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## FRESHWATER CRABS IN AFRICA

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**Introduction**

Freshwater crabs are a strangely neglected component of the world's inland aquatic ecosystems. Despite their wide distribution throughout the tropical and warm temperate zones of the world, and their great diversity, their role in the ecology of freshwaters is very poorly understood. This is nowhere more true than in Africa, where crabs occur in almost every freshwater system, yet even fundamentals such as their higher taxonomy are yet to be determined. This review will attempt to stimulate interest in this fascinating group of organisms by summarising what little we do know about freshwater crabs in Africa.

In terms of basic morphology, freshwater crabs are similar to their marine counterparts (Fig. 1), but they are taxonomically distinct, freshwater crabs being classified into families that are exclusively freshwater (see Appendix). There is a large size range, with some species reaching adulthood with a carapace width (CW) of 20–30 mm, whereas others reach maturity at CW 50 mm or more. Older specimens of the larger species can have CWs in excess of 100 mm.

**Distribution**

There are around one hundred species of freshwater crabs currently recognised from Africa (see Appendix), although this number will probably increase considerably in due course as taxonomic understanding advances. They occur throughout the non-arid areas of the continent, including the River Nile as far as its delta in Egypt, but the greatest diversity of species occurs in forested areas of equatorial Africa, where most species apparently have restricted geographical distributions. In savanna regions, in contrast, the number of species is lower but individual ranges are greater. This is particularly clear in West Africa, whose species are generally divisible into widespread species, found in the wet savanna zone and normally penetrating into some rainforest areas as well, and narrowly distributed rainforest species. The two rainforest blocks of West Africa – the Upper Guinea and the Lower Guinea – support over thirty species, but only two are known to occur in both regions (Cumberlidge 1999).

In East Africa, each highland area supports endemic or restricted species (six in the Usambara Mountains of Tanzania and at least two in each of the other mountain ranges in the region), with relatively few more widespread species in the lowlands. Recent detailed genetic analysis in southern Africa has shown a similar pattern, with a high diversity of geographically restricted small-bodied species in the main mountain ranges and fewer more widespread large-bodied species in the intervening lowlands. The mountain species occur in two widely separated clusters, in the Western Cape region and in the Drakensburg Mountains, but despite this are more closely related to each other than to any of the lowland forms (Daniels et al. 2002b). These results imply that the generally small size of high altitude species throughout Africa is not simply a convergent adaptation to the habitat, but evidence of ancestral relationships. This conclusion is supported by the recent genetic sequencing of a single individual from a mountain stream in Tanzania that showed it to be more closely related to mountain species than to riverine species in South Africa (S. Daniels, personal communication). However, small size cannot be taken as unequivocal evidence for relationship. Williams (1991) reports significant size variation within the East African *Potamonautes loveni*; in western Kenya this species is small bodied (CW of adults beginning at 31 mm) whereas on Mount Elgon it is appreciably larger (CW of adults beginning at 45 mm). On Mt Elgon *P. loveni* is sympatric with a morphologically similar, small-bodied species, suggesting that its increased size in this location is a result of competitive displacement.

There is a small but interesting fossil record of freshwater crabs in Africa. Extinct species of, or close to, *Potamonautes* have been recorded from the Miocene of Kenya and the Late Cretaceous of Niger (Morris 1976). Most remarkable, however, is the large number of specimens attributable to *P. niloticus* from the Upper Miocene of Lake Albert, Uganda (Carriol & Secretan 1992). That this species has remained morphologically similar over a period of six million years suggests either a long stability in the environment of Lake Albert or adaptability to change in this species, the latter evidenced by the variety of habitats in which it lives today.

**Habitat**

Most known species are associated with flowing water, although this could be a consequence of collections having been made in rivers more than in lakes and wetlands. Two or more species may co-exist in the same river, normally with one species occupying the river itself and others occurring mainly in marginal habitats, such as trickles, the stream bank or even humid forest (Williams 1968; Cumberlidge 1999). Several species are generally able to adapt to a wide range of habitats; for example,

*Potamonautes niloticus* occupies most of the Nile catchment, including the River Nile itself and associated irrigation canals in Egypt (Flower 1931; Hussein & Obuid 1993), the littoral region of Lake Victoria, and headwater streams draining ultimately into Lake Victoria (M. Dobson, personal observation). Most species, however, appear to have more restricted habitat requirements, being confined either to high gradient streams or to larger or more sluggish rivers.

Major lakes are generally occupied by species which extend into rivers in the catchment. The main exception to this is Lake Tanganyika, which supports several endemic species and even an endemic family (Appendix). Each endemic species has specific lake bed habitat requirements, with *Platythelphusa tuberculata* occurring mainly in muddy-bottomed areas and the other species in sandy or rocky parts; several of the smaller species are typically found living in empty snail shells on the lake bed (Cumberlidge et al. 1999). Among smaller lakes, *Potamonautes rukwanzi* was recently described from Lake Rukwanzi, a tiny crater lake in western Uganda (Corace et al. 2001). The isolated nature of this lake means that this crab may be endemic; hence other lakes in the region may also support their own endemic species.

Several species are associated with permanent or seasonal pools in relatively dry parts of the continent, inhabiting burrows within or adjacent to the water body. These represent several genera, including the two species of *Deckenia* on the coastal plain of East Africa (Ng et al. 1995), *Sudanonautes monodi* in the savanna of West Africa (Cumberlidge 1986) and *Potamonautes calcaratus* in Kruger National Park, South Africa (Daniels et al. 2002a).

Little is known about crab populations in wetlands, despite the obvious importance of such systems in Africa, although *Potamonautes niloticus*, so common in the rocky littoral of Lake Victoria, is absent from coastal swamps around the lake apparently because it is unable to tolerate the low oxygen concentrations (Shaw 1959). There is, however, at least one exclusively wetland species – *P. lividus* – confined to small patches of swamp forest in eastern South Africa (Gouws & Stewart 2001).

In West Africa, parallel niches can be identified in the two forest blocks. Thus, for example, each has a large, stream-dwelling species that forages on the forest floor (*Liberonautes latidactylus* in Liberia, *Sudanonautes africanus* in Nigeria), a large swamp-living semi-terrestrial forest species (*L. paludicollis* in Liberia; *S. aubryi* in Nigeria), and a variety of small river-dwelling species (Cumberlidge 1999). In the few areas of high altitude in West Africa, there is probably the same altitudinal zonation that occurs in East Africa; thus Mt Nimba in Guinea supports the endemic *L. nimba* in grassland above the rainforest, this being replaced by several other congeners at lower altitude.



FIG. 1 (above). *Potamonautes loveni* from Mt Kenya. The scale bar represents 10 mm. Photo: M. Dobson.

FIG. 2 (below). A female *Potamonautes* sp. (probably *P. neumanni*) from the Rift Valley, central Kenya, with its abdomen pulled back to reveal eggs *in situ*. This individual was carrying 150 eggs. The scale bar represents 10 mm. Photo: M. Dobson.

Finally, at least two species – in West Africa and in Tanzania and Kenya – are known to occupy tree holes (Cumberlidge & Sachs 1991; Bayliss 2002; Cumberlidge & Vannini 2004), while a third, from Madagascar, is apparently confined to leaf axils of *Pandanus* palms (Cumberlidge et al. 2002). These species spend the day in their water-filled burrows, but then forage on land at night. Both the tree hole species are apparently colonial, with never more than one adult per hole but many holes being occupied within the vicinity of each other.

True freshwater crabs do not occur in the marine littoral, salt marshes, or mangrove forests and are unable to live in sea water. *Potamonautes niloticus* from Lake Victoria can survive well in salt water up to 50% of the concentration of seawater, but at concentrations higher than this they exhibit signs of severe physiological stress and die within a few days (Shaw 1959). A similar level of tolerance is shown by the South African *P. warreni* (Morris & van Aardt 1998).

### Reproduction and longevity

True freshwater crabs, in contrast to marine species, do not have a free-swimming larval stage, but emerge from the egg as a fully formed, albeit small, crab. Typically, a brood will comprise up to a few hundred eggs, around 1 mm in diameter (see Fig. 2). The tree-dwelling *Globonautes macropus* produces even fewer eggs; it has been recorded with broods of 30–50 (Cumberlidge & Sachs 1991). Among species of *Platythelphusa* in Lake Tanganyika, egg sizes are similar (averaging 1.5–1.9 mm diameter), and the number of eggs per brood is determined by the size of the species at maturity; the large *P. armata* may carry up to 900, whereas the small species normally have fewer than 100 eggs (S. Marijnissen, personal communication). This contrasts with marine crabs, which may produce hundreds of thousands of much smaller eggs.

Brood sizes are small because of the parental care shown by freshwater species. Eggs and hatchlings are carried by the female in her abdominal brood pouch until they are large enough to fend for themselves, often for several weeks, during which time the female carries a heavy burden. Disney (1971) reports a female *Sudanonautes orthostylis* with a CW of 24 mm captured in the process of releasing her brood; thirteen juveniles, each 3.5 mm CW were found in her brood pouch. In the same paper, he reports a specimen of *S. africanus*, CW 81 mm, carrying 216 young, each with a CW of 4–5 mm; the chamber was not tightly sealed and several juveniles were exploring her leg bases.

Like their marine counterparts, freshwater crabs exhibit heterochely – the state of one claw being larger than the other. This occurs in both sexes and, of the various African species examined, all have shown a tendency towards right-handedness, but with a significant minority (averaging

around 20%) being left-handed. The significance of this asymmetry is unclear, but it may be related to sexual signalling and defence. The large claws of females may be an indication of reproductive vigour, but equally they may have an important role in defence – females can devote up to three months towards the care of a brood, during which time the ability to defend their offspring may be highly adaptive (Daniels 2001).

There is some evidence of a clear breeding season in seasonally wet areas. In Liberia, several species generally carry eggs only in January–March, producing free-living immature crabs in time to coincide with the rainy season from April to June (Cumberlidge & Sachs 1991).

The life span of crabs is unknown, although Raybould (1969) recaptured two specimens of *Potamonautes* sp. (probably *P. suprasulcatus*) 48 weeks after marking, demonstrating that ecdysis had not occurred during this time; this suggests that they can live for several years. Major Stanley Flower evidently found distraction from the pressures of colonial service in Egypt and the Sudan by keeping crabs as pets; he records a specimen of *P. niloticus* that survived 14 months in captivity, while a specimen of *Potamon potamios*, an eastern Mediterranean species that reaches the eastern Sinai, lived with him for over four years (Flower 1931).

### Diet

Freshwater crabs in captivity will readily eat meat, including live invertebrate prey, as well as a variety of vegetable matter, and the available evidence suggests that they are opportunistic feeders. In practice, this means that they are generally scavengers, with plant-derived detritus comprising the main food consumed. Studies of gut contents have demonstrated an essentially herbivorous and detritivorous diet among larger individuals, whereas those with a CW less than around 25 mm, although still largely herbivorous, supplement their diet with aquatic invertebrates (Fig. 3 and personal observation; see also Okafor 1988). This difference in diet may be related to the activity of animals: small and medium sized individuals actively pursue animal prey, whereas larger ones, presumably lacking adequate mobility, have greater difficulty in capturing other animals (Williams 1965). In common with other detritivorous benthic invertebrates, crabs are not averse to cannibalism when kept in captivity (Williams 1961) and even in the wild (Hill & O'Keefe 1992; Somers & Nel 1998).

The one known exception to this opportunistic feeding habit is the Lake Tanganyika endemic *Platythelphusa armata*, which is a specialist molluscivore, feeding on the extremely abundant snails found in this lake (but not averse to taking other food items when the opportunity arises: S. Marijnissen, personal communication). A consequence of this is the armouring that occurs in the shells of potential prey species, and the associated

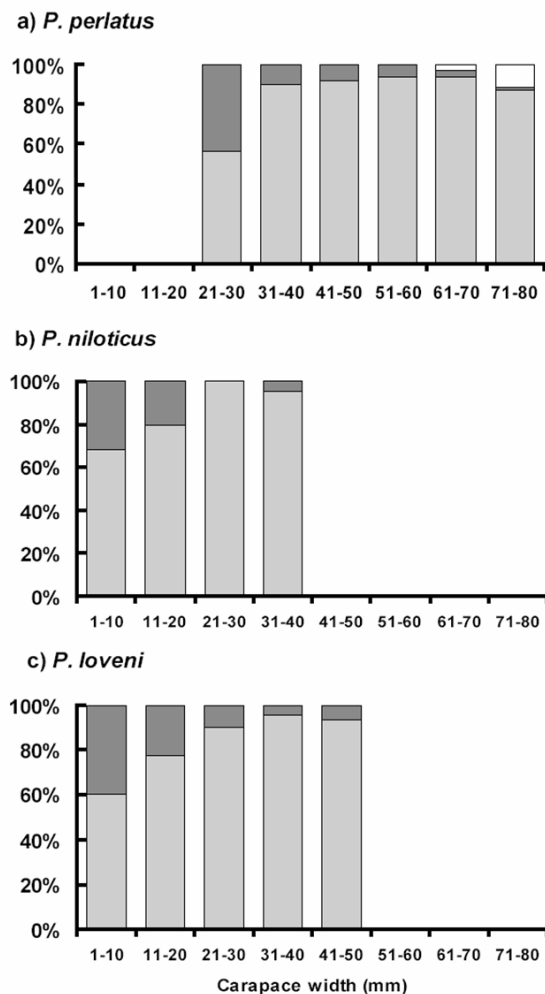


FIG. 3. Diet of three species of *Potamonautes* spp., based upon gut contents analysis and demonstrating the reduction in relative importance of invertebrates with increasing diets. All three species were caught in fast-flowing streams; specimens of *P. loveni* and *P. niloticus* caught in slower, siltier streams showed a similar pattern but with a lower proportion of invertebrate matter in their diets. Pale shading: detritus and vegetable matter; dark shading: invertebrate remains; unshaded: others (vertebrate remains and crab parts). Based on data in: a) in Hill & O'Keefe (1988); b) Williams (1965); c) Williams (1962).

strengthening of robust claws in the predator (West et al. 1991). The Miocene of Lake Albert includes fossils of a similarly armoured snail, which Carriol & Secretan (1992) speculated could have been a consequence of predation by *Potamonautes niloticus*; this is unlikely, as *P. niloticus* in modern lake environments has not initiated the same defence response, but it presumably does take the occasional snail, as do other species in lentic environments where molluscs are common. In Lake Tanganyika, for example, *Potamonautes platynotus* commonly eats snails, while in coastal freshwater wetlands in southern Mozambique, *Varuna litterata* has been recorded with snail shells in its gut, despite its diet predominantly comprising leaf litter (Dobson, unpublished).

Direct observations of feeding in the wild are rare, but Dominey & Snyder (1988) report observations of crab feeding activity in Lake Barombi Mbo (Cameroon). The crabs feed by searching through organic debris on the lake bed and by tearing wood out of submerged logs in search of burrowing invertebrates.

The overwhelming importance of detritus in the diet of most species suggests that they are key shredders in African rivers. The detritus shredding guild, so important to the ecology of rivers in the North Temperate zone, is apparently almost completely absent from most tropical systems (see Dobson et al. 2002 for references). However, crabs may simply have been overlooked (Dobson et al. 2002). They are certainly able to shred leaf litter very effectively (Hill & O'Keefe 1992; Abdallah et al. 2004) and this, combined with their general abundance and high biomass (see below), makes them potentially very important in the dynamics of energy resources in African rivers.

### Predation and parasitism

Crabs are predated by a variety of organisms, particularly otters and, in central and West Africa, otter shrews, but also fish, young crocodiles, monitor lizards, mongooses, civets, drills and birds such as storks and kingfishers (Rathbun 1921; Voelker & Sachs 1977; Purves et al. 1994; Butler & Marshall 1996). Turnbull-Kemp (1960) reports unpublished work from Zimbabwe that found 13.1% of 1000 introduced trout had crabs in their stomachs, while crab remains were identified from 100% of otter (*Aonyx capensis*) droppings examined, with a volumetric occurrence of 97.5%. There is a difference in the size of crabs eaten by these species, with trout feeding on the smaller individuals while otters (and other predators such as eels) catch larger individuals from the stream bed (Butler & Marshall 1996).

Little is known about the susceptibility of freshwater crabs to disease, or about parasitism. In many areas they may be infested with *Simulium* larvae



and pupae (see below), but there is no evidence that these have a detrimental influence on the crabs themselves. Similarly, Turnbull-Kemp (1960) reported large numbers of crabs in Zimbabwe carrying a small greenish leech (Hirudinea) up to 10 mm in length, but whether these were parasitising the crabs or simply using them as an attachment site is unclear.

At least some crabs are subject to kleptoparasitism. In Lake Barombi Mbo, they fall victim to prey stealing activities by cichlid fishes, with two species of fish that employ 'sit-and-wait' predatory tactics being especially suited to this activity (Dominey & Snyder 1988).

### Population density

Estimates of crab population density are hampered by the problems of effective sampling in the field. Baited traps (Fig. 4) are effective but biased, as they rarely catch small individuals (e.g. Disney 1971; Somers & Nel 1998). Conventional methods for sampling macroinvertebrates, such as Surber samplers, do not catch representative numbers of crabs, probably

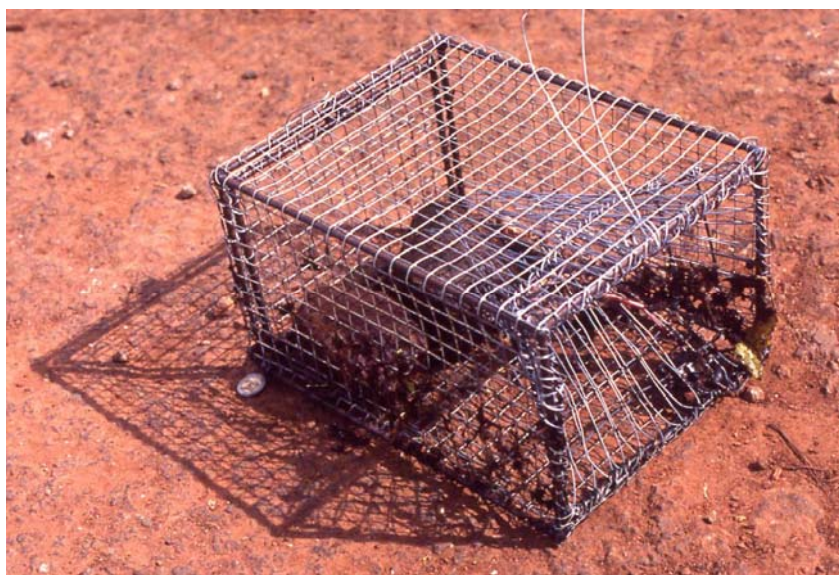


FIG 4. An example of a crab trap. This trap, with a mesh diameter of 10 mm, was weighted with two large stones and baited with smoked fish. Other effective baits recorded in the literature include freshly caught fish, raw liver and fleshy fruits. Photo: M. Dobson.

due to the mobility of larger individuals (Hill & O'Keefe 1992; Dobson & Mathooko, unpublished). Probably the most effective method is that of isolating a stream section with stop nets, followed by intensive hand searching, although this is difficult in larger streams and rivers. Turnbull-Kemp (1960) employed a combination of isolating a section of river and then adding funnel traps, which were emptied daily over several days until the catch declined enough for a population estimate to be made. He did, however, acknowledge that he was missing all small individuals, his smallest caught individuals having a CW of 17.3 mm.

The earliest published estimate of crab population densities was that of Turnbull-Kemp (1960), who calculated the density of *Potamonautes perlatus* individuals greater than 17 mm CW at Inyanga (Zimbabwe) as 0.8–1.3 m<sup>-2</sup>, with a combined wet weight of 5.5–13.6 g m<sup>-2</sup>. This is low in comparison with an estimated density of the same species in the Buffalo River (Cape Province, South Africa) at 1.7–5.2 crabs m<sup>-2</sup> (based only on specimens >25 mm CW) and a (dry) biomass of 54–136 g m<sup>-2</sup> (Hill & O'Keefe 1992). In the nearby Eerste River, Somers & Nel (1998) incorporated all size classes and recorded mean crab densities of up to 15.6 m<sup>-2</sup>, with a mean carapace width of c. 19 mm. Assuming a conservative 0.2 g per crab, this would give a total crab biomass at least four times that of all other benthic macroinvertebrates combined (based on figures in King 1983). In the Eastern Usambara Mountains of Tanzania, Abdallah et al. (2004) estimated overall biomass of crabs to be 88% of the total invertebrate biomass, rising to 94% in debris dams.

Among more terrestrial species, the only estimate available is that of Okafor (1988) for a *Sudanonautes* sp. that occupies burrows along the banks of rivers and ponds. He estimated a maximum population density during the wet season of 22 m<sup>-2</sup>, of which nearly 40% had a CW greater than 40 mm, giving a biomass of around 215 g m<sup>-2</sup>. During the dry season, in contrast, crabs were much more difficult to find, and the apparent biomass dropped to 4 g m<sup>-2</sup>.

Despite the variability and errors associated with such estimates, what they show consistently is that, where crabs occur, they are clearly very significant members of the invertebrate fauna in terms of overall biomass. This, in association with their detritus processing activities and their role as food for a wide range of predators, makes them extremely important members of African freshwater communities.

### Terrestrial activity

Many species actively forage on land, and several species have become semi-terrestrial. Ability to reabsorb salt from the urine and to restrict water loss, both of which are physiological adaptations to fresh water, have pre-adapted these crabs to terrestrial life (Morris & van Aardt 1998).

Furthermore, in addition to gills most species possess a pseudo-lung, a modified gill cavity allowing them to breathe in the air (Adamczewska et al. 1997), and in extreme cases the pseudo-lung has developed to the extent that it allows some species to be almost exclusively terrestrial (e.g. Cumberlidge 1986, 1991). The main restriction to complete terrestrialsation in freshwater crabs is their inability to excrete ammonia into the air. They need to return to water periodically to perform this function, but when they do so the rate of excretion can be up to 70 times faster than normal, requiring only a brief period of immersion (Morris & van Aardt 1998).

Various species are apparently associated more frequently with burrows in damp soil adjacent to water, rather than within the water body itself. Moore (1903) omitted an unidentified species (presumably a *Potamonautes*) from his list of the fauna of Lake Tanganyika, on the grounds that it was 'practically terrestrial'. The West African *Sudanonautes aubryi* lives in burrows in savanna adjacent to forest, digging its burrow in or immediately adjacent to seasonally flooded areas. Bertrand (1979) excavated approximately 100 of these burrows in Ivory Coast, in order to investigate architecture and occupancy. He determined that burrows of this species (which he misidentified as *S. africanus* – see Cumberlidge 1999), whose CW ranged from 27–61 mm, average 102 cm in length, often with two or three chambers, and extend to a depth of up to 94 cm, normally deep enough to reach the water table. Most of the burrows were unoccupied, the density of captures being one crab for every two burrows excavated in the flooded zone and one for every nine excavated in the drier zone. The absence of individuals smaller than 27 mm in the burrows, along with the presence of much smaller individuals in an adjacent river, led Bertrand (1979) to suggest that juveniles of this species are riverine, the terrestrial habit occurring only in older individuals.

Riverine species are also able to persist during drought conditions by burrowing into the substratum. For example, the preferred locality of *Sudanonautes floweri* in the Democratic Republic of Congo is debris dams in rivers, but it retreats into burrows during the dry season and crabs periodically extend their burrows in order to remain close to the falling water table (Rathbun 1921). During an extreme drought in northern Tanzania, when normally permanent streams ceased to flow, *Potamonautes suprasulcatus* and an unidentified species remained buried in refugia, either squeezing into interstitial spaces or excavating shallow depressions in sand under boulders. Live crabs were collected from such refugia for two weeks after surface water had disappeared. No attempt was made by these crabs to move into parts of the river where open water pools remained, or to burrow to subsurface water (Raybould et al. 1978).

Even under wet conditions, many predominantly aquatic freshwater crabs regularly venture on to land, apparently to forage. In some cases, there may be clear seasonal activity; in Malawi, for example, *Potamonautes choloensis* is frequently seen in large numbers wandering around on land, particularly during or soon after rain at the beginning of the wet season; this is possibly caused by their re-activation after dormancy, and the requirement for food, which at this time is abundant on land but not in the water (Cantrell 1980).

Terrestrial activity is not a universal phenomenon. The Lake Tanganyika endemics in the genus *Platythelphusa* and *Potamonautes platynotus* are obligate aquatic species (Cumberlidge et al. 1999), while *Potamonautes niloticus* apparently never ventures out of the water (Hynes et al. 1961).

### Economic and medical importance

Human consumption of freshwater crabs has been recorded from various parts of Africa, including *Sudanonautes aubryi* in Ivory Coast (Bertrand 1979) and *S. africanus* and *S. kagoroensis* in Nigeria (Okafor 1988; Cumberlidge 1991), although conversely some tribes apparently will not eat them (Rathbun 1921; Cantrell 1980). In the East African Great Lakes, in contrast, large crabs such as *Platythelphusa* species in Lake Tanganyika and *Potamonautes niloticus* in Lake Victoria are frequently entangled in gill nets in large numbers, but they are discarded as bycatch (S. Marijnissen, pers. comm. and M. Dobson, personal observation). In Liberia, the dwarf river crab *Liberonautes nanoides* is caught in large numbers during the dry season using basket traps, and sold in local markets for human consumption (Sachs & Cumberlidge 1991). This is a small species and is used as an ingredient in soup (N. Cumberlidge, personal communication). In Nigeria, *Sudanonautes africanus* is commonly sold in markets and roadside stalls, either fresh or smoked (Okafor 1988). Crab consumption in this region tends to increase when economic decline reduces the availability of other protein sources (Udonzi 1987); economic austerity will therefore lead to increased prevalence of paragonimiasis among susceptible human populations (see below).

Crabs are put to various medicinal uses. One of the most interesting is the role of *Potamonautes raybouldi*, the tree hole crab of the East Usambara Mountains in Tanzania and the Shimba Hills in Kenya (Bayliss 2002; Cumberlidge & Vannini 2004). Here it is not the crab itself that is important, but the water from the tree hole in which it lives. Tree hole crab water is administered to pregnant women, and particularly those with a history of miscarriages. The value of this water may relate to the behaviour of the crab, which neutralises the naturally acidic water in tree holes by capturing snails and adding their crushed shells to the water, raising the pH but also enhancing levels of dissolved calcium (Bayliss 2002). In Egypt,

Flower (1931) reported that crabs were actively sought and eaten by childless women, in the belief that this would cause them to become pregnant; whether there is any medical basis in this idea is unclear.

Perhaps the most important interaction between humans and crabs is the latter's role as vectors of disease. Crabs of the genera *Sudanonautes* and *Liberonautes* have been identified as secondary hosts of lung flukes (*Paragonimus* spp.), several species of which cause pulmonary paragonimiasis, in the rain forest regions of West and west-central Africa (Voelker et al. 1975; Voelker & Sachs 1977; Cumberlidge 1999). The mode of transmission from crabs to humans is consumption of incompletely cooked crab flesh (Ollivier et al. 1995); in southern Nigeria, crabs are often eaten raw, particularly by children, ensuring high rates of infection (Udonzi 1987).

Crabs also act indirectly as vectors of onchocerciasis (river blindness), a disease caused by a blood fluke spread by blackflies (Diptera) belonging to several species within the *Simulium neavei* complex. Larvae of these flies have a phoretic association with crabs and other freshwater invertebrates, most notably mayflies, both larvae and pupae attaching themselves to the carapace and leg bases of these other organisms. The presence of *Simulium* larvae living attached to crab carapaces was first reported from *Potamonautes* spp. in western Kenya by van Someren & McMahon (1950). These insects are apparently unable to live other than in association with other organisms, except perhaps as first instar larvae (Raybould & Mhiddin 1978). Periods of attachment of larvae are highly variable. In enclosures in a Tanzanian stream, Raybould & Mhiddin (1978) found that 30% became dislodged after two days or fewer; in contrast, 25% remained attached for at least 26 days and, in one case an individual maintained its footing for 72 days. Pupae were generally present on crab carapaces for 8–10 days. Interestingly, when crabs burrowed into sediments to avoid drought (see above), their phoretic *Simulium* associates were also able to survive extended periods without immersion (Raybould et al. 1978).

Crabs may play a valuable role as indicators of pollution. *Potamonautes warreni* has the misfortune of being large-bodied, easy to capture with bait, and common in the Orange River, which drains much of the heavily polluted mining region of northern South Africa. Therefore it has been intensively investigated as a possible bioindicator of metals in sediments (e.g. van Eeden & Schoonbee 1991; Sanders et al. 1999; Shuwerack et al. 2001).

One species, *Potamonautes lirrangensis* ('Malawi blue crab'), which occurs in Lake Malawi and in rivers in the upper Congo catchment, can be found for sale as an aquarium species (often under the name *P. orbitospinus*).

## Threats and Conservation

Unusually for such a little known group of invertebrates, the freshwater crabs of Africa have the dubious distinction of six species appearing on the IUCN Red List of Threatened Species. Five are from the Guinea forest region of West Africa: *Afrithephusa afzelii*, *A. leonensis* (Sierra Leone); *A. gerhildae*, *A. monodosus* (Guinea); *Globonautes macropus* (Guinea and Liberia); the sixth, *Louisea edeaensis*, is from Cameroon. There may be others that are endangered, but are too little known for an effective assessment.

The role of crabs as vectors of disease also makes them susceptible to deliberate extermination. Fortunately for the survival of crabs in fast-flowing streams, however, onchocerciasis has been successfully eliminated from various foci, particularly in East Africa, without recourse to exterminating the unwilling hosts of the blackflies. In the early 1950s experiments using DDT in an attempt to kill crabs in western Kenya were quickly abandoned when it was discovered that, not only were fish more susceptible than crabs, but also that a common reaction to dosing with insecticide was for the crabs to leave the river, returning when the danger had passed (McMahon et al. 1958).

Crabs may be threatened by introduction of exotic species. In East Africa, it is probable that introduction of rainbow trout (*Oncorhynchus mykiss*) into streams without natural predatory fish species has led to a reduction in crab numbers through predation (Williams et al. 1964). No native crayfish occur in sub-Saharan Africa, but experimental aquaculture, particularly using the Louisiana red swamp crayfish (*Procambarus clarkii*), has inevitably led to escapes and establishment of wild populations. Lake Naivasha in Kenya is a well-documented example of the detrimental effects of this species on natural systems (Mikkola 1978; Harper et al. 1990), but its impact upon native crabs remains unknown. *Procambarus* appears to be unable to establish itself in running waters in East Africa, but in South Africa it is present in the Crocodile River, Northern Province (Mikkola 1996). In addition to direct competition, crayfish may transmit parasites and diseases for which crabs will have no immunity. The Australian *Cherax tenuimanis* has brought to South Africa its turbellarian parasite *Temnocephala chaeropsis*, which readily infects *Potamonautes warreni* in the laboratory (Avenant-Oldewage 1993). Whether this parasite will establish in wild crab populations and have any detrimental effect is not yet known, but once established, like the crayfish themselves, it will be extremely difficult to eliminate. Unfortunately, there is an attitude among some commentators that, as native crayfish are not present in Africa, there is an unexploited niche to be filled (Adegboye 1983; Mikkola 1996), so it is almost inevitable that crayfish will become



more widespread in Africa over time, and that they will come into direct contact (and presumably competition) with native crabs.

### Identifying African freshwater crabs

Extensive taxonomic work led by Neil Cumberlidge at Northern Michigan University has led to the publication of a series of identification keys. Cumberlidge (1996b) provides a key to the families of the region, but this was compiled before the recognition of Platythelphusidae as a separate family. Cumberlidge et al. (1999) provide a further key to families, but this does not include the Gecarcinucidae. Cumberlidge (1994) provides a key to the genera of Potamonautidae. Cumberlidge et al. (1999) provide a key to species of Platythelphusidae. Cumberlidge (1996a) provides a key to the genera and species of Globonautinae. The entire West African fauna is described and keyed in Cumberlidge (1999) and that of Madagascar in Cumberlidge & Sternberg (2002). Elsewhere, Gouws & Stewart (2001) provide a key to *Potamonautes* in KwaZulu-Natal, but this province supports only five of the 13 species currently identified from South Africa. Ng et al. (1995) provide a table for distinguishing the two East African species of *Deckenia*.

Unfortunately, identification of crabs from the rest of Africa is still fraught with difficulties. The keys produced by Cumberlidge are gradually appearing online, including useful photographic illustrations of the key features. They can be accessed at:

<http://www.nmu.edu/biology/Neil/MainFWC-website/FWCIdentification.html>

If crabs are collected from African freshwaters, then the following notes should assist in facilitating identification. Males and females within a species grow at similar rates and are the same size as adults, although adult size can cover a wide range. Adult males are required to ensure correct identification, but females are required to determine the adult size of a given species. The gender of crabs can be established by examining the underside of the animal (Fig. 5). The abdomen is folded under the cephalothorax. In the males, the abdomen outline is a narrow triangle, so that a large proportion of the sternum is visible; peeling the abdomen back will reveal two pairs of slender gonopods. The female abdomen is widened, so that most or all of the sternum is covered; peeling the abdomen back reveals four pairs of often feathery appendages, the pleopods.

Adult females can be distinguished from juveniles by the size of the abdomen, which is greatly widened to cover the sternum and overlap with the coxae of the walking legs, forming the abdominal brood pouch. If the abdomen is peeled back to reveal eggs or juveniles, then adulthood is confirmed.

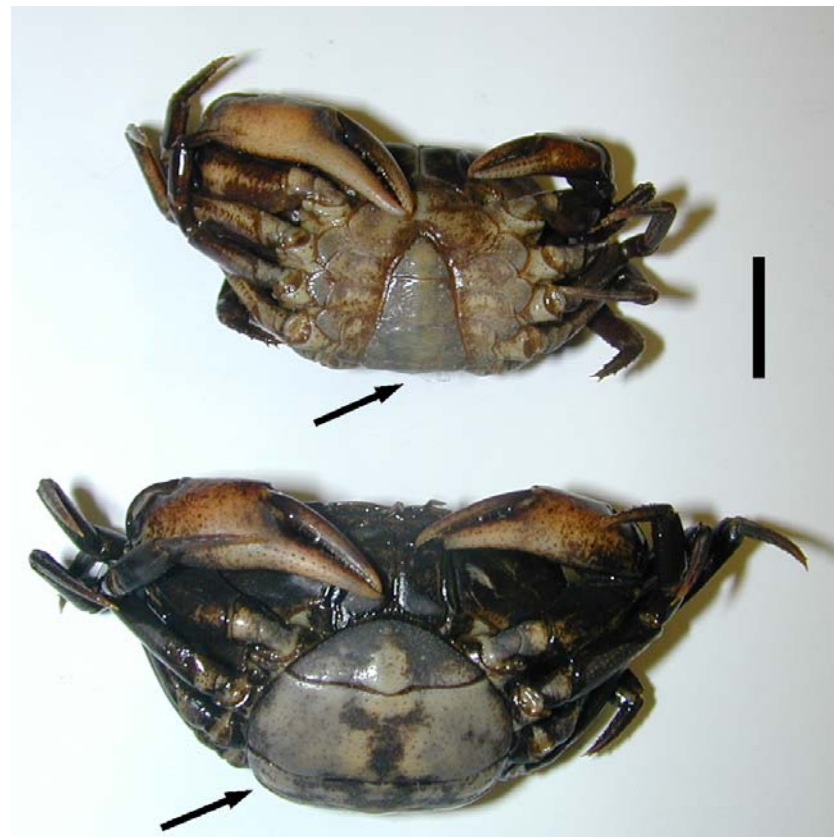


FIG. 5. Underside of two crabs (*Potamonautes* sp.) from the Kenyan Rift Valley, demonstrating sexual dimorphism. Top: a male, showing the narrow abdomen (upper arrow). Bottom: a female, showing the wide abdomen (lower arrow). The scale bar represents 10 mm. Photo: M. Dobson.

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### Appendix: Classification and diversity

There are currently five families of freshwater crabs recognised from Africa and Madagascar, of which three are endemic to the continent, whilst the others are shared with southern Asia.

The dominant family, in terms of number of species and distribution, is the Potamonautidae, an exclusively Afrotropical family found throughout sub-Saharan Africa. It contains about eighty species in 11 genera, four of which (*Erimetopus*, *Sudanonautes*, *Liberonautes* and *Potamonemus*) are mostly found in the forested regions of Central and West Africa (Cumberlidge 1999; Cumberlidge & Reed 2004). A fifth genus, *Potamonantes*, occurs throughout the region, with the exception of Madagascar; it currently contains around 60 recognised species, although this is likely to change substantially in the future (Cumberlidge, personal communication). The remaining six genera are endemic to Madagascar (Cumberlidge & Sternberg 2002).

The other African endemic families are the Platythelphusidae, comprising one genus (*Platythelphusa*) and six species, all endemic to Lake Tanganyika, and the Deckeniidae, comprising one genus (*Deckenia*) and two species in Tanzania, Kenya and Somalia.

The Gecarcinucidae comprises one African subfamily, the Globonautinae, with three genera (*Afrithelphusa*, *Globonautes* and *Louisea*) and seven species, endemic to the Guinea forest region of West Africa. The remainder of this family is Indomalayan in distribution. The inclusion of the African Globonautinae in the Gecarcinucidae was viewed as uncertain by Cumberlidge (1999).

The Potamidae is a widespread family occurring in the Indomalayan and southern Palaearctic regions, but is represented in Africa only by the endemic *Potamon* (*Eutelphusa*) *algeriense* occurring in Algeria, Tunisia and Morocco (Brandis et al. 2000). However, this family also occurs on the island of Socotra, politically part of Yemen but geographically closer to the Horn of Africa (Cumberlidge & Wranik 2002).

Several marine species may be encountered in freshwaters near the coast. For example, *Varuna litterata*, a member of the marine family Varunidae (which also includes the Chinese mitten crab *Eriocheir sinensis*) occurs as an adult in freshwater wetlands along the Indian Ocean coast (M. Dobson, personal observation), but needs to return to the sea to reproduce (Connell & Robertson 1986), and so cannot be classed as a true freshwater species. Mention should also be made of the observations of Flower (1931) that several specimens of the marine species *Carcinus maenas* were found many kilometres inland along the River Nile in Egypt. These were almost certainly translocated in baskets of fish brought up from the coast for sale, rather than natural freshwater incursions by this species.

Similar phenomena probably occur wherever marine produce is being carried inland.

There are no native crayfish in mainland Africa. There is, however, a biogeographically interesting endemic crayfish genus – *Astacoides* – confined to the highlands of south east Madagascar (Hobbs 1987), in one of the few parts of the world where freshwater crabs and crayfish co-exist naturally. There is apparently an altitudinal zonation, with crayfish restricted to higher altitudes while crabs tend to occupy lower elevations, with some sympatry at around 750 m altitude (Rabeharisoa 1996).

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**Note on references** Many of the papers cited here give names for crab species that are now considered to be inaccurate, a consequence of the poor state of taxonomic knowledge of this group. When citing works, therefore, I have changed names according to more recent literature or personal communications from specialists. Therefore, where there is a discrepancy between the name used in the original citation and the name applied in this review, the latter is in accordance with current thinking.

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