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REDESCRIPTION OF *SUDANONAUTES GRANULATUS* (BALSS, 1929) (POTAMOIDEA: POTAMONAUTIDAE) FROM WEST AFRICA

Neil Cumberlidge

ABSTRACT

Sudanonautes granulatus (Balss, 1929), a fresh-water crab from West Africa, is redescribed from type material and from a large series of other specimens. The species is recognized by a combination of characters of the carapace, chelipeds, and gonopods. It is compared to other species of *Sudanonautes* Bott, 1955, and to the other genera of fresh-water crabs occurring in West Africa. *Sudanonautes granulata* shows much intraspecific variation, and it is likely that this has contributed to past difficulties in recognizing this species. The distribution indicates that this species is restricted to the tropical rain forest zone of West Africa, from Côte d'Ivoire to Cameroon, including Bioko Island (Fernando Po).

Fresh-water crabs belonging to the genus *Sudanonautes* Bott, 1955, are associated with nonmarine aquatic habitats throughout West and Central Africa. Despite recent contributions to the taxonomy of this genus (Cumberlidge, 1989, 1991, in press), many problems remain. Several species of fresh-water crabs from the rain forest regions of Cameroon and Nigeria are superficially similar in appearance and are difficult to identify. For example, small crabs collected from this area which possess a smooth carapace and a short end segment on gonopod 2 could belong to either *Sudanonautes* or to *Potamonemus* (see Cumberlidge and Clark, 1992).

Those which lack a flagellum on the exopod of the third maxilliped belong to *Potamonemus*. However, the identification of those that clearly conform to the genus *Sudanonautes* as defined by Bott (1955) is less clear, since they could be either *S. orthostylis* (Bott, 1955), *S. kagoroensis* Cumberlidge, 1991, or *S. aubryi* (H. Milne-Edwards, 1853). An additional species, *S. granulatus* (Balss, 1929) is recognized here, which offers a fourth possible identity for such material.

Sudanonautes granulatus (Balss, 1929) was originally described only briefly as a subspecies of *Potamonautes decazei* (A. Milne-Edwards, 1886). It was later recorded by Chace (1942) as *Potamon granulata* (Balss, 1929) without argument. Bott (1955) regarded *granulatus* as a synonym of *S.* (*S.*) *d. decazei* (A. Milne-Edwards, 1886). That author (Bott, 1964) later recognized *S.* (*S.*) *d. decazei* as the junior synonym of *S.* (*S.*) *p. pelii* (Herklots, 1861). Thus the most recent record of *granulata* treats it as a synonym of *S. pelii* (Herklots, 1861).

The present study arises from a reexamination of the original series of *Potamonautes decazei granulata* held in the Zoologisches Museum der Humboldt-Universität, Berlin, which were used by Balss (1929) to describe the subspecies. Additional specimens of *S. granulatus* from West Africa were found in other museum collections, and still others form part of the author's own collection. A total of 89 specimens of *S. granulatus* from 11 localities in Côte d'Ivoire (Ivory Coast), Ghana, Togo, Nigeria, Cameroon, Bioko, and Central African Republic were examined.

Sudanonautes granulatus is recognized here based upon a combination of characters of the adult male gonopods, carapace, and chelipeds. A great deal of intraspecific variation was found, both between immature and mature specimens from the same locality and between mature specimens from different localities. It is likely that this variation has contributed to past difficulties in recognizing this species.

Differences between *S. granulatus* and other similar species in the genus are identified and discussed. *Sudanonautes granulatus* is redescribed from adult males from Côte d'Ivoire and Nigeria, from a female from Togo, and from pubescent and juvenile specimens. Notes on the distribution and ecology of *S. granulatus* are provided for the first time.

The following abbreviations are used: MNHN = Muséum National d'Histoire

Naturelle, Paris, France; NMU = Northern Michigan University, Marquette, Michigan USA; NNM = Nationaal Naturhistorisch Museum, Leiden, The Netherlands; ZIM = Zoologisches Staatsinstitut und Zoologisches Museum, Hamburg, Germany; ZMB = Zoologisches Museum der Humboldt-Universität, Berlin, Germany; CW = carapace width at widest point; CL = carapace length, measured along median line; CT = cephalothorax thickness, maximum depth of cephalothorax; FW = front width, width of front measured along anterior margin; M = male; F = female; ad = adult; pub = pubescent; A = segment of abdomen; P = pereiopod; *r* = correlation coefficient; *d.f.* = degrees of freedom.

Materials and Methods

Material Examined.—Côte d'Ivoire: NNM 35246 Koudougou, 10 km southwest of Bouaflé (7°N, 5°40′W), December 1980, 1 M, (Figs. 1a, b, 2 a–d, 3a, b, e, 4a, b), 1F. Ghana: NHM 1902.8.17.1, Ankobra River, South West District (5°N, 2°14′W), 1 M ad (CW = 32.3 mm), 17.VIII.1902, collected by S. H. Jones. Togo: ZMB–15182, 1 F; ZMB–20244, 4 F, collected by Schroder, 24.II.1904; ZMB–20170, 1 F, 2.I.1893; ZMB–20171, 2 M, 2 F; ZMB–20173, 3 F, 1 M, 30.XI.1892; ZMB–20194, 1 F, all collected by Conradt, 15.V.1893; ZMB–21313, 1 M; ZMB–8977, 10–20 specimens; ZMB–8978, 1 M, ZMB–21312, 3 F, all from Bismarksburg (=Aného, 40 km east of Lomé), collected by Büttner, 20.VII–20.IX.1890; ZMB–8980, Misahohe, 5 F, collected by E. Baumann. Nigeria: NMU 28.IV.1979, Oban Hills, Cross River State: Ekang (=Akansoko=MCC) Road, 25 km northeast of Calabar, (4°56′N, 8°27′E), 1 M ad, 28.IV.1979 (Figs. 3e–g, 4e, f). NMU 5. VI. 1979, Ekang Road, 30 km northeast of Calabar (4°58′N, 9°25′E), 1 M, 1 F. NMU 29. VI. 1979, Ekang Road, 30 km northeast of Calabar (4°58′N, 9°25′E), 1 M. NMU 3. VIII. 1980, Ayip-Eku Oil Palm Estate, between Osomba and New Ndebezi villages (5°27′N, 8°43′E), 1 M. NMU 20. X. 1980 (Fig. 3e, f) Ekang Road, 80 km, Ayip-Eku Oil Palm Estate (5°28′N, 8°42′E) 1 F, all collected by Dr. J. C. Reid. NMU 9.IV.1983, Umaji, Cross River State (6°29′N, 9°15′E), 2 M ad, 3 F ad, 1 M juv, 3 F juv, 9.IV.1983, river Amire u Kiriki, tributary of Katsina-Ala and Benue rivers, collected by N. Cumberlidge. NHM 1938.7.1.24–25, Obubra division, southern Nigeria, 1 M, collected by S. Sanderson. Cameroon: ZIM K–3492, Kiliwindi, northwest Cameroon, 1 F ovigerous, collected by Ernst Lantsch, 3.XII.1908. ZIM K–27877, Nbenjibok, 1 M, collected by Prof. Dr. Vogel, 29.XI.1962 (Figs. 1c, d, 3h–j, 4g, h). ZIM K–30393, Ekok, Cross River, 1 F hatchlings, collected by Dr. J. Voelker 1.V.1975. ZIM K–30394, Kembong, near Mamfe, 1 F, 2 M, collected by Dr. J. Voelker 26.IV.1975. ZMB–10194, Bipindi, 2 F, collected by Zenker. ZMB–20158, Soppo, 1 M, 3 F, Zenker. ZMB–20168, Ossidinge, 4 M, collected by Dr. Mansfield, 14.III.1905. ZMB–21304, Johann Albrechts Hohe, 1 F, collected by Conradt 28-29.VIII.1898. ZMB–21305, 3 F, collected by Preuss. NHM 1938.7.1(14–23), tributary of Cross river, Tinta, Assumbi, Mamfe Division, 716 m (5°45′N, 7°24′E), 7 M ad, 5 F ad, 4 juv, 1.VII.1938, collected by S. Sanderson. NMU 25.III.1970, Bille, near Kumba, 1 F ad, collected by R. H. L. Disney, 25.III.1970. Fernando Po (=Bioko): ZIM K–5362, collected by A. Schultze, 20.VIII.1911. Central African Republic: ZIM K–5357, Douma, Oubangi, 1 M, 2 F, collected by Dr. Schubotz, 4.X.1911.

The right mandible and the right first and second gonopods were illustrated following removal from the specimens in order to describe these structures under magnification. The length of the propodus of the right and left chelipeds of males and females measured along the ventral line was compared to body size (CL) (Fig. 7). Four dimensions of the carapace—carapace length, carapace width, carapace thickness, and front width—were recorded from all available specimens using digital calipers (Fig. 6a). The relative proportions of the latter three measurements (adjusted for body size, CL) of *S. granulatus* were calculated (Fig. 6b). These proportions were also calculated for a series of three other species of *Sudanonautes*. One-factor ANOVA repeated measures analysis was used to test for significant differences between the mean carapace proportions of *S. granulatus* and those of three closely related species (Table 1). A comparison of the features characterizing these species of *Sudanonautes* was made.

Sudanonautes granulatus (Balss, 1929) (Figs. 1a–d, 2a–d, 3a–m, 4a–j, 6a, b, 7)

Potamonautes decazei granulatus Balss, 1929: 119–120.

Potamon granulatus Chace, 1942: 211.

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

Sudanonautes orthostylis Cumberlidge, 1989: 231–237, figs. 1a–g, 2a–c; tables 1, 2 (part); Cumberlidge, 1991: 1943, fig. 2f.

Diagnosis.—Mandibular palp 2-segmented, terminal segment single; third maxilliped with flagellum on exopod; terminal segment of gonopod 2 extremely short. Variable species, characters of carapace, chelipeds, gonopods varying according to maturity, size at maturity varying with geographic locality. Chelipeds: major (right) cheliped of adult male longer, higher than left cheliped. Dactylus of right cheliped of adult male narrow, greatly arched enclosing wide, ovoid space; that of pubescent male not broadened or greatly arched, fingers touching in several places when closed. Cheliped length of right dactylus longer than carapace width in adult male, shorter than carapace width in pubescent male. Gonopods: terminal segment of gonopod 1 of adult male widened in midsection, with distinct longitudinal groove; this groove faint in pubescent male. Carapace: adult male with completely smooth anterolateral margin, lower margin of orbit,

postfrontal crest; pubescent male, female with rows of small rounded teeth on anterolateral margin, lower margin of orbit, flank grooves, postfrontal crest. Front width of all ages, both sexes relatively wide (about one-third carapace width). Exorbital, epibranchial teeth small, low; intermediate tooth small but distinct; vertical flank groove meeting anterolateral margin at base of intermediate tooth. Size at maturity varying between populations—Nigeria/Cameroon mature between size classes CL = 19.0–21.0 mm; Côte d'Ivoire, mature between CL = 31.0–35.0 mm.

Types.—Balss (1929) did not designate a holotype for *Potamonautes decazei granulata* Balss, 1929. Bott (1955) selected a female lectotype (ZMB–11257, CW = 26 mm) from Misahohe, Togo, collected by Smend, from the syntype series. Since the lectotype is a female, and since *S. granulatus* shows variation in both body size and geographic locality, the species is described here from the largest male specimens from two localities, an adult male (CW = 58.1 mm NNM 35246) from Côte d'Ivoire, and an adult male (CW = 41.5 mm NMU 28.IV.1979) from Nigeria. The female lectotype (ZMB–11257) from Togo, and a pubescent male (CW = 34.2 mm NMU 5.VI.1979) from Nigeria are also described.

Type Locality.—Misahohe, Togo.

Distribution.—Côte d'Ivoire, Ghana, Togo, Nigeria, Cameroon, Bioko Island (Fernando Po), Central African Republic.

Description.—The following description is based on the adult males from Côte d'Ivoire (CW = 58.1 mm NNM 35246), and Nigeria (CW = 41.5 mm NMU 5.VI.1979).

Size.—Measurements given in Table 1.

Carapace (Fig. 1a, b).—Cephalothorax ovoid, widest at anterior third (CW/CL = 1.50, Côte d'Ivoire; 1.52, Nigeria) relatively thick, with maximum depth in anterior region (CT/CL = 0.47, Côte d'Ivoire; 0.51, Nigeria). Anterior margin of front straight, curving under, front relatively narrow, about one-quarter carapace width (FW/CW = 0.26, Côte d'Ivoire; 0.27, Nigeria). Surface of carapace smooth with no deep grooves. Postfrontal crest smooth, ending before meeting anterolateral margins; midgroove broad, shallow. Exorbital tooth blunt, low, intermediate tooth reduced to tiny notch, epibranchial tooth almost undetectable. Anterolateral margin of carapace entirely smooth, lacking teeth or serrations. Posterior margin about two-thirds as wide as carapace width.

Each flank with 2 grooves, 1 longitudinal, 1 vertical, dividing flank into 3 parts. Longitudinal flank groove beginning at respiratory opening, curving backward across flank, dividing suborbital, subhepatic regions from pterygostomial region. Short vertical flank groove marked by row of small rounded teeth, beginning just beneath intermediate tooth, curving down to meet longitudinal flank groove. This short vertical groove dividing suborbital region from subhepatic region. First sternal groove complete; second sternal groove reduced to 2 small notches at sides of sternum. Third maxillipeds filling entire oral field, except for transversely oval efferent respiratory openings. Flagellum on exopod of third maxilliped (Fig. 2c). Ischium of third maxilliped smooth, with faint vertical groove. Mandibular palp 2-segmented; terminal segment single, undivided (Fig. 2a, b). First 5 segments of male abdomen broad, short, tapering inward; last 2 segments (A6, A7) long, narrow, last segment (A7) rounded at distal margin (Fig. 2d).

Chelipeds and walking legs (Figs. 1a, c, 4a–d).—Chelipeds greatly unequal, right of male from Côte d'Ivoire much longer (61.6 mm), higher (21.9 mm) than left (48.5 mm, 16.0 mm, respectively, Figs. 1a, 4a, b). Right cheliped of male from Nigeria much longer (42.0 mm), higher (18.0 mm) than left (33.0 mm, 12.0 mm, respectively, Fig. 4c, d). Length of ventral margin of propodus of major (right) cheliped alone (61.6 mm Côte d'Ivoire, 42.0 mm Nigeria) greater than carapace width (58.1 mm Côte d'Ivoire, Nigeria 41.5 mm). Dactylus of right cheliped narrow, strongly arched, enclosing ovoid interspace when closed, palm swollen. Fingers of right cheliped with series of pointed teeth along length. Anterior dorsal margin of merus of right and left chelipeds with 2 rows of small round teeth, 1 larger tooth close to distal end, outer margin with 1 row of fainter granules (Fig. 1a). Carpus of cheliped with 2 large pointed teeth, second much smaller than first (Fig. 1a). Left cheliped showing

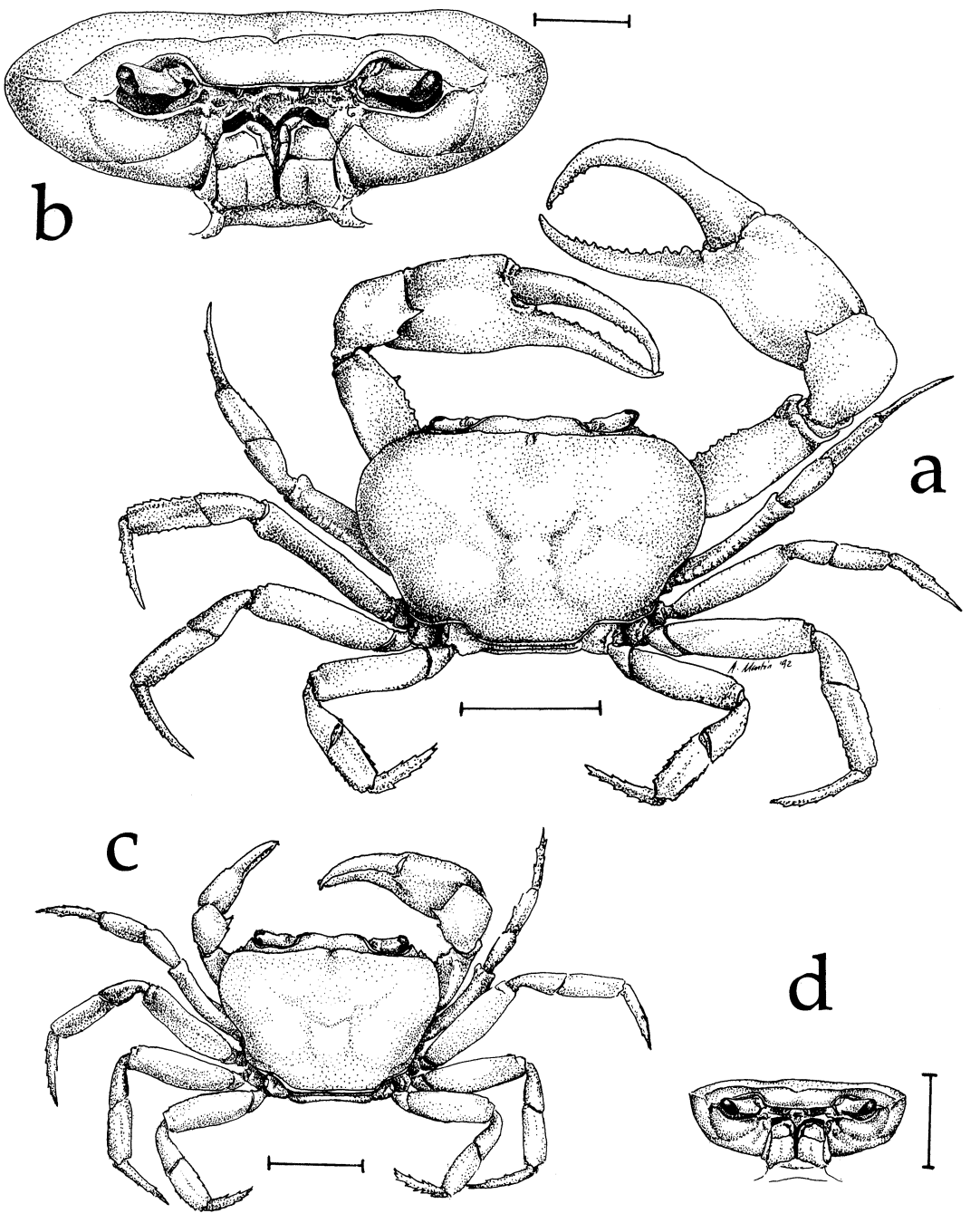

Fig. 1. *Sudanonautes granulatus* (Balss, 1929), adult male from Côte d'Ivoire (carapace width = 58.08 mm), NNM 35246. a, whole animal, dorsal aspect; b, cephalothorax, frontal aspect. Pubescent male from Nigeria, ZIM, ZIM, ZIM K–27877 (carapace width 23.5 mm). c, whole animal, dorsal aspect; d, cephalothorax, frontal aspect. Scale bars equal 20 mm (a), and 10 mm (b–d).

less enlargement, but dactylus also narrow, arched, enclosing long space, teeth smaller than those of right cheliped. Walking legs (pereiopods 2–5, Fig. 1a) slender, P4 longest, P5 shortest. Dactyli P2–5 tapering to point, each bearing rows of downward-pointing sharp bristles; dactylus P5 shortest segment.

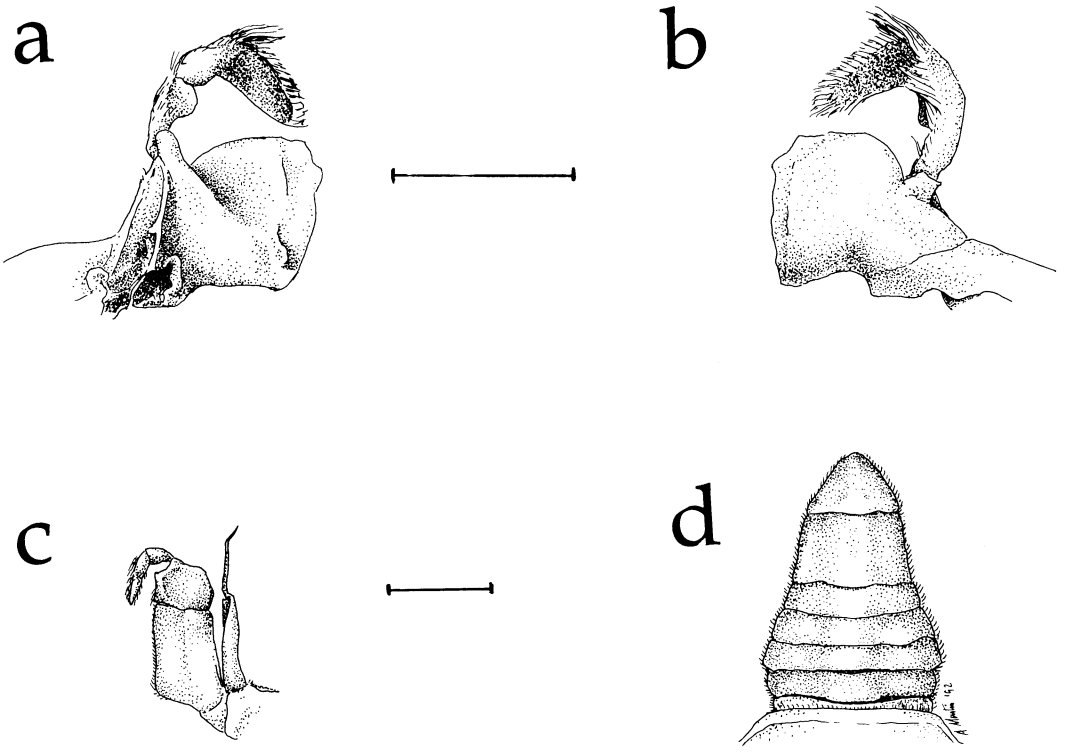

Fig. 2. *Sudanonautes granulatus* (Balss, 1929), adult male from Côte d'Ivoire (carapace width = 58.08 mm), NNM 35246. a, left mandible, anterior view; b, left mandible, posterior view; c, left third maxilliped; d, abdomen. Scale bars equal 5 mm (a, b), and 10 mm (c–d).

Gonopods (Fig. 3a–g).—Terminal segment gonopod 1 curving outward away from midline, tapering to pointed tip; terminal segment widened laterally in midsection (Fig. 3a, b). Longitudinal groove (sperm channel) running along proximal two-thirds of terminal segment. Entire groove visible only if gonopod turned to view medial margin (Fig. 3c). Penultimate segment gonopod 1 slim; narrowest at junction between segments, widest at basal terminal. Two margins of groove for gonopod 2 beginning far apart at basal end of penultimate segment of gonopod 1, then tapering distally, finally fusing together shortly before junction with terminal segment. Medial, lateral margins of penultimate segment of gonopod 1 fringed by bristles.

Gonopod 2 (Fig. 3d) shorter than gonopod 1 (reaching only junction between segof gonopod 1). Terminal segment gonopod 2 extremely short, only one-tenth as long as penultimate segment. Terminal segment gonopod 2 not solid, sides thin, folded inward enclosing inward-facing hollow; tip rounded. Penultimate segment gonopod 2 widest at base, tapering sharply inward about one-third along length, last two-thirds forming long, thin, tapering, upright process supporting short terminal segment.

Adult female (Figs. 4i, j, 7).—Carapace, chelipeds of adult female lectotype (CW = 26 mm) from Misahohe, Togo, differing from adult males described here. Notably, anterolateral margin behind epibranchial tooth raised, bearing row of small, even, rounded low teeth. Lower orbital margin, postfrontal crest similarly toothed. Postfrontal crest extending laterally across entire carapace, meeting both anterolateral margins at epibranchial teeth; latter no larger than other teeth along anterolateral margins. Right, left chelipeds of female approximately equal in both length (12.5 mm, 14.5 mm), height (4.5 mm, 5.5 mm). Cheliped length much shorter than carapace width. Both chelipeds smaller, more slender than smaller (left) cheliped of adult male of same size. Dactylus of largest cheliped of adult female lacking characteristic arching of adult male. Mature female abdomen very wide

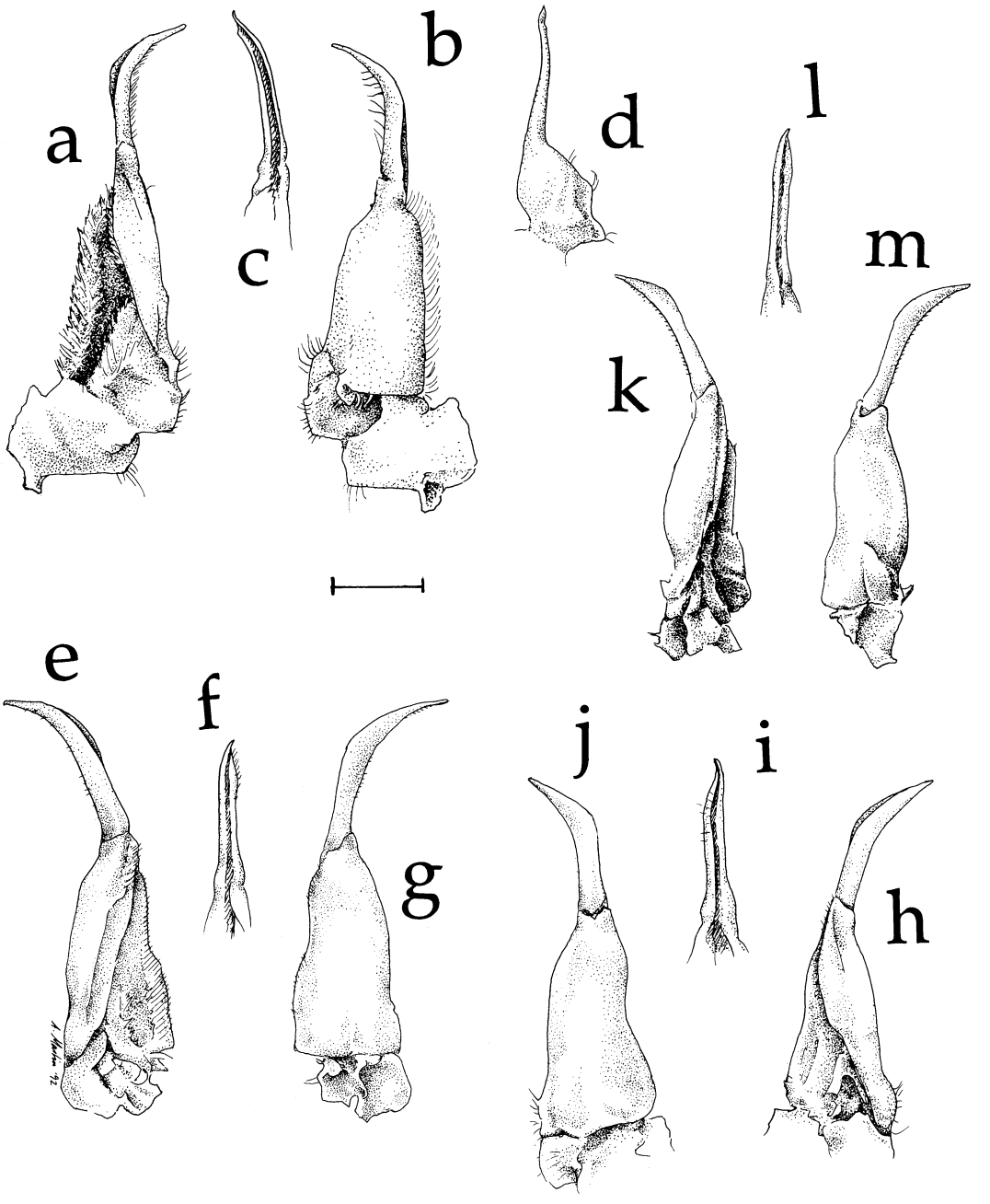

Fig. 3. Comparisons of the gonopods of *Sudanonautes granulatus* (Balss, 1929) from different localities in West Africa. a–d, adult male from Côte d'Ivoire (carapace width = 58.08 mm), NNM 35246. a, left gonopod 1, ventral view; b, left gonopod 1, dorsal view; c, left gonopod 1 turned to show sperm channel; d, left gonopod 2, ventral view. e–g adult male from Nigeria, NMU 28.IV.1979 (carapace width 41.5 mm). e, right gonopod 1, dorsalview; f, right gonopod 1, turned to show sperm channel; g, right gonopod 1, ventral view. h–j, adult male from Umaji, Nigeria, NMU 9.IV.1983 (carapace width 29.5 mm). h, left gonopod 1, dorsal view; i, left gonopod 1, turned to show sperm channel; j, left gonopod 1, ventral view. k–m, pubescent male from Cameroon, ZIM, ZIM K–27877 (carapace width 23.5 mm). k, right gonopod 1, dorsal view; l, right gonopod 1, turned to show sperm channel; m, right gonopod 1, ventral view. Scale bar equals 10 mm.

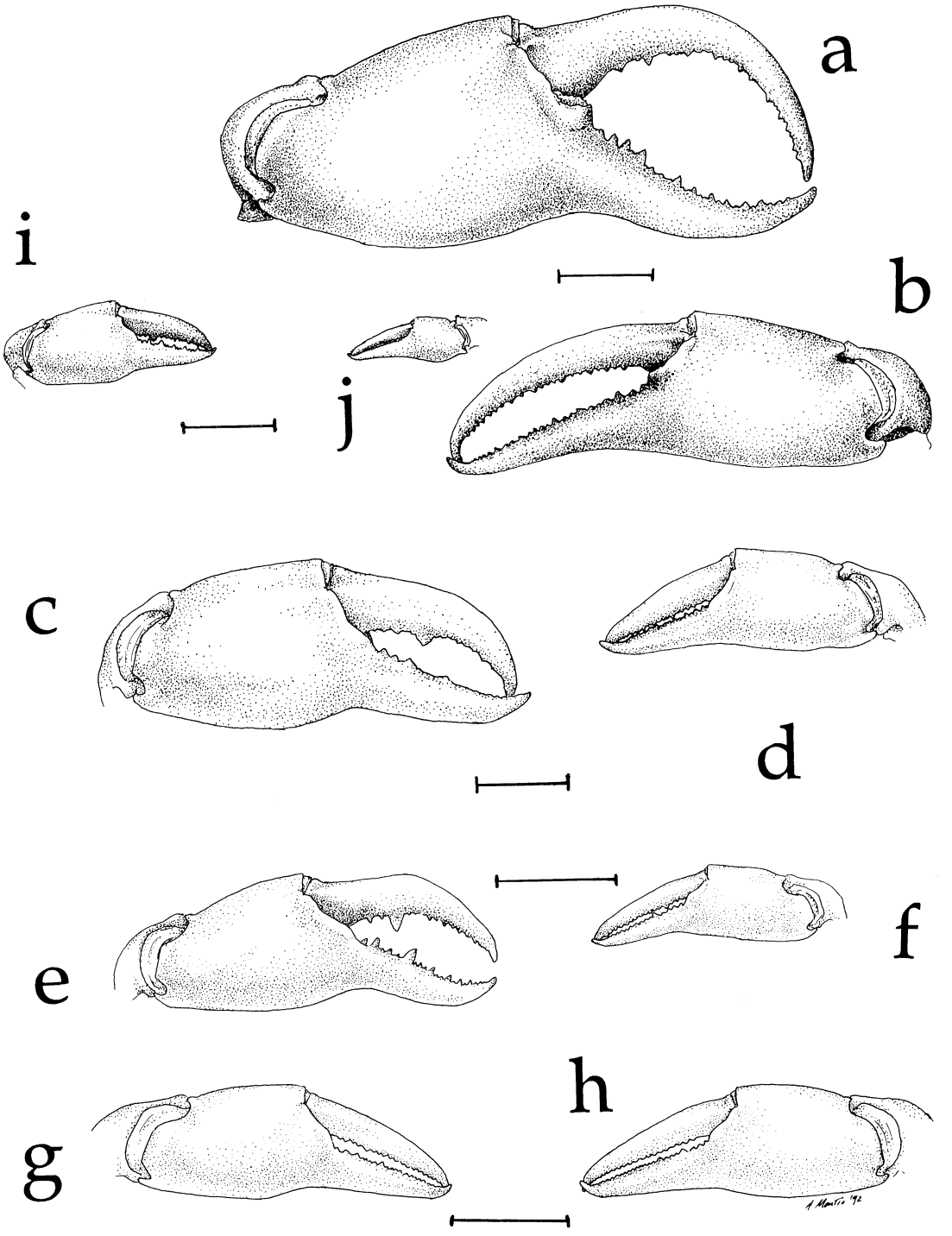

Fig. 4. Chelipeds of *Sudanonautes granulatus* (Balss, 1929). a, b, adult male from Côte d'Ivoire (carapace width = 58.08 mm), NNM 35246. a, right cheliped, frontal view; b, left cheliped, frontal view. c, d, adult male from Oban, Nigeria, NMU 28.IV.1979 (carapace width 41.5 mm). c, right cheliped, frontal view; d, left cheliped, frontal view. e, f, adult male from Umaji, Nigeria, NMU 9.IV.1983 (carapace width 29.5 mm). e, right cheliped, frontal view; f, left cheliped, frontal view. g, h, pubescent male from Cameroon, ZIM, ZIM K–27877 (carapace width 23.5 mm). g, right cheliped, frontal view; h, left cheliped, frontal view. i–j, adult female from Oban, Nigeria, NMU 25.III.1970 (carapace width 28.0 mm); i, right cheliped, frontal view; j, left cheliped, frontal view. Scale bars equal 10 mm (a–f, i, j), 5 mm (g, h).

reaching coxae of pereiopods 2–5. Segments of female abdomen becoming gradually longer distally, first, fifth becoming gradually wider, abdomen being widest at line separating fourth, fifth segments. Sixth segments, telson together form near semicircle.

Juvenile, pubescent size classes (Figs. 1c, d, 4g, h, 6a, b, 7).—Right, left chelipeds of males, females of juveniles equal, showing no differential enlargement. Juvenile males, females showing no difference in relative development of abdomen (closest in shape to adult male abdomen). Juvenile size class for populations from Cameroon, Nigeria, carapace length less than or equal to 14.0 mm. Pubescent size classes included females with enlarged abdomen, broader than juvenile form, but not overlapping coxae, as in adult females.

Sexual maturity judged by development of female abdomen, overlapping bases of coxae of walking legs; adults with broad, hair-fringed pleopods. All female specimens bearing eggs or hatchlings included in this group. Female from Ekok, Cameroon (CW = 22.9 mm) with hatchlings in abdominal brood pouch, 3 other females (CWs = 29.7, 31.0, 36.3 mm) ovigerous. Pubertal molt, from pubescent to sexually mature, occurring somewhere between size classes CW = 22.0, 25.0 mm for populations from Cameroon, Nigeria. Abdomen of large immature female from Côte d'Ivoire (CW = 44.5 mm) not overlapping coxae of walking legs, anterolateral margin, postfrontal crest not smooth, instead marked by small teeth. These characters implying later pubertal molt in population from Côte d'Ivoire.

Relative proportions of carapace of juvenile, pubescent *S. granulatus* differing from adults in several ways (Fig. 6b). Carapace width (CW/CL), thickness (CT/CL) increasing as crabs grow. Relationships described by CW/CL = 1.24 − 0.007 CL, *d.f.* = 87, *r* value of 0.645 indicating highly significant correlation ($P < 0.001$); CT/CL = 0.44 + 0.003 CL, *d.f.* = 87, *r* value of 0.34 indicating significant correlation ($P < 0.001$) between size groups. Relative front width of juveniles similar to that of adults. FW/CL = 0.44 − 0.001 CL, *d.f.* = 87, *r* value of 0.19 indicating no significant correlation ($P > 0.05$) between size groups. In summary, carapace of adult *S. granulatus* relatively thicker, wider than juveniles, but width of frontal margin similar in all age groups.

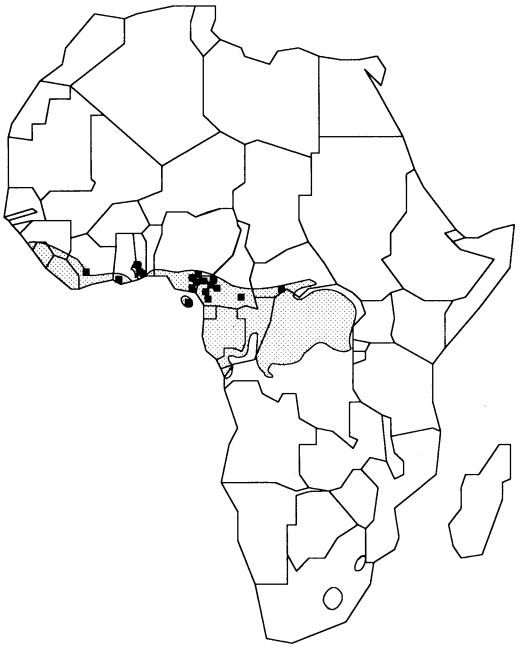

Fig. 5. Distribution of *Sudanonautes granulatus* (Balss, 1929). The map of Africa shows country outlines. The shaded area depicts the forest zone. The black squares represent records of individual specimens of *S. granulata.*

Pubescent male.—Following description based on pubescent male (CW = 34.2 mm NMU 5. VI. 1979) from Nigeria. Characters of carapace, chelipeds of pubescent males (Figs. 1c, d, 4g, h) resembling those described above for females (Fig. 4i, j). Longitudinal groove (sperm channel) of terminal segment of gonopod 1 of pubescent males present but shallow, faint (Fig. 3h–j).

Color.—In life, adult male from Nigeria (NMU 28.IV.1979) dorsal carapace brown with purple, cream pattern, sternum white with purplish tinge, arthrodial membranes between joints of chelipeds, pereiopods brick red, yellow, tips of chelipeds brown, red. In life, adult female, juveniles with dark brown dorsal carapace, chelipeds, dorsal pereiopods; sternum, undersides of legs light brown.

Ecological Notes.—The distribution (Fig. 5) indicates that this species is restricted to the tropical rain forest zone of West Africa from Côte d'Ivoire to Cameroon, including the island of Bioko (Fernando Po). In the Oban

Table 1. The ratio of carapace width (CW), carapace thickness (CT), and front width (FW), to body size (carapace length, CL) of *Sudanonautes granulatus* (Balss, 1929) and four closely related species of *Sudanonautes* from Cameroon and Nigeria. One-factor ANOVA repeated measures analysis was used to test for significant differences between the mean of the carapace proportions of *S. granulatus* and the four other species (N = 14 in all cases). * = Proportion significantly different from *S. granulatus* at 95% confidence limits. ** = Holotype and paratypes from Bipindihof, Cameroon, only. *** = Adult male and female specimens from Nigeria only.

CW/CL	CT/CL	FW/CL
Sudanonautes granulatus (Balss, 1929)		
1.40 (SD = 0.06)	0.52 (SD = 0.05)	0.39 (SD = 0.02)
******Sudanonautes orthostylis* (Bott, 1955)		
1.44 (SD = 0.06)	0.51 (SD = 0.03)	0.47* (SD = 0.03)
Sudanonautes kagoroensis Cumberlidge, 1991		
1.50* (SD = 0.05)	0.48* (SD = 0.03)	0.40 (SD = 0.02)
*******Sudanonautes aubryi* (A. Milne-Edwards, 1886)		
1.52* (SD = 0.07)	0.61* (SD = 0.05)	0.38 (SD = 0.05)

Hills northeast of Calabar, Nigeria, *S. granulatus* occurs in streams flowing through mature rain forest. Crabs were collected by hand from small streams (1–10 m wide, 20–50 cm deep), with fast, medium, or slow flowing water, and even from a dried-up stream bed. The stream beds themselves varied from mudstone to sand, together with either clay or yellow silt. These streams usually lacked vegetation (although one collection was made in a grass swamp). Crabs were collected from a variety of habitats: lodged among grass, under stones, burrowing among root material in the center of the stream, hiding among stones, or burrowing in the moist bed of a dried-up stream. One locality was a roadside ditch, with rust-red algae, and grass in the water. (Based on J. C. Reid's field notes.)

Remarks.—*Sudanonautes granulatus* conforms to the diagnosis of the genus *Sudanonautes* (Bott, 1955). This genus includes fresh-water crabs with the following combination of characters: a flagellum on the exopod of the third maxilliped, a two-segmented mandibular palp with a single (simple) terminal segment, a short terminal segment of gonopod 2; a terminal segment of gonopod 1 curving outward away from the midline, and a distinct intermediate tooth between the exorbital and the epibranchial teeth on the anterolateral margin.

Potamonautes decazei granulata Balss, 1929, was established to recognize an observed difference in size between material from Togo and Cameroon (mature at CW = 25 mm) and the type of *P. decazei* (CW = 58.0 mm). This size difference, and the lack of any large examples of *granulatus,* was considered by Balss (1929) to be due to genuine geographic variation. He also noted granulations on the carapace of *granulatus* which he contrasted with the smooth carapace of *decazei.* Since the surface of the carapace of *S. granulatus* is smooth, Balss (1929) must have been referring to the small teeth marking the margins of the carapace, orbits, vertical flank grooves, and postfrontal crest of immature *S. granulatus.* However, Balss (1929) did not illustrate the new subspecies, and his description was brief. Bott (1955) considered the marginal teeth of the carapace of *S. granulatus* not to exceed those normally seen on small specimens of *S. decazei,* and included *S. granulatus* in *S.* (*S.*) *d. decazei* (A. Milne-Edwards, 1886). Later, Bott (1964) placed *S.* (*S.*) *d. decazei* in synonymy with *S. pelii* (Herklots, 1861). This classification was adopted by other workers (unpublished) who identified a number of museum specimens of *S. granulatus* as belonging to *S.* (*S.*) *p. pelii.*

Sudanonautes granulatus was compared here to the type material of *Thelphusa decazei* A. Milne-Edwards, 1886, and *T. pelii* Herklots, 1861, and found to be clearly different from these taxa. Bott's (1964) opinion that *T. decazei* is a junior synonym of *S. pelii* is, therefore, supported (for more details see Cumberlidge, 1989). Comparisons of the first gonopod, major cheliped, and carapace of the adult male *S. granulatus* with those of the holotype of *S. pelii* revealed the following differences. The first gonopod of *S. granulatus* is widened in the midsection and bears a longitudinal groove, whereas that of *S. pelii* tapers evenly to the tip and lacks a groove; the dactylus of the major cheliped of *S. granulatus* is narrow and greatly arched, and is longer than the carapace width, whereas that of *S. pelii* is broad and slightly arched and is shorter than the carapace width; and the postfrontal crest

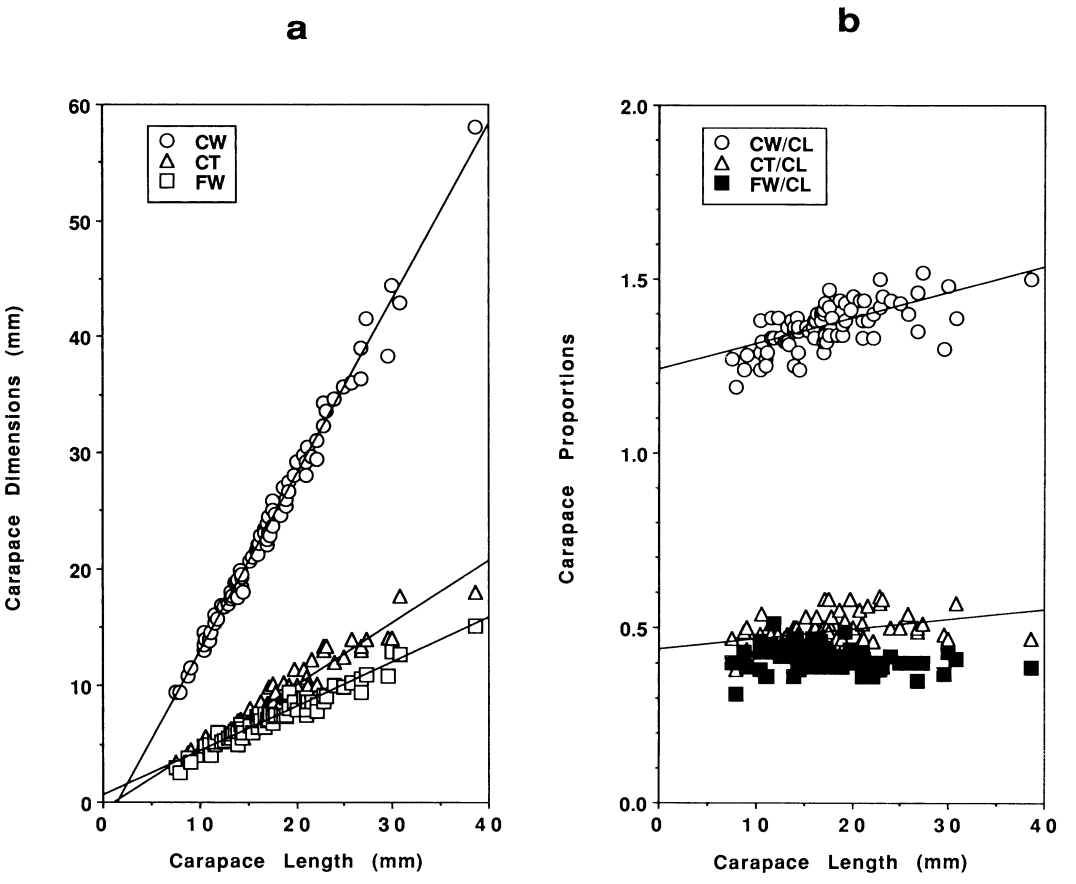

Fig. 6. Comparisons of 89 specimens of *Sudanonautes granulatus* (Balss, 1929), ranging in size from CW = 14.0–58.06 mm from West and Central Africa. a. Dimensions of the carapace (CW, CT, FW) compared to body size (CL). Relationships are described by the following regression equations: CW = −2.305 + 1.513 CL, r = 0.99; CT = −0.73 + 0.53CL, r = 0.97; FW = 0.531 + 0.383CL, r = 0.97. All r values indicate a highly significant correlation ($P < 0.001$), at 87 degrees of freedom. b. Relative proportions of the carapace (CW/CL, CT/CL, and FW/CL) compared to body size (CL). The relationships are described by the following regression equations: CW/CL = 1.24 + 0.007CL, r = 0.645; CT/CL = 0.44 + 0.003CL, r = 0.339; FW/CL = 0.44 − 0.001CL, r = 0.187. The r values for CW/CL and CT/CL indicate a highly significant correlation ($P < 0.001$), at 87 degrees of freedom. The r value for FW/CL indicates no significant correlation ($P > 0.05$), at 87 degrees of freedom. CW = carapace width at the widest point; CL = carapace length, measured along the median line; CT = cephalothorax thickness, the maximum depth of the cephalothorax; FW = front width, the width of the front measured along the anterior margin; r = correlation coefficient; J = juvenile; P = pubescent; A = adult.

of *S. granulatus* meets the anterolateral margin at the epibranchial tooth, whereas that of *S. pelii* meets this margin behind the epibranchial tooth.

A number of specimens of *S. granulatus* from Nigeria (NMU 28.IV.1979, NMU 5.VI.1979, NMU 29. VI. 1979, NMU 3. VIII. 1980, NMU 20. X. 1980; NHM 1938.7.1.24-25) were described as *S. orthostylis* (Bott, 1955) by Cumberlidge (1989). Comparisons of these specimens with the holotype of *S. orthostylis* argue for their removal from that species and their reassignment to *S. granulatus*.

Comparisons.—Several species of freshwater crabs from Cameroon and Nigeria bear a superficial resemblance to *S. granulatus*. These are *S. orthostylis* (Bott, 1955), *S. kagoroensis* (Cumberlidge, 1991), *S. aubryi* (H. Milne-Edwards, 1853), and *Potamonemus mambilorum* (Cumberlidge and Clark, 1992). Table 1 compares *Sudanonautes granulatus* with these three species of *Sudanonautes*.

Sudanonautes granulatus may be distinguished from the holotype of *S. orthostylis* (Bott, 1955) as follows. (1) The proximal two-thirds of the end segment of gonopod

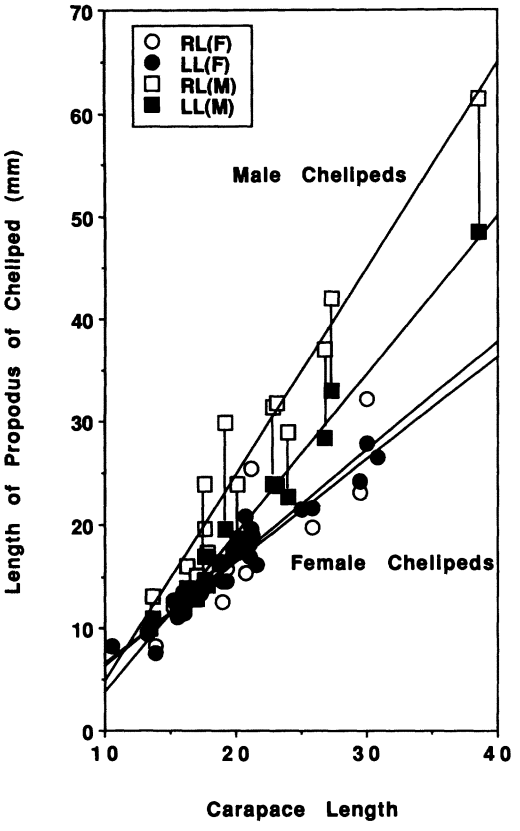

Fig. 7. *Sudanonautes granulatus* (Balss, 1929) from West Africa. Length of the right and left chelipeds of males and females compared to body size (CL). The relationships of the length of the right (RL) and left (LL) chelipeds of males are described by the following regression equations: RL(M) = −14 + 1.97CL, and LL(M) = −11.53 + 1.54CL. The values of *r* for both chelipeds were found to be very highly significant ($P < 0.001$), with *r* values of 0.97 for RL(M), and 0.99 for LL(M) (both at 47 degrees of freedom). The relationships of the length of the right (RL) and left (LL) chelipeds of females are described by the following regression equations: RL(F) = −2.9 + 0.96CL, and LL(F) = −2.84 + 0.96CL. The values of *r* for both chelipeds were found to be very highly significant ($P < 0.001$), with *r* values of 0.94 for RL(F), and 0.97 for LL(F) (both at 47 degrees of freedom). CL = carapace length; RL(M) = length of propodus of the right cheliped of males measured along the ventral line; LL(M) = length of propodus of the left cheliped of males measured along the ventral line; RL(F) = length of propodus of the right cheliped of females measured along the ventral line; LL(F) = length of propodus of the right cheliped of females measured along the ventral line; J = juvenile; P = pubescent; A = adult; *r* = correlation coefficient.

1 of *S. orthostylis* is straight, lacks a groove, and curves sharply outward at the tip, whereas that of *S. granulatus* curves along its entire length, and the gonopod bears a longitudinal groove. (2) The vertical flank groove of *S. orthostylis* originates at the epibranchial tooth, whereas that of *S. granulatus* originates at the intermediate tooth. (3) The dactylus of the major cheliped of the adult male of *S. orthostylis* is broad and flat, but not arched, whereas that of *S. granulatus* is narrow and dramatically arched. (4) The major cheliped of adult *S. granulatus* is longer than the carapace width, whereas that of *S. orthostylis* is shorter than the carapace width. (5) The carapace of *S. granulatus* is significantly less wide (mean CW/CL = 1.40) and the front width is narrower (mean FW/CL = 0.39) than in *S. orthostylis* (1.44 and 0.47, respectively, at 95% confidence level, Table 1).

The carapace and the first gonopod of *S. granulatus* closely resemble those of *S. kagoroensis*. The two taxa may be distinguished as follows. The vertical flank groove of *S. kagoroensis* originates at the epibranchial tooth, whereas that of *S. granulatus* originates at the intermediate tooth; the dactylus of the major cheliped of the adult male of *S. kagoroensis* is only moderately arched, whereas that of *S. granulatus* is dramatically arched; and the major cheliped of adult male *S. granulatus* is as long as or longer than the carapace width, whereas that of *S. kagoroensis* is shorter than the carapace width. Finally, the carapace of *S. kagoroensis* is significantly flatter (mean CT/CL = 0.46) and wider (mean CW/CL = 1.44) than that of *S. granulatus* (0.49 and 1.37, respectively, at the 95% confidence level, Table 1).

Characters of the carapace and gonopods of *S. granulatus* resemble those of *S. aubryi*. For example, both possess a smooth rounded carapace lacking teeth, both have a vertical flank groove originating at the intermediate tooth, and both possess a grooved terminal segment of gonopod 1. The two taxa may be distinguished as follows. The dactylus of the major cheliped of the adult male of *S. aubryi* is only moderately arched, whereas that of *S. granulatus* is dramatically arched; the major cheliped of adult male *S. granulatus* is as long as or longer than the carapace width, whereas that of *S. aubryi* is shorter than the carapace width. Finally, the carapace of *S. aubryi* is significantly flatter (mean CT/CL = 0.62) and wider (mean CW/CL = 1.51) than that of *S. granulatus* (0.49

and 1.37, respectively, at the 95% confidence level, Table 1).

The major cheliped of adult male specimens of *P. mambilorum* closely resembles that of *S. granulatus,* since in both species it is longer than the carapace width and the dactylus is dramatically arched, enclosing a wide, ovoid space. The two taxa may be distinguished as follows. While the terminal segment of the second gonopod of *P. mambilorum* resembles that of *Sudanonautes,* the lack of a flagellum on the exopod of the third maxilliped of *P. mambilorum,* and the lack of a clearly defined intermediate tooth on the anterolateral margin of the carapace clearly separate the two taxa.

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