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A new freshwater crab (Decapoda: Brachyura: Potamonautidae) from the Paleogene of Tanzania, Africa

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With 2 figures and 1 table

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Abstract: Discovery of numerous fragmentary remains of freshwater crab in Paleogene, probably Oligocene, sediments in Tanzania, Africa, permits the description of a new genus and species, *Tanzanonautes tuerkai*. The fossils represent the oldest freshwater crabs known.

Key words: Decapoda, Brachyura, Potamonautidae, Paleogene, freshwater, Tanzania, Africa.

1. Introduction

African freshwater and terrestrial habitats are currently inhabited by at least six families of shrimp, anomurans, and brachyurans (Glaessner 1969; Bott 1970; Kensley 1981; Cumberlidge 1999). The family interrelationships of freshwater brachyurans are intensely debated; however, several workers are currently using morphology-based cladistic analyses to test the numerous proposed classification schemes. A comprehensive summary of the history of classification of the extant freshwater crabs of Africa is given by Cumberlidge (1999). Even more recently, phylogenetic studies based upon morphology of the second male gonopods (Klaus et al. 2006) and molecular sequencing (Klaus et al. 2006; Daniels et al. 2006) have brought into question the classification of freshwater crabs based upon more traditional morphological criteria. The latter two studies have also introduced new hypotheses regarding their origins, evolution, and paleobiogeographic history.

Fossil occurrences of freshwater decapods from Africa are notably sparse. Morris (1976) and Carriol & Secrétan (1994) reported Miocene occurrences of the freshwater crab *Potamonautes* MacLeay from Kenya and Uganda, respectively. Martin & Trautwein (2003) described a fragmentary specimen of freshwater crab from Mio/Pliocene sediments in Kenya which they referred to Potamonautidae gen. and sp. indet. The only other report is a reference to a new genus within the Potamidae from the Cretaceous of Nigeria (Joleaud & Hsu 1935); however, the illustration, a line drawing, of this specimen appears to be of a necrocarcinid. It is further notable that it was collected in association with other marine decapods. Moreover, Morris (1976) indicated that the specimen could no longer be located; thus, the affinities of the specimen cannot be resolved. Hence, the discovery of a new locality preserving fossil freshwater brachyurans from Paleogene (Oligocene) deposits in Tanzania is particularly important. The discovery extends the geographic and stratigraphic range of freshwater

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crabs in Africa and, significantly, represents the earliest occurrence of freshwater crabs. Table 1 summarizes the worldwide fossil occurrences of freshwater brachyurans. Prior to this discovery, the earliest occurrence was from the Miocene, by which time the group is known from Europe, Africa, and South America.

2. Systematic paleontology

Class Decapoda LATREILLE, 1802
Order Brachyura LATREILLE, 1802
Family Potamonautidae BOTT, 1970

Type genus: *Potamonautes* MACLEAY, 1838.

Diagnosis: Mandibular palp biarticulate; postfrontal crest partly very distinct; united at epigastric region; terminal segment of gonopod one (1) shorter than penultimate segment (translated from BOTT 1970: 133).

Remarks: The above diagnosis does not include a sufficient number of characters of the dorsal carapace and pereiopods to make a judgment about the placement of the fossil specimens considered herein. CUMBERLIDGE (1999), however, presented a detailed description of the family that provides a broader basis for assignment. Several characters that he recognizes support placement of the new genus within the family, including the general outline of the carapace with its greatest width in the anterior third and a narrow posterior margin. These features are consistent with those preserved on the fossil carapace. However, there is no evidence of a postfrontal crest, comprised of postorbital and epigastric crests. Examination of several species of extant potamonautids in the collections of the Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt am Main, Germany, by one of us (RMF) indicated that the crest varied in degree of development from extremely prominent to rather subtle. Thus, the crest in the fossil specimen may have been subtle enough that it is not preserved and visible on the specimen. The absence of a diagnostic crest, which is present in virtually all African freshwater crabs (CUMBERLIDGE, 1999: 113), may suggest that early members either had a very reduced crest or lacked the ridge altogether. Alternatively, because the front of the fossil carapace is badly fractured and broken, it is quite possible that the postfrontal ridge is simply not recognizable.

The morphology of the chelipeds also supports placement of the new fossils within the family. The merus is triangular in outline; has toothed margins; and bears a flattened, smooth region, the meral tympanum, on the proximal end of the posterior surface. The carpus bears two teeth on the medial margin, of which the first is largest. Finally, the chelipeds are heterochelous with the major claw being both longer and higher than the minor claw. Two of these characters, the form of the merus and the morphology of the carpus, were recognized by CUMBERLIDGE (1999) as key synapomorphies of the family in a recent cladistic analysis. Those characters exclude the new fossil from other African crab groups. It would seem even more unlikely that the new crab belonged to a family of freshwater decapods that is currently unknown on the continent.

Support for placement of the Tanzanian material within the Potamonautidae is not unequivocal, given the absence of anatomical information about the postfrontal ridge, ventral surface of the carapace, mouth parts, and gonopods. However, there is sufficient evidence for an initial referral to Potamonautidae pending the recovery of more complete and better preserved material. The only other family of freshwater crabs that is currently known from East Africa is the Deckeniidae ORTMANN, 1897, which is represented by very few species. The diagnosis of the family (BOTT 1955) does not address features visible on the specimens at hand; however, examination of the illustrations of the two species, *Deckenia imatatrix* HILGENDORF, 1869, and *D. mitis* HILGENDORF, 1898, suggest that, although neither species bears a postfrontal crest, the convexity and outline of the carapaces are unlike the specimens at hand and unlike those of the Potamonautidae. The front is produced in such a way as to produce a sinusoidal fronto-orbital margin, the anterolateral margin bears two relatively strong spines, the greatest width is attained at about midlength, the posterior margin is broader, and the branchial regions appear to be inflated. Thus, it seems unlikely that the new specimens would be referrable to this family. It is noteworthy that BOTT (1955: 219) incorrectly attributes the authorship of the family to himself, rather than to ORTMANN. Further, he refers to the two taxa as distinct species in his descriptions but considers *D. mitis* as a subspecies of *D. imitatrix* on his Plate 1.

Genus *Tanzanonautes* gen. nov.

Type species: *Tanzanonautes tuerkayi* new species, by original designation.

Etymology: The generic name is derived from Tanzania, the site of discovery of the fossils, and *nautes*, Greek for sailor or seaman, a common suffix within the family. The gender is masculine.

Diagnosis: Potamonautid with nearly flat transversely; postfrontal crest apparently lacking or strongly reduced; strongly reduced definition of regions. Posterolateral margin long, straight. Mesogastric region the most strongly defined of the axial regions.

Tanzanonautes tuerkayi sp. nov.
Fig. 1

Etymology: The trivial name honors Dr. MICHAEL TÜRKAY, Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt am Main, Germany, an authority on freshwater crabs.

Type specimens: The holotype, RRBP (Rukwa Rift Basin Project) 05177, a partial carapace with parts of right and left chelipeds and meri of left pereiopods 2-5 (Fig. 1.1-1.3). Paratypes include: RRBP 02001, a partial finger; RRBP 02029, finger of left propodus; RRBP 03015, right cheliped with dactylus (Fig. 1.5); RRBP 03024, an isolated

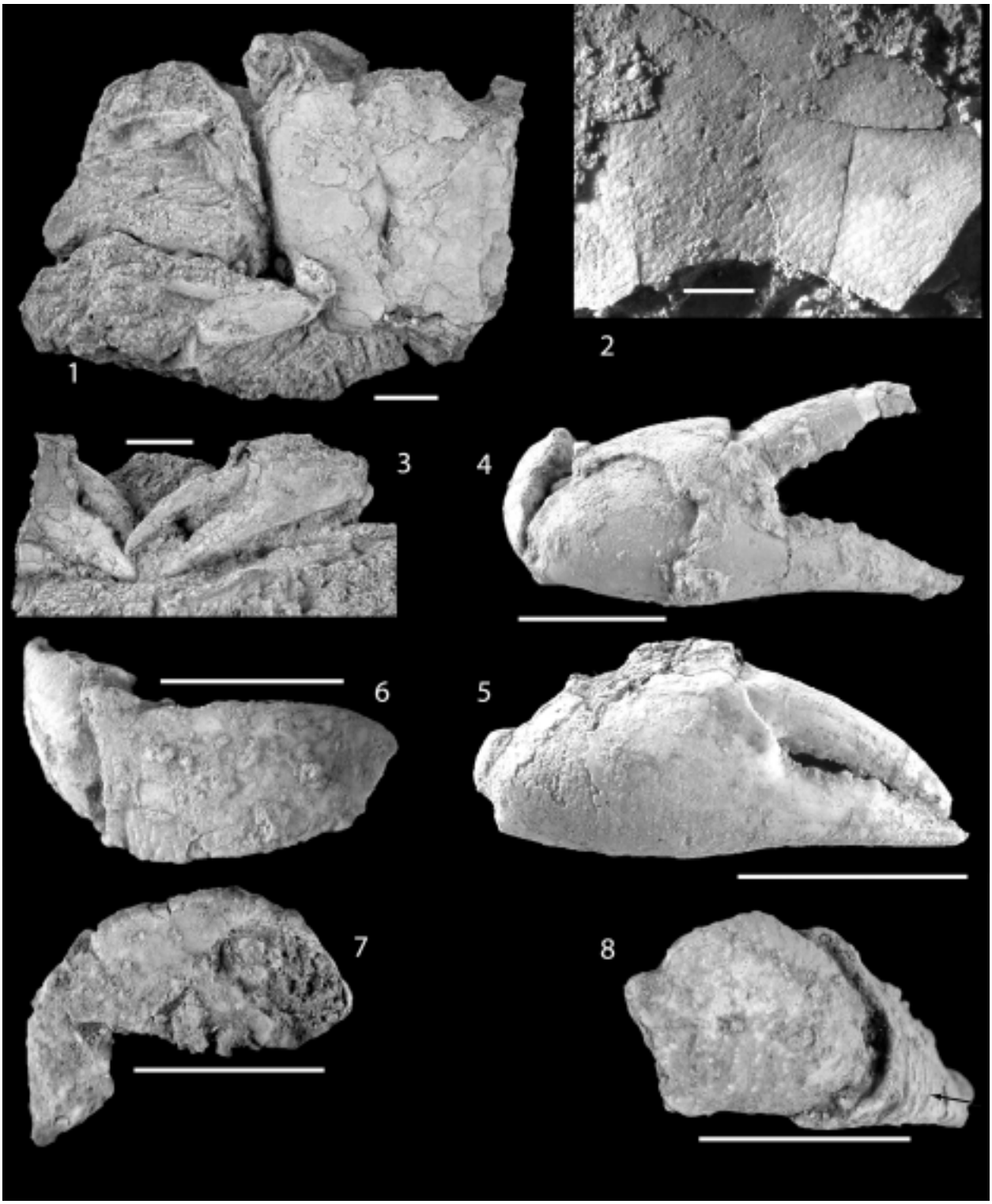

Fig. 1. *Tanzanonautes tuerkayi* n. gen., n. sp. (**1-3**) holotype—RRBP 05177, **1** – dorsal carapace with meri of pereiopods on left side; **2** – closeup of carapace surface showing low nodes developed on the surface of the endocuticle; **3** – frontal view of holotype showing weakly heterochelous chelipeds; **4** – right propodus/dactylus of paratype—RRBP 03127; **5** – outer surface of right propodus of paratype –RRBP 03015; **6-8** – views of merus and carpus of paratype RRBP 03127, **6** – outer surface of merus, **7** – inner surface of merus, **8** – outer surface of carpus showing development of terraced lines on merus (arrow). Scale bars equal 1 cm.

finger; RRBP 03127, a nearly-complete right cheliped (Fig. 1.4, 1.6-1.8); RRBP 03015, RRBP 04083, 04134, 04166, 04194, 04266A, 04266B, 04280, and 04395A, small portions of claw material; and RRBP 04138 and 04161, possible fragments of carapace. All will be housed in the Antiquities Unit at the National Museum of Tanzania, Dar es Salaam, Tanzania.

Diagnosis: Carapace widest in anterior one third; postfrontal and postorbital crests absent; axial regions weakly defined. Chelipeds weakly heterochelous, with moderately inflated hand and long, uniformly tapering fingers bearing fine denticles. Surface of chelipeds with finely pustulose terraced lines.

Description: The carapace (RRBP 05177) is of moderate-size and is sub-rectangular in outline, with a length of ~ 44 mm and width of ~ 50 mm (the widest point being located ~ 15 mm from the anterior margin); it is transversely flattened with a gentle longitudinal vault most strongly arched anteriorly.

Although the anterior edge is incomplete, it does not appear to project beyond the poorly preserved orbits. The well-defined anterolateral margin is short and smoothly rounded. The posterolateral margin is straight and gently rounds onto the lateral flanks. The posterolateral corner is obscured by basal segments of pereiopod 5. The broad (~ 28 mm) posterior margin is weakly convex.

The surface of the carapace is generally smooth, with poorly defined regions. The mesogastric and protogastric regions are expressed as a single area and are ~ 10 mm wide posteriorly, broadening uniformly toward the anterior margin. The urogastric region is rectilinear and bounded by broad, shallow branchiocardiac grooves. The cardiac region is slightly wider than the urogastric region, narrowing posteriorly. Hepatic and branchial regions are not clearly defined.

The chelipeds on RRBP 05177 are heterochelous; the height of the hand at the level of attachment of the dactylus is greater on the right cheliped and the fingers of the right hand are more robust than those on the left. The meri of pereiopods 2-5 (RRBP 05177) are elongate and flattened, with the merus of pereiopod 5 being somewhat larger than the others. The most complete chelal element (RRBP 03127; Figs. 1.4, 1.6-1.8) consists of a right cheliped exhibiting a merus longer (15.2 mm) than wide (9.1 mm) that tapers proximally and is triangular in cross-section. The inner surface is smooth and concave, with a convex upper surface bearing short, transverse rows of perforate pustules directed distally to form short terraced lines (Fig. 1.8). The lower surface is flattened, bearing few, irregularly spaced, small nodes.

The carpus is slightly longer (10.8 mm) than wide (9.6 mm), with its greatest width distally. The inner corner bears a blunt spine on the outer surface with a smaller spine below it; another blunt spine is present on the distal margin at mid-width (Fig. 1.8). The outer surface exhibits transverse terraced lines as on the merus.

The propodus is subtriangular with a length/width ratio of 2.4. The manus (hand) is longer (17.1 mm) than high (11.6 mm). Its outer surface is smooth, with the upper surface proximal to the dactylus possessing terraced lines,

Fig. 2. Location of the field area (X) in the Songwe Valley portion of the Rukwa Rift Basin, Mbeya Region, southwestern Tanzania (inset shows location of Tanzania in East Africa).

similar to more proximal elements of the appendage. The inner surface is gently convex. The fixed finger is long (13.5 mm), slender (4.7 mm wide), and tapers to a sharp point curved toward the inner surface. The occlusal surface possesses small (<1 mm), blunt primary denticles arrayed with 2-3 smaller, secondary denticles intercalated between them. The dactylus is similar to the fixed finger in general morphology, but with a row of setal pits on the outer surface extending throughout the length of the element.

A second, smaller right cheliped (RRBP 03015) was recovered preserving the propodus and dactylus (Fig. 1.5). It is similar in general shape to RRBP 03127; however, the distal margin of the hand extends more obliquely toward the fixed finger than in RRBP 03015.

Locality and stratigraphic position: All specimens were recovered from localities TZP-01 and TZP-02, in Unit II (Roberts et al. 2004) of the Red Sandstone Group (RSG) located in the Songwe Valley portion of the Rukwa Rift Basin, southwestern Tanzania (Fig. 2). The localities are situated at approximately lat. 8º 56' S, long. 33º 12' E (precise locality coordinates are on file at Ohio University). RSG Unit II consists of continental, mixed fluvial channel and overbank deposits and has been assigned a Paleogene age based upon faunal similarities (e.g., the phiomorph rodent *Metaphiomys*) with the early Oligocene Jebel el Qatrani Formation in Egypt (Roberts et al. 2004; Stevens et al. 2006). This age estimate is consistent with thermal history reconstructions of rift flanks (Van der Beek et al. 1998) and K-Ar dates on alkaline volcanics in the study area (Tiercelin et al. 1988).

3. Taphonomy

The specimens forming the basis for this description are all fragmentary. They are preserved in extremely friable, medium-grained sandstone, and preparation of the material is difficult. Presence of the basal elements of pereiopods 1-5 and the chelipeds in life position on the sole specimen preserving part of the carapace suggests that the specimen was a corpse, rather than a molt. The breakage of the carapace and the loss of some of the remains probably resulted from crushing during compaction and dewatering of the sediment followed by exhumation by erosion during the period of exposure at the surface.

The distal elements of the first pereiopods are sufficiently calcified that they exhibit a good state of preservation. However, the carapace and the proximal elements of the pereiopods appear less well calcified and are, therefore, subject to a greater degree of fragmentation and destruction as the friable sand was eroded or fell away from the specimen.

Examination of the remaining cuticle on the carapace indicates that the preservation of the material was very delicate. The surface of the cephalothorax is preserved in great detail and the very fine, low nodes (Waugh 2002) that characterize the cuticle in this species are clearly visible (Fig. 1.2). This observation, coupled with the preservation of articulated remains, suggests that the corpse was buried rapidly and was not transported far from its living site.

4. Final comments

The Paleogene material reported here as a new genus and species, *Tanzanonautes tuerkayi*, of potamonautid brachyuran represents the earliest fossil occurrence of a freshwater crab. This new record raises the possibility that Africa may represent the first site of invasion of freshwater/terrestrial habitats by crabs, although this cannot be stated with confidence given the rather sparse overall fossil record and the taxonomic diversity of the group. The Miocene presence of freshwater brachyurans in Europe, India, and South America, as well as Africa (see Table 1), indicates that the group was relatively widespread in freshwater/terrestrial habitats not long after the time interval (likely Oligocene) represented by *Tanzanonautes tuerkayi*. A scenario of the group initially invading such habitats in Africa requires testing and a better understanding of fossil brachyuran diversity and paleogeography; at present, the data are insufficient to determine whether this is an actual pattern, or a consequence of poor sampling and gaps in the brachyuran fossil record.

The hypotheses arising from molecular based phylogenies provide additional intriguing points of speculation. Klaus et al. (2006) suggest that the origin of Old World crabs was in Africa and that the timing of origin of the Gecarcinucoidea was linked to a time during which Africa experienced a warm, humid climate, probably during the middle Eocene. Interestingly, their analysis nested the two species of Potamonautidae, *Potamonautes obesus* and *P. perlatus* within the Gecarcinucoidea as the sister group to the Deckeniidae. Daniels et al. (2006) performed a molecular based phylogenetic study using different freshwater crab taxa and concluded that the radiation of crab taxa occurred in post-Gondwana time, probably in the Early Cretaceous and that the currently recognized families, based upon morphological criteria, are not monophyletic. The specimens described in the present study extend substantially the history of freshwater crabs, but they do not permit distinguishing between the various hypotheses of origin and evolution postulated by the molecular studies.

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Table 1. Checklist of fossil terrestrial and freshwater brachyurans.

Superfamily Portunoidea Rafinesque, 1815
Family Trichodactylidae H. Milne Edwards, 1853
Sylviocarcinus H. Milne Edwards, 1853
Sylviocarcinus piriformis (Pretzmann, 1968 (Rodríguez 1997) – Miocene, Colombia

Superfamily Potamoidea Ortmann, 1896
Potamidae Ortmann, 1896
Potamon Savigny, 1816
Potamon antiquum Szombathy, 1916 – late Pliocene, Hungary
Potamon? castellinense (Szombathy, 1916) – late Miocene, Italy
Potamon proavitum Glaessner, 1928 – early Pliocene, Austria
Potamon silvalense Glaessner, 1933 – Miocene, India
Archithelphusa Bott, 1955
Archithelphusa punctata (Heer, 1865) (Bott 1955)–middle Miocene, Germany
Geothelphusa Stimpson, 1858
Geothelphusa tenuimanus (Miyake & Minei, 1965) (Naruse et al. 2004) – Pleistocene, Japan
Geothelphusa dehaani (White, 1847) (Karasawa 1997) – Pleistocene, Japan
Proballaya Bott, 1955
Proballaya quenstedti (Zittel, 1885) (Bott 1955; Schweigert et al.1997) – early Miocene, Germany
Propotamonautes Bott, 1955
Propotamonautes speciosus (v. Meyer, 1862) (Bott 1955) – middle Miocene, Germany
Potamonautidae Bott, 1970
Potamonautes MacLeay, 1838
Potamonautes niloticus (H. Milne Edwards, 1837) (Carriol & Secrétan 1994) – late Miocene, Uganda
Potamonautes tugenensis Morris, 1976 – Miocene, Kenya
Potamonautidae gen. and sp. indet. (Martin & Trautwein 2003) – Mio/Pliocene, Kenya
Tanzanonautes Feldmann, O'Connor, Stevens, Gottfried, Roberts, Ngasala, Rasmusson & Kapilima, herein
Tanzanonautes tuerkayi Feldmann et al., herein – Paleogene, Tanzania

Superfamily Pseudothelphusoidea Ortmann, 1893
Family Pseudothelphusidae Ortmann, 1893
Eudaniela Pretzman, 1971
Eudaniela garmani (Rathbun, 1898) (Rodriguez & Diaz 1977) – subrecent, Venezuela

Superfamily Grapsoidea MacLeay, 1838
Family Gecarcinidae MacLeay, 1838
Cardisoma Latreille, 1825
Cardisoma guanhumi (Latreille, 1817) (Rathbun 1918; Türkay 1978; Donovan & Dixon 1998; Collins & Donovan 1997; Collins 1999) – Pleistocene, Jamaica
Cardisoma planum Rathbun, 1945 – Neogene, Fiji