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## Chapter 6.

Freshwater crabs of Africa: diversity, distribution, and conservation.

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## 6.1 Overview of the African freshwater crab fauna

Freshwater crabs are among the most important invertebrates inhabiting African inland waters, and these large and conspicuous crustaceans are present in almost all freshwater habitats, from mountain streams to large lowland rivers and smaller water bodies (Rathbun 1921; Balss 1936; Bott 1955; Cumberlidge 1999; Yeo et al. 2008). The present work focuses on the freshwater crabs of continental Africa, which includes northern Africa in the Palaearctic zoogeographical zone, and the rest of the African continent that lies in the Afrotropical zone. The countries of northern Africa that host freshwater crabs are Morocco, Algeria, Tunisia, and Egypt, where there are three species of freshwater crabs in two genera (Potamonautes and Potamon) and two families, Potamonautidae Bott, 1970, and Potamidae Ortmann, 1896 (Yeo et al. 2008; Cumberlidge 2009a,b; Cumberlidge et al. 2009). The part of the Afrotropical zone dealt with here includes all 43 African countries south of the Sahara Desert, but excludes the islands of the western Indian Ocean (Socotra, the Seychelles, and Madagascar) that also lie in the Afrotropical zone. This part of Africa includes 119 species of freshwater crabs in 10 genera that all belong to the Potamonautidae (Cumberlidge 1999, 2009a,b; Daniels et al. 2006; Cumberlidge et al. 2008; Yeo et al. 2008; Cumberlidge and Ng 2009; Cumberlidge et al. 2009).

The total taxonomic diversity of continental Africa (11 genera, 120 species, two families) (Table 6.1) is markedly lower than seen in the freshwater crab faunas of the Neotropical (50 genera, 298 species, two families) and Oriental/Palaearctic (154 genera, 849 species, two families) regions (Yeo et al. 2008; Cumberlidge et al. 2009). Continental Africa's freshwater crab fauna is highly endemic at the family, genus, and species levels with 100% endemicity for the predominant family, the Potamonautidae (Bott 1955; Cumberlidge 1999; Cumberlidge et al. 2009). The African continent is, for the purposes of this project, subdivided into the five main regions, and each of these has a distinct freshwater crab faunal composition, with only a few species (14 out of 120) found in more than one region. For example, the most diverse regions are eastern Africa (44 species, three genera), central Africa (33 species, three genera), and western Africa (24 species, six genera), while southern Africa (20 species, one genus) and northern Africa (four species, two genera) each have a less diverse regional fauna (Bott 1955; Cumberlidge 1997, 1998, 1999, 2009a,b; Cumberlidge and Boyko 2000; Corace et al. 2001; Cumberlidge et al. 2002; Cumberlidge and Vanini 2004; Cumberlidge and Reed 2004, 2006; Cumberlidge and Tavares 2006; Cumberlidge and Dobson 2008; Cumberlidge et al. 2009)



The Common Creek Crab Liberonautes latidactylus (Least Concern) is the most common and most frequently caught freshwater crab in small streams throughout the rainforest and savanna zones of western Africa. © PIOTR NASKREKI

Table 6.1. Numbers of species, genera, families and subfamilies, and their regions of occurrence, for each of the 43 countries in Africa that has freshwater crabs. N = northern Africa, W = western Africa, C = central Africa, E = eastern Africa, S = southern Africa."

	Country	No. Species	No. Genera	Region	Family, subfamily
1	Morocco	1	1	N	Potamidae, Potaminae
2	Algeria	1	1	N	Potamidae, Potaminae
3	Tunisia	1	1	N	Potamidae, Potaminae
4	Egypt	1	1	N	Potamidae, Potaminae
		2	1		Potamonautidae, Potamonautinae
5	Nigeria	10	3	W	Potamonautidae, Potamonautinae
6	Liberia	8	1	W	Potamonautidae, Potamonautinae
		1	1		Potamonautidae, Hydrothelphusinae
7	Guinea	5	2	W	Potamonautidae, Potamonautinae
		2	1		Potamonautidae, Hydrothelphusinae
8	Côte d'Ivoire	6	3	W	Potamonautidae, Potamonautinae
9	Ghana	6	3	W	Potamonautidae, Potamonautinae
10	Togo	4	2	W	Potamonautidae, Potamonautinae
11	Sierra Leone	2	2	W	Potamonautidae, Potamonautinae
		1	1		Potamonautidae, Hydrothelphusinae
12	Benin	2	2	W	Potamonautidae, Potamonautinae
13	Chad	2	1	W	Potamonautidae, Potamonautinae
14	Mali	2	2	W	Potamonautidae, Potamonautinae
15	Mauritania	2	1	W	Potamonautidae, Potamonautinae
16	Burkina Faso	1	1	W	Potamonautidae, Potamonautinae
17	Niger	1	1	W	Potamonautidae, Potamonautinae
18	D. R. Congo	24	3	С	Potamonautidae, Potamonautinae
19	Cameroon	13	4	С	Potamonautidae, Potamonautinae
20	Congo	11	3	С	Potamonautidae, Potamonautinae
21	Gabon	8	2	С	Potamonautidae, Potamonautinae
22	Central African Republic	4	2	C	Potamonautidae, Potamonautinae
23	Equatorial Guinea/Bioko	3	1	C	Potamonautidae, Potamonautinae
24		1	1	C	Potamonautidae, Potamonautinae
	Angola (Cabinda)	3	2	E	
25	Sudan	3	۷		Potamonautidae, Potamonautinae
26	Somalia	1	1	Е	Potamonautidae, Potamonautinae Potamonautidae, Hydrothelphusinae
27	Ethiopia	6	1	Е	
	Ethiopia		·	E	Potamonautidae, Potamonautinae
28	Kenya	13 2	1		Potamonautidae, Potamonautinae Potamonautidae, Hydrothelphusinae
29	Uganda	12	2	Е	Potamonautidae, Potamonautinae
30	Rwanda	4	1	E	Potamonautidae, Potamonautinae
					Potamonautidae, Potamonautinae
31	Burundi	1	1	E	,
32	Tanzania	24 1	1	Е	Potamonautidae, Potamonautinae
22	Molowi		1	Е	Potamonautidae, Hydrothelphusinae
33	Malawi	4	4		Potamonautidae, Potamonautinae
34	Angola	5	1	S	Potamonautidae, Potamonautinae
35	Botswana	2		S	Potamonautidae, Potamonautinae
36	Lesotho	1	1	S	Potamonautidae, Potamonautinae
37	Mozambique	3	1	S	Potamonautidae, Potamonautinae
38	Namibia	4	1	S	Potamonautidae, Potamonautinae
39	South Africa	14	1	S	Potamonautidae, Potamonautinae
40	Swaziland	1	1	S	Potamonautidae, Potamonautinae
41	Zambia	3	2	S	Potamonautidae, Potamonautinae
42	Zimbabwe	3	1	S	Potamonautidae, Potamonautinae

#### 6.1.1 Biogeographic patterns

Freshwater crabs are found in all major habitat types in continental Africa, including floodplains, swamps, lakes, moist forest rivers, Mediterranean systems, highland and mountain systems, large lakes, large river rapids, dry savanna rivers, and even xeric systems where there are freshwater resources above ground. Species diversity is highest in the rivers and streams of the major river basins of Africa, especially those that flow through lowland rainforest and drain forested highlands. Because of their widespread representation in Africa's aquatic ecosystems, freshwater crabs are also represented in most of the continent's freshwater ecoregions (e.g., the North African, Nilo-Sudan, Upper Guinea, West Coast Equatorial, Congo, Great Lakes, Eastern and Coastal, Cuanza, Zambezi, and Southern Temperate freshwater ecoregions) (Thieme et al. 2005; Abell et al. 2008). However, with only a few exceptions, there is no close correlation between freshwater crab distribution patterns and freshwater ecoregion boundaries found in the



The White Volta River as an example of suitable habitat for at least two freshwater crabs species. © KLAAS-DOUWE DIJKSTRA

African region. The only instances where freshwater crabs distribution coincides with ecoregion boundaries are those species that have a restricted distribution.

Table 6.2. The threatened species of freshwater crabs found in continental Africa, with their regions of occurrence, and a summary of their conservation status. C = central Africa, W = western Africa, S = southern Africa, E = eastern Africa, N = northern Africa.

		Regional		
	Species	Distribution	Red List Category	Red List Criteria
1	Liberonautes grandbassa	W	CR	B1ab(iii)+2ab(iii)
2	Liberonautes lugbe	W	CR	B1ab(iii)
3	Afrithelphusa monodosa	W	EN	B1ab(iii)+2ab(iii); C2a(i)
4	Globonautes macropus	W	EN	B1ab(iii)+2ab(iii); C2a(i)
5	Liberonautes nanoides	W	EN	B1ab(iii)+2ab(iii)
6	Liberonautes rubigimanus	W	EN	B2ab(iii)
7	Louisea balssi	С	EN	B1ab(i,ii,iii,iv,v)
8	Louisea edeaensis	С	EN	B1ab(i,ii,iii,iv,v)
9	Potamonautes gonocristatus	С	EN	B1ab(i,ii,iii,v)
10	Potamonautes idjiwiensis	C/E	EN	B1ab(i,iii)+2ab(i,iii)
11	Potamonautes mutandensis	C/E	EN	B1ab(iii,v)+2ab(iii,v); C1+2a(ii)
12	Potamonautes platycentron	Е	EN	B1ab(iii)+2ab(iii)
13	Liberonautes nimba	W	VU	B1ab(iii)+2ab(iii); D2
14	Potamonautes choloensis	Е	VU	B1ab(i)
15	Potamonautes gerdalensis	Е	VU	B1ab(i); D2
16	Potamonautes ignestii	Е	VU	B1ab(i); D2
17	Potamonautes infravallatus	Е	VU	B1ab(i); D2
18	Potamonautes lividus	S	VU	B1ab(iii)+2ab(iii)
19	Potamonautes montivagus	Е	VU	B2ab(i)
20	Potamonautes pilosus	Е	VU	B1ab(i,iii); D2
21	Potamonautes raybouldi	Е	VU	B2ab(iii)
22	Potamonautes reidi	W	VU	B1ab(iii)+2ab(iii)
23	Potamonautes triangulus	W	VU	B1ab(iii)+2ab(iii)
24	Potamonautes unisulcatus	Е	VU	B1ab(i,ii,iii); D2
25	Potamonautes xiphoidus	Е	VU	B1ab(iii)+2ab(iii); D2
26	Potamonemus sachsi	W/C	VU	B1ab(iii)+2ab(iii)



The Purple March Crab Afrithelphusa monodosa (Endangered) which lives in swamps and year-round wetland habitats in north-western Guinea where it is known from only a few specimens from two localities. This species is clearly a competent air-breather and has a pair of well-developed pseudolungs. It is mainly threatened by habitat loss and degradation. © PIOTR NASKREKI

#### 6.2 Conservation status

The conservation status of Africa's freshwater crab fauna was assessed by Cumberlidge *et al.* (2009) using the IUCN Red List Categories and Criteria at the global scale (IUCN 2003), and individual species assessments are freely available through the IUCN Red List website (www. iucnredlist.org). Results reveal current high levels of threat

with 26 (21%) of the 120 species assessed as globally Threatened (Table 6.2 and 6.3, and Figure 6.1a). There is insufficient information to assess the status of 27 species which were categorised as Data Deficient (DD) due to a lack specimens, and locality and population data (Cumberlidge *et al.* 2009; Table 6.3, and Figure 6.1a). If all Data Deficient (DD) species also proved to be Threatened, the level of threat could be as high as 44%.

Figure 6.1. The proportion (%) of freshwater crab species in each regional IUCN Red List Category in mainland continental Africa (Cumberlidge *et al.* 2009, Appendix 1): a) all 120 species from the region; and b) following removal of the 27 DD species.

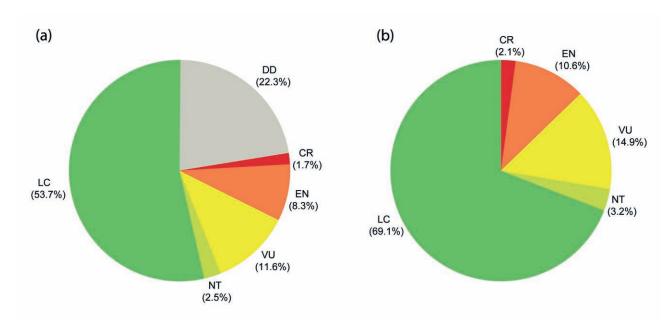


Table 6.3. The number of African crab species in each IUCN Red List category by region (Cumberlidge *et al.* 2009, Appendix 1). The total number of species per Category does not include species found in more than one region. Numbers with an \* = total species per region including those species that are found in more than one region. For example, LC includes five species that are found in both W + C, two species that are found in both E + N, and one species each that is found in both E + C, E + S, and S + C + E); EN includes two species that are found in both C + E); DD includes one species that is found in both C + S). C = central Africa, W = western Africa, S = southern Africa, E = eastern Africa, N = northern Africa.

	REGION					Total species per
IUCN Red List Category	N	W	С	Ε	S	Red List Category
Critically Endangered	0	2	0	0	0	2
Endangered	0	4	2	4	0	10
Vulnerable	0	3	1	9	1	14
Near Threatened	0	0	0	2	0	2
Least Concern	2	10	16	24	15	64
Data Deficient	0	5	12	5	4	25
Total species per region*	2*	24*	31*	44*	20*	117

Of the 94 species that could be assessed, the majority (65 species, 69%, Figure 6.1b) belong to seven genera and were judged to be Least Concern (LC), and most of these live in rivers, marshy lowlands, or mountain streams in the forested parts of Africa (Cumberlidge 1999; Cumberlidge et al. 2009). Forty-three out of the 76 species of Potamonautes are LC, as are one of the three species of Potamonemus, eight of the 11 species of Sudanonautes, eight of the nine species of Platythelphusa, three of the eight species of Liberonautes, and one each of the two species of Erimetopus and Potamon. Twenty-six (28%) of the 94 assessed species were listed in one of three threatened categories, either as Critically Endangered (CR) (two species), Endangered (EN) (10 species) or Vulnerable (VU) (14 species) (Figure 6.1b and Table 6.3). Just three species (3%) were assessed as Near Threatened (NT). No species of freshwater crabs from Africa could be confirmed

Aubry's Crab Sudanonautes aubryi (Least Concern) is a widespread species found throughout much of western and Central Africa. This specimen was collected on the western border of the Campo Maan National Park on the border to Equatorial Guinea. This large species inhabits streams, rivers, and ponds, and digs burrows near waterways; at night and during rainstorms it is often found on land because it is capable of breathing air. © JENS KIPPING

Extinct (EX) or Extinct in the Wild (EW). However, it should be noted that a species cannot be formally assessed as Extinct until exhaustive surveys have been carried out.

Detailed assessments of species' regional status are also available for eastern Africa (Darwall *et al.* 2005), southern Africa (Cumberlidge and Daniels 2008), western Africa (Smith *et al.* 2009), northern Africa (Garcia *et al.* 2010), and central Africa (Brooks *et al.* 2011).

#### 6.3 Patterns of species richness

Continental Africa has a rich, highly diverse, and distinctly recognisable freshwater crab fauna, with all species endemic to the continent, and distributed over 43 countries (Cumberlidge 1999; Table 6.1). Distribution data used here have been derived from all available specimen records but are still likely to be incomplete. Although a majority of the African species are quite well studied, there are still some that are known only from either the type locality or from just a few records, and in these cases further collections are necessary to ascertain their actual distributions. The available data indicate that the composition of the freshwater crab fauna in Africa is not uniform, changes from region to region, and varies with ecosystem, aquatic drainage basins, and vegetation cover. For example, freshwater crabs are found in all of the major ecosystems in continental Africa, but are noticeably more abundant in the rainforest, especially in highland regions (Cumberlidge 1999). Species diversity appears to depend on vegetation cover and the availability of water, with the highest number of species occurring in rainforest ecosystems, especially in highland areas, and the fewest in savanna ecosystems. One interesting pattern shown by the distribution of species in African forests is areas of high biotic diversity surrounded by apparently identical forest areas that have a gradient of declining species numbers (Cumberlidge 1999). For example, there are three relatively small areas of the African rainforest that stand out as having an unusually high number of species and a higher than normal number of endemic species: the Upper Guinea forest in western Africa, the Lower Guinea forest in Nigeria and Cameroon, and the forests of eastern D. R. Congo (Cumberlidge 1999).

At the genus level the taxonomic diversity is highest in western and central Africa (six genera), lower in eastern Africa (four genera), and lowest in northern Africa (two genera) and southern Africa (one genus) (Table 6.4). Although eastern Africa is the most species rich region (with 44 species in three genera and two subfamilies), western Africa stands out as the most diverse (with 24 species, six genera and two subfamilies) (Table 6.4). Distribution patterns considered at the genus level indicate that each of the five African regions has genera with species that have a wide distribution, and many other species that have a restricted distribution. Five out of eleven genera have a wide distribution in more than one region. For example, Potamonautes is found in all five regions, Sudanonautes is found in three regions, while Platythelphusa and Potamonemus occur in two regions. Potamonautes, Sudanonautes, and Liberonautes include some widespread species, and some species that are endemic to a particular region. In contrast, six genera have a relatively restricted range and are endemic to a particular region. For example, Afrithelphusa, Globonautes and Liberonautes are all

Table 6.4. Number of species and genera found in each region in Africa. N = northern Africa, W = western Africa, C = central Africa, E = eastern Africa, S = southern Africa. \* = regional endemic.

		REGION				
Genus	# Species	Ν	W	С	Ε	S
Potamonautes	76	2	4	23	33	19
Sudanonautes	11	0	5	5	1	0
Platythelphusa	9	0	0	9	9	0
Liberonautes*	8	0	7	0	0	0
Afrithelphusa*	4	0	4	0	0	0
Potamonemus	3	0	1	2	0	0
Deckenia*	2	0	0	0	2	0
Erimetopus*	2	0	0	2	0	0
Louisea*	2	0	0	2	0	0
Potamon	1	1	0	0	0	0
Globonautes*	1	0	1	0	0	0
Genera /region		2	6	6	4	1

endemic to western Africa, *Louisea* and *Erimetopus* are both found only in central Africa, and *Deckenia* is found only in eastern Africa. Although *Potamon* has a number of wide distributional ranges in the Mediterranean and Middle East as far east as the Himalayas (Brandis *et al.* 2000), within Africa this genus is found only in the Palaearctic zone of northern Africa.



Potamonautes lirrangensis (Least Concern) is a relatively abundant and widespread species found in large slow flowing rivers in rainforests across central and eastern Africa. It is subject to a small commercial fishery in Malawi. © DENIS TWEDDLE

### 6.3.1 All freshwater crab species: interpretation of distribution patterns

Potamonautes includes by far the largest number of species in Africa (Bott, 1955, 1959, 1969, 1970; Stewart et al. 1995; Cumberlidge 1997, 1998, 1999, 2009a,b; Stewart 1997; Corace et al. 2001; Cumberlidge et al. 2002; Cumberlidge and Vanini 2004; Reed and Cumberlidge 2004, 2006; Cumberlidge and Boyko 2000; Cumberlidge and Tavares 2006; Cumberlidge and Dobson 2008). The 76 species of this large genus are found in all five regions of Africa, and are distributed throughout sub-Saharan Africa from the Cape to Cairo, and from Senegal to the Horn of Africa (Figure 6.2). The only region where Potamonautes does not occur is in the coastal fringe of north-west Africa (the Maghreb) that lies in the Palaearctic zoogeographical region. Some species of Potamonautes are widespread and are associated with the major river basins throughout the continent, some have adopted a semi-terrestrial airbreathing habit, while others have a narrow distribution and are endemic to a very restricted area. The largest numbers of species of Potamonautes occur in eastern Africa and in the forested Congo River basin. The vast majority of species of Potamonautes occur in eastern, central, and southern Africa (33, 24, and 20 species respectively), and there are only four species of Potamonautes in western Africa (all endemic), and two in northern Africa (both widespread species found along the Nile River). One species (Potamonautes ecorssei) is even found in the Sahara desert in Mali, but only where the Niger River flows through Timbuktu (Cumberlidge 1999).

Sudanonautes includes 11 species distributed in western and central Africa, with one species (S. floweri) reaching as far east as Uganda and Sudan in eastern Africa (Cumberlidge 1989, 1991, 1993b,c, 1994b, 1995,a,b,c,d, 1999) (Figure 6.2). The largest numbers of Sudanonautes species are found in the forested region of south-east Nigeria, south-west Cameroon, and on the island of Bioko. Species of Sudanonautes occur in most of the major ecosystems of western and central Africa (tropical rainforest, Guinea and Sudan savanna), and are found in most aquatic habitats (standing water, streams and major rivers) and on land. Sudanonautes africanus, S. nigeria, S. granulatus, S. orthostylis, S. chavanesii and S. faradjensis occur exclusively in rainforest habitats, while S. aubryi and S. floweri are found in both rainforest and woodland savanna. Sudanonautes kagoroensis occurs only in Guinea savanna in Nigeria, while the semi-terrestrial air-breathing S. monodi is the only species found in both Guinea and in dry Sudan savanna. Eight of the 11 species of Sudanonautes are widespread throughout western and central Africa, while the other two species, S. orthostylis and S. sangha, each have a restricted distribution in central Africa (Cumberlidge 1999; Cumberlidge and Boyko 2000).

The eight species of *Liberonautes* are all restricted to western Africa; the western limit of the genus is Senegal,



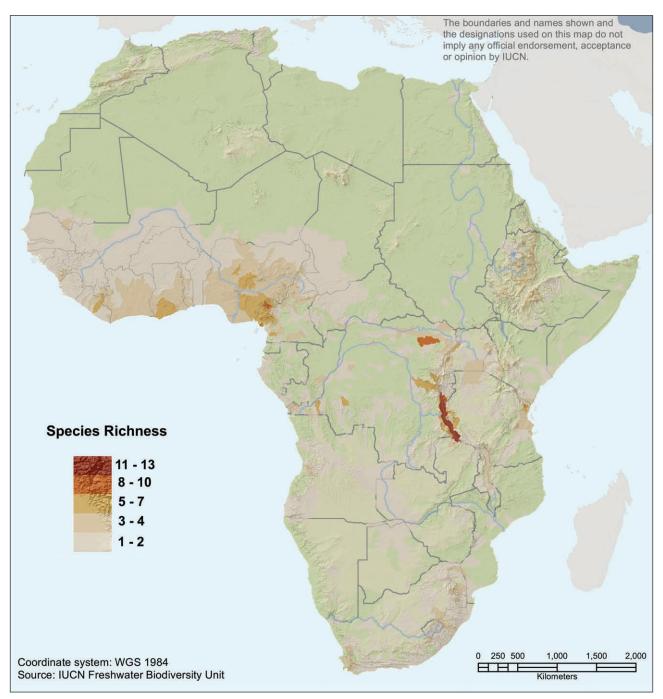
The freshwater crab Potamon algeriense (Least Concern) is endemic to the streams and rivers of Morocco, Algeria and Tunisia. It is Least Concern and affected by human induced threats such as habitat loss and degradation linked to population growth and industrial and agrarian development.

© JEAN-PIERRE BOUDOT

the eastern limit is Ghana, and the northern limit is Mali (Cumberlidge 1999; Cumberlidge and Huguet 2003) (Figure 6.2). One species (*L. latidactylus*) is widespread over the entire range of the genus, while the remaining seven species each have a limited distribution in Liberia, Guinea, and Côte d'Ivoire. Species of *Liberonautes* are found mostly in rainforest, although *L. latidactylus* is also found in both Guinea and Sudan savanna zones. Most species are found in aquatic habitats (streams or major rivers) while *L. paludicolis* is more terrestrial and *L. rubigimanus* and *L. nimba* are found at high altitudes, and *L. chaperi* and *L. nanoides* are found exclusively in the major rivers.

The three species of Potamonemus occur in only in western and central Africa in the forested highlands of south-east Nigeria, south-west Cameroon, and western Togo (Figure 6.2). These species occur in small streams and probably leave the water at night to feed (Cumberlidge and Clark 1992; Cumberlidge 1993a; 1999). Globonautes macropus, the Liberian Tree Hole Crab, occurs only in the western part of the Upper Guinea forest in Liberia and Guinea, and lives in small water reservoirs in tree holes in closed canopy forest (Cumberlidge and Sachs 1991; Cumberlidge 1991, 1996a,b; 1999). The four species of Afrithelphusa occur only in the western part of the Upper Guinea forest of western Africa. Afrithelphusa gerhildae and A. monodosa are both found only in Guinea, while A. afzelii and A. leonensis are only known from Sierra Leone (Cumberlidge 1987, 1991; 1996a,b; 1999). The two species of Louisea are found only in south-west Cameroon in the forested highlands and the moist lowland rainforests (Cumberlidge 1994a, 1999). One of the two species of Erimetopus (E. brazzae) is relatively widespread in the lower Congo River, while the other species, E. vandenbrandeni, is more restricted in its distribution (Cumberlidge and Reed 2004; Cumberlidge et al. 2009). All nine species of Platythelphusa are endemic to

Figure 6.2. The distribution of freshwater crab species across mainland continental Africa. Species richness = number of species per river/lake sub-catchment.



Lake Tanganyika (Cumberlidge et al. 1999; Marijnissen et al. 2004), while both species of *Deckenia* are endemic to eastern Africa (Ng et al. 1995; Marijnissen et al. 2005). One species of *Potamon* (*P. algeriensis*) is found in continental Africa and is endemic to the Mahgreb in northern Africa (Brandis et al. 2000; Cumberlidge 2009a).

#### 6.3.2 Threatened species

Some 28% (26 out of 94 species) of African freshwater crabs were assessed as being in one of the three threatened categories (CR, EN, VU) (Cumberlidge *et al.* 2009; Figure 6.1a; Table 6.5). Most of these (20 species) are found in either eastern Africa (11 species) or western Africa (nine species), and there are only three threatened species in

central Africa (the most speciose region) and just one in southern Africa (Figure 6.3). There are no threatened species in the northern Africa region. Of the threatened species, 10 were assessed as EN, of which four are from western Africa (A. monodosa, G. macropus, L. nanoides, and L. rubigimanus), four from eastern Africa (P. idjwiensis, P. mutandensis, P. platycentron, and P. gonocristatus) and two from central Africa (L. edeaensis and L. balssi). None of the species from southern Africa was assessed as EN. A further fourteen species were assessed as VU, of which nine are from eastern Africa (P. choloensis, P. gerdalensis, P. ignestii, P. infravallatus, P. montivagus, P. pilosus, P. raybouldi, P. unisulcatus, and P. xiphoidus), four from western Africa (P. reidi, P. triangulus, Potamonemus sachsi, and L. nimba), one from southern Africa (P. lividus),

Table 6.5. Number of species from each genus in each IUCN Red List Category.

	IUCN RED LIST CATEGORY						
Genus	LC	NT	VU	EN	CR	DD	
Potamonautes	43	0	12	4	0	18	
Sudanonautes	8	0	0	0	0	3	
Platythelphusa	8	0	0	0	0	1	
Liberonautes	3	0	1	2	2	0	
Afrithelphusa	0	0	0	1	0	3	
Potamonemus	1	0	1	0	0	1	
Deckenia	0	2	0	0	0	0	
Erimetopus	1	0	0	0	0	1	
Louisea	0	0	0	2	0	0	
Potamon	0	1	0	0	0	0	
Globonautes	0	0	0	1	0	0	
Total species	64	3	14	10	2	27	

and one from central Africa (*P. sachsi*, which is also found in western Africa). Two species (*L. grandbassa* and *L. lugbe*) were assessed as CR, both of which are from western Africa. Just two species, *Deckenia imitatrix* and *D. mitis* (both from eastern Africa) were assessed as NT. The main threats to these species were identified as urban, industrial, and agricultural development and the associated aquatic habitat degradation and pollution.

#### 6.3.3 Restricted range species

Excluding DD species, some 29 species were found to have a restricted range (<20,000km²) (Table 6.6), and these restricted range species are irregularly distributed throughout Africa (Figure 6.4). The limited distributions of these species are not simply a product of omission errors stemming from a lack of knowledge or under-collection. These species are

Figure 6.3. The distribution of Threatened freshwater crab species across mainland continental Africa. Species richness = number of species per river/lake sub-catchment.

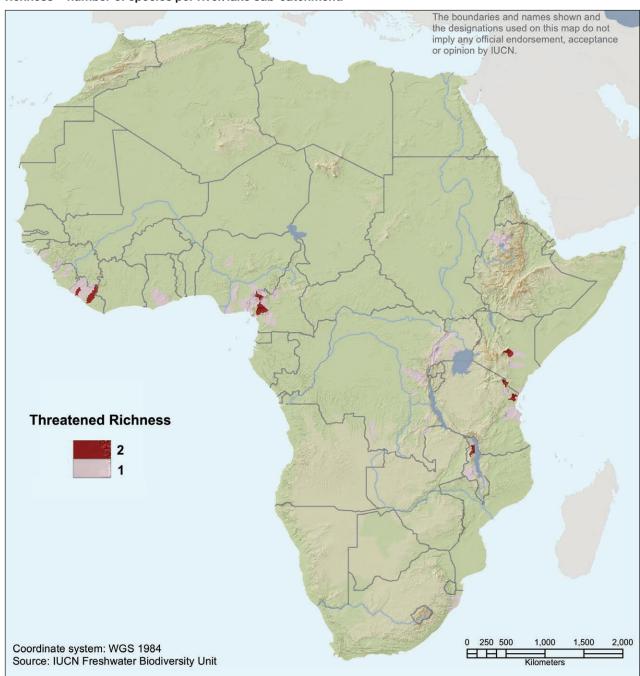


Table 6.6. Species of freshwater crabs of Africa restricted to single river basins, excluding those considered to be Data Deficient. RL = IUCN Red List status; LC = Least Concern; VU = Vulnerable; EN = Endangered; CR = Critically Endangered; Range = an estimation of the species distribution range based on all known specimens; #Loc = Number of discontinuous localities from which the species was collected; PA = found in a protected area; Y = yes, N = no; regions of Africa are noted as N = northern Africa, W = western Africa, C = central Africa, E = eastern Africa, S = southern Africa.

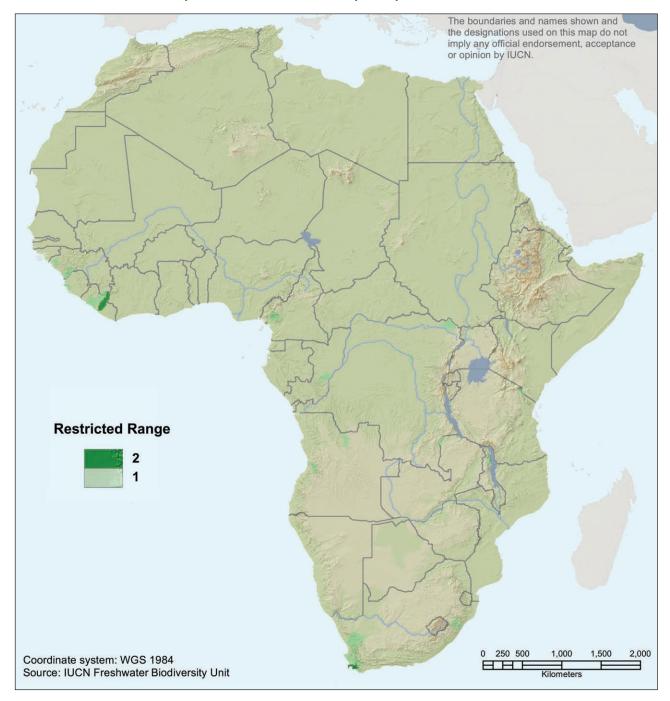
Species	RL Category	Range (km2)	# Loc	PA	Region
Liberonautes grandbassa	CR	~ 100	1	N	W
Liberonautes lugbe	CR	~ 100	1	N	W
Afrithelphusa monodosa	EN	< 5,000	2	N	W
Globonautes macropus	EN	< 5,000	5	Ν	W
Liberonautes nanoides	EN	< 5,000	1	N	W
Liberonautes rubigimanus	EN	< 20,000	3	Υ	W
Louisea edeaensis	EN	< 5,000	2	Ν	С
Louisea balssi	EN	< 5,000	3	Ν	С
Potamonautes gonocristatus	EN	< 5,000	<10	N	Е
Potamonautes idjiwiensis	EN	< 500	<5	N	Е
Potamonautes mutandensis	EN	< 500	<5	N	Е
Potamonautes platycentron	EN	< 500	<5	N	Е
Erimetopus brazzae	LC	< 20,000	<10	Ν	С
Potamonautes margaritarius	LC	< 800	<5	Ν	С
Potamonemus mambilorum	LC	< 20,000	8	Ν	С
Potamonemus sachsi	VU	< 20,000	<10	Ν	С
Sudanonautes kagoroensis	LC	< 5,000	7	Ν	W
Liberonautes nimba	VU	< 20,000	4	Υ	W
Potamonautes choloensis	VU	< 20,000	<10	N	Е
Potamonautes gerdalensis	VU	< 20,000	<5	N	Е
Potamonautes ignestii	VU	< 20,000	<5	N	Е
Potamonautes infravallatus	VU	< 20,000	<10	Ν	Е
Potamonautes lividus	VU	< 20,000	<10	Υ	S
Potamonautes montivagus	VU	< 20,000	<10	Ν	Е
Potamonautes pilosus	VU	< 20,000	<5	Ν	Е
Potamonautes raybouldi	VU	< 2,000	<10	N	Е
Potamonautes reidi	VU	< 20,000	<10	Υ	W
Potamonautes triangulus	VU	< 20,000	6	N	W
Potamonautes unisulcatus	VU	< 20,000	<5	N	Е
Potamonautes xiphoidus	VU	< 2,000	<5	N	Е

specifically recorded, through many surveys conducted over the years, as being absent in localities where they may have been expected to occur. Any disruption to the habitats of these species (either from development, pollution, or political unrest) could have serious consequences, given that 24 of these restricted range species have been assessed as Threatened (Table 6.6). Any species with a restricted range is potentially vulnerable to extreme population fragmentation and could suffer a rapid decline, and even extinction, in a relatively short time should dramatic changes in land-use suddenly affect its habitat. It is therefore of immediate concern that 24 of the 94 crab species that could be assessed are known from distribution ranges of less than 20,000km<sup>2</sup> (and some of these have an estimated range of 5,000km<sup>2</sup> or less). Despite the dangers of population fragmentation, current population levels of stenotopic species assessed as LC or NT were estimated to be stable because they have been



The Blue River Crab Potamonautes lividus (Vulnerable) is a relatively restricted range species endemic to swamp forests in north-eastern Kwa-Zulu Natal, South Africa. © WINKS EMMERSON

Figure 6.4. The distribution of freshwater crab species with severely restricted distributional ranges across mainland continental Africa. Species richness = number of species per river/lake sub-catchment.



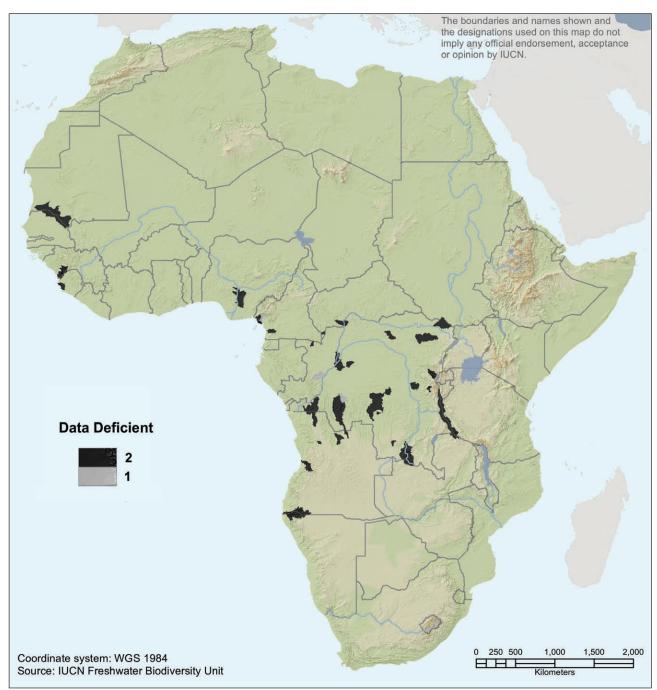
collected recently and there are no identifiable immediate threats that would impact the health of those streams and endanger their long-term existence. The reasons for the restricted ranges of the stenotopic species are largely unknown, but it is thought likely that they have speciated relatively recently in response to isolation in a specialised (marginal) habitat or through island colonization, rather than their being the remnant populations of formerly widespread species now in decline (Cumberlidge 2008; Cumberlidge et al. 2009).

#### 6.3.4 Data Deficient species

Some 27 of the 94 species (28%) assessed were judged to be DD (Table 6.3, Figure 6.1a). Thirteen of the DD species are from central Africa (*E. vandenbrandeni, P. acristatus,* 

P. adeleae, P. adentatus, P. lueboensis, P. punctatus, P. schubotzi, P. semilunaris, Potamonemus asylos, S. orthostylis and S. sangha), five are from western Africa (A. afzelii, A. gerhildae, A. leonensis, P. senegalensis, and S. nigeria), six are from eastern Africa (P. praelongata, P. amalerensis, P. bipartitus, P. didieri, P. rodolphianus, and P. rothschildsi), and three are from southern Africa (P. kensleyi, P. dubius, and P. macrobrachii) (Figure 6.5). None of the species from northern Africa were found to be DD. The relatively high proportion of DD species reflects the general lack of specimens available, a scarcity that continues to fuel uncertainty about the distribution of these little-known species (Bott 1955; Cumberlidge 1999; Cumberlidge et al. 2009). It is of great concern that in many cases these DD species have not been found in recent years. These species have been listed as DD in view of the absence of recent information on their Extent

Figure 6.5. The distribution of Data Deficient freshwater crab species across mainland continental Africa. Species richness = number species per river/lake sub-catchment.



of Occurrence, habitat, ecological requirements, population size, population trends, and long-term threats (Cumberlidge et al. 2009). It is also of concern that many of these species are known only from a few individuals collected many years ago, and that no new specimens have been found recently. The DD status is also assigned where there is insufficient information either on their taxonomic distinction (e.g. E. vandenbrandeni), or where they are known from either only one or only a few localities (P. schubotzi, S. orthostylis and S. sangha) and the full range extent is uncertain. It is possible that in some cases the DD status may be due to undersampling but, as mentioned above, this is not thought to be the case for many of the DD species. Further research is needed on all of these species because, at least, they may prove to be restricted range endemics vulnerable to habitat loss.

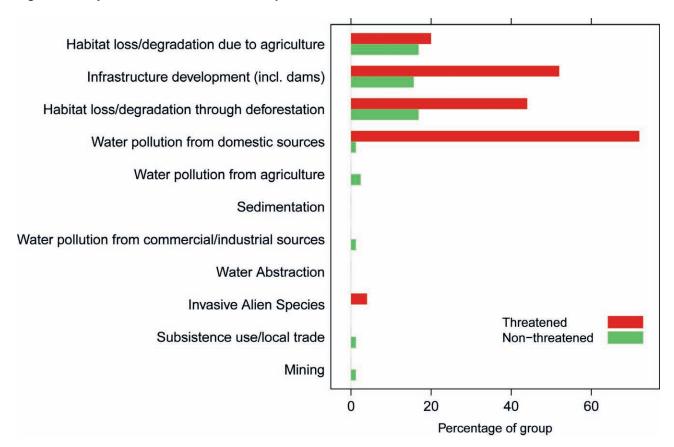
#### 6.4 Major threats

The main threats to African freshwater crabs include water pollution, urban, industrial, and agricultural development, and habitat loss and deforestation resulting from human population and urban and agricultural expansion (Figure 6.6).

#### 6.4.1 Habitat destruction

Threats to the endemic species include habitat destruction in the form of deforestation driven by timber extraction, mining, increasing agriculture, the demands of increasing industrial development, the alteration of fast flowing rivers for the creation of hydroelectric power, and the drainage of wetlands for farming and other uses (Figure

Figure 6.6. Major threats to freshwater crab species in mainland continental Africa.



6.6). Destruction of the forests in many parts of Africa is further exacerbated by logging roads that provide access to remote and previously undisturbed parts of the forest. Other threats that result in deforestation and habitat destruction include political unrest and refugee movements, which are often accompanied by deforestation and soil erosion that contributes environmental damage to freshwater ecosystems. Potential future threats to aquatic communities in rivers associated with cities and towns in Africa include pollution by sewage and industrial

and general waste. Some agricultural pesticides used by farmers may prove to be lethal to freshwater crabs, but more research needs to be carried out. All of the above factors combine to increase the overall level of threat to range-restricted endemic species, and the careful management of Africa's forests and water resources in the future will have the biggest impact on their long-term survival.

#### 6.4.2 Pollution

Pollutants from mining activities for diamonds, gold, bauxite, iron ore, and coltan, and from organic wastes from leaking sewage systems in urban areas in Africa can accumulate in rivers and other freshwater bodies. These pollutants impact freshwater crab populations because they are benthic feeders that ingest other invertebrates and detritus that may contain high levels of contaminants. Immediate attention should be given to the improvement of the water quality in these areas, not least because the bioaccumulation of metals in crabs could pose an increasing problem for the health of people that may eat them.

## 6.4.3 Natural predators and competition with introduced species

A large number of African predators – including yellownecked otters, water mongooses, African civets, kites, egrets, herons, giant kingfishers, monitor lizards,



Deforestation near the village Simpa in western Ghana, in the region of the Upper Guinean Rainforest. © JOHANNES FÖRSTER



Pollution from urban and domestic sources is a major threat to threatened freshwater crab species. © RANDALL BRUMMETT

and crocodiles - depend on freshwater crabs as vital components of their diet. This is because freshwater crabs are the largest macro-invertebrates in African aquatic ecosystems and form an integral part of the food chain (Cumberlidge et al. 2009). The ecological importance of freshwater crabs in food webs in Africa is underlined by the impact of alien North American crayfish (Procambarus *clarkii*) in the rivers of western Kenya, which out-competed and replaced the native crabs. The drop in freshwater crab populations in these systems led to a subsequent decline in clawless otter populations that fed on crabs, most likely due to increased competition with other predators attracted by the abundance of crayfish (Foster and Harper 2006, 2007; Ogada 2006). Recent reports indicate that the highly competitive Procambarus clarkii is rapidly spreading elsewhere in Eastern Africa and may even reach Lake Tanganyika, where it could threaten populations of freshwater crabs in the endemic genus Platythelphusa (Howard, pers. comm.).

#### 6.4.4 Taxonomic issues

The evolving taxonomy of freshwater crabs may prove to be a challenge for conservation planning in the future because, although a lot of progress has been made recently, some taxa currently assumed to be widespread and common may prove to be complexes of several distinct cryptic taxa, each with specific ecologies and distributions requiring direct conservation action. Three such possibilities are *P. perlatus*, *P. lirrangensis* and *S. granulatus* that are all currently assessed as LC primarily on account of their wide distributional ranges. However, the distribution patterns of these species consist of many relatively isolated subpopulations that show a great deal of morphological variation, and further investigations may show these species to be species complexes (Daniels *et al.* 2002).

#### 6.5 Research actions required

Significant areas of this vast continent still remain insufficiently explored, and new species of freshwater crabs are sure to be discovered if collection efforts in remote areas are intensified and taxonomic advances become more readily available in the form of identification keys. Although taxonomic knowledge has advanced considerably recently, and museum collections of freshwater crabs have improved, a great deal of work still needs to be done. There is a need for further surveys



The Louisiana Crayfish Procambarus clarkia has become seriously invasive throughout inland waters in Africa. It is omnivorous and will hunt and compete with the native freshwater crab species. © GEOFFREY HOWARD

to discover new species, refine species distributions, define specific habitat requirements, describe population levels and trends, and identify specific threats to Africa's important and unique freshwater crab fauna. It is vital to the health of these ecosystems that fishery managers consider measures that specifically include the conservation and sustainable use of local populations of river crabs.

#### 6.6. Conservation recommendations

The biology and distribution patterns of the freshwater crabs of Africa are becoming better known, as are the potential threats to their long-term survival. With 27 species (28%) of the 94 non-DD species of freshwater crabs from Africa currently assessed as being at risk of global extinction, the long-term survival of the continent's largely endemic freshwater crab fauna is a concern. Nevertheless, it is hoped that conservation recovery plans for threatened species will be developed for those species identified to be in need of conservation action through this Red List assessment process (Collen *et al.* 2008; Cumberlidge *et al.* 2009).

The conservation of many species of freshwater crabs depends primarily on preservation of areas of natural habitat large enough to maintain water quality. Although it is not yet known exactly how sensitive African freshwater crabs are to polluted or silted waters, there is evidence from Asia that similar crabs are not likely to survive when exposed to these factors (Ng and Yeo 2007). Development, agriculture and exploitation of natural products are necessary realities in developing economies, but compromises may have to be made if freshwater crab species are not to be extirpated in the future. Judicious and careful use of resources is unlikely to cause species extinctions as long as water drainages are not heavily polluted or redirected, some forest and vegetation cover is maintained, and protected areas are respected (Cumberlidge et al. 2009).

Common species assessed as LC have a wide distribution in the rivers, wetlands, and mountain streams of the region and, so far, have proved to be relatively tolerant of changes in land-use affecting aquatic ecosystems. It is encouraging that these more adaptable species can persist in the already disturbed and visibly polluted parts of the lowland rivers

and streams. The increasing loss of natural vegetation and pollution as a result of land development and agriculture are, however, likely to affect the lowland rivers in the long term, and many of the wholly aquatic species that live there could eventually be vulnerable. Even species assessed as LC could suffer catastrophic declines should there be abrupt changes in land development, hydrology, or pesticide-use regimes. It is not known how the highland taxa will cope with habitat disturbance and pollution but, considering their specialised habitat requirements, it is likely that most of these species will not adapt as readily as the more widespread lowland species. In many countries with a rapid pace of development, often only a fine line separates a species assessed as LC from one assessed as VU, or a VU species from one that is assessed as EN. Development projects could have a dramatic impact on species with specific habitat requirements and a restricted distribution. Conservation activities should therefore be aimed primarily at preserving the integrity of sites and habitats while at the same time closely monitoring key freshwater crab populations.

The 27 species of African freshwater crabs judged to be DD were assigned to this category primarily as the result of insufficient field survey. The scarcity of available specimens is in some parts of the continent due to the long-term poor security situation, and as a result little is known of the habitat needs, population trends, or threats to these species. When more information has been gathered, it is expected that almost all DD species will have a relatively restricted distribution and be endemic to the river basin where they are found.

The conservation assessment of freshwater crabs in Africa (Cumberlidge *et al.* 2009) represents a first step toward the identification of threatened species within the region and toward the development of a conservation strategy for endemic species. The restricted range of many species, together with the on-going human-induced loss of habitat in many parts of the region, are primary causes of concern for the long-term survival of this fauna. Africa's freshwater crabs have a high degree of endemism, with many species living in specialised habitats such as river rapids, lowland marshes, forested highlands, and islands. Additional research is recommended to determine the minimum effective size and design of protected areas for freshwater species such as crabs.

## Species in the spotlight

# A unique species flock of freshwater crabs in Lake Tanganyika: a model for studies in evolution and extinction

Marijnissen, S.A.E.1

ake Tanganyika is unique among the African Great Lakes in harbouring 10 endemic species of freshwater crabs, including Potamonautes platynotus and nine species in the genus Platythelphusa which form the only known lacustrine species flock of freshwater crabs in Africa. Platythelphusid crabs have a striking variety of morphological and ecological features making them ideal subjects for studies in adaptive evolution (Cumberlidge et al. 1999; Marijnissen et al. 2004). For instance, both males and females of Platythelphusa armata are armed with one significantly enlarged claw that they use to crush snail  $shells. \ Platythelphus a\ conculcata$ has evolved an extremely flat body that enables it to hide inside narrow crevices underneath rocks and stones. Platythelphusa maculata, on the other hand, is a tiny round-bodied species, which is often found taking refuge within empty shells of the large endemic snail Neothauma tanganyicensis.

As Africa's oldest (estimated 9-12 million years) and most species diverse lake, Lake Tanganyika is a famed natural laboratory for studying processes of adaptive evolution (e.g. Glor 2010, and references therein). Initially, it was thought that the platythelphusids were a relict group of marine crabs that got trapped in the lake after a recession of the sea and remained unchanged over millions of years (Moore 1903). However, genetic evidence indicates that all Lake Tanganyika crabs are derived from freshwater ancestors.



Potamonautes platynotus (LC) is primarily aquatic but has been observed to climb out of the water to feed amongst rocks along the lake shore. © HEINZ BUSCHER

The evolutionary divergence of the platythelpusids coincides with a period of climate change and drought, when the lake levels dropped substantially and Lake Tanganyika was split into separate basins (Cane and Molnar 2001; Marijnissen et al. 2006). Other taxa, including several cichlid groups (Duftner et al. 2005; Koblmüller et al. 2004, 2005, 2007), as well as the Synodontis catfish species flock (Day and Wilkinson 2006), diverged during the same period, about 3.3-2.5 million years ago.

The morphological differences between the platythelphusid crabs seem to have evolved within a relatively short period of time. A longstanding hypothesis is that the high levels of species diversity in the African Great Lakes are the result of competition and ecological niche diversification (Schluter 2000). Research on the crabs shows

morphological differentiation that could indeed be linked to ecological niche divergence (Marijnissen 2007). However, there is also evidence of considerable ecological versatility among platythelphusid species that coexist in rocky shore areas (Marijnissen *et al.* 2008).

Lake Tanganyika offers a wide diversity of habitats, ranging from cobble beaches, rocky outcrops, and stromatolite reefs, to extensive beds of empty Neothauma tanganyicensis shells, sandy beaches and deep layers of mud. Crabs can be found in all these habitats, but the majority of the species are found in the rocky areas. The crabs are important components of the food-web as prey as well as predators. They are included in the diet of numerous endemic fish, such as spiny eels (Mastacembelus plagiostomus), bagrid catfish (Chrysichthys brachynema and C. stappersi), and catfish

UNDP/GEF Project on Lake Tanganyika, Regional Coordination Unit, c/o Secretariat of the Lake Tanganyika Authority, Route Principale, Kigobe Nord, Bujumura, Burundi

(Synodontis dhonti), as well as cichlids (Boulengerochromis microlepsis and Lamprolus lemarii). The crabs themselves are top invertebrate predators, and their relative abundance can have important implications for organisms lower in the food web, including algae, insect larvae, ostracods, and snails (Marijnissen et al. 2008, 2009).

Lake Tanganyika is increasingly under pressure from environmental problems generated by human populations (reviewed in Lowe-McConnell 2003). The majority of species diversity is found in rocky near-shore areas, which are severely impacted by sedimentation resulting from ongoing deforestation in the lake catchment (Cohen et al. 2005). Sedimentation can negatively affect aquatic organisms through a range of factors including deterioration of habitat quality and heterogeneity, reduction of food intake, alteration of competitive relationships, decrease of reproductive success,

and breakdown of mate recognition systems as water visibility is reduced (Donohue and Molinos 2009). Research in Lake Tanganyika has demonstrated negative impacts of sedimentation on algal productivity as well as on species diversity and densities of ostracods, snails, and fishes (McIntyre et al. 2004, and references therein). As crabs are closely linked, either as predators or prey, to many other organisms that are vulnerable to the impacts of increased sedimentation, it is likely that they will respond by shifting their foraging patterns (e.g. McIntyre et al. 2004). However, demonstrating and predicting the effects that habitat disruptions will have on the endemic crabs requires taking into account the complexity of the ecosystem. Changes in the species flock may be delayed relative to those of other species as crabs occupy multiple positions within the food web, and a considerable amount of overlap exists among the ecological niches of the different

Lake Tanganyika crab species (Marijnissen *et al.* 2008).

Lake Tanganyika's crabs are also threatened by invasion of the non-native Louisiana Crayfish (Procambarus clarkii) and the Red Claw Crayfish (Cherax quadricarinatus). Both of these crayfish have been introduced to Africa for aquaculture purposes and are spreading rapidly throughout the continent (e.g. Arrignon et al. 1990; G. Howard, IUCN, pers. comm.). Considering their current presence in catchments adjacent to Lake Tanganyika, it is likely that these crayfish will move into the lake basin in the near future. Due to their resilience to different environmental circumstances, high dispersal capacity and opportunistic diet, crayfish are capable of causing dramatic biodiversity shifts (e.g. Smart et al. 2002; Snyder and Evans 2006; Cruz and Rebelo 2007), and could cause an ecological disaster if they establish themselves in Lake Tanganyika.

Without conservation effort to address environmental threats in the Lake Tanganyika basin, this could lead to the loss of a dynamic endemic species flock that provides unique insight into the evolution and ecological functioning of this unusually diverse lake system.

# Lake Tanganyika is increasingly under pressure from environmental problems generated by human populations



Platythelphusa armata (LC) is the largest and most distinctive species in the genus. Juveniles are often found sheltering within the empty shells of the gastropod Neothauma tanganyicense. © SASKIA MARIJNISSEN

## Species in the spotlight

# The East African tree hole crab — spectacular adaptation

Bayliss, J1

otamonautes raybouldi,
the East African tree hole
crab, is a bizarre example
of crab evolution. It is
exceptionally rare for a crab to
live in a tree (an arboreal species),
and most of those that do depend
on an external water supply –
for example, several species of
mangrove crab reside in trees for
protection but lay their eggs in
the sea.

There are over 1,200 species of freshwater crab, out of which only a handful exhibit some kind of arboreal association. The East African tree hole crab is unique in this case. It lives solely in the water filled tree holes formed

where a tree branches. When branching occurs it often creates a small hole, or bole, which fills with water. The East African tree hole crab has evolved to occupy this niche, adapting its behaviour and morphology accordingly.

What is remarkable about this species is its natural history. This species has an apparent lack of dependence on any water body, except that collected in tree holes as water run-off from the host tree. What is yet more remarkable is the way in which it obtains the calcium in order to build its exoskeleton (Bayliss 2002). It forages at night or in heavy rain, when it leaves its hole to search for leaf-litter

snails. When it find these snails it takes pieces of the snail shell back to its water-filled tree hole and masticates them, which releases the calcium ions into solution. It then ingests the calcium in order to obtain sufficient quantities to build its own exoskeleton. It also eats its old exoskeleton when it moults. As crabs have a hard exoskeleton they need to moult in order to be able to grow and mature. Below the hard exoskeleton is soft tissue that expands over time. Eventually the hard exoskeleton will prevent any further expansion, at which stage the process of moulting (or ecdysis) occurs.

It was first observed and collected by Professor John Raybould in 1966, but it was not until 2004 when it was eventually described under the patronym *Potamonautes raybouldi* (Cumberlidge and Vannini 2004). It is a forest species found in just a few sites in east Africa, such as the East Usambara Mountains in northern Tanzania, and several sites in southern Kenya (e.g. the Shimba Hills).

It has primitive lungs that enable it to spend time outside water, and elongated legs that allow it to climb up and down the tree trunks. The males have one claw that is larger than the other, which is presumably used for display and eventual mating. The females have been found protecting their young (parental care), living in the same tree holes with a brood of juvenile crabs that is presumably their own. These tree holes need cleaning on a regular basis as leaves



Juvenile crabs in a communal tree hole. © JULIAN BAYLISS

and other debris accumulate. The juvenile crabs are often too small to cope with moving larger leaves and debris, and would be unable to clean the tree-hole without assistance from the adult female crab. They also need protection from predators, possibly including other crabs.

The local people in the East Usambara Mountains use the water that Potamonautes raybouldi lives in as a medicinal potion. They often collect the water, which they call 'Mazi yangodi' (the water from holes with crabs), to give to pregnant women. The water contains calcium, which is required by pregnant women to reduce the risk of pregnancyinduced hypertension (PIH), high blood pressure (pre-eclampsia), and kidney failure, all of which can result in miscarriage. Exactly how and when the connection between the 'crab water' and calcium deficiency in pregnant woman was arrived at is a mystery.

The East African tree hole crab is a spectacular example of adaptation, essentially of an aquatic species not only to a terrestrial environment but also to an arboreal existence. It has lost its dependency on larger water bodies such a streams and rivers, and via the process of natural selection, through trial and error (otherwise known as evolution), it has managed to exploit a niche that crabs have rarely occupied. The further connection between the local population of the East Usambara Mountains and their use of the Mazi Yangodi further highlights this species scenario as an amazing example of natural history and a connection with a human society. However, this story of natural history is not finished. Exactly how the males and females find each other in order to mate in closed canopy, dark forest, when each crab resides in a different tree and they are relatively shortsighted, remains an exciting mystery yet to be solved.





Adult crabs defending their tree hole. © JULIAN BAYLISS