Chapter 1
Global Diversity and Conservation of Freshwater Crabs (Crustacea: Decapoda: Brachyura)

Neil Cumberlidge

Abstract The global diversity of the almost 1400 species of primary brachyuran freshwater crabs that spend their entire lives in freshwater habitats is outlined, along with that of 220 species of secondary brachyuran freshwater crabs that spend part of their life in fresh water and part in salt water. Estimates of freshwater crab diversity based on the current rates of discovery and levels of exploration indicate that the field is still in a growth phase, and it is likely that there are a substantial number of undescribed taxa. The distribution pattern of the brachyuran freshwater crab families across zoogeographic regions is discussed, and the conservation status and current threats to the group are highlighted. It is likely that a greater proportion of the global fauna of freshwater crabs is actually threatened with extinction than is currently realized.

Keywords Primary and secondary freshwater crabs · Red List · Species estimates · Data deficiency

1.1 Introduction

The majority of crabs that live exclusively in freshwater habitats are brachyurans and these are referred to here as the primary freshwater crabs. These crabs comprise almost 1400 exclusively freshwater species assigned to five families: Pseudothelphusidae, Potamonautidae, Potamidae, Gecarcinucidae, and Trichodactylidae that are all in the Heterotremata (Ng et al. 2008; Cumberlidge et al. 2009; Cumberlidge 2014a; PKL Ng pers. com.). Primary freshwater crabs complete their life cycle independently of the marine environment, are never found in littoral saltwater habitats, and include species that are either semi-terrestrial or mostly terrestrial in habit. Four of the five primary freshwater families (Potamidae, Potamonautidae, Gecarcinucidae, and Pseudothelphusidae) share common ancestry,

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while the fifth family, the Trichodactylidae, is positioned on a separate part of the Brachyuran phylogenetic tree (Cumberlidge and Ng 2009; Tsang et al. 2014). There are another 220 species of brachyuran freshwater crabs worldwide (PKL Ng pers. com.) that belong to nine unrelated families (Tsang et al. 2014) whose members are mostly marine species: Sesarmidae, Varunidae, Gecarcinidae, Glyptograpsidae, and Dotillidae (Thoracotremata) and Hymenosomatidae, Chasmognathidae, Portunidae, and Xanthidae (Heterotremata) (Yeo et al. 2008; PKL Ng pers. com.). These paraphyletic families all include species that are found in fresh water, but all of these species also need to be in salt water at some point in their life (Yeo et al. 2008; PKL Ng pers. com.). Because of their euryhaline existence, these brachyurans are referred to here as secondary freshwater crabs. In South America there is a third group of exclusively (primary) freshwater crabs that are assigned to a single family (Aeglidae) in the decapod infraorder Anomura (that also includes hermit crabs). The aeglids are discussed in detail elsewhere in this volume (Chap. 2) and are distinguished here from other species that share the vernacular name 'freshwater crabs' by referring to them as anomuran primary freshwater crabs.

Although the brachyuran and anomuran primary freshwater crabs belong to widely separate evolutionary lineages of decapod crustaceans they nevertheless share similar adaptations for life in a freshwater habitat. For example, they all undergo direct development (with no larval stages) and they all produce large, yolky eggs that hatch directly into juvenile crabs. In contrast, the secondary freshwater brachyurans while fully adapted to freshwater/terrestrial living, do not show direct development [with a few exceptions (Ng and Tan 1995; Schubart and Koller 2005)]. The life cycle of these secondary freshwater animals is characterized by highly abbreviated development in which their eggs release larvae at an advanced stage that must pass through one or more stages before metamorphosing into hatchling crabs. This strategy of abbreviated development has evolved independently in each of the families with secondary freshwater species and these similarities are the result of evolutionary convergence.

1.1.1 Habitat

The primary brachyuran freshwater crabs occur in a wide variety of aquatic and terrestrial habitats around the world in the tropics and subtropics. These decapods are present in almost all freshwater bodies in the inland waters of the continents, from clear, fast-flowing montane streams to sluggish lowland rivers and streams, as well as peat and freshwater swamps, stagnant ponds and rice fields, tree holes, leaf axils, and underground caves (Cumberlidge et al. 2009). Most of the primary freshwater crabs do not survive for long in salt water, but there is evidence that species of potamids and gecarcinucids from Thailand are somewhat tolerant of saline conditions because they can survive immersion in salt water for up to three weeks in the laboratory (Esser and Cumberlidge 2011). Terrestrial freshwater crabs that live in tropical rain forests either move through forest floor litter or climb trees,

and can live well away from permanent freshwater sources (Ng 1988; Cumberlidge 1991; Ng and Tay 2001; Bayliss 2002; Cumberlidge and Vannini 2004; Cumberlidge et al. 2005). These species do not require regular immersion in fresh water and can obtain water either from their food or from drinking dew or rainwater. Freshwater crabs are primarily nocturnal, and remain hidden during the day and come out at night to forage. These crabs are omnivorous scavengers that feed mainly on plant matter, but some species are opportunistic carnivores that feed either on live prey such as fish, molluscs, and prawns or on dead animals that they encounter (Ng 1988). Crabs also constitute an important food resource for many species of fishes, caymans, turtles, birds, and mammals in tropical freshwater ecosystems (Ng 1988; Magalhães 2003; Cumberlidge et al. 2009; Balian et al. 2010).

The distribution patterns of the secondary brachyuran freshwater crabs are mainly centred on the coastal/littoral regions of continents and islands, and are markedly different from those of the inland primary freshwater crabs that dominate the inland waters of the continents and are never found naturally in salt water of any kind (Esser and Cumberlidge 2011). Most species of secondary freshwater crabs do not wander very far inland, with a few exceptions (Schubart et al. 1998; Schubart and Koller 2005; Ng and Tay 1995). This littoral distribution pattern no doubt reflects their ties to saltwater and their need to spend part of their life cycle in freshwater and part of it in the sea.

1.2 Global Diversity

Although the primary freshwater crabs are one of the most species-rich groups within the Brachyura (Ng et al. 2008; Cumberlidge et al. 2009) these large and conspicuous tropical freshwater macro invertebrates were completely unknown until the late 18th century. Primary freshwater crabs were first discovered in 1783, and only six species (now in three different families) had been described by 1800 (Table 1.1). Even Linnaeus (1758) was unaware of the existence of these tropical and subtropical crustaceans. The very first freshwater crab species known to science was *Dilocarcinus septemdentatus* (Herbst 1783) (Trichodactylidae) from South America, followed two years later by *Potamon fluviatile* (Herbst 1785) (Potamidae) from southern Europe, and then by *Oziotelphusa senex* (Fabricius 1789) (Gecarcinucidae) from southern India. It took another 36 years for the first pseudothelphusid [*Guinotia dentata* (Latreille 1825)] to be discovered (in Trinidad), which was followed the next year by the discovery of the first potamonautid [*Potamonautes berardi* (Audouin 1826)] in Egypt. In terms of the modern understanding of the group, representatives of all five recognised families had been described between 1783 and 1826. After that no more primary freshwater crab families have been recognised [although at the high point 12 primary freshwater crab families had been proposed (Bott 1970; Cumberlidge et al. 1999)]. The rate of discovery of new species and genera of freshwater crabs increased slowly

Table 1.1 Number of described species and families of brachyuran primary freshwater crabs per century from 1783 to 2015

Year	Species	Family (families)
1783	1	1
1800	6	1
1900	167	1
2000	991	12
2015	1393	5

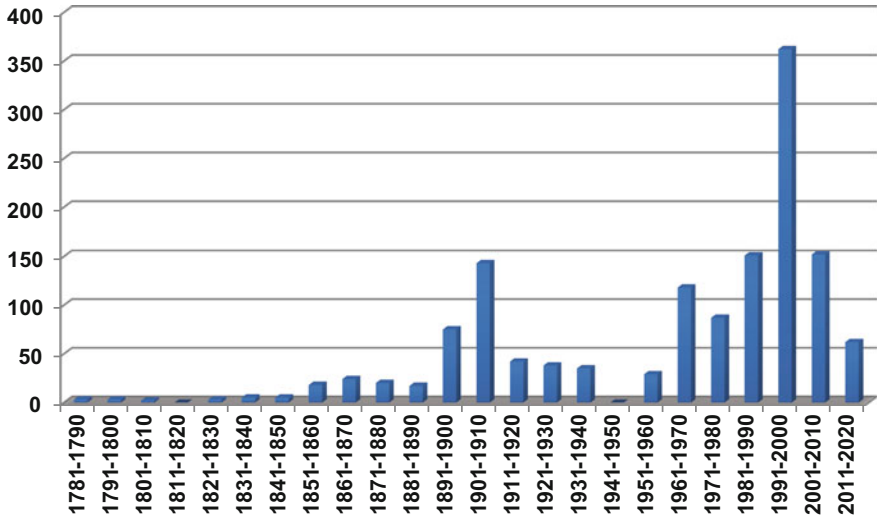

Fig. 1.1 Record of the number of species of freshwater crabs described per decade around the world from 1783 until the present day (*vertical axis*). All five families of primary brachyuran freshwater crabs are included. The *horizontal axis* shows time in ten-year blocks beginning with the discovery of the first species of freshwater crab in 1783

throughout the 19th century, reached a peak in the late 20th century, and continues to grow at a steady pace in the 21st century (Fig. 1.1; Table 1.2).

In 2009, there were 1280 known species of freshwater crabs, whereas in 2015 there are now 1394 species, and the consistently steady rate of species descriptions is showing no signs of slowing down (Fig. 1.1; Table 1.2). The five families of primary freshwater crabs have strikingly different numbers of species (Table 1.2). The breakdown of the described species by family in 2015 is as follows: Potamidae (548 species), Gecarcinucidae (361 species), Pseudothelphusidae (268 species), Potamonautidae (152 species), and Trichodactylidae (47 species) (Table 1.2). The rate of discovery of new species varies with the family under discussion. For example, while new species of Potamidae, Potamonautidae, Pseudothelphusidae, and Gecarcinucidae are still being discovered, no new species of Trichodactylidae have been described since 1996, despite active sampling in tropical South American

Table 1.2 Primary and secondary freshwater crab species discovery rates

Families of primary brachyuran freshwater crabs	Described species 2009	Described species 2015	# New species since 2009	Rate N. sp./ year	Estimated species (end 21st century); described + undescribed*
Potamonautidae	133	152	+19	3	152 + 255 = 407
Gecarcinucidae	344	372	+28	4.5	372 + 382 = 764
Potamidae	505	551	+46	8.0	551 + 680 = 1231
Pseudothelphusidae	251	271	+20	3	271 + 255 = 526
Trichodactylidae	48	48	0	0	48 + 0 = 48
Total primary FW crabs	1280	1394	+113	19	1394 + 1615 = 3009
Total secondary FW crabs	170	222	+52	9	737

*Assuming the current rate of species discovery continues for the next 85 years

lowlands including the Amazon basin (Table 1.2). This indicates that current numbers of species of trichodactylids may be close to the complete fauna for this family. Even so, it should be remembered that there are still large areas within the range of the Trichodactylidae that are as yet unexplored for freshwater crabs.

The number of undiscovered species of primary freshwater crabs is difficult to estimate accurately, but despite this, there have been attempts to estimate their true global diversity (Table 1.2). For example, Yeo and Ng (1999) used different methods to estimate the actual number of primary freshwater crabs globally. One approach was to extrapolate values from surveys of a well-sampled region and use this to estimate undescribed diversity in the unexplored freshwater crab habitats around the world. This involved calculating the number of species per unit area found in the intensively surveyed species-rich country of Thailand (1.8 species/km^2) and using this to estimate freshwater crab diversity based on estimates of the area of suitable freshwater crab habitat elsewhere. This gave an estimated global diversity of around 2155 species. However, the accuracy of this figure suffers from the fact that the actual species richness of primary freshwater crabs is not constant (Table 1.2) and varies a great deal across habitats in different parts of the world (Cumberlidge et al. 2009).

Another approach to estimate the number of undescribed species of primary freshwater crabs globally is to assume that the current rate of species discovery will continue for the rest of the 21st century. Cumulative data on the description of new species of primary freshwater crabs since their first discovery in 1783 up to the present time indicate that the boom in species discovery that began in the 1970s is still progressing strongly (about 15 species per year globally) (Table 1.2). This is a reasonable rate to use to estimate future additions for the rest of this century because the factors driving the current rate of species discovery are still adding to our knowledge of species richness, and are likely to continue to do so for many years to come, given the current encouraging levels of active taxonomic research in all

Table 1.3 Undiscovered biodiversity—vertebrates, invertebrates, and crustaceans

Group	Described species	Estimated species	% described
Vertebrates	62 k	80.5 k	81
Invertebrates	1.4 M	8–10 M	13–16
Crustaceans	47 k	150 k	~20

zoogeographical regions. The above factors include: (1) intensified biotic surveys targeted at the large areas of the tropics that are still poorly surveyed for freshwater crabs, (2) taxonomic revisions of described taxa including the resolution of synonymies and of the validity of subspecies, and (3) molecular studies aimed at discovering cryptic species using DNA sequences coupled with more refined taxonomic expertise (Cumberlidge and Daniels 2014). The latter approaches are likely to add to the species list even in the absence of new field collections.

A conservative worldwide estimate of the total number of species of primary freshwater crabs (those that are already discovered plus those not yet discovered) based on the assumption that the current rate of species description (about 19 new species a year globally) will continue throughout the 21st century (about 1614 more species) would give a total global fauna of more than 3000 species. This means that in 2015, with almost 1400 known species, we could be still only half way to our goal. Reality is probably somewhere in between the estimates obtained using the extrapolation method (2155 species) and those made using the species discovery rate method (3008 species). There could be between 755 and 1614 more species of primary freshwater crabs yet to be discovered.

When estimated numbers of undiscovered species of vertebrates (~80,500) are compared to the number of discovered species (~62,000) about 81 % are already known (Table 1.3). In contrast, estimated numbers of undiscovered species of invertebrates (~8,000,000) compared to the number of discovered species (~1,400,000) indicate that only about 17.5 % of this group are already known. When similar estimates are carried out for crustaceans as a whole (~150,000 undiscovered species; ~47,000 discovered species) then only about 31 % are already known. The present estimates that about 50 % of the primary freshwater crabs are still unknown indicates that although the above approaches bring us closer to our goals of understanding complete faunas, a more accurate system of estimating species numbers is clearly needed before the true diversity can be known.

1.3 Distribution and Zoogeography

The primary freshwater crabs have a circumtropical distribution and are today found in warm freshwater habitats in 122 countries in five zoogeographic regions (Neotropical, Afrotropical, Palaearctic, Oriental, and Australasian) (Cumberlidge et al. 2009). Interestingly, the present understanding of freshwater crab global distribution was established at the country level in the 19th century and no new

countries that host these crustaceans have been added since then. These crabs are mainly found in the inland waters of the major continents and are notably absent from remote oceanic islands in the Pacific Ocean (such as the Galapagos, the Hawaiian Archipelago, the Society Islands), as well as from islands in the Atlantic and Indian Oceans. Primary freshwater crabs are also absent from cool freshwater habitats around the world in the Nearctic and from the cooler temperate zones of the Palaearctic, Neotropical, and Australasian regions (including New Zealand) (Yeo et al. 2008).

Globally, the primary freshwater crabs have two main centres of diversity: one centred in the Oriental region (923 species, 2 families, 66 % of the global fauna) and the other in the Neotropical region (319 species, 2 families, 23 % of the global fauna). In the Oriental region the countries with the highest species richness are China (243), Thailand (101), Malaysia (92), Indonesia (83), and India (90) (Cumberlidge et al. 2009; Cumberlidge et al. 2010). All of these Asian countries have representatives of the two most species-rich families—Potamidae and Gecarcinucidae. The species-rich countries in Indochina tend to have an even mix of species from both of these families (Yeo and Ng 2007). On the other hand, China's fauna is dominated by potamids and has only a few gecarcinucids (Cumberlidge et al. 2010), while India's fauna is dominated by gecarcinucids and has relatively few potamids (Cumberlidge et al. 2009).

In the Neotropical region the countries that have the highest species richness are Colombia (102), Mexico (67), Brazil (50), and Venezuela (44) (Cumberlidge et al. 2009, 2014). All of these countries have representatives of both Neotropical families—Pseudothelphusidae and Trichodactylidae. Mexico, Costa Rica, Colombia, and Venezuela have all been actively surveyed recently for freshwater crabs, and all have faunas dominated by pseudothelphusids especially in high-altitude habitats (the Cordilleras of the northern Andes, the Mexican Sierras, and the Guiana Massif). On the other hand, Brazil's freshwater crab fauna is dominated by trichodactylids that thrive in the vast lowland Amazon and Orinoco basins, and has fewer pseudothelphusids (perhaps because these crabs prefer highlands over lowland drainages). Although there has been active surveying for freshwater crabs in Brazil in recent years, this vast tropical area still has many under-sampled regions that have the potential for the discovery of many more new species. Similarly, the lower species numbers in Ecuador (26), Peru (22), Costa Rica (15), and Panama (15), and in most countries in Central America are almost certainly underestimates due to under-sampling (Cumberlidge et al. 2014; Magalhães et al. 2015).

The Afrotropical region is the most species-poor region in the world for primary freshwater crabs with only around 152 species in 2 families (11 % of the global fauna). There are two high diversity countries in this region one in Central Africa (Democratic Republic of Congo, 36) and one in East Africa (Tanzania, 25). However, with the possible exception of South Africa and Nigeria, most countries in this region are poorly surveyed (including the vast and largely unexplored Congo River basin), and the low numbers of species are almost certainly underestimates due to under-sampling. Increased recent surveying in a number of previously unexplored highland regions of southern Africa has produced several new species,

and this approach promises to reveal a much greater diversity than is presently known (Daniels and Bayliss 2012; Phiri and Daniels 2013, 2014; Daniels et al. 2014; Cumberlidge 2014a).

1.3.1 Patterns of Species Richness and Endemism

The freshwater crab faunas within the different zoogeographical regions of the world typically include species that have one of two main distribution patterns: (1) widely distributed commonly encountered species with high population numbers, and (2) narrowly distributed rare species with a relatively restricted range and low population numbers. Widely distributed species include *Potamonautes niloticus* (Nile River drainage, East and North Africa) and *Sudanonautes africanus* (Lower Guinea forests, Congo river drainage, Central Africa) (Cumberlidge 1999, 2009). The wide distributional ranges of these species have been achieved as a result of the general lack of barriers to dispersal in the large river drainages and the long time periods available for species to spread out in these stable tropical ecosystems. These species have colonized vast areas of the tropics despite their relatively slow rate of dispersal (limited to adults) and their low fecundity (typical of reproduction by direct development). Abiotic barriers to their dispersal that restrict them to tropical warm water habitats include cool water temperatures (less than 0 °C, e.g., cold water rivers and high altitude mountain streams), a lack of year-round water (arid lands, deserts, extremely high mountain ranges), and prolonged contact with salt water (Esser and Cumberlidge 2011). Relatively restricted range species include *Potamonautes kundudo* (from a cave in Ethiopia, North Africa) and *Liberonautes nimba* (from high altitudes on Mount Nimba, West Africa) (Cumberlidge 1999, 2009; Cumberlidge and Clark 2012). Such species are found in just a few localized and isolating niches, despite the fact that they are living within a wider area of apparently favourable habitat. Over time the genetic isolation of populations of restricted-range freshwater crabs has resulted in the high levels of speciation and endemism that we observe today, especially in highland faunas (Cumberlidge 1999; Ng and Yeo 2007; Yeo et al. 2008; Cumberlidge et al. 2009).

Endemism in primary freshwater crabs is also evident at the family level. The Neotropical Pseudothelphusidae and Trichodactylidae and the Afrotropical Potamonautidae are strictly endemic to their zoogeographical regions. On the other hand the Potamidae is found in two regions: the southern Palaearctic region (North Africa, southern Europe, Middle East, Himalayas) and the Oriental region (southern China, Japan, and tropical Asia as far south as Wallace's line) (Cumberlidge et al. 2009; Cumberlidge et al. 2010). Similarly, the Gecarcinucidae is also found in the Oriental and Australasian regions (India, Sri Lanka, Indo-China, China, the Philippines, the Indonesian Archipelago, New Guinea, and northern Australia) (Cumberlidge et al. 2009). Endemism at the country level is high in primary freshwater crabs with 84 % of Palaearctic, Oriental, and Australasian species

endemic to the country where they occur, as are 76 % of the Neotropical and 54 % of the Afrotropical species (Cumberlidge et al. 2009).

1.3.2 Islands

Significant numbers of species of primary freshwater crabs are found on large and small nearshore islands in the Neotropical, Afrotropical, Oriental, and Australasian regions. Because primary freshwater crabs are exclusively freshwater animals that have an aversion to salt water their presence on islands needs to be explained. One possibility is that crabs on islands close to continental landmasses were already in both places when past sea levels were lower than today, and became isolated when part of their range became an island as sea levels rose. However, this cannot explain the presence of primary freshwater crabs on remote oceanic islands (such as the Seychelles Archipelago and Madagascar that are fragments of the former Gondwanan landmass) because these ancient islands have been isolated for millions of years by deep seawater barriers (Cumberlidge 2008; Esser and Cumberlidge 2011). In these cases it is likely that the island freshwater crab faunas reached there by independent overseas rafting events millions of years ago, in a similar way to that proposed for saltwater-intolerant amphibians found on oceanic islands (Measey et al. 2007; Cumberlidge 2008; Daniels 2011; Cumberlidge and Daniels 2014).

1.3.3 Secondary Freshwater Crabs

Secondary freshwater crabs differ from primary freshwater crabs in that the former have the physiological ability to live both in saltwater and freshwater habitats for long periods of time, whereas primary freshwater crabs consistently avoid salt water. In addition, some species of secondary freshwater crab (e.g., *Varuna litterata*, Varunidae) have a widespread distributional range that not only includes tens of thousands of square kilometres of ocean, but also includes low salinity coastal waters and inland freshwaters. *Varuna litterata* is a common inhabitant of oceanic and freshwater habitats in the Indian Ocean (East Africa and Madagascar) and in the Pacific Ocean (Japan and Polynesia). Apart from phylogenetic separation at the family level (Tsang et al. 2014) differences between primary and secondary freshwater crabs relate to their life cycle strategies and their larval development. All brachyuran freshwater crabs are well adapted to life in freshwater, but primary freshwater crabs always reproduce by direct development, whereas most secondary freshwater crabs have abbreviated or reduced larval development with a few free-living larval stages and they complete their life cycle on land or in fresh water. Because these larval stages require saltwater for development the adult crabs need to return to the sea to breed. The retention of marine larval stages has the advantage of achieving a wide dispersal range in those species that produce planktonic larvae

that are carried long distances by ocean currents before settling down on the benthos as young crabs (Vogt 2013). The only known exceptions to this strategy are species belonging to three genera of sesarmids: *Geosesarma notophorum* (a terrestrial freshwater crab from Sumatra, Indonesia), *Metopaulias* d*epressus* (a Jamaican terrestrial freshwater crab which lives in water pools in bromeliad leaves), and ten endemic species of *Sesarma* from Jamaica (Schubart and Koller 2005). These sesarmid freshwater species remain in fresh water for their entire life cycle and reproduce by direct development without producing any free-living larval stages (Ng and Tan 1995; Schubart and Koller 2005).

Five thoracotreme families (Varunidae, Sesarmidae, Gecarcinidae, Glyptograpsidae, and Dotillidae) include species that are found in freshwater habitats for either part or all of their life cycle. The Varunidae (7 genera, 55 species) are found in the coastal regions in the Palaearctic, Afrotropical, Oriental, Australasian and Pacific regions. A few species of varunids migrate long distances up rivers and spend most of their adult lives in fresh water (Schubart et al. 2002). The majority of varunids produce larvae that need to develop in sea water which means that the adults must either migrate from inland freshwaters to coastal waters, or release their larvae into rivers that carry them downstream to the sea (Anger 1995; Diesel et al. 2000). This family includes the euryhaline genera *Varuna* (2 species, including *V. litterata*) and *Eriochier* (4 species, including the Chinese mitten crab, *Eriochier sinensis*) that have wide distributional ranges and which live mostly in freshwater. The Varunidae also includes *Orcovita* (10 species) that are all karst and cave specialists, some of which live in freshwater habitats far inland and some of which have adapted to life in anchialine waters. The varunid genus *Ptychognathus* includes 25 species, most of which are estuarine, but some live in freshwater habitats and may venture several kilometres inland. Other varunid genera with species that are found in fresh water are *Utica* (7 species), *Pyxidognathus* (3 species), *Pseudograpsus* (2 species), and *Neoeriocheir* and *Platyeriocheir* (each with 1 species).

The Sesarmidae (8 genera, 95 species) is a large globally distributed family found in saltwater, brackish water, and freshwater habitats in the Palaearctic, Afrotropical, Neotropical, Oriental, Australasian, and Pacific regions. While the majority of species are found in soft-sediment coastal marshes and mangroves, some species live as adults in rivers (Diesel and Schuh 1998; Schubart et al. 2000), and others are found further inland and live exclusively in freshwater habitats. This family includes *Karstama* (15 species) that are all karst and cave specialists, some live inland in freshwater habitats, and some live near the coast in anchialine waters. The family also includes *Labuanium* (6 species) that are all tree climbers that live in phytotelm freshwater habitats and some species range several kilometres inland, often close to rivers. Another genus is *Pseudosesarma* (7 species) that are mostly found in mangrove forests, but some live in freshwater habitats. *Scandarma* (3 species) are tree climbers that live in freshwater pools in *Pandanus* palm leaves sometimes far inland. The Jamaican genus *Sesarma* (10 species) are primary freshwater specialists that live in mountain streams, bromeliad leaf axils, rock rubble, empty snail shells, and caves, and are all completely independent of salt

water. Other sesarmid genera include *Geosesarma* (51 species, from Thailand, Taiwan, and Indonesia, that includes the exclusively freshwater species *G. notophorum*), *Sesarmops* (2 species, from phytotelm habitats in Madagascar), and *Metopaulius* (1 species, from a phytotelm habitat in Jamaica).

The Gecarcinidae (6 genera, 22 species) are the true land crabs that are found in coastal regions of the continents and islands throughout the tropics (in the Neotropical, Afrotropical, Oriental, Australasian, and Pacific regions), and includes some species that wander into freshwater habitats. This family comprises the genera *Johngarthia* (5 species), *Discoplax* (5 species), *Cardisoma* (4 species), *Gecarcinus* (3 species), *Epigrapsus* (3 species) and *Gecarcoidea* (2 species). The Glyptograpsidae (2 genera, 3 species) are found in the coastal regions in Central America and the east Atlantic. This family includes two genera *Glyptograpsus* (2 species) and *Platycheirograpsus* (1 species). *Glyptograpsus* spends its adult life in inland freshwater nhabitats (Schubart et al. 2002) but its adults must migrate downstream to release their larvae into the sea (Anger 1995; Diesel et al. 2000). Finally, the Dotillidae is a family of marine crabs with 59 species that includes two species of *Potamocypoda* from the coastal areas of the Australasian region that have adapted to a euryhaline life that includes both saltwater and freshwater habitats.

Four heterotreme families (Hymenosomatidae, Chasmocarcinidae, Portunidae, and Xanthidae) include species found in freshwater habitats for either part of, or all of, their life cycle. The Hymenosomatidae (9 genera, 26 species) are found in the coastal areas of the Neotropical, Afrotropical, Oriental, and Australasian regions. This family includes the genera *Amarinus* (11 species), *Neorhynchoplax* (4 species), and *Hymenosoma* (4 species) and most of these species are found in either estuarine or freshwater habitats. The Chasmocarcinidae (formerly Goneplacidae) (2 genera, 4 species) are from coastal areas in the Australasian Pacific regions and includes *Australocarcinus* (3 species) and *Trogloplax* (1 species). Finally the Portunidae and Xanthidae are two large marine crab families that include a few species that spend most of their lives in freshwaters. For example, *Scylla serrata* and *Callinectes sapidus* (Portunidae) and *Rhithropanopaeus harrisii* (Xanthidae) are common inhabitants of freshwaters but still need to migrate to the sea to breed.

1.4 Conservation Status

The International Union for Conservation of Nature (IUCN) Red List assessments of primary freshwater crabs by Cumberlidge et al. (2009) included the entire known fauna at that time (1280 species in 220 genera, 5 families) from 6 zoogeographic regions (Cumberlidge 2014b). Since that study was completed 114 more species of primary freshwater crabs have been described (Table 1.2) that are currently being assessed using IUCN Red List protocols, but are not yet part of the Red List. Therefore the conservation assessment data used here are based on the 1280 species that have already been assessed that are on the IUCN Red List site.

Although the study by Cumberlidge et al. (2009) included the entire global freshwater crab fauna, the extinction risk of 628 out of the 1280 species of freshwater crabs from all five families (almost 50 %) was not assessed due to a lack of relevant conservation information for them. The Red List protocols simply list such species as Data Deficient (DD) and exclude them from subsequent calculations of extinction threat. Cumberlidge et al. (2009) therefore based their assessments on the remaining 651 species in all five families, two-thirds of which (425 species) were not threatened (either LC or NT). However, high extinction threat levels were found for 209 assessed species: 32 critically endangered (CR), 52 endangered (EN), and 123 vulnerable (VU). Well over half (59 %) of these threatened species belong to just two families—Gecarcinucidae (Oriental and Australasian, 43 % of species Threatened) and Pseudothelphusidae (Neotropical, 34.2 % of species Threatened). The proportion of threatened African Potamonautidae (27.5 %) and Oriental Potamidae (26.5 %) is less than the global average (32.1 %), while only 10.3 % of the species of Neotropical Trichodactylidae appear to be at-risk (Cumberidge and Daniels 2007; Cumberlidge et al. 2009).

There are 43 countries (out of 122 with a freshwater crab fauna) that have a responsibility for the protection of at least one threatened species. So far, only one country (Singapore) has developed a conservation action plan aimed at protecting a freshwater crab: the critically endangered potamid, *Johora singaporensis* (Ng et al. 2015). This is the only threatened species of primary freshwater crab (out of 209) that is currently receiving any active conservation action (Ng et al. 2015). Elsewhere in Asia there are important concentrations of at-risk species (34.8 % of threatened species globally) in the highland forests of Sri Lanka and Taiwan, and in the rain forests of Indochina, Thailand, the Malay Peninsula, Borneo, and New Guinea. In the Neotropical region the highest numbers of threatened species are found in Colombia, Ecuador, Venezuela, Mexico, El Salvador, and Honduras. In the Caribbean, the entire freshwater crab fauna of the Dominican Republic and Haiti is threatened, but the faunas of these countries are species-poor (1-2 species). In the Afrotropical region the highest numbers of at-risk species are found in Liberia, Guinea, and Malawi, where there are alarmingly high proportions of threatened freshwater crabs (50–66.7 %).

The majority of threatened species of freshwater crabs are restricted-range (stenotopic) endemics whose habitat has been impacted by deforestation, alteration of drainage patterns, and pollution. Many of the threatened species of pseudothelphusids, potamonautids, potamids, and gecarcinucids are competent air-breathers that either live in burrows, or move between water and land in highlands, islands, caves, karsts, and phytotelms. These habitat specialists have small populations and restricted distributional ranges, and are especially susceptible to localized anthropogenic habitat disturbances (Collen et al. 2008, 2014).

The brachyuran secondary freshwater crabs have not yet been subjected to a global conservation assessment using the IUCN Red List protocols and so there is no information on the conservation status of any species in this important widespread group of freshwater decapods.

1.4.1 Data Deficiency

The primary freshwater crabs, like other invertebrate groups that have been studied at the global level (Richman et al. 2014; De Grave et al. 2014), include large numbers of DD species, which are species that lack data on population size and trends, distributional range, habitat quality, and threats (Cumberlidge et al. 2009). Many of these DD species (especially those collected before the 1950s) are not known beyond their original description, and their actual geographic range (other than type locality) is unclear due to inadequate on-the-ground knowledge. Once a species has been initially assessed as DD it is not included in any further analyses, because data necessary for the IUCN Red List assessment protocols are lacking.

High numbers of DD species are therefore a cause for concern because this designation may be masking the true number of threatened species, and could change IUCN Red List threat levels significantly when new field data enable their inclusion in future assessments. For example, the current estimates of threatened species of primary freshwater crabs (32 %) were made without the inclusion of 628 DD species (which represent almost 49 % of the global fauna) (Cumberlidge et al. 2009).

If improved future sampling targeted all DD species of freshwater crabs and provided sufficient new data to allow their assessment, then there would be two possible outcomes. If the result revealed that all DD species belonged to a threatened category (VU, EN, or CR), then the number of threatened species would increase dramatically (up from 32 to 66 %). On the other hand, if the result revealed that none of the DD species were threatened (all LC), then the number of threatened species would be halved (from 32 to 16 %). The wide difference in the results when these assumptions are applied undermines confidence in reported threat levels because a large proportion of the known global freshwater crab fauna has not been included. This is one reason that global Red List assessments are ideally carried out every 10 years, and why new field surveys that target threatened species should also include DD species.

The global study of the freshwater crabs identified 12 countries (Table 1.4) that have no DD species because the conservation status of their entire known freshwater crab faunas has been assessed. These countries can be used as models to estimate threat levels in countries that currently have a lot of DD species, and this can offer insights into the impacts that large numbers of DD species may have on the reported Red List threat levels. For example, Sri Lanka (50 species, 80 % threatened) is a comprehensively assessed country with an alarmingly high number of threatened species. On the other hand, Tanzania (25 species, 28 % threatened) is a comprehensively assessed country that has fewer than the average expected threatened species. When all 12 comprehensively assessed countries that lack DD species are considered together, the average percentage of threatened species amounts to 48 % of the fauna (range 100 to 8 %) in one of the three IUCN Red List threatened categories (Table 1.4). This average estimate is much higher than the current global estimate (32 % threatened, without DD species). In species-rich

Table 1.4 Extinction threat levels of primary freshwater crabs found in comprehensively assessed countries that have no data deficient (DD) species

Country	Total spp.	Thr. (%)	Endemic (%)	DD
Sri Lanka	50	80	98	0
Tanzania	25	28	16	0
South Africa	13	8	54	0
Turkey	9	11	22	0
Liberia	9	67	33	0
Australia	7	29	100	0
Honduras	6	33	17	0
Ghana	6	17	17	0
Malawi	4	50	50	0
Ethiopia	4	25	50	0
Singapore	4	75	75	0
Dominican Republic	2	100	100	0
Haiti	1	100	100	0
Totals	140	48	56	

China (8 % threatened) and in most of the African continent (21 % threatened), the high proportion of DD species means that the true number of threatened species is likely to be much greater than currently estimated (Cumberlidge et al. 2009; Cumberlidge 2011).

Multiple gaps in the exploration of freshwater crab faunas around the world make it likely that intensified surveying will not only add to the number of known species, it will also add to the number of threatened and DD species. The eventual inclusion in the Red List of little-known species currently treated as DD is likely to alter the current levels of biodiversity threat. Another factor that adds to the number of known species (and to the number of threatened species) is a lack of freshly caught samples because fresh tissues are required for the discovery of cryptic species using DNA sequence data. This is because the improved taxonomic clarity offered by molecular and morphological approaches allows detailed evaluations that can reveal cryptic species hidden within a morphologically similar widespread species. In these cases, the original range of a widespread species is fragmented when one or more cryptic species are identified within this range. The original species and cryptic species typically have restricted distributions, and some of these may prove to be concealed threatened taxa (Phiri and Daniels 2014; Cumberlidge and Daniels 2014). Taken together with the present high numbers of DD species, it seems highly likely that the true number of threatened freshwater crabs globally may be much higher than estimated.

Finally, highlighting DD species can serve as a focal point for further field studies aimed at filling gaps in our knowledge. With careful planning the implementation of conservation actions for threatened species could also have the added

value of increasing our knowledge of DD species if they are found in the same area as the threatened species of interest.

1.4.2 Extinction

Some estimates place the current rate of species extinction as being at such high levels (i.e., eight species lost forever every day) that some authors have characterised modern times as the Earth's sixth major mass extinction episode (De Vos et al. 2015). Those authors estimated the current extinction rate to be approximately 100 extinctions per million species per year (1000 times higher than natural background rate), and predicted that future rates may be even worse (10,000 times higher than the natural background rate). The projections of those authors are based on estimates of about 8.7 million species found on the planet today (Mora et al. 2011), although only 1.9 million species have been formally described taxonomically.

Despite these high extinction rate estimates the IUCN Red List site actually lists only 901 species of animals or plants that are either extinct (EX) or extinct in the wild (EW) in recent times (Table 1.5). One reason for this relatively low number of extinctions is that in 2015 only 3.9 % of the 1.9 million described species have been assessed and are part of the Red List dataset (Stuart et al. 2010). Another reason is that before a species can be declared as extinct it is necessary to apply the IUCN Red List protocols that require exhaustive surveys examining the disappearance of a species suspected as being extinct (i.e., repeated investigations in the right habitats at the right time of year, and no sightings for over 60 years). At our present levels of knowledge no species of primary freshwater crabs are extinct (EX) or extinct in the wild (EW) using the IUCN Red List protocols. There are, however, 351 EX or EW species of vertebrates and 411 EX or EW species of invertebrates, including 12 extinct species of freshwater shrimps on the Red List. In the case of the primary freshwater crabs it is likely that some DD (and even CR) species may already be

Table 1.5 Number of species on the Red List that are extinct or extinct in the wild in 2015

Group	Total described species (k)	Species on Red List (% of total species known)	No. species RL EX/EW	% assessed species extinct
Invertebrates	1400	17,218 (1.2 %)	411	2.44
Vertebrates	62	39,223 (63 %)	354	0.93
Plants	300	19,738 (6.6 %)	136	1.40
Total: all organisms	1900	74,106 (3.9 %)	901	1.21

Invertebrates are the most poorly known group of organisms and most species have yet to be discovered (possibly because it is had to identify invertebrates without specialist knowledge). Invertebrates also have the smallest number of species represented on the IUCN Red List, but have the highest documented rate of extinction of any group studied

extinct, but we cannot establish this as fact because we lack the necessary field data to make an evaluation. Freshwater crab habitats around the tropics are among the most severely disrupted ecosystems in the world. It is therefore likely that the current intense degradation of tropical freshwater ecosystems worldwide that are subjected to forest destruction, water diversion, and pollution (Stiassny 1999; Dudgeon et al. 2006) makes it likely that some freshwater species assessed as DD that have not been collected for many years since their original description may actually be extinct. The same lack of field data that warrants their status as DD may actually be masking their extirpation, but this information gap is preventing their formal assessment as extinct (Sodhi et al. 2004; Bahir et al. 2005; Ng and Yeo 2007). For example, the DD species *Louisea edeaensis* and *L. balssi* (Cameroon), *Afrithelphusa afzelii* (Guinea), *Thaipotamon siamense* (Thailand) and *Demanietta manii* (Thailand) may well already be extinct because there have been no records of them for over a century despite survey activities, or because their original habitats are now highly altered or located in densely populated urban areas (Ng and Naiyanetr 1993; Cumberlidge 1999; Sodhi et al. 2008).

1.5 Threats and Conservation Issues

The main threats to primary freshwater crabs include habitat destruction (accelerated by global climate change), alterations of river or stream flow patterns (from dams and other drainage diversions), and pollution (from mining, pesticides, and fertilizers) (Cumberlidge et al. 2009; Cumberlidge 2011). Other threats to these freshwater animals include displacement of native species by introduced species. For example, in Kenya, East Africa the introduction of the red swamp crayfish (or Louisiana red-claw crayfish) (*Procambarus clarkii*) into Lake Naivasha in 1970 impacted native populations of aquatic plants and freshwater crabs. Soon after the introduction of *P. clarkii* to the lake their populations rose to levels high enough to support a thriving commercial export fishery. However, the high densities of crayfish in the lake had a devastating impact on the aquatic vegetation due to overgrazing and there was a subsequent collapse of crayfish populations. The eventual recovery of the lake's aquatic plants allowed crayfish populations to expand and once again they overgrazed the lake's vegetation. The dominance of *P. clarkii* in Kenyan freshwater ecosystems and its cyclical effects on the lake's primary producers also caused population crashes of native freshwater crabs (*Potamonautes loveni*) (Gherardi et al. 2011). It may also have caused population crashes of the clawless otters that feed on these crabs (Ogada 2006). When freshwater crabs became scarce, the lake's otters switched from to eating crabs to eating crayfish, but the otters overall food supply was nevertheless reduced due to competition from numerous other predators attracted to feed on the abundant crayfish.

Other threats to freshwater crabs are over-harvesting for food and for the aquarium trade. Common species of freshwater crabs are harvested by human

populations around the world, either for use as food or for the treatment of medical problems (such as stomach ailments and physical injuries). Locally abundant species of African freshwater crabs (e.g., *Potamonautes lirrangensis* in Lake Malawi and *Platythelphusa armata* in Lake Tanganyika) support small-scale fisheries. Even so, these species could still be vulnerable to population crashes. Species of brightly coloured primary and secondary Asian freshwater crabs are collected intensively for the aquarium trade and some of these restricted range habitat specialists may now be threatened with extinction (Cumberlidge et al. 2009).

Many widespread lowland species of freshwater crabs (e.g., *Parathelphusa maculata*) seem to be tolerant of change because these crabs continue to survive despite suffering severely altered lowland freshwater habitats as a result of land development, natural forest loss, and agriculture. On the other hand, many species of freshwater crabs are less tolerant of habitat alteration and are vulnerable to population crashes, and these species tend to be those that have a restricted distribution in highly threatened tropical freshwater habitats. For example, restricted range species such as the cave specialist *Cerberusa caeca*, and the cold mountain stream specialist *Johora grallator* are both vulnerable to, and have little tolerance of, habitat changes. Other restricted range species that inhabit inaccessible places (such as offshore islands, high mountains, caves, and karsts) with low human impact are less likely to be threatened. Studies of the conservation status of the freshwater crab faunas of Sri Lanka (Bahir et al. 2005), Malaysia (Ng and Yeo 2007), China (Cumberlidge et al. 2011a), Tanzania (Reed and Cumberlidge 2006), southern Africa (Cumberlidge and Daniels 2007), and the Neotropical region (Cumberlidge et al. 2014) have reached similar conclusions: it is the restricted range species living in disturbed habitats that are more likely to be threatened.

The conservation of freshwater crabs in general requires conservation actions tailored to bring about the long-term survival of a species threatened with extinction. Other approaches to species conservation focus more on habitat conservation. For example, there is a need for a network of carefully managed protected sites that are large enough to preserve natural forests in drainage basins that will maintain water quality in the rivers, streams, lakes, and wetlands where crabs live. This in turn would require the establishment of more nature reserves and national parks, and the development of integrated species conservation action plans for the world's increasing number of species of freshwater crabs that are threatened with extinction.

1.6 Conclusions

1. Primary and secondary freshwater crabs are abundant in tropical and subtropical freshwater habitats around the world in five zoogeographic regions (Neotropical, Afrotropical, Palearctic, Oriental, and Australasian). Primary freshwater crabs dominate the inland waters of continents and islands, while secondary freshwater crabs mostly occupy littoral freshwater and saltwater habitats, and many species migrate seasonally between the two.

2. Primary and secondary freshwater crabs are diverse and species rich (1394 and 223 species respectively in 2015) and they together constitute more than 20 % of all brachyurans The rate of new species discovery in four of the five families of primary freshwater crabs is high, and is likely to continue for the rest of the 21st century, given the vast areas on un-surveyed suitable habitats around the world, and the improving taxonomic precision. The species discovery rate in one family, the Trichodactylidae, has slowed in the past 20 years and this family may be close to being known comprehensively.
3. The extinction risk of 651 out of the 1280 species of freshwater crabs known in 2009 that were assessed using IUCN Red List protocols indicates that two-thirds (425) are not immediately threatened (either LC or NT); but that about one third (209) have a high extinction threat level: 32 critically endangered (CR), 52 endangered (EN), and 123 vulnerable (VU) species.
4. The main threats to primary freshwater crabs include habitat destruction (accelerated by global climate change), alterations of river or stream flow patterns (from dams and other drainage diversions), and pollution (from mining, pesticides, and fertilizers). Other threats to freshwater animals include displacement of native species by introduced species, and over-harvesting either for food or for the aquarium trade.
5. No species of primary freshwater crabs are known to be extinct (EX) or extinct in the wild (EW), but extinctions are difficult to confirm using IUCN Red List protocols. However, some 628 species of primary freshwater crabs (which represent almost 49 % of the global fauna) are designated as Data Deficient (DD). The large number of DD species of primary freshwater crabs is a cause for concern because their exclusion from conservation assessments due to a lack of relevant data may be masking the true number of threatened (and possibly extinct) species.
6. Some DD species may actually be extinct because there have been no records of them for over a century and their original habitats are now highly altered or located in densely populated urban areas. It is likely that a greater proportion of the global fauna of freshwater crabs is threatened with extinction than is currently realized.

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