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Unravelling the *Potamonautes lirrangensis* (Rathbun, 1904) species complex (Potamoidea: Potamonautidae), with the description of two new species

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Abstract. The taxonomic status of the widely distributed freshwater crab *Potamonautes lirrangensis* (Rathbun, 1904) sensu lato is revised because morphological and molecular evidence indicates that this taxon is a complex comprising more than one species. Four taxa are now recognized: *Potamonautes lirrangensis* (Rathbun, 1904) s. str. and *P. kisangani* sp. nov. from the Middle Congo River in Central Africa, *P. amosae* sp. nov. from the drainages of Lakes Kivu and Tanganyika, and *P. orbitospinus* (Cunnington, 1907) from Lake Malawi which had been previously synonymised with *P. lirrangensis* s. lat. Diagnoses, illustrations and distribution maps are provided for each of these taxa and they are compared to similar species from Central and Southern Africa.

Keywords. Freshwater crabs, Africa, *Potamonautes amosae* sp. nov., *P. kisangani* sp. nov., *P. orbitospinus* (Cunnington, 1907), revision, taxonomy.

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Introduction

This work focuses on the taxonomic status of the widely distributed species *Potamonautes lirrangensis* (Rathbun, 1904) s. lat., which has a reported range that includes the Middle Congo River (Rathbun 1904, 1921; Capart 1954), Lake Kivu (Chace 1942; Bott 1955; Reed & Cumberlidge 2006; Cumberlidge & Meyer 2011; Daniels *et al.* 2015), rivers near Lake Tanganyika, Tanzania (Marijnissen *et al.* 2006;

Reed & Cumberlidge 2006), Lake Tanganyika (Capart 1952; Coulter 1991; Marijnissen *et al.* 2006; Reed & Cumberlidge 2006), and Lake Malawi (Balss 1929; Chace 1942; Bott 1955; Marijnissen *et al.* 2006; Reed & Cumberlidge 2006; Cumberlidge & Meyer 2011; Kochey *et al.* 2017). The study was prompted by doubts regarding the continued inclusion of the large number of specimens currently attributed to *P. lirrangensis* s. lat. from widely separated parts of Africa on the basis of only a few morphological characters.

The original description of *Potamon* (*Potamon*) *lirrangensis* was based on a single dried adult female specimen (carapace width (CW) 43.7 mm), which is now in poor condition, collected in 1891 from Liranga in the Middle Congo River in the République du Congo (Fig. 1). Thirteen years later, Rathbun (1904: pl. VI fig. 8) described the species from this specimen and unfortunately, since 1904 there has been no new material collected from the type locality. Despite this, subsequent authors (Rathbun 1921; Balss 1929; Chace 1942; Bott 1955; Reed & Cumberlidge 2006; Cumberlidge & Meyer 2011) have assigned superficially similar specimens from elsewhere in Central Africa (Fig. 1) and the Rift Valley lakes (Figs 2–3) to *Potamonautes lirrangensis* s. lat. based on the limited set of characters available from the adult female type. Among these were specimens from Lake Malawi (Fig. 2) that had previously been described as *Potamon* (*Potamonautes*) *orbitospinus* Cunnington, 1907, a taxon that Balss (1929, 1936) and Chace (1942) accepted, but which Bott (1955) treated as a junior synonym of *Potamonautes lirrangensis* s. lat. This opinion was followed by subsequent authors (Coulter 1991; Reed & Cumberlidge 2006; Ng *et al.* 2008; Cumberlidge & Meyer 2011).

The taxonomic status of *P. lirrangensis* and *P. orbitospinus* is reviewed here from the results of recent morphological and molecular studies of freshwater crabs from the entire range of *P. lirrangensis* s. lat. including the D.R. Congo (Fig. 1), western Tanzania, and Lakes Tanganyika, Kivu (Fig. 3), and Malawi (Fig. 2; Marijnissen *et al*. 2006; Reed & Cumberlidge 2006; Cumberlidge & Meyer 2011; M. Genner, unpubl. data). These works indicate that *P. lirrangensis* s. lat. as presently configured is not monophyletic, and comprises a species complex.

In the present study the taxonomically important characters of 83 specimens currently attributed to *P. lirrangensis* s. lat. are compared from 15 localities representing the known range of this species together with available molecular evidence (Marijnissen *et al.* 2006; Daniels *et al*. 2015). The results collectively indicate that *P. lirrangensis* s. lat. comprises at least 4 species: *P. lirrangensis* s. str., with a distribution restricted to the Middle Congo River in the République du Congo, *P. kisangani* sp. nov. from Kisangani in the D. R. Congo, *P. amosae* sp. nov. from the basins of Lakes Kivu and Tanganyika, and *P. orbitospinus* from Lake Malawi. These taxa are described and illustrated, updated distribution maps are provided, and their conservation status is discussed in the light of the new data provided here.

Material and methods

Morphological analyses

Eighty-three specimens were examined from the Middle Congo River (Liranga, Kisangani; Fig. 1), rivers near Lake Tanganyika, Tanzania, and Lakes Kivu, Tanganyika (Fig. 3), and Malawi (Fig. 2) (Table 1) that had been attributed to either *P. lirrangensis* s. lat. or to *P.* (*P.*) *orbitospinus*. Morphological analyses included a detailed examination of characters of the carapace, thoracic sternum, mouthparts, chelipeds, pereiopods, and gonopods. The habitats at the collection localities of the specimens attributed to *P. lirrangensis* s. lat. range from major rivers to deep African Rift Valley lakes. Measurements were made with digital callipers and are given in millimetres (mm). The habitus and gonopod photographs were taken with a digital camera and a Keyence VHX 5000 digital microscope (Keyence, Itasca, IL, USA), and post processing was undertaken using Adobe Photoshop CC 2015.0.1 Release. Measurements of the subterminal articles (SA) of gonopods 1 and 2 (G1, G2) were made along a straight line beginning

at the midpoint of the basal margin and ending at the midpoint of the distal margin (at the junction between the two parts). Measurements of the terminal articles (TA) of G1 and G2 were made on the ventral face along the midline beginning at the midpoint of the basal margin that forms the SA/TA junction and ending at the TA tip. The length of the TA of G1 and G2 relative to the length of the SA of each of these structures is presented as the ratio of the terminal article/subterminal article (TA/SA). Adult females were recognized by their conspicuously widened pleon whose lateral margins (A4–6) cover the episternites of the thoracic sternum; a telson which covers the anterior thoracic sternum (S1–4) and by the 4 pairs of broad feathery biramous pleopods on pleomeres 2–5. Adult female specimens may or may not be carrying eggs or hatchlings in the pleonal brood pouch. The beginning of the adult size range is indicated by females with a CW that is either equal to, or greater than, the CW of the smallest known adult female (Cumberlidge 1999; Marijnissen *et al.* 2006). This value for females was used here

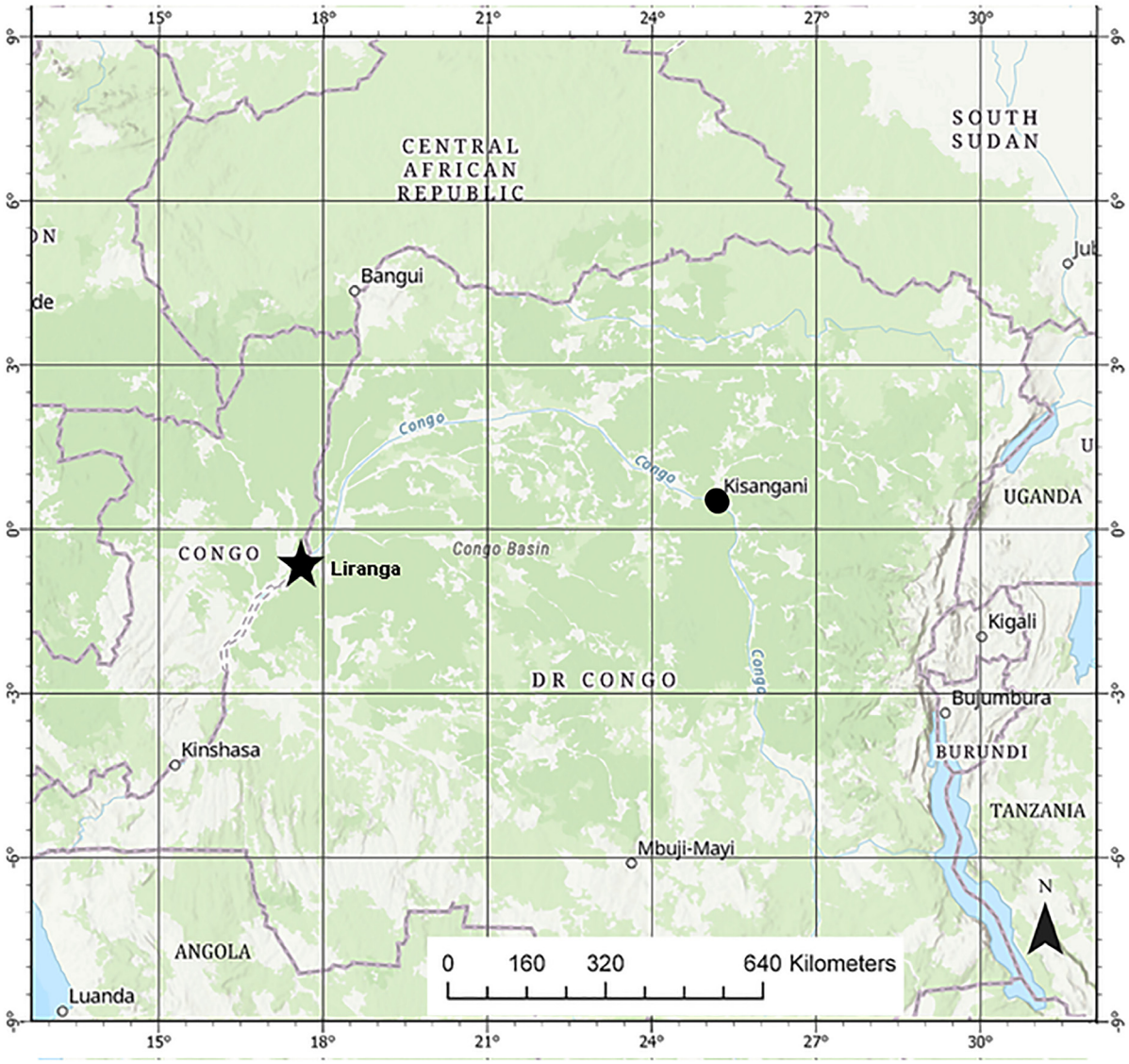

Fig. 1. Map showing the updated geographic distribution of *Potamonautes lirrangensis* (Rathbun, 1904) s. str. The black star on the left is Liranga, République du Congo (MNHN B-3826), the type locality. The black circles show the distribution of *Potamonautes kisangani* sp. nov. in the vicinity of Kisangani, D.R. Congo. See text for exact localities.

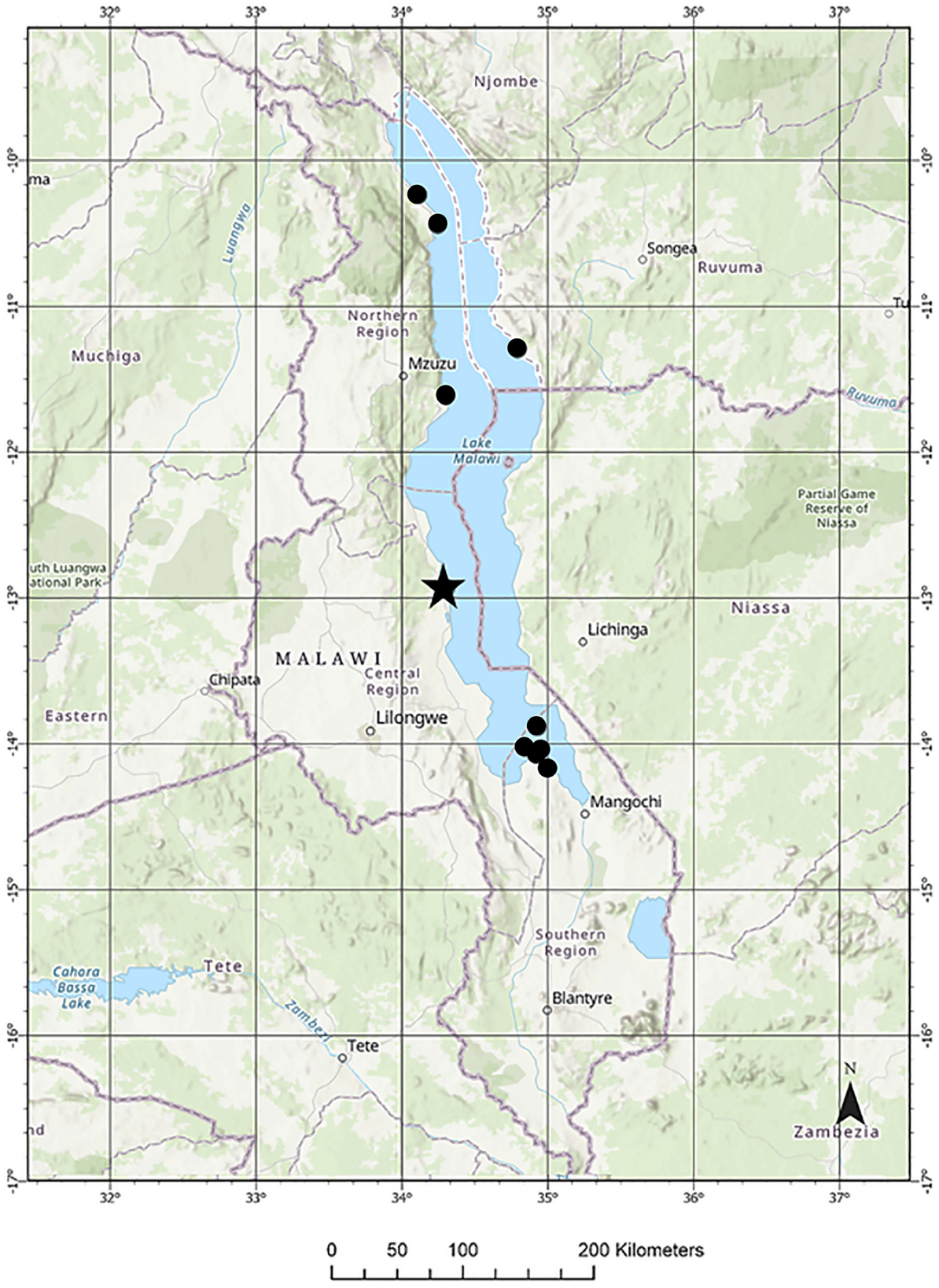

Fig. 2. Map showing the updated geographic distribution of *Potamonautes orbitospinus* (Cunnington, 1907). The black star shows the type locality. See text and Table 2 for exact localities.

to establish the beginning of the adult size range for male specimens. The terminology is adapted from Cumberlidge (1999) and the higher classification used follows that of Ng *et al.* (2008).

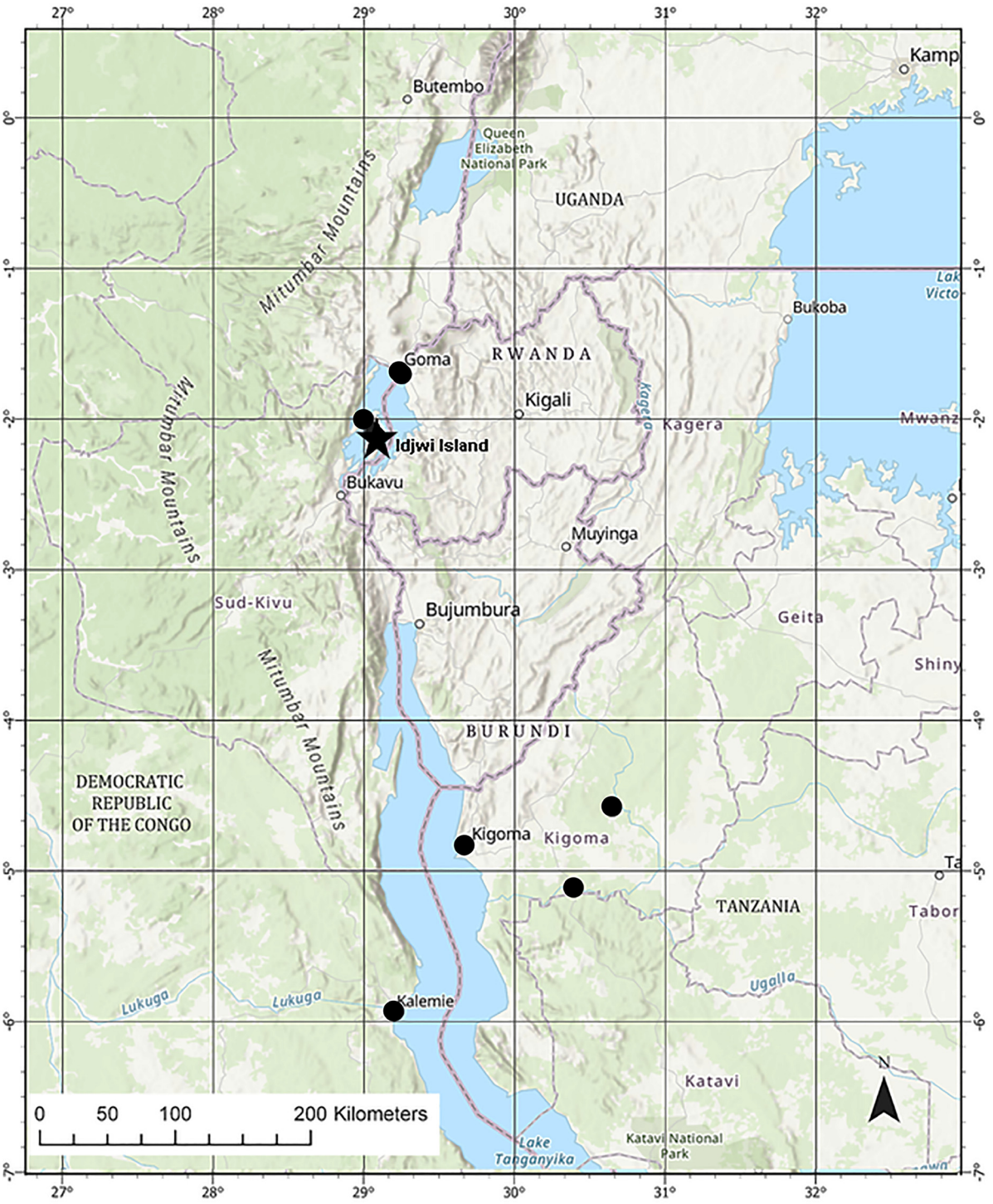

Fig. 3. Map showing the updated geographic distribution of *Potamonautes amosae* sp. nov. The black star shows the type locality. See text for exact localities.

Table 1. History of the description of the first gonopod (G1) of specimens of *Potamonautes lirrangensis* (Rathbun, 1904) s. lat. with the revised identifications in the present work.

Revised identification	Previous identification	Specimen	G1 Illustrated	Country	Locality
P. lirrangensis (Rathbun, 1904) s. str.	*P. lirrangensis* (Rathbun, 1904) s. lat.	Holotype	None	République du Congo	Liranga
P. kisangani sp. nov.	*P. lirrangensis* (Rathbun, 1904) s. lat.	Holotype	Rathbun (1921: fig. 8g); present work Fig. 11A	D.R. Congo	Kisangani
P. amosae sp. nov.	*P. lirrangensis* (Rathbun, 1904) s. lat.	Holotype NHMUK 2018.306	Present work Fig. 11B–H	Rwanda	Lake Kivu
P. amosae sp. nov.	*P. lirrangensis* (Rathbun, 1904) s. lat.	Non-type MCZ 11224	Chace (1942: fig. 1b)	D.R. Congo	Lake Kivu, Idjwi Island
P. amosae sp. nov.	*P. lirrangensis* (Rathbun, 1904) s.lat.	Non-type MCZ 32878	Bott (1955: figs 38–39)	Rwanda	Lake Kivu, Goma
P. amosae sp. nov.	*P. lirrangensis* (Rathbun, 1904) s.lat.	Non-type NMU TRW1972.04	Reed & Cumberlidge (2006: figs 153–154, pl. 5c)	Tanzania	Kigoma, Malagarasi River
P. orbitospinus (Cunnington, 1907)	*P. lirrangensis* (Rathbun, 1904) s. lat.	Non-type NMU TRW 1972.05	Cumberlidge & Meyer (2011: fig. 7a–b)	Malawi	Lake Malawi
P. orbitospinus (Cunnington, 1907)	*P. lirrangensis* (Rathbun, 1904) s. lat.	Lectotype NHMUK 1908.1.31.27	Present work Fig. 11A–D	Malawi	Nkhata Bay, Lake Malawi

Molecular and phylogenetic analyses

Tissue was harvested from either the gills or the ambulatory legs of ethanol preserved specimens. DNA was extracted using a DNeasy kit (Qiagen, Hilden, Germany), following the protocol of the manufacturer. One mitochrondrial (16S rRNA) and one nuclear (histone 3, H3) locus were sequenced, using the primers 16SA and 16SB (Palumbi *et al.* 1991), and H3AF and H3AR (Colgan *et al.* 1998), as reported in Daniels *et al.* (2015). PCR reactions were conducted in 25 µL volumes, including 12.5 µL of MyTaq mastermix (Bioline, London), 0.5 µL of each primer (10 mM), 11 µL molecular grade water, and 1 µL of template DNA (1:10 dilution of eluted DNA). PCR conditions were as follows: 1 minute at 95°C, then 35 cycles of 95°C for 30 s, 50°C for 30 s and 72°C for 1 minute, followed by 72°C for 5 minutes. Amplification success was checked on 1% agarose gel. Purification and sequencing of the PCR products was outsourced to either Macrogen (Seoul, Korea) or Eurofins Genomics (Wolverhampton, UK). Sequences were checked using Chromas ver. 2.6 (Technelysium Ltd, Brisbane), and novel sequences have been deposited in GenBank (Table 2).

Sequences were aligned using ClustalW (Thompson *et al*. 2003), and concatenated in SequenceMatrix (Vaidya *et al*. 2011). The phylogenetic analyses utilised both the 16S and H3 genes. Maximum Likelihood (ML) analyses were conducted in IQ-TREE ver. 2.12 (Minh *et al*. 2020), on the IQ-TREE webserver, using an automatic model selection including the 16S locus as one partition, and each codon position of the H3 genes as separate partitions (Chernomor *et al*. 2016). Branch support was estimated from 1000

Table 2. List of specimens analysed for the molecular phylogeny, with their localities and their Isolate and Genbank Accession numbers.

Source	Species	Latitude	Longitude	Location	Country	Date of Collection	Isolate Number	16S Accession	H3 Accession
This study	*Potamonautes amosae* sp. nov.	-5.113	30.391	Malagarasi River, Uvinza	Tanzania	30 Jul. 2016	2016-07-08-UV1	MW182542	MW188515
This study	*Potamonautes amosae* sp. nov.	-5.113	30.391	Malagarasi River, Uvinza	Tanzania	30 Jul. 2016	2016-07-08-UV2	MW182540	MW188516
This study	*Potamonautes amosae* sp. nov.	-5.113	30.391	Malagarasi River, Uvinza	Tanzania	30 Jul. 2016	2016-07-08-UV3	MW182541	MW188517
This study	*Potamonautes bellarussus*	-9.395	33.827	Mguwisi River, Kyela	Tanzania	16 Jul. 2011	2011-07-04-168	MW182544	MW188512
This study	*Potamonautes bellarussus*	-9.395	33.827	Mguwisi River, Kyela	Tanzania	16 Jul. 2011	2011-07-04-170	NA	MW188513
This study	*Potamonautes bellarussus*	-8.856	34.082	Ruaha River, Ruaha	Tanzania	1 Dec. 2011	2011-12-01-CR2	MW182543	MW188514
This study	*Potamonautes* cf. *unispinus*	-13.787	29.000	Mkushi	Zambia	15 Jun. 2010	2010-06-55-575	MW182548	MW188500
This study	*Potamonautes* cf. *unispinus*	-13.787	29.000	Mkushi	Zambia	15 Jun. 2010	2010-06-55-576	NA	MW188501
This study	*Potamonautes choloensis*	-16.016	35.495	Mulanje	Malawi	22 May 2009	2009-05-30-421A	MW182547	MW188497
This study	*Potamonautes choloensis*	-16.065	35.588	Mulanje	Malawi	18 May 2010	2010-05-11-059	MW182546	MW188498
This study	*Potamonautes choloensis*	-15.353	35.303	Zomba plateau	Malawi	5 Jun. 2010	2010-06-ZT-406	MW182545	MW188499
This study	*Potamonautes obesus*	-15.021	35.102	Near Liwonde	Malawi	19 Jan. 2011	2011-01-31-214	NA	MW188510
This study	*Potamonautes obesus*	-15.021	35.102	Near Liwonde	Malawi	19 Jan. 2011	2011-01-31-215	MW182549	MW188511
This study	*Potamonautes orbitospinus*	-14.023	34.843	Cape Maclear, Lake Malawi	Malawi	1 Jul. 2010	2010-06-CM-CM1	MW182550	MW188503
This study	*Potamonautes orbitospinus*	-14.023	34.843	Cape Maclear, Lake Malawi	Malawi	26 Jun. 2010	2010-06-CM-CM10	NA	MW188502
This study	*Potamonautes orbitospinus*	-14.023	34.843	Cape Maclear, Lake Malawi	Malawi	1 Jul. 2010	2010-06-CM-CM3	NA	MW188504
This study	*Potamonautes orbitospinus*	-14.023	34.843	Cape Maclear, Lake Malawi	Malawi	26 Jun. 2010	2010-06-CM-CM5	MW182551	MW188505
This study	*Potamonautes orbitospinus*	-14.023	34.843	Cape Maclear, Lake Malawi	Malawi	26 Jun. 2010	2010-06-CM-CM6	MW182552	NA
This study	*Potamonautes orbitospinus*	-14.023	34.843	Cape Maclear, Lake Malawi	Malawi	26 Jun. 2010	2010-06-CM-CM7	MW182553	MW188506
This study	*Potamonautes orbitospinus*	-14.023	34.843	Cape Maclear, Lake Malawi	Malawi	26 Jun. 2010	2010-06-CM-CM8	MW182554	MW188507
This study	*Potamonautes orbitospinus*	-14.023	34.843	Cape Maclear, Lake Malawi	Malawi	26 Jun. 2010	2010-06-CM-CM9	MW182555	MW188508
This study	*Potamonautes orbitospinus*	-13.533	34.867	Chiofu, Lake Malawi	Malawi	17 Jan. 2011	2011-01-25-5-175B	MW182556	MW188509
Marijnissen *et al.* 2006	*Potamonautes orbitospinus*	–	–	Thumbi West, Lake Malawi	Malawi	2006	–	DQ203235	–
Marijnissen *et al.* 2006	*Potamonautes amosae* sp. nov.	–	–	Ruzizi, Lake Kivu	DR Congo	2006	–	DQ203236	–
Daniels *et al.* 2006	*Potamonautes amosae* sp. nov.	–	–	Lake Kivu	DR Congo	23 Aug. 2002	ZMA Crust. De. 204681	AY803534	–
Mvogo Ndongo *et al.* 2017	*Sudanonautes floweri*	4.472	9.957	–	Cameroon	30 Aug. 2015	ZUR T262-3	KY069952	–
Daniels *et al.* 2006	*Sudanonautes floweri*	–	–	–	Gabon	Mar. 2004	NMU 03.2004.1	–	AY803696

ultrafast bootstrap replicates (Hoang *et al*. 2018). Only bootstrap proportions >70% were regarded as strongly supported. Bayesian inference (BI) analyses were conducted in BEAST ver. 2.6.3 (Bouckaert *et al*. 2019), using the same partitions and equivalent models as in the ML analyses, and a chain length of 50 million generations. Every 1000th tree was sampled, and the first 50% of trees were discarded as burn-in. Posterior probability branch support was calculated using Tree Annotator (part of the BEAST package), with values of >0.9 regarded as strongly supported. Trees were visualised using FigTree ver. 1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/), and the Bayesian maximum credibility tree is shown.

Range area calculations

The updated geographic distribution of *P. lirrangensis* s. str. and *P. kisangani* sp. nov. (Fig. 1), *P. amosae* sp. nov. (Fig. 3), and *P. orbitospinus* (Fig. 2) are provided, and the extent of occurrence (EOO) for each species was calculated using GeoCAT (Bachman *et al*. 2011) as the area contained within the minimum convex polygon around all sites of present occurrence. The area within the EOO that is actually occupied by the taxon (the area of occupancy; AOO) was estimated using GeoCAT as the sum of the area occupied within a 2 × 2 km grid overlaid around each locality.

Abbreviations of museums and institutions

A.M. Congo Exped.	=	American Museum Congo Expedition
AMG	=	Albany Museum, Grahamstown, South Africa.
AMNH	=	American Museum of Natural History, New York, USA
Exped.	=	Expedition
NBL	=	Naturalis Biodiversity Center, Leiden, the Netherlands (formerly Rijksmuseum van Natuurlijke Historie)
NHMUK	=	The Natural History Museum, London, UK
MNHN	=	Museum national d'histoire naturelle, Paris, France
MCZ	=	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
NMU	=	Northern Michigan University, Marquette, Michigan, USA
UB	=	School of Biological Sciences, University of Bristol, Bristol, UK
USNM	=	United States National Museum of Natural History, Smithsonian Institution, Washington D.C., USA

Abbreviations

A	=	pleomere (abdominal somite)
A5/6	=	sutures between pleomeres
CH	=	carapace height measured at maximum height of cephalothorax
CL	=	carapace length measured along median line from anterior to posterior margin
CW	=	carapace width measured at widest point
D.R. Congo	=	Democratic Republic of the Congo
E	=	thoracic episternite
FW	=	front width measured along anterior frontal margin between orbits
G1	=	first male gonopod
G2	=	second male gonopod
IUCN	=	International Union for the Conservation of Nature
juv.	=	juvenile
ovig.	=	ovigerous
P2–5	=	pereiopods 2–5 (first to fourth ambulatory legs)
S	=	thoracic sternite
S3/4	=	sternal sulci between adjacent thoracic sternites

S4/E4 = episternal sulci between adjacent thoracic sternites and episternites
SA = subterminal article of G1 or G2
TA = terminal article of G1 or G2
TS = terminal article of mandibular palp

Results

Phylum Arthropoda Latreille, 1829
Subphylum Crustacea Brünnich, 1772
Order Decapoda Latreille, 1802
Infraorder Brachyura Latreille, 1802
Superfamily Potamoidea Ortmann, 1896
Family Potamonautidae Bott, 1970
Subfamily Potamonautinae Bott, 1970
Genus *Potamonautes* MacLeay, 1838

Potamonautes lirrangensis (Rathbun, 1904) sensu stricto
Figs 1, 4A, 7A, Table 1

Potamon (*Potamonautes*) *lirrangensis* Rathbun, 1904: pl. 14 fig. 8.

Potamon (*Potamonautes*) *lirrangensis* – Rathbun 1905: 169; 1921: 413–415, pls 25, 26 figs 3, 8. — Balss 1914: 404; 1929: 347–348 (partim, nec D.R. Congo: Kituri upper Lualaba, Katanga Province, Russisi River, Lake Kivu); 1936: 188–189 (partim, nec D.R. Congo: Banana, Lakes Kivu, Mweru).

Potamon lirrangensis – Chace 1942: 188–189. — Capart 1954: 836, fig. 28.

Potamonautes (*Lirrangopotamonautes*) *lirrangensis* – Bott 1955: 268–269 (partim, nec Lake Kivu, Kindu, Lokandu, Kinshasa, Buta, Lubo, Lulua, Luzizi, Ruzizi Rivers, Luvungu, Lake Tanganyika (Mpala, Uvira), Lake Malawi).

Potamonautes lirrangensis – Cumberlidge 1998: 201 (partim, nec Tanzania: Tukuyu formerly Neu-Langenburg). — Reed & Cumberlidge 2006: 23 (partim, nec figs 41–51, 153–154, 177 pl. V, Malawi: Lake Malawi, nec Tanzania: Kigoma District, rivers draining into Lake Tanganyika, Taveta, Mungonya River, Uvinza, Malagarasi River). — Ng *et al*. 2008: 171 (partim).

Diagnosis

Based on female type from Liranga. Exorbital tooth large, spine-like; lateral margin of exorbital tooth lined by small teeth, angled outward at 45° to midline of carapace, straight, neither bulging outward (convex) nor curving inward (concave); epibranchial tooth small, pointed, as large as other denticles lining anterolateral margin (Fig. 4A). Anterolateral margin posterior to epibranchial tooth curving strongly outward (Fig. 4A); postfrontal crest distinct, completely traversing carapace between epibranchial teeth; posterior surface of carapace with deep urogastric grooves; cheliped carpus inner margin with two large, subequal, forward-pointing spines (Fig. 7A); cheliped merus inner lower margin with spine-like tooth distally.

Material examined

Holotype (by original designation)
REPUBLIC OF THE CONGO • 1 ♀ adult (dried, CW 43.7, CL 38, FW 14.5 mm); Liranga, Middle Congo River, at the confluence of the Congo and Oubangi Rivers; 5 Sep. 1891; J. Dybowski leg.; MNHN B-3826.

Description

See Diagnosis.

Size

Medium-sized species, adult at CW 43 mm.

Colour

The preserved specimen from Liranga is uniformly light brown.

Distribution

The revised distributional range of *P. lirrangensis* s. str. (Fig. 1) now comprises just the Middle Congo River: Liranga (not 'Lirranga' as implied from the specific epithet) in the République du Congo. This species now excludes specimens formerly identified as *P. lirrangensis* s. lat. from Kisangani in the D.R. Congo (Fig. 1), rivers near Kigoma draining into Lake Tanganyika, in Tanzania, Lake Tanganyika in Zambia (Fig. 3), and Lake Malawi in Malawi (Fig. 2).

Ecology

The type locality of *P. lirrangensis* s. str. in the Middle Congo River (Liranga) lies in the Sudanic Congo-Oubangi Ecoregion (Freshwater Ecoregions Of the World (FEOW #535) (Thieme *et al*. 2005; Abell *et al*. 2008). This is more than 1000 km from Kisangani where *Potamonautes kisangani* sp. nov. is found in the Upper Congo Rapids Ecoregion (FEOW # 539), which indicates that the habitats of these 2 taxa are different, despite both being located in the Middle Congo River. Interestingly, these 2 taxa are separated by a third ecoregion, the Cuvette Centrale (FEOW #537).

Comparisons

Taxonomically important characters of the male cheliped, thoracic sternum, and gonopods, and the colour when alive, together with DNA data for *P. lirrangensis* s. str. will not be available until topotypal material is collected that includes an adult male. The carapace of the female type specimen from Liranga was illustrated by Capart (1954: fig. 28) and photographed by Rathbun (1904: pl. 14 fig. 8) and (together with the cheliped carpus) have been included in the present study (Figs 4A, 7A).

The lateral margin of the exorbital tooth of *P. lirrangensis* s. str. from Liranga (Fig. 4A) is similar to that of *P. kisangani* sp. nov. from Kisangani (Fig. 4B; Rathbun 1904: fig. 8a) and is angled outward at 45° to the midline of the carapace and is straight and neither bulges outward (convex) nor curves inward (concave). This contrasts with that of *P. amosae* sp. nov. from Lake Kivu (Fig. 4C) and the Malagarasi River (Reed & Cumberlidge 2006: pl. 5a), where the lateral margin of the exorbital tooth is not straight and bulges distinctly outward (convex) before meeting the postfrontal crest. This also contrasts with *P. orbitospinus* from Lake Malawi (Fig. 4E) where the lateral margin of the exorbital tooth curves inward (concave) and is neither straight nor convex.

The identifications of specimens as *P. lirrangensis* s. lat. by a number of authors (Rathbun 1921; Chace 1942; Bott, 1955; Reed & Cumberlidge 2006; Cumberlidge & Meyer 2011) are all now considered unreliable because they conflate characters from the 4 taxa that comprise the species complex under study here. Specifically, the descriptions of the male characters of *P. lirrangensis* s. lat. by the above authors combined characters from specimens from Kisangani, Lake Kivu, Tanzania, and Lake Malawi (Table 1).

Three taxonomic consequences of the treatment of *P. lirrangensis* s. lat. by Bott (1955) are addressed here. For example, that Bott (1) established the subgenus *Potamonautes* (*Lirrangopotamonautes*) Bott, 1955 with *Potamon* (*Potamonautes*) *lirrangensis* from Liranga, Middle Congo River as the type species; (2) included 3 taxa in this subgenus: *Potamonautes* (*Lirrangopotamonautes*) *lirrangensis*, *P.* (*L.*) *j. johnstoni* (Miers, 1885) and *P.* (*L.*) *johnstoni platycentron* Hilgendorf, 1897; and (3) treated *Potamon* (*Potamonautes*) *orbitospinus* as a junior synonym of *P.* (*L.*) *lirrangensis*. The subgenus *Potamonautes*

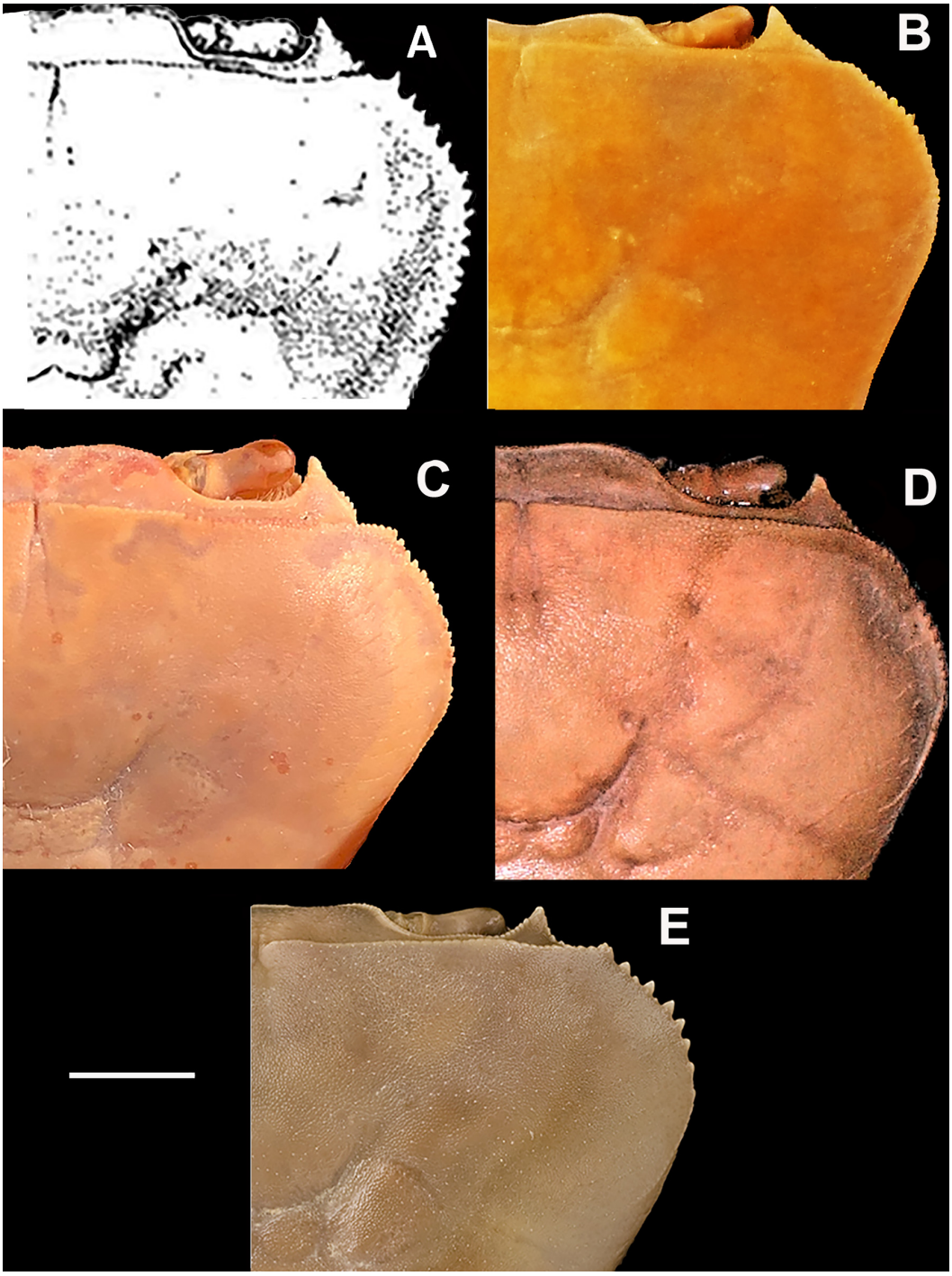

Fig. 4. Dorsal view of the right side of the carapace. **A**. *Potamonautes lirrangensis* s. str., holotype, adult, ♀, CW 53.6 mm, from Liranga, République du Congo (MNHN B-3826) (Capart 1954: fig. 28). **B**. *P. kisangani* sp. nov., holotype, adult, ♂, CW 60.5 mm, from Kisangani, Democratic Republic of the Congo (USNM 98944). **C**. *P. amosae* sp. nov., holotype, adult, ♂, CW 46.5 mm, from Lake Kivu, D.R. Congo (NHMUK 2018.306). **D**. *P. amosae* sp. nov., adult, ♂, CW 39.5 mm, from Kigoma District near Lake Tanganyika, Tanzania (NMU TRW 1971.05). **E**. *P. orbitospinus* (Cunnington, 1907), lectotype, adult, ♂, CW 56.9 mm, from Nkhata Bay, Lake Malawi, Malawi (NHMUK 1908.1.31.27). Scale bar: A = 8.7 mm; B = 7.9 mm; C = 6.8 mm; D = 5.7 mm; E = 7.9 mm. Photograph E by Phillip Crabb, NHMUK.

(*Lirrangopotamonautes*) Bott, 1955, however, has not been recognized by subsequent authors due to doubts about the monophyly of a group comprising these 3 taxa (Reed & Cumberlidge 2006; Ng *et al*. 2008). Currently, *P. johnstoni* (Reed & Cumberlidge 2006: 21–23, figs 31–40, 151–152, 176 pl. IV) and *P. platycentron* (Reed & Cumberlidge 2006: 30–31, figs 82–92, 161–162, 181 pl. IX) are each recognized as valid species, while the taxonomic status of *P. orbitospinus* is addressed in the present study.

Conservation status

The current IUCN extinction risk assessment of LC for *P. lirrangensis* s. lat. was based on the extremely wide range of that taxon (Cumberlidge 2018). The present work reduces the range of *P. lirrangensis* s. str. significantly (Fig. 1), from an estimated extent of occurrence (EOO) of almost 1.5 million km^2 based on 58 localities, to a single locality that precludes the calculation of the EOO. This change will no doubt impact the conservation assessment of this species when it is revised.

Potamonautes kisangani sp. nov.
urn:lsid:zoobank.org:act:77F6D732-392A-4B60-AA4A-AA2104D12C01
Figs 1, 4B, 5A, 6A–B, 7B, 8, 11A, Table 1

Potamon (*Potamonautes*) *lirrangensis* – Rathbun 1921: 413–415, pls 25–26, figs 3, 8.

Diagnosis

Exorbital tooth large, spine-like; lateral margin of exorbital tooth lined by small teeth, angled outward at 45° to midline of carapace, straight, neither bulging outward (convex) nor curving inward (concave); epibranchial tooth small, granular, followed by large granules lining anterolateral margin (Fig. 4B); anterolateral margin posterior to epibranchial tooth curving strongly outward (Fig. 4B); postfrontal crest distinct, completely traversing carapace between epibranchial teeth; posterior surface of carapace with deep urogastric grooves (Fig. 4B). Male thoracic sternal sulcus S3/4 deep, distinct, V-shaped. Ischium of third maxilliped with thin but distinct vertical sulcus. Major chela with 3 large molars at proximal end of both fingers (Fig. 6A–B); major chela dactylus (moveable finger) and fixed finger (pollex of propodus) both elongated, straight, slender (Fig. 6A–B); cheliped carpus inner margin with 2 large, subequal, forward-pointing spines (Fig. 7B); cheliped merus inner lower margin with spine-like tooth distally. P5 carpus, propodus, and dactylus all shortened (Fig. 8A–B). G1 TA conspicuously widened by high, rounded dorsal lobe (as wide as TA width at TA-SA junction); G1 TA distal third straight, ending in pointed tip (Fig. 11A). G1 SA at junction with G1 TA with horizontal margin on ventral side, U-shaped indentation filled by conspicuous dorsal membrane on dorsal side.

Etymology

The new species is named for Kisangani, D.R. Congo, the locality where it was first collected. The specific epithet is used as a Latin noun in apposition. The vernacular name is the Kisangani freshwater crab.

Material examined

Holotype

DEMOCRATIC REPUBLIC OF THE CONGO • ♂ adult (CW 60.5 mm); Kisangani, vicinity of Wagenia fishery; 25 Apr. 1955; Smithsonian-Bredin Congo Exped., W.L. Schmitt leg.; USNM 98944.

Paratypes

DEMOCRATIC REPUBLIC OF THE CONGO • 2 ♂♂ (CW 59.5, 39.4 mm), 10 ♀♀ (CW 62.7, 61.1, 59.2, 56.9, 56.8, 56, 51.6, 48.3, 44.5, 40.3 mm), 3 ♀♀ ovig. (CW 66.5, 62.8, 54.7 mm); same collection data as for holotype; USNM 98944.

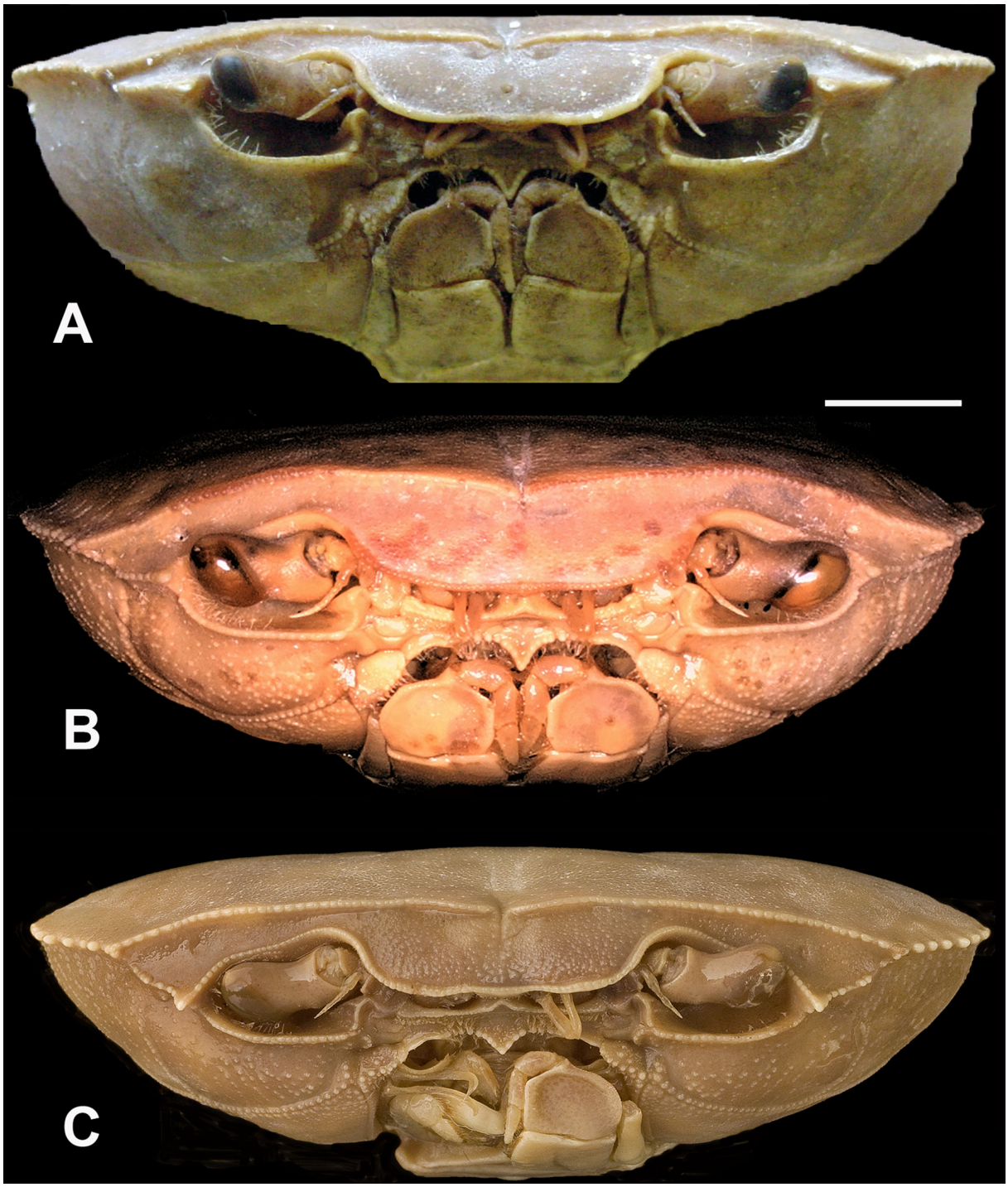

Fig. 5. Frontal view of carapace. **A**. *Potamonautes kisangani* sp. nov., holotype, adult, ♂, CW 60.5 mm, from Kisangani, Democratic Republic of the Congo (USNM 98944). **B**. *P. amosae* sp. nov., holotype, adult, ♂, CW 46.5 mm, from Lake Kivu, D.R. Congo (NHMUK 2018.306). **C**. *P. orbitospinus* (Cunnington, 1907), lectotype, adult, ♂, CW 56.9 mm, from Nkhata Bay, Lake Malawi, Malawi (NHMUK 1908.1.31.27). Scale bar: A = 8.5 mm; B = 6.3 mm; C = 7.8 mm. Photograph C by Phillip Crabb, NHMUK.

Other material

DEMOCRATIC REPUBLIC OF THE CONGO • 1 ♂, 1 ♀, 1 ♀ ovig.; Kisangani; Feb. 1915; A.M. Congo Exped., H. Lang leg.; USNM 54305 • 3 ♀♀ (CW 59.8, 54.9, 45.1 mm), 1 ♀ ovig. (CW 54.8 mm); same collection data as for preceding; Apr. 1915; USNM 54306 • 5 ♀♀ (CW 51.9, 49, 48.9, 45.6, 36.8 mm), 2 ♂♂ (CW 60.2, 29.2 mm); same collection data as for preceding; USNM 54307 • 1 ♂ (CW 59.1 mm); Kisangani, vicinity of Wagenia fishery; W.L. Schmitt Bredin Exped. leg.; USNM 98939 • 3 ♀♀ (CW 40.4, 40, 24.8 mm); rocky gorge of Tshope Falls, Kisangani; 19 Apr. 1955; Smithsonian-Bredin Congo Exped., W.L. Schmitt leg.; USNM 98940 • 1 ♀ (CW 53.6 mm), 3 juvs; Kisangani, vicinity of Wagenia fishery; Smithsonian-Bredin Congo Exped., W.L. Schmitt leg.; USNM 98941 • 2 ♀♀ ovig. (CW 56.5, 53.7 mm), 1 ♀ (CW 62.6 mm); Kisangani; 20 Apr. 1955; Smithsonian-Bredin Congo Exped., W.L. Schmitt leg.; USNM 98942 • 1 ♀ (with hatchlings, CW 60.1 mm); Kisangani; 20 Apr. 1955; Smithsonian-Bredin Congo Exped., W.L. Schmitt leg.; USNM 98943 • 1 ♂ (subadult CW 47.2 mm); Kisangani; 22 Jun. 1955; G. Browne leg.; NHMUK 1955.6.22.65 • 1 ♂, 1 ♀; Kisangani; Apr. 1915; A.M. Congo Exped., H. Lang leg.; MCZ CRU-10613.

Description

See Diagnosis.

Size

Large-sized species, adult at CW 53 mm, largest known specimen CW 66 mm.

Colour

The colour of living specimens from Kisangani D.R. Congo was provided by Rathbun (1921: 415). The dorsal carapace is either dark blue, dark green, or dark brown, the thoracic sternum is pink with blue/gray tones, and the pleon is yellow/white. The fixed and movable fingers of the chelae are dark brown/black in recently preserved specimens (Fig. 6A–B), while the arthrodial membranes of the chelipeds are vermillion (vivid red/orange).

Distribution

This species is only known from the vicinity of Kisangani in the D.R. Congo (Fig. 1).

Ecology

Kisangani lies in the Upper Congo Rapids Ecoregion (FEOW #539) (Thieme *et al*. 2005; Abell *et al*. 2008). The field notes of Herbert Lang on the habitat of *P. kisangani* sp. nov. from Kisangani provided by Rathbun (1921: 415) indicate that although this species is found in large rivers, it favours shallow waters near river banks where drifting logs jam. At the Boyoma Falls near Kisangani these crabs were common above and below the cataracts, while in the Tshopo River crabs were abundant among the rocks and boulder fields above the Tshopo Falls, but were absent below the falls where the water was shallow and had a sandy substrate.

Remarks

This new species was recognized to accommodate a large number of specimens from Kisangani, D.R. Congo that were collected by two U.S. Expeditions: the American Museum Congo Expedition (1909–1915) led by Herbert O. Lang and James P. Chapin, and the Smithsonian-Bredin Expedition to the Belgian Congo, Sudan, Uganda, and Egypt (1955) led by Waldo L. Schmitt. The first U.S. expedition initially deposited a large number of specimens (in 10 samples) in the AMNH and subsequently gifted some of these (USNM 54305, 54306, 54307 and MCZ CRU-10613) to these other museums. All of the specimens from the first U.S. Congo expedition were attributed by Rathbun (1921) to *P. lirrangensis* s. lat., and she provided a description, photographs, and illustrations of this species (Rathbun 1921:

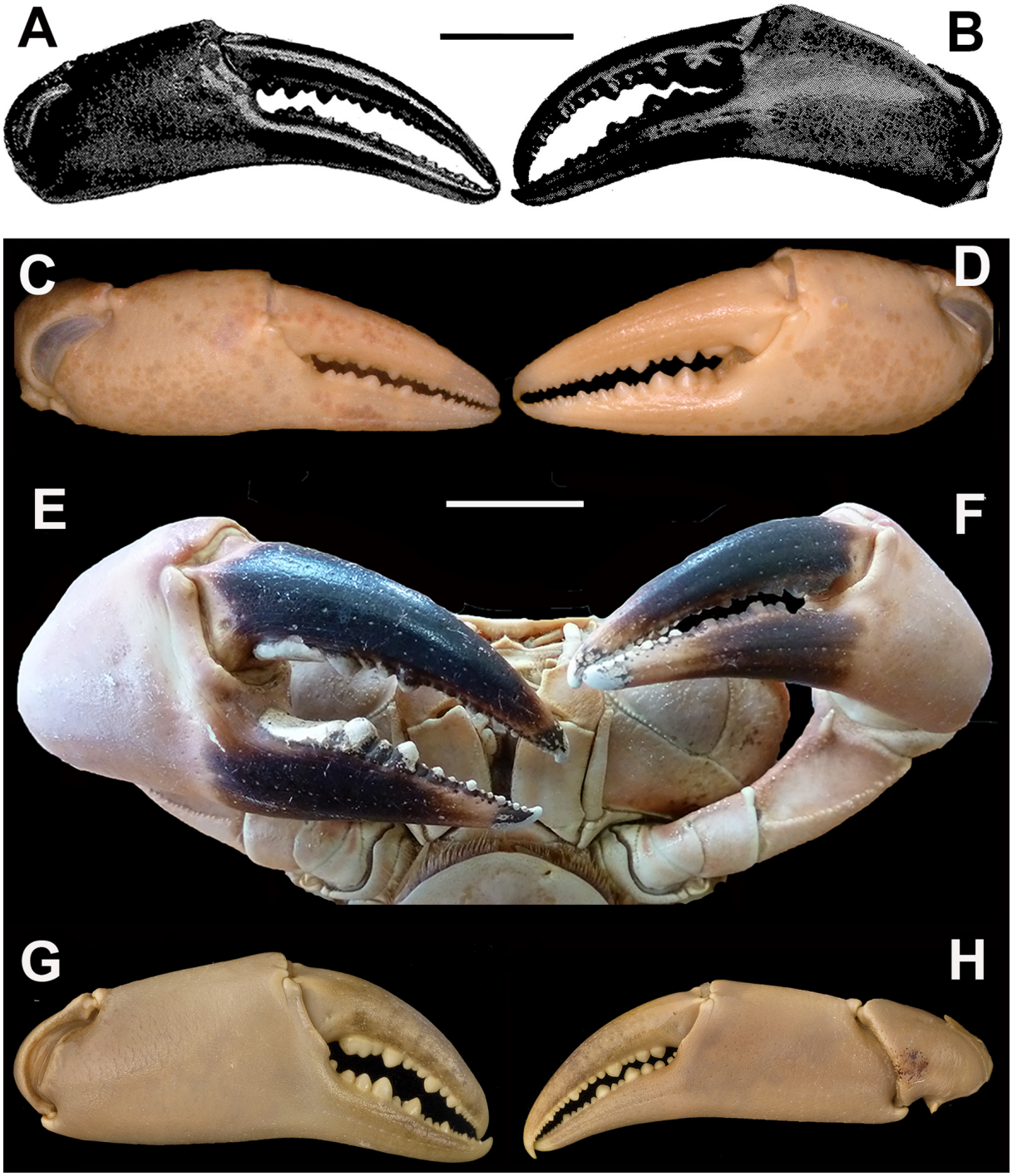

Fig. 6. Outer view of left and right chelae. **A–B**. *Potamonautes kisangani* sp. nov., holotype, adult, ♂, CW 60.5 mm, from Kisangani, Democratic Republic of the Congo (USNM 98944). **C–D**. *P. amosae* sp. nov., holotype, adult, ♂, CW 46.5 mm, from Lake Kivu, D.R. Congo (NHMUK 2018.306). **E–F**. *P. amosae* sp. nov., adult, ♀, CW 80.1 mm, from the Malagarasi River, Tanzania (NMU TRW 1971.05). **G–H**. *P. orbitospinus* (Cunnington, 1907), lectotype, adult, ♂, CW 56.9 mm, from Nkhata Bay, Lake Malawi, Malawi (NHMUK 1908.1.31.27). Scale bars: A–B = 10.9 mm; C–D = 8.9 mm; E–F = 11.0 mm; G–H = 8.9 mm. Photographs G–H by Phillip Crabb, NHMUK.

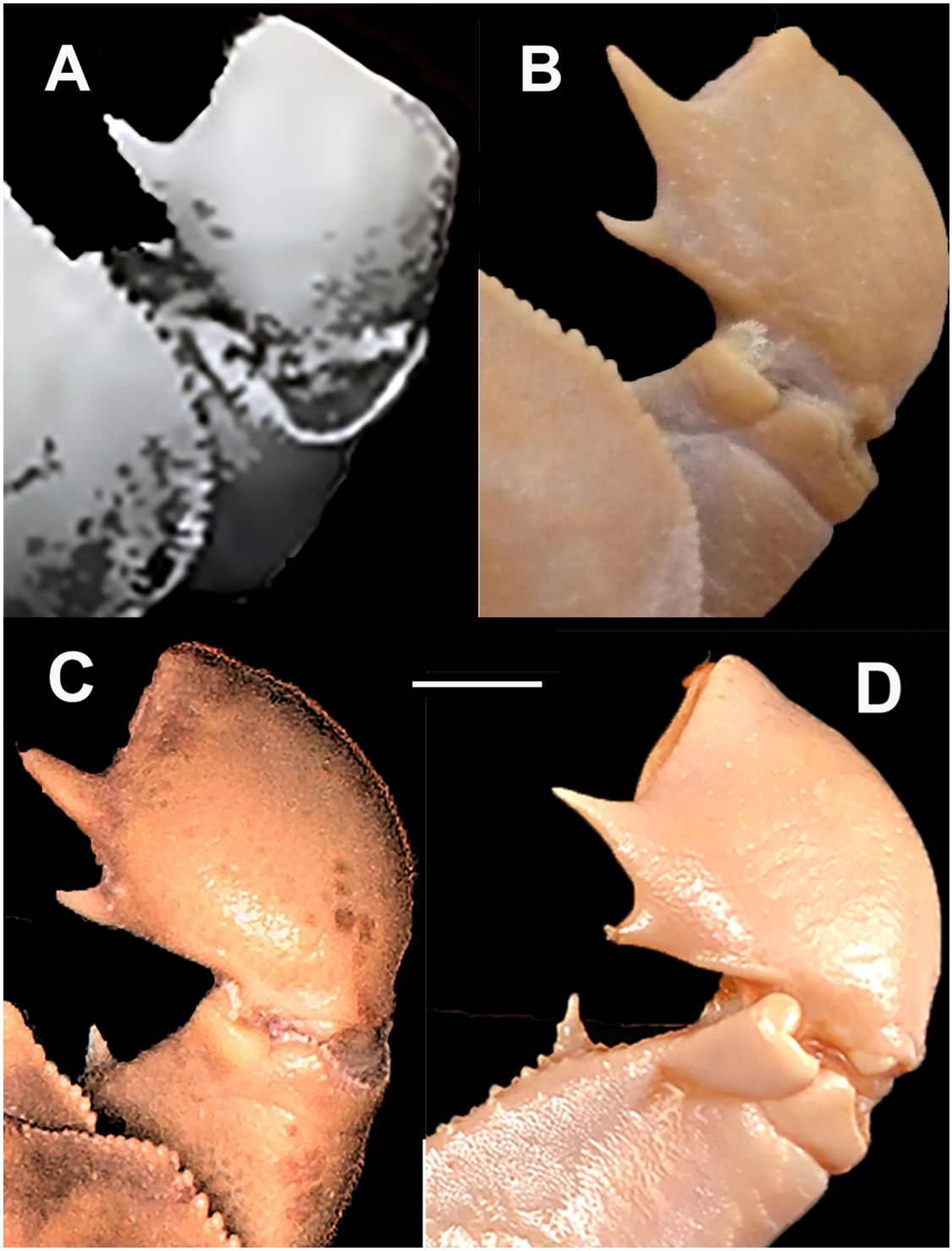

Fig. 7. Dorsal view of right cheliped carpus. **A**. *Potamonautes lirrangensis* s. str., holotype, adult, ♀, CW 53.6 mm, from Liranga, République du Congo (MNHN B-3826) (Rathbun, 1904: pl. 14, fig. 8). **B**. *P. kisangani* sp. nov., holotype, adult, ♂, CW 60.5 mm, from Kisangani, Democratic Republic of the Congo (USNM 98944). **C**. *P. amosae* sp. nov., holotype, adult, ♂, CW 46.5 mm, from Lake Kivu, D.R. Congo (NHMUK 2018.306). **D**. *P. orbitospinus* (Cunnington, 1907), lectotype, adult, ♂, CW 56.9 mm, from Nkhata Bay, Lake Malawi, Malawi (NHMUK 1908.1.31.27). Scale bar: A = 5.7 mm; B = 4.8 mm; C = 3.6 mm; D = 4.9 mm. Photograph D by Phillip Crabb, NHMUK.

413–415, pls 25–26, figs 3, 8). The second U.S. Congo expedition in 1955 also collected a number of specimens (in 7 samples) from Kisangani (examined in the present work) that were also initially attributed to *P. lirrangensis* s. lat. Figures of the carapace, chelipeds, and G1 of the adult male holotype from Kisangani, D.R. Congo (Figs 4B, 5A, 6A–B, 7B, 8A–B, 11A) are provided for comparison with

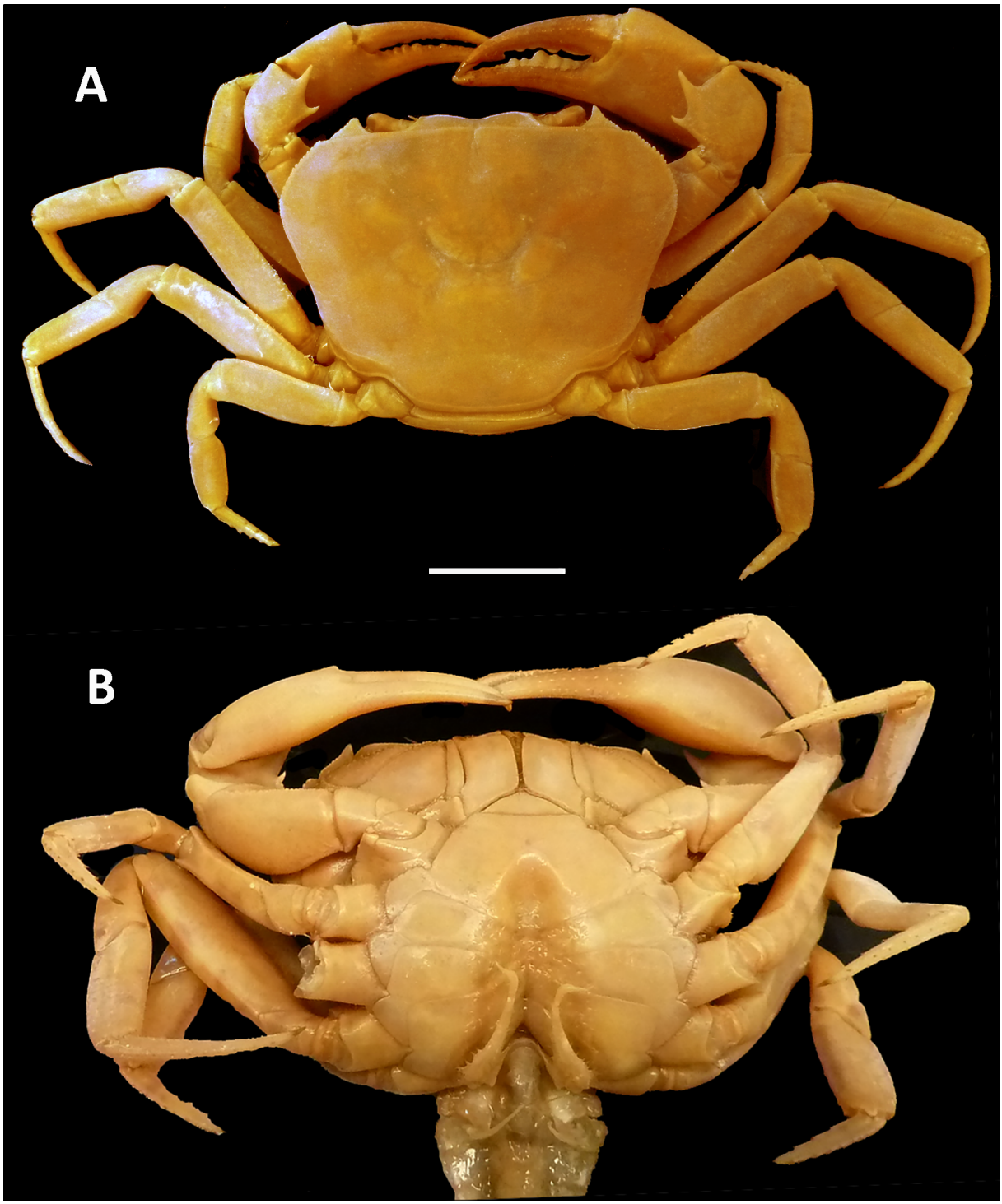

Fig. 8. *Potamonautes kisangani* sp. nov. **A**. Adult, ♀, whole animal, dorsal view. **B**. Adult, ♂, whole animal, ventral view. Scale bar = 10 mm.

the other taxa included here. One character that distinguishes this species from *P. lirrangensis* s. str. is the epibranchial tooth, which is small and granular, followed by large granules lining the anterolateral margin in *P. kisangani* sp. nov. (Fig. 4 B) (vs pointed and as large as the other teeth lining the anterolateral margin in *P. lirrangensis* s. str. from Liranga; Fig. 4A). The absence of DNA sequence data for any of the specimens from Kisangani means that it is not possible to test the monophyly of *P. kisangani* sp. nov. using molecular data.

Comparisons

The epibranchial tooth and anterolateral margin of *P. kisangani* sp. nov. from Kisangani (Fig. 4B) and of *P. amosae* sp. nov. from Lake Kivu (Fig. 4C) and the Malagarasi River (Fig. 4D; Reed & Cumberlidge 2006: pl. 5a) are similar in both species: the epibranchial tooth is a small granule that is followed by large granules lining the anterolateral margin. In contrast, the epibranchial tooth of *P. lirrangensis* s. str. from Liranga (Fig. 4A) and of *P. orbitospinus* from Lake Malawi (Fig. 4E) is pointed and as large as the other teeth lining the anterolateral margin.

The male thoracic sternal sulcus S3/4 of *P. kisangani* sp. nov. from Kisangani (Fig. 8B) and of *P. orbitospinus* from Lake Malawi (Fig. 10B) is deep, distinct, and V-shaped, whereas this sulcus is faint in *P. amosae* sp. nov. from Lake Kivu (Fig. 9B) and the Malagarasi River (Reed & Cumberlidge 2006: pl. 5c).

The ischium of the third maxilliped of *P. kisangani* sp. nov. from Kisangani (Fig. 5A) and of *P. orbitospinus* from Lake Malawi (Fig. 5C) has a thin but distinct vertical sulcus, whereas this sulcus is faint and obscure in *P. amosae* sp. nov. from Lake Kivu (Fig. 5B) and the Malagarasi River (Reed & Cumberlidge 2006: pl. 5c–d).

The chela dactylus (moveable finger) and fixed finger (pollex of propodus) of *P. kisangani* sp. nov. from Kisangani (Fig. 6A–B) are both elongated and slender, whereas the chela fingers in *P. amosae* sp. nov. from Lake Kivu (Fig. 6C–D) and from the Malagarasi River (Fig. 6E–F; Reed & Cumberlidge 2006: pl. 5a figs 46–47; NMU TRW1972.04), and in *P. orbitospinus* from Lake Malawi (Fig. 6G–H), are thick and broad.

The major chela has 3 large molars at the proximal ends of both fingers, with older specimens showing fusion of these teeth into a flat surface of the fixed finger in *P. kisangani* sp. nov. from Kisangani (Figs 6A–B, 8A) and in *P. amosae* sp. nov. from the Malagarasi River (CW 80.1 mm) (Fig. 6E–F; Reed & Cumberlidge 2006: pl. 5a figs 46–47), whereas the proximal parts of both fingers of the major chela in *P. orbitospinus* from Lake Malawi (Fig. 6G–H) has enlarged, rounded, separate (unfused) teeth.

The P5 carpus, propodus, and dactylus of *P. orbitospinus* from Lake Malawi (Figs 10B, 13) are all elongated and slender, whereas these ambulatory leg articles in *P. kisangani* sp. nov. from Kisangani (Fig. 8A–B) and of *P. amosae* sp. nov. from Lake Kivu (Fig. 9A–B) and the Malagarasi River (Reed & Cumberlidge 2006: pl. 5a) are all short and stocky.

The G1 TA in *P. kisangani* sp. nov. from Kisangani (Fig. 11A) and *P. amosae* sp. nov. from Lake Kivu (Fig. 11B–D, F) and the Malagarasi River (Reed & Cumberlidge 2006: pl. 5c–d fig. 152) is only slightly widened by a low dorsal lobe and the TA ends in either a straight, or only slightly upcurved tip. This contrasts with the G1 TA in *P. orbitospinus* from Lake Malawi, which is conspicuously widened by a high, rounded dorsal lobe (as wide as the TA width at the TA-SA junction) and the G1 TA ends in a strongly curved upwards tip (Fig. 12A–H).

Potamonautes amosae sp. nov.
urn:lsid:zoobank.org:act:1B3001B9-7101-4551-AE46-2BEFCAD3598A
Figs 3, 4C–D, 5B, 6C–F, 7C, 9, 11B–F, 14, Table 1

Potamon (*Potamonautes*) *lirrangensis* – Balss 1936: 188 (partim, nec 189, fig. 24, Lirranga, Stanleyville; Kituri uberer Lualaba. Katanga-region). — Chace 1942: 188–189, fig. 1. – Capart 1952: 62–64, figs 12, 14c–d.

Potamonautes (*Lirrangopotamonautes*) *lirrangensis* – Bott 1955: 268–270, pl. XVI figs 2a–d, 38–39, 83. — Coulter 1991: 253, 255, tabs 9.XX, 9.XXI.

Potamonautes lirrangensis – Cumberlidge 1998: 201. — Reed & Cumberlidge 2006: figs 41–51, 153–154, 177 pl. V (partim). — Cumberlidge & Meyer 2011: 1845–1848 (partim, nec Malawi: Lake Malawi).

Diagnosis

Exorbital tooth large forward-pointing spine; lateral margin of exorbital tooth lined by granules before meeting postfrontal crest; epibranchial tooth small, granular, followed by small granules lining anterolateral margin (Fig. 4C–D). Anterolateral margin posterior to epibranchial tooth curving strongly outward (Fig. 4C–D); postfrontal crest distinct, completely traversing carapace between epibranchial teeth; posterior surface of carapace with deep urogastric grooves; third maxilliped ischium smooth (either lacking vertical sulcus or with faint sulcus); thoracic sternal sulcus S3/4 faint, shallow (Fig. 9B); major chela fixed finger with 3 large molars proximally, fused in older specimens into flat surface (Figs 6A–B, 8A); cheliped carpus inner margin with two large, subequal, forward-pointing spines (Fig. 7C); cheliped merus inner lower margin with spine-like tooth distally; P5 carpus, propodus, and dactylus not elongated (Fig. 9A–B); G1 TA (Fig. 11C–F) slightly widened by slim dorsal lobe (⅓ TA width at TA-SA junction); tip straight, only slightly curved upwards.

Etymology

The new species is named to honour the memory of Marilyn Suzanne Amos, of Mobile, Alabama, USA, who passed away during these studies. She was the mother of the second author (EJ). The specific epithet is used as a Latin noun in apposition. The vernacular name is Amos's crab.

Material examined

Holotype

DEMOCRATIC REPUBLIC OF THE CONGO • ♂ subadult; Idjwi Island, Lake Kivu; 2.082854° S, 29.071167° E; Feb. 1939; A. Loveridge leg.; MCZ CRU-11224.

Other material

DEMOCRATIC REPUBLIC OF THE CONGO • 1 ♂ subadult (CW 46.5 mm); Lake Kivu; donated by Royal Belgian Institute of Natural Sciences, Brussels; NHMUK 2020.3 • 1 ♂ subadult (CW 44.5 mm); Goma, Lake Kivu; 30 Nov. 1952; I. Gordon leg.; wide coast; NHMUK 2020.4.

RWANDA • 1 ♂ juv. (CW 30.0, CL 23.7, CH 11.2, FW 9.8 mm); Gisenye, Lake Kivu; Mar. 1936; J.C. Bequaert leg.; MCZ CRU-9177 • 1 ♀ juv. (CW 26.9 mm); Gisenye, Lake Kivu; 12 May 1955; Smithsonian-Bredin Congo Exped., W.L. Schmitt leg.; in water at shoreline; USNM 98937 • 1 ♀ adult (CW 62 mm); Kalemie (formerly Albertville), Lake Tanganyika; 8 Mar. 1919; M. Dhont de Bie leg.; NHMUK 1919.3.8.1-3.

TANZANIA • 1 ♂ subadult (CW 39.5 mm); Mungonya River, Mwandiga, near Kigoma; 4.828819° S, 29.666191° E; Apr. 1971; T.R. Williams leg.; NMU TRW 1971.05 • 1 ♀ adult (CW 80.1 mm); Malagarasi River, Uvinza, Kigoma District; 5.115673° S, 30.380144° E; Apr. 1971; T.R. Williams leg.; NMU TRW 1971.15.

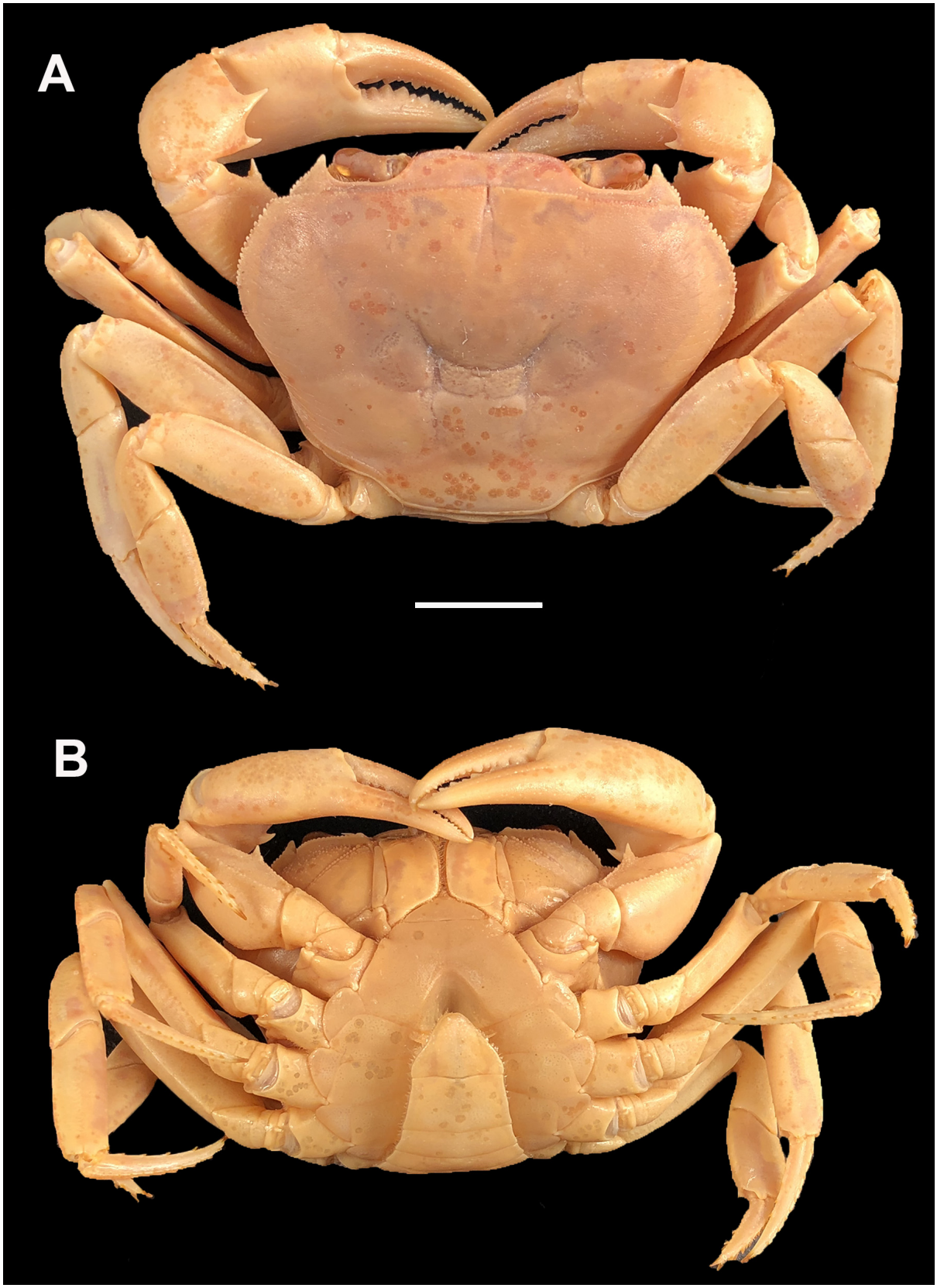

Fig. 9. *Potamonautes amosae* sp. nov., holotype, adult, ♂, CW 46.5 mm, from Lake Kivu, D.R. Congo (NHMUK 2018.306). **A**. Entire animal, dorsal view. **B**. Entire animal, ventral view. Scale bar = 11.3 mm.

Description

Carapace height equal to front width (CH/FW 1.0); carapace length 2.4 × front width (CL/FW 2.5); carapace width ~3 × front width (CW/FW 3.1); posterior region of carapace with deep urogastric grooves; exorbital tooth large forward-pointing spine; lateral margin of exorbital tooth lined by small granules; epibranchial tooth small, granular, followed by large granules lining anterolateral margin (Fig. 4C–D); anterolateral margin posterior to epibranchial tooth curving strongly outward (Fig. 4C–D); postfrontal crest distinct, completely traversing carapace between epibranchial teeth; posterior surface of carapace with deep urogastric grooves; carapace branchiostegal wall divided by pleural (vertical) suture into suborbital region (with granules on surface), subhepatic region (with granules, crinae on surface); divided by epimeral (longitudinal) suture; pterygostomial region with granules on surface (Fig. 5B). Epistomial tooth prominent, granulated, V-shaped. Mandible palp comprising 2 articles; terminal article single, undivided, with setae (but no hard flap) at junction between articles. Third maxillipeds filling entire oral field, except for transversely ovate respiratory openings at superior lateral corners; exopod with long flagellum; third maxilliped ischium smooth (either lacking vertical sulcus or with faint sulcus). Thoracic sternal sulcus S3/4 faint, shallow; episternal sulci S4/E4, S5/E5, S6/E6, and S7/E7 faint.

Major chela dactylus (moveable finger) and pollex of propodus (fixed finger) thick, broad, leaving long thin interspace between fingers when closed; both fingers with 3 large teeth proximally, other teeth small unfused distally; major chela fixed finger proximal molars fused into flat surface in older specimens from the Malagarasi River (CW 80.1 mm) (Fig. 6E–F); cheliped carpus inner margin with two large subequal forward-pointing spines (Fig. 7C); cheliped merus lower margins heavily granulated, inner lower margin with spine-like tooth distally; P3 longest, P5 shortest (carpus, propodus, and dactylus not elongated); P2–5 dactyli tapering to pointed tip, each bearing 4 rows of downward-pointing, short, sharp spines.

Male pleon slim, triangular, telson narrow triangle with rounded apex, pleomeres Al–6 quadrate. G1 TA proximal third straight, not widened, margins parallel, at midpoint bent sharply outward at 60° angle to longitudinal axis of G1 SA; G1 TA (Fig. 11B–E) widened by low dorsal lobe (⅓ TA width at TA-SA junction); tip straight, only slightly upcurved. G1 SA at junction with G1 TA with horizontal margin on ventral side, U-shaped indentation filled by conspicuous dorsal membrane on dorsal side. G2 TA long, flagellum-like (Fig. 11F). Margins of G1 TA, SA lined by setae.

Size

Large species, adult size range between CW 50 to 80 mm.

Colour

Preserved specimens are uniformly light brown like the holotype, but the large adult female from the Malagarasi River in Tanzania has black pigmentation on both fingers of the chelae (Fig. 6E–F).

Distribution

Potamonautes amosae sp. nov. was collected from rocky areas of Lake Kivu in the D.R. Congo and Rwanda (Fig. 3). Lake Kivu is a relatively small (100 km long by 50 km wide), deep lake (depth 480 m) situated in the Albertine Rift of the Western Rift Valley. This lake is divided by the border between the D.R. Congo and Rwanda, with the large Idjwi Island lying in the D.R. Congo. The Ruzizi River drains south out of Lake Kivu and links it to the northern part of Lake Tanganyika in Burundi, but this species has not been recorded from this river. *Potamonautes amosae* sp. nov. is found along the eastern shores of Lake Tanganyika in localities associated with the Malagarasi River in western Tanzania (Capart 1952; Reed & Cumberlidge 2006; M. Mbalassa & S. Marijnissen pers. com.) where it flows through the Kigoma District, and on the western shores of Lake Tanganyika at Kalemie in the D.R. Congo (Capart 1952).

Ecology

Little is known about the habitat and ecology of *P. amosae* sp. nov. In the region of Lake Tanganyika this species was often captured in marshes and wetlands near the lake, but never in the lake itself (Capart 1952). In Lake Kivu this species is found on islands in the lake as well as in the lake (Chace 1942). The range of *P. amosae* sp. nov. includes part of the Lake Victoria Basin Freshwater Ecoregion (FEOW #521) (Thieme *et al*. 2005; Abell *et al*. 2008).

Conservation status

An IUCN extinction risk assessment of *P. amosae* sp. nov. has not yet been carried out. This species has a wide distributional range (with an estimated extent of occurrence (EOO) of almost 46 600 km^2) and has been recorded from seven localities (Fig. 3) in three different countries. Given that there are no known immediate threats to this species, it would probably be assessed as Least Concern.

Remarks

There are a number of characters that distinguish *P. amosae* sp. nov. from *P. orbitospinus* in Lake Malawi. For example, the male thoracic sternal sulcus S3/4 of *P. amosae* sp. nov. is faint and shallow (vs deep and complete in *P. orbitospinus*); the low dorsal lobe of the G1 TA of *P. amosae* sp. nov. means that it is only slightly widened (vs a G1 TA dorsal margin that is conspicuously widened by a high dorsal lobe in *P. orbitospinus*); the anterolateral margin of *P. amosae* sp. nov. is lined by small granules (vs lined by a row of small distinct teeth in *P. orbitospinus*); the merus, propodus, and dactylus of P5 of *P. amosae* sp. nov. are all short (vs all elongated and slender in *P. orbitospinus*); and the third maxilliped ischium of *P. amosae* sp. nov. is smooth (vs with a third maxilliped ischium that has a deep vertical sulcus in *P. orbitospinus*).

In the past, *P. amosae* sp. nov. from Lake Kivu has been identified as *P. lirrangensis* s. lat. by a number of authors (Chace 1942; Bott 1955; Reed & Cumberlidge 2006; Cumberlidge & Meyer 2011). These identifications were made based on characters shared with the type of *P. lirrangensis* s. str. from Liranga (such as denticles or granules lining the anterolateral margin, 2 large pointed spines on the cheliped carpus inner margin, and a large pointed spine on the cheliped merus inner margin). There are a number of illustrations of *P. amosae* sp. nov. available, but most of these specimens have been identified as *P. lirrangensis* s. lat. For example, Chace (1942) illustrated the carapace and G1 of a specimen from Lake Kivu (MCZ CRU-11224), and Capart (1952: fig. 12) figured an entire specimen from Kalemie (formerly Albertville) on the western shores of Lake Tanganyika and remarked on its similarity to the species found in Lake Kivu. Later, Reed & Cumberlidge (2006: figs 41–51, 153–154, 177 pl. V) described in detail an adult female (CW 81 mm) and male (CW 56.5 mm) of *P. lirrangensis* s. lat. (NMU TRW1971.15) from the Malagarasi River at Uvinza in the Kigoma District of Tanzania near Lake Tanganyika.

DNA sequence data are available from specimens formerly assigned to *P. lirrangensis* s. lat. from Lakes Kivu, Tanganyika, and Malawi (Marijnissen *et al*. 2006; Daniels *et al*. 2015; Kochey *et al*. 2017). Marijnissen *et al*. (2006) used 2 mitochondrial DNA sequence markers (12S rRNA and 16S rRNA) to investigate relationships between specimens identified morphologically as *P. lirrangensis* s. lat. from Ruzizi in Lake Kivu in the D.R. Congo (GenBank DQ203210, DQ203236), from Uazua in the Zambian part of Lake Tanganyika (DQ203211, DQ203237), and from Thumbi West Island near Cape Maclear in southern Lake Malawi (GenBank DQ203209, DQ203235). Marijnissen *et al*. (2006: fig. 1) found that the specimen from Lake Kivu (here recognised as *P. amosae* sp. nov.) formed a separate basal lineage from the clade formed by the other 2 specimens from Lake Malawi (here recognised as *P. orbitospinus*).

Daniels et al. (2015) sequenced four DNA markers (GenBank AY803494, AY803534, AY803568, AY803682) for a specimen (ZMA.Crust.De.204681) held in the NBL that was identified in that work as

P. lirrangensis s. lat. and incorrectly listed as being from Lake Malawi. In fact, specimen ZMA.Crust. De.204681 was collected from Lake Kivu (site 13, E. major; 23 Aug. 2002; Pascal Isumbisa leg.) and is therefore properly identified as *P. amosae* sp. nov.

There is molecular support for the recognition of *P. amosae* sp. nov. as a valid species from mitochondrial 16S rRNA and the nuclear coding gene Histone H3 sequences (Fig. 14). Across the 2 genes, 5 specimens are assigned to *P. amosae* sp. nov.: 3 from Uvinza, Kigoma District, Tanzania (2016-07-08-UV1; 2016-07-08-UV2; 2016-07-08-UV3), and two from Lake Kivu. The first specimen from Lake Kivu is ZMA. Crust.De.204681 represented by AY803534 and AY803682 (Daniels *et al*. 2015); the second specimen is from Ruzizi, Lake Kivu represented by DQ203236 (Marijnissen *et al*. 2006).

Potamonautes orbitospinus (Cunnington, 1907)
Figs 2, 4E, 5C, 6G–H, 7D, 10, 12–14, Table 1

Potamon (*Potamonautes*) *orbitospinus* Cunnington, 1907: 259–261, pl. 16 fig 1.

Potamon (Potamonautes) orbitospinus – Balss 1929: 349 (partim, nec D.R. Congo: Lake Kivu).
Potamon orbitospinus – Chace 1942: 218.

Common name

The Malawi blue crab.

Diagnosis

Exorbital tooth large forward-pointing spine; lateral margin of exorbital tooth not angled, in line with midline axis of carapace curving slightly inward (concave) before meeting postfrontal crest; epibranchial tooth pointed, as large as other teeth lining anterolateral margin (Fig. 4E). Anterolateral margin posterior to epibranchial tooth curving strongly outward (Fig. 4E); postfrontal crest distinct, completely traversing carapace between epibranchial teeth; posterior surface of carapace with deep urogastric grooves; third maxilliped ischium with thin, deep vertical sulcus; thoracic sternal sulcus S3/4 deep, V-shaped, completely traversing sternum (Fig. 10B); cheliped carpus inner margin with two large, subequal, forward-pointing spines (Fig. 7D); cheliped merus inner lower margin with spine-like tooth distally; P5 carpus, propodus, and dactylus all slender, distinctly elongated; G1 TA (Fig. 12A–C, E–G,) conspicuously widened by high, rounded dorsal lobe (as wide as TA width at TA-SA junction); tip distinctly curved upwards.

Material examined

Lectotype (here designated)
MALAWI • ♂ adult (CW 56.9, CL 38.4, FW 13.8 mm); western shore of Lake Malawi; 31 Jan. 1908; Tanganyika Exped., J.E.S. Moore leg.; NHMUK 1908.1.31.27.

Paralectotypes
MALAWI • 3 juvs (including CW 33.2, CL 22.8, CH 11.6, FW 10.0 mm); Lake Malawi; 19 Dec. 1891; M. Woodward leg.; NHMUK 1891.12.19.1 to NHMUK 1891.12.19.3 • 1 ♂ subadult (CW 27.5 mm); Universities Mission, Likoma, Lake Nyassa (now Lake Malawi); 14 Jan. 1893; J.A Williams leg.; NHMUK 1893.1.14 • 1 ♀ adult (CW 52.8 mm); west coast of Lake Malawi from Nkhata Bay to Ruarwe; Jun. 1896; A. Whyte leg.; NHMUK 1897.4.29.1 • several subadults; Nkhata Bay, Lake Malawi; 23 Jun. 1904; Third Tanganyika Exped., local fishermen and Dr W.A. Cunnington leg.; NHMUK 1897.4.29.23.

Additional material

MALAWI • 2 ♀♀ adults (CW 61.1, 65.8 mm), 2 ♀♀ subadults (CW 36.7, 45.1 mm), 1 ♂ subadult (CW 36.6 mm), 9 juvs; Lake Malawi, N of Hudzi; 20 Oct. 1926; Cristy leg.; NHMUK 1926.10.20.1 to NHMUK 1926.10.20.5 • 1 ♂ subadult (CW 31.1 mm); NW coast of Lake Malawi, near Nkhata Bay; 31 Jan. 1908; NHMUK 1908.1.31.16-18 • 1 ♀ adult (CW 55.6 mm); Lake Malawi, Monkey Bay; 20 Oct. 1926; NHMUK 1926.10.20.6 • 1 ♂ subadult (CW 49 mm), 1 ♀ adult with hatchlings (CW 64.8 mm); NW coast of Lake Malawi, near Nkhata Bay; 26 Jul. 1954; Miers leg.; NHMUK 1954.7.26.5, NHMUK 1954.7.26.6 • 1 ♀ adult (CW 61.1 mm), 1 ♂ adult (CW 55.4 mm); Lake Malawi; 5 Jun. 1956; G. Fryer leg.; NHMUK 1956.6.5.10, NHMUK 1956.6.5.11 • 1 ♀ adult (CW 57 mm), 1 ♂ subadult (CW 40 mm), 2 juvs (CW 32.5, 33.4 mm); Lake Malawi; 26 Jul. 1954; W.A. Cunnington leg.; NHMUK 1954.7.26.3, NHMUK 1954.7.26.4 • 1 ♂ subadult (CW 51.1 mm); Lake Malawi, Monkey Bay; Mar. 1968; D.H. Eccles leg.; among rocks in sand; NMU TRW 1972.04 • 1 ♂ subadult (CW 46.2 mm); Lake Malawi, 2 km ENE of Monkey Bay; May 1968; D.H. Eccles leg.; NMU TRW 1972.05 • 1 ♀ subadult (CW 51.1 mm); Lake Malawi; Sep. 1988; Irv. Kornfield leg.; NMU 09.1988k.1 •1 ♀ (damaged); Lake Malawi, N of Monkey Bay; 5 Apr. 1972; D.H. Eccles leg.; depth 91 m; NMU TRW1972.02 • 1 ♂ (CW 51.4 mm); Lake Malawi, Monkey Bay; 24 Mar. 1968; D.H. Eccles leg.; among rock in sand with little vegetation; NMU TRW1972.04 • 1 ♂ (CW 46.5 mm); Lake Malawi, ENE of Monkey Bay; 23 May 1968; D.H. Eccles leg.; NMU TRW1972.05 • 1 ♂ subadult (CW 46.5 mm); Lake Malawi, Cape Maclear; M. Genner leg.; NHMUK 2010-06-CM-CM6 • 1 ♀ subadult (CW 50.15 mm); same collection data as for preceding; NHMUK 2010-06-CM-CM8 • 1 ♀ adult (CW 52.2 mm); same collection data as for preceding; Jun. 2010; NHMUK CM13 • 1 ♀ adult (CW 54.4 mm); same collection data as for preceding; NHMUK CM14 • 1 ♀ subadult (CW 44.1 mm); same collection data as for preceding; NHMUK CM21 • 1 ♀ adult (CW 54.8 mm); Lake Malawi, NW coast near Nkhata Bay; 1961; Sweeney leg.; NHMUK 2011.1509 • 1 ♀ subadult (CW 32.7 mm); Lake Malawi, Cape Maclear; 17 Jun. 2010; M. Genner leg.; UB CM17 • 1 ♀ subadult (CW 37.4 mm), 1 ♀ adult (CW 57.6 mm); 2 ♂♂ adults (CW 55.1, 54.9 mm); same collection data as for preceding; UB CM22, UB CM11, UB CM20, UB CM12 • 1 ♀ adult (CW 57.1 mm), 1 ♀ subadult (CW 33.1 mm); same collection data as for preceding; 26 Jun. 2010; UB CM10, UB CM5 • 1 ♂ subadult (CW 49.2 mm); same collection data as for preceding; 21 Jun. 2010; UB CM4 • 1 ♀ subadult (CW 48.3 mm); same collection data as for preceding; UB CM9 • 1 ♀ subadult (CW 46.7 mm); same collection data as for preceding; UB CM15 • 1 ♀ subadult (CW 35.4 mm); same collection data as for preceding; UB CM16 • 1 ♀ subadult (CW 45.4 mm); same collection data as for preceding; UB CM24 • 1 ♂ adult (CW 59.4 mm); same collection data as for preceding; UB CM7 • 2 ♀♀ adults (CW 55.4, 54.4 mm), 2 ♀♀ subadults (CW 44.9, 45.9 mm); same collection data as for preceding; UB CM7 • 1 ♂ adult; same collection data as for preceding; 26 Jun. 2010; R. Bills leg.; AMG CAW 467A.

Redescription

Carapace height equal to front width (CH/FW 1.0); carapace length 2.5 × front width (CL/FW 2.5); carapace width 3.5 × front width (CW/FW 3.5); exorbital tooth large forward-pointing spine; exorbital tooth lateral margin not angled, in line with midline axis of carapace, curving slightly inward (concave) before meeting postfrontal crest; epibranchial tooth pointed, as large as other teeth lining anterolateral margin (Figs 4E, 10A). Anterolateral margin posterior to epibranchial tooth curving strongly outward (Fig. 4E); postfrontal crest distinct, completely traversing carapace between epibranchial teeth; posterior surface of carapace with deep urogastric grooves; carapace branchiostegal wall divided by vertical pleural suture into suborbital and subhepatic regions, both smooth with sparse granules, pterygostomial region smooth (Fig. 10B); epistomial tooth prominent, granulated, V-shaped. Mandible palp comprising 2 articles; terminal article single, undivided, with setae (but no hard flap) at junction between articles. Third maxillipeds filling entire oral field, except for transversely ovate respiratory openings at superior lateral corners; exopod with long flagellum; ischium with deep vertical sulcus.

Thoracic sternal sulcus S3/4 deep, completely traversing sternum; episternal sulci S4/E4, S5/E5, S6/E6, and S7/E7 distinct.

Major chela dactylus (moveable finger) and pollex of propodus (fixed finger) thick, broad, leaving long interspace between fingers when closed; both fingers with 3 large teeth unfused proximally, several medium-sized teeth distally (Fig. 6G–H); cheliped carpus inner margin with two large subequal forward-pointing spines (Fig. 7D); cheliped merus inner lower margin with spine-like tooth distally; P5 carpus, propodus, and dactylus all slender, distinctly elongated; P2–5 dactyli elongated, tapering to pointed tip, each bearing 4 rows of downward-pointing, short, sharp spines.

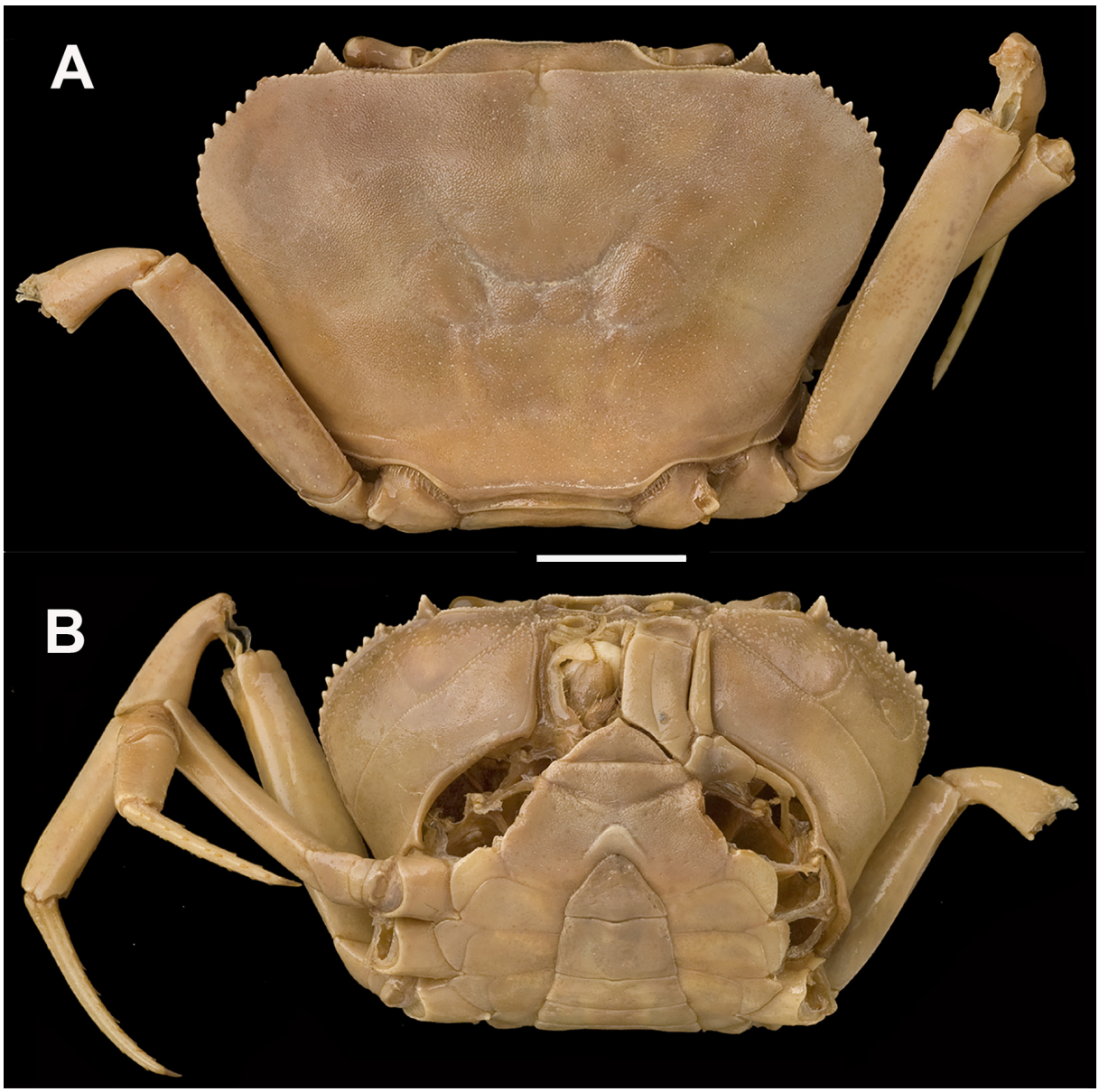

Fig. 10. *Potamonautes orbitospinus* (Cunnington, 1907), lectotype, adult, ♂, from Nkhata Bay, Lake Malawi, Malawi, CW 56.9 mm (NHMUK 1908.1.31.27). **A**. Entire animal, dorsal view. **B**. Entire animal, ventral view. Scale bar = 11.9 mm. Photographs by Phillip Crabb, NHMUK.

Pleon of male slim, triangular, telson narrow triangle with rounded apex, pleomeres Al–6 quadrate. G1 TA proximal third straight, not widened, margins parallel, at midpoint bent sharply outward at 90° angle to longitudinal axis of G1 SA; G1 TA (Fig. 12A–C, E–G) conspicuously widened by high, rounded dorsal lobe (as wide as TA width at TA-SA junction); tip distinctly curved upwards; G1 SA at junction with G1

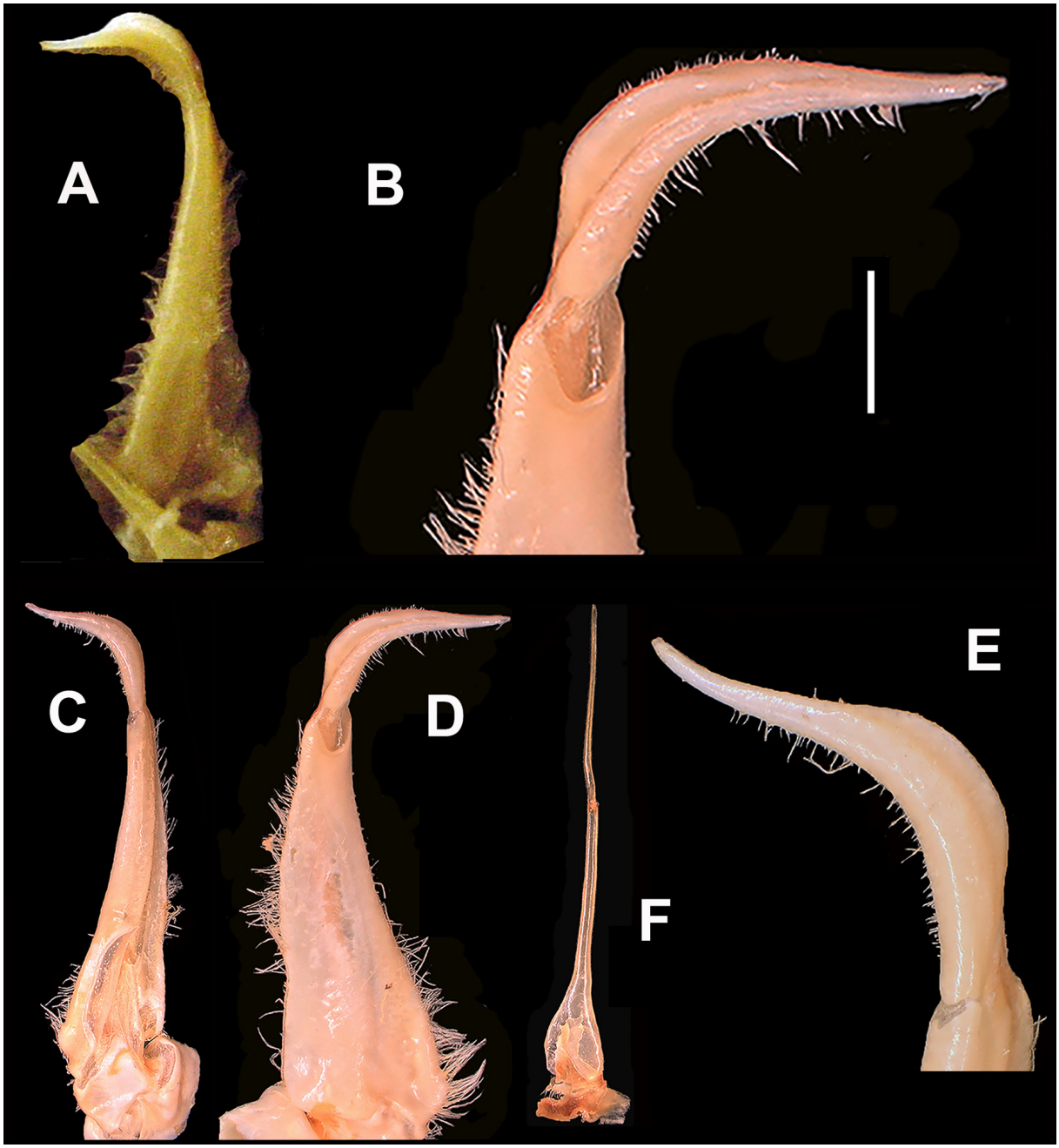

Fig. 11. A. *Potamonautes kisangani* sp. nov., holotype, adult, ♂, CW 60.5 mm, from Kisangani, Democratic Republic of the Congo (USNM 98944). G1, ventral view. – **B–F**. *P. amosae* sp. nov., holotype, adult, ♂, CW 46.5 mm, from Lake Kivu, D.R. Congo (NHMUK 2018.306). **C, E**. G1, ventral view. **B, D**. G1, dorsal view. **F**. G2, ventral view. Scale bar: A, C–D = 3.0 mm; B = 3.1 mm; E = 1.2 mm; F = 1.3 mm.

TA with horizontal margin on ventral side, U-shaped indentation filled by conspicuous dorsal membrane on dorsal side. G2 TA: long, flagellum-like (Fig. 12D, H). Margins of G1 TA, SA lined by setae.

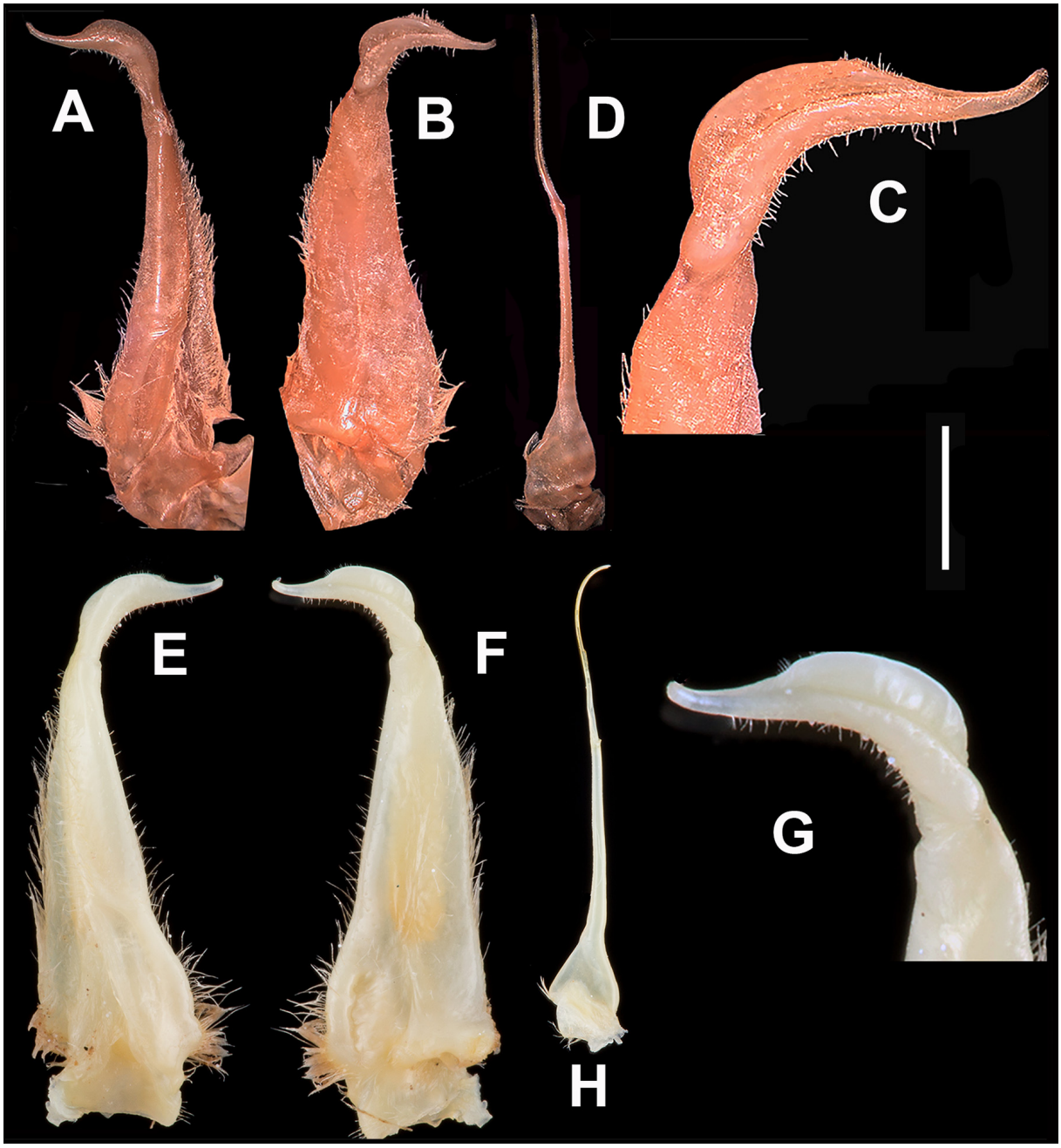

Fig. 12. *Potamonautes orbitospinus* (Cunnington, 1907). **A–D**. Lectotype, adult, ♂, CW 56.9 mm, from Nkhata Bay, Lake Malawi, Malawi (NHMUK 1908.1.31.27). **A**. G1, ventral view. **B–C**. G1, dorsal view. **D**. G2, ventral view. **E–H**. Adult, ♂, Cape Maclear, Lake Malawi, Malawi (AMG CAW 467A). **E**. G1, ventral view. **F–G**. G1, dorsal view. **H**. G2, ventral view. Scale bar: A–B, E–F = 3 mm; C, G = 1.3 mm; D, H = 1.2 mm.

Size

Large species, pubertal molt starting around CW 53 mm (largest adult male CW 56.9 mm, largest adult female CW 53.9 mm).

Colour

The carapace surface and branchiostegal walls of living specimens are deep blue, and are especially bright in newly-hardened specimens (Fig. 13). There are distinct white outlines marking the postfrontal crest, anterolateral margins, frontal margin, orbital margins, exorbital teeth, epistome, and the third maxilliped ischium and merus. The thoracic sternum is pinkish blue/grey and cream, and the arthrodial membranes on the inner side of the joints between the coxae and the basis of the chelipeds and P2–5 are cream.

Distribution

Potamonautes orbitospinus is abundant and widely distributed throughout Lake Malawi (Fig. 2) and has not been recorded from outside of the lake.

Ecology

Lake Malawi is the southernmost Great Lake in the East African Rift system and lies in 3 countries: Malawi, Mozambique, and Tanzania. The Ruhuhu River in Tanzania flows west into the northeastern part of Lake Malawi while the Shire River drains south out of the lake and is a tributary of the Zambezi River.

Fig. 13. *Potamonautes orbitospinus* (Cunnington, 1907), living specimen from Lake Malawi, Malawi. Photograph Oliver-Mengedoht.de/Panzerwelten.de.

In 1904, Cunnington and his assistants collected the first known specimens of *P. orbitospinus* from the waters of Lake Malawi itself, noting that some specimens were found on the beach (Cunnington 1907). The specimens reported on here are all restricted to Lake Malawi, and this species is a lake specialist that has never been collected in the rivers of the drainage basin that flow into the lake.

Conservation status

An IUCN conservation assessment of *P. orbitospinus* has not yet been carried out. The species is known from a large number of specimens from 16 localities all in Lake Malawi (29 600 km^2). Given that its estimated extent of occurrence (EOO) is more than 21 100 km^2, and that no specific threats are known, it would probably be assessed as Least Concern. It is significant that the population levels of *P. orbitospinus* are sufficient to be regularly caught as bycatch in local fisheries in Lake Malawi, and this species is also captured to supply a steady demand by the global aquarium trade.

Remarks

The recognition of *P. orbitospinus* and *P. lirrangensis* s. str. as valid species returns to the original taxonomic situation over 110 years ago when they were first described from two widely separated locations (Rathbun 1904; Cunnington 1907). Chace (1942) also treated *P. lirrangensis* and *P. orbitospinus* as valid species, but Bott (1955), Reed & Cumberlidge (2006) and Cumberlidge & Meyer (2011) considered *Potamon* (*Potamonautes*) *orbitospinus* to be a junior synonym of *Potamonautes lirrangensis* s. lat. The result has been that the available descriptions and distribution maps of *Potamonautes lirrangensis* s. lat. (Reed & Cumberlidge 2006: fig. 177) incorrectly combine characters and localities of *P. lirrangensis* s. str. from the Congo River with those of *P. orbitospinus* from Lake Malawi, and *P. amosae* sp. nov. from Lake Kivu and Kigoma District near Lake Tanganyika.

Potamonautes orbitospinus is recognised here based on characters of the lectotype described by Cunnington (1907) from Lake Malawi as well as other comparable material from this lake. The redescription includes new taxonomically important characters because although the description by Cunnington (1907) of *P. orbitospinus* was based on an adult male, he did not illustrate the first gonopod or sternal characters of the type specimen. See concluding remarks below for comparisons with other superficially similar species.

The combined phylogeny based on mitochondrial 16S rRNA and the nuclear coding gene Histone H3 (Fig. 14) includes a specimen from Thumbi West Island near Cape Maclear in southern Lake Malawi (GenBank DQ203209, DQ203235), alongside eight other specimens from Cape Maclear and Chiofu on the east coast of Lake Malawi. The phylogeny suggests a monophyletic clade for *P. orbitospinus* from Lake Malawi, separate from the clade for *P. amosae* sp. nov. (Fig. 14).

A specimen identified as *P. lirrangensis* s. lat. from 'Uazua' in the Zambian part of Lake Tanganyika (POlirrangensisZAM31; Marijnissen *et al*. 2006) has a partial 16S sequence (DQ203237) with high similarity (99%) to a specimen of *P. orbitospinus* from Lake Malawi (POlirrangensisMAL27; DQ203235; Marijnissen *et al*. 2006). This same specimen (POlirrangensisZAM31), however, has a partial 12S sequence (DQ203211) which has only 97% similarity to POlirrangensisMAL27 (DQ203209). This may indicate that *P. orbitospinus* shares a close evolutionary affinity to specimens within Lake Tanganyika, but further sampling is required to determine the evolutionary relationships of these two groups.

Kochey *et al*. (2017) carried out a molecular study of the Malawi blue crab (which they identified as *P. lirrangensis* s. lat.) that found the morphologically similar populations in Lake Malawi to be equally close genetically, and confirmed that the lake hosts only a single species of freshwater crab (here identified as *P. orbitospinus*). Those authors also found that the blue crab populations in Lake Malawi had only moderate haplotype diversity and low levels of nucleotide diversity for two mitochondrial

loci (NADH dehydrogenase subunit 1 (*ND1*) and cytochrome b (*CytB*) (Kochey *et al*. 2017). The lack of divergence of blue crab populations in Lake Malawi and the morphological similarity of specimens found in different parts of the lake suggests a recent colonisation (Kochey *et al.* 2017).

Discussion

The results of the present molecular study (Fig. 14) support the recognition of *P. orbitospinus* from Lake Malawi and of *P. amosae* sp. nov. from Lake Kivu and Tanzania. The 4 taxa formerly assigned to

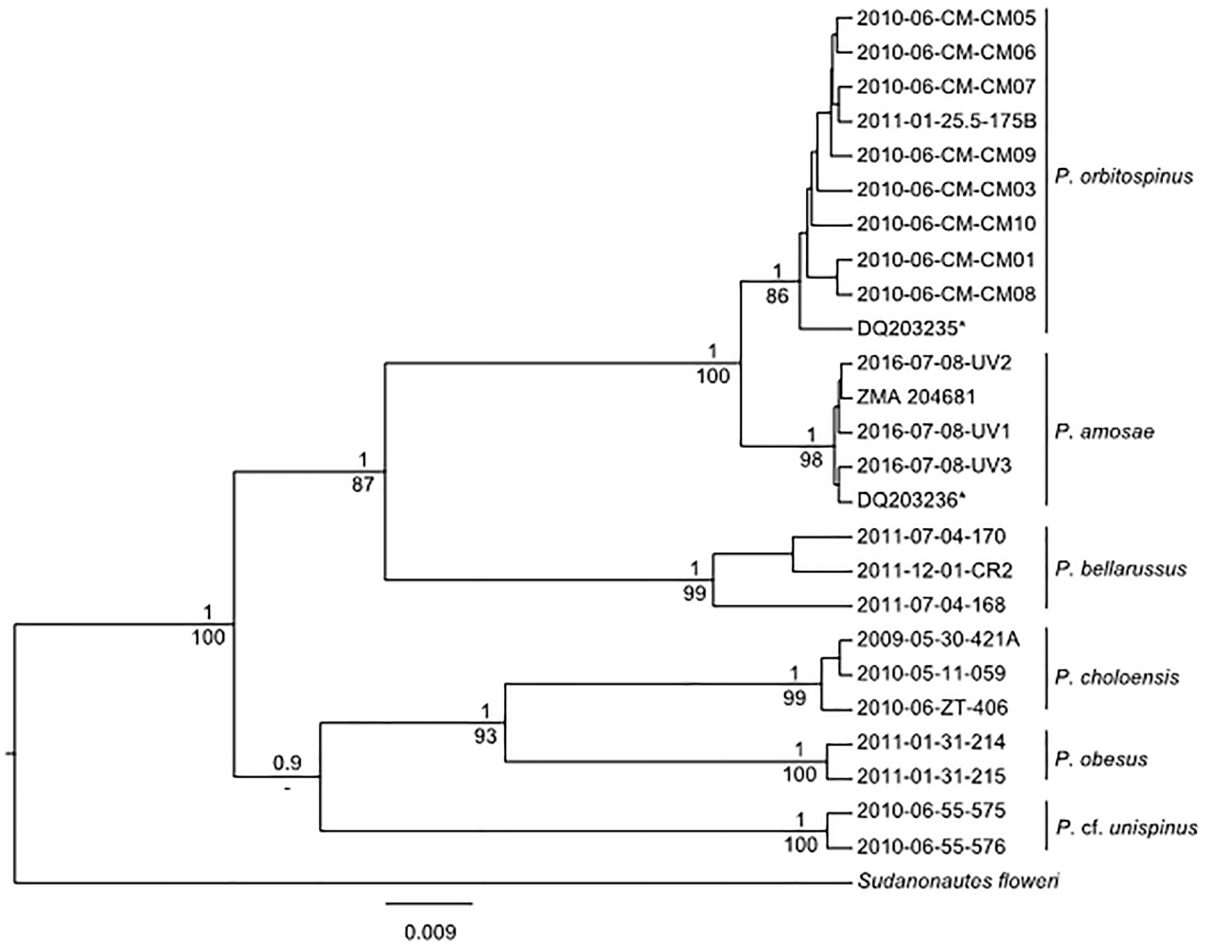

Fig. 14. Phylogenetic relationships of species of African freshwater crabs included in the present study. *Potamonautes orbitospinus* (Cunnington, 1907) and *P. amosae* sp. nov. were both formerly included in the *Potamonautes lirrangensis* (Rathbun, 1904) s. lat. species complex. The analysis combines 16SrRNA (489 bp alignment) and Histone 3 sequences (290 bp alignment). Numbers above branches indicate Bayesian Inference (~BI) posterior probability support values, and numbers below branches indicate Maximum likelihood (ML) bootstrap support values. Only intraspecific node support values are shown for clarity. '-' indicates the node was not supported by ML analysis. Codes on the branch tips indicate either isolate numbers or *Genbank accession numbers (Table 2). Other species shown on the tree (*P. bellarussus* Daniels, Phiri & Bayliss, 2014, *P. choloensis* Chace, 1953, *P. obesus* A. Milne-Edwards, 1868, and *P*. cf. *unispinus* Stewart & Cook, 1998) have a distribution that overlaps with that of the focal species (*P. lirrangensis* s. lat.). The outgroup species is *Sudanonautes floweri* de Man, 1901 from Cameroon and Gabon. The scale bar indicates genetic distance.

P. lirrangensis s. lat., namely *P. lirrangensis* s. str. from Liranga, *P. kisangani* sp. nov. from Kisangani, *P. orbitospinus* from Lake Malawi, and *P. amosae* sp. nov. from Lake Kivu and Tanzania, can be distinguished by the suite of morphological characters provided earlier.

The present study has resolved a long-standing controversy regarding the taxonomic identity of the Malawi blue crab, which was formerly identified as *P. lirrangensis* s. lat., and, after 65 years, is now again recognized as *P. orbitospinus*. In addition, the identity of the largest species of freshwater crab found in Lake Kivu is recognized here as *P. amosae* sp. nov. and this is grouped with populations of large crabs from the Lake Tanganyika drainage in Tanzania and the D.R. Congo. Finally, a better understanding of the taxonomic status of *P. lirrangensis* s. str. from Liranga and *P. kisangani* sp. nov. from Kisangani await further collections from the largely unexplored Middle Congo River.

Acknowledgements

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Conflicts of interest

The authors declare no conflicts of interest.

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