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#### **Recommended Citation**

Cumberlidge N, Clark PF. 2010. Two new species of freshwater crabs from Mt. Elgon, East Africa (Brachyura: Potamoidea: Potamonautidae) with a redescription of Potamonautes niloticus (A. Milne-Edwards, 1887) and notes on their natural history. Journal of Natural History, 44:1807-1829.

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# Two new species of freshwater crabs from Mount Elgon, East Africa (Brachyura: Potamoidea: Potamonautidae) and a re-diagnosis of *Potamonautes niloticus* (H. Milne Edwards, 1837) with notes on their natural history and onchocerciasis

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(Received 13 August 2009; final version received 1 February 2010)

Two new species of potamonautid freshwater crabs from eastern Uganda, Africa are described, and *Potamonautes niloticus* (H. Milne Edwards, 1837) is re-diagnosed with key characters illustrated photographically. A total of four species of crabs are now known to occur on Mount Elgon, which borders both Kenya and Uganda. Two of these species are endemic to the mountain and the distribution patterns of all four species indicate a distinct altitudinal preference. All taxa are compared with similar species and their distributions and natural history are reviewed. Furthermore, three of the crabs recorded from Mount Elgon have been implicated in the transmission of onchocerciasis in East Africa.

**Keywords:** Potamoidea; Potamonautidae; *Potamonautes elgonensis* sp. nov; *Potamonautes williamsi* sp. nov; *Potamonautes niloticus*; *Potamonautes loveni*; freshwater crab; onchocerciasis; Mount Elgon; Kenya; Uganda; East Africa

#### Introduction

A large number of freshwater crabs from Mount Elgon and western Kenya collected by Trefor R. Williams (formerly University of Liverpool, UK) and his colleagues in the 1960s were made available for examination. This is not the first major collection from the region; others date back to the early twentieth century (see Colosi 1924; Sjöstedt 1925; Rathbun 1935; Roux 1935). These latter studies resulted in the description of several new species from Mt Elgon and the highlands of western Kenya including *Potamonautes* (*Geothelphusa*) *loveni* Colosi, 1924, *Potamonautes* (*Geothelphusa*) *granviki* Colosi, 1924, *Potamonautes* (*Potamonautes*) harvardi Rathbun, 1935 and *Potamonautes* (*Geothelphusa*) loveni longimerus Roux, 1935. Recently, Cumberlidge and Clark (2009) considered all of these taxa to be junior synonyms of *Potamonautes loveni* (Colosi, 1924), and recognized only two species of freshwater crabs from the mountain: *P. loveni* and *Potamonautes niloticus* (H. Milne Edwards, 1837).

Potamonautes niloticus is relatively easy to identify, distinct and has never presented any serious taxonomic difficulties (Bott 1955). However, this was not the case for *P. loveni*, which proved to be much more problematic (Cumberlidge and Clark 2009). The collection made by T.R. Williams and examined here has further clarified

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the taxonomy of the freshwater crabs inhabiting Mt Elgon. As a result, two new species are described based on a unique combination of characters of the adult male (first gonopod, carapace, thoracic sternum and chelipeds). These new species were collected in forests on the western slopes of the mountain in Uganda from streams, rivers and nearby land during a survey on river blindness (onchocerciasis) in humans (Barnley and Prentice 1958; McMahon et al. 1958; Hynes et al. 1961; Williams et al. 1961; Williams, 1964). The opportunity is taken here to re-diagnose *P. niloticus* and illustrate the key characters in a photograph because it is one of the three species from Mt Elgon that are closely linked with river blindness in a focus of the disease in the highlands of western Kenya and eastern Uganda (Williams 1968, 1991; Crosskey 1990).

Specimens are deposited in the Natural History Museum, London, UK (NHM); Department of Biology, Northern Michigan University, Marquette, MI, USA (NMU); Museum of Comparative Zoology, Harvard, MA, USA (MCZ); Musée Royal de l'Afrique Centrale, Tervuren, Belgium (MRAC); Swedish Museum of Natural History (Naturhistoriska Riksmuseet) Stockholm, Sweden (SMNH); and the United States National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM). Abbreviations used: a1–a6, abdominal somites 1–6; a7, telson of the abdomen; asl, above sea level; cw, distance across the carapace at the widest point; ch, carapace height, the maximum height of the cephalothorax; coll., collected by; fw, front width measured along the anterior margin; all these measurements in mm; e, thoracic episternite; EAFRO, East African Fisheries Research Organisation; GO1, first gonopod (= first pleopod of male); juv., juveniles; ovig., ovigerous; p1-p5, pereiopods 1-5; pres., presented by; s, thoracic sternite; 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 thoracic sternites and episternites; stn, station.

# Family **POTAMONAUTIDAE** Bott, 1970 *Potamonautes* MacLeay, 1838

Potamonautes niloticus (H. Milne Edwards, 1837) (Figure 1)

Telpheusa nilotica H. Milne Edwards 1837: 12.

Thelphusa nilotica: White 1847: 29; H. Milne Edwards 1853: 210; A. Milne-Edwards 1854: 170, pl. 12, fig. 2; Herklots, 1861: 13; Hilgendorf 1869: 109; Miers 1886: 214; Bell 1894: 166.

Parathelphusa nilotica: A. Milne-Edwards 1887: 141; Hilgendorf 1898: 21, fig. 7; Nobili 1906: 1; 1909: 357.

Potamon (Acanthothelphusa) nilotica: Ortmann 1897: 300.

Potamon (Parathelphusa) niloticus: Rathbun 1905: 263, pl. 12, fig. 15; Lenz 1912: 3.

Potamon (Acanthothelphusa) niloticum: Colosi 1919: 52, 1920: 27.

Potamon (Potamonautes) niloticum: Colosi 1924: 12, fig. 7.

Potamonautes niloticus: Balss 1929: 348; Chace 1942: 218.

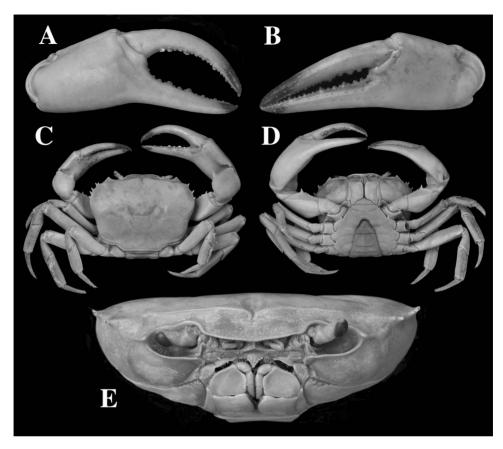


Figure 1. *Potamonautes niloticus* (H. Milne Edwards, 1837). Adult male from Yala River, Kenya (NHM 2008.3388). Cheliped: (A) right (major) frontal view; (B) left (minor), frontal view; whole animal: (C) dorsal view; (D) ventral view; (E) carapace, frontal view. Photograph Phil Crabb, NHM Photographic Unit.

Potamon nilotica: Flower 1931: 733.

Potamon (Acanthothelphusa) niloticus: Rathbun 1933: 258, 1935: 25.

Potamon niloticus: Capart 1954: 841, figs 35, 16.

Potamonautes (Acanthothelphusa) niloticus: Bott 1955: 260, pl. XIII fig. 1a–c, fig. 30a,b; Monod 1980: 382–383, pl. IV, fig. 22.

*Potamonautes niloticus*: Cumberlidge 1997: 579, 1998: 202, 2009a: 548–549, 551–557, Fig. 1; Ng et al. 2008: 171.

#### Material examined

Nontype. Uganda. Six males (cw 44.3–12.4), three females (cw 23–12.9), stn El.34, Kamijaro River, Manafwa sector, Mt Elgon, 1204 m asl, coll. T. R. Williams, 28 December 1960 (NHM 2008.3143–3150); six males (cw 37.6–25.1, 1 damaged), three females (cw 30.2–23.2), stn El.49, Manafwa River, Manafwa sector, Mt Elgon, 1280 m asl, coll. T. R. Williams, 1 January 1961 (NHM 2008.3163–3171); one male

(cw 19), three females (cw 28–11.3), stn El 60, Liisi River, Manafwa sector, Mt Elgon, 1219 m asl, coll. T. R. Williams, 1 January 1961 (NHM 2008.3139-3142); one male (cw 38), one female (cw 32.2), stn El.78, Nalakwa River, Manafwa sector, Mt Elgon, 1402 m asl, coll. T. R. Williams, 3 January 1961, with P. loveni (NHM 2008.3301-3302); one male (cw 54), stn El.79, Nalakwa River, Manafwa sector, Mt Elgon, 1402 m asl, coll. T. R. Williams, 3 January 1961 (NHM 2008. 3307); eight males (cw 32.2-13.6), two females (cw 30.6, 13.8), stn El 81 Zuzu River, Namaiala sector, Mt Elgon, 1374 m asl, coll. T. R. Williams, 3 January 1961 (NHM 2008.3151-3162); two males (cw 49, 40.3), three females (cw 59.2-42.6), stn El 123, Buyi River, Mt Elgon, 1374 m asl, coll. T. R. Williams, 10 January 1961 (NHM 2008.3322-3326); two males (cw 38.1, 37.4), stn El 130, Siroko River, Siroko sector, Mt Elgon, 1097 m asl, coll. T. R. Williams, 11 January 1961 (NHM 2008.3137-3138); two female adults (cw 58.9, 52.1), three female subadults (cw 27.2–29.9), two juvs (cw 15.7, 15.4), River Somso, Budongo Forest (crabs with Simulium pupae), coll. G. Barnley (NHM 1955.11.8.30–33); one male (cw 42.1), lakeshore, Jinja, 701 m asl, coll. R. H. Lowe, 1 August 1953, pres. P. S. Corbet, EAFRO (NHM 2010.30); one female (cw 39.3), Ripon Falls, Lake Victoria, coll. 3 May 1954, pres. P. S. Corbet, EAFRO (NHM 2010.32); one male (cw 54.7), caught in gill nets set between Sagits and Vumba Island, coll. J. Hinchcliffe, 15 February 1956, pres. P. S. Corbet, EAFRO (NHM 2010.33); one male (cw 41.0), Rivers Agoye, Nyara, Wariki, Aduka of the Ala River and Ora River drainage systems near Arua, West Nile, coll. P. Hainsworth, July-August 1955 (NHM 2010.38); one female (cw 51.1), caught in gill net set in Pilkington Bay, Lake Victoria, coll. J. D. Roberts, 25 February 1955, pres. P. S. Corbet, EAFRO (NHM 2010.31). Kenya. One male (cw 53.4), stn EA62.141, Sergoi River at Soy (between Eldoret and Kitale) Kakamega to Kitale region (0°35'0" N. 35°1'0" E, DD 0.58, 35.02), Western Province, Kenya, 26 March 1961, with *Potamonau*tes loveni (NHM 2008.3388); two adult males (cw 67.7, 56.2) two adult females (cw 61.5, 61.3), Yala River, Kaimoisi, 2000 m asl, coll. I. Gordon, 9 June 1964 (NHM 2010.1-4). Egypt. Several subadults and juvs, first cataract of the Nile, Aswan, coll. W. Langmore (NHM 1892.10.23.1–6); adult female (cw 48.7), Nile near Cairo, coll. S. S. Flower (NHM 2010.5); adult female, Nile near Samannud, coll. 14 July 1899 (NHM 1908.1.9.1); adult ovig. female (cw 48.6), Nile near Cairo, Giza Zoological Museum, Zoological Survey of Egypt, coll. S. S. Flower, 19 January 1922 (NHM 1922.11.22.12-17); subadult female (cw 41.7), Nile at Turah near Cairo, Giza Zoological Museum, Zoological Survey of Egypt, coll. C. S. Boyes, 17 February 1919, pres. S. S. Flower, 19 January 1922 (NHM 1922.11.22.12-17); subadult female (cw 44.9), Nile at Turah near Cairo, Giza Zoological Museum, Zoological Survey of Egypt, coll. C. S. Boyes, 17 February 1919, pres. S. S. Flower, 19 January 1922 (NHM 1922.11.22.12–17); ovig. female (cw 39.7), Nile near Cairo, Giza Zoological Museum, Zoological Survey of Egypt, coll. S. S. Flower, 19 January 1922 (NHM 1922.11.22.12–17); female subadult (cw 46), Nile at Turah near Cairo, Giza Zoological Museum, Zoological Survey of Egypt, coll. C. S. Boyes, 17 February 1919, pres. S. S. Flower, 19 January 1922 (NHM 1922.11.22.12–17). Israel or Gaza. Subadults, male (cw 21.9), female (cw 18.2), Palestine (exact locality uncertain, may be present day Israel or Gaza), (NHM 1865.64).

#### Diagnosis

Based on adult male specimens. Postfrontal crest complete, distinct; epigastric, postorbital crests fused; postorbital crests extending laterally to meet anterolateral margins; exorbital, epibranchial teeth both strong, sharp; anterolateral margin immediately behind epibranchial tooth with row of distinct spines; thoracic sternal suture s3/s4 complete; dactylus of major cheliped strongly arched enclosing broad oval interspace when closed; first carpal tooth on carpus of cheliped strong, pointed, second carpal tooth weak, low, blunt; ventral margins of merus of pereiopod 1 both granulated; distal meral tooth strong, pointed; terminal article of GO1 long, s-shaped, widened in middle, ventral lobe thickened, higher than dorsal lobe, dorsal membrane broad. Large-sized species, adult size range from cw 54 to cw 63 mm.

#### Distribution

Potamonautes niloticus is a large, conspicuous river crab that has a wide distribution throughout the entire length of the Nile and its tributaries and is known to occur in more than 60 localities in six countries (Egypt, Sudan, Ethiopia, Uganda, Kenya and Rwanda) and Lake Victoria (Cumberlidge 2009a). This species is endemic to the Nile River basin and has never been found outside this system in sub-Saharan Africa and there are no records from Tanzania, despite its presence in Lake Victoria, Kenya and Uganda (Reed and Cumberlidge 2006; Cumberlidge 2009a,b). The records reported in the present study indicate that P. niloticus also occurs in the Mediterranean zoogeographical subregion of the Palaearctic, which is well outside the Afrotropical region. Most of these additional localities are from the Nile River in Lower Egypt from Cairo, Turah and Samannud (which lies on the Damietta branch of the Nile in the central Delta), but one is from "Palestine", which, if confirmed, would further extend the range of this species outside the Afrotropical region. Moreover, all of these specimens were collected between 88 and 140 years ago and the authors are not aware of any new material that has been collected from the freshwater habitats that lie between southern Israel and the Nile Delta.

#### **Ecology**

Potamonautes niloticus occurs in a range of aquatic habitats including the major channels of the Nile itself and its lowland tributaries, in small and large lakes associated with the river basin, as well as in small clear fast-flowing mountain streams with rocky beds, and sluggish warm lowland streams with muddy bottoms (Bott 1955; Williams 1964; Cumberlidge 1997, 1998, 2009a). This species is completely dependent on aquatic habitats and it has never been reported to leave the water whether it is found in streams, rivers or lakes. In the southern parts of its range in Kenya and Uganda, P. niloticus serves as a host for the aquatic larvae of the biting blackfly, Simulium sp., which are the vectors of Onchocerca volvulus, the parasite that causes river blindness in humans (Crosskey 1990). There is no evidence that P. niloticus is associated with this disease in the northern part of its range in Egypt and the Sudan.

#### Conservation status

Potamonautes niloticus is listed (IUCN 2009) as least concern (LC) in view of its wide distribution, estimated stable population size and abundance (it supports small-scale local fisheries in Lake Victoria in Uganda and Kenya), and the lack of known widespread long-term threats. The stable population estimates are based on the fact that there are large numbers of specimens in museum collections, and on recent collections

of this species from Uganda and Kenya, which implies that East African populations are stable, although anecdotal evidence indicates that the populations in Egypt north of the Aswan Dam may well be in decline because the most recent collection date (1922) available is from Lower Egypt (Cumberlidge 2008; Cumberlidge et al. 2009).

#### Remarks

The type specimen deposited in the Muséum national d'Histoire naturelle, Paris is a dried male, collected from Egypt by Rüppell in 1830 and is in poor condition (Capart 1954). Consequently the diagnosis given here is based on a non-type adult male specimen collected from the Yala River, Kaimoisi, Kenya (see Figure 1) that conforms to the published description of the type. The NHM material from Palestine is worthy of comment because it was initially catalogued as four specimens (one male, three female) of Gecarcinus. All were registered under NHM accession number 1865.64, subsequently re-examined, and identified (by person unknown) as comprising two species. Two adult females (one ovig.) were determined as Thelphusa berardi [now Potamonautes berardi (Audouin, 1826)], and the others as T. nilotica (now P. niloticus). Both jars retained the original registration number and the identifications are confirmed here to species level. The record of *P. berardi* from "Palestine", which was only previously known to occur as far north as Medinet el Fayum on the Nile, suggests that these two species of *Potamonautes* were sympatric with the potamid Potamon potamios (Olivier, 1804) which occurs in the eastern Mediterranean region as far south as Israel, Palestine, and El Quseima (Kosseima) in north east Sinai (NHM 1922.11.22.32-33 and NHM 1928.6.7.1-2) in Egypt (Brandis et al. 2000). However, the age of the museum material reported on here means that the distribution status of these three species of freshwater crabs requires updating.

**Potamonautes elgonensis** sp. nov. (Figures 2–4)

Potamonautes loveni: Williams 1991: 181–187 (part).

#### Material examined

Type material. Uganda. Holotype. Adult male (cw 47), stn El.142, Jabtarit River, Kiriki sector, Mt Elgon, 2134 m asl, coll. T. R. Williams, 14 January 1961 (NHM 2008.1000). Paratypes. Adult male (cw 47.7), five subadult males (cw 39.0–25.8), four subadult females (cw 37.7–28.7), 12 juvs, stns El.140 and El.141, Jabtarit River, Kiriki sector, Mt Elgon, 2073 m asl coll. T. R. Williams, 14 January 1961 (NHM 2010.6–27); one subadult male (cw 38.5), one subadult female (cw 40.5), small rivers and streams above 1372 m asl, western slopes of Mt Elgon, coll. G. R. Barnley, 1957 (NMU TRW 1959.04); eight males (cw 31.2–10.6), five females (cw 37.6–15.1), 15 juvs, stn El.18, Lasu River, Malawa sector, Mt Elgon, 1539 m asl, coll. T. R. Williams, 27 December 1960 (NHM 2008.3172–3181); one male (cw 46.7) River Sume, western slopes of Mt Elgon, 1524 m asl, coll. M. A. Prentice, 12 September 1960, pres. T. R. Williams (NHM 2008.3259); two males (cw 15.9, 13.5), five females (cw 35.9–19.5), 19 juvs, stn El.36, Ririma River, Malawa sector, Mt Elgon, 1829 m asl, T. R. Williams, 29 December 1960 (NHM 2008.3219–3228); stn El.62, four males (cw 38.8–16.7),

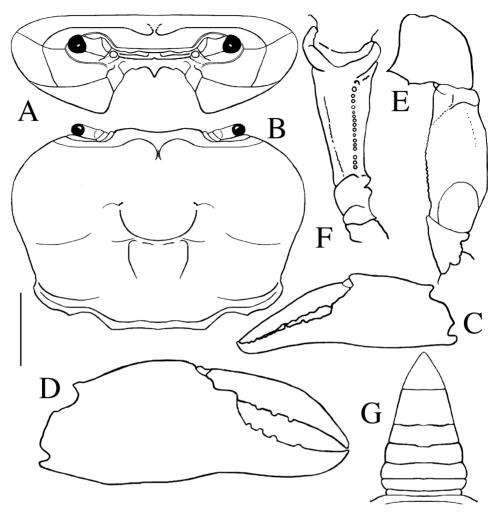


Figure 2. *Potamonautes elgonensis* sp. nov. Male, paratype, cw 49.5, from Mount Elgon, Uganda (NMU TRW 1959.04). (A) Cephalothorax, frontal view; (B) carapace, dorsal view; (C) cheliped, left (minor) frontal view; (D) cheliped, right (major) frontal view; (E) carpus and merus of right cheliped, dorsal view; (F) carpus and merus of right cheliped, inferior view; (G) abdomen. Scale bar represents 12.4 mm.

12 females (cw 38.8–14.8), 12 juvs, Manafwa River, Malawa sector, Mt Elgon, 1402 m asl, coll. T. R. Williams, 1 January 1961 (NHM 2008.3229–3238); four males (cw 34.1–13.8), nine males (cw 29.7–12.2), seven juvs, stn El.104, Namaugutu River, Namatala sector, Mt Elgon, 1555 m asl, coll. T. R. Williams, 8 January 1961 (NHM 2008.3312–3312); nine males (cw 45.0–38.00), eight females (cw 29.4–14.1), 10 juvs, stn El.65, Sago-Sago River, Malawa sector, Mt Elgon, 1402 m asl, coll. T. R. Williams, 1 January 1961 (NHM 2008.3412–3421); one male (cw 29.9), three females (cw 34.4–23.8), stn El.90 Tayaka River, Namatala sector, Mt Elgon, 1463 m asl, from soil among roots at stream edge, coll. T. R. Williams, 7 January 1961 (NHM 2008.3005–3008); two males (damaged), two females (cw 47.8, one damaged) stn El.97, Sisiwachi

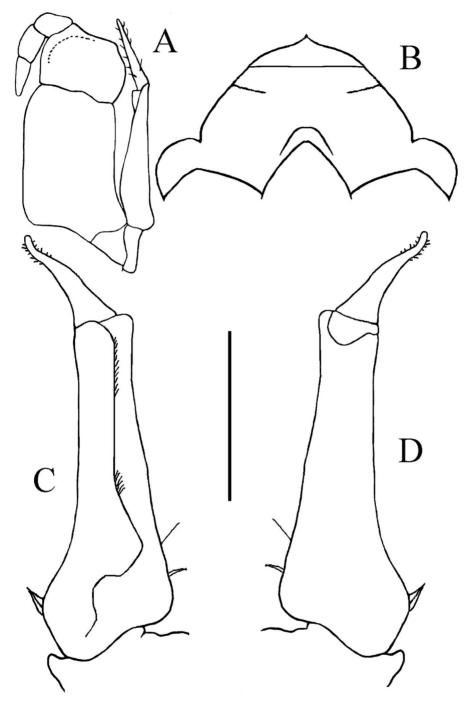


Figure 3. *Potamonautes elgonensis* sp. nov. Adult male, paratype, cw 49.5 mm, from Mount Elgon, Uganda (NMU TRW 1959.04). (A) Left third maxilliped; (B) anterior sternum; (C) left first gonopod ventral view; (D) left first gonopod dorsal view. Scale bar represents 12.4 mm (A,B) or 4.5 mm (C,D).

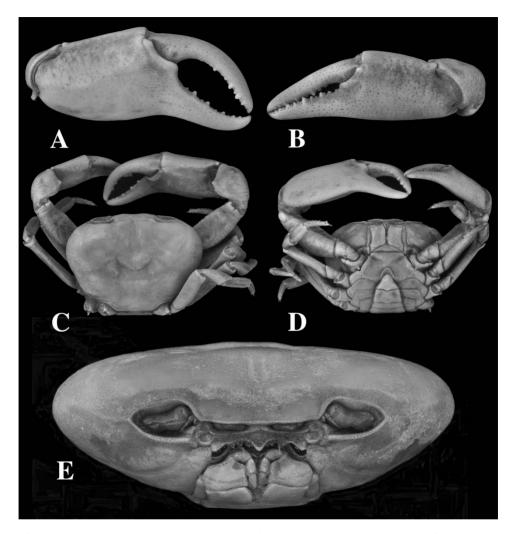


Figure 4. *Potamonautes elgonensis* sp. nov. Adult male, paratype, cw 49.5 mm, from Mount Elgon, Uganda (NMU TRW 1959.04). Cheliped: (A) right (major) frontal view; (B) left (minor) frontal view; whole animal: (C) dorsal view; (D) ventral view; (E) carapace, frontal view. Photograph Phil Crabb, NHM Photographic Unit.

River, Namatala sector, Mt Elgon, 1585 m asl, coll. T. R. Williams, 8 January 1961 (NHM 2008. 3001–3004); stn El.101, Namatala River, Namatala sector, Mt Elgon, 1463 m asl, coll. T. R. Williams, 8 January 1961 (NMU TRW 8.I.1961); several males (cw 30.6–14.2), eight females (cw 37.0–16.4), 24 juvs, stn El.102, Namatala River, Namatala sector, Mt Elgon, 1463 m asl, coll. T. R. Williams, 8 January 1961 (NHM 2008.3422–3431); 10 males (cw 37.0–15.9), nine females (cw 37.2–14.7), nine juvs, stn El.145, north Sirokomu River, Kiriki sector, Mt Elgon, 2134 m asl, coll. T. R. Williams, 14 January 1961 (NHM 2008.3432–3441); three males (cw 27–10.40, six females (cw 20.9–11.2), seven juvs, stn El.171, Atar River, Nyenye sector, Mt Elgon, 1829 m asl,

coll. T. R. Williams, 16 January 61 (NHM 2008.3239-3248); five males (cw 35.4-12.5), one female (cw 29.2), six juvs, stn El.172, Kyeseberi River, Nyenye sector, Mt Elgon, 1829 m asl, coll. T. R. Williams, 16 January 1961 (NHM 2008, 3249-3258); one subadult male (cw 20.5), two subadults/juvs (cw 16.0, 16.5), stn El. 29, Namikoma River, Malawa sector, Mt Elgon, 1372 m asl, with *P. niloticus*, coll. T. R. Williams 28 December 1960 (NMU El. 29); juv. males (cw 21.5), stn El.179, Sipi stream, Nyenye sector, Mt Elgon, 1463 m asl, bearing Simulium neavei, coll. T. R. Williams, 17 January 1961 (NMU El.179); two juvs (cw 24.5, 26.0) Sipi Falls, Sipi River, Nyenye sector, Mt Elgon, coll. T. R. Williams (NMU TRW 1961.02); one subadult male (cw 28.5) one subadult female (cw 27.5) coll. Dr. Buttner, 20 July 1969 (NMU 20 July 1969); two adult ovig. females (cw 44.5, 43.0), one subadult female (cw 34.5), seven juy. males (cw 37.5–20.5) western slopes Mt Elgon, rivers and streams above 1524 m asl, coll. M. A. Prentice (0°11′0″ N, 30°14′0″ E, DD 0.18, 30.23) (NMU TRW 1960.08); adult male (cw 49.5) western slopes of Mt Elgon, small rivers and streams above 1372 m asl, coll. G. R. Barnley, 1957 (3°0′0″ N, 34°0′0″ E, DD 3, 34) (NMU TRW 1959.04); eight males (cw 46.8–32.5), eight females (cw 50.2–37.3), River Sume, western slopes of Mt Elgon, 1524 m asl, coll. M. A. Prentice, 12 September 1960, pres T. R. Williams (NHM 2008.3260-3269); adult male, (cw 44.8), three subadult males (cw 36.7, 35.3, 27.9) stream, western side Mt Elgon, coll. P. Hainsworth and P.S. Corbet, February 1956 (NHM 2010.34–37).

#### Diagnosis

Based on holotype. Postfrontal crest complete, distinct; epigastric, postorbital crests joining with each other; postorbital crests extending laterally to meet anterolateral margins; exorbital, epibranchial teeth both missing; anterolateral margin immediately behind epibranchial tooth completely smooth; ischium of third maxilliped either smooth or with faint vertical suture; thoracic sternal suture s3/s4 reduced to two faint short side notches; dactylus of major cheliped slightly arched enclosing long narrow interspace when closed; first, second carpal teeth on carpus of cheliped weak, low, blunt; ventral margins of merus of pereiopod 1 both weakly granulated; distal meral tooth either low or missing; terminal article of GO1 curved outward, broadened medially; dorsal membrane broad. Large species, adult size range beginning cw 45 mm, largest specimen cw 50 mm.

#### Description

Carapace ovoid, wide (cw/fw 3.15), medium high (ch/fw 1.2); surface completely smooth semi-circular, urogastric, transverse branchial grooves present. Front straight, relatively narrow, about one-third carapace width (fw/cw 0.32), anterior margin sharply deflexed. Postfrontal crest distinct. Anterolateral margin between exorbital, epibranchial teeth smooth, lacking intermediate tooth; exorbital, epibranchial teeth reduced to small granules, anterolateral margin completely smooth, continuous with posterolateral margin. Suborbital margin raised, completely smooth. Suborbital, subhepatic, pterygostomial carapace regions all completely smooth; sidewall divided into three parts by longitudinal (epimeral) suture (dividing suborbital, subhepatic regions from pterygostomial region), and by vertical (pleural) groove (dividing suborbital from subhepatic regions), dorsal end of vertical groove meeting epibranchial tooth. First thoracic sternal suture s1/s2 deep; second suture s2/s3

deep, running horizontally across sternum; third suture s3/s4 missing except for two faint notches on sides; episternal sulci s4/e4, s7/e7 absent, s5/e5, s6/e6, complete. Third maxillipeds filling entire oral field, except for transversely oval respiratory openings at superior lateral corners; long flagellum on exopod of third maxilliped, ischium of third maxilliped either smooth or with very faint vertical suture. Epistomial tooth prominent, smooth, triangular. Mandibular palp two-segmented; terminal segment single, undivided, with setae (but no hard flap) at junction between segments. Dactylus of adult male major cheliped thickened, slightly arched, enclosing long narrow interspace when closed. First carpal tooth of cheliped weak, low, blunt; second carpal tooth smaller, also weak, low, blunt, followed by several small granules; ventral margins of merus of pereiopod 1 both weakly granulated; distal meral tooth either low or missing; superior surface of merus smooth. Pereiopods p2-p5 slender, p3 longest, p5 shortest, dactyli of p2-p5 tapering to point, each bearing four rows of downward-pointing short, sharp spines. Adult male abdomen triangular, somites a1–a6 of male abdomen four-sided, telson (a7) a triangle with rounded apex; somites a5–a6 broadest. Terminal article of GO1 curving outward, widened medially in the middle; broad dorsal membrane; margins of subterminal segment of GO1 setose.

#### Distribution

Potamonautes elgonensis is known only from the western and northern slopes of Mt Elgon in Uganda at medium altitudes between 1402 and 2134 m asl in five river drainage sectors: Malawa, Manafwa and Namatala (west), and Kiriki and Nyenye (north) (Williams 1991).

#### Comparisons

Williams (1991) considered the first gonopod characters of P. elgonensis and P. loveni to be identical, and treated these taxa as a single species (P. loveni), interpreting differences in the degree of expression of the postfrontal crest, and in species size and colour to be the result of intraspecific character variability. The present study indicates that the material used in the redescription of P. loveni by Williams (1991) actually comprised specimens that belonged to two different species; P. loveni (Colosi, 1924) (re-described by Cumberlidge and Clark 2009), and *P. elgonensis* sp. nov. For example, the first gonopod characters of adult male specimens of P. loveni and P. elgonensis, although similar, are not identical, i.e. the terminal article of P. loveni is almost straight and slim, whereas that of P. elgonensis is curved distinctly outward and widened medially in the middle. In addition, P. loveni is a smaller species, with an adult size range between cw 35 mm and cw 49 mm (while the adult size range of P. elgonensis is between cw 45 mm and cw 50 mm); the postfrontal crest is faint or missing in P. loveni (it is distinct in P. elgonensis), and the carapace of P. loveni is a darker colour than that of P. elgonensis (which is pale). Finally, the dactylus of the major cheliped of adult male of P. loveni is highly arched, encloses an oval interspace when closed, and lacks dentition (whereas the dactylus of adult males of P. elgonensis is widened but only slightly arched, encloses a long rectangular interspace when closed, and has several large rounded teeth).

Specimens of *P. elgonensis* are known only from the western and northern (Ugandan) side of Mt Elgon (in the Malawa, Manafwa, Namatala, Kiriki and Nyenye drainage

sectors) where their distribution overlaps with that of *P. loveni*. In contrast, Mt Elgon represents the western limit of the range of *P. loveni*; this species is also found in the eastern and southern (Kenyan) sides of Mt Elgon (in the Suam and Nzoia drainage sectors) and from the Cherangani Hills to the Mau Range, including the Kakamega Forest and the Nandi Hills, as far east as Lake Naivasha in the Rift Valley (Cumberlidge and Clark 2009).

#### Remarks

The taxonomic confusion surrounding the identities of the freshwater crabs from western Kenya arises from a number of sources, including long-standing opinions on species synonymies, some that have proved to be in error (Bott 1955), the confusion of two different species (Williams 1991), and the lack of understanding of the morphological changes that accompany growth in these species (Reed and Cumberlidge 2006; Cumberlidge and Clark 2009).

#### Etymology

The species is named in recognition of its known distributional range that indicates that it is restricted to the western and northern slopes of Mt Elgon in Uganda.

Potamonautes williamsi sp. nov.

(Figures 5–7)

#### Material examined

Type material. Uganda. Holotype. Adult male holotype (cw 21.1), stn El.114b, Simu tributary, Siroko sector, Mt Elgon, 1341 m asl, coll. T. R. Williams, 9 January 1961 (NHM 2008.3331); Paratypes, eight males (cw 20–16.8), one adult female (cw 19.7), stn El.114b Simu tributary, Siroko sector, Mt Elgon, 1341 m asl, coll. T. R. Williams, 9 January 1961 (NHM 2008.3332-3339); many small specimens, stn El.114b, Simu tributary, Siroko sector, Mt Elgon, 1341 m asl, coll. T. R. Williams, 9 January 1961 (NHM 2008.3332-3339); stn El.54, stream, tributary of the Manafwa River, Manafwa sector, Mt Elgon, 1265 m asl, coll. T. R. Williams, 1 January 1961, (NMU TRW 1.i.1961): 14 males (cw 19.23–11.7), nine females (cw 20.6–12.17), four ovig. females (cw 20.7-19.6) stn El.90, Tayaka River, Namatala sector, Mt Elgon, 1463 m asl, from soil among roots at stream edge, coll. T. R. Williams, 7 January 1967 (NHM 2008.3056); 18 males (cw 34.71–12.36), three ovig. females (cw 20.1–18.3), four females (cw 15-13.4) stn El.96, Namafumbole, Namatala sector, Mt Elgon, 1585 m asl, coll. T. R. Williams, 8 January 1961 (NHM 2008.3058–3067); eight males (cw 20.3–13.5), one ovig. female (cw 16.6), one female (cw 17.2), seven juvs, stn El.97, Sisiwachi, Namatala sector, Mt Elgon, 1585 m, coll. T. R. Williams, 8 January 97 (NHM 2008.3088–3097); adult male stn El.109, Simu stream, tributary of the Siroko River, Siroko sector, Mt Elgon, 1829 m asl, coll. T. R. Williams, 1960 (NMU TRW 1960a); 41 males (cw 27.4–9.1), 17 females (cw 17.4–11.2), 35 juvs, stn El.114a, Simu tributary, Siroko sector, Mt Elgon, 1341 m asl, coll. T. R. Williams, 9 January 1961 (NHM 2008.3072–3081); two males (cw 29.0, 27.3), two females (cw 31.0, 16.3), stn El.114b, Simu tributary, Siroko sector, Mt Elgon, 1341 m asl, with P. loveni, coll. T. R. Williams, 9 January 1961 (NHM 2008.3327-3330); 29 males (cw 32.1-7.8),

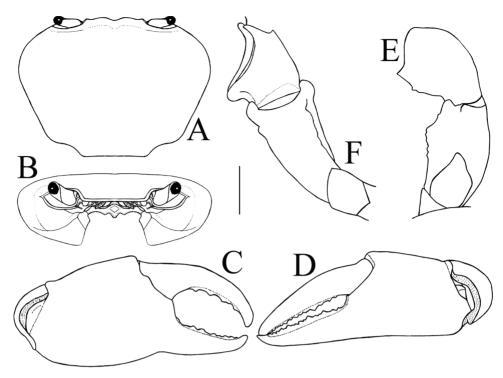


Figure 5. *Potamonautes williamsi* sp. nov. Adult male, paratype, cw 20 mm, from Mount Elgon, foot of Sipi Falls, Sipi River, Nyenye sector (NHM 2008.3332–3339). (A) Carapace, dorsal view; (B) cephalothorax, frontal view; cheliped, (C) right frontal view; (D) left frontal view; (E) carpus and merus of right cheliped, dorsal view; (F) carpus and merus of right cheliped, inferior view. Scale bar represents 5.7 mm (A,B) or 3.7 mm (C–F).

eight adult females, all ovig. (cw 19.7–16.4), 29 females (cw 18.7–10.8) 14 juvs, stn El.115, Simu tributary, Siroko sector, Mt Elgon, 1341 m asl, coll. T. R. Williams, 9 January 1961 (NHM 2008.3113-3122); one adult male (cw 17.4, cl 12.8, ch 7.2, fw 5.9) one male, stn El.173a, foot of Sipi Falls, Sipi River, Nyenye sector, Mt Elgon, 1737 m asl, coll. T. R. Williams, 17 January 1961 (NHM 2008.3053); four males (cw 18.6–14.2) stn El.173b, in stream and splash zone below Sipi Falls, Nyenye River, Mt Elgon, 1737 m asl, coll. T. R. Williams, 17 January 1961 (NHM 2008.3133–3136); one male (cw 17.4), oine female (cw 16.4) stn El.173c, foot of Sipi Falls, Sipi River, Nyenye sector, Mt Elgon, coll. T. R. Williams, 17 January 1961 (NHM 2008.3054– 3055); nine males (cw 17.8–9.3), 10 adult females, all ovig. (cw 20.5–17.0), 12 females (cw 16.8–9.8), 20 juvs, stn El.173, Nyenye River, Nyenye sector, Mt Elgon, 1737 m asl, with P. loveni, in stream and splash zone below Sipi Falls, coll. T. R. Williams, 17 January 1961 (NHM 2008.3123–3132); one adult, stn 173, male from stream in splash zone below Sipi Falls, Sipi River, Nyenye sector, Mt Elgon, 1738 m asl, with P. loveni, coll. T. R. Williams, 17 January 1961 (NMU TRW 17.i.1961); stn El.179, Sipi stream, Nyenye sector, Mt Elgon, 1463 m asl, coll. T. R. Williams, 1960 (NMU TRW 1960c); one adult male (cw 19.8), 1 subadult (cw 17.2), one adult female (cw 19.8), one ovig. female (cw 17.8), 2 juvs, stn El.180, Muyembe River, Siroko sector, Mt Elgon, 1067 m

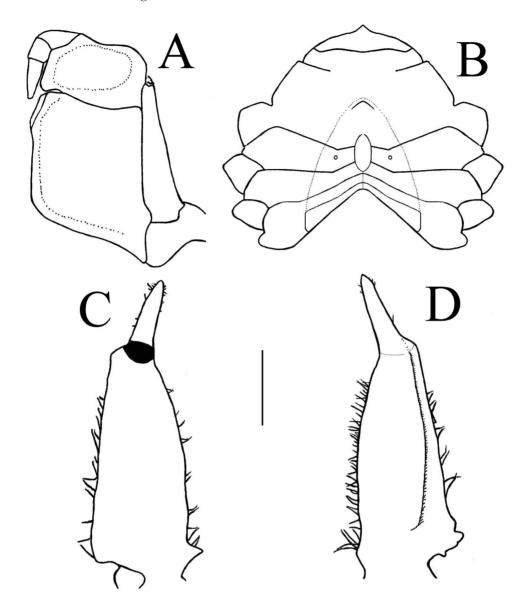


Figure 6. *Potamonautes williamsi* sp. nov. (A,B) Adult male, paratype, cw 20 mm, from Mount Elgon, foot of Sipi Falls, Sipi River, Nyenye sector (NHM 2008.3332–3339): (A) left third maxilliped; (B) sternum; (C,D) adult male Mount Elgon, stn El.109, Simu stream, tributary of the Siroko River, (NMU TRW 1960a): (C) GO1 ventral view; (D) GO1, dorsal view. Scale bar represents 4.5 mm (A,B) or 3 mm (C,D).

asl, coll. T. R. Williams, 18 January 1961 (NHM 2008.3082–3087); seven males (cw 19.6–11.9), one adult ovig. female (cw 23.3), seven females (cw 17.2–10.2), stn El.187 Sipi stream, Nyenye sector, Mt Elgon, 1737 m asl, coll. T. R. Williams, 17 January 1961 (NHM 2008.3098–3107); adult ovig. female (cw 27), stream 2, near Jackson Pool, Jinja, Mt Elgon, c. 3886 m asl, coll. M. C. Williams and A. Tjonneland, 15 January

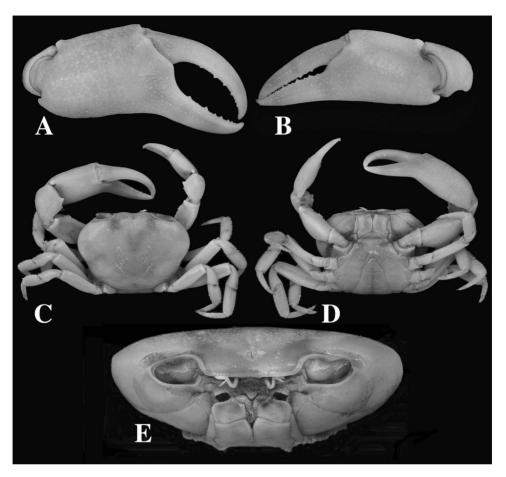


Figure 7. *Potamonautes williamsi* sp. nov. Adult male, paratype, cw 20 mm (NHM 2008.3332–3339). Cheliped: (A) right (major) frontal view; (B) left (minor) frontal view; whole animal: (C) dorsal view; (D) ventral view; (E) carapace, frontal view. Photographs Phil Crabb, NHM Photographic Unit.

1955, pres. Philip S. Corbet, EAFRO 5 May 1955, (NHM 2010. 63); one juv., Sasa River, Jinja, Mt Elgon, c. 3536 m asl, coll. P. S. Corbet, 29 July 1954, pres. P. S. Corbet, EAFRO, 5 May 1955, (NHM 2010. 64); two adult males (cw 23.2, 20.4), stream 1, near Jackson Pool, Mt Elgon, c. 3871 m asl, coll. Miles C. Williams and Ardfinn Tjonneland, January 1955, pres. P. S. Corbet, EAFRO, 5 May 1955 (NHM 2010.28–29); Sipi Falls, Sipi River, Nyenye sector, Mt Elgon, coll. H. Löffler, Zoological Institute, Vienna, 23 May 1961 (NMU TRW 1961.02); two males Butandiga, near Bulambuli, Mbale west of Mt Elgon (1°12′ N, 34°22′ E) (USNM 70905); Sipi stream, Nyenye sector, Mt Elgon, 2000 m asl, coll. A. Loveridge, 18 December 1933 (USNM 70907); Elgonyi, Mt Elgon, 2333 m asl, coll. A. Loveridge, 25 January 1934 (USNM 70911); one male (cw 38.7), Butandiga, near Bulambuli, Mbale west of Mt Elgon, coll. A. Loveridge, 8 January 1935 (USNM 70912); one male, Mt Elgon, Elgonyi (USNM 82295); two adult females (cw 17.5, 17), two adult males (cw 20.5, 19.5) Elgonyi,

Butandiga? Mt Elgon, coll. MCZ Expedition, 1933–34 (MCZ 8235); one adult female (cw 18), one adult male (cw 16.5), two subadult males (cw 15.5, 14.5) Elgonyi, Mt Elgon, coll. MCZ Expedition, 1933–34 (MCZ 8236); adult female (cw 17), one adult male (cw 18.5) Butandiga, near Bulambuli, Mbale west of Mt Elgon (MCZ 9026).

#### Diagnosis

Holotype. Postfrontal crest either faint or missing completely; exorbital, epibranchial teeth reduced to small granules, anterolateral margin behind epibranchial tooth not raised, completely smooth, continuous with posterolateral margin; carapace surface completely smooth; carapace medium high (ch/fw 1.2); suborbital margin raised, completely smooth; ischium of third maxilliped either smooth or with very faint vertical suture; thoracic sternal suture s3/s4 missing, except for two short side notches; thoracic episternal suture s4/e4 to s7/e7 faint or absent; dactylus of major cheliped thickened, medium arched, enclosing oval interspace; first carpal tooth on carpus of cheliped weak, low, blunt; second carpal tooth smaller, also weak, low, blunt, followed by several small granules; ventral margins of merus of pereiopod 1 both weakly granulated; distal meral tooth either low or missing; terminal article of GO1 straight-sided, slim, cone-shaped, angled at about 60° to longitudinal axis of gonopod, tapering evenly to pointed tip; terminal article of GO1 not widened in middle, medial, lateral lobes both low, even; dorsal membrane broad; margins of subterminal segment of GO1 setose; small species, adult size range beginning at cw 20 mm.

#### Description

Carapace ovoid, wide (cw/fw 3.15), medium high (ch/fw 1.2); surface completely smooth semi-circular, urogastric, transverse branchial grooves faint. Front straight, relatively narrow, about one-third carapace width (fw/cw 0.32), anterior margin sharply deflexed. Postfrontal crest either faint or missing completely. Anterolateral margin between exorbital, epibranchial teeth smooth, lacking intermediate tooth; exorbital, epibranchial teeth reduced to small granules, anterolateral margin completely smooth, continuous with posterolateral margin. Suborbital margin raised, completely smooth. Suborbital, subhepatic, pterygostomial regions of carapace sidewall all completely smooth; sidewall divided into three parts by longitudinal (epimeral) suture (dividing suborbital, subhepatic regions from pterygostomial region), and by vertical (pleural) groove (dividing suborbital from subhepatic regions), dorsal end of vertical groove meeting epibranchial tooth. First thoracic sternal suture s1/s2 obscure; second suture s2/s3 deep, running horizontally across sternum; third suture s3/s4 reduced to two short notches on sides; episternal sulci s4/e4 to s7/e7 faint/ absent. Third maxillipeds filling entire oral field, except for transversely oval respiratory openings at superior lateral corners; long flagellum on exopod of third maxilliped, ischium of third maxilliped either smooth or with very faint vertical suture. Epistomial tooth prominent, smooth, triangular. Mandibular palp two-segmented; terminal segment single, undivided, with setae (but no hard flap) at junction between segments. Dactylus of adult male major cheliped thickened, medium arched, enclosing oval interspace. First carpal tooth of cheliped weak, low, blunt; second carpal tooth smaller, also weak, low, blunt, followed by several granules; ventral margins of merus of pereiopod 1 both weakly granulated; distal meral tooth either low or missing; superior surface of merus smooth. Pereiopods p2–p5 slender, p3 longest, p5 shortest, dactyli of p2–p5 tapering to point, each bearing four rows of downward-pointing short, sharp spines. Adult male abdomen triangular, somites a1–a6 of male abdomen four-sided, telson (a7) a broad triangle with rounded apex; somites a5–a6 broadest. Terminal article of GO1 straight-sided, slim, cone-shaped, angled at about 60° to longitudinal axis of gonopod, tapering evenly to pointed tip; terminal article of GO1 not widened in middle, medial, lateral lobes both low, even; dorsal membrane broad; margins of subterminal segment of GO1 setose. This is a relatively small species, adult size range beginning at cw 17 mm.

#### Distribution

This species is known only from the western slopes of Mt Elgon in Uganda (01°8′ N, 34°33′ E) at medium altitudes between 1128 and 2333 m asl.

#### Comparisons

Adult egg-bearing females of P. williamsi measure between cw 17 and 21 mm, which makes this a considerably smaller species than P. niloticus and P. loveni (where specimens with cws of 20 mm would be juveniles). Potamonautes williamsi is closest to P. loveni, a medium-sized species of freshwater crab from Mt Elgon that has an adult size range from cw 35 to 49 mm (Cumberlidge and Clark 2009). Potamonautes williamsi and P. loveni are similar in that both species have a completely smooth carapace lacking a postfrontal crest, their exorbital and epibranchial teeth are reduced to small granules, the anterolateral margins of the carapace are completely smooth, lacking teeth of any kind, the thoracic sternal groove s3/s4 is reduced to two side notches, and a similar first carpal tooth on the carpus of the cheliped which is small, low and rounded (Cumberlidge and Clark 2009). However, there are a number of characters that distinguish them, for example, the terminal article of GO1 of adult male of P. williamsi is straight-sided, slim, and cone-shaped, and tapers evenly to a pointed tip (without widening in the middle), whereas that of *P. loveni* is slightly sinuous and is widened in the middle by an enlarged medial lobe; the subterminal segment of GO1 of P. williamsi has setose margins, whereas these margins are smooth in P. loveni; the dactylus of the cheliped of P. williamsi is thickened, has large teeth, and forms a medium arch that encloses an oval interspace, whereas the dactylus of the cheliped of *P. loveni* is slim, lacks teeth, and forms a high arch that encloses a round interspace.

The adult male holotype of *P. williamsi* was compared here with an adult male specimen of *P. niloticus* from Kenya. The two taxa can be distinguished as follows. The anterolateral margin of *P. niloticus* behind the epibranchial tooth is clearly toothed (whereas this margin is completely smooth in *P. williamsi*); the first and second carpal teeth on the carpus of the cheliped of *P. niloticus* are each produced into sharp spines (whereas these teeth are small and low in *P. williamsi*); the ventral margins of the merus of pereiopod 1 of *P. niloticus* are both heavily granulated (whereas these margins are smooth in *P. williamsi*); the distal meral tooth of *P. niloticus* is a small sharp spine (whereas this tooth is reduced to a small granule in *P. williamsi*); and *P. niloticus* (whose adult size range is from cw 46 to 65 mm) is a much larger species than *P. williamsi*.

#### Etymology

The species is named for Trefor R. Williams (retired, formerly of the University of Liverpool, UK), in recognition of his significant contributions to freshwater crab biology and to advances in the study of onchocerciasis in East Africa.

#### Habitat and ecology

The following notes are based on those provided by Hynes et al. (1961) and Williams et al. (1961). Potamonautes williamsi is found in the forest zone of Mt Elgon at midaltitudes from 1100 to 1800 m. Female crabs with either eggs or hatchlings attached to their abdomen are common in January, indicating that the breeding season of P. williamsi is between November and February (Cumberlidge 1999). Potamonautes williamsi spends little time in the water, and in the forest was frequently seen on the banks of rivers, streams and (most commonly) small trickles. This species typically burrows into the loose soil of the banks of small forest-streams and is found among the roots of tree ferns in places where the stream banks are sufficiently damp and soft, and it often digs burrows some distance from streams. Several very dense populations of P. williamsi were found in areas of loose earth and stones in the damp soil of the splash zone of waterfalls. The Sipi Falls is the type locality and consists of a series of three waterfalls in the foothills of Mt Elgon located close to, but not inside, the boundary of the Ugandan Mt Elgon National Park, about 55 km north of Mbale, and not far from the town of Kapchorwe. It would appear that P. williamsi requires the extremely humid conditions that are typical of the wet forested areas at medium altitudes on Mt Elgon, because it was not found on the drier northern slopes, or at lower altitudes (i.e. below 1100 m) in the cleared farmlands below the forest.

#### Ecological notes

Mount Elgon is an ancient eroded volcano (4321 m asl with an area of 169 km²) situated on the Kenya–Uganda border, about 140 km north-east of Lake Victoria. The Ugandan sector of Mt Elgon is an important watershed for the Kiriki, Nyenye, Siroko, Namatala, Manafua and Malawa Rivers (which flow south into Lake Victoria). The Kenyan sector is drained by the Nzoia River (which flows south into Lake Victoria) and the Suam River (which flows north into Lake Turkana) (Williams 1991). At lower altitudes, Mt Elgon's slopes support montane forest (some of which has been cleared for agriculture) that gives way at higher altitudes to open moorland with giant lobelia and groundsel plants.

The four species of freshwater crabs found on Mt Elgon (*P. niloticus*, *P. loveni*, *P. elgonensis* and *P. williamsi*) have different altitudinal preferences that overlap. *Potamonautes niloticus* is found in the warm waters at lower altitudes up to 1400 m, *P. williamsi* is found at mid-altitudes between 1100 and 1800 m, *P. elgonensis* is found at mid-altitudes between 1402 and 2134 m, and *P. loveni* is found in cooler waters between 1000 and 3000 m. *Potamonautes loveni* also occurs in the upper reaches of rivers on the highlands of western Kenya and eastern Uganda (Cumberlidge and Clark 2009). At medium altitudes, all four species are found together on the slopes of Mt Elgon. Within the range of altitudes between 1280–1950 m asl, where the water is cooler than the lowland streams but warmer than at higher altitudes, *P. loveni* coexists with *P. niloticus. Potamonautes loveni* reaches its lowest altitudes on Mt Elgon in the

Namatala River drainage sector where the forest remains largely intact, below which it is replaced by *P. niloticus*, which prefers warmer waters (Williams 1991).

Potamonautes niloticus is completely dependent on rivers and (unlike P. williamsi and P. loveni) it rarely, if ever leaves the water. The ranges of P. niloticus, P. williamsi and P. loveni overlap in several rivers at medium altitudes between 1158 and 1402 m, presumably because these heights represent the upper limits of the warmer waters favoured by P. niloticus. Potamonautes niloticus is a widespread species associated with the Nile River basin (Bott 1955; Cumberlidge 1997, 1998, 2009a; Cumberlidge et al. 2008) and occurs in a range of aquatic habitats including the major lowland rivers and lakes, small clear fast-flowing mountain streams with rocky beds, and sluggish lowland streams with muddy bottoms.

#### Crabs and human river blindness

Potamonautes niloticus, P. elgonensis and P. loveni are associated with onchocerciasis on Mt Elgon, while P. loveni is linked with this disease elsewhere in the highland areas of western Kenya (Williams 1968, 1991; Cumberlidge and Clark 2009). In eastern Kenya, in the region of Mount Kenya, P. alluaudi (Bouvier, 1921) has also been linked with river blindness (Williams 1968; Cumberlidge 2009a). The larval stages of Simulium neavei, the blackfly vector of the parasite Onchocerca volvulus that causes human river blindness, attach to the carapace of freshwater crabs living in the cold well-oxygenated waters of fast-running highland streams (Williams 1991). Wherever P. niloticus occurs in fast-flowing streams with turbulent water it is often associated with S. neavei (Williams et al. 1961; Hynes et al. 1961). Simulium neavei was never found associated with P. williamsi and it is unlikely that this species is involved with the focus of onchocerciasis on Mt Elgon (Williams et al. 1961).

#### Conservation

None of the collection localities for any of the species found on Mt Elgon fall within any of the three protected areas on the mountain – the Ugandan and Kenyan Mt Elgon National Parks, and the Mt Elgon Forest Reserve in Kenya. It is encouraging to note that much of Mt Elgon's montane ecosystem now appears to be recovering from previous episodes of human disturbance. This contrasts with other parts of East Africa where the montane forests are experiencing rapid habitat destruction and degradation, and encroachment from growing human populations that now endangers much of the rich and scarcely known biota of this unique region.

#### Remarks

The present work adds two new species to *Potamonautes*, an important and widespread genus of African freshwater crabs that is found throughout Africa from Senegal to the Horn of Africa, and from Egypt to South Africa. The recent upsurge in interest in the Afrotropical freshwater crabs has seen the description of a number of new species of *Potamonautes* and this widespread genus now has close to 70 species (Coulter 1991; Stewart 1997a, 1997b; Stewart and Cook 1998; Daniels et al. 1998; Cumberlidge 1999; Cumberlidge et al. 1999; Daniels et al. 2000, 2002; Corace et al. 2001; Gouws et al. 2001; Cumberlidge et al. 2002; Cumberlidge and Vannini 2004; Reed and Cumberlidge 2004, 2006; Cumberlidge and Tavares 2006; Cumberlidge and

Dobson 2008; Cumberlidge 2008, 2009b; Cumberlidge and Clark 2009; Ng et al. 2008). It is likely that this genus will have even more species attributed to it as taxonomic discrimination improves and as biodiversity studies survey the continent in more detail.

#### Acknowledgements

Trefor R. Williams (retired, formerly of the University of Liverpool, UK) is thanked for donating to NHM and NMU the specimens described here, and for many thoughtful discussions with the first author. Miranda Lowe (NHM) is thanked for loaning specimens and Dr Rafael Lemaitre and Marilyn Schotte (USNM) are thanked for their support during work by the first author on the USNM collection. Furthermore, Ardis Johnson (MCZ) is thanked for their assistance and kind hospitality during visits by the first author to these museums. The Peter White Scholar Award (NMU) is acknowledged for its support for the first author, and we are grateful to Phil Crabb (NHM Photography Unit) for taking the photographs reproduced in figures 1, 4 and 7.

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## Journal of Natural History

Publication details, including instructions for authors and subscription information: http://www.informaworld.com/smpp/title~content=t713192031

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Online publication date: 06 July 2010

**To cite this Article** Cumberlidge, Neil and Clark, Paul F.(2010) 'Two new species of freshwater crabs from Mount Elgon, East Africa (Brachyura: Potamoidea: Potamonautidae) and a re-diagnosis of *Potamonautes niloticus* (H. Milne Edwards, 1837) with notes on their natural history and onchocerciasis', Journal of Natural History, 44: 29, 1807 — 1829

To link to this Article: DOI: 10.1080/00222931003678792

**URL:** http://dx.doi.org/10.1080/00222931003678792

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