

A Guide to,
and Checklist for,
the Decapoda of
Namibia, South Africa
and Mozambique
(Volume 3)

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By

W. D. Emmerson

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SUPERFAMILY POTAMOIDEA

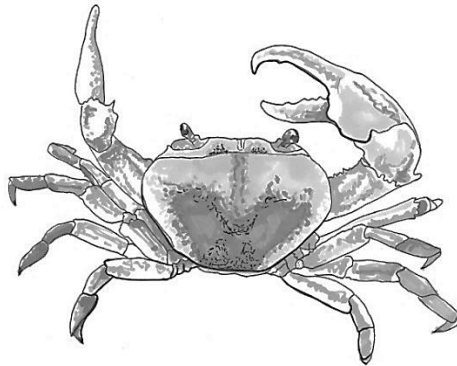
ORTMANN, 1896

Martin & Davis (2001) placed four families in their superfamily Potamoidea, namely Potamidae, Potamonautidae, Deckeniidae and the Platythelphusidae. In their work on Afrotropical freshwater crabs, Cumberlidge et al. (2008) revised the Potamoidea down to two families, the Potamidae and Potamonautidae, which was accepted by Ng et al. (2008). The freshwater Trichodactylidae are generally considered to have evolved independently from the rest of the freshwater families Gecarcinucidae, Potamidae and Potamonautidae (Old World) and Pseudothelphusidae (New World), but the phylogenetic links between these latter families and their emergence from a marine ancestor(s) are contentious (Tsang et al., 2014). Although some authors have estimated the origin of freshwater crabs to be more than 120 Mya (Ng & Rodriguez, 1995; Ng et al., 1995), this postulate would either predate the Heterotremata radiation, or would suggest that the Brachyura are older than previously considered (Klaus et al., 2011). The oldest freshwater crab fossil to date, *Tanzanonautes tuerkai*, is relatively recent and dates from the Late Oligocene (Feldmann et al., 2007) following a post-Cretaceous Heterotreme radiation and a later (30–65 Mya) freshwater crab radiation (Schram, 1986). However, Klaus et al. (2011) rejected the Gondwanan origin based on fossil markers which showed large estimated time discrepancies. Work by Tsang et al. (2014) showed that the Old World families Gecarcinucidae, Potamidae and Potamonautidae emerged basally in the Heterotremata, followed by the Pseudothelphusidae-Retroplumidae, then the Trichodactylidae-Orithyiidae-Chasmocarcinidae-Bellidae. This then places the split between the freshwater crabs and the Heterotremata at around 137 Mya and implies a deep dichotomy between the Old World families and the Pseudothelphusidae (New World) around 124 Mya. In the Old World clade, the Potamonautidae branched off first around 86 Mya, followed by a division between the Potamidae and Gecarcinucidae around 80 Mya. The Trichodactylidae evolved on the Heterotremata line branching off from the Orithyiidae around 86 Mya. These results point to at least two separate origins of freshwater crabs, with marine ancestors invading freshwater early during Brachyuran evolution. Porter et al.

(2005) put the heterotreme common ancestor around 240 Mya, rather than 137 Mya, showing that the freshwater crabs in fact emerged a lot earlier than previously thought.

The Potamidae have some fossil species such as *Potamon antiquum* and *Geothelphusa dehaani* (De Grave et al., 2009; Schweitzer et al., 2010). The Potamoidea consist of 2 families, Potamidae and Potamonautidae, with the latter family including 19 genera and 157 species (Davie et al., 2015a). Both occur in freshwater, but there is a geographical separation, with the former found in Europe and Asia and the latter occurring in Africa south of the Sahara (Ng et al., 2008). Davie et al. (2015a) has given an analysis of the Potamoidea. Only the Potamonautidae are represented in southern Africa.

FAMILY POTAMONAUTIDAE BOTT, 1970



AW

Potamonautes lividus

Carapace, subovate to quadrilateral, wider than long, dorsum smooth to granular, gastro-cardiac groove distinct, epigastric and postorbital cristae varying from distinct to almost absent, anterolateral margin prominently convex, usually with one tooth (epibranchial) which may appear serrate, rarely obsolete, rarely with 3 or more; front, usually entire. Mandibular palp with 2 or 3 segments, terminal one simple, often with a dense brush-like base. Antennule, the lateral margin of the antennular fossa is filled by the antenna second segment. Abdomen, 6 free somites in males and females, plus telson, male pleon always triangular. G1, strongly chitinised, with clearly defined terminal and subterminal segments. G2, half length of G1, in cross-section the dorsal faces of the subterminal and terminal segments have a setose spoon-shaped structure which does not go around to the ventral side; both the dorsal and ventral margins are long and curve inwards, with their tips overlapping to form a closed tube dorsally (Cumberlidge et al., 2008; Davie et al., 2015a).

Bott (1955) did pioneering work on African freshwater crabs and established the family Potamonautidae and two subfamilies Hydrothelphusinae

and Potamonautinae (Bott, 1970). Martin & Davis (2001) placed the family Potamonautidae in the superfamily Potamoidea, Štević (2005) had the Potamonautinae as a subfamily in the family Potamidae and superfamily Potamoidea, Klaus et al. (2006) had the Potamonautidae as a family within the superfamily Potamoidea, while Cumberlidge et al. (2008) revised the Potamonautinae under the Potamonautidae in the superfamily Potamoidea, which was accepted by Ng et al. (2008). Using molecular evidence, Cumberlidge et al. (2008) radically synonymised the Deckeniidae and Globonautinae in the Hydrothelphusinae and the Platythelphusidae with the Potamonautidae. This move makes distributional patterns more parsimonious, but challenges key morphological characters, such as the value of the structure of the mandibular palp, which had previously been diagnostic. Using morphology and DNA datasets, the West African Globonautinae was referred to the Potamonautinae. So, although unorthodox, the system of Cumberlidge et al. (2008) with two subfamilies, Hydrothelphusinae and Potamonautinae, appears to be the best proposal so far and is used by Ng et al. (2008) and Davie et al. (2015a). Members of the former family occur in West Africa, Madagascar and the Seychelles, while those of the latter subfamily are distributed in Africa south of the Sahara, so only the Potamonautinae are represented in southern Africa.

The fossil record of potamonautids is sparse; the Hydrothelphusinae have no fossil members (Schweitzer et al., 2010). However, the Potamonautinae have three fossil species, *Potamonautes niloticus*, *P. tugenensis* and *Tanzanonautes tuerkai* (De Grave et al., 2009; Schweitzer et al., 2010), with *T. tuerkai*, from the Tanzanian Oligocene (40–25 Mya), presently the oldest freshwater crab known (Feldmann et al., 2007; De Grave et al., 2009). An extinct species of *Potamonautes*, *P. tugenensis* is known from the Miocene, 25–6 Mya of Kenya and the Late Cretaceous, around 70 Mya, of Niger (Dobson, 2010; Schweitzer et al., 2010). *Potamonautes niloticus* is known from Miocene (6 Mya) strata from Lake Albert (Daniels et al., 2006).

Assuming that freshwater crabs evolved from marine crabs, and in order to understand this connection between these two groups, Cumberlidge & Ng, (2009) plotted the phylogenetics of the Potamoidea. They found that marine crabs were basal, followed sequentially by the Pseudothelphusidae, Gecarcinucidae-Parathelphusidae and Potamidae, with the Potamonautidae emerging last. Unlike freshwater crayfish such as the Astacoidea, which have marine relatives such as the Nephropidea, or the freshwater Aeglididae, which are related to the Galatheidae, it has been more difficult to identify the marine-freshwater link in crabs. This link is important to the understanding of the evolutionary history of freshwater

crabs and their phylogenetic positioning. Von Sternberg et al. (1999) has offered evidence that they may have arisen from a grapsoid crab, as, although they belong to different major groups (heterotremes and thoracotremes respectively) they both share apomorphic characters such as epigastric and postorbital crests on the carapace. Thus a common heterotreme crab ancestor could have given rise to the heterotreme potamoids and marine thoracotreme families such as the Grapsidae and Sesamidae, some of which, like *Geosesarma notophyllum*, live in freshwater and never need to return to the sea, as their eggs have abbreviated direct development (Cumberlidge & Ng, 2009). An initial estimate of the origin of the African Potamonautidae was between the late Cretaceous and early Tertiary, around 65 Mya (Bott, 1955). Ng et al. (1995) suggested that the bilobed mandibular palp freshwater crabs were at least 120 M years old, corresponding to the breakup of Africa and S America. Using cladistics and phenetics in order to better understand the origins and position of freshwater crabs within the Eubrachyura and Thoracotremata, Von Sternberg & Cumberlidge (2001a) found although homoplasy detracted from any reliable brachyrhynchan groupings, various trees did show that the pseudothelphusids were placed with the potamoids, which usually contained the thoracotremes. Potamoidea such as *Potamonautes-Sudanonautes*, *Socotra* and *Seychellum* formed a clade with the Psuedothelphusidae branching off earlier and the Thoracotremata as a sister group.

Molecular clock estimates put a common ancestor of the potamonautids as entering African inland waters during the Upper Cretaceous, between 75.0 and 78.6 Mya (Daniels et al., 2006; Cumberlidge et al., 2008; Yeo et al., 2008). These crabs then radiated out over the continent and split into two lineages, the Potamonautinae and the Deckiinae. The Deckiinae separated into two lineages, the Deckiini (*Globonautes*, *Afriothelphusa*, *Deckenia* and *Seychellum*) and the Hydrothelphusini, which are found only in Madagascar. As Madagascar, the Seychelles and India split from Africa around 160 Mya, the ancestors of *Seychellum* must have crossed to the Seychelles on driftwood, while the Madagascan ancestors of the Hydrothelphusini must have undertaken a similar journey around 44 Mya during the Oligocene (Daniels et al., 2006; Cumberlidge et al., 2008). During the late Miocene the subcontinent underwent mesic and xeric cycles due to glaciation, during which time river systems varied in interconnectedness. Using a molecular clock of around 1% sequence divergence per million years, Daniels et al. (2002) estimated that the tropical clade separated around 3 Mya during the early Pliocene.

Thus, consensus phylogeny has shown that the Potamonautidae are divided into the Potamonautinae (Africa) and the Deckeniinae, which were further divided into the Deckeniini (E & W Africa and the Seychelles) and the Hydrothelphusini (Madagascar) (Von Sternberg et al., 1999; Von Sternberg & Cumberlidge, 2001b; Daniels et al., 2006; Klaus et al., 2006). But there is less certainty of their affinities with freshwater crabs elsewhere in the Old World. A close evolutionary relationship between the freshwater crabs of Madagascar, W Africa, E Africa and the Seychelles was found, which was surprising because it raises important phylogenetic questions (Cumberlidge et al., 2008). Brosüng (2008) also suggested that this freshwater invasion could have happened during the Late Cretaceous-Early Cenozoic, 80–60 Mya, close to the Cretaceous-Tertiary boundary (when E Gondwana split off from Africa to form Madagascar, the Seychelles and India, which were all islands), proposing that the three freshwater families (including the Gecarcinucidae) which are present in Eurasia, India and the Orient were already established before India collided with Asia, allowing their spread through these regions. Klaus et al. (2011) and Tsang et al. (2014), however, have shown that freshwater crabs, Potamonautidae included, emerged much earlier—around 137 Mya—effectively sinking the Gondwana theory. Porter et al. (2005) had also suggested that because the heterotreme ancestor possibly emerged as early as 240 Mya, that freshwater crabs had evolved much earlier than had previously been considered.

In terms of biodiversity, the Potamonautidae account for 10% of the world's freshwater crab fauna (Cumberlidge & Ng, 2009). *Potamonautes* is a large genus with 71 species worldwide (Ng et al., 2008). Although Barnard (1950) recognised 10 species of *Potamonautes*, Kensley (1981a) only listed 7 species of *Potamonautes*, although both authors listed several subspecies which have now been recognised as full species. The genus *Potamonautes* shows high levels of endemism (84%) to the southern African region (Angola, Botswana, Lesotho, Mozambique, Namibia, South Africa, Swaziland, Zambia and Zimbabwe) and to South Africa itself (74%; Gouws et al., 2002; Cumberlidge & Daniels, 2007). Many species of *Potamonautes* have only been described during the last decade, using both genetic and morphological data; these include *P. dentatus* from the Drakensberg (Stewart et al., 1995; Gouws & Stewart, 2001), *P. parvispina* from the Olifants River (Stewart, 1997a), *P. granularis* from the Olifants River (Daniels et al., 1998), *P. unispinus* from Mpumalanga and the Northern Province (Stewart & Cook, 1998, Daniels & Stewart, 2000), *P. clarus* from the Drakensberg (Gouws et al., 2000), *P. lividus* from Transkei, KZN and Swaziland swamp forests (Gouws et al., 2001)

and *P. parvicorpus* from fast-flowing mountain streams in the Western Cape (Daniels et al., 2001). *Gecarcinautes brincki*, which also occurs in Western Cape mountain streams, was re-examined morphologically and genetically and found to conform to *Potamonautes*, so was therefore transferred to that genus (Stewart, 1997b; Daniels et al., 2001).

Some have extremely restricted ranges, such as *P. dubius* in parts of the Kunene (Barnard, 1950; Cumberlidge & Tavares, 2006; Hogan, 2012) and upper Zambesi, *P. clarus* in the upper reaches of the Tugela, KZN (Gouws et al., 2000; Gouws & Stewart, 2001), *P. parvispina* in the upper reaches of the Oliphants River (Stewart, 1997a) and *P. granularis* in the lower reaches of the Oliphants River (Daniels et al., 1998). In Mozambique two new species have also been described recently from isolated mountains: *P. namuliensis* was described from specimens collected from Mount Namuli in Zambezia Province, Mozambique, at 1500m above sea level, while *P. choloensis* was found on the inselberg of Mount Mabu, Mozambique (Daniels & Bayliss, 2012), a biodiversity “hotspot” which was discovered using Google Earth (Bright, 2012). There are presently eighteen species of *Potamonautes* in southern Africa including *P. bayonianus*, *P. brincki*, *P. calcaratus*, *P. choloensis*, *P. clarus*, *P. depressus*, *P. dentatus*, *P. dubius*, *P. granularis* (not *granulatus*), *P. lividus*, *P. namuliensis*, *P. obesus*, *P. parvicorpus*, *P. parvispina*, *P. perlatus*, *P. sidneyi*, *P. unispinus* and *P. warreni* (Gouws et al., 2001; Daniels et al., 2002; Cumberlidge & Daniels, 2007; Ng et al., 2008; see checklist).

In Angola there are 7 species of freshwater crabs, including *Potamonautes adeleae*, *P. anchetiae*, *P. kensleyi* and *P. macrobrachii* (Cumberlidge & Tavares, 2006; Cumberlidge & Daniels, 2009).

In Lake Tanganyika the freshwater crabs have radiated, forming a hotspot for diversity, with 10 potamonautids endemic to the lake (Marijnissen et al., 2006). Members of this family consume earthworms, grubs, aquatic invertebrates including insect larvae and snails, leaf litter, detritus and algae (Hill & O’Keeffe, 1992).



POTAMOIDEA

POTAMONAUTIDAE

POTAMONAUTINAE

Potamonautus lividus, Gouws, Stewart & Reavell, 2001

Synonymy. Nil (Ng et al., 2008).

Common Name. Blue river crab (IUCN, 2011).

Description. Carapace, vaulted and narrow posteriorly, branchial region highly convex with a CW/CL ratio of 1.45, anterior margin straight, urogastric grooves fairly well-developed, cardiac grooves weak, otherwise smooth, anterolateral margins smooth, postfrontal crest smooth, medially indistinct, front lobe projects downwards, exorbital teeth small but sharp, no epibranchial teeth, anterolateral margins behind postfrontal crest smooth, curving, each flank with a longitudinal groove dividing subhepatic and pterygostomial regions, with a vertical groove running from a longitudinal groove which joins the anterolateral margin between the exorbital tooth and postfrontal crest. Maxilliped 3 fills entire buccal frame, except for the oval respiratory openings, exopods with short flagellum. Mandibular palp with 2 segments, the terminal segment with a tuft of setae on its posterior surface. Chelipeds, unequal, dactylus of right one strongly arched, 1.63 times length of left cheliped dactylus. Both dactyls with 20 cutting teeth, 3–4 of which are larger than others, right chela propodus inflated, 2 times wider than left one, pollex also has 20 teeth with 4–5 teeth prominent, carpi of both chelipeds with one prominent and 3 rudimentary teeth, meri granulose with a small, blunt spine on anterior surface. Pereiopods, slender, with P3 the longest and P5 the shortest, propodi and meri smooth, dorsal margins with fine bristles, dactyls with sharp points, with spiny bristles on margins. First 5 sternal segments broad and short, last 2 longer and terminal one rounded distally. In males pleopod 1 (gonopod 1) terminal segment short and curves away from midline, sub-terminal segment with hirsute margins, posterior surface with twisting longitudinal groove; pleopod 2, terminal segment filament like, with slight curve, sub-terminal segment wide at base then tapering distally (Gouws et al., 2001). *Size*, 37.3mm CW, 27.6mm CL (females), 36mm CW, 24.7mm CL (males). Females reach up to 18.3g, while males can reach 21.4g. The major cheliped is bigger in males with the propodus reaching up to 40.2mm, while in females the propodus only reaches 29.1mm. This species exhibits sexual dimorphism, with males growing bigger chelae than females (Gouws et al., 2001). This species is mainly heterochelous with the right chela larger; in females, 74% are right handed and 13% are left handed, while in males, 79% are right handed and 8% left handed, with around 13% roughly equal in size. *Colour*, carapace orange to red with a characteristic silver-blue sheen, chelipeds and legs bright orange to red, with tips lighter than the main appendages (Gouws et al., 2001; Cumberlidge & Daniels, 2009). *Type locality*, Mapelane, KZN (Gouws et al., 2001).

This species is very similar to *P. sidneyi* but can be separated out using seven carapace variables such as carapace height, eye distance and

posterior carapace width (Gouws et al., 2001). Regression analysis of carapace data between *P. lividus* and *P. sidneyi* showed them to be significantly different from each other, with the latter larger while the former has a more vaulted carapace, which narrows posteriorly and with a narrower frontal lobe. Allozyme differences also showed a clear genetic difference. *P. lividus* is characterised by having a highly vaulted carapace, a medially reduced postfrontal crest, inflated and arched chelipeds, a downward projecting frontal lobe, rounded and downward sloping epibranchial corners and a characteristic silver-blue sheen and bright orange to red chelipeds and legs.

Distribution. This recently described potamonautid occurs in a few restricted sites in KZN: at Dakaneni, Manzibomvu (St Lucia tributaries), Mapelane, Mdibi and the University of Zululand (Richards Bay tributaries; Gouws et al., 2001; Gouws & Stewart, 2001). More recently this species has also been found in a swamp forest at Dwessa Reserve, Transkei, E Cape, where the specimen above was identified and photographed, and it has also been found in Swaziland, which indicates that it has a wider, if patchy, distribution (Daniels & Bayliss, 2012). More recently it has also been tentatively identified from ephemeral pans around St Lucia, KZN (Peer et al., 2014). Here it had a similar appearance to *P. lividus*, but was bigger with a different coloration, so could be a new species.

Zonation & Habitat. This burrow-living species only occurs in a few restricted areas of swamp forest and associated wetlands in the Transkei and KZN, which are characterised by *Ficus trichopoda*, *Syzygium cordatum*, *Bridelia sp.*, *Barringtonia recemosa*, *Hibiscus tiliaceus*, *Rauvolfia caffra*, *Voacanga thouarsii*, *Raphia australis* and *Podocarpus falcatus*. Here it builds shallow U-shaped burrows, which are partially filled with water, in the spongy peaty soils of these forest floors. This species is found further from water than *P. sidneyi*, with its burrows often among vegetation, whilst *P. sidneyi* has a closer association with water (Gouws et al., 2001; Cumberlidge & Daniels, 2009). When water levels rise, flooding their burrows, *P. lividus* moves to higher ground. This crab also appears to be more active on cloudy days and at night. During rainstorms it apparently leaves its burrow to feed on land.

This species is rare and its population is probably very low, based on its selected coastal swamp forest habitat (only 9–10 localities are known), the density of burrows within each location, and the small number of specimens that are found at each locality (Cumberlidge & Daniels, 2009).

Conservation. The Potamonautidae of southern Africa exhibit high endemism (74% in South Africa; 84% in southern Africa) and, as some are considered rare or very rare, have been conservation assessed (Cumberlidge & Daniels, 2007). The extent of occurrence for *P. lividus* is <20000km², with an area of occupancy of only around 2000km² in nine to ten locations, and its conservation status is rare, vulnerable or threatened. This was the only *Potamonautes* species to be given this critical assessment; although other species such as *P. kensleyi* occupy a smaller area and fewer locations, this crab is regarded as being data deficient, so a proper assessment could not be made. *Potamonautes lividus* is highly endemic and because of the restricted, specialised, fragile and vulnerable swamp forest habitat in which it is restricted, it too has the potential to be vulnerable. It has thus been assessed using the IUCN Red List criteria and found to be vulnerable (Cumberlidge & Daniels, 2007, 2009; IUCN, 2011). However, in a recent study, *P. lividus* was found in a new location in Swaziland, suggesting a wider distribution, making the case for a possible re-evaluation of the species on the IUCN Red List (Cumberlidge et al., 2009).

Phylogeny. Gouws & Stewart (2001) compared five species of *Potamonautes* from southern Africa using a genetic identity dendrogram and found that *P. lividus* split from *P. sidneyi*, with *P. dentatus* emerging earlier, before a split with *P. clarus* and *P. depressus*. Because of their specialist habitat ecology living in coastal swamp forests and the presence of a diagnostic locus HEX, which is fixed for alternate alleles in sympatric populations of the two species, *P. lividus* and *P. sidneyi*, this suggests that a lack of gene flow and reproductive isolation exists between them. Further analysis using genetic and morphological data showed this species to be distinct from the other KZN species, namely *P. clarus*, *P. depressus*, *P. sidneyi* and *P. dentatus* (Gouws & Stewart, 2001).

Daniels et al. (2002) investigated the molecular phylogeny of the southern African *Potamonautes* using all fourteen species found in southern Africa. The 16S topology was found to place *P. lividus* and *P. dentatus* as sister taxa to the large-bodied riverine species such as *P. sidneyi*. They found that sister taxon relationships were well resolved, with *P. lividus*, a small-bodied crab, amongst the most basal within the large-bodied riverine clade. Using a molecular clock, the separation of the tropical species clade occurred around 3 Mya (early Pliocene), while the separation between the temperate species (Cape Fold and Drakensberg) was placed at 12 Mya (mid-Miocene), indicating that this basal species probably emerged early. When comparing African freshwater crabs with

those from Madagascar, the Seychelles, Europe, Asia and the West Indies using molecular phylogenetic methods, Daniels et al. (2006) found that the Indian group, the Gecarcinucidae, emerged basally, followed by the Asian and Papua New Guinean family, the Parathelphusidae and the intermediate Asia/Europe/Socotra family Potamindae, before the family the Potamonautidae were resolved into two major clades, Madagascan and African. Within the African clade, *Potamonemus-Sudanonautes* were basal, followed by *Liberonautes*, *Potamonautes calcaratus*-*P. obesus*, leading to two clades, one containing, among others, *P. niloticus* and *P. ohhneri*, with the other leading via *P. ecorseii* to the southern African species, which include *P. clarus*, *P. depressus*, *P. brincki*, *P. parvispina*, *P. parvicorpus*, *P. dentatus*, *P. lividus*, *P. granularis*, *P. perlatus*, *P. sidneyi*, *P. bayonianus*, *P. unispinus* and *P. warreni*. These authors found lineages which they postulated as being indicative of post-Gondwana fragmentation, and estimated that the radiation into the Afrotropical freshwater crabs of Africa, Madagascar and the Seychelles occurred during the Cretaceous, between 78.6 and 75.03 Mya, when Madagascar and the Seychelles were already separated from the African continent. They suggested that these oceanic barriers could have been bridged through rafting in hollow tree trunks, for example. *Potamonautes warreni* can withstand 14‰ salinity (Morris & Van Aardt, 1998) and ancestral freshwater crabs may have been able to endure even higher salinities. Daniels et al. (2006) further advanced that the present distribution of freshwater crabs most probably resulted from the invasion of ancestral marine crabs which had a wide distribution and had since become extinct. However, they also did not eliminate the possibility of an older vicariance event from the breakup of Gondwana, as Madagascar split from Africa when a northwards transgressing sea breached southern Mozambique during the mid-Cretaceous some 100 Mya (Forster, 1975), although this is not in line with Cumberlidge & Ng's (2009) hypothesis of a later island invasion. The absence of freshwater crabs from some oceanic islands is due to their recent volcanic origins less than 10 Mya.

In a recent molecular phylogenetic analysis, Daniels & Bayliss (2012) tested a number of southern African *Potamonautes* and found that they formed two main clades. The first led via *P. calcaratus* to *P. obesus*-*P. namuliensis* and *P. choloensis*. The other led via *P. lirrangensis*, *P. platynotus* and *P. raybouldi* as well as *P. odhneri*, *P. emini* and *P. subukia* to *P. clarus*-*P. depressus*, followed by *P. brincki*, *P. parvicorpus*-*P. parvispina*, *P. mulanjeensis* and *P. lividus*, which in turn led via *P. dentatus* to *P. granularis*-*P. perlatus*, *P. bayonianus* and *P. unispinus*-*P. warreni*. This analysis, like that of two previous studies (Daniels et al.,

2002, 2006), showed two distinct clades, one of small-bodied mountain-living riverine species and one of large-bodied riverine crabs. Species of *Potamonautes* from East Africa were also found to be basal to the monophyletic southern African clade, although with poor statistical support.

Etymology. *Potamonautes*, *Potamonautes*, *Potamon*- Gr. *potamos*, a river; *-nautes*, Gr. *nautes*, *nautiskos*, a sailor, i.e. a river inhabitant; *lividus*, L. *lividus*, blue or light blue, alluding to the characteristic silver-blue sheen on the carapace (Gouws et al., 2001).



POTAMOIDEA
POTAMONAUTIDAE
POTAMONINAE

***Potamonautes perlatus* (H. Milne Edwards, 1837)**

Synonymy. *Potamon perlatus*, *Potamon (Potamonautes) perlatus*, *Potamonautes (Potamonautes) perlatus perlatus*, *Thehphusa cristata*, *Thehphusa corrugata* (McLeay, 1838; Krauss, 1843; Stebbing, 1910; Lenz, 1912; Bott, 1955; Cumberlidge, 1997, 1998; Ng et al., 2008).

Common Name. Cape River Crab (Barnard, 1950).

Description. Carapace, vaulted yet flattish, with gently convex branchial regions, epibranchial corner not strongly down-curving, postfrontal crest well developed, sharp and overhanging, continuous to the epibranchial angle, which is obtuse, almost straight in adults, sometimes slightly

concave between midline and epibranchial angle; the granulation on the frontal and orbital margins, postfrontal crest and anterolateral margins are beaded, but this becomes feeble and disappears towards the posterior, leaving the dorsal surface smooth, with a few scattered bristles in the middle; pterygostomial region feebly granulate. Maxilliped 3, with shallow longitudinal groove on joint 3 between the maxilliped 3 bases, sternum ends in point, also with 2 transverse grooves. Chelipeds, outer surfaces of joints 4 and 5 finely to coarsely squamose-granulate, joint 4 lower surface with granules in two rows, with only the inner or anterior row ending in a tooth or tubercle, wrist inner margin has 2 teeth—the proximal one small, blunt or obsolete, larger chela finger in males can be strongly curved. Pereiopods, P2 and P3, joint 5 inner surface has denticle in middle of apical margin, but may also be on P4 and P5; in adults joint 4 of P5, 2 to 2.5 times as long as wide. Sternum, between maxilliped 3 bases ending in a point which is blunt or sharp, 2 transverse grooves, the rear one shallow and indistinct medially. In males, pleopod 1 has a low ridge on the external side, with no strong keel on terminal section, the terminal segment has rounded, inward projecting lobe near the base of the ventral section (Barnard, 1950; Bott, 1955; Stewart et al., 1995). *Size*, up to 100mm CW, 70mm CL (Barnard, 1950). Heterochely has been found to occur in this species (Siegfried, 1972) indicating heteromorphic growth. *Colour*, light to dark brown, may have a green or reddish tinge, chelipeds violet, especially in larger specimens (Barnard, 1950; Bott, 1955). *Type locality*, Cape.

Distribution. This potamonautid has one of the broadest geographic distributions of freshwater crabs in the region (Barnard, 1950) and is found principally in the western and southern Cape from the Cape Peninsula (Harrison & Barnard, 1972) to Clanwilliam and eastwards to Belmont and the Gamtoos River (Stebbing, 1910; Barnard, 1935, 1950; Kensley, 1981a; Gouws et al., 2002; Daniels, 2003; Cumberlidge & Daniels, 2009). It also continues into the Transkei where it overlaps with *P. sidneyi* (Barnard, 1935, 1950). *Potamonautes perlatus* and *P. sidneyi* populations do overlap in the Eastern Cape and although some gene flow between them has been observed, there is no clinal variation (Gouws et al., 2002). There are unconfirmed reports that it also occurs in Namibia (Barnard, 1935; Cumberlidge & Daniels, 2007, 2009) as well as in Zimbabwe (Butler & Marshall, 1996), but this latter record is probably another species. It has also been reported from the Congo (Cumberlidge, 1998), but again this needs confirmation.

Zonation & Habitat. This is a large bodied crab is found in the upper, lower and middle reaches of large river systems including the Olifants, Berg, Breede and Gamtoos Rivers (Cumberlidge & Daniels, 2009), where it burrows into the banks. Along the Buffalo River, this crab emerges from its burrow an hour after sunset to spend the night on the bed of the stream, returning to its burrow before sunrise (Hill & O’Keeffe, 1992).

Cumberlidge & Daniels (2009) reported that *P. perlatus* is common in the Olifants, Berg, Breede and Gamtoos Rivers. In the W Cape estimates for this species vary between 0.35 to 5.2 crabs. m⁻² (Arkell, 1979; King, 1983). *Potamonautes* spp. can be locally very abundant, with densities of up to 23 crabs. m⁻² in some river systems which, together with ease of capture and palatability, results in them forming a major part of the diet of many vertebrates. Densities of *P. perlatus* in the Eerste River ranged from 2.89 to 15.57 crabs. m⁻² (Somers & Nel, 1998). This crab was studied in the upper reaches of the Buffalo River, E Cape, where densities were found to range between 1.72 and 5.25 crabs. m⁻² or 54–136g DM. m⁻² (Hill & O’Keeffe, 1992). In Zimbabwe densities of *Potamonautes* vary from 0.1 to 2.2 crabs. m⁻² (Butler & Du Toit, 1994). On the slopes of Mt Kenya, Dobson et al. (2007) found that *Potamonautes* densities (mainly *P. odhneri*) were extremely high in forested areas (107.2. m⁻²) compared to open (1.6. m⁻²) and shaded sites (9.6. m⁻²). A generation time of between 3 and 6 years was estimated for this large-bodied species, whereas small-bodied species such as *P. parvicorpus* take 1 to 2 years to mature (Cumberlidge & Daniels, 2007). Observations of *P. perlatus* at the head of the Buffalo River have shown that it is mainly nocturnal, with most activity at night (Hill & O’Keeffe, 1992). Crabs in the W Cape were found to follow a linear size-dependent hierarchy in which the largest crab is the most dominant (Somers & Nel, 1998). Intraspecific aggression, predation and refuge availability appears to exert strong selection pressure in determining the population structure of wild *P. perlatus*. *Potamonautes perlatus* is common in ponds and streams around the Cape Peninsula and can respire and survive in both air and water (Zond & Charles, 1931).

Breeding females, 25mm CW, have been found in mountain streams, and near Cape Town gravid females have been seen during December. The embryos measure 3mm CW, while small, free-living juveniles (4 by 3.5mm) have been seen in the Bredasdorp area during May (Barnard, 1950).

Conservation. As *Potamonautes* has a high degree of endemism in southern Africa, their populations could become vulnerable due to anthropogenic factors such as pollution (industrial, agricultural or urban)

or habitat destruction. To assess their vulnerability, the conservation status of all nineteen species of *Potamonautes* was assessed using the IUCN Red List criteria (Cumberlidge & Daniels, 2007). *Potamonautes perlatus* was found to have a least concern status, with an extent of occurrence $>180,000 \text{ km}^2$ and an area of occupancy of $>10,000 \text{ km}^2$ giving it a common frequency.

Phylogeny. Barnard (1950) noted that although he accepted Balss' identification of *P. perlatus* from the Upper Congo, he suggested that they would not be phylogenetically conspecific. Daniels et al. (1999a), investigating six populations of *P. perlatus* along the length of the Berg River, W Cape using allozyme electrophoretic variation, found that despite considerable morphological variation along the length of this river, genetic variation was fairly constant, suggesting that gene flow could be responsible for this low genetic variation. A similar study along the length of the Oliphants River, W Cape, also showed two genetically distinct populations, with a narrow hybrid zone between two populations, but as the occurrence of hybrids was low, selection against hybrids was suggested, with a species boundary existing between the two populations (Daniels et al., 1999b).

In the W Cape, *P. perlatus* and *P. brincki* are similar, but have been shown to be morphometrically and genetically distinct (Stewart, 1997a). Also in the W Cape, *P. perlatus* can be distinguished from *P. parvispina* (Stewart, 1997b). Ecologically they are also different, with *P. brincki* preferring mountain streams.

Potamonautes perlatus, like *P. sidneyi*, exhibits what appears to be clinal morphological differentiation through its geographical distribution (see Barnard, 1950). To test this hypothesis, ten populations of this species were collected along a transect 23,00km long and genetic identities were compared pairwise (Gouws et al., 2002). Diffuse boundaries between species were found between *P. perlatus* and *P. granulatus* as well as between *P. perlatus* and *P. sidneyi*, over which gene flow and hybridisation could occur. However, significant genetic sub-structuring was shown between populations and within species, indicating low levels of gene flow. Similarly, no patterns of clinal variation could be found. Using combined analysis, Daniels et al. (2002), studying 14 species of southern African *Potamonautes*, showed strong support for two monophyletic clades, one of small-bodied mountain stream species and another clade of large-bodied riverine species, including *P. perlatus* and *P. granularis*. *Potamonautes perlatus* was thus shown to be closely related to *P. granularis*. Sequences of *P. perlatus* were compared with *P. sidneyi* as

sympatric species pairs, and it was found that the divergence was 3.26 to 11.68%. Sequence divergences were higher for the non-hybridising species pairs *P. perlatus* and *P. parvispina* (14.2% to 23.04%), *P. perlatus* and *P. brincki* (8.92% to 20.36%) and *P. perlatus* and *P. parvicorpus* (7.62% to 14.12%). Cluster analysis also placed *P. perlatus* as a sister taxa to *P. granularis*. Tree topologies and some associations had consistently high bootstrap support, which did not uphold Bott's (1955) subgeneric divisions. Using a "molecular clock", Daniels et al. (2002) extrapolated their data to estimate that the separation of the tropical species clade occurred 3 Mya (Pliocene), while separation of the temperate species (Cape Fold and Drakensberg, including *P. perlatus*) took place around 12 Mya in the mid-Miocene, when changes in climatic cycles led to isolation and speciation. The close phylogenetic relationships which were shown between *P. perlatus* and *P. granularis* as well as *P. perlatus* and *P. sidneyi*, who can hybridise when occurring sympatrically, suggests poorly developed isolation mechanisms among these hybridising species with recent isolation and separation.

The genetic structure of *P. perlatus* was also investigated for 21 populations from major drainage systems in South Africa (Daniels, 2003). Limited genetic variation was shown in the Berg and Olifants catchments, but moderate levels of variation were found in the Gamtoos and Breede River systems. Gene-flow estimates showed high dispersal levels both within and between drainage areas, suggesting *P. perlatus* may have the potential to disperse short distances across land, especially during periods of flooding or high humidity. However, analysis using sequences from ten populations revealed two distinct clades, one where the rivers drain to the west and another in drainages to the southern escarpment. This split coincides with the Cape Fold Mountains, which form a barrier between these eastward and westward catchments, indicating a historic isolation between the two catchment populations with the two clades diverging during the early Pliocene, 6 Mya. This phylogenetic patterning of *P. perlatus* has been further analysed to establish whether the present genetic structure is due to the drainage systems, which developed during the Pliocene, or whether it evolved earlier during the Miocene (Daniels et al., 2006). A wide variety of populations were sampled from 31 populations and five major perennial catchments in the Eastern and Western Cape. Two major phylogroups were found, the first encompassing populations in westward-flowing rivers such as the Oliphants and Berg, while the second came from the southward-flowing rivers, which could be further broken down into the Breede and Gamtoos/Gouritz populations. Analyses showed limited gene flow as well as long-distance dispersal, while grouping

suggested isolation either by distance or fragmentation. The west-flowing drainages, including the Berg, Olifants, Eeste, Liesbeeck and Tokai, were isolated from the south-flowing rivers by the Cape Fold Mountains, while the southward flowing systems like the low-lying Breede, Gamtoos and Gouritz allow some gene flow between them. This suggests that a late Miocene event has impacted contemporary populations, as they do not conform to the Pliocene hydrographic boundaries (Daniels et al., 2006). These authors concluded that these crabs radiated during post-Gondwana times, probably during the Early Cretaceous around 120 Mya, and that the currently recognised families are not monophyletic. This pattern fits better with the older Miocene drainage system rather than the more recent Pliocene pattern. Klaus et al. (2006) also used *P. perlatus* in an analysis and suggested that the Old World crabs originated in Africa and that a sister group to the Potamoidea, the Gecarcinoidea, emerged during the mid-Eocene, when Africa experienced a warm, humid climate.

Using the sperm ultra-structure of this species, Jamieson (1993) found various structures which are features of higher heterotremes. Jamieson et al. (1995) further showed an affinity with *Calocarcinus africanus* and *Pilodius areolatus*. Klaus et al. (2009) showed that *P. perlatus* (Potamonautinae) grouped with *Platythelphusa armata*, which, with the Deckeniinae (Potamonautidae), were basal to the Gecarcinocidae. In their evolutionary history of the Eubrachyura, Tsang et al. (2014) found that *P. perlatus* emerged basally with two other potamonautids, with the Gecarcinocidae and Potamidae emerging after as sister clades. In a phylogenetic study across the heterotreme-thotacacotreme boundary, van der Meij & Schubart (2014) used *Potamonautes perlatus* and found that it grouped basally to the potamids within the heterotremes.

Etymology. *Potamonautes*, see *P. lividus*; *perlatus*, L. *perlatus*, carried through, completed, in reference to the postfrontal crest which completely crosses the carapace unbroken.



POTAMOIDEA
POTAMONAUTIDAE
POTAMONAUTINAE

***Potamonautes sidneyi* (Rathbun, 1904)**

Synonymy. *Potamon* (*Potamonautes*) *perlata*, *Potamon* (*Potamonautes*) *perlatus*, *Potamon* (*Potamonautes*) *Sidneyi*, *Potamon* (*Potamonautes*) *sidneyi*, *Potamonautes* (*Orthopotamonautes*) *sidneyi* (Barnard, 1950; Bott, 1955; Cumberlidge, 1998).

Common Name. Natal river crab.

Description. Carapace, roughly heart-shaped, wider than long, with distinctly rounded anterolateral borders, tapering to posterior; front, entire, postfrontal crest distinct, forming distinct angle at epibranchial corner on joining the anterolateral margin, continuous across epigastric region to epigastric angle; strong granulation in frontal, orbital, anterolateral, and pterygostomial region, as well as postfrontal crest with granulate corrugations on epibranchial zone, epibranchial corners exhibit scabrosity or granulation. The mandibular palp has 2 members or segments (diagnostic). Antennule, lateral margin of each fossa filled by antenna segment 2. Chelipeds, robust, with corrugations on outer surfaces of joints 4 and 5. Pereiopods, robust, strongly granulate, with the upper margins of joints 4 spinulose. Male gonopod 2, when seen in cross-section, dorsal side of junction between subterminal segment and terminal article, with

setose spoon structure, which does not extend to ventral side. When viewed in cross-section, the edges of both dorsal and ventral margins of the terminal article are long, inward-curving and their tips overlap to form a closed dorsal tube (Barnard, 1950; Gouws & Stewart, 2001; Klaus et al., 2006; Cumberlidge et al., 2008). *Size*, up to 55mm CW, 40mm CL (Barnard, 1950). *Colour*, variable, from brownish and purplish to black. *Type locality*, Durban (Port Natal), KZN? Although used as a synonym for *P. sidneyi* by Barnard (1950), it was viewed by Krauss (1843) to be the true *P. perlatus* of Milne Edwards.

This species can be identified by the robust carapace, the possession of broad, short limbs, and the typical granulation and beading on the anterolateral and frontal carapace margins, as well as the scabrosity of the epibranchial corners (Gouws & Stewart, 2001). Both Colosi (1924) and Barnard (1935, 1950) questioned the validity of *P. perlatus* and *P. sidneyi* being placed as separate species, because of a morphological transition between the two species which subsequently led to inconsistencies in species identification, such that *P. sydneyi* was recorded as far westwards as the western Cape (Barnard, 1950). However, despite this transition between the typical rough *P. sidneyi* form in KZN and the smooth *P. perlatus* form of the Cape, with a large overlapping area stretching from Still Bay to KZN, an analysis by Gouws & Stewart (2001) has shown that the two species can be separated morphologically fairly easily.

Distribution. Like many potamonautids, this species is endemic to southern Africa (Stebbing, 1910; Barnard, 1950; Kensley, 1981a) where it is found in the middle to lower reaches of rivers and streams in KZN (Gouws & Stewart, 2001; Mackay & Cyrus, 2001), Mpumalanga (Stewart & Cook, 1998), Swaziland and Mozambique (Cumberlidge & Daniels, 2007, 2009). This species has been recorded from Durban (as Port Natal; Stebbing, 1910), to as far east as Lake Sibayi and northern KZN (Lenz, 1912; Barnard, 1950) and as far south as Port Shepstone and Weza State Forest (Stewart et al., 1995; Gouws & Stewart, 2001) and is widespread across the province in the low-lying Midland region, from the foothills of the Drakensberg to the coast (Stewart et al., 1995).

For such a widespread species surprisingly little is known on its biology or ecology.

Zonation & Habitat. It occurs in a number of aquatic habitats such as major rivers, reservoirs, mountain streams and swamps, typically in the mid to lower reaches of rivers in KZN where the flow is slow (Cumberlidge & Daniels, 2009). Although not recorded from the upper