

Notes on the taxonomy of *Potamonautes obesus* (A Milne-Edwards, 1868) and *Potamonautes calcaratus* (Gordon, 1929) (Brachyura: Potamoidea: Potamonautidae) from eastern and southern Africa

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Abstract

The East African freshwater crab *Potamonautes obesus* (A Milne-Edwards, 1868) (family Potamonautidae) is redescribed from a large series of specimens from Tanzania and Somalia, and *Potamonautes (Potamonautes) bottegoi* de Man, 1898 is judged to be a junior objective synonym of *P. obesus*. The related taxon, *Potamonautes calcaratus* (Gordon, 1929) from Mozambique and South Africa, is recognised here as a valid species and is redescribed from type material. The distributions of *P. obesus* and *P. calcaratus* are described and discussed.

Key words: Crustacea, Brachyura, Potamoidea, Potamonautidae, *Potamonautes*, freshwater crab, taxonomy, East Africa, southern Africa

Introduction

The present study aims to stabilize the taxonomy of *P. obesus* (A Milne-Edwards, 1868), a commonly encountered and widespread species of East African freshwater crab. This species is morphologically thought to be closely related to two other described taxa, *Potamonautes (Potamonautes) bottegoi* de Man, 1898 and *Potamonautes (Potamonautes) calcaratus* Gordon, 1929, and identification of specimens that are superficially similar to *Potamonautes obesus* is often confusing and uncertain (Cumberlidge 1997, 1998). Part of the reason for this confusion (it is argued here) is that *P. obesus* exhibits a great deal of intraspecific variation, especially in male specimens. This type of intraspecific morphological differentiation is known to be common in freshwater crabs from southern Africa (Daniels *et al.* 2001). For example, the molts that occur in adult males of *P. obesus* (cw 43 mm and above) bring about a transformation of the major cheliped that is unusual in African freshwater crabs.

The change in form of the major cheliped is different enough to have prompted some authors to describe different life stages of *P. obesus* as different species. Thus, A. Milne-Edwards (1868) described *T. obesus* from a large adult male (cw 62 mm) from Zanzibar, Tanzania, while de Man (1898) described *P. (P.) bottegoi* from a juvenile/subadult male (cw 27 mm) from Somalia. Since that time, these two taxa have either been treated as two separate species (Rathbun 1904; Chace 1942; Barnard 1950; Pretzmann 1977; Cumberlidge 1997, 1998) or as synonyms of a single species, *P. obesus* (Balss 1929; Bott 1955; present work).

This situation became further complicated when Gordon (1929) described *Potamon (Potamonautes) calcaratus* Gordon, 1929 based on an adult male (cw 35.8 mm) and several other subadult specimens from Mozambique. Although distinct, Gordon's taxon is close to *P. obesus* in a number of characters, especially those of the carapace and male major cheliped and abdomen. These similarities have led to disagreements regarding the taxonomic status of *P. calcaratus*, which has been treated as a distinct species (Gordon 1929; Chace 1942; Barnard 1950; Pretzmann 1977; Daniels *et al.*, 2002a; present work), as a subspecies of *P. obesus* (Bott 1955; Stewart & Cook 1998), or as a junior synonym of *P. obesus* (Cumberlidge 1997, 1998). Furthermore, Bott (1955) erected the subgenus *Obesopotamonautes* Bott, 1955 (type species *Thelphusa obesa*) to accommodate *P. (O.) o. obesus* and *P. (O.) o. calcaratus*, and additionally included in this subgenus *Potamon (Potamonautes) langi* Rathbun, 1921 from the Congo river basin.

The present work is based on examination of the type material of *P. (P.) bottegoi* and *P. (P.) calcaratus*. The type of *P. obesus* is dried, so the description here is based on a large series of new specimens of *P. obesus* from Tanzania collected by Trefor R. Williams, and on other museum specimens. All specimens assigned to *P. obesus* correspond closely to the original description of *T. obesa* A Milne-Edwards, 1868, and to the illustrations of the carapace and gonopod 1 of this specimen by Capart (1954). The results of the present study lead us to recognize *P. obesus* and *P. calcaratus* as two valid species, and to treat *P. bottegoi* as a junior objective synonym of *P. obesus*. *Potamonautes obesus* and *P. calcaratus* are redescribed, and important taxonomic characters are illustrated. Species distribution maps of the two taxa are provided and their distributions discussed. Fig. 28 was prepared by SKR using Arcview 8.1 GIS software. The geocoordinates for species localities were taken from the present material, from museum specimens (following direct examination by NC), and from the literature. Pretzmann (1977) provided the coordinates for all of the geographical localities of specimens of *P. obesus* from Somalia.

Abbreviations

cw = the distance across the carapace at the widest point; cl = carapace length measured along the median line, from the anterior to the posterior margin; ch = carapace height, the maximum height of the cephalothorax above the sternum; fw = front width, the width of

the front measured along the anterior margin between the orbits; s = thoracic sternite; e = episternite; s4/s5, s4/s5, s5/s6, s6/s7, s7/s8 = sternal sutures between adjacent thoracic sternites; s4/e4, s5/e5, s6/e6, s7/e7 = episternal sutures between adjacent sternites and episternites; a1 to a6 = abdominal segments 1 to 6; t = telson; p1 to p5 = pereopods 1 to 5; pmw = width of posterior margin of carapace between posterolateral corners; asl = height in metres above sea level; MNHN = Muséum National d'Histoire Naturelle, Paris, France; NHML = The Natural History Museum, London, UK; NMHN = US National Museum of Natural History, Smithsonian Institution, Washington, D.C.; NMU = Northern Michigan University, Marquette, MI, USA; ZMA = Zoölogisch Museum Amsterdam, The Netherlands; LongDD = longitudinal digital degrees; LatDD = latitudinal digital degrees.

***Potamonautes obesus* (A Milne-Edwards, 1868) (Figs. 1-8, 17-25, 30)**

- Thelphusa obesa* A. Milne-Edwards, 1868: 86, pl. 20, fig. 1-4.
Thelphusa obesa: A. Milne-Edwards, 1869: 178.
Thelphusa obesa: Hilgendorf, 1879: 801.
Thelphusa obesa: A. Milne-Edwards, 1887: 146.
Thelphusa obesa: Pfeffer, 1889: 33.
Thelphusa obesa: Hilgendorf, 1891: 20.
Potamon (Potamonautes) obesum: Ortmann, 1897: 303, 305.
Thelphusa obesa: Hilgendorf, 1898: 16.
Potamon obesum: de Man, 1898: 434, 437.
Potamon (Potamonautes) bottegoi, de Man 1898: 262-270, fig. 3.
Potamon (Potamonautes) bottegoi: de Man, 1898: 436.
Potamon (Potamonautes) obesus: Rathbun, 1904: pl. 15, fig. 8, 9.
Potamon (Potamonautes) obesus: Rathbun, 1905: 180, fig. 45.
Potamon (Potamonautes) bottegoi: Rathbun, 1905: 180.
Potamon (Potamonautes) obesus: Sandler, 1912: 199.
Potamon (Potamonautes) obesus: Bouvier, 1921: 49.
Potamon (Potamonâutes) bottegoi: Colosi, 1925: 2.
Potamon (Potamonautes) bottegoi: Parisi, 1925: 98.
Potamonautes obesus: Balss, 1929: 348.
Potamon (Potamonautes) bottegoi: Rathbun, 1933: 258.
Potamon (Potamonautes) bottegoi: Rathbun, 1935: 26.
Potamonautes obesus: Barnard, 1935: 484.
Potamon (Potamonautes) obesus: Chace, 1942: 190.
Potamon bottegoi: Chace, 1942: 208.
Potamon (Potamonautes) obesus: Barnard, 1950: 192.
Potamon (Potamonautes) bottegoi: Barnard, 1950: 192, fig. 34 f, g.
Potamon (Potamonautes) obesus: Capart, 1954: 841, fig. 36, 17
Potamonautes (Obesopotamonautes) obesus obesus: Bott, 1955: 257–259, pl. XXII fig. 2a–d, fig. 19, 80.
Potamonautes (Obesopotamonautes) obesus obesus: Pretzmann, 1977: 238, figs 7–12.
Potamonautes obesus: Cumberlidge, 1997: 580.
Potamonautes bottegoi: Cumberlidge, 1997: 581–582.
Potamonautes bottegoi: Cumberlidge, 1998: 198.
Potamonautes obesus: Cumberlidge, 1998: 202–203.

Type material: TANZANIA: *Thelphusa obesa* A. Milne-Edwards, 1868, dried, form II adult male, holotype (designated here, cw 50.6 mm, cl 39.5 mm), Zanzibar, (Grandidier) (MNHN-B4632). Photographs of the holotype and of an ovigerous female (cw 49.5 mm) from Nyassa were provided by Rathbun (1904, 180–182, plate VII, figs. 8, 9), and the holotype was illustrated by Capart (1954). **SOMALIA:** de Man (1898) described *Potamon (Potamonautes) bottegoi* de Man, 1898 based on four sub-adult males from Matago I Bool (=Bohol), between Brava and Lugh (Captain Bottego), x.1895; one of these males, a paratype (cw 27 mm) (ZMA 102868) was examined in the present study. Bott (1955) listed the ‘type’ of *Potamon (Potamonautes) bottegoi* as the specimen with the following dimensions: cw 31, cl 24, ch 13, fw 10 mm. Pretzmann (1977) referred to all of the specimens from Matago I Bool as the ‘holotype’, but did not specify an individual specimen.

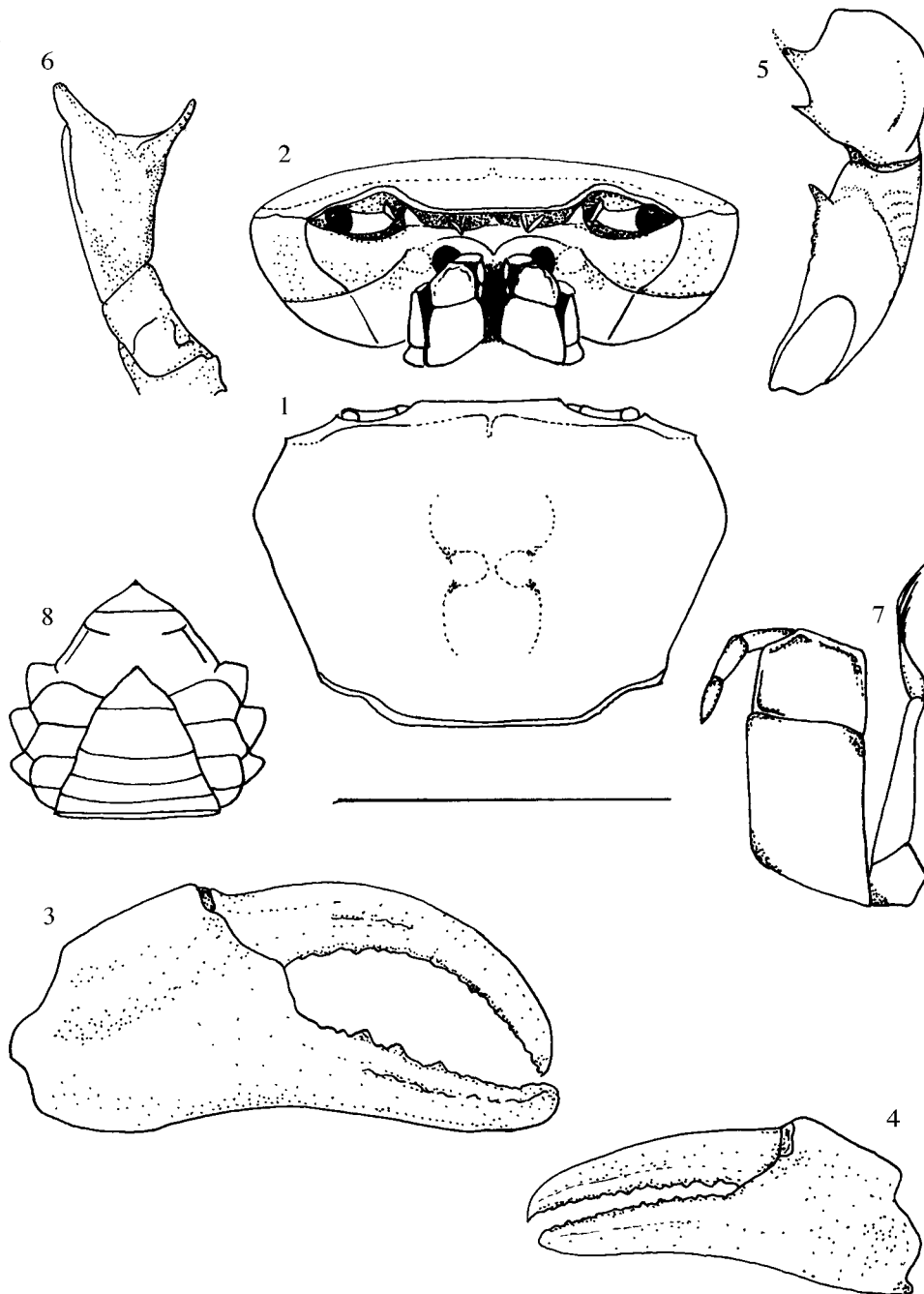
Additional material: SOMALIA: Ola Uager, 2 adult males (cws 44, 42 mm), iii.1970 (M. Vannini) (NHMW 4366); Lac Badana, form II adult male (cw 52 mm), major cheliped length 61.5 mm (>cw), x.1971 (M. Vannini) (NHMW 4367); Afmedu, form II adult male (cw 59.6 mm), major cheliped length 68.6 mm (>cw), 3 males (cws 42, 41, 39 mm), subadult female (cw 38 mm), viii.1970 (M. Vannini) (NHMW 4368); Giohar, juvenile male (cw 28 mm), subadult female (cw 35 mm), viii.1971 (M. Vannini) (NHMW 4370); Bur Akaba, subadult female (cw 37 mm), x.1971 (M. Vannini) (NHMW 4371); Gelib, juvenile, 1962 (Lanza) (NHMW 4372); Baidoa, subadult female (cw 34 mm), 1959 (A.M. Simonetta) (NHMW 4373); Baidoa, form II adult male (cw 54 mm), major cheliped length 58 mm (>cw), x.1971 (M. Vannini) (NHMW 4374). **KENYA:** Southeast, Silver Beach, 5 km north of Mombasa, juvenile female (cw 14.5 mm) 31.vi.1987 (M. Lödl) (NHMW 13351); Tana River, juvenile female (damaged) (W.A. Chanler) (USNM 20647); Lorian Marsh, adult male (cw 41.9, cl 31.3, ch 17.9, fw 12.9), adult female, ovigerous (cw 32.6, cl 24.7, ch 13.7, fw 10.7), juvenile (cw 14.7, cl 10.4, ch 6.6, fw 5.2), juvenile (cw 14.8, cl 11.4, ch 7.3, fw 5.6) (USNM 59367); Voi, juvenile female (cw 21.9, cl 17.9, ch 9.4, fw 8.2), juvenile male (cw 19.9, cl 15.5, ch 8.6, fw 7.7), 7.iv.1934 (A. Loveridge) (USNM 70910); adult male (cw 42.2, cl 32.6, ch 20.9, fw 15.0), (NMU 7.2001a.1). **TANZANIA:** Mlali, near Morogoro, Uluguru Mountains, adult male (cw 49.1, cl 36.7, ch 21.7, fw 16.1 mm), 20.v.1968 (J.N. Raybould) (NMU TRW 1968a.06); Mlali, near Morogoro, Uluguru Mountains, adult male (cw 41.3, cl 30.5, ch 17.5, fw 14.7 mm), adult female (cw 43.4, cl 32.8, ch 18.2, fw 15 mm), 20.v.1968 (J.N. Raybould) (NMU TRW 1968b.06); adult male (cw 42, cl 31.9, ch 18.4, fw 14.5 mm), USDM campus, Dar es Salaam, 6.iv.1986 (NMU KMH 3455); Dam at Handemi, between Pare Mountains and Uluguru Mountains, 4 juveniles (cw 8.9, cl 7.7, ch 4.2, fw 3.6 mm; cw 12, cl 8.9, ch 5.1, fw 4.5 mm; cw 18, cl 14.3, ch 8.7, fw 6.7 mm; cw 24.2, cl 18.7, ch 11.4, fw 8.5 mm), 2 females (cw 33.5, cl 25.9, ch 15.3, fw 11.1 mm); cw 36.8, cl 28.4, ch 16.9, fw 13.8 mm), male (cw 40.8, cl 30.9, ch 19.4, fw 13.8 mm), 19.ii.1962 (NMU TRW EA62.37); Mlali, south of Morogoro, Uluguru Mountains, 4 females (cw 34.1, cl 23.9, ch 14.7, fw 11.5 mm; cw 33.9, cl 24.8, ch 15, fw 12.1 mm; cw 41.7, cl 30.3, ch 18.3, fw 14.5; cw 48.1, cl 36.3, ch 20.3, fw

17 mm), juvenile (cw 12.2, cl 9.5, ch 5.3, fw 4.3 mm) 21.ii.1962 (NMU TRW EA62.40); East Usambara Mountains, 2 females (cw 35.9, cl 27.3, ch 16, fw 12.9 mm; cw 39, cl 29.5, ch 16.8, fw 13.5 mm), 1970 (J.N. Raybould) (NMU TRW 1970.10); Muheza, near Amani, East Usambara Mountains, temporary stream, juvenile (cw 23, cl 17.7, ch 10.6, fw 8.1) (NMU TRW 1962.07); Kihurio, Gonja, South Pare Mountains, near Saseni river, 2 juveniles (cw 15.3, cl 12.2, ch 7.3, fw 6.2 mm; cw 8.6, cl 7.5, ch 4.3, fw 3.5 mm), 1962 (NMU TRW EA62.28); RS Nambunjo, Muengei, Maturbi, female (cw 42.7, cl 31.6, ch 19.1, fw 15.6 mm), male (cw 27.3, cl 20.2, ch 12.9, fw 9.3 mm), 4 juveniles (cw 18, cl 14.1, ch 8.2, fw 6.6 mm; cw 14.3, cl 12.2, ch 6.8, fw 4.9 mm; 2 damaged), xi.1989 (J. Kingdon) (NMU 11.1989.6); Litipo Forest Reserve, Lindi District, 39°29'E, 6°02'S, female (cw 40.1, cl 30.2, ch 17.8, fw 12.9 mm), (Frontier Tanzania) (NMU 1990.2); Kiono Forest, Makange Forest Reserve, Bagamoyo District, 2 juveniles (cw 28, cl 17.3, ch 9.6, fw 7.8 mm; cw 26.4, cl 20.8, ch 11.3, fw 9.9 mm), female (cw 36.4, cl 27.34, ch 16, fw 12.8 mm) iii.1990 (Frontier Tanzania) (NMU 3.1990.1–3); Tono'omba Forest Reserve, Yiewa District, Undi region, 39°01.E 8°25.S, 150–540 m asl, male (cw 44, cl 32.3, ch 18.7, fw 14.8 mm), 4 juveniles (cw 25.7, cl 19.5, ch 11.5, fw 9.2 mm; cw 24.8, cl 19.1, ch 11.3, fw 8.1 mm; cw 20, cl 15.2, ch 9.2, fw 7.4 mm; cw 17.4, cl 13.3, ch 17.5, fw 6.4 mm) vi–ix.1992 (Frontier Tanzania) (NMU 6–9.1992.1–5); Genda-Genda South Forest, Handeni District, 38°38.E 5°33.S, juvenile (cw 16.1, cl 12.6, ch 7.6, fw 6.6 mm), male (cw 40.2, cl 30.56, ch 19, fw 13.9 mm), 29.vii–18.ix.1991 (Frontier Tanzania) (NMU 29.7-18-9.1991.1-2); Genda Genda Dry Forest 58°38.E 5°32.S, adult male (cw 46.1, cl 34.7, ch 24.6, fw 16.7 mm), 2 ovigerous females (cw 41.1, cl 31.1, ch 17.1, fw 14.7; cw 37.9, cl 27.7, ch 16.3, fw 12.3 mm), subadult male (cw 34.5, cl 27.0, ch 17.2, fw 12.6 mm), 2 juvenile males (cw 32.3, cl 24.6, ch 15.7, fw 11.65; cw 24.3, cl 18.9, ch 11.65, fw 9.4 mm), juvenile female (cw 18.0, cl 14.3, ch 8.35, fw 6.5 mm), 2 juveniles (damaged), (Frontier Tanzania) (NMU 7.2001b.1–9); Mount Tongwe, Muweza District, Tanga region, male (cw 38.9, cl 29.4, ch 19.5, fw 14.7 mm), 10.ii.1992 (Frontier Tanzania) (NMU 10.02.1992.1); Kazimzumbwi Forest Reserve, Kisarawe District, 39°03.E 6°57.S, 2 females (cw 30.5, cl 23.5, ch 13.4, fw 11.8 mm; cw 30.4, cl 23.6, ch 13.6, fw 11 mm), male (cw 27.1, cl 21.2, ch 12.5, fw 10.5 mm), 3 juveniles (cw 17.7, cl 14.7, ch 8.5, fw 7.1 mm; cw 14.1, cl 10.2, ch 5.9, fw 5.3 mm; cw 15.4, cl 12.5, ch 6.5, fw 5.8 mm), i–ii.1991 (Frontier Tanzania) (NMU 1–2.1991.1–6); Kazimzumbwi Forest Reserve, Kisakawe District, 39°03.E 6°57.S, male (cw 28, cl 22.1, ch 13.9, fw 10.8), female (cw 27.2, cl 21, ch 12.2, fw 9.5 mm), 7 juveniles (cw 17.5, cl 13.9, ch 7.5, fw 6.1 mm, damaged; cw 13.6, cl 10.7, ch 5.8, fw 5 mm; cw 12.8, cl 10, ch 5.7, fw 4.7 mm; cw 11.3, cl 9.2, ch 5.1, fw 4.7 mm; cw 11, cl 8.8, ch 5.1, fw 4.7 mm; cw 10.8, cl 8.8, ch 5.5, fw 3.9 mm; one damaged), i–ii.1991 (Frontier Tanzania) (NMU 1–2.1991.1–9); Matumbi Forest, Rifiji District, male (cw 49.1, cl 36.3, ch 23.4, fw 15.5 mm), adult female (damaged), juvenile female (cw 14.0, cl 10.75, ch 5.9, fw 5.6) (Frontier Tanzania) (NMU 1990.1); stream near Saggo-Nganga? Nyanga?, Njanga?, adult female, ovigerous (cw 36.8 mm), subadult female (cw 33.1 mm) (Fülleborn) (ZSM 1518/1); adult

female (cw 35.5 mm), subadult female (cw 25.8 mm) (ZSM 1518/2); Tendaguru, water hole, adult female (cw 52.2 mm), Reck coll. (ZSM 1518/4); Kilwa, adult female, ovigerous (cw 47.8 mm) (Eimer) (ZSM 1518/3); Pemba Island, subadult female (cw 29.5 mm), juvenile male (cw 19.3 mm) (Lenz) (ZSM 1200/2); vicinity of Nyassa and Lake Tanganyika, adult female, ovigerous (cw 40.3, cl 28.9, ch 17, fw 12.9) (USNM 30010). **MALAWI:** Mhandwe stream, 20 km south of Monkey Bay on Lake Malawi, female (cw 38.3, cl 26.7, ch 14.9, fw 11.9 mm), 14.vi.1971 (D.H. Eccles) (NMU TRW 1972.06).

TABLE 1. A gazetteer of collection localities for *Potamonautes obesus*.

Country	Locality	Latitude	Longitude	Lat DD	Long DD
Kenya	Lorian Marsh	00°40'00''N	39°35'00''E	0.67	39.58
	Tana River	02°32'00''S	40°31'00''E	-2.53	40.52
	Voi	03°23'00''S	38°34'00''E	-3.38	38.57
Malawi	Mhandwe stream	14°05'00''S	34°55'00''E	-14.08	34.91
Somalia	Afgoi	02°08'30''N	42°03'59''E	2.14	42.07
	Afmedu	00°31'03''N	42°03'59''E	0.52	42.07
	Baidoa	03°07'00''N	43°39'00''E	3.12	43.65
	Giohar	02°46'00''N	45°31'00''E	2.77	45.52
	Lac Badana	00°44'00''S	42°32'00''E	-0.73	42.53
	Manas River	02°53'00''N	43°28'00''E	2.88	43.47
	Matagoi Bool	01°40'00''N	43°28'00''E	1.67	43.47
	Ola Uager	01°14'00''S	41°32'00''E	-1.23	41.53
	Tanzania	Dam at Handemi	05°26'00''S	38°01'00''E	-5.43
East Usambara Mts.		04°45'00''S	38°30'00''E	-4.75	38.50
Genda Genda Forest, Handeni District		05°34'00''S	38°39'00''E	-5.57	38.65
Kazimzumbwi Forest Reserve, Kisarawe District		06°57'00''S	39°03'00''E	-6.95	39.05
Kihurio, Gonja		04°28'00''S	38°04'00''E	-4.47	38.07
Kilwa		05°32'00''S	37°31'00''E	-5.30	37.52
Kiono Forest, Makange Forest Reserve, Bagamoyo District		06°20'00''S	38°30'00''E	-6.33	38.50
Litipo Forest Reserve, Lindi District		06°02'00''S	38°29'00''E	-6.03	38.48
Matumbi Forest Reserve, Rifiji District		08°20'00''S	38°55'00''E	-8.33	38.91
Mount Tongwe, Muweza District		05°18'00''S	38°44'00''E	-5.30	38.73
Muheza		05°10'00''S	38°47'00''E	-5.17	38.78
Pemba Island		05°10'00''S	39°48'00''E	-5.53	39.80
Tono'omba Forest Reserve, Yiewa District		08°25'00''S	39°01'00''E	-8.42	39.02
USDM campus, Dar es Salaam		06°48'00''S	39°03'00''E	-6.80	39.05
Vicinity of Nyasa and Lake Tanganyika		04°14'00''S	33°13'00''E	-4.23	33.22
Zanzibar		06°10'00''S	39°20'00''E	-6.17	39.33



FIGURES 1–8. *Potamonautes obesus* (A. Milne-Edwards, 1868), adult male, form II (cw 49.1 mm, NMU TRW 1968.06) from Mlali, near Morogoro, Uluguru Mountains, Tanzania. 1, carapace and eyes, dorsal view; 2, cephalothorax, carapace and eyes, frontal view; 3, right cheliped, frontal view; 4, left cheliped, frontal view; 5, carpus and merus of right cheliped, dorsal view; 6, merus of right cheliped, inferior view; 7, left third maxilliped; 8, sternum and abdomen. Scale = 3 cm, 1–6, 8; 6 cm, 7.

Diagnosis. Carapace of adult high (ch/fw 1.3), smooth, rounded, epibranchial corner sloping downward; epibranchial tooth small but pointed, positioned well behind postfrontal crest; sidewall clearly in 4 parts; episternal sulcus s4/e4, s7/e7 incomplete, s5/e5, s6/e6 complete, dactylus of major cheliped of form I adult male (cw 39–42 mm, Fig. 19, 20) flat, broad, palm very high; dactylus of major cheliped of form II adult male (cw 43–59.6 mm, Fig. 21) highly curved, slim, elongated (propodus of cheliped longer than cw), palm very high; terminal article of gonopod 1 directed outward at a 45° angle to vertical, slim, tapering to slightly upcurved tip; lateral fold on terminal article wider, higher than medial fold; subterminal segment of gonopod 1 columnar, broad from base to apex.

Redescription. The dorsal carapace and first gonopod of the adult male holotype from Zanzibar, Tanzania (MNHN-B4632) were illustrated by Capart (1954). This specimen is dried, so the following description is based on a form II adult male (cw 49.1 mm, NMU TRW 1968.06, Figs. 1–8) from Mlali, near Morogoro, Uluguru Mountains, Tanzania. Carapace relatively wide (cw/fw 3.0), highly arched (ch/fw 1.0); front slightly indented, slightly deflexed, medium width (about one third cw, fw/cw 0.3). Postfrontal crest present but faint, epigastric lobes continuous with postorbital crests, ends curving back towards epibranchial teeth, but not quite meeting. Dorsal surface of carapace smooth; semi-circular, urogastric, cardiac, cervical grooves faint; mid-groove of postfrontal crest short, deep, forked at posterior end. Exorbital tooth small, low; epibranchial tooth small, pointed, positioned well behind postorbital crests; anterolateral margin behind epibranchial tooth raised, smooth continuous with posterolateral margin (not curving inward over carapace at posterior end); posterior margin of carapace about one third as wide as carapace. Suborbital, subhepatic, pterygostomial regions of carapace sidewall either faintly granular or smooth; sidewall in four parts, vertical sulcus on sidewall granular, beginning on anterolateral margin close to exorbital tooth, dividing suborbital region from hepatic region, vertical sulcus continuing across pterygostomial region, dividing it into two parts. Ischium of third maxilliped smooth, lacking vertical groove, exopod with long flagellum. Second thoracic sternal sulcus s2/s3 deep, completely crossing sternum, third thoracic sternal sulcus s3/s4 incomplete, sides deep, angled inward, middle shallow, distinct bulges on s4 where chelipeds articulate. Episternal sulcus s4/e4, s7/e7 incomplete, s5/e5, s6/e6 distinct. Male abdomen a broad-based triangle, side edges curving slightly inward; sides of telson slightly indented.

Chelipeds highly unequal; dactylus of major cheliped of form I adult male (cw 38–42 mm, Fig. 19, 20) flat, broad, narrow interspace, propodus of cheliped shorter than cw, palm very high; dactylus of major cheliped of form II adult male (cw 49.1 mm, Fig. 21) highly curved, slim, enclosing long oval interspace, elongated, propodus of cheliped longer than cw, palm very high; propodus of right cheliped of form II male (cw 49.1 mm) higher (22 mm), longer (51.3 mm), than that of left cheliped (12.6 mm, 29.5 mm, respectively); teeth along inner margin of dactylus weak, blunt; finger of propodus long (extending beyond dactylus), lined by small teeth interspersed with three larger pointed molars;

dactylus of minor (left) cheliped straight, extending beyond finger of propodus; fingers of dactylus, propodus of left cheliped with short pointed teeth along inner margins, touching when closed. Palms of both chelipeds smooth. Inner margin of carpus of cheliped with two teeth, first large, blunt, directed forward, second blunt, approximately half size of first. Inner margin of merus of cheliped with smooth oval surface (meral tympanum); medial, inferior margin of merus of cheliped smooth with single large distal tooth; superior surface of merus with rows of prominent, rough grains. Merus P5 longer than fw; propodi of P4, P5 short, wide (shorter than fw), anterior, posterior margins of propodi of P5 clearly serrated; dactylus of P4 long, dactylus of P5 very short, shortest of walking legs.

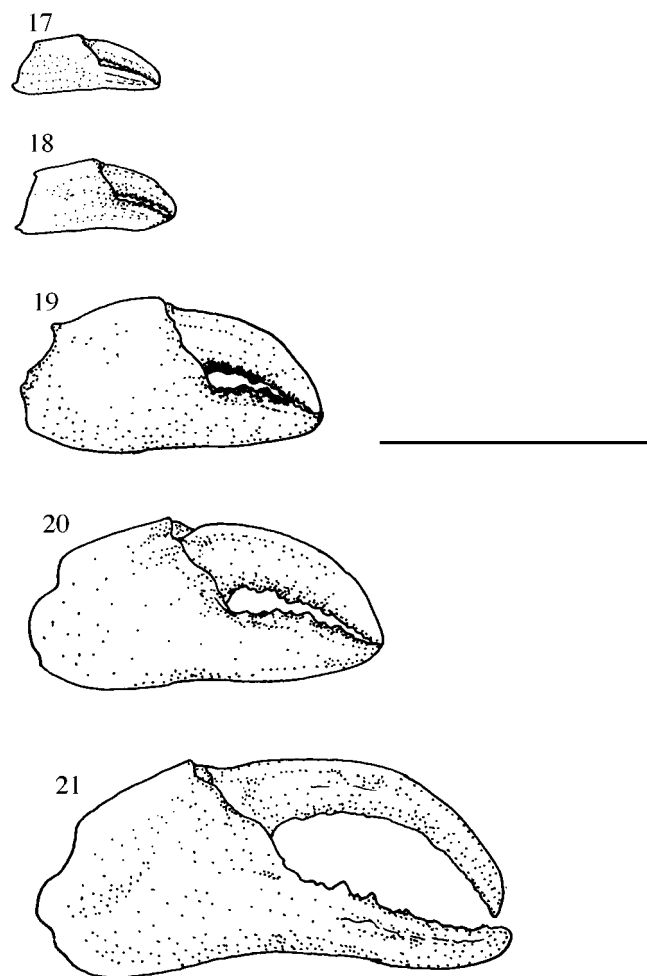


FIGURE 17–21. *Potamonautes obesus* (A. Milne-Edwards, 1868), right (major) cheliped of males of different body sizes. 17, juvenile male, (cw 18 mm); 18, subadult male, (cw 24.8 mm); 19, adult male, form I (cw 38.9 mm); 20, f adult male, form I (cw 44 mm); 21, adult male, form II (cw 49.1 mm). Scale bar = 3 cm.

Terminal article of gonopod 1 about one third as long as subterminal segment; entire terminal article directed outward at a 45° angle to vertical, slim, tapering to slightly upcurved tip; lateral fold on terminal article wider, higher than medial fold; longitudinal groove visible on superior side of terminal article, ventral side of subterminal segment; medial, lateral margins of subterminal segment fringed by short setae; subterminal segment columnar, broad from base to apex; dorsal membrane visible on subterminal segment. Gonopod 2 longer than gonopod 1; terminal article of gonopod 2 long, flagellum-like, over one half as long as subterminal segment.

Size. The adult size range based on measurements of the specimens from Tanzania, Kenya and Somalia is between cws 39–59.6 mm (although one adult ovigerous female from Somalia measured cw 32 mm).

Variation. The chelipeds of *P. obesus* change dramatically as crabs grow (Figs. 17–21), with allometric growth producing heterochely, where the right (major) cheliped is longer and higher than the left (the minor cheliped). Changes in the propodus and dactylus of the major cheliped are the most dramatic. We recognise here two distinct forms of the major cheliped of adult males, which we term form I and form II. The major cheliped of form I adult males (e.g., cw 38–42 mm, Fig. 19, 20) shows the following developments. The palm of the propodus is swollen, very high, and the inferior margin of the propodus forms a smooth downward curve extending to the tip of the fixed finger, which is very broad and flat; the dactylus of the major cheliped is also broad and flat along its length. The palm of the propodus of the major cheliped of form II adult males (e.g., cw 49.1 mm, Fig. 21) is swollen, high and the inferior margin forms a smooth downward curve extending to the tip of the fixed finger, which is broad, flat, and elongated. The fixed finger of the propodus of the major cheliped of form II males is elongated, so that the propodus length is longer than the carapace width; the dactylus of form II males is highly curved, slim and elongated, and encloses a large oval interspace.

Characters that vary with age and with geographical locality include the degree of granulation on the carapace sidewall (which ranges from heavily granulated to completely smooth); and the degree of definition of the postfrontal crest (which varies between sharp-edged in subadults to faint in adults).

Type locality. *Potamonautes obesus*: Zanzibar, Tanzania, East Africa. *Potamon* (*Potamonautes*) *bottegoi* de Man, 1898: Matago I Bool (Bohol), Somalia.

Distribution. The distribution of all known localities of *P. obesus* is summarized in Fig. 28. *Potamonautes obesus* is found in Somalia, Kenya, Tanzania (principally in the coastal region, plus Zanzibar and Pemba islands), and Malawi. Barnard (1950) reports that this species occurs in Harare, Zimbabwe.

Comments. Bott (1955) considered *Potamonautes obesus* to be a senior synonym of *Potamon* (*Potamonautes*) *bottegoi* de Man, 1898, and this view is accepted here. *Potamonautes obesus* from Tanzania and Somalia was found to share a number of diagnostic characters (see above) with the subadult paratype of *P. (P.) bottegoi* from Somalia, and the two

taxa are considered here to belong to the same species. For example, the dorsal surface of the carapace of both taxa is smooth and highly vaulted, and the major cheliped of form II adult males is longer than the carapace width. In addition, there is no vertical groove on the ischium of the third maxilliped, the male abdomen outline forms a broad-based triangle, all episternal grooves are present to some degree, and the carapace sidewalls are divided by surface grooves into four parts. Differences between the male major cheliped and gonopod 1 of *P. obesus* from Tanzania and of the subadult types of *P. (P.) bottegoi* from Somalia can be attributed to differences between these characters in subadult males and form I and form II adult males, rather than to differences at the species level.

Natural history. Williams *et al.* (1964) provide field notes on the habitat of *P. obesus* found in an arid area close to Mount Meru in northern Tanzania. Those authors collected specimens of *P. obesus* together with *Deckenia mitis* Hilgendorf, 1898 (Deckeniiidae) from wetland areas where the standing surface water was relatively warm and stagnant. Williams *et al.* (1964) reported that *P. obesus* and *D. mitis* were dug out from their burrows sited near the waters edge, and were rarely seen actually in the water. The burrows of these crabs often cause extensive damage to drainage ditches. Although data regarding the current population trends of *P. obesus* are unavailable, this species has a relatively wide distribution, is well represented in museum collections, and has been collected in the past ten years. For these reasons we would judge its conservation status to be in the Least Concern category of the Red List Assessment (IUCN 2001).

2. *Potamonautes calcaratus* (Gordon, 1929) (Figs. 9–16, 26–29, 30).

Potamon (Potamonautes) calcaratus Gordon, 1929: 405–411, figs. 1–5.

Potamon calcaratus: Chace, 1942: 208.

Potamon (Potamonautes) calcaratus: Barnard, 1950: 193, fig. 34h, I, 35d.

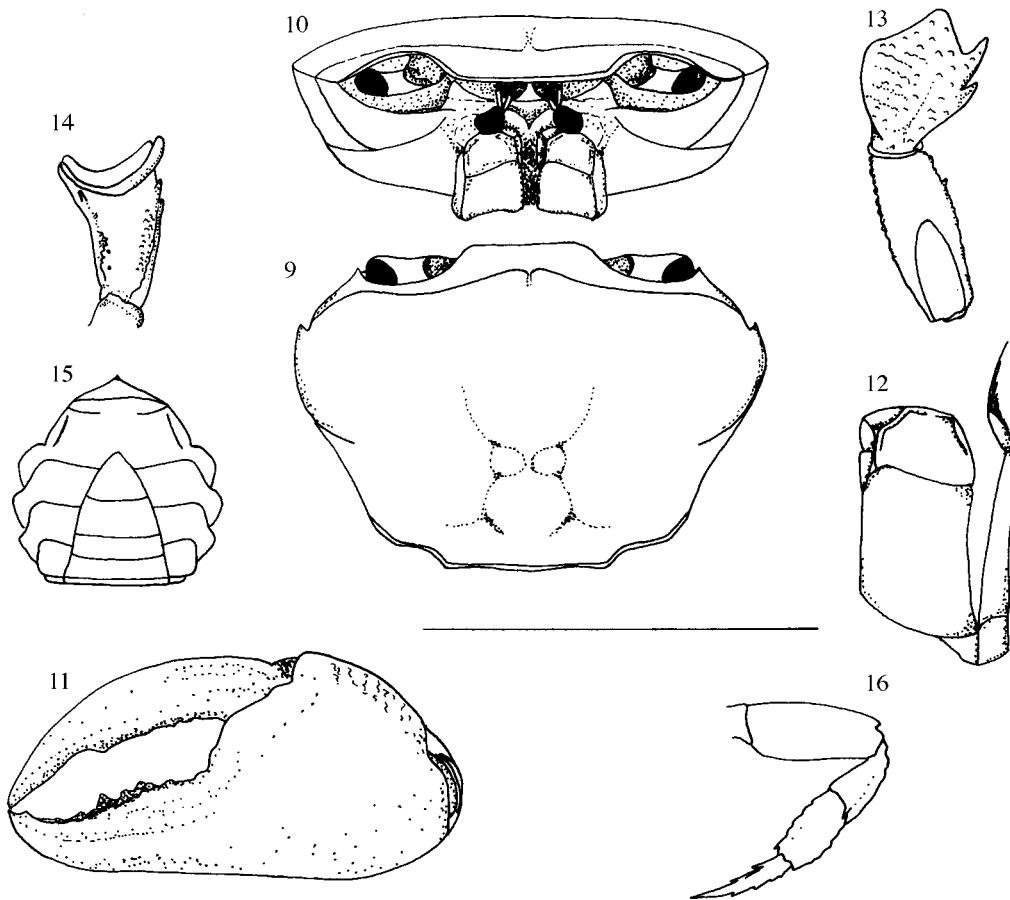
Potamon (Obesopotamonautes) obesus calcaratus: Bott, 1955: 259–260, fig. 81.

Potamonautes calcaratus: Daniels *et al.*, 2002a: 172.

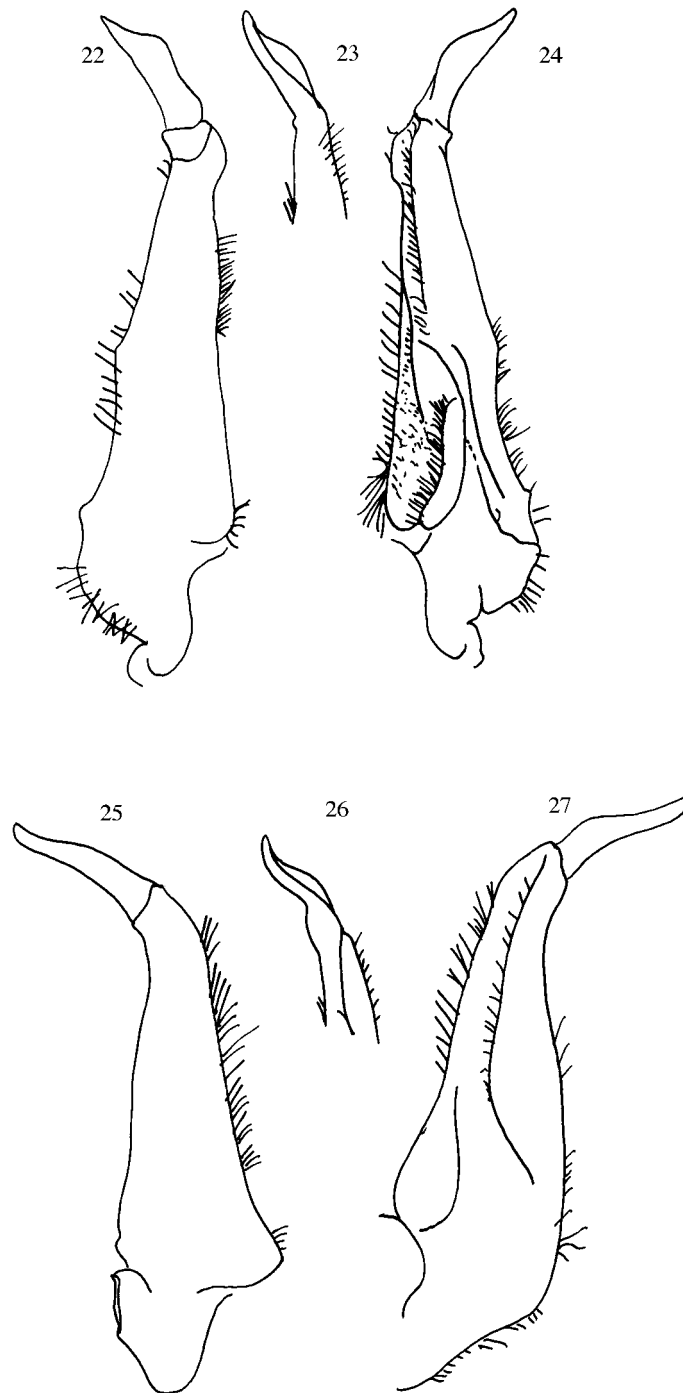
Type Material. MOZAMBIQUE: Lectotype (designated here) Charre, north of Sena (=Vila de Sena) on the Zambezi river, adult male (form I) (cw 35.8, cl 25.4, ch 13.1, fw 11.6 mm), 3.v.1929 (Hugh B. Cott) (NHML 1929.3.5.9–13). Paratypes, Charre, north of Sena (=Vila de Sena) on the Zambezi river, 3 subadult males (cw 31.7, cl 22.9, ch 11.7, fw 10.1 mm; cw 23.5, cl 17.2, ch 9, fw 7.6 mm; cw 21.8, cl 15.7, ch 8.1, fw 7.6 mm), 3.v.1929 (Hugh B. Cott) (NHML 1929.3.5.9–13), subadult female (cw 25.5 mm) (Hugh B. Cott) (ZSM 1518/6).

Additional material. MOZAMBIQUE: adult male (form II) (cw 42.9 mm), adult female (cw 40.3 mm) (ZSM 1518/5); Macequece, juvenile male, soft shell, 1929 (NHMW 4375); Quelimane, Zambezia District, subadult male (cw 34.2 mm) (Peters) (ZSM 1517/1). SOUTH AFRICA: (not examined; localities provided by S.R. Daniels, pers comm.) Kruger National Park, north of Kwaggaspan, 25°08.73'S 31°33.47'E; north of Kwag-

gaspan, 25°06.59'S 31°32.62'E; south of Kwaggaspan, 25°10.62'S 31°33.86'E; Muhlabarnadvube pan, 25°11.73'S 31°37.22'E; unnamed pan west of Renosterkoppies, 25°07.03'S 31°35.29'E; north of Jones Dam, 24°50.22'S 31°42.77'E; unnamed pan south of Lugman, 24°43.718.S 31°40.266'E; between Nklanguleni and Lugman, 24°42.961'S 31°39.518'E; south of Talamati, 24°35.261'S 31°38.976'E; north of Kumana, 24°35.465'S 31°47.285'E; Girivana Pan, 24°21.600'S 31°41 493'E; Gudzani, 24°16.98'S 31°48.56'E.



FIGURES 9–16. *Potamonautes calcaratus* (Gordon, 1929), lectotype, adult male, form I (cw 35.8 mm, NHML 1929.3.5.9–13). 9, carapace and eyes, dorsal view; 10, cephalothorax, carapace and eyes, frontal view; 11, right cheliped, frontal view; 12, left third maxilliped; 13, carpus and merus of right cheliped, dorsal view; 14, merus of right cheliped, inferior view; 15, sternum and abdomen; 16, right fifth pereopod (modified from Gordon 1929). Scale bar = 3 cm, 9–11, 13–16; 6 cm, 12.



FIGURES 22–29. *Potamonautes obesus* (A. Milne-Edwards, 1868), adult male, form II (cw 49.1 mm, NMU TRW 1968.06) from Mlali, near Morogoro, Uluguru Mountains, Tanzania. 22, left gonopod 1, dorsal aspect; 23, left gonopod 1, terminal article, superior aspect; 24, left gonopod 1, ventral aspect. *Potamonautes calcareatus* (Gordon, 1929), lectotype, adult male, form I (cw 35.8 mm, NHML 1929.3.5.9–13). 25, left gonopod 1, dorsal aspect; 26, left gonopod 1, terminal article, superior aspect; 27, left gonopod 1, ventral aspect.

Diagnosis. Carapace medium height (ch/fw 1.1); epibranchial tooth large forming deep epibranchial sinus, positioned well behind postfrontal crest; carapace sidewall in three parts (ventral extension of vertical groove across pterygostomial region either faint or absent); anterolateral margin behind epibranchial tooth raised, smooth, curving inward over carapace at posterior end, not continuous with posterolateral margin; episternal sulci s4/e4, s5/e5, s6/e6, s7/e7 not visible; large, pointed distal tooth on both anterior-inferior and posterior-inferior margins of merus of cheliped; dactylus of major cheliped of adult male either flat, broad, enclosing narrow interspace (form I), or highly curved, slim, elongated enclosing wide interspace (form II); propodus of cheliped either shorter than cw (form I) or longer than cw (form II); lower margin of propodus of cheliped either convex throughout (form I) or concave in middle (form II); carpus of second and third pereopods with small, pointed tooth on outer margin; terminal article of gonopod 1 directed outward at 60° angle to vertical, slim, tapering, ending in slightly upcurved tip; lateral fold on terminal article wider, higher than medial fold; base of subterminal segment of gonopod 1 broad, tapering to slim apex that curves slightly outward.

Redescription. The following is based on the lectotype, a form I adult male (cw 35.8 mm, NHML 1929.3.5.9–13) from Mozambique. Carapace relatively wide (cw/fw 3.1), medium height (ch/fw 1.1); front slightly indented, slightly deflexed, about one third of the carapace width (fw/cw 0.3); postfrontal crest present but faint, epigastric lobes continuous with postorbital crests, ends curving back towards epibranchial teeth, but not quite meeting; surface of carapace smooth; semi-circular, urogastric, cardiac, cervical grooves faint; mid-groove of postfrontal crest short, faint. Exorbital, epibranchial teeth small, pointed; epibranchial tooth forming deep sinus, positioned well behind postfrontal crest; anterolateral margin behind epibranchial tooth raised, smooth, curving inward over carapace at posterior end, not continuous with posterolateral margin; posterior margin of carapace about one third as wide as carapace. Suborbital, subhepatic, pterygostomial regions of carapace sidewall smooth; vertical sulcus on sidewall beginning on anterolateral margin close to exorbital tooth, dividing suborbital from hepatic region, ventral extension of vertical groove in pterygostomial region either faint or absent. Ischium of third maxilliped smooth, lacking vertical groove, exopod of third maxilliped with long flagellum. Second thoracic sternal sulcus s2/s3 deep, completely crossing sternum, third thoracic sternal sulcus s3/s4 incomplete, sides deep, angled inward, middle shallow, distinct bulges on s4 where chelipeds articulate. Episternal sulci s4/e4, s5/e5, s6/e6, s7/e7 not visible. Male abdomen outline forming broad-based triangle, sides of telson straight.

Chelipeds highly unequal, propodus of left cheliped of form I adult male lectotype higher, longer, than propodus of right cheliped (left cheliped missing in lectotype, present in other paratypes); dactylus of major cheliped of form I adult males (cw 35–42 mm) flat, broad, palm very high; dactylus of major cheliped of form II adult male (cw 43 mm, ZSM 1518/5) highly curved, slim, elongated, enclosing long oval interspace; propodus of major cheliped longer than cw, palm very high; teeth along inner margin of dactylus weak, blunt;

finger of propodus long (extending beyond dactylus), lined by small teeth interspersed with three larger pointed molars; dactylus of minor (left) cheliped straight, extending beyond finger of propodus; fingers of dactylus, propodus of left cheliped with short pointed teeth along inner margins, touching when closed. Palms of both chelipeds smooth, except for carinae on superior margin. Inner margin of carpus of cheliped with two teeth, first large, pointed, directed forward, second tooth pointed, approximately half size of first; dorsal surface of carpus with distinct carinae. Merus of cheliped with smooth oval surface (meral tympanum) on inner surface; anterior-inferior and posterior-inferior margins of merus of cheliped smooth, each with small, pointed distal tooth; superior surface of merus with rows of prominent, rough grains. Carpus of P2, P3 each with small, pointed tooth on outer margin; merus of P5 longer than fw; propodius of P4, P5 short (shorter than fw), wide; anterior, posterior margins of propodi of P5 clearly serrated; dactylus of P4 long, dactylus of P5 very short; P5 shortest walking leg.

Terminal article of gonopod 1 about one third as long as subterminal segment; entire terminal article directed outward at 60° angle to vertical, slim, tapering, ending in slightly upcurved tip; lateral fold on terminal article wide, higher than medial fold; longitudinal groove visible on superior side of terminal article, ventral side of subterminal segment; medial, lateral margins of subterminal segment fringed by short setae; base of subterminal segment broad, tapering to slim apex that curves slightly outward; dorsal membrane on subterminal segment narrow. Gonopod 2 longer than gonopod 1; terminal article of gonopod 2 long, flagellum-like, over one half as long as subterminal segment.

Size. The adult size range is from cws 35–42 mm. The carapace proportions are given in table 2.

TABLE 2. A gazetteer of collection localities for *Potamonautes calcaratus*.

Localities Sout Africa	Latitude	Longitude	LatDD	LongDD
Between Nklanguleni and Lugman	24°42'961''S	31°39'518''E	-24.97	31.79
Girivana Pan	24°21'600''S	31°41'493''E	-24.52	31.82
Gudzani	24°16'98''S	31°48'56''E	-24.29	31.82
Muhlambarnadvube pan	25°11'73''S	31°37'22''E	-25.20	31.62
North of Jones Dam	24°50'22''S	31°42'77''E	-24.84	31.72
North of Kumana	24°35'465''S	31°47'285''E	-24.71	31.86
North of Kwaggaspan	25°08'73''S	31°33'47''E	-25.15	31.56
North of Kwaggaspan	25°06'59''S	31°32'62''E	-25.12	31.55
South of Kwaggaspan	25°10'62''S	31°33'86''E	-25.18	31.57
South of Talamati	24°35'261''S	31°38'976''E	-24.66	31.90
Pan, south of Lugman	24°43'718''S	31°40'266''E	-24.92	31.74
Pan, west of Renosterkoppies	25°07'03''S	31°35'29''E	-25.12	31.59

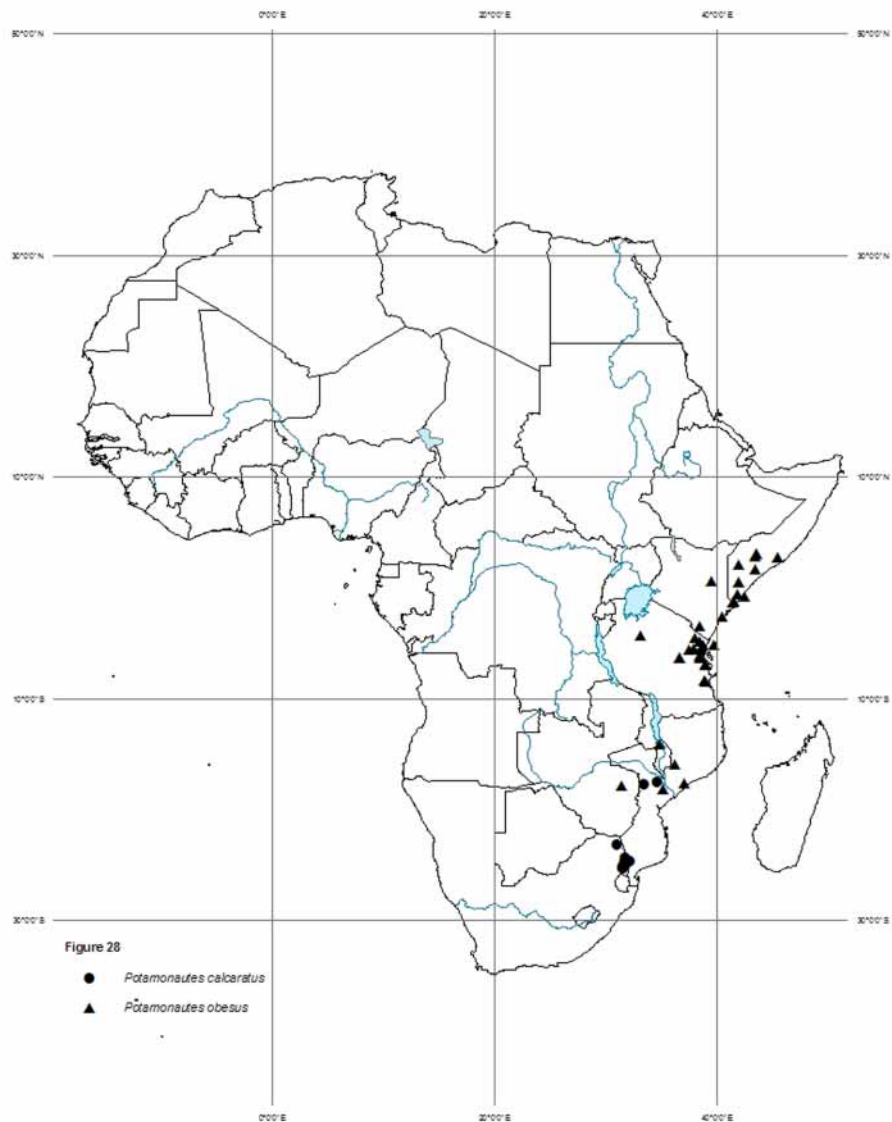


FIGURE 28. Summary of the distribution of *Potamonautes obesus* (A. Milne-Edwards, 1868) (black triangles) and *Potamonautes calcaratus* (Gordon, 1929) (black circles). Data are taken from the present study and from the literature (Barnard 1950; Pretzmann 1977).

Variation. The chelipeds of juvenile *P. calcaratus* are of equal size and shape. However, the chelipeds undergo allometric growth that results in a marked heterochely in older crabs. For example, the palm of the propodus of the major cheliped of subadult males (cw 20–34 mm) and adult males (cw >35 mm) is both high and wide, and the basal margin of the propodus is either straight or curves downward, appearing convex. The fixed finger of

the propodus is very broad, tapering sharply at the tip. In subadult and form I adult males the dactylus is flat and broad, and its teeth meet those of the fixed finger. The dactylus of the major cheliped of form II adult males is slim, elongated, and strongly arched, enclosing a wide oval interspace.

Type locality. Charre, Mozambique.

Distribution. Mozambique, northeast South Africa (only in Mpumalanga Province). Barnard (1950) reported *P. calcaratus* to occur in the Chirinda forest, in the lower Zambezi valley in Zimbabwe.

Natural history. *Potamonautes calcaratus* is the most terrestrial of the freshwater crab species found in South Africa, and lives in burrows it digs near waterholes or pans; it is the only South African freshwater crab to dig a burrow that reaches a depth of 70 cm (Daniels *et al.* 2002b). Most of the localities from South Africa shown in Fig. 30 are in the Kruger National Park and were kindly provided to us by S. R. Daniels. Other localities from South Africa and elsewhere in the region in Fig. 30 are taken from Gordon (1929) and Barnard (1950). Although data regarding the current population trends of *P. calcaratus* are unavailable, this species has a relatively narrow distribution, is not well represented in museum collections, and has not been collected in the past ten years. For these reasons we would judge its conservation status to be in the Vulnerable category (Red List Criteria B1a; C) of the Red List Assessment (IUCN 2001).

Comments. *Potamonautes calcaratus* is closest to *P. obesus*. The two taxa share the following characters: both have a smooth rounded carapace, both lack a vertical groove on the ischium of the third maxilliped, and both have a male abdomen outline that forms a broad-based triangle. In addition, the major cheliped of adult males of both species exhibits a very unusual metamorphosis that shows two different forms – termed here form I and form II. Gordon (1929) described *P. (P.) calcaratus* from a form I adult male whose major cheliped has a broad flat dactylus. The form II male major cheliped of *P. calcaratus* is described here for the first time from a specimen from Mozambique (ZSM 1518/5). The palm of the propodus of the major cheliped of form I adult males is very high, both fingers are broad and flat and they almost touch, enclosing a long, narrow interspace. This configuration changes with subsequent molts, and in form II adult males the major dactylus of the cheliped is slim, elongated, strongly arched, and encloses a wide, oval-shaped interspace.

Potamonautes calcaratus can be distinguished from *P. obesus* as follows. The carapace of *P. calcaratus* is flatter (ch/fw 1.1) than that of *P. obesus* (ch/fw 1.5); the terminal article of gonopod 1 in *P. calcaratus* is directed outward at an angle of 45° to the vertical, whereas in *P. obesus* it forms an angle of 60°; the apex of the subterminal segment of gonopod 1 of *P. calcaratus* curves distinctly outward, whereas in *P. obesus* this segment is straight along its length; the dorsal membrane on the subterminal segment of gonopod 1 is narrow in *P. calcaratus* but is broad and distinct in *P. obesus*; and the thoracic sternum of *P. calcaratus* lacks episternal sulci s4/e4 and s7/e7, which are both present in *P. obesus*.

Furthermore, the subhepatic and suborbital regions of the carapace sidewall of *P. calcaratus* are both smooth, and the pterygostomial region is not divided, whereas the subhepatic and suborbital regions of the carapace sidewall of *P. obesus* are both granular, and the pterygostomial region is divided by a granular sulcus. Finally, the carpi of the second and third pereopods of *P. calcaratus* have a small, pointed tooth on the outer margin, which is lacking in *P. obesus*. For these reasons, *P. obesus* and *P. calcaratus* are considered here to belong to two valid species.

Bott (1955) established the subgenus *Obesopotamonautes* Bott, 1955, to accommodate *P. (O.) o. obesus*, *P. (O.) o. calcaratus*, and *P. (O.) langi* (Rathbun, 1921). However, this subgenus as defined by Bott (1955) is considered here to be doubtful. For example, the holotype of *Potamon (Potamonautes) langi* Rathbun, 1921 (AMNH 3353), was examined in the present study. The grouping of *Potamonautes langi* (Rathbun, 1921) with the taxa under consideration here is questionable, because *P. langi* from the rivers of the Congo basin in Central Africa bears little resemblance to either *P. obesus* or *P. calcaratus* (Rathbun 1921; Bott 1955). For example, *P. langi* can be distinguished from *P. obesus* and *P. calcaratus* by the following characters: the anterolateral margin of the carapace has several long and pointed teeth, the postfrontal crest is sharp-edged in adults and meets the anterolateral margins, the exorbital tooth is large, sharp and pointed, and the teeth on the carpus of the cheliped are of equal size, and both are long and pointed. Furthermore, Daniels *et al.* (2002a) investigated the phylogenetic relationships of the southern African freshwater crab fauna and found no support for some of the subgenera proposed by Bott (1955).

The distributions of *P. obesus* and *P. calcaratus* have some areas of overlap in Mozambique (Figure 28), but it is unknown if sympatric populations do occur. Daniels *et al.* (2002b) used allozyme analysis and the direct sequencing of mtDNA to study the population genetics of *P. calcaratus* from South Africa. It would be useful to apply a similar approach to the two taxa that are the focus of the present study to investigate the possibility of hybridization within sympatric populations.

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Paul Clark and Miranda Lowe of The Natural History Museum, London, are thanked for loaning the type series of *P. calcaratus*. We are grateful to Trefor R. Williams for kindly donating most of the material of *P. obesus* used in this study, much of which was originally collected by J.N. Raybould and by Frontier Tanzania. We are also grateful to Peter Dworschak, NHMW, Vienna, Austria, for providing access to specimens from Somalia, and to Dirk Platvoet, ZMA, Amsterdam, the Netherlands, for loaning the type of *P. (P.) bottegoi*. Savel R. Daniels, University of Stellenbosch, South Africa, is thanked for sending to us a specimen of *P. calcaratus*, and for kindly sharing the locality data of this species from South Africa. Marilyn Schotte and Scott Miller of the USNM, Washington D.C. are

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References

- Bott, R. (1955) Die Süßwasserkrabben von Afrika (Crust., Decap.) und ihre Stammesgeschichte. *Annales du Musée du Congo belge, (Tervuren, Belgique,) C-Zoologie*, (3,3),3(1), 209–352.
- Balss, H. (1929) Über Ostafrikanischer Potamonidae (Decapoda). Mit Anhang: Potamoiden von Madagaskar. *Zoologische Jahrbücher, Abteilung für Systematik* 58, 339–358.
- Barnard, K.H. (1935) Scientific results of the Vermay-Lang Kalahari Expedition, March to September 1930, Crustacea. *Annals of the Transvaal Museum*, 16, 481–492.
- Barnard, K.H. (1950) Descriptive catalogue of South African decapod crustacea. *Annals of the South African Museum*, 38, 1–837
- Bouvier, E.L. (1921) *Decapoda*. In: *Voyage de Ch. Alluaud et R. Jeannel en Afrique orientale (1911–1912)*. Résultats scientifiques, Crustacés, III (Paris), 23–62.
- Capart, A. (1954) Révision des types des espèces de Potamonidae de l'Afrique Tropicale conservés au Muséum d'Histoire Naturelle de Paris. *Volume Jubilaire de Victor Van Strahlen, Director de l'Institut royal des Sciences naturelles de Belgique, 1925–1934, II*, 819–847.
- Chace, F.A. (1942) III. Decapod Crustacea. In: Scientific results of the fourth expedition to forested areas in eastern Africa. *Bulletin of the Museum of Comparative Zoology, Harvard College*, 91(3), 185–233.
- Colosi, G. (1925) Crostacei raccolti nella Somalia dalla Missione della R. Societa geografica (1924). *Bolletino dei Musei di Zoologia ed Anatomia comparata della R. Universita di Torino*, 39 (32, 1924), 1–4.
- Cumberlidge, N. (1997) The African and Madagascan freshwater crabs in the Museum of Natural History, Vienna (Crustacea: Decapoda: Brachyura: Potamoidea). *Annalen des Naturhistorischen Museums in Wien*, 99B, 571–589.
- Cumberlidge, N. (1998) The African and Madagascan freshwater crabs in the Zoologische Staatssammlung, Munich (Crustacea: Decapoda: Brachyura: Potamoidea). *Spixiana*, 21(3), 193–214.
- Cumberlidge, N. (1999) *The freshwater crabs of West Africa. Family Potamonautidae*. Faune et Flore Tropicales 35, Institut de recherche pour le développement IRD (ex-ORSTOM), Paris, 382 pp.
- Daniels, S.R., Stewart, B.A., Ridgway, T.M. & Florence, W. (2001) Carapace dentition patterns, morphometrics and allozyme differentiation amongst two toothed freshwater crab species (*Potamonautes warreni* and *P. unispinus*) (Decapoda: Brachyura: Potamonautidae) from river systems in South Africa. *Journal of Zoology, London*. 255, 389–404.
- Daniels, S.R., Stewart, B.A., Gouws, G., Cunningham, M. and Matthee, C.A. (2002a) Phylogenetic relationships of the southern African freshwater crab fauna (Decapoda: Potamonautidae: *Potamonautes*) derived from multiple data sets reveal biogeographic patterning. *Molecular Phylogenetics and Evolution*, 25, 511–523.
- Daniels, S.R., Stewart, B.A. & Cook, P.A. (2002b) Congruent patterns of genetic variation in a burrowing freshwater crab revealed by allozymes and mt DNA sequence analysis. *Hydrobiologia*, 468, 171–179.
- Gordon, I. (1929) A new river-crab of the subgenus *Potamonautes* from Portuguese East Africa. *Annals of the Magazine of Natural History*, 3(10), 405–411.
- Hilgendorf, F. (1879) Die von Hr. W. Peters in Mocambique gesammelten Crustaceen. *Monatsbericht de Königlich Preussischen Akademie der Wissenschaften zu Berlin*, 1878, 782–851,

- plates 1–4.
- Hilgendorf, F. (1891) Aufzählung der von Emin Pascha und Dr. Stuhlmann gesammelten Fische und Krebse. *Sitzungs-Bericht der Gesellschaft naturforschender Freunde zu Berlin*, 1891(1), 18–21.
- Hilgendorf, F. (1898) Die Land- und Süßwasser-Dekapoden Ostafrikas. In: *Die Thierwelt Deutsch Ost-Afrikas*, 4(7), 1–37.
- IUCN (2001) IUCN Red List Categories and Criteria: Version 3.1. *IUCN Species Survival Commission*. IUCN, Gland, Switzerland and Cambridge, UK.
- de Man, J.G. (1898) Description d'une espèce nouvelle du Genre *Potamon* Sav. provenant du pays des Somalis. *Annali del Museo Civico di Storia Naturale di Genova*, 19(29)(2), 262–270.
- Milne-Edwards, A. (1868) La description de quelques Crustacés du genre *Thelphusa* recueillis par M. de Brazza dans les régions du Congo. *Bulletin de la Société Philosophique Paris, séries* 7(10), 148–151.
- Milne-Edwards, A. (1869) Révision du genre *Thelphusa* et description de quelques espèces nouvelles faisant partie de la collection du Muséum. *Nouvelles Archives du Muséum d'Histoire naturelle Paris*, 5, 161–190.
- Ortmann, A.E. (1897) Carcinologische Studien. *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie de Thiere*, 10, 256–372.
- Ortmann, A.E. (1903) The geographical distribution of freshwater decapods and its bearing upon ancient geography. *Proceedings of the American Philosophical Society*, 41, 267–400.
- Parisi, B. (1925) Un nuovo Potamonidi dell'Abissinia. *Atti Societa Italia Scienza Naturello, Museo civico Milano*, 61, 332–334.
- Pfeffer, G. (1889) Uebersicht der von Herrn Dr. Franz Stuhlmann in Aegypten, auf Sansibar und dem gegenüberliegenden Festlande gesammelten Reptilien, Amphibien, Mollusken und Krebse. *Jahrbuch des Hamburg Wissenschaften Anst*, 6(2), 1–36.
- Pretzmann, G. (1977) Über einige ostafrikanische Süßwasserkrabben. *Monitore Zoologico Italiano*, 10, 233.
- Rathbun, M.J. (1904) Les crabes d'eau douce (Potamonidae). *Nouvelles Archives du Muséum d'Histoire naturelle (Paris)* (4) 6, 255–312.
- Rathbun, M.J. (1905) Les crabes d'eau douce (Potamonidae). *Nouvelles Archives du Muséum d'Histoire naturelle (Paris)* 7(4), 159–322.
- Rathbun, M.J. (1921) The brachyuran crabs collected by the American Museum Congo expedition 1909–1915. *Bulletin of the American Museum of Natural History*, 43, 379–474.
- Rathbun, M.J. (1933) Reports on the scientific results of an expedition to the southwestern highlands of Tanganyika Territory. V. Crabs. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 75(5), 250–262, 7 plates.
- Rathbun, M.J. (1935) Scientific results of an expedition to rain forest regions in Eastern Africa. 2. Crustacea. *Bulletin of the Museum of Comparative Zoology, Harvard College*, 79, 23–28.
- Sendler, A. (1912) Zehnfusskrebse aus dem Wiesbadener naturhistorischen Museum. *Jahrbuch des Nassauischen Vereins für Naturkunde in Wiesbaden*, 65, 189–207.
- Stewart, B.A. & Cook, P.A. (1998) Identification of a new species of river crab (Decapoda: Brachyura: Potamonautidae) from South Africa using morphological and genetic data. *Journal of Crustacean Biology*, 18(3), 556–571.
- Williams, T.R., Hynes, H.B.N. & Kershaw W.E. (1964) Freshwater crabs and *Simulium neavei* in East Africa. II. Further observations made during a second visit to East Africa in February–April 1962 (the dry season). *Annals of Tropical Medicine and Parasitology*, 58, 159–167.