



Disentangling the *Sudanonautes granulatus* (Balss, 1929) species complex (Potamoidea: Potamonautidae), with the description of two new freshwater crabs from Nigeria and Côte d'Ivoire, West Africa

NEIL CUMBERLIDGE^{1*}, PIERRE A. MVOGO NDONGO^{2,3} & PAUL F. CLARK⁴

¹Department of Biology, Northern Michigan University, Marquette, MI, 49855 USA.

²Département de Gestion des Écosystèmes Aquatiques, Institut des Sciences Halieutiques, Université de Douala à Yabassi, PO. Box. 7236 Douala-Bassa, Cameroun

³Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Invalidenstr. 43, 10115 Berlin, Germany.

<https://orcid.org/0000-0003-1581-2557>

⁴Department of Life Sciences, The Natural History Museum, London, SW7 5BD, UK.

<https://orcid.org/0000-0001-6862-3982>

*Corresponding author. [✉ ncumberl@nmu.edu](mailto:ncumberl@nmu.edu); <https://orcid.org/0000-0002-0568-6414>

Abstract

The taxonomic status of the widely distributed West and Central African freshwater crab *Sudanonautes granulatus* (Balss, 1929) sensu lato is revised in the light of improved morphological evidence which indicates that this taxon is a complex comprising at least 4 species: *Sudanonautes granulatus* (Balss, 1929) sensu stricto from Togo, *S. koudougou* n. sp. from Côte d'Ivoire, *S. umaji* n. sp. from Nigeria, and *S. tiko* from Cameroon, Nigeria, and Bioko. Diagnoses, illustrations and distribution maps are provided for these species and they are compared with congeners from West and Central Africa.

Key words: freshwater decapods, *Sudanonautes koudougou* n. sp., *S. umaji* n. sp., *S. tiko*, revision, taxonomy, Togo

Introduction

This work focuses on the taxonomic status of the widely distributed species *Sudanonautes granulatus* (Balss, 1929) sensu lato which has a reported range extending from Cote d'Ivoire in West Africa to the Central African Republic in Central Africa, including Bioko Island in Equatorial Guinea (Cumberlidge 1993a, 1999, 2008). This study was prompted by doubts regarding the continued inclusion of specimens currently attributed to *S. granulatus* s.l. from 7 countries in different regions of Africa. The original description of *Potamonautes decazei granulata* Balss, 1929 was based on 17 samples of freshwater crabs from Togo, West Africa collected between 1890 and 1904 during the German colonial period, that were deposited in the Museum für Naturkunde, Berlin, Germany. Later, some of these specimens became part of the collections of 2 other German museums; the Zoologisches Staatsinstitut und Zoologisches Museum, Hamburg and the Zoologische Staatssammlung München, Munich. These samples are from 2 localities in the highlands of western Togo that were both German colonial outposts: Missahoe [= Missahohé or Missahöhe] and Bismarckburg (Krell 1994). The specimens were first studied by Balss (1929) who described them as *Potamonautes decazei granulata*, a subspecies of *Thelphusa decazei* A. Milne-Edwards, 1886 from Central Africa.

Potamonautes decazei granulata was subsequently assigned to *Potamon* Savigny, 1816 by Chace (1942) who recognized it as a species, *Potamon granulata* (Balss, 1929). Later, Bott (1955) transferred these same specimens to *Sudanonautes* Bott, 1955 and treated *P. d. granulata* as a junior synonym of *Sudanonautes* (*Sudanonautes*) *decazei decazei* (A. Milne-Edwards, 1886). Bott (1955) designated a lectotype for *P. d. granulata* (MNB Crust.11257) from Missahoe, Togo making the remaining specimens from Togo paralectotypes. No additional taxonomic information (Chace 1942; Bott 1955) or illustrations (Balss 1929; Chace 1942; Bott 1955), was provided by any of these authors for *P. d. granulata*.

Cumberlidge (1993a) was the first to recognize the taxonomic confusion surrounding *P. d. granulata* and the necessity for a comprehensive revision of this taxon. That author accepted its assignment by Bott (1955) to *Sudanonautes*, and treated it as a valid species, *S. granulatus* (Balss, 1929). Cumberlidge (1993a) based his conclusions on a series of specimens that he compiled from museum collections and newly collected material which greatly expanded the distributional range of *S. granulatus* beyond Togo to also include Côte d'Ivoire, Ghana, Nigeria, Cameroon, Bioko Island, Equatorial Guinea, and the Central African Republic. Although Cumberlidge (1993a) provided a full description and illustrations of the gonopods, chelipeds, thoracic sternum, mandible and third maxillipeds of adult males of *S. granulatus* s.l., his revision was based on specimens from Côte d'Ivoire (NBL CRUS.D35246) and Nigeria (NMU 5.VI.1979), and he did not refer directly to either the lectotype or the paralectotypes from Togo. Since then, descriptions of new *Sudanonautes* species from West and Central Africa (Cumberlidge & Boyko 2002; Mvogo Ndongo *et al.* 2017) together with the reexamination by the present study of an adult male paralectotype of Balss (1929), and the available samples used by Cumberlidge (1993a) indicate that many of these specimens (including the 2 that were illustrated) do not belong to the same species.

In the present study, the lectotype and paralectotypes of *P. d. granulata* from Misahohe and Bismarckburg, Togo were compared, and found to be conspecific. An adult male paralectotype from Bismarckburg, Togo was selected and compared to other adult male specimens currently attributed to *S. granulatus* s.l. from localities representing the current range of this species in West and Central Africa (Cumberlidge 1993a, 1999). The results indicate that *S. granulatus* s.l. is a species complex comprising at least 4 species: *S. granulatus* *sensu stricto*, with a distribution restricted to the western highlands of Togo, *S. koudougou* **n. sp.** from Koudougou in Côte d'Ivoire, *S. umaji* **n. sp.** from Nigeria, and *S. tiko* Mvogo Ndongo, Schubart & Cumberlidge in Mvogo Ndongo, Schubart, von Rintelen, Tamesse & Cumberlidge, 2017, from Nigeria and Bioko Island, Equatorial Guinea. All of these taxa are described and illustrated with revised and updated distribution maps being provided, and their taxonomic status is discussed in the light of the new data. This work raises the number of species of *Sudanonautes* from twelve (Cumberlidge 1999; Cumberlidge & Boyko 2001; Mvogo Ndongo *et al.* 2017) to fourteen.

Materials and methods

Characters of the gonopods, carapace, sternum, cheliped, third maxilliped, and mandible were examined in detail and photographed with a digital camera and a Keyence VHX 5000 digital microscope. Post-processing was undertaken using Adobe Photoshop CC5. Measurements were made with digital callipers and are given in millimeters (mm). Measurements of the subterminal segments of G1 and G2 were made along a straight line beginning at the midpoint of the basal margin of the subterminal segment (SS) and ending at the midpoint of its distal margin (at the SS-terminal article (TA) junction). Measurements of the terminal articles of G1 and G2 were made on the ventral face along the midline beginning at the midpoint of the basal margin that forms the SS-TA junction and ending at the TA tip. The length of the TA of G1 and G2 relative to the length of the SS of each of these structures is presented as the ratio of the terminal article/subterminal segment (TA/SS). The terminology used follows Cumberlidge (1999) and Davie *et al.* (2015). The following abbreviations are used: A, pleomere; asl, altitude above sea level in meters; CW, carapace width measured at widest point; CL, carapace length measured along median line from anterior to posterior margin; CH, carapace height measured at maximum height of cephalothorax; FW, front width measured along anterior frontal margin between inner angles of orbits; G1, first gonopod; G2, second gonopod; P2–5, pereopods 2–5 (ambulatory legs 1–4); TA, terminal article of G1 or G2; TS, terminal segment of mandibular palp; S, thoracic sternite; SS, subterminal segment of G1 or G2; NHM, The Natural History Museum, London, UK; NMU, Northern Michigan University, Marquette, Michigan USA; MNB, Museum für Naturkunde Berlin, Germany (formerly Zoologisches Museum der Humboldt-Universität, Berlin, Germany), NBL, Naturalis Biodiversity Center, Leiden, The Netherlands (formerly Rijksmuseum van Natuurlijke Historie); ZIM, Zoologisches Staatsinstitut und Zoologisches Museum, Hamburg, Germany; ZSM, Zoologische Staatssammlung München, Munich, Germany.

Systematics

Infraorder Brachyura Latreille, 1802

Superfamily Potamoidea Ortmann, 1896

Family Potamonautidae Bott, 1970

Subfamily Potamonautinae Bott, 1970

Genus *Sudanonautes* Bott, 1955

Sudanonautes granulatus (Balss, 1929) sensu stricto

(Figs. 1A, B, 4A, 5A, B, G, 6A–C, 7D, E, 8)

Potamonautes decazei granulata Balss, 1929: 119–120.

Potamon granulatus, Chace, 1942: 211.

Sudanonautes (Sudanonautes) decazei decazei, Bott, 1955: 300–301 (in part).

Sudanonautes granulatus, Ng *et al.* 2008: 172 (in part); Cumberlidge 1998: 207 (in part).

Not *Sudanonautes orthostylis*, Cumberlidge, 1989: 231–237 (in part), figs. 1 a–g, 2a–c; tabs. 1, 2 = *S. tiko*.

Not *Sudanonautes granulatus*, Cumberlidge, 1993a: 806–807, 812 (in part), figs. 1a, b, 2a–d, 3a–c, 4a, b = *S. tiko*.

Not *Sudanonautes granulatus*, Cumberlidge, 1993a: 806, 810 (in part), figs. 3 h–j, 4e, f = *S. umaji* n. sp.

Not *Sudanonautes orthostylis*, Cumberlidge, 1993b: 520–521 (in part), tab. 2 = *S. tiko*.

Not *Sudanonautes granulatus*, Cumberlidge, 1997: 576, = *S. umaji* n. sp.

Not *Sudanonautes granulatus*, Cumberlidge, 1999: 174, 175, 198–201 (in part), figs. 31B, 32G, 33G, 34G, 35G, 36J, 37G, 39B, 53W, 54–57, 60G, 67H, tab. IX = *S. tiko*.

Lectotype. MNB Crust.11257 (CW 26, CL 18, CH 11, FW 8 mm), Missahoe, Klouto District (6.933081°N, 0.572483°E), 740 m asl, coll. G. Smend, selected from the syntype series by Bott (1955).

Paralectotypes. MNB Crust.8980, 3 adult females (CWs 31.0 ovigerous, 30.5, 23.1 mm), 2 subadult females, (CWs 19.5, 18.8 mm), Missahoe, Klouto District (6.933081°N, 0.572483°E), 740 m asl, 30 Mar. 1893, coll. E. Baumann. ZSM 1214/8, 5 adult males (CW 25.0, CL 18.0, CH 9.5, FW 7.8 mm, CW 25.5, CL 18.2, CH 8.93, FW 7.6 mm, CW 23.6, CL 16.9, CH 8.9, FW 6.9 mm, CW 22.0, CL 15.7, CH 8.2, FW 6.5 mm, CW 23.3, CL 15.9, CH 7.5, FW 6.7 mm, subadult male, CW 16.1, CL 11.6, CH 5.6, FW 5.3 mm), Missahoe, Klouto District (6.933081°N, 0.572483°E), 740 m asl, coll. E. Baumann. MNB Crust.8977, adult male (CW 23.0 mm), Bismarckburg (8.178194°N, 0.686241°E), 590 m asl, coll. R. Büttner. MNB Crust.8978, subadult male (CW 18.8, CL 13.6, CH 6.4, FW 6.1 mm) plus several other specimens, Bismarckburg (8.178194°N, 0.686241°E), 590 m asl, 20 Jul. to 20 Sep. 1890, coll. R. Büttner. MNB Crust.20170, female, 2 Jan. 1893. MNB Crust.20171, 2 males, 2 females, coll. S. Conradt. MNB Crust.20173, Bismarckburg (8.178194°N, 0.686241°E), 590 m asl, coll. R. Büttner. MNB Crust.20194, adult female (CW 22.2, CL 16.1, CH 8.0, FW 7.6 mm), Bismarckburg (8.178194°N, 0.686241°E), 590 m asl, 15 May 1893, coll. S. Conradt. MNB Crust.20244, 4 females, Bismarckburg (8.178194°N, 0.686241°E), 590 m asl, 24 Feb. 1904, coll. C.W.M. Schröder. MNB Crust.21312, 3 adult females (largest CW 27 mm), Bismarckburg (8.178194°N, 0.686241°E), 590 m asl. MNB Crust.21313, male, Bismarckburg (8.178194°N, 0.686241°E), 590 m asl, coll. R. Büttner. ZSM 1214/1, adult male (CW 25.0, CL 17.2, CH 9.0, FW 7.8 mm), adult female ovigerous (CW 23.1, CL 16.2, CH 7.8, FW 6.7 mm), subadult male (CW 18.1, CL 13.5, CH 6.7, FW 5.6 mm), Bismarckburg (8.178194°N, 0.686241°E), 590 m asl.

Rediagnosis. Carapace surface smooth with no deep grooves, granules, or carinae. Exorbital tooth large, intermediate tooth (between exorbital, epibranchial teeth) small, distinct, pointed, epibranchial tooth reduced to granule (Fig. 1A). Anterolateral margin lined by row of small granules; vertical sulcus on branchiostegite granulated, in line with intermediate tooth, dorsal part curving posteriorly just before meeting anterolateral margin at epibranchial tooth, dividing suborbital from subhepatic region (Figs. 1B, 4A). Thoracic sternal suture S3/4 reduced to 2 small notches at sides of sternum; outer margins of S3, S4 thickened, raised (Fig. 1B). Third maxilliped exopod with long flagellum, ischium with faint vertical sulcus (Fig. 7D). Cheliped carpus inner margin distal tooth large spine, proximal tooth small (Fig. 5G). G1 TA elongated (TA/SS 0.75), basal half angled slightly outward at 13° to G1 SS longitudinal axis, midpoint curved sharply outward at 72° to G1 SS longitudinal axis, distal third tapering to pointed tip; TA midsection slightly widened, dorsal fold slightly higher than ventral fold (Fig. 6A, B); longitudinal sulcus of TA visible on ventral side for proximal two-thirds of TA (Fig. 6A, B). G2 (Fig. 6C) much shorter than G1 (G2 TA extremely short (G2 TA/SS 0.14), tip only reaching G1 TA-SS junction). Small species, adult size range 21–32 mm.

Redescription. Male paralectotype (MNB Crust.8977). Carapace. Cephalothorax ovoid, carapace $3.5 \times$ as wide as FW (CW/FW 3.5), medium length (CL/FW 2.5), medium height (CH/FW 1.2) (Fig. 1A). Anterior margin of front straight, curving down; posterior margin about two-thirds as wide as CW (Fig. 1A). Carapace surface smooth with no deep grooves, granules, or carinae. Anterolateral margin lined by row of small granules. Postfrontal crest smooth, distinct, complete, meeting anterolateral margins; mid-groove broad, shallow. Exorbital tooth large, intermediate tooth between exorbital, epibranchial teeth small, distinct, pointed, epibranchial tooth reduced to granule (Figs. 1B, 4A). Longitudinal sulcus on branchiostegite beginning at respiratory opening, curving backwards, dividing suborbital, subhepatic regions from pterygostomial region; vertical sulcus on branchiostegite granulated, in line with intermediate tooth, dorsal part curving posteriorly just before meeting anterolateral margin at epibranchial tooth, dividing suborbital from subhepatic region (Fig. 1B).

Thoracic sternum. Sternal suture S1/2 short, complete; S2/3 deep completely traversing sternum; S3/4 reduced to 2 small notches at sides of sternum; outer margins of S3, S4 thickened, raised (Fig. 1B). Third maxillipeds filling entire oral field, except for transversely oval efferent respiratory openings; exopod with long flagellum, ischium with faint vertical sulcus (Fig. 7D). Mandibular palp with 2 articles, terminal article simple, article junction with fringe of long setae, but lacking either anterior lobe or ledge (Fig. 7E). First 5 pleomeres of male pleon (A1–5) broad, short, tapering inward; A6, long, narrow, telson triangular, distal tip rounded (Fig. 1B).

Pereiopods. Chelae unequal, left longer than right (Fig. 5A, B). Dactylus of left (major) chela broadened, slightly arched, enclosing long narrow interspace when closed, palm swollen (Figs. 1A, 5A). Movable finger (dactylus), fixed finger (propodus) of left chela each lined by pointed teeth, medium size proximally, small size distally. Cheliped merus lower margins both lined by small teeth, distal meral tooth larger, pointed (Fig. 1B). Cheliped carpus inner margin distal tooth large spine, proximal tooth small, $1/3^{\text{rd}}$ size of distal tooth (Figs. 1A, 5G). P2–5 (Fig. 1A) not elongated, P5 shortest leg; dactyli P2–5 tapering to point, each bearing rows of downward-pointing sharp corneous spines.

Gonopods. G1 TA elongated (TA/SS 0.75), basal half angled slightly outward at 13° to G1 SS longitudinal axis, midpoint turned sharply outward at 72° to G1 SS longitudinal axis, distal third tapering to pointed tip; TA midsection slightly widened, dorsal fold slightly higher than ventral fold (Fig. 6A, B); longitudinal sulcus of TA visible on ventral side for proximal two-thirds of TA (Fig. 6A, B) sulcus continuing to tip but visible only if gonopod turned to superior view. G1 SS widest at base, narrowest distally, slim, tapering evenly to TA-SS junction (ratio of width of basal margin / distal margin = 2.5); mesial, lateral margins of G1 SS completely smooth; G1 SS distal margin straight ventrally, with U-shaped indentation dorsally; G1 SS ventral side with slim flap folded inward, distally almost meeting outer margin, angled diagonally downwards, leaving heavily setose ventral side of G1 SS exposed (Fig. 6A). G2 (Fig. 6C) much shorter than G1, only reaching G1 TA-SS junction; G2 TA extremely short (G2 TA/SS 0.14), tip rounded; G2 SS widest at base, tapering sharply inward about one-third along length, with last two-thirds forming long, thin, tapering, upright process that supports short G2 TA (Fig. 6C).

Size. Small species, adult size range between CWs 21–32 mm.

Type locality. Togo, Missahoe, near Kpalimé, north of Klouto [= Kloto].

Habitat. Savanna vegetation predominates in most of Togo, except for the southwestern highland region between 600 and 986 m asl where *S. granulatus* s.s. was collected, where there are tropical semi-deciduous moist forests that receive an annual rainfall between 1,300 and 1,600 mm. This area is part of the southeastern corner of the Volta Freshwater Ecoregion 507 (Thieme *et al.* 2005; Abell *et al.* 2008). The forested highland region where this species occurs is an eastern outlier of the biodiversity-rich Upper Guinea forest of West Africa which extends east from Guinea, Sierra Leone, Liberia, and Côte d’Ivoire, as far east as Ghana and western Togo.

Distribution. *Sudanonautes granulatus* s.s. is restricted to the highlands of western Togo near the eastern border of Ghana between Missahoe (6.933081°N, 0.572483°E, 740 m asl) and Bismarckburg (8.178194°N, 0.686241°E, 590 m asl.) These two localities are 140 km apart (Fig. 8). It should be noted that the Bismarckburg, Togo locality for *S. granulatus* s.s. was incorrectly recorded by Cumberlidge (1993a) as “Bismarcksburg (= Aného, 40 km east of Lomé)” when in fact Bismarckburg (the correct spelling) for this German colonial station is in the highlands of western Togo (Krell 1994).

Remarks. Balss (1929) distinguished *P. d. granulata* from Togo by its strongly granulated anterolateral carapace margins and small adult body size range between CWs 21–32 mm, confirmed by the size of 3 ovigerous females (CWs 24, 31, and 32 mm) among this material. Balss (1929) contrasted these specimens with the type of *Thelphusa decazei* A. Milne-Edwards, 1886, from the Alima River in the République du Congo, which has a

larger adult body size (CW 40.4 mm) and smooth anterolateral carapace margins (Capart 1954: figs. 12, 15). Balss (1929) treated the specimens from Togo as a subspecies of *T. decazei* because he attributed differences in carapace margin granulation and adult size range between the specimens from Togo and others from Cameroon (that he identified as *Potamonautes decazei*) as geographic variation within the same species. Balss (1929) expanded the range of *Potamonautes decazei* accordingly, and listed the distribution of this species as ‘Togo, Cameroon, Gabon (Franceville)’. It is likely that the listing from Gabon was an error arising out of the ambiguity of the recording of the type locality of *T. decazei* as ‘the Alima River, Franceville’ because the Alima River is in the République du Congo, while Franceville is in Gabon.

Bott (1955: 300–301), like Balss (1929) also noted differences in carapace margin granulation and adult size range between the samples of *P. d. granulata* from Togo and *P. decazei* Cameroon but treated *P. d. granulata* as a junior synonym of *S. (S.) d. decazei* (A. Milne-Edwards, 1886) rather than a subspecies. Later, Bott (1964) judged *S. (S.) d. decazei* from Central Africa to be a junior synonym of *S. (S.) p. pelii* (Herklots, 1861) from Ghana. Subsequently Cumberlidge (1994, 1999) considered *S. (S.) p. pelii* to be a junior synonym of *S. aubryi* (H. Milne Edwards, 1853). These differing opinions regarding the taxonomic status of *S. granulatus* s.l., are addressed here.

This study is based on a detailed description of the male paralectotype of *P. d. granulata* from Bismarckburg, Togo (Fig. 8). The carapace, cheliped, sternal, and gonopod characters of this specimen, as well as the adult body size range of the samples, are all similar to those of other adult males in the samples examined by Balss (1929) from Togo, and are all judged to be conspecific. The male paralectotype of *S. granulatus* s.s. was also compared with other specimens from Côte d’Ivoire, Nigeria, Cameroon, and Bioko identified by Cumberlidge (1993a) as *S. granulatus* s.l. These specimens were found to be significantly different from each other and from *S. granulatus* s.s. and are assigned in this work to either a new species, or a revised species. Comparisons of the paralectotype of *S. granulatus* s.s. with other specimens from Nigeria, Cameroon, Ghana, and the Central African Republic identified by Cumberlidge (1993a) as *S. granulatus* s.l. indicated that they should be excluded from *S. granulatus* s.s. on morphological grounds (see below).

All of the specimens attributed by Cumberlidge (1993a) to *S. granulatus* s.l. examined in the present study belong to *Sudanonautes* because they share the following combination of characters (Bott 1955; Cumberlidge 1999; Cumberlidge & Boyko 2001): a distinct intermediate tooth (between the exorbital and epibranchial teeth) on the anterolateral margin, a prominent horizontal postfrontal crest that is complete and meets both anterolateral margins; a thoracic sternal suture S3/4 that is absent except for two short notches on the margins; an elongated G1 TA (TA/SS 0.70–0.85); an extremely short G2 TA (G2 TA/SS 0.14); and a third maxilliped exopod with a long flagellum.

Specimens included by Cumberlidge (1993a) in *S. granulatus* s.l. are reassigned in the present work to the following taxa. Those from Missahoe, Togo (MNB Crust.8980, MNB Crust.11257, ZSM 1214/8) and Bismarckburg, Togo (MNB Crust.8977, MNB Crust.8978, MNB Crust.20170, MNB Crust.20171, MNB Crust.20173, MNB Crust.20194, MNB Crust.21312, MNB Crust.21313, MNB Crust.20244) are assigned to *S. granulatus* s.s. The specimen from Koudougou, Côte d’Ivoire (NBL CRUS.D.35246) is described here as *S. koudougou* **n. sp.** (Figs. 3A–D, 5E, F, I, 7 A–C, 8). Specimens from Umaji, Nigeria (NMU 9.IV.1983), from the Oban Hills, Nigeria (NMU 5.VI.1979, NMU 29.VI.1979, NMU 3.VIII.1980, NMU 20.X.1980) are all included in *S. umaji* **n. sp.** (Figs. 2A, B, 4B, 5C, D, H, 6D, F, 7, 8). Other specimens from Nigeria (NMU 28.IV.1979), Cameroon (ZIM K27877), and Bioko Island (ZIM K5362) are assigned here to *S. tiko*. A female from Bipindi, Cameroon (MNB Crust.15182) erroneously listed by Cumberlidge (1993a) as *S. granulatus* s.l. is re-identified here as *S. aubryi*. Finally, the taxonomic status of several other specimens listed by Cumberlidge (1993a) as *S. granulatus* s.l. from Nigeria (NHM 1938.7.1.24–25), Cameroon (ZIM K3492, ZIM K30393, ZIM K30394, MNB Crust.10194, MNB Crust.20158, MNB Crust.20168, MNB Crust.21304, MNB Crust.21305), Ghana (NHM 1902.8.17.1), and the Central African Republic (ZIM K5357) is now ambiguous and they should be regarded as *incertae sedis*. It is likely that all of these should be removed from *S. granulatus* s.l., however, their true identities cannot be established until further studies have been undertaken.

Sudanonautes umaji **n. sp.**

(Figs. 2A, B, 4B, 5C, D, H, 6D, F, 7F, 8)

Sudanonautes orthostylis, Cumberlidge, 1989: 231–232, 239–240 (in part), tabs. 1, 2.

Sudanonautes granulatus, Cumberlidge, 1993a: 806, 810 (in part), figs. 3 h–j, 4e, f.

Holotype. NMU 9.IV.1983, adult male (CW 27.6, CL 18.3, CH 9.0, FW 9.0 mm, P1 propodus length \times height: R 29.8 \times 11.0 mm, L 19.5 \times 6.0 mm), Nigeria, Umaji, 12 km north-west of Obudu Cattle Ranch, 281 m asl (6.481086°N, 9.251100°E), Amire u Kiriki River, tributary of Katsina-Ala and Benue Rivers, 9 Apr. 1983, coll. N. Cumberlidge.

Paratypes. NMU 9.IV.1983, adult male (CW 25.0, CL 17.8, CH 8.6, FW 8.6 mm), 3 subadult females (CW 21.9, CL 16.1 mm, chela propodus length \times height: right 13.5 \times 4.0 mm, left 13.0 \times 4.0 mm, CW 20.9, CL 15.2 mm, CW 20.8, CL 15.4 mm), juvenile female (CW 18.0, CL 13.2 mm), Nigeria, Umaji, 12 km northwest of Obudu Cattle Ranch, 281 m asl (6.481086°N, 9.251100°E), Amire u Kiriki River, a tributary of the Katsina-Ala and Benue Rivers, 9 Apr. 1983, coll. N. Cumberlidge.

Other material. NMU 5.VI.1979, adult male (CW 34.66 mm), subadult female (CW 21.65 mm), Nigeria, Oban Hills, Ekan Road, 30 km northeast of Calabar (5.1448315°N, 8.5245183°E), 5 Jun. 1979, coll. J. C. Reid. NMU 29.VI.1979, adult male (CW 23.56 mm), Nigeria, Oban Hills, Ekan Road, 30 km northeast of Calabar (5.1448315°N, 8.5245183°E), 29 Jun. 1979, coll. J. C. Reid. NMU 3.VIII.1980, adult male (CW 30.02 mm), Nigeria, Oban Hills, Ayip-Eku Oil Palm Estate, between Osomba and New Ndebezi villages (5.4000°N, 8.7000°E), 3 Aug. 1980, coll. J. C. Reid.

Diagnosis. Carapace: surface smooth, anterolateral margins, suborbital margins, postfrontal crest all granulated. Exorbital tooth low, broad, intermediate tooth pointed, smaller than exorbital tooth, epibranchial tooth reduced to granule; vertical sulcus on branchiostegite in line with intermediate tooth, dorsal part curving posteriorly just before meeting anterolateral margin at epibranchial tooth (Figs. 2B, 4B). Mandibular palp with 2 articles, terminal article simple, article junction with fringe of long setae, but lacking either anterior lobe or ledge (Fig. 7F); third maxilliped with flagellum on exopod, ischium with deep vertical sulcus (Fig. 2B). Chelipeds: movable finger (dactylus) of major chela broadened, slightly arched, enclosing long narrow interspace when closed; fixed finger (pollex of propodus) of chela with 2 large sharp teeth proximally, otherwise small teeth distally (Fig. 5C, D); lower margin of propodus of major chela longer than CW; cheliped carpus inner margin distal tooth large, pointed, proximal tooth small (Figs. 2A, 5H). Gonopods: G1 TA long (TA/SS 0.84), initially angled outwards at 17° to G1 SS longitudinal axis, midpoint curved sharply outwards at 70° to G1 SS longitudinal axis; G1 TA slim, midsection only slightly widened (Fig. 6D, E); TA with longitudinal sulcus running to tip, visible on ventral side on proximal two-thirds, entire groove visible only if gonopod turned to superior view (Fig. 6F). G2 TA extremely short (TA/SS 0.14).

Description. Adult male holotype. Carapace. Cephalothorax ovoid, width about 3 \times FW (CW/FW 2.9), length 2 \times FW (CL/FW 2.0), medium height, subequal to FW (CH/FW 1.1) (Fig. 2A). Anterior margin of front straight, curving under; carapace posterior margin width about two-thirds CW. Carapace surface smooth, lacking granules or carinae; anterolateral, suborbital margins each lined by row of small granules; postfrontal crest distinct, granulated, complete, meeting anterolateral margins; mid-groove of crest broad, shallow. Exorbital tooth low, broad, intermediate tooth distinct, small, about half size of exorbital tooth, epibranchial tooth reduced to granule (Fig. 2A); branchiostegite with longitudinal sulcus beginning at respiratory opening, curving backwards, dividing suborbital, subhepatic regions from pterygostomial region; vertical sulcus on branchiostegite in line with intermediate tooth, top part curving backwards just before meeting anterolateral margin at epibranchial tooth; vertical sulcus dividing suborbital from subhepatic regions (Figs. 2B, 4B).

Thoracic sternum. Sternal suture S1/2 faint complete; S2/3 deep, completely traversing sternum; S3/4 reduced to 2 small side notches, outer margins of S4 thickened, raised (Fig. 2B). Third maxillipeds filling entire oral field, except for transversely oval efferent respiratory openings; exopod with long flagellum, ischium with deep vertical sulcus (Fig. 4B). Mandibular palp with 2 articles, terminal article simple, article junction with fringe of long setae, but lacking either anterior lobe or ledge (Fig. 7F). First 5 pleomeres of male pleon (A1–5) broad, short, tapering inward; A6 long, narrow, telson triangular, tip rounded. Mature female pleon wide with oval outline, telson reaching S1/2, sides reaching coxae of P2–5, A6 longest, A5 widest, maximum width along A6–5 junction.

Pereiopods. P1 chelae unequal, right (major) longer, higher than left (Fig. 5C, D); P1 right propodus longer (29.8 mm) than CW (27.6 mm); movable finger (dactylus) of right chela broadened, slightly arched, enclosing elongated oval interspace when closed, one large tooth in proximal third, rest with small teeth along cutting edge (Fig. 5C); movable finger (pollex of propodus) of right chela with 2 large pointed teeth proximally, small teeth distally (Fig. 5C). Cheliped merus lower margins both lined by small teeth, distal meral tooth larger, pointed (Fig. 2A). Cheliped carpus inner margin distal tooth large spine, proximal tooth small, 1/3rd size of distal tooth (Figs. 2A, 5H). P2–5 neither elongated or shortened, P5 shortest leg; dactyli P2–5 tapering to point, each bearing rows of downward-pointing sharp bristles; P5 dactylus shortest article (Fig. 2A).

Gonopods. G1 TA long (TA/SS 0.84), initially angled outward at 17° to G1 SS longitudinal axis, midpoint curved sharply outward at 70° to G1 SS longitudinal axis; G1 TA midsection only slightly widened (Fig. 6D, E); G1 TA with longitudinal sulcus running from base to tip visible on ventral side in proximal two-thirds, entire groove visible only if gonopod turned to superior view (Fig. 6F). G1 SS widest at base, narrowest distally, slim, tapering evenly to TA-SS junction (ratio of width of basal margin / distal margin = 4); mesial, lateral margins of G1 SS completely smooth; G1 SS distal margin straight ventrally, with V-shaped indentation dorsally; G1 SS ventral side with slim flap folded inward, distally almost meeting outer margin, angled diagonally downwards, leaving heavily setose ventral side of G1 SS exposed (Fig. 6A). G2 shorter than G1 (G2 only reaching G1 TA-SS junction). G2 TA extremely short (G2 TA/SS 0.14); G2 SS widest at base, tapering sharply inward about one-third along length, last two-thirds forming long, thin, tapering, upright process supporting short G2 TA.

Size. Small species, adult size range CW 24–34.7 mm.

Type locality. Nigeria, Cross River State, Umaji, 12 km northwest of Obudu Cattle Ranch, 281 m asl (6.481086°N, 9.251100°E), Amire u Kiriki River, a tributary of the Katsina-Ala and Benue Rivers.

Etymology. The species is named for Umaji in Cross River State, southeast Nigeria where it was collected. The species epithet is used as a noun in apposition.

Distribution. Cross River State, southeast Nigeria (Fig. 8).

Habitat. Umaji in southeast Nigeria lies in the Northern Gulf of Guinea Drainages; Bioko Freshwater Ecoregion 518 (Thieme *et al.* 2005; Abell *et al.* 2008) in the evergreen rainforest zone that also includes parts of the Cameroon highlands and the mountain forests of Bioko Island, Equatorial Guinea. This area receives over 10 m of rainfall annually, and its aquatic systems include the Cross River basin in Nigeria, and the coastal rivers and streams that flow into the Gulf of Guinea from Cameroon and Bioko Island. Crabs were collected from under stones in a sandy, gravelly river bed. The river had been temporarily dammed by villagers so that crabs could be collected from the exposed dry river bed, after which the river flow was restored. *Sudanonautes umaji* n. sp. was collected at this locality together with specimens of *S. africanus* and *S. aubryi*. Several of the localities where this species occurs are in the Oban Hills, some of which are part of the Cross River National Park. This area is heavily forested and borders with equatorial rainforests in neighboring Cameroon.

Sudanonautes koudougou n. sp.

(Figs. 3A–D, 5E, F, I, 7A–C, 8)

Sudanonautes granulatus, Cumberlidge, 1993a: 806–807, 812 (in part), figs. 1a, b, 2a–d, 3a–c, 4a, b.

Holotype. NBL CRUS.D.35246, adult male (CW 58.1, CL 38.73, CH 18.2, FW 15.11 mm; lower margin of propodus of right chela = 61.6 mm), Côte d'Ivoire, Koudougou, 10 km southwest of Bouafl (6.957348 N, -5.763060 W), Dec. 1980.

Diagnosis. Carapace surface, anterolateral margins, suborbital margins, postfrontal crest, all completely smooth. Carapace distinctly wide (~4 × FW, CW/FW 3.9), elongated (CL/FW 2.6). Exorbital tooth blunt, low, intermediate tooth reduced to granule, epibranchial tooth almost undetectable; postfrontal crest mid-part distinct, ends faint towards anterolateral margins; vertical sulcus on branchiostegite running from intermediate tooth to longitudinal sulcus (Fig. 4C). Mandibular palp with 2 articles, terminal article simple, article junction with fringe of long setae but lacking lobe or ledge (Fig. 3C); third maxilliped exopod with flagellum, ischium smooth, with only faint vertical sulcus (Fig. 3B). Thoracic sternal suture S3/4 reduced to 2 small notches at sides of sternum, outer margins of S4 flat, not raised. Chelipeds: moveable finger (dactylus) of right chela narrow, strongly arched enclosing wide, ovoid space when closed and tips touching; palm of propodus swollen (Fig. 5E, F, I); propodus of right chela lower margin elongated, longer than CW (Figs. 3A, 5E, F, I). Gonopods: mesial, lateral margins of G1 SS fringed by long setae; G1 TA only slightly widened in mid-section, with distinct longitudinal sulcus running length of TA (Fig. 7A, B); G2 TA extremely short (TA/SS 0.1 (Fig. 7C).

Description. Male holotype. Carapace. Cephalothorax ovoid, carapace distinctly wide (~4 × FW, CW/FW 3.9), elongate (CL/FW 2.6), medium height (CH/FW 1.2). Anterior margin of front straight, curving under; carapace posterior margin width about one third CW (Figs. 3A, 4C). Surface of carapace smooth with no deep grooves; postfrontal crest mid-part distinct, ends faint towards anterolateral margins; midgroove broad, shallow. Exorbital

tooth blunt, low, intermediate tooth reduced to granule, epibranchial tooth almost undetectable. Anterolateral margin of carapace entirely smooth, lacking teeth or granules (Fig. 3A). Longitudinal sulcus on branchiostegite beginning at respiratory opening, curving backwards, dividing suborbital, subhepatic regions from pterygostomial region; vertical sulcus on branchiostegite in line with intermediate tooth; vertical sulcus meeting longitudinal sulcus, dividing suborbital from subhepatic region (Fig. 4C).

Thoracic sternum. Sternal suture S1/2, short, faint, S2/3 horizontal, completely traversing sternum; S3/4 reduced to 2 small notches at sides of sternum, outer margins of S4 flat, not raised. Third maxillipeds filling entire oral field, except for transversely oval efferent respiratory openings, exopod with long flagellum, ischium smooth, with faint vertical sulcus (Fig. 3B). Mandibular palp with 2 articles, terminal article simple, article junction with fringe of long setae, but lacking either anterior lobe or ledge (Fig. 3C). First five pleomeres of male (A1–5) broad, short, tapering inward, distal pleomere (A6) long, narrow, telson triangular, distal tip rounded (Fig. 3D).

Pereiopods. Major (right) chela propodus longer, higher than left chela (Figs. 3A, 5C, D); moveable finger (dactylus) of right chela narrow, strongly arched enclosing wide, ovoid space when closed and tips touching; palm of propodus swollen (Fig. 5E, F, I); lower margin of propodus of right chela longer than CW (Fig. 5E, F, I); movable, fixed fingers of right chela each lined by series of small pointed teeth. Left chela showing less enlargement, but dactylus narrow, slightly arched, enclosing long space, lined by small teeth (5F). Cheliped merus lower margins both with rows of small round teeth, distal tooth larger, pointed (Fig. 5I); cheliped carpus inner margin distal tooth small, pointed, proximal tooth smaller, pointed (Fig. 5I). P2–5 neither elongated nor shortened, P4 longest leg, P5 shortest leg; dactyli P2–5 tapering to point, each bearing rows of downward-pointing corneous spines (Fig. 3A).

Gonopods. G1 TA long (TA/SS 0.76), basal half straight in line with G1 SS longitudinal axis, midpoint curved outward at 63° to G1 SS longitudinal axis, distal third tapering to pointed tip; TA midsection only slightly widened (Fig. 7A, B); longitudinal sulcus of TA visible on ventral side for proximal two-thirds of TA, sulcus continuing to tip, but visible only if gonopod turned to superior view. G1 SS broad (ratio of width of basal margin / distal margin = 4); G1 SS ventral side with slim flap folded inward, distally almost meeting outer margin, angled diagonally downwards, leaving heavily setose ventral side of G1 SS exposed (Fig. 7A). G2 shorter than G1 (G2 only reaching G1 TA-SS junction). G2 TA extremely short (G2 TA/SS 0.14), tip rounded (Fig. 7C); G2 SS widest at base, tapering sharply inward about one-third along length, with last two-thirds forming long, thin, tapering, upright process supporting short TA (Fig. 7C).

Size. Large species, size at maturity ca. CW 58 mm.

Type locality. Côte d'Ivoire, Koudougou, 10 km southwest of Bouaflé (6.957348 N, -5.763060 W) in the Marahoué Region in the Sassandra-Marahoué District.

Etymology. The new species is named for the town of Koudougou in central Côte d'Ivoire, where it was collected. The species epithet is used as a noun in apposition.

Habitat. The Marahoué Region where Koudougou is situated lies in the middle of the Eburneo Freshwater Ecoregion 514 (Thieme *et al.* 2005; Abell *et al.* 2008). This area is bounded by the basins of the Comoé, Bandama, and Sassandra Rivers that flow south into the Atlantic Ocean. The vegetation in this ecoregion reflects the amount of rain received, with dry Sudan savanna woodland in the plateau in the northern part of this ecoregion that records the lowest annual rainfall. South of this the vegetation is a forest-savanna mosaic that receives more annual rainfall, to the south of which is Guinean rain forest that gets the highest annual rainfall. *Sudanonautes koudougou n. sp.* was collected in the southern part of this ecoregion in the Guinean rain forest zone where much of the forest vegetation has now been converted to other uses.

Distribution. This species is known only from the Marahoué Region in central Côte d'Ivoire.

Remarks. The holotype (NBL CRUS.D.35246) was originally identified as *S. granulatus* s.l. by Cumberlidge (1993a: figs. 1a, b, 2a–d, 3a–c, 4a, b) and was therefore part of the material included in that earlier redescription. The figures of this specimen by Cumberlidge (1993a) have been reorganized, relabeled, and used in the present work to illustrate the holotype of *S. koudougou n. sp.* (Figs. 3A–D, 5E, F, I, 7A–C). Cumberlidge (1993a) attributed differences between the paralectotype of *S. granulatus* s.s. from Togo and *S. koudougou n. sp.* from Côte d'Ivoire to be the result of geographical variation within *S. granulatus* s.l. There are a number of morphological differences in characters of the carapace, cheliped, thoracic sternum, and G1 between the paralectotype of *S. granulata* s.s. and the holotype of *S. koudougou n. sp.* that support the recognition of these 2 specimens as separate species that are also distinct from all other species of *Sudanonautes*.

Comparisons. In addition to *S. koudougou n. sp.*, Côte d'Ivoire is home to 5 other species of freshwater crabs

in 3 genera (Cumberlidge 1999): *Liberonautes latidactylus* (de Man, 1903), *L. chaperi* (A. Milne-Edwards, 1886), *L. nimba* Cumberlidge, 1999, *Potamonautes ecorseii* (Marchand, 1902), and *S. aubryi* (Cumberlidge 1999). Species of *Sudanonautes* and *Liberonautes* can be distinguished from *Potamonautes* by the presence of an intermediate tooth between the exorbital and epibranchial teeth on the anterolateral margin (vs the lack of an intermediate tooth in all *Potamonautes* species) (Cumberlidge 1999: 128–129). Species of *Sudanonautes* can be distinguished from *Liberonautes* by the angle of the G1 TA: it is directed outwards in *Sudanonautes* species (Cumberlidge 1999: figs. 38A–E, 39A–E) and inwards in *Liberonautes* species (Cumberlidge 1999: figs. 28A–D, 29A–D). *Sudanonautes koudougou* **n. sp.** can be distinguished from *S. aubryi* by the position of the postfrontal crest which (although faint) is aligned to meet the epibranchial teeth in *S. koudougou* **n. sp.** (Fig. 4C) (vs a postfrontal crest whose lateral ends meet the anterolateral margins behind the epibranchial teeth in *S. aubryi*; Cumberlidge 1999: fig. 30A).

***Sudanonautes tiko* Mvogo Ndongo, Schubart & Cumberlidge in Mvogo Ndongo, Schubart, von Rintelen, Tamesse & Cumberlidge, 2017**

Sudanonautes orthostylis, Cumberlidge, 1989: 231–237 (in part), figs. 1 a–g, 2a–c; tabs. 1, 2.

Sudanonautes granulatus, Cumberlidge, 1993a: 806–807, 812 (in part), figs. 1a, b, 2a–d, 3a–c, 4a, b.

Sudanonautes orthostylis, Cumberlidge, 1993b: 520–521 (in part), tab. 2.

Sudanonautes granulatus, Cumberlidge, 1999: 174, 175, 198–201 (in part), figs. 31B, 32G, 33G, 34G, 35G, 36J, 37G, 39B, 53W, 54–57, 60G, 67H, tab. IX.

Sudanonautes tiko, Mvogo Ndongo *et al.* (2017): 1–11, figs. 1–4, 6.

Holotype. MNB Crust.29628, adult male (CW 36.2 mm, CL 24.8 mm, CH 12.2 mm, FW 10.4 mm), Cameroon, Tiko, Tamba Forest, Southwest Region (4.180556N, 9.394444E), 100 m asl, 22 Aug. 2015, coll. P. A. Mvogo Ndongo.

Paratype. MNB Crust.29629, adult male (CW 35.4 mm, CL 25.1 mm, CH 12.0 mm, FW 10.3 mm), Cameroon, Edea, Mbus Michon, Littoral Region (3.757222N, 10.32056E), 137 m asl, 10 Jul. 2015, coll. P. A. Mvogo Ndongo.

Other material. LZUY-00, adult male (CW 28.7 mm, CL 20.7 mm, CH 9.7 mm, FW 9.2 mm), Cameroon, Edea, Mbus Michon, Littoral Region (3.757222°N, 10.32056°E), 9 Jul. 2015, coll. P. A. Mvogo Ndongo. NHM 1938.7.1.14–23, 2 adult males (CWs 33.6, 29.8 mm), 5 subadult males (CWs 27.8, 26.7, 25.9, 24.8, 22.9 mm), 5 juv. males (CWs 18.4, 17.9, 18.4, 17.9, 17.8 mm), 3 adult females (CWs 42.8, 36.0, 29.7 mm), subadult female (CW 20.7 mm), Cameroon, tributary of Cross River, Tinto, Asumbi, Mamfe Division, 716 m asl (5.545367°N, 9.588061°E), 1 Jul. 1938, coll. S. Sanderson. NMU 28.IV.1979, adult male (CW 41.5 mm), Nigeria, Oban Hills, Cross River State, Ekang (= Akansoko = MCC) Road, 25 km northeast of Calabar (5.108406°N, 8.523134°E), 28 Apr. 1979, coll. J. C. Reid. NMU TRW 1980.02b, adult male CW 39.6 mm, Nigeria, Cross River State, 30 km north of Calabar (5.1678128°N, 8.538973°E), 5 Mar. 1979, coll. J. C. Reid. NMU 07.2001h, adult male (CW 36.1 mm), 2 adult females (CWs 39.0 ovigerous, 30.1 mm), Equatorial Guinea, Bioko Island, Lago Loreto (3.407378°N, 8.673116°E), Jul. 2001.

Diagnosis (Mvogo Ndongo *et al.* 2017: figs. 1a, b, 2a–e, 3a–c). Carapace subovoid; postfrontal crest distinct, completely traversing carapace, meeting epibranchial teeth; exorbital tooth low, blunt, intermediate, epibranchial teeth both granule-sized. Vertical sulcus on branchiostegite aligned to meet anterolateral margin at epibranchial tooth. Third maxilliped exopod with long flagellum, ischium with deep vertical sulcus. Thoracic sternal suture S1/2 short, faint, S2/3 distinct, completely traversing carapace, S3/4 reduced to 2 short notches on lateral margins; margins of S1–4 thickened, raised; anterior margin of sternopleonal cavity low, not raised. Fingers of male major chela slim, elongated, fixed finger (pollex of propodus) with 2 large teeth proximally, movable finger (dactylus) distinctly arched enclosing elongated oval interspace when closed, with single large tooth one-third distance from base; cheliped carpus inner margin with 2 small pointed subequal teeth; cheliped merus lower margins both lined by small sharp teeth. G1 SS medium width (ratio of width of basal margin / distal margin = 3); G1 TA elongated (G1 TA/SS 0.33), one third length of gonopod, proximal G1 TA straight basally, distal half curving sharply outward, midsection widened, distally tapering evenly to narrow, pointed tip. G2 TA extremely short (TA/SS 0.1).

Size. A medium-sized species, adult size range CW 28–42.8 mm.

Type locality. Cameroon, Tamba Forest, Tiko, in the Southwest Region (04.180556°N, 9.394444°E), 100 m asl.

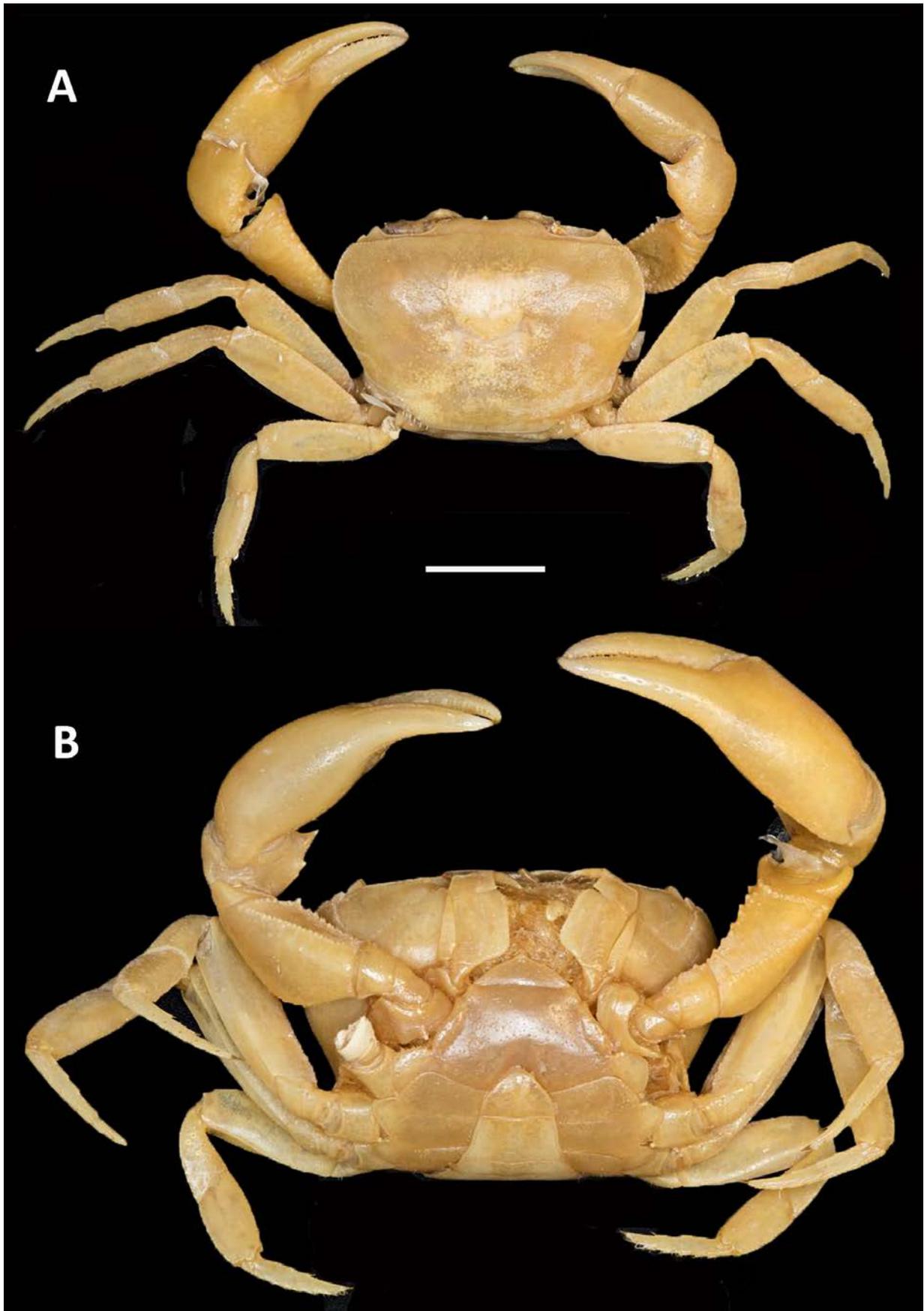


FIGURE 1. *Sudanonautes granulatus* (Balss, 1929) s.s. paralectotype from Bismarckburg, Togo (MNB Crust.8977). Whole animal, **A.** dorsal view; **B.** ventral view. Scale bars: A = 9.2 mm, B = 7 mm.

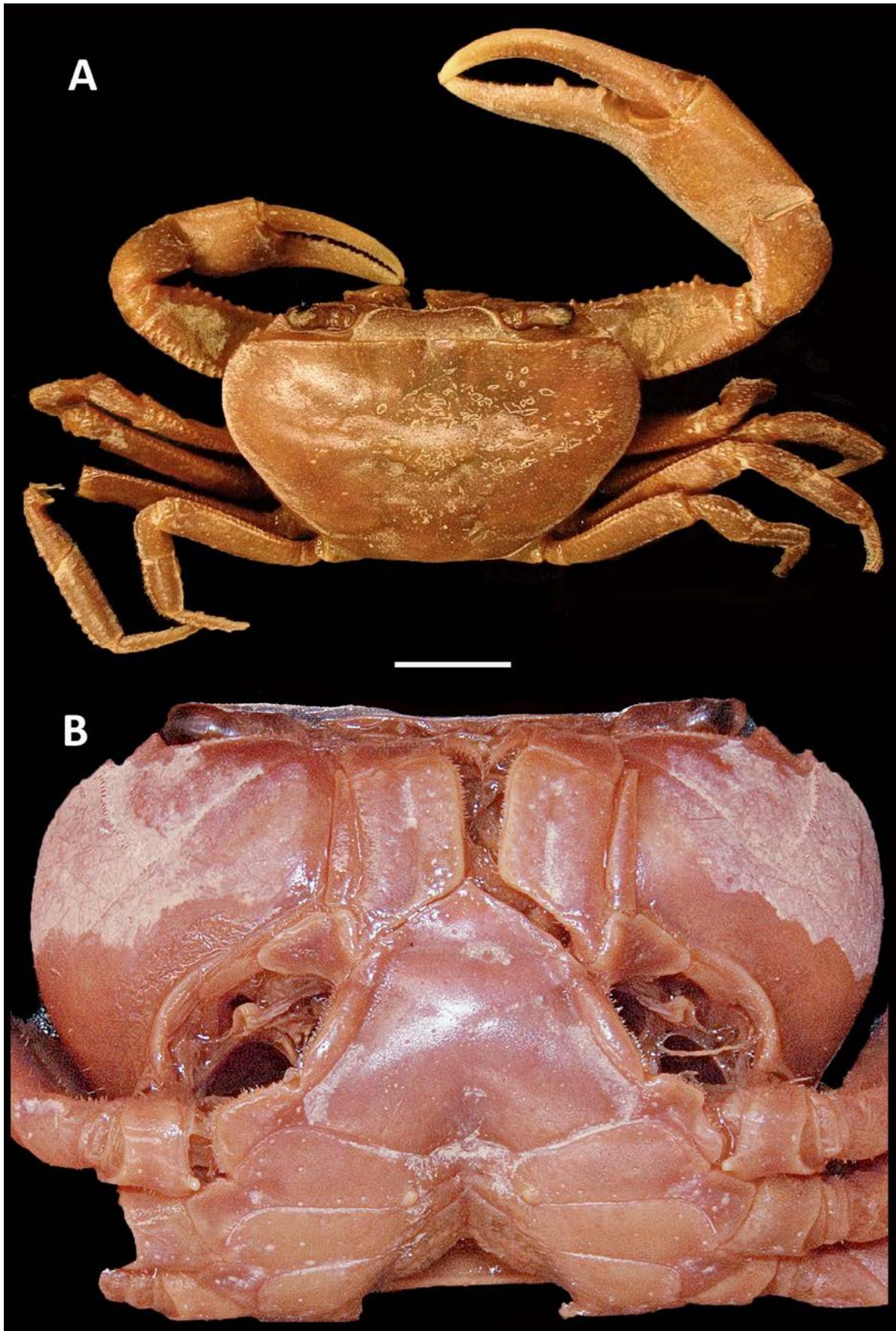


FIGURE 2. *Sudanonautes umaji* n. sp. holotype from Umaji, Nigeria (NMU 9.IV.1983). Whole animal, **A**, dorsal view; **B**, ventral view. Scale bars: A = 8 mm, B = 4.1 mm.

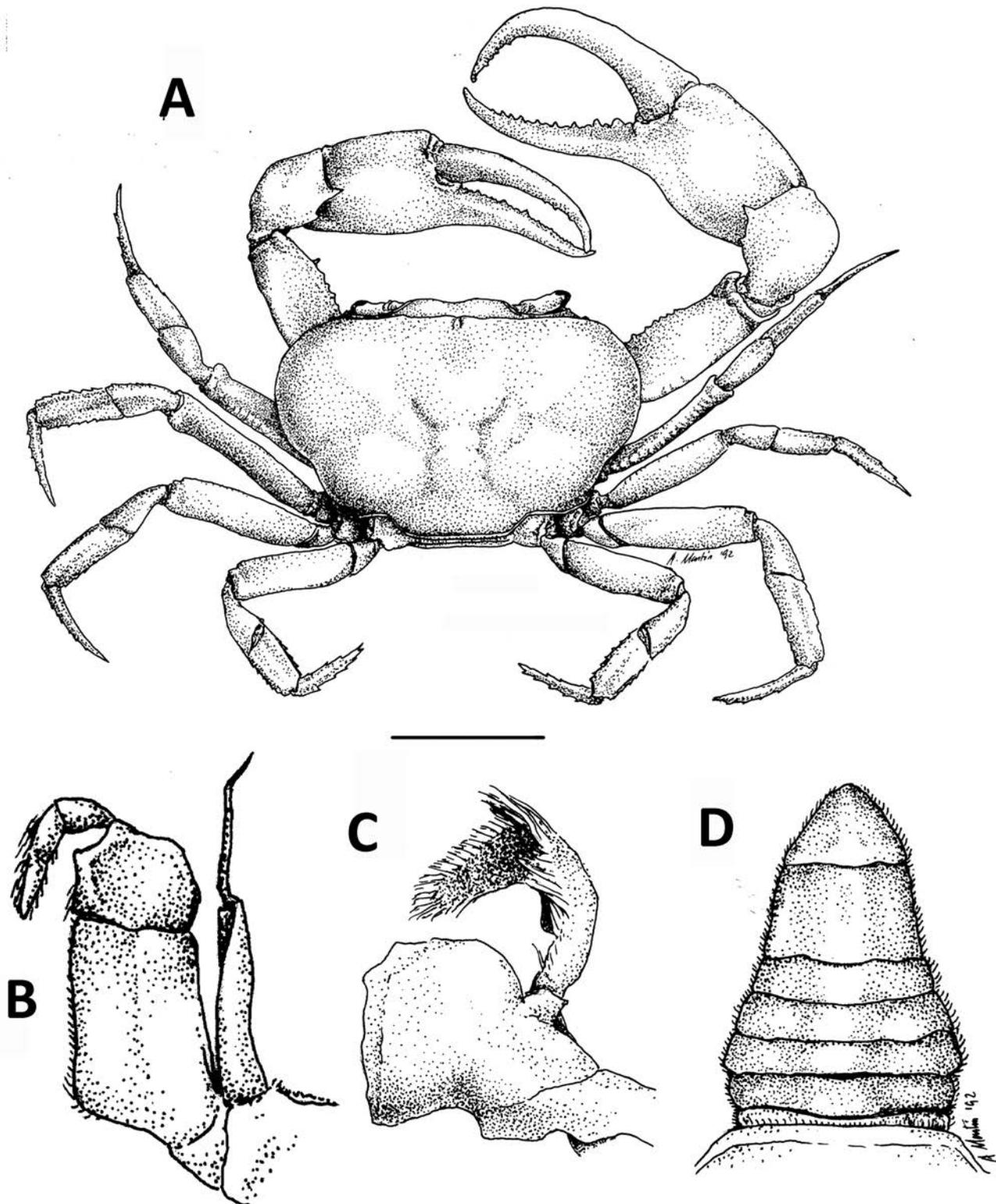


FIGURE 3. *Sudanonautes koudougou* n. sp. holotype from Koudougou, Côte d'Ivoire (NBL CRUS.D.35256). **A.** whole animal, dorsal view; **B.** left third maxilliped, frontal view; **C.** left mandible, external view; **D.** pleon, ventral view. Scale bars: A = 23.2 mm, B, C = 4 mm, D = 7 mm. Figures A–D are based on those originally published in Cumberlidge (1993a) and are reproduced here with the permission of Oxford University Press, the copyright owner of the Journal of Crustacean Biology.

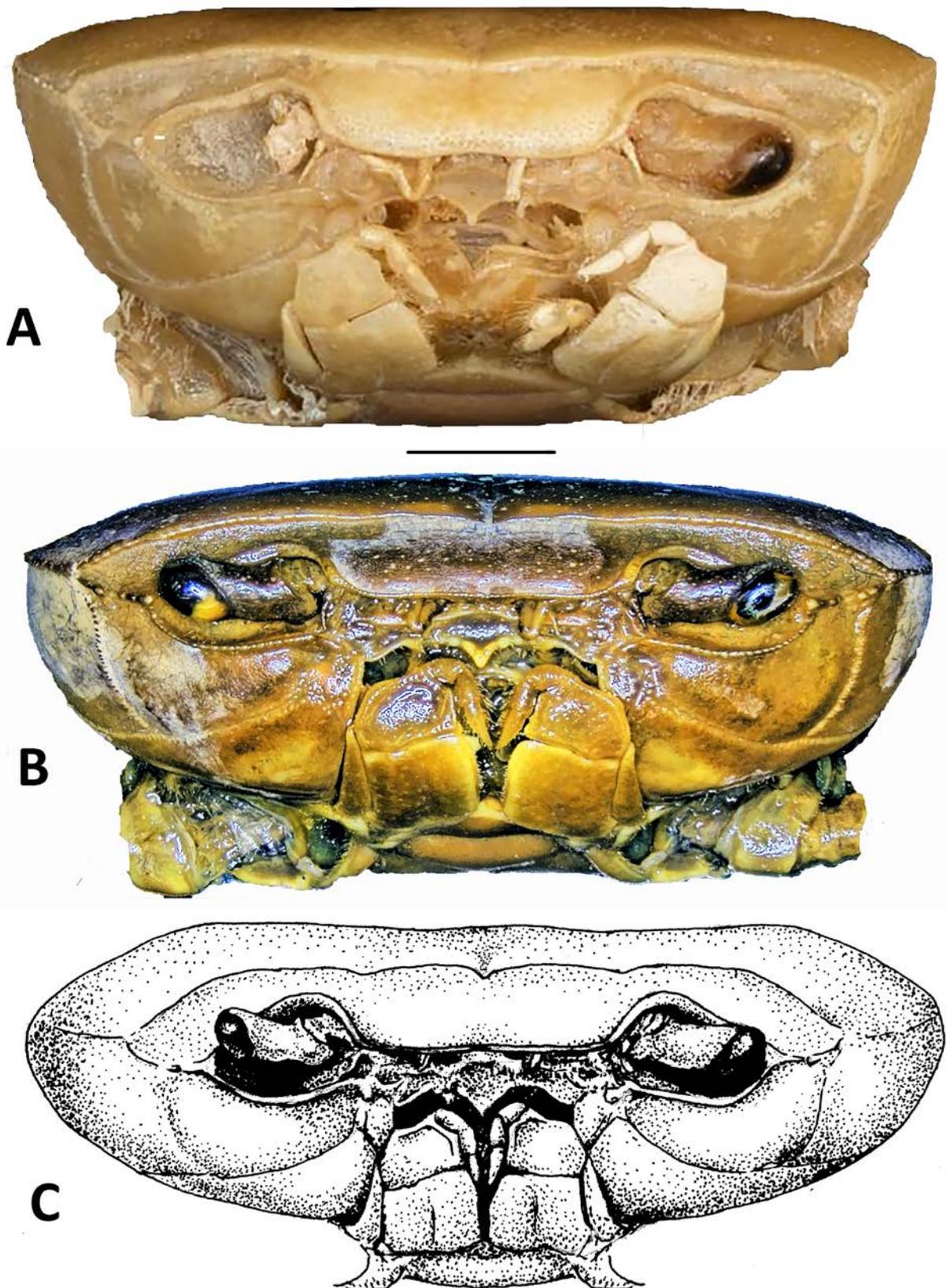


FIGURE 4. Carapace frontal view. **A.** *Sudanonautes granulatus* (Balss, 1929) s.s. paralectotype from Bismarckburg, Togo (MNB Crust.8977); **B.** *S. umaji* n. sp. holotype from Umaji, Nigeria (NMU 9.IV.1983); **C.** *S. koudougou* n. sp. holotype from Koudougou, Côte d'Ivoire (NBL CRUS.D.35256). Scale bars: A = 3.7 mm, B = 4.5 mm, C = 9.1 mm. Figure C was originally published in Cumberlandidge (1993a) and is reproduced here with the permission of Oxford University Press, the copyright owner of the Journal of Crustacean Biology.

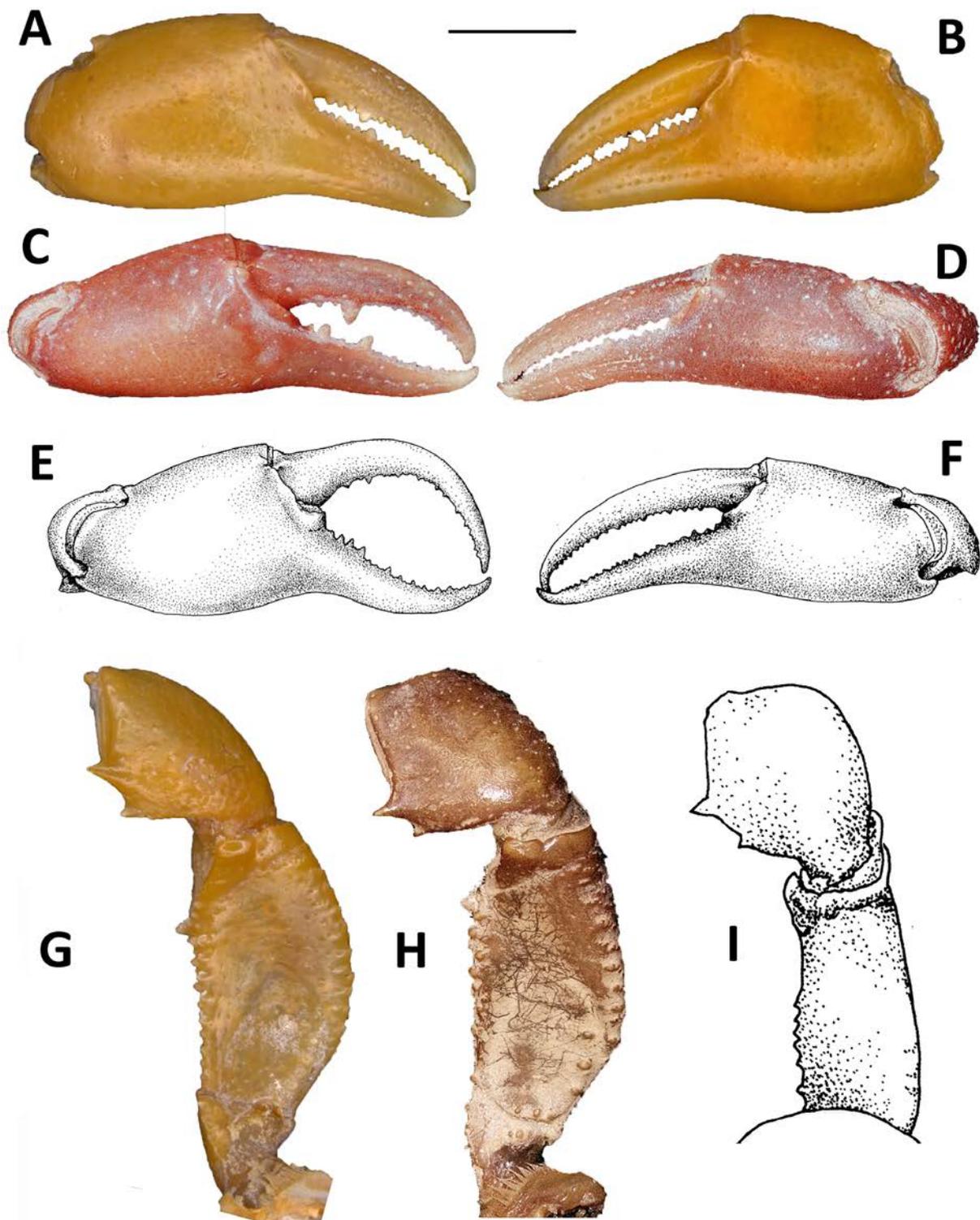


FIGURE 5. *Sudanonautes granulatus* (Balss, 1929) s.s. paralectotype from Bismarckburg, Togo (MNB Crust.8977). **A.** right chela, external view; **B.** left chela, external view. *Sudanonautes umaji* n. sp. holotype from Umaji, Nigeria (NMU 9.IV.1983). **C.** right chela, external view; **D.** left chela, external view. *Sudanonautes koudougou* n. sp. holotype from Koudougou, Côte d'Ivoire (NBL CRUS.D.35256). **E.** right chela, external view; **F.** left chela, external view. Right cheliped carpus and merus superior view of **G.** *S. granulatus* (Balss, 1929) s.s. (MNB Crust.8977); **H.** *S. umaji* n. sp. (NMU 9.IV.1983); **I.** *S. koudougou* n. sp. (NBL CRUS.D.35256). Scale bars: A, B = 6.2 mm, C, D = 8 mm, E, F = 3 mm, G–I = 4.9 mm. Figures E, F, and I are based on those originally published in Cumberlidge (1993a) and are reproduced here with the permission of Oxford University Press, the copyright owner of the Journal of Crustacean Biology.



FIGURE 6. *Sudanonautes granulatus* s.s. (Balss, 1929) paralectotype from Bismarckburg, Togo (MNB Crust.8977). **A.** right G1 ventral view; **B.** right G1 dorsal view; **C.** right G2 ventral view. *Sudanonautes umaji* n. sp. holotype from Umaji, Nigeria (NMU 9.IV.1983). **D.** right G1 ventral view; **E.** right G1 dorsal view; **F.** right G2 ventral view. Scale bars: A–C = 2.5 mm, D, F = 2 mm.

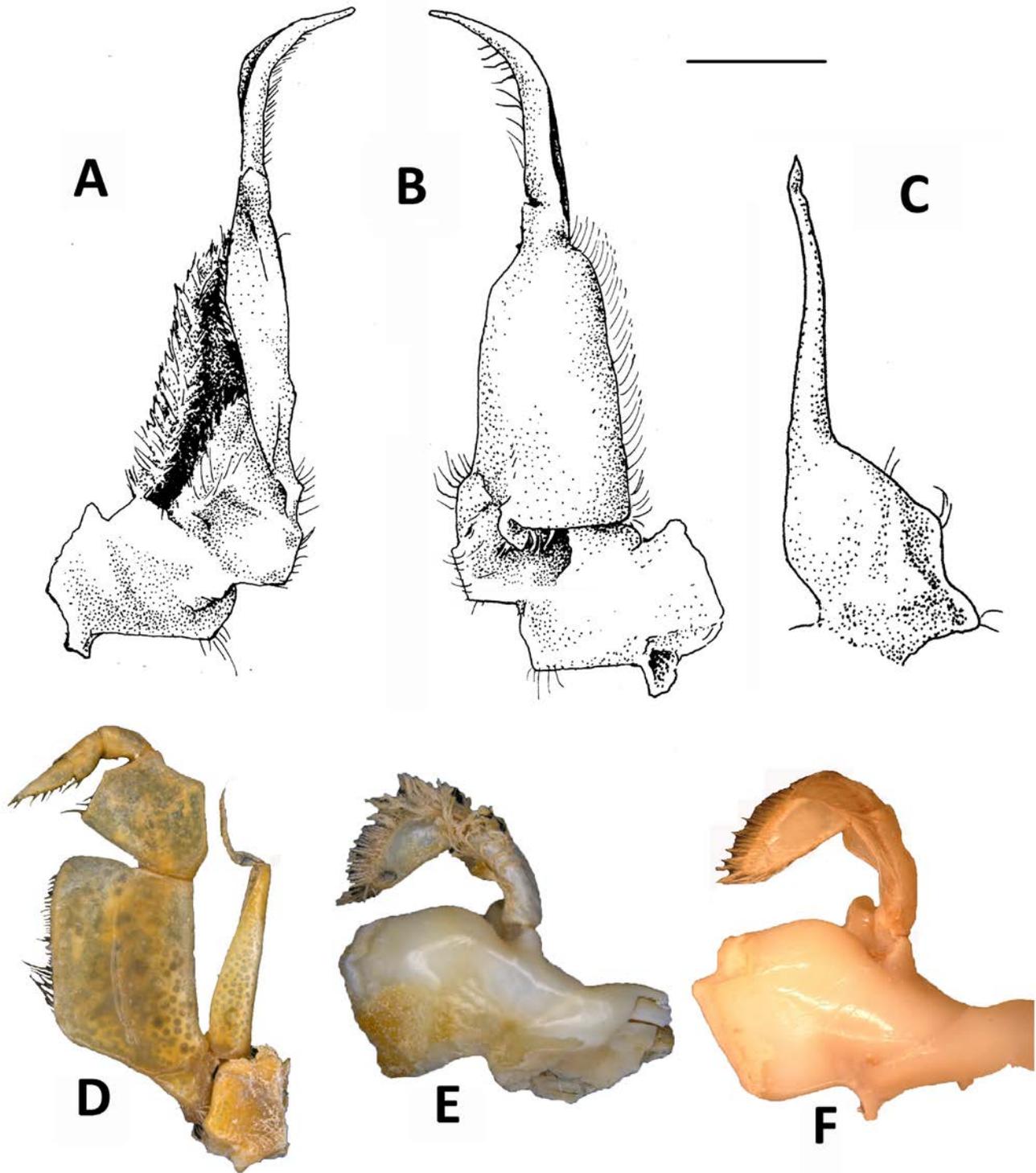


FIGURE 7. *Sudanonautes koudougou* n. sp. holotype from Koudougou, Côte d'Ivoire (NBL CRUS.D.35256). **A.** right G1 ventral view; **B.** right G1 dorsal view; **C.** right G2 ventral view. *Sudanonautes granulatus* s.s. (Balss, 1929) (MNB Crust.8977). **D.** left mandible, external view; **E.** left third maxilliped, external view. *Sudanonautes umaji* n. sp. holotype from Umaji, Nigeria (NMU 9.IV.1983). **F.** left mandible, external view. Scale bars: A, B, 2.9 mm, C = 2.5 mm, D, F = 5 mm. Figures A–C are based on those originally published in Cumberlidge (1993a) and are reproduced here with the permission of Oxford University Press, the copyright owner of the Journal of Crustacean Biology.

Habitat. *Sudanonautes tiko* is found in the humid area of the coastal rain forests bordering the Gulf of Guinea in Nigeria, Cameroon, and Bioko Island in the Northern and Southern Gulf of Guinea drainage ecoregions. Tiko (the type locality) and Edea are both in the coastal zone of Cameroon which includes volcanic highlands such as

Mount Cameroon (4,095 m asl), and receives a heavy annual rainfall (exceeding 5,000 mm). *Sudanonautes tiko* lives under rocks in small streams at Tiko where it occurs sympatrically with other species of freshwater crabs such as *S. africanus* and *S. floweri*. At Edea, *S. tiko* is found under small stones in wetland areas near the Sanaga River (Mvogo Ndongo *et al.* 2017).

Distribution. The present work expands the distribution of this species from two localities in the Littoral Region of southwest Cameroon (Tiko, Tamba Forest and Bwenga Forest in the Mungo River Basin, and Edea in the Sanaga River basin) to include localities in the Mamfe region of Cameroon, the adjoining Oban Hills in southeast Nigeria, and Bioko Island (Fig. 8).

Remarks. The full description of this species is given in Mvogo Ndongo *et al.* (2017). The specimen from the Oban Hills in southeast Nigeria (NMU 28.IV.1979) that was previously identified as *S. orthostylis* by Cumberlidge (1989) and as *S. granulatus* s.l. by Cumberlidge (1993a, 1999) is reassigned here to *S. tiko*. Similarly, the specimen from Bioko Island, Equatorial Guinea (ZIM K5362) that was previously identified as *S. granulatus* s.l. by Cumberlidge (1993a), and 3 specimens from Bioko that were collected more recently (NMU 07.2001h), are also re-identified here as *S. tiko*.

Comparisons. The 4 new and revised taxa in the present study (*S. granulatus* s.s., *S. umaji* n. sp., *S. koudougou* n. sp., and *S. tiko*) can be distinguished from each other by several morphological characters. *Sudanonautes granulatus* s.s. from Togo is superficially similar to *S. umaji* n. sp. from Nigeria, but the two differ as follows. The G1 TA is short (TA/SS 0.70) in *S. granulatus* s.s. (Fig. 6A, B) (vs a G1 TA that is longer (TA/SS 0.84) in *S. umaji* n. sp. (Fig. 6D, E)); the G1 SS is slim (ratio of width of basal margin / distal margin = 2.2) in *S. granulatus* s.s. (Fig. 6A, B) (vs a G1 SS that is broad (ratio of width of basal margin / distal margin = 4) in *S. umaji* n. sp. (Fig. 6C, D)); and the ischium of the third maxilliped has a faint vertical sulcus in *S. granulatus* s.s. (Fig. 7D) (vs an ischium of the third maxilliped with a deep vertical sulcus in *S. umaji* n. sp. (Fig. 2B)).

Sudanonautes granulatus s.s. and *S. umaji* n. sp. can both be distinguished from *S. koudougou* n. sp. from Côte d'Ivoire as follows. The mesial and lateral margins of the G1 SS are completely smooth in both *S. granulatus* s.s. (Fig. 6A, B) and *S. umaji* n. sp. (Fig. 6D, E) (vs G1 SS margins that are fringed by long setae in *S. koudougou* n. sp. (Fig. 7A, C)); the anterolateral margins of the carapace are distinctly granulated in both *S. granulatus* s.s. (Figs. 1A; 4A) and *S. umaji* n. sp. (Fig. 2A, B) (vs anterolateral margins that are completely smooth in *S. koudougou* n. sp. (Fig. 3A)); an intermediate tooth that is small but pointed in both *S. granulatus* s.s. (Fig. 3A) and *S. umaji* n. sp. (Fig. 4B) (vs an intermediate tooth that is reduced to a granule in *S. koudougou* n. sp. (Figs. 3A, 4C)); a carapace that is narrow and short in *S. granulatus* s.s. (CW/FW 3.2, CL/FW 2.2) and *S. umaji* n. sp. (CW/FW 2.9, CL/FW 2.0) (vs a carapace that is both wider (CW/FW 3.9) and longer (CL/FW 2.6) in *S. koudougou* n. sp. (Fig. 3A)); and the major chela has a dactylus that is only slightly arched with several large teeth (Figs. 1A, 2A, 4B) (vs a major chela dactylus that is highly arched and lacks large teeth in *S. koudougou* n. sp. (Figs. 3A, 5E, F)).

In addition, *S. granulatus* s.s., and *S. umaji* n. sp. can be distinguished from *S. tiko* from Cameroon, Nigeria, and Bioko by the size of the intermediate tooth between the exorbital and epibranchial teeth: it is small, distinct, and pointed in these 2 species (Figs. 1A, 2A) (vs reduced to a small granule in *S. tiko* (Mvogo Ndongo *et al.* 2017: figs. 1a, 2a)). *Sudanonautes koudougou* n. sp. can all be distinguished from *S. tiko* by the postfrontal crest: it is distinct in the middle but faint at the ends in the former species (Fig. 3A) (vs distinct across the entire carapace in *S. tiko* (Mvogo Ndongo *et al.* 2017: figs. 1a, 2a)).

Other *Sudanonautes* species. *Sudanonautes granulatus* s.s., *S. umaji* n. sp., *S. koudougou* n. sp., and *S. tiko* can all be distinguished from the 10 other West and Central African species in this genus (*S. africanus* (A. Milne-Edwards, 1869), *S. aubryi* (H. Milne Edwards, 1853), *S. chavanesii* (A. Milne-Edwards, 1886), *S. faradjensis* (Rathbun, 1921), *S. floweri* (de Man, 1901), *S. kagoroensis* Cumberlidge, 1991, *S. monodi* (Balss, 1929), *S. nigeria* Cumberlidge, 1999, *S. orthostylis* Bott, 1955, and *S. sangha* Cumberlidge & Boyko, 2001) as follows.

The adult body size range is either small or medium (between CWs 21–58 mm), and the surface of the posterior region of the carapace is smooth in the 4 species under study here (Figs. 1A, 2A, 3A) (vs an adult body size range between CWs 85–90 mm, and a posterior carapace surface that is roughened with distinct warty patches and raised ridges in *S. africanus* (Cumberlidge 1995b: fig. 1a; 1999: fig. 30B)). The lateral ends of the postfrontal crest meet the anterolateral margins at each of the epibranchial teeth in the 4 species under study here (Figs. 1A, 2A, 3A) (vs a postfrontal crest that meets the anterolateral margins behind the epibranchial teeth in *S. aubryi* (Cumberlidge 1999: fig. 38A)). The epibranchial teeth are both reduced to a small granule in the 4 species under study here (Figs. 1A, 2A, 3A) (vs epibranchial teeth that are large and sharp in *S. chavanesii* (Cumberlidge 1995c: fig. 1a; 1999: fig.

30C)). The anterolateral margin is lined by small granules in the 4 species under study here (Figs. 1A, 2A, 3A) (vs an anterolateral margin lined by sharp teeth in *S. faradjensis* (Cumberlidge 1995d: fig. 1a; 1999: fig. 30E)).

The G1 TA is slim and is only slightly widened in the midsection in the 4 species under study here (Figs. 6A, B, D, F, 7A, B) (vs a G1 TA that is distinctly widened in the midsection by a ventral fold that is twice as wide as the dorsal fold in *S. floweri* (Cumberlidge 1995a; 1999: fig. 38C) and in *S. monodi* (Cumberlidge 1999: fig. 39A)). In addition, the carapace is medium high (CH/FW 1.1–1.2) in the 4 species under study here (vs highly arched (CH/FW 1.5) in *S. floweri* (Cumberlidge 1995a: fig. 1b)). The outer margins of thoracic sternites S3 and S4 are thickened and in 3 of the 4 species under study here (except *S. koudougou*) (Figs. 1B, 2B) (vs thoracic sternites S3 and S4 whose margins are flat and not raised in *S. kagoroensis* (Cumberlidge 1999: fig. 32I)). The mandibular palp articulation is simple, and completely lacks a lobe or ledge in the 4 species under study here (Figs. 3C, 7E, F) (vs a mandibular palp with a small but distinct anterior lobe arising at the junction between the articles in *S. nigeria* (Cumberlidge 1999: fig. 33J)). The G1 TA has a visible longitudinal sulcus, the midpoint of the G1 TA is curved sharply outward from the G1 SS longitudinal axis, and the distal third tapers to a pointed tip in the 4 species under study here (Figs. 6A, B, D, F, 7A, B) (vs a G1 TA that lacks a longitudinal sulcus, that is entirely straight, except at the tip which is curved sharply outwards in *S. orthostylis* (Cumberlidge 1999: fig. 39C)). Finally, the exorbital tooth is low and blunt in the 4 species under study here (Figs. 1A, 2A, 3A) (vs an exorbital tooth that is large and triangular in *S. sangha* (Cumberlidge & Boyko 2001: fig. 4c)).

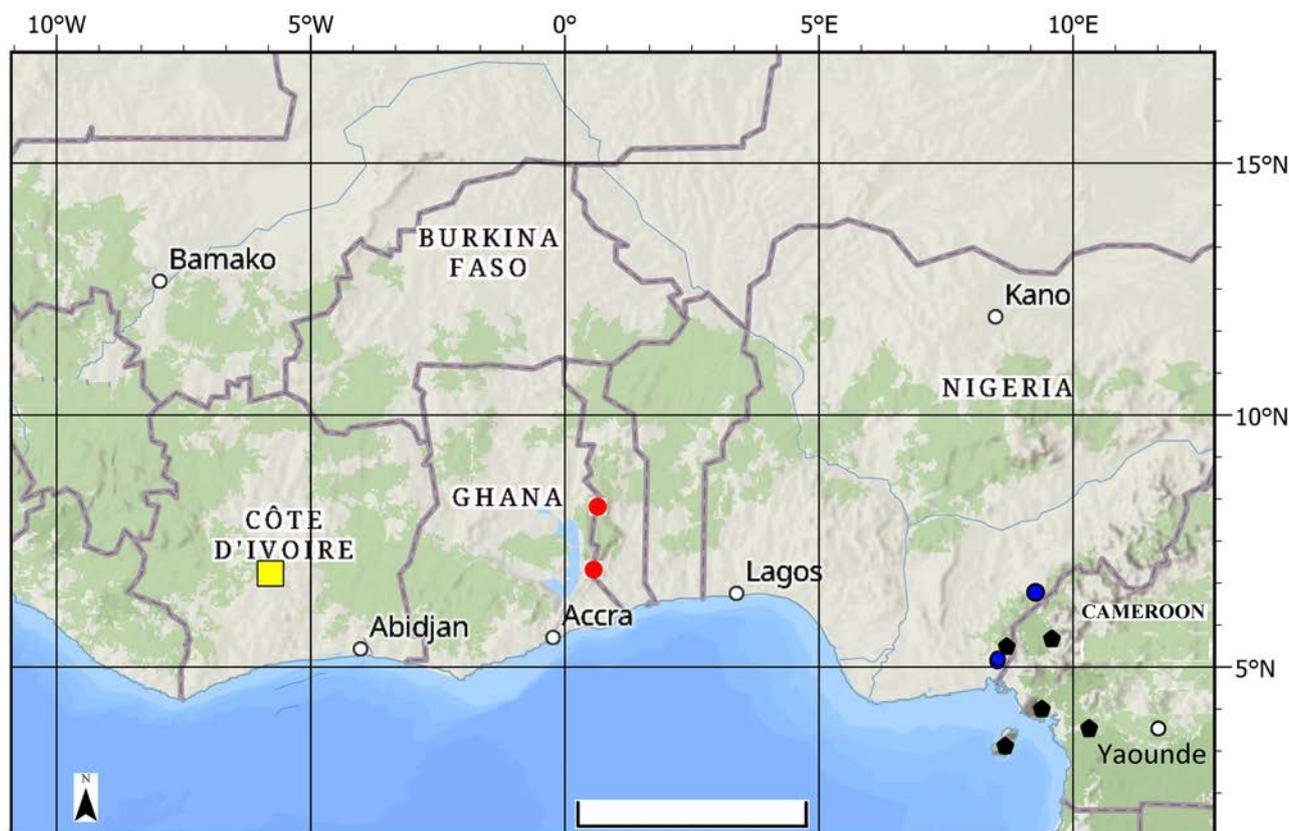


FIGURE 8. Map showing the geographic distribution of *Sudanonautes koudougou* n. sp. (yellow square), *S. granulatus* s.s. (Balss, 1929) (red circles), *S. umaji* n. sp. (blue circles), and *S. tiko* (black pentagons). Scale bar = 500 km. See text for exact localities.

Discussion

This revision of the taxonomic status of freshwater crabs from West and Central Africa formerly identified as *S. granulatus* s.l. by Cumberlidge (1993a, 1999) has revealed this taxon to be a species complex comprising at least 4 different species: *S. granulatus* s.s., *S. koudougou* n. sp., *S. umaji* n. sp., and *S. tiko*. Accordingly, the distribution of *S. granulatus* s.s. is now restricted to western Togo, and the former wide and disjunct distributional range of *S.*

granulatus s.l. (Cumberlidge 1993a, 1999: fig. 67H, 2008) comprising western populations in Côte d'Ivoire, Ghana, and Togo separated from eastern populations in Nigeria, Cameroon, Bioko Island, and Central African Republic is no longer recognized. One consequence of these findings is that the IUCN Red List conservation assessment of *S. granulatus* s.l. as Least Concern (Cumberlidge 2008) will now need to be revised.

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