occur natively in North America and it is here that crayfish reach their highest level of diversity. In Europe, indigenous crayfish species (ICS) are only represented by members of the Astacidae, with the cambarids being non-indigenous crayfish species (NICS) recently introduced into Europe. As previously explained, the family Parastacidae contains all freshwater crayfish found naturally occurring in the southern hemisphere.

Family Astacidae Latreille, 1802

The Family Astacidae (three genera, 16 species according to Hobbs, 1989) are distributed both in Europe and west of the Rocky Mountains in the northwestern United States and northward into southern British Columbia, Canada.

Astacidae in Europe

The *Atlas of Crayfish in Europe* (Souty-Grosset et al. 2006) shows that only five crayfish species, all belonging to the family Astacidae, are native to Europe, according to the taxonomy adopted by Holdich (2002), with three from the genus *Astacus* and two from *Austropotamobius*. For *Astacus*, these include the noble crayfish, *Astacus astacus* (Linnaeus 1758), the narrow-clawed crayfish, *A. leptodactylus* (Eschscholtz 1823), and the thick-clawed crayfish, *A. pachypus* (Rathke 1837). The genus *Austropotamobius* includes the white-clawed crayfish, *A. pallipes*, and the stone crayfish, *A. torrentium* (Schrank 1803). The present distributions of these ICS are the result of both natural events that occurred during the Pleistocene up until recent historical times, and translocations attributable to human activities. Identification keys are given in order to identify ICS and NICS in Europe; Box 3 below is extracted from the crayfish guide of Romania (Pârvulescu 2010) illustrating how to distinguish *Astacus astacus* from *Astacus leptodactylus*, *Austropotamobius torrentium* and the introduced North American species, *Orconectes limosus* (Rafinesque 1817), the spinycheek crayfish.

Recent molecular studies by Filipova et al. (2011) were aimed at verifying the taxonomic status of European crayfish through DNA barcoding. They compared sequences obtained from the cytochrome *c* oxidase subunit I (COI) gene fragment from sampled American populations with populations now present in European waters. They demonstrated that DNA barcoding is useful for the rapid and accurate identification of exotic crayfish in Europe, and also provided insights into overall variation within these species.

The genus *Astacus*

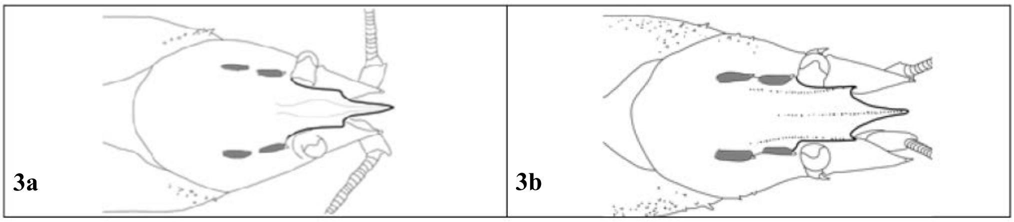
The genus *Astacus* must have been formed during the Paleogene in response to a changing regime of inland waters. The genus dispersed widely in Europe during Neogene times, but the Pliocene cooling of the climate is believed to have divided a single species (*A. astacus*) of the genus into three species or subspecies: *A. a. colchicus* is the most archaic of them, having survived in Western Transcaucasia; *A. a. balcanicus* must have emerged in the Balkan peninsula, while *A. astacus*, the most advanced species, occupied all the northern parts of Europe.

Box 3. Key to crayfish in Europe (courtesy of Lucian Pârvulescu).

1. Two pairs of post-orbital ridges: 3

    3a. First post-orbital ridges more prominent and ending atypically with a spine, the second post-orbital ridges are blunt. Strong rostrum with parallel edges more or less sharp apex. Sides of the cephalothorax and of the cervical groove with spines: *Astacus astacus*

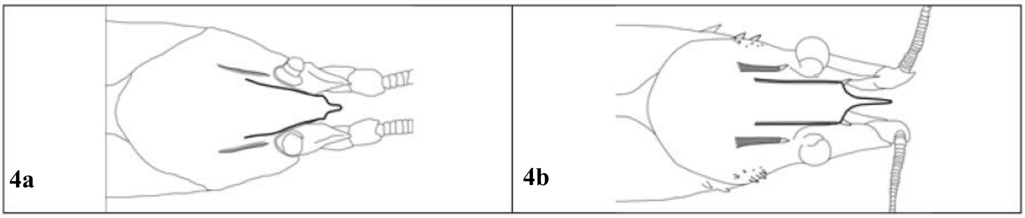
    3b. Both post-orbital ridges visible and with one apical spine each. Strong rostrum with parallel edges, sharp apex. On the sides of the cephalothorax and of the cervical groove 1–3 prominent spines and several tubercles or small spines: *Astacus leptodactylus*



2. One pair of post-orbital ridges: 4

    4a. The post-orbital ridges as a crease, triangular shaped rostrum with a less obvious apex and without median carina: *Austropotamobius torrentium*

    4b. Post-orbital ridges prominent, ending atypically in obvious spine, rostrum with parallel edges and sharp apex. Many hepatic spines on the sides of the cephalothorax: *Orconectes limosus*



Astacus astacus (Linnaeus 1758) (noble crayfish):

In the genus *Astacus*, the noble crayfish, *Astacus astacus* (Linnaeus 1758), is widely distributed in Europe, from France in the southwest to Russia in the east, and from Italy, Albania and Greece in the south to Scandinavia in the north (Cukerzis 1988, Skurdal and Taugbøl 2002) and has been stocked into numerous new localities, especially in marginal areas, so that this crayfish now has a larger distribution than it originally had, and is currently found in 39 territories across most of northern Europe. Although its range was much greater before the onset of the crayfish plague, a fungal infection which is responsible for the widespread reduction of the number of crayfish populations throughout Europe (Holdich et al. 2009). The species is widely harvested, and many countries have national and federal regulations governing trapping seasons and size restrictions (Skurdal and Taugbøl 2002). The most abundant populations exist in Nordic and Baltic countries (e.g., it is the dominant crayfish in Latvian waters, having been found in 220 out of 258 crayfish localities) (Taugbøl et al. 2004, Arens and Taugbøl 2005). *Astacus astacus* was introduced into Cyprus from Denmark in the 1970s, and although the original stock has disappeared, it apparently occurs by the Lefkara dam (Stephanou 1987).

According to the recent IUCN assessment (Edsman et al. 2010), although the noble crayfish is a widespread species, it has undergone significant declines in population numbers due to unfavourable interactions with non-indigenous species, crayfish plague, habitat loss and over-harvesting. Estimates of the rate of decline in Sweden, Finland and Norway are as high as 78%, ~ 20% and 61%, respectively, over a 3 generation period. Similar rates of decline are being seen within a number of other countries. Globally, this species is estimated to be declining at a rate of 50–70%, however, in some parts of its range, numbers are stable and there have been some successful re-stocking programs, so the true rate of decline may in fact be slightly lower.

Astacus leptodactylus Eschscholtz, 1823 (narrow-clawed crayfish)—species complex: According to Holdich et al. (2009), the narrow-clawed crayfish, *Astacus leptodactylus* Eschscholtz, 1823, has a southeastern European range and is indigenous to Russia and the Ponto-Caspian area. It was originally distributed over an area corresponding more or less to Turkey, the Ukraine, Turkmenistan and southwestern Russia, but is also found in Iran, Kazakstan, Georgia, Belarus, Bulgaria, Romania, Hungary and Slovakia. The Caspian Sea, the Black Sea and the lower and middle Danube are in its original distribution area, along with the lower reaches of the rivers Don, Dniester and Volga and their tributaries (Köksal 1988, Holdich 2002). However, this crayfish has been widely introduced into many countries as a replacement for noble crayfish populations lost due to crayfish plague. The species is currently found in 32 territories across most of Europe, with the exception of Scandinavia and the Baltic Peninsula, although its range was probably greater before the onset of the crayfish plague (Holdich et al. 2009). The systematics of this species complex is in a state of flux, with populations from Western and Central Europe referred to as *A. leptodactylus*, whilst in Eastern Europe, a number of species are recognized within a separate genus *Pontastacus* (Starobogatov 1995, Śmietana et al. 2006). *Astacus leptodactylus* is considered a species complex (see IUCN assessment: Gherardi and Souty-Grosset 2010a). In the 1950s, this species was believed to belong to the subgenus *Astacus* (*Pontastacus*), and included *A.* (*P.*) *pachypus, A.* (*P.*) *pyzlowi* and *A.* (*P.*) *kessleri*. The following four subspecies were assigned to *A.* (*P.*) *leptodactylus*: *eichwaldi, cubanicus, salinus*, and *leptodactylus*. Karaman (1962, 1963), however, did not acknowledge *A.* (*P.*) *cubanicus* as a subspecies. In the 1970s, *Pontastacus* was raised to the generic level. In the 1980s, Brodskij made a number of revisions within *Pontastacus*, but the number of taxa varied with each paper. In the mid-1990s, Starobogatov (1995) split *Pontastacus* into two genera including *Pontastacus*, which contained *P. angulosus* (Rathke, 1837), *P. cubanicus* (Birstein and Winogradow 1934), *P. danubialis* (Brodskij, 1967), *P. eichwaldi* (Bott, 1950), *P. intermedius* (Bott, 1950), *P. kessleri* (Schimkewitsch, 1886), *P. pyzlowi* (Skorikov, 1911) and *P. salinus* (Nordmann, 1942). The second genus, *Caspiastacus*, contained two species (*C. pachypus* Rathke, 1837 and *C. daucinus* (Brodsky, 1981)). However, there is a great deal of criticism over recent taxonomic revisions made by Ukranian and Russian taxonomists, as they appear to be based on little evidence. The most abundant populations are found in Eastern Europe and the Near East. Large commercial stocks of *A. leptodactylus* exist in Belarus (Alekhnovich 2006). This species is prone to the effects of crayfish plague and in recent times there have been reports of introduced populations being affected in England (Environment Agency 2007), and Switzerland (Hefti and Stucki 2006). Simić et al. (2008) report that although *A. leptodactylus* is spreading in some regions of Serbia, in others, their numbers are being reduced by the presence of *O. limosus*. Although crayfish plague devastated populations in Turkey in the 1980s, resulting in very low harvests (down from 5000 tonnes in 1984 to 320 tonnes in 1991), a partial recovery has been recorded in the 2000s (i.e., 2317 tonnes in 2004), and previously plague-infected lakes are productive again (Harlioğlu 2008). Perdikaris et al. (2007) have also reported *A. leptodactylus* from the River Evros in Greece, where it was probably deliberately introduced. Tertyshny and Panchishny (2009) have reported large-scale mortalities amongst the stocks from aquaculture of *A. leptodactylus* in the Ukraine, which are partly attributable to disease.

Astacus pachypus Rathke, 1837 (thick-clawed crayfish), occurs in the Caspian Sea and in the brackish waters of the estuaries of the Dniester and the Bug, and is recorded from two European countries, as well as some western Asian countries. At the present time, this species is indigenous to Russia, Ukraine, Azerbaijan, Turkmenistan and Kazakhstan (Machino and Holdich 2006, Holdich et al. 2009). In Azerbaijan, it is known from the coastal waters off Baku (Holdich 2002); in Kazakhastan, this species is known from the coastal waters of the Caspian Sea (Sokolsky et al. 1999); in Turkmenistan, it is known from coastal waters (Cherkashina 1999a). In the Ukraine, this species is known from the Dneiper-Bug Lagoon of the Azov-Black Sea Basin (Cherkashina 1999b). In the 1950s, this species was thought to belong to a different subgenus from *Astacus* (i.e., was thought to belong to *A.* (*Pontastacus*) *pachypus*, along with the species *pylzowi, kessleri* and *leptodactylus*). The subgenus *Pontastacus* has since been elevated to generic level, and subsequently to a new genus (*Caspiastacus*) in 1995 by Starobogatov (Souty-Grosset et al. 2006). The taxonomy of Eurasian crayfish is questionable, as there appears to be little validity for revisions to the existing taxonomy. There is considerable morphological variation across the Eurasian species, and it is thought that there is hybridization between *A. pachypus* and *A. leptodactylus*. The only way to truly delineate the precise range of each species is to conduct comparative molecular genetic studies (see IUCN assessment by Gherardi and Souty-Grosset 2010b).

The genus *Austropotamobius*

Among the European crayfish, the genus *Austropotamobius* Skorikov, 1907, is widely distributed throughout west and central Europe, from the Iberian Peninsula in the west and the British Isles in the north to Italy and the Balkan Peninsula in the south and east (Holdich 2002). It comprises two species, the circum-alpine stone crayfish, *Austropotamobius torrentium* (Schrank, 1803), and the white-clawed crayfish, *Austropotamobius pallipes* (Lereboullet, 1858). However, the situation within each species is more complicated, especially for the white-clawed crayfish (*A. pallipes*). Its taxonomy is still under debate in spite of well-advanced research, particularly in genetics (see details in Chapter 2 of this volume).

According to molecular data, the historical events leading to the main splits in the genus took place during the second half of the Miocene. At that time, the landmass of the Adriatic microplate separated the Paratethys from the paleo-Mediterranean sea (Dercourt et al. 1986). The resulting two major drainages thus might have formed the basis for the split of the ancestral *Austropotamobius* into the *pallipes* and *torrentium* lineages (Souty-Grosset et al. 2006).

Austropotamobius torrentium (Schrank, 1803) (stone crayfish): three subspecies are known: *Austropotamobius torrentium torrentium, A. t. danubicus*, and *A. t. macedonicus*. This species is mainly confined to Central Europe where it is known from France and western Germany in the west of its range, to Turkey in the east (Füreder et al. 2006). Indeed, the species is currently known from 20 countries, but with a restricted range in Central and Southeastern Europe, where it was most likely more widely distributed in the past. It is the most southerly of the European ICS, extending as far as Bulgaria and Romania, and has recently been found in Turkey (Harlioğlu 2007). Perdikaris et al. (2007) have confirmed the presence of *A. torrentium* in the River Evros in Greece for the first time in 112 years. While this species is relatively widespread across Europe, it is undergoing significant declines throughout much of its range (IUCN assessment, Füreder et al. 2010a).

Austropotamobius pallipes (Lereboullet, 1858) (white-clawed crayfish—species complex) has a wide distribution throughout Europe. It was previously thought that the western limit of the species range was in Portugal (although it is now thought to be extinct there), but is now northwestern Spain. Montenegro is the eastern limit, whilst Spain and Scotland are the southern and northern limits, respectively. Its distribution is restricted in Austria, Corsica, Germany, Lichtenstein and Montenegro (Souty-Grosset et al. 2006). This species, currently found in 17 countries, has a narrower range than those of *A. astacus* and *A. leptodactylus*, and is more centred in Western, Central and Southern Europe. Machino et al. (2004) have catalogued the many introductions of *A. pallipes* that have been made throughout Europe. There is a wide genetic diversity within the second taxon, so that some authors have suggested dividing it into two phylogenetic species: *Austropotamobius pallipes* and *A. italicus* (Grandjean et al. 2000, Zaccara et al. 2004, Fratini et al. 2005). If the division of the species into *A. italicus* (Faxon, 1814) and *A. pallipes* is accepted, then the distribution map will have to be redrawn (Fratini et al. 2005, Bertocchi et al. 2008). In northern Europe, these two species can be clearly defined at a molecular level, but farther south, several subspecies have been recognized. Allopatric speciation of the two taxa led to *A. pallipes* being distributed in west-central Europe (France, Great Britain and Northern Italy) and *A. italicus* in Switzerland, Austria, Italy, the Balkans and Spain (Grandjean et al. 2002a,b). Phylogeographic studies confirmed the presence in Italy of both *A. pallipes*, confined to North-Western Italy, and *A. italicus*, distributed across the peninsula (Fratini et al. 2005). However, research is still in a state of flux, so that the general consensus is to define the taxon as a species complex, with a number of distinct genetic strains related to their recent history, but which are not distinguishable morphologically (Souty-Grosset et al. 2006).

Some consider *Austropotamobius pallipes* as a species complex comprised of two genetically distinct species; *A. pallipes* and an Italian species for which the name is being discussed. The Italian species is thought to be comprised of a number of subspecies, though this depends on the author. Both the Italian form and *A. pallipes* can be found in Spain, France, Italy and Switzerland. It is also suggested that there are two subspecies of *A. pallipes*: *A. pallipes pallipes*, which exists in France, the British Isles, Spain, Switzerland, and Germany, and *A. p.* subsp. which is known from Liguria in Italy and the Alpes Maritimes region of France. There still exists some debate as to whether the Italian form should be raised to species level, though recent genetic work (Grandjean et al. 2000a, Fratini et al. 2005, Bertocchi et al. 2008) would support a separate species, *Austropotamobius italicus* with 4 subspecies. The White-clawed crayfish has been assessed as Endangered under criterion A2ce. In the last ten years, this species is suspected to have undergone a decline of somewhere between 50–80% based on presence/absence data available for England, France and Italy (IUCN assessment, Füreder et al. 2010b).

Astacidae in North and Central America

The family Astacidae and the particular case of the genus *Pacifastacus* (example of *Pacifastacus leniusculus*, ICS in North America and NICS in Europe).

Pacifastacus leniusculus Dana 1852 (signal crayfish): three subspecies have been historically recognised in North America including: *Pacifastacus l. leniusculus*, *P. l. trowbridgii* and *P. l. klamathensis* (Miller 1960). These sub-species are difficult to distinguish because both their morphological characters and their distribution range overlap. Sonntag (2006) examined mtDNA variation in signal crayfish populations from the Klamath River Basin in California and Oregon in North America and was able to distinguish the three subspecies using this DNA marker. In Europe, the first studies were based on the RFLP analysis of mtDNA (Grandjean and Souty-Grosset 1997) suggested that the high variation found in three French signal crayfish populations could reflect the presence of more subspecies in Europe. However, the recent study by Filipova (2012) used an mtDNA analysis of signal crayfish sampled from 17 European countries and showed that only the lineage corresponding to *P. l. leniusculus* seems to have been introduced into Europe. A recent study by Larson et al. (2012) found substantial cryptic diversity across the range of the species, with three main groups that were highly distinct from *P. leniusculus*, each being found in discrete geographic regions. In North America, *Pacifastacus leniusculus leniusculus* is distributed in southern British Columbia in Canada, and in California, Idaho, Oregon, and Washington in the USA. *Pacifastacus leniusculus klamathensis* is distributed in British Columbia in Canada, Idaho and south to central California in the USA. *Pacifastacus leniusculus trowbridgii* ranges from British Columbia in Canada to California, Idaho, Oregon and Washington in the USA, and has been introduced into California and Nevada in the USA, and also introduced into Japan. Furthermore, this subspecies is also known to occur in Greece (Koutrakis et al. 2007). *Pacifastacus leniusculus* has been introduced into many countries throughout Europe, as well as to California, Nevada and Utah in the USA. This species was introduced during the 1970s and 1980s, is widely cultivated, and is established in the wild, from where it is harvested (Harlioğlu and Holdich 2001).

Family Cambaridae

The family Cambaridae is distributed in North America east of the Rocky Mountains, from southern Canada in the north to Central America in the south, and with one genus (*Cambaroides*) being disjunct and restricted to eastern Asia. This family contains the most described freshwater crayfish species, with 444 species currently distributed among 12 genera (see Table 1).

In the family Cambaridae, there are three highly specious genera that account for roughly 86% of the known species and these include: *Procambarus* (178 species, 40.1%), *Cambarus* (106, 23.9%) and *Orconectes* (97, 21.9%). The remaining nine genera contain fewer species and include *Barbicambarus* (2 taxa), *Bouchardina* (1), *Cambarellus* (17), *Cambaroides* (7), *Distocambarus* (5), *Fallicambarus* (19), *Faxonella* (4), *Hobbseus* (7) and *Troglocambarus* (1).

North and Central America

Members of the family Cambaridae occur natively in North America and it is here that crayfish reach their highest level of diversity. Reasons for this high level of biodiversity include isolation from glacial advances and geological and topographic diversity. Approximately 68% (444 species and subspecies) of the world's known species occur in North America (Taylor 2002), with the overwhelming majority of this continent's crayfish fauna (98%) assigned to the family Cambaridae (the remainder are from the family Astacidae, see above). With over two-thirds of its species endemic to the southeastern United States, the distribution of crayfish diversity in North America closely follows that observed in other freshwater aquatic taxa, such as fishes (Warren and Burr 1994) and mussels (Williams et al. 1993).

The state of Alabama in the USA is home to one of the most diverse crayfish faunas in the world, with a current count of 89 species, all found in an area of roughly 135,000 km^2 (Schuster et al. 2008). These species are from seven different genera, of which only the virile crayfish, *Orconectes virilis*, is considered to be non-native. Eleven of these species are endemic to the state, and thus are found nowhere else. The state of Alabama lists almost one third (28) of these as species of greatest conservation need (Wildlife and Freshwater Fisheries Division 2005). Several other states from the southeastern U.S. have similarly high levels of diversity and these include: Tennessee (84 species), Georgia (72), Mississippi (63), Arkansas (60), Florida (56) and Kentucky (52). Unfortunately, there is still very little known about many of these species, especially the limits of their distributions and detailed life histories (Moore et al. 2013).

The number of crayfish species described or reported from North America declines from south to north. For example, in Canada only 11 species in total are known (Hamr 1998). Most (nine crayfish species) are found in Ontario, including five species of *Orconectes*, two *Cambarus* and one *Fallicambarus*, plus the northern clear water crayfish, *Orconectes propinquus* (Girard, 1852) which is dispersing up the St. Lawrence River from Quebec. Ontario and Quebec (eight species) have the highest species richness of crayfishes in Canada. Of the 11 Canadian crayfishes, the only two that do not occur in Ontario are the spinycheek crayfish (*Orconectes limosus*), which is found in Quebec, New Brunswick and Nova Scotia, and the signal crayfish, which is found in British Columbia. Two provinces (Newfoundland and Labrador and Prince Edward Island) and the three Canadian territories lack crayfish faunas due to their extreme northern latitudes.

The genus *Procambarus*

The genus *Procambarus* contains the largest number of species of any genus of freshwater crayfish worldwide. Currently, there are 170 described species and 16 taxa listed as subspecies (Fetzner 2005). They are distinguished from other genera by having a male gonopod with four terminal elements. The native range of the genus is in North America, ranging along the eastern seaboard and the coastal regions of the Gulf of Mexico, up the Mississippi River drainage as far as southern Wisconsin, and south through Texas and Mexico to Honduras (Hobbs 1972). The genus was divided into 16 different subgenera by Hobbs (1972) and these include: *Acucauda* (1 species), *Austrocambarus* (24), *Capillicambarus* (3), *Girardiella* (22), *Hagenides* (10), *Leconticambarus* (14), *Lonnbergius* (2), *Mexicambarus* (1), *Ortmannicus* (59), *Paracambarus* (2), *Pennides* (20), *Procambarus* (1), *Scapulicambarus* (6), *Tenuicambarus* (1) and *Villalobosus* (13). The last subgenus, *Remoticambarus*, which contained the monotypic cave-adapted species, *Procambarus* (*R.*) *pecki*, was recently found to be most closely related to members of the *Cambarus* subgenus *Aviticambarus*, and is now considered a member of that group (Buhay and Crandall 2009).

At least one species, the red swamp crayfish (*Procambarus clarkii*, Girard 1852), now has what could be considered a worldwide distribution, after being introduced into many countries either intentionally via the aquaculture industry, or accidently via the pet trade. In many areas where it has been introduced, it has had severe adverse impacts on native crayfish, either by direct competition or through the spread of the crayfish plague, and has been implicated in the declines of other native species of aquatic flora and fauna.

Mexico and Central America together comprise another "hot spot", which contains 55 native cambarid species from two genera (*Cambarellus* and *Procambarus*), whereas only four species have been described from Guatemala, two from Belize, one in Costa Rica (probably introduced) and the Dominican Republic (also introduced) and four from Cuba. According to Mejía-Ortíz et al. (2003), the Mexican crayfish fauna is restricted to the two previously mentioned native genera, of which only members of the genus *Procambarus* have been recorded from underground habitats (Reddell 1981, Hobbs 1989). In Mexico, *Procambarus* is represented by members from nine of the 16 recognized subgenera, with *Austrocambarus* having the greatest representation with 16 species and subspecies (Villalobos et al. 1993, Rojas et al. 1999, 2000), and possibly several as yet undescribed species (Allegrucci et al. 1992). In Mexico, 15 species of *Procambarus* have been previously recorded from hypogean waters. Ten of these are stygophiles (those that can be found in caves but that lack the adaptations to cave life), and in most cases they are also known from epigean waters. Only five are considered true stygobites (those being found exclusively in caves and with clear adaptations to cave habitats). These species include *Procambarus* (*Ortmannicus*) *xilitlae* (Hobbs and Grubbs 1982), distributed to the north of the Cordillera, and *Procambarus* (*Austrocambarus*) *rodriguezi* (Hobbs 1943), *Procambarus* (*Austrocambarus*) *oaxacae oaxacae* (Hobbs 1973), *Procambarus* (*Austrocambarus*) *oaxacae reddelli* (Hobbs 1973) and *Procambarus* (*Austrocambarus*) sp. 2 (Allegrucci et al. 1992), all from south of the Cordillera. Mejía-Ortíz et al. (2003) described a new stygobitic species of *Procambarus* (*Austrocambarus*) inhabiting Gabriel Cave near Buenos Aires, Oaxaca, Mexico and discuss its affinities with other members of the subgenus. They also reviewed the distribution of stygobitic and stygophilic species of *Procambarus* in Mexico.

Several recent attempts have been made, not only by Mexican scientists but by many other organizations, to identify all Mexican crayfish species. For example, *Procambarus regiomontanus* was only found in the state of Nuevo Leon and this endemic species is now endangered due to the introduction of *Procambarus clarkii* into streams in this region.

The genus *Cambarus*

The genus *Cambarus* is the second largest crayfish genus in the Northern Hemisphere and it currently contains 12 subgenera (*Aviticambarus* (6 species), *Cambarus* (11), *Depressicambarus* (17), *Erebicambarus* (5), *Exilicambarus* (1), *Glareocola* (3), *Hiaticambarus* (11), *Jugicambarus* (26), *Lacunicambarus* (4), *Puncticambarus* (23), *Tubericambarus* (4), *Veticambarus* (1)) and 111 species. Members of this genus can be distinguished by the presence of two terminal elements on the male form I gonopod that are curved at an angle of roughly 90º from the main axis of the appendage. *Cambarus* ranges from the coastal region of New Brunswick, Canada, south to the Florida panhandle, west to Texas, and northward to Minnesota and southern Ontario, Canada (Hobbs 1969). The genus has its center of diversity in the Southern Appalachian Mountains of the eastern United States (Hobbs 1969).

Members of the subgenus *Jugicambarus* are a variable group, with some forms occupying diverse habitats and ecological niches, such as rivers and streams, lakes, burrows and caves. The burrowing crayfish, such as *C.* (*J.*) *dubius*, *C.* (*J.*) *monongalensis* and *C.* (*J.*) *carolinus* (among others), can have quite striking color variations, ranging from deep red, orange, and royal blue, and multiple combinations thereof. Most of these species are primary burrowers (Hobbs 1969, 1989), and spend the majority of their lives underground in the burrows they construct.

Another large subgenus, *Puncticambarus*, contains large crayfish (> 15 cm) that mostly inhabit bigger river systems. Species such as *C.* (*P.*) *robustus*, *C.* (*P.*) *cumberlandensis,* and the highly imperiled *Cambarus* (*P.*) *veteranus* are all part of this group. *Cambarus robustus* has a rather large distribution, ranging from southern Ontario and New York to North Carolina and Tennessee in the south, and then to Illinois in the west. However, Hobbs (1989) and others have considered this to be a large species complex for quite some time, and several new species have already been described from this complex, such as *Cambarus smilax* (Loughman et al. 2011). *Cambarus veteranus* is limited in its distribution to the upper tributaries of the Guyandotte River drainage of West Virginia. This species is quite rare and is being adversely impacted by human land use practices, such as logging operations and mountain top removal mining, which dump large quantities of sediment into rivers, making them uninhabitable for crayfish and other aquatic organisms.

The genus *Orconectes*

The genus *Orconectes* is comprised of 11 subgenera, 93 species and 11 subspecies. Members of the genus also have a male gonopod with two terminal elements, but rather than being curved at 90º like in *Cambarus*, they are usually longer and straight to only slightly curved. The distribution of the genus ranges from the eastern side of the Rocky Mountains to the east coast and from southern Canada southward to the Gulf coast, but is mostly absent from the core southeastern states of Alabama, Georgia, South Carolina and Florida.

The eleven subgenera include the monotypic *Billecambarus* (1 species), *Buannulifictus* (8), *Crockerinus* (16), *Faxonius* (3), *Gremicambarus* (7), *Hespericambarus* (8), *Orconectes* (10), *Procericambarus* (31), *Rhoadesius* (2), monotypic *Tragulicambarus* (1) and *Trisellescens* (10).

One of the most frequently mentioned species, *Orconectes virilis* (Hagen, 1870), commonly called the northern or virile crayfish, and a member of the subgenus *Gremicambarus*, grows on average to 10–12 cm in length, excluding its antennae and large chelipeds. The color of the body and abdomen are brownish-red, dappled with dark brown spots. The chelae, or the palm of the large chelipeds, are wide, flattened and possess a straight dactyl margin. The chelae and legs have a bluish tint with yellow tubercles (Hamr 2002). *O. virilis* has a wide natural range from Alberta to Quebec, Canada, throughout more than half of the United States from Texas to Maine, and Chihuahua, Mexico (Hamr 2002). But in Massachusetts, *O. virilis* is believed to be an invasive species (Hobbs 1989), and is listed as such by the Global Invasive Species Database (http://www.issg.org/database/). Its habitats include rivers, streams, lakes, ponds, and marshes.

Another species from the genus that has received considerable attention, especially as an invasive species is *Orconectes rusticus* (Girard, 1852), or the rusty crayfish. This species is a member of the large subgenus *Procericambarus* and has a native range in parts of Indiana, Michigan and Ohio, but has been widely introduced into other areas of the United States (e.g., Illinois, Wisconsin, Pennsylvania, Maryland, and others), and has caused significant declines or local extinctions of other native crayfish species, and have also impacted other aquatic flora and fauna. These crayfish typically grow larger and are able to outcompete other crayfish for food, shelter and other resources. Introgression also appears to be a common method that this species employs to displace other native crayfish from the habitats it invades (Perry et al. 2001a,b).

The spinycheek crayfish, *Orconectes limosus* (Rafinesque, 1817), a member of the subgenus *Faxonius*, is native to the northeastern states, and has also been introduced into many parts of Europe, where it has dispersed widely from its original sites of introduction, either through natural dispersal or human-aided translocations. The species also carries the crayfish plague, and has adversely impacted many of the native European species.

In Missouri, the long pincered crayfish, *Orconectes longidigitus* (Faxon 1898), is native to the White River drainage, and is one of the largest species in North America. In more recent years, are creational fishery in the state has become increasingly popular. Another species, *Orconectes meeki* (Faxon, 1989) is found in the upper White River drainage of Missouri and Arkansas. It is listed as critically imperiled and is among the rarest crayfish in the state. Additionally, the coldwater crayfish, *Orconectes eupunctus* (Williams, 1952), is also critically imperiled and is restricted to only three river drainages in Missouri and Arkansas. The species is typically associated with cold spring-fed rivers in the region and is being impacted by the recent introduction of another crayfish.

Japan and Southeast Asia

The taxonomy of the Asian cambarid genus *Cambaroides*, known from southeastern Russia, Mongolia, North and South Korea, China and Japan, still remains unresolved (e.g., Starabogatov 1995, Kawai et al. 2003, Braband et al. 2006, Kawai 2012). The taxa from Mongolia, Russia and Japan are considered endangered. Starobogatov (1995) suggested that there were 7 species, but recent studies by Kawai and workers suggest that there may only be four.

Cambaroides japonicus (De Haan, 1841) is the only crayfish native to Japan and is restricted to Hokkaido (Kawai 1996). The invaders, such as *Procambarus clarkii* and *Pacifastacus leniusculus* (Dana, 1852), are now also present. The same native genus is encountered in Korea, with the named species *Cambaroides similis* (Koelbel, 1892) and *C. wladiwostokensis*, and in central China, with two species *Cambaroides koshevonikowi*. Here again, *P. clarkii* is present, and farmed on a large scale (production exceeding 100000 tonnes per year).

Family Parastacidae

The family Parastacidae comprises 14 extant genera (~180 species) of which 10 are found in Australia, New Guinea and New Zealand, three in South America and one in Madagascar (Crandall and Buhay 2008, Toon et al. 2010).

South America

According to the review of Almerão et al. (2015), in South America, the first observations of crayfish were made by von Martens (1869) with the description of *Astacus pilimanus* and *A. brasiliensis*, collected in Porto Alegre and Santa Cruz do Sul (Brazil). Following this work, there were many other works on the taxonomy and systematics of South American crayfish: including those by Huxley (1880), Faxon (1898, 1914), Ortmann (1902), Riek (1969, 1972), Buckup and Rossi (1980), Crandall et al. (2000), and Rudolph and Crandall (2005, 2007). Currently, there are 13 species (aforementioned) and for a few, some remarks are necessary. *Parastacus saffordi* was described by Faxon (1898) based on the examination of one individual collected in Montevideo (Uruguay). Buckup and Rossi (1980) identified two specimens of *P. saffordi* from Siderópolis (state of Santa Catarina) and another from the collection of the National Museum of Rio de Janeiro (Cubatão River, state of Santa Catarina). Over a twenty-year period, Buckup performed numerous sampling campaigns in both states (Santa Catarina and Rio Grande do Sul), but never found a specimen with the morphological features originally ascribed to *P. saffordi*. Investigations of the collections from Museo de Historia Natural and from Facultad de Ciencias de la Universidad de la Republica in Montevideo did not reveal the presence of this species. Moreover, *P. saffordi* shows some morphological similarities with *P. varicosus* and thus it is probable that the two species are conspecific. Another taxonomic problem concerns *P. laevigatus* that was described based on individuals deposited in National Museum of Rio de Janeiro (NMRJ) (Buckup and Rossi 1980). Unfortunately, these individuals were lost and never found. In 1990, Buckup collected only one individual of *P. laevigatus* further south (Laguna, state of Santa Catarina) from the type locality (Joinville, state of Santa Catarina). However, it was not possible to confirm it was *P. laevigatus* because the type material deposited in NMRJ was lost. All of these taxonomic uncertainties are being investigated further (Buckup, pers. comm.).

The thirteen South American crayfish species all belong to three genera—*Parastacus* (8 species), *Virilastacus* (4) and *Samastacus* (1)—and they are distributed in Southern Brazil, Uruguay, central to southern Chile and in Southern Argentina (Crandall et al. 2000). This group forms a well-supported clade within the larger Parastacid phylogeny, with supported subclades representing the three genera (Crandall et al. 2000, Sinclair et al. 2004, Toon et al. 2010).

The first collections of freshwater crayfish in South America were made in the 18th century (Buckup 1998). Since then, populations have been identified in several localities in Brazil, Uruguay, Argentina and Chile. It has been postulated that this distribution pattern has been influenced by marine water permanence during the transgressions that occurred from the Cretaceous to the Middle Paleogene periods (Collins et al. 2011). The *Parastacus* group seems to have a disjunct distribution, in which two species (*P. brasiliensis* and *P. laevigatus*) are supposed to be endemic to southern Brazil, two (*P. pugnax* and *P. nicoleti*) are endemic to Chile, and the other four species (*P. saffordi*, *P. varicosus*, *P. defossus* and *P. pilimanus*) are distributed in Southern Brazil and Uruguay (Buckup 1999). The monotypic genus *Samastacus* (type species, *S. spinifrons*) occurs in Chile and Argentina (Rudolph 2010), while all the species of the *Virilastacus* group (*V. araucanius*, *V. retamali*, *V. rucapihuelensis* and *V. jarai*) are endemic to Chile (Rudolph 2010).

Australia

Australia, including Tasmania, holds the world's largest crayfish species, which includes several good examples of flagship species in conservation terms. Within Australia, freshwater crayfish are distributed in all states and territories, but mainly in costal temperate regions of southwestern, southeastern and eastern Australia, and they occupy a variety of different aquatic habitats (Taylor 2002). As summarized by Beatty (2005), two genera (*Astacopsis* and *Parastacoides*) are endemic to Tasmania, but the latter genus was subsequently revised (see Hansen and Richardson 2006). For example, the Tasmanian giant freshwater crayfish, *Astacopsis gouldi* (Clark, 1936), is found in the rivers of northern Tasmania. While two genera (*Engaeus* and *Geocharax*) are recorded in southeastern Australia and Tasmania.

In New South Wales, the Murray River crayfish, *Euastacus armatus* (Von Martens, 1866), is the most commonly known species, and is the world's second largest freshwater crayfish, endemic to the streams and tributaries of the Murray-Darling catchment where it plays a vital role in ecosystem processes and is an important tourist attraction. However, population numbers have been declining due to habitat modification and overfishing (IUCN: Alves et al. 2010).

Several studies addressing the taxonomy of *Cherax* species in Australia have described new species or synonymised others, which have resulted in some confusion and disagreement regarding the status of certain taxa. *Cherax* species from different regions can often be quite different in appearance. There is even evidence that specimens from within the same waterway can look quite different. However, based on past revisions and new descriptions, classifications are based largely after Riek (1969), Austin (1996) and Munasinghe et al. (2004). Several member of the genus *Cherax* have been studied extensively and include the marron (*C. tenuimanus* Smith 1912), the red-claw crayfish (*C. quadricarinatus* Von Martens 1868), the western yabby and also the koonac (*C. preissii*, Erichson, 1846), and the yabby (*C. destructor*, Clark, 1936), that latter which supports a large aquaculture industry and aquarium pet trade. In northeastern New South Wales, two endemic species of *Cherax*, *C. cuspidatus* and *C. leckii*, were recently discovered (Coughran 2006). In Western Australia the hairy marron, *C. tenuimanus*, is endemic to the Margaret River and is under threat of extinction due to its rapid replacement following the introduction of the widespread smooth marron, *C. cainii* (Austin and Bunn 2010). This species is indigenous to southwestern Western Australia between Harvey and Albany (Kent River), and is considered a good biological indicator of water quality for the rivers in the region. Yabbies, *Cherax destructor,* are native to the eastern states of Australia and are considered invasive in Western Australia, where they compete with the native marron (*C. tenuimanus*). *C. destructor* is of special interest because the species is the most widespread and abundant of all Australian freshwater crayfish, with a natural distribution covering over two million square kilometers, from South Australia and the southern portion of the Northern Territory in central Australia, to the Great Dividing Range in the east (Nguyen et al. 2004). *Cherax quadricarinatus* is indigenous to the rivers of northwestern Queensland and the northern territory in tropical Australia, and also extends into the catchments of southeastern Papua New Guinea. According to Beatty (2005), 22 species of *Cherax* have been described and are native to Australia.

Tasmania has a rich freshwater crayfish fauna, with about 37 species from four genera, which is relatively high in the context of the total Australian fauna (Whiting et al. 2000). They range from the world's largest crayfish, *Astacopsis gouldi*, which are found in the northern part of the island, to the tiny burrowing crayfish from the genus *Engaeus* that are found throughout the island. Within *Engaeus* there are 15 species known, 13 of which occur only in Tasmania, and two shared with Victoria on the Australian mainland. Areas of high diversity are in the northeast (*Engaeus* spp.) and the central west (*Engaeus* and *Parastacoides* spp.) (Richardson et al. 2006).

Finally, several genera are restricted to certain regions. For example, the genus *Tenuibranchiurus* is only present in southeastern Queensland, *Gramastacus* in western Victoria, and *Engaewa* in the southwestern part of Australia. In southwestern Australia, the burrowing freshwater crayfish genus *Engaewa* is a Gondwanian relict restricted to the high rainfall zone. Of five species of *Engaewa* recognized in the genus, three are of conservation concern.

In Victoria, the Grampians National Park harbours seven species from six different genera (*Euastacus bispinosus* (Clark, 1936), *Cherax destructor, Geocharax falcata* Clark, 1936*, Gramastacus insolitus* Riek, 1972 (the smallest Western swamp crayfish) and *Engaeus lyelli* Clark, 1936) all of which occur in sympatry. This region is considered a "hot spot" for crayfish diversity in Queensland, and here the crayfish *Euastacus sulcatus* is quite abundant. This species is a keystone species and functions as an ecosystem engineer (Furse 2010).

In New Zealand, the family Parastacidae is also present, with just two endemic species of *Paranephrops* on the main islands, and no introduced species.

Madagascar

Freshwater crayfish of the genus *Astacoides* are endemic to the highlands of eastern Madagascar, with six uniquely tropical species listed as of 2005: *Astacoides madagascariensis* (Milne Edwards and Audouin, 1839), *A. caldwelli* (Bate, 1865), *A. betsileoensis* (Petit, 1923), *A. granulimanus* (Monot and Petit, 1929), *A. crosnieri* (Hobbs 1987) and *A. petiti* (Hobbs 1987). Growth rates for *Astacoides granulimanu*s and

A. crosnieri are among the slowest known of any crayfish. *Astacoides madagascariensis* is endemic to Madagascar, and extends a little further north than that of any other Malagasy crayfish. The distribution of this species lies at latitudes 18º to 21º S, longitudes 47º to 49º E. Type specimens were probably collected in the vicinity of Tananarive (Hobbs 1987). This species is found in the Toamasina and Antananarivo provinces (Boyko et al. 2005). These authors also described a new species commemorating Hobbs and named it *Astacoides hobbsi*. Madagascar's freshwater habitats have great significance for global biodiversity, yet conservation efforts, as in so much of the world, has focused on terrestrial ecosystems. Jones et al. (2007) call for more attention to be paid to Madagascar's exceptional, yet understudied, freshwater biodiversity which is now coming under increasing threat.

Conclusions

If marine crustaceans are economically of great importance, freshwater crayfish have stimulated much economic activity and are the subject of many books and thousands of research articles.

Freshwater crayfish have served as model organisms for over 125 years in scientific research, from areas such as neurobiology and vision research to conservation biology and evolution. Recently, evolutionary histories in the form of phylogenies have served as a critical foundation for testing hypotheses in diverse research areas (e.g., Crandall 2006). Molecular methods have been applied widely to the phylogenetics and systematics of crayfish so that the status of perhaps the majority of species has been established with some confidence, though the phylogenetic relationships, particularly of the North American radiation, require further elucidation (Crandall and Buhay 2008). According to Burnham and Dawkins (2013), "freshwater species in general (and crayfish specifically) often have limited ranges with high species endemism within, and species turnover between, catchments. Freshwater species also face ever-increasing threats, and genetic diversity (both at and below the species level) is being lost as a result of these threats". They further state that "molecular taxonomy provides a tool by which this diversity can be rapidly (and relatively cheaply) uncovered before it is lost. Identifying previously unrealised diversity within crayfish via molecular techniques can act as a stimulus to further taxonomic investigations and conservation efforts". They also gave specific examples from the Australian crayfish fauna, where molecular data were used to highlight significant genetic diversity, which may correspond to previously overlook morphological variation. Their examples and results can be used to promote the undertaking of wide-scale molecular revisions of as many crayfish taxa as possible, looking for any previously unrecognised lineages within currently described species (akin to evolutionary significant units—ESUs) that may then warrant further revision.

Crayfish and threats

Two centers of crayfish diversity have been described, the first in the southern Appalachian Mountains of the southeastern United States (Northern Hemisphere center) and the second in southeastern Australia (Southern Hemisphere center) (Crandall and Buhay 2008); hot spots of diversity have also been identified for single families or genera (e.g., in Italy by Fratini et al. 2005). In recent times, however, their original distribution has been altered due to the massive human-mediated introduction of species outside of their native range, and the subsequent spread of some of these crayfish beyond the original area of introduction (Lodge et al. 2000, Holdich et al. 2009). Consequently, native crayfish diversity is in serious decline due to increased impacts due to habitat loss and degradation, often acting in synergy with the detrimental effects of invasions by alien species, over-harvesting, and chemical pollution. Roughly 50% of the species in the United States are imperiled (Taylor et al. 2007). In 2010, the International Union for Conservation of Nature (IUCN) wanted to comprehensively assess the status of the world's freshwater biodiversity in order to rapidly expand the taxonomic and geographic coverage of the IUCN Red List of Threatened Species (www.iucnredlist.org) in order to inform conservation strategies and management decisions. The priority taxa being assessed were freshwater fishes, molluscs, dragonflies and damselflies and crayfish worldwide. The global assessment was completed through a combination of regional assessments with a current major focus on Africa, Asia and Europe. According to Cumberlidge (2010), when examined at the level of individual zoogeographic regions, the accumulation of taxonomic knowledge is particularly contingent upon the productivity of a few regional experts. Although for some taxa, the accumulation curves flatten out (for instance Palearctic crayfish) thus demonstrating near completeness of the inventory, the majority of accumulation curves in other zoogeographical regions, as well as for individual taxa, demonstrate that we are nowhere near completing a full biodiversity inventory of the world's freshwater Decapoda.

Crayfish taxonomy and conservation

Studies utilising genetic data to examine the systematics of freshwater crayfish with morphology that is ambiguous or difficult to interpret suggest that morphologically based taxonomic studies of freshwater crayfish need to be interpreted with caution (e.g., Horwitz et al. 1990, Zeidler and Adams 1990, Campbell et al. 1994, Austin and Knott 1996). As noted by Austin and Knott (1996) the need for caution is because taxonomic characters may be more variable than realised, morphological and habitat differences may not equate with specific distinctions, and genetically distinct species need not be morphologically distinct.

Morphological plasticity has been demonstrated in decapod crustaceans. Examples from freshwater crayfish include those provided by Austin (1996) and Austin and Knott (1996), which suggest that the genus *Cherax* may display morphological plasticity in relation to environmental factors. *Cherax crassimanus* Riek, *Cherax quinquecarinatus* (Gray) and *Cherax preissii* Erichson each utilize an extremely wide range of freshwater habitats, ranging from deeper, permanent rivers to semi-permanent swamps. They found a direct correspondence between habitat variation and a large component of the morphological variation observed both within and between species. The morphological variation was found to correspond to habitat variation and was made up of a diverse range of traits, including several that have been considered previously (Riek 1967b, 1969) to be of taxonomic importance. A similar correlation of attributes to those reported by Austin and Knott (1996) was noted by Hobbs, Jr. (1975) among North American freshwater crayfish species. However, Austin and Knott (1996) were the first to show such a relationship within species.

The implication of these insights is that the conventional approach to the taxonomy of freshwater crayfish, where small anatomical differences are assumed to be reliable guides to specific distinctions, both in the Southern Hemisphere (e.g., Clark 1936, Riek 1951, 1956, 1967a,b, 1969, 1972, Sumner 1978, Swain et al. 1982, Morgan 1986, 1988, Hobbs, Jr. 1987) and in the Northern Hemisphere (Hobbs, Jr. 1989) may be flawed, and thus may extend to the existing taxonomic classifications of freshwater crayfish. Furthermore, the presence of potential morphological plasticity within freshwater crayfish suggest that, where habitat characteristics have been used as supporting information for the delineation of freshwater crayfish (based on an assumption that crayfish species tend to occupy narrow and distinct habitats), these errors may have been compounded (Austin and Knott 1996). Clearly the use of such convergent characteristics interpreted as the result of descent from a common ancestor will result in the construction of erroneous taxonomies and phylogenies (Fetzner and Crandall 2002). Addressing taxonomic and phylogenetic questions via the utilization of non-morphological characters (e.g., serology and genetics) has a long history in astacological research (e.g., Clark and Burnet 1942, Patak and Baldwin 1984, Patak et al. 1989, Austin 1996, Austin and Knott 1996) and more recently molecular data has been acknowledged in playing an important role in conservation biology through ensuring accurate definitions of species boundaries, facilitating detection of cryptic species, and providing boundaries for management units within species (Fratini et al. 2005). It has been noted that we are currently facing a global biodiversity crisis with a rapid loss of diversity occurring in all environments and at all levels, from ecosystems to genes (Browning et al. 2001), with population declines and species' extinctions occurring at an unprecedented rate (Dirzo and Raven 2003, DeSalle and Amato 2004, May 2010). It is evident that the scale of biodiversity loss globally makes the conservation of all threatened species virtually impossible; therefore certain units (whether ESUs, species, regions, etc…), must be made priorities.

According to Burnham and Dawkins (2013) crayfish taxonomy has often been in a state of flux, with different understandings of morphological and habitat variation within freshwater crayfish being common. An example of how examining additional data, and adding multiple data types (e.g., morphology, ecology/habitat, molecular), can affect our best estimate of taxonomy comes from the (now defunct) Tasmanian endemic genus *Parastacoides*. In 1936, Clark erected the monotypic genus, *Parastacoides*, with *Astacus tasmanicus* Erichson designated the type specimen; however, in 1939 Clark added another two species, *Parastacoides inermis* Clark and *Parastacoides insignis* Clark, Riek (1951) described an additional two species *Parastacoides setosimerus* Riek and *Parastacoides leptomerus* Riek, but sixteen years later synonymised *P. setosimerus* and *Parastacoides tasmanicus* (Erichson) whilst adding two more species: *Parastacoides sternalis* Riek and *Parastacoides pulcher* Riek (Riek 1967a). Based on a numerical phenetic study, Sumner (1978) reviewed the genus and identified three groups, to which he gave sub-specific rank: *Parastacoides tasmanicus tasmanicus* (Erichson) (*P. tasmanicus*, *P. pulcher*, *P. leptomerus, P. setosimerus*), *Parastacoides tasmanicus inermis* (Clark) (*P. inermis*, *P. sternalis* Riek), *Parastacoides tasmanicus insignis* (Clark) (*P. insignis*): thus reducing the number of species back to one. Ecological work by Richardson and Swain (1980), however, suggested that habitat and morphological variation was more complicated than previously realised and was inconsistent with the recognition of only a single species of *Parastacoides* divided into three subspecies. Most recently, using a combination of molecular and morphological analyses, Hansen and Richardson (2006) divided *Parastacoides* into fourteen species within two newly erected genera, *Ombrastacoides* Hansen and Richardson and *Spinastacoides* Hansen and Richardson.

Final conclusion

Resolving taxonomy is a prerequisite for conserving and managing indigenous crayfish species

We have described how major geological and climatic changes have affected the present biogeographical spread of crayfish, resulting in evolutionary diversity. With more detailed research on populations, their overall taxonomy becomes less clear-cut and is clearly in a state of flux with serious legal implications for crayfish conservation. While this situation may fascinate researchers, a confused taxonomy means that conservation and management of threatened crayfish becomes weaker and more problematic. If a species is accepted as being under threat and is then protected under national or international legislation but is later shown to be a species complex or recommended to be split into a number of sub-species or sibling species, the legal status of its protection becomes unclear. Do we need to accept all populations with a degree of genetic segregation in order to define management and conservation units? It takes time and resources to get relevant legislation rewritten and passed, and the outcome may be unpredictable. If a recognisable 'deme' within a species is no longer seen as threatened, does this weaken the case for restricting trade and movement of non-indigenous crayfish species within its area of distribution?

To conclude, the worldwide crayfish distribution fauna reveals a great variety of available information for different native crayfish species, ranging from the well-studied high diversity of the United States and Australia and the few species of Europe, to the still incomplete knowledge of the crayfish fauna of Mexico and South America.

The way forward is still to conduct complete molecular studies for each genus and then to link those results to a reliable morphological framework for each species.

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