

Redescription of *Sudanonautes floweri* (De Man, 1901) (Brachyura: Potamoidea: Potamonautidae) from Nigeria and Central Africa

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SYNOPSIS. The African fresh-water crab *Sudanonautes floweri* (De Man, 1901) is redescribed from the male syntype from Sudan (designated here the lectotype) and a large series of other specimens. The species is recognised by a combination of characters of the carapace, chelipeds, mandibles, and gonopods. *Sudanonautes floweri* is compared to related species occurring in Nigeria and Central Africa. The species is found in guinea and woodland savanna from northern Nigeria to southern Sudan, in tropical rain forest from south-east Nigeria to northern Angola (including Bioko), and along the Zaire river and its tributaries. *Sudanonautes floweri* is one of the second intermediate hosts of the human lung fluke (*Paragonimus*) in Africa.

INTRODUCTION

Recent major works on the taxonomy of the fresh-water crabs of Africa (Bott, 1955, 1959, 1964; Monod, 1977, 1980) recognise three species of *Sudanonautes* Bott, 1955 – *S. aubryi* (H. Milne Edwards, 1853), *S. africanus* (A. Milne Edwards, 1869), and *S. pelii* (Herklots, 1861). Since that time a number of other species in this genus have been added (Cumberlidge, 1991, 1993a, b). The subject of the present work, *S. floweri* (De Man, 1901), was formerly considered by both Bott (1955) and Monod (1977, 1980) to be a subspecies of *S. aubryi*. *Sudanonautes floweri* is judged here to be a good species, and is redescribed from a male syntype from Sudan.

Gonopod 1 of *S. floweri* is distinct (Fig. 2 d-f), and when considered in conjunction with other characters of the carapace and sternum (Fig. 1 a-c) and mandibles (Fig. 2 a-c), can be used to identify the species unequivocally. This is important, since *S. floweri* is one of the four species of *Sudanonautes* that serve as the second intermediate host of the human lung fluke (*Paragonimus*) in Nigeria and Central Africa (Voelker, *et al.*, 1975; Voelker & Sachs, 1977; Nozais, *et al.*, 1980). However, the ambiguous descriptions of *S. floweri* and

S. aubryi in the literature (A. Milne Edwards, 1853; De Man, 1901; Bott, 1955; Monod, 1977, 1980) have led to the misidentification of specimens of *S. floweri* as *S. aubryi* by parasitologists (Voelker, *et al.*, 1975, fig. 6; Voelker & Sachs, 1977, fig. 4).

The right mandible and the right first and second gonopods of the type of *S. floweri* were removed to illustrate these structures from different angles and under magnification (Fig. 2 a-i). Specimens of *S. floweri* from Nigeria collected by the author were either dug from their burrows at the sides of streams, or were trapped in fishing nets set overnight in ponds. One specimen (NMU 9.IV.1983) was caught by hand under rocks in a dried river bed, immediately following the temporary damming of the river by villagers. Four measurements, carapace length, carapace width, carapace height, and front width, were recorded from each specimen using digital callipers. Carapace proportions were calculated according to carapace length. These data were pooled and used for descriptions of growth (Fig. 3 a,b). Statistical comparisons between species were made between sexually mature adults only (Table 1). The distribution of *S. floweri* described here is based on the direct examination of a large number of specimens from 73 different localities in 9 countries. Litera-

ture records are generally not reliable, and have not been included.

The following abbreviations are used: AMNH, American Museum of Natural History, New York, NY, USA; FMC, Field Museum, Chicago, IL, USA; MCZ, Museum of Comparative Zoology, Harvard, MA, USA; MNHN, Muséum National d'Histoire Naturelle, Paris; NHM, The Natural History Museum, London, UK; NNH, Nationaal Natuurhistorisch Museum, Leiden, The Netherlands; NMU, Northern Michigan University, Marquette, MI, USA; RCM, Royal Congo Museum, Tervuren, Belgium; SMF, Senckenberg Museum, Frankfurt am M., Germany; USNM, The United States National Museum of National History, Smithsonian Institution, Washington, DC, USA; ZIM, Zoological Institute and Museum, Hamburg, Germany; ZMB, Museum für Naturkunde der Humboldt-Universität, Berlin, Germany; CW = carapace width at widest point; CL = carapace length, measured along median line; CH = cephalothorax height, maximum height of cephalothorax; FW = front width, width of front measured along anterior margin; m = male; f = female; coll. = collected by.

SYSTEMATIC ACCOUNT

Sudanonautes floweri (De Man, 1901)

(Figs 1 a-i, 2 a-j, 3 a,b, Table 1)

Potamon (*Potamonautes*) *floweri*; De Man, 1901:94–98, 100–101, pl. X (fig. 1–7); Rathbun, 1904, pl. XVII (figs 2, 6); Rathbun, 1905:193–195; Rathbun, 1921:406–410, fig. 6, pl. XX (fig. 2); Parisi, 1925:99.

Potamon (*Potamonautes*) *aubryi*; Balss, 1914, p. 405 (except ZIM K13557 from Mukonje farm, Cameroon, not *Potamon aubryi* H. Milne Edwards, 1853).

Potamonautes floweri; Balss, 1936:171, fig. 6.

Potamon floweri; Flower, 1931:734; Chace, 1942:211; Capart, 1954:834, fig. 21.

Sudanonautes (*Convexonautes*) *aubryi floweri*; Bott, 1955:304–306, fig. 65, 100, a-b, pl. XXVIII (fig 2 a-d); Monod, 1977:1218; Monod, 1980:384–385.

DIAGNOSIS. Mandibular palp 2-segmented; terminal segment single, undivided, with small hard, hair-fringed flap at junction between segments (Fig. 2 a-c). Terminal segment of gonopod 1 with raised lobe on cephalic part, separated from caudal part by a conspicuous longitudinal groove; subterminal segment of gonopod 1 distinctly broadened on outer margin (Fig. 2 d-f). Conspicuous raised ridges on sternum at points where chelipeds articulate (Fig. 1 c). Carapace greatly arched (CH/CL = 0.61, Fig. 1 b), very wide (CW/CL = 1.51, Fig. 1 a). Vertical suture separating sub-branchial and suborbital regions meeting anterolateral margin at base of intermediate tooth (Fig. 1 b).

DISTRIBUTION. Nigeria, Cameroon, Bioko (= Fernando Po), Central African Republic, Sudan, Zaire, Congo, Gabon, Cabinda, Angola. It is likely that *S. floweri* is also present in Equatorial Guinea. Rathbun (1921) and Balss (1936) provided details of the distribution of the species in Zaire. Monod (1980) reported *S. floweri* from the basins of the Nile, Zaire, Chari, and Lake Chad. The present work adds several new localities in Nigeria, Bioko, and northern Angola.

MATERIAL

LECTOTYPE. NHM reg. 1901.8.26.2, 1m (CW 48.5, CL 30.5, CH 17.8, FW 11.7 mm), from Bahr el Gebel, Sudan, coll. Capt. S. S. Flower, 26.viii.1901. This specimen is here designated the lectotype of *S. floweri*. De Man did not specify types, so the material he examined was syntypic.

OTHERS. The catalogue number of material held at NHM and NMU begins with the date (year, month, day) of collection or acquisition. **NIGERIA.** NHM 1895.5.5.1–4, Asaba, 150 miles up the Niger, coll. N. H. Crosse. NHM 1905.6.5.98–100, Sapele, junction of Jameson and Aethiopian rivers, coll. Dr. Ansoroye. NHM 1910.4.30.19–22, Oban southern Nigeria, coll. P. A. Talbot. NHM 1938.7.1, Obubra, southern Nigeria, coll. I. Sanderson. RCM 52.889, Jos, 1967, coll. E. B. Guong. NMU 8–12.V.1975, Rosse, at Iguoriokhi, Bendel State, 1f, 8–12.v.1975, coll. Bruce Powell. NMU 24.IV.1980, first or second roadside culvert, Calabar, 1f (CW 45.5 mm) dug from burrow, coll. J. C. Reid. NMU 30.IV.1982, Ogoja, Cross River State, 1m, CW 50 mm, dug from hole at edge of swamp at Ogoja, rain forest/ woodland savanna, coll. B. D. Barrett. NMU 4.I.1983, Kaduna river (year-round flow), Kaduna State, 4m, coll. Fatima Abdulkadir. NMU 1.III.1983, dug from holes, Kaduna, Kaduna State, coll. Fatima Abdulkadir. NMU 4.IV.1983, foot of Obudu plateau, Cross River State, 1m, fast white water, big rocks, small rocks, sand gravel bottom, caught by villagers, who dammed stream, dried river bed, caught crabs under rocks, (with *S. africanus*, *S. granulatus*), coll. N. Cumberlidge. NMU 12.XII.1983, Yankari Game Reserve, Bauchi State, Hippo Pool, dug from holes, 1m, 1f, coll. N. Cumberlidge. NMU 30.IV.1984, pond near tributary of river Niger (20 km east of river), Otta, Benue State, 1f, (CW 54 mm), coll. John Iyage. NMU 12.VI.1984, dug from holes in banks of river Samu, tributary of Niger, Pasakwauri, near Kagoro, Kaduna State, 1m, 1f, coll. N. Cumberlidge. ZIM K3484, Benin, 1m, 2f, xii.1909, coll. C. Manger. ZIM K30252, Njaba creek, 15.iii.1973, coll. J. Voelker. ZIM K30314, Cross river, near Arochukwu, 6.iv.1974, coll. J. Voelker. **CAMEROON.** NHM 1938.7.1.9–13, Mamfe, coll. I. Sanderson. NHM 2.VIII.1968, Kindongo, south Bakundu, west Cameroon, in hole on forest floor about 100 yds from nearest (non-permanent) water, coll. T. S. Jones. RCM 54.190, Kombetiko, 5 km from Batouri, river Tanadi, 3 specimens, 2.ii.1976, coll. F. Puylaert. RCM 53.389, Olounou, 15–30 specimens, 15–17.viii.1971, coll. F. Puylaert. RCM 54.198, Bissiri Mayerey, 20.i.1976, coll. F. Puylaert. SMF 2098, Bibundi, 20.viii.1948, coll. Justus Weil. SMF 2868, Bibundi, coll. Justus Weil. SMF 1787, Victoria, 1907, O. Valley. NMU 24.X.1970, near Mamfe, crossing road by Baduma village, Kumba-Mamfe road, 1f, coll. R. H. L. Disney. ZIM K3526, 1m, 1f, 24.xii.1911, coll. Dr. E. Fickendey. ZIM K25447, Duala, 1m, 4.x.1912, C. Manger. ZIM K30397, Kembong, near Mamfe, 26.iv.1975, coll. J. Voelker. ZMB 5552, Djeerfluss, 1m, coll. Schweinfurth. ZMB 7789, Benue, 4–9.viii.1889, coll. Staudinger. ZMB 8234, Barombi Lake, 1f, coll. Zeuner. ZMB 10023, 1f, coll. Preuss. ZMB 10216, Johann Albrechtshöhe (modern name unknown, 4°40'N, 9°20'E), 1f, coll. Conrad. ZMB 13718, Victoria, 1f, coll. Deutsche Tiefsee Expedition. ZMB 14342, Douala, 2f, 5.xi.1910, coll. Shaeffer. ZMB 16440, Barombi Station, 1m, 1891, coll. Preuss. ZMB 16947, Douala, 1m, coll. Thorbeke.

ZMB 20161, Buea, 6f, 16.xi.1892, coll. Preuss. ZMB 20195, Buea, 1m, 1f, coll. Preuss. ZMB 20199, Victoria, 4m, coll. Preuss. ZMB 21300, river Sanaga, Douala grassland district, 1200 m, 1m, 11.i.1917, coll. Elbert. ZMB 21308, Douala, 1f, coll. Thorbecke. CENTRAL AFRICAN REPUBLIC. RCM 55.399, Giako river, Bougoua, 26.ii.1982, coll. L. de Vos & J. Kempeneus. RCM 53.086, near Bangui, 22.xii.1967. SUDAN. NHM 1912.12.31.52, Nyonki Nile, 2030 feet, 1f, hatchlings, 28.iv.1912, coll. Sir F. T. Jackson. NHM 1912.12.31.53, Gondokoro, 1800 feet, 12.iv.1912, coll. Sir F. T. Jackson. NHM 1913.9.10.1-3, Lado Nipo, 15 miles north of Kajokaji, coll. S. S. Flower, zoological survey of Egypt. NHM 1913.9.10.9-10, new cut to Zeraf, north of Shamfe, coll. G. W. Graham. NHM 1918.12.13.1-3, Mongalla, coll. S. S. Flower, Zoological Survey of Egypt. NHM 1922.11.22.7-11, Mongalla, Kanisa, vi.1914, coll. S. S. Flower, Zoological Survey of Egypt. FMC, 400 miles west of Juba, 7m, 18f, 22.xii.1884. ZAIRE. RCM 1666, Buta, 1934, coll. F. Hutsebout. RCM 1.661-1.665, Bambesa, 1.viii.1924, coll. J. Brejko. RCM 47.495, Epulu, ix.1956, coll. Dr. M. Poll. RCM 46.159-46.160, Ngense, 1955. MNHN BP5049, river Dougou, affluent of Uele, 1m, coll. L. Didier, Mission du Bourg Bozas, 1903. MCZ 10612, Faradje, 1m 1f, 21-23.ix.1915. SMF 2405, Luki, coll. E. Darteville. SMF 2398, Ganda Sundi, coll. E. Darteville. SMF 2385, Faradje, upper Uele, v.1925, coll. Dr. Schoudeten (exchange, RCM 1083, 1079). SMF 2383, Bambesa, coll. Krydag. SMF 1782, Duma, coll. Telinbotz. All of the following AMNH material coll. H. Lang, J. Chapin, AMNH Congo Expedition. AMNH 3338, Faradje, 5m, 2f. AMNH 3339, Faradje. AMNH 3355, Faradje, 3m. AMNH 3357, Faradje, 3m, 1f, x.1912. AMNH 3358, affluents of Nepoko river, near Gamangui (Ituri Forest), 3m, 1f. AMNH 3359, Banana, 3m. AMNH 3359, Poko, 1m, 4f, x-xii.1913. AMNH 3377, affluents of Nepoko river, near Gamangui (Ituri Forest), 3m, 1f. AMNH 3406, south of Poko, x-xii.1913. AMNH 3409, affluents of Nepoko river, near Gamangui (Ituri Forest), 1m. AMNH 3422, Van Kerckhovernille, 2m, 1f, iv.1912. AMNH 3448, Faradje, 1f, 1911. AMNH 3453, Poko, 1m, 4f, viii.1909. AMNH 3458, north of Ganza, 1f (ovig), 16.xii.1909. AMNH 3462, affluents of the Tshope river, near Stanleyville. AMNH 3465, Yakukuku, 1m; Garamba, 1f, xi.1911. BIOKO. NHM 1905.7.19.12, coll. Fernando Po Exploration Committee. ZMB 20164, 1m, 1f, vii.1900, coll. Conradt. GABON. NHM 1908.6.2.22, Lambarene, Ogoué river, coll. M. Ansoerge. NHM 1908.6.2.23-24, Abanga river, Ogoué river. NHM 1908.6.2.25, Fang forest, Ogoué river, caught on a mountain-top during heavy tropical rain, 29.iv.1907. NHM 1908.6.2.25a, Masoma river, Ogoué river. AMNH 3367, Libreville, 5m, 5f, ii.1916, coll. H. Lang, J. Chapin. AMNH 3369, 3m, 2f, 1916, coll. H. Lang, J. Chapin. FMC, Gabon or Middle Congo, French Equatorial Africa, 1951-1952, coll. H. A. Beatty. CABINDA. MNHN BP5048 (1m, CW 54.7, CL 36.0 mm), BP5047 (1f, CW 56.6, CL 39.5 mm) Landana, Cote de Loango, 4.ix.1898, coll. M. Petit. ANGOLA. NHM 1912.4.2.1-3, Luali river.

anterior third (CW/CL = 1.51), extremely high, with maximum height in anterior region (CH/CL = 0.61). Anterior margin of front straight, curving under, front relatively narrow, about one-quarter carapace width (FW/CW = 0.25). Surface of carapace smooth with no deep grooves. Postfrontal crest consisting of fused epigastric, postorbital crests, lateral ends with slight crenulations; mid-groove broad, shallow. Postfrontal crest contrasting colour to carapace, located very close to, almost touching, postorbital margin; laterally, postfrontal crest meeting, or nearly meeting, anterolateral margin of carapace at, or near, epibranchial tooth. Exo-orbital tooth blunt, low, intermediate tooth smaller than exo-orbital tooth, epibranchial tooth small, low, a granule. Anterolateral margin of carapace raised and granulated, bigger granules at epibranchial corner, smaller granules behind, continuous with posterolateral margin, or curving slightly inward in hepatic region. Posterior margin about two-thirds as wide as carapace width.

Face of of carapace with 2 sutures, 1 longitudinal, 1 vertical, dividing face and sides into 3 parts (Fig. 1 b). Longitudinal suture dividing suborbital, subhepatic regions from pterygostomial region, beginning under inferior medial margin of orbit, and curving backward across side. Short, curving, vertical suture dividing suborbital region from subhepatic region (Fig. 1 b); suture beginning beneath intermediate tooth, curving down to meet longitudinal suture, marked by row of small rounded granules. Third maxillipeds (Fig. 1 d) filling entire oral field, except for transversely oval efferent respiratory openings at superior lateral corners; long flagellum on exopod of third maxilliped; ishium of third maxilliped smooth, with faint vertical groove; merus with flanged edges. Mandibular palp 2-segmented, terminal segment single, undivided, small hard, hair-fringed flap at junction between segments (Fig. 2 a-c).

PEREIOPODS (Fig. 1 f-i). Chelipeds of lectotype unequal, right longer, higher than left. Dactylus of right cheliped not arched, fingers enclosing long interspace when closed, palm of propodus swollen. Fingers of right cheliped with 4 larger teeth on lower digit and 4 larger teeth on upper digit, interspersed with a series of smaller pointed teeth along their lengths. Inferior margins of merus with rows of small teeth, cluster of granules surrounding larger tooth at distal end. Carpus of cheliped with 2 large pointed teeth on inner margin, second smaller than first. Left cheliped similar to right, but smaller in all respects. Walking legs (pereopods 2-5) slender (Fig. 2 j), third pair longest, fourth pair shortest. Posterior margin of propodus of walking legs serrated, dactyli of walking legs tapering to point, each bearing rows of downward-pointing sharp bristles; dactylus of fourth pair shortest (Fig. 2 j).

UNDERSIDE. First transverse groove on sternum (between sternal segments 2 and 3) complete; second groove (between sternal segments 3 and 4) consisting of 2 small notches at sides of sternum; sternum with conspicuous raised ridges at points where chelipeds insert (Fig. 1 c). Segments 1-6 of abdomen four sided, last segment triangular, sides indented, rounded at distal margin (Fig. 1 e); segment 3 broadest, segments 3-7 tapering inwards (Fig. 1 e).

Terminal segment of gonopod 1 long (2/3 as long as subterminal segment), first half straight continuation of subterminal segment, second half curving outward, tapering to pointed tip; terminal segment with raised lobe on the cephalic part, separated

DESCRIPTION OF MALE LECTOTYPE

CARAPACE (Fig. 1 a,b). Ovoid, extremely wide, widest in

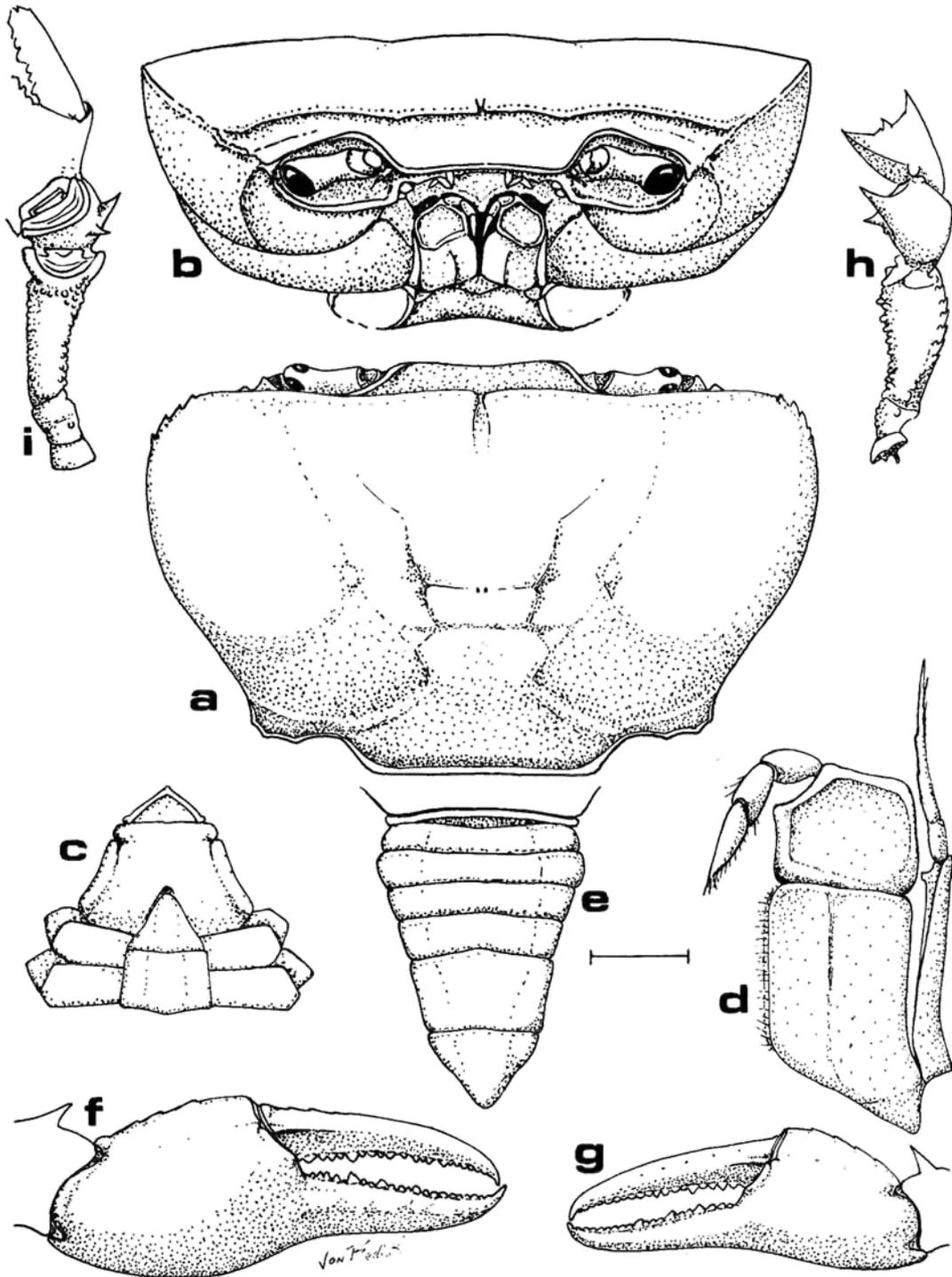


Fig. 1 *Sudanonautes floweri*, lectotype, adult male from Bahr el Gebel, Sudan (CW 48 mm), NHM reg 1901.8.26.2. (a), whole animal, dorsal aspect; (b), carapace, frontal aspect; (c) sternum; (d) left third maxilliped; (e), abdomen; (f), right cheliped, frontal view; (g), left cheliped, frontal view; (h) carpus, and merus of right cheliped, superior view; (i) carpus, and merus of right cheliped, inferior view. Scale bar equals 15 mm (h, i), 10 mm (c, f, g), 7.5 mm (a, b, e), and 3.75 mm (d).

from the caudal part by a distinct longitudinal groove visible from caudal and superior views (Fig. 2 d,f), not visible from cephalic view (Fig. 2 e). Subterminal segment of gonopod 1 broadened conspicuously on outer margin, fringed with bristles (Fig. 2 d,e), with raised flap extending halfway across segment in distal part,

tapering diagonally to point at junction with terminal segment, forming roof of chamber for gonopod 2; subterminal segment beneath flap forming lower floor of chamber for gonopod 2 (Fig. 2 d). Gonopod 2 (Fig. 2 g-i) shorter than gonopod 1 (reaching only to the junction between last 2 segments of gonopod 1).

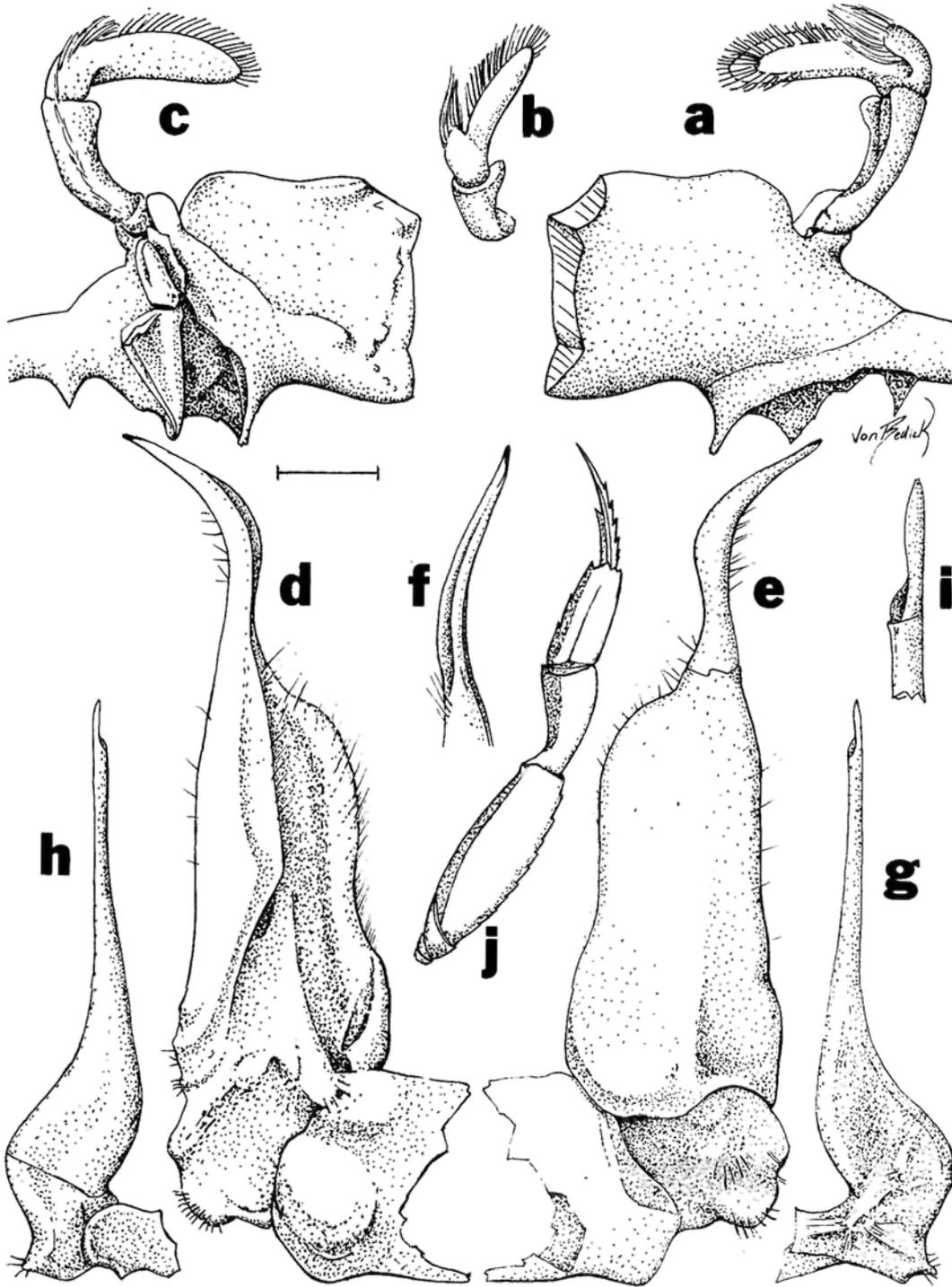


Fig. 2 *Sudanonautes floweri*, lectotype, adult male from Bahr el Gebel, Sudan (CW 48 mm), NHM reg 1901.8.26.2. (a), right mandible anterior view; (b), right mandible superior view; (c), right mandible posterior view; (d), left gonopod 1, caudal view; (e), right gonopod 1, caudal view; (f), right gonopod 1, superior view; (g), right gonopod 2, cephalic view; (h), right gonopod 2, caudal view; (i), right gonopod 2, caudal view, detail of terminal segment; (j) left pereopod 2. Scale bar equals 10 mm (j), 1.5 mm (a-c, d-h), and 0.5 mm (i).

Terminal segment gonopod 2 cup-shaped, with pointed tip, extremely short, only 1/15 as long as subterminal segment. Subterminal segment gonopod 2 widest at base, then tapering sharply inward, forming long, thin, pointed, upright process supporting short terminal segment.

ADULT FEMALE. Right, left chelipeds same proportions as male of same size, unequal in both length, height. Mature female abdomen very wide reaching coxae of pereopods 2–5. Segments of female abdomen becoming gradually longer distally, first, fifth becoming gradually wider, abdomen being

widest at groove separating fourth, fifth segments. Sixth segment, telson together forming near semicircle.

GROWTH (Fig. 3 a,b, Table 1). Measurements and proportions given in Table 1, Fig. 3 a,b. Sexual maturity judged by development of female abdomen: abdomen of mature females overlapping bases of coxae of walking legs, pleopods broad, hair-fringed. Pubertal moult, from pubertal stage to sexual maturity, occurring between CW 33–42 mm. Largest known specimen, (male from Cameroon) CW 60.4, CL 39.9. In Zaire, eggs produced in December; in Sudan, hatchlings present in April. Dimensions of carapace varying with age (Fig. 3 a). Relative proportions of carapace width (CW/CL) and height (CH/CL) of juvenile and pubescent *S. floweri* not significantly different ($P > 0.05$) from adults (Fig. 3 b). Front width becoming smaller with age: FW/CL of adult *S. floweri* significantly more narrow ($P < 0.001$) than that of juvenile and pubescent animals (Fig. 3 b).

COLOUR. (Living adults from Ogoja, Nigeria). Dorsal carapace dark purplish brown, with a contrasting yellow-orange postfrontal crest and yellow orbital border. Flanks light brown, third maxillipeds pale brown with purple tinge, eye-stalks white cream, cornea black, sternum and abdomen light brown with purple tinge. Arthroal membranes between joints of chelipeds and pereopods dark brown; dorsal surface

Table 1 Means (\pm SE) of ratio of carapace width (CW), carapace height (CH), and front width (FW), to body size (CL) of adult *Sudanonautes floweri* compared to the adults of six closely related species of *Sudanonautes* from Nigeria and Central Africa.

	CW/CL $X \pm SE$	CH/CL $X \pm SE$	FW/CL $X \pm SE$
<i>Sudanonautes floweri</i>	1.52 \pm 0.01 (n = 65)	0.61 \pm 0.0	10.38 \pm 0.003
<i>Sudanonautes aubryi</i>	1.37 ^a \pm 0.01 (n = 63)	0.52 ^a \pm 0.01	0.38 \pm 0.002
<i>Sudanonautes africanus</i>	1.38 ^a \pm 0.01 (n = 26)	0.43 ^a \pm 0.003 (n = 14)	0.36 ^c \pm 0.004 (n = 15)
<i>Sudanonautes granulatus</i>	1.42 ^a \pm 0.01 (n = 33)	0.51 ^a \pm 0.01	0.41 ^a \pm 0.01
<i>Sudanonautes monodi</i>	1.49 ^a \pm 0.01 (n = 23)	0.58 ^b \pm 0.004	0.39 \pm 0.004
<i>Sudanonautes kagoroensis</i>	1.52 \pm 0.02 (n = 9)	0.50 ^a \pm 0.01	0.39 \pm 0.004
<i>Sudanonautes orthostylis</i>	1.45 ^a \pm 0.02 (n = 10)	0.51 ^a \pm 0.01	0.46 ^a \pm 0.01

Proportion significantly different from that of *S. floweri*: ^a = $P < 0.001$; ^b = $P < 0.01$; ^c = $P < 0.05$.

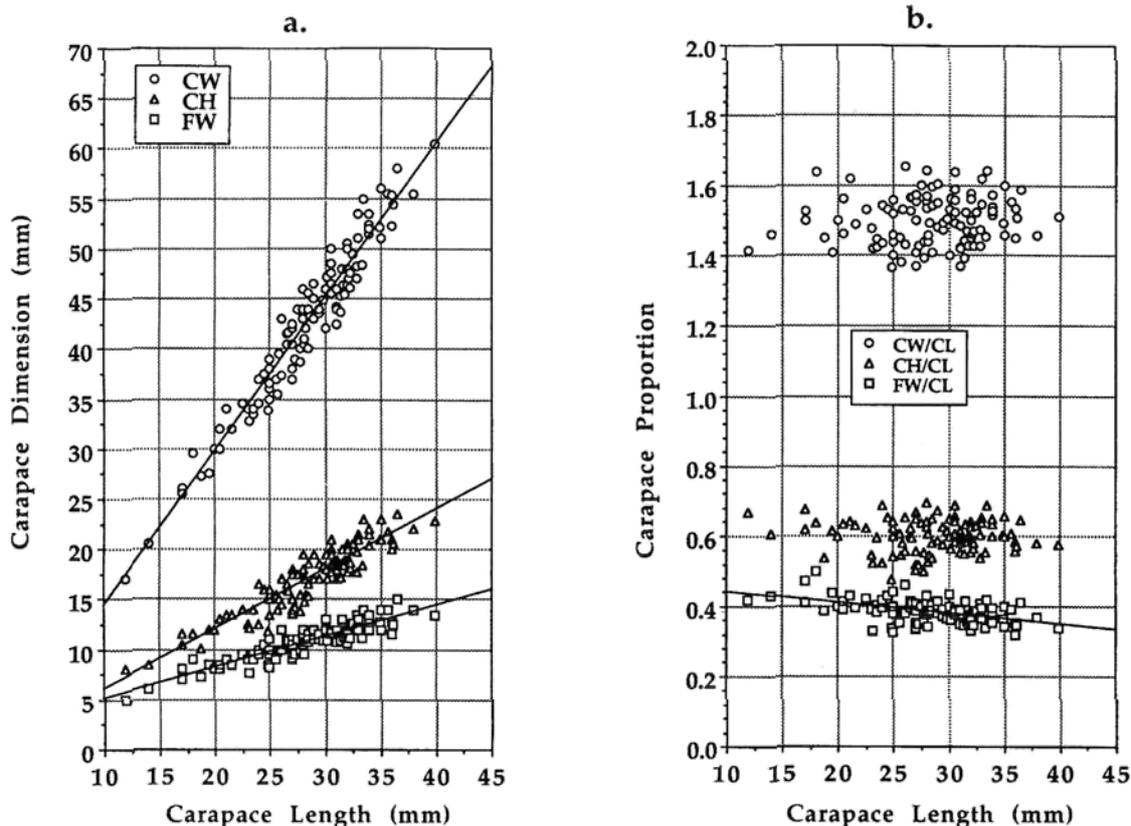


Fig. 3. Comparisons of 108 specimens of *Sudanonautes floweri*. a, dimensions of the carapace (CW, CH, FW) compared to body size (CL), r values (all at $df = 107$) indicate a highly significant correlation ($P < 0.001$) between size classes. b, relative proportions of carapace width and height (CW/CL, CH/CL) compared to body size (CL), r values (both at $df = 107$) indicate no significant correlation ($P > 0.05$) between size classes; relative proportions of front width (FW/CL) compared to body size (CL), r value (at $df = 107$) indicates a highly significant correlation ($P < 0.001$) between size classes.

of chelipeds and pereiopods light brown, ventral surface light brown. Specimens from the Ogoué river, in the Fang forest, Gabon, with brown-pink carapace, shading into neutral orange in middle; walking legs orange-vermillion.

VARIATION. The anterolateral margin is raised, marked by a series of granules or small teeth in some specimens (from Juba, Shambe, and Kojo-Kaji, Sudan; Ituri forest, Banana, and Faradje, Zaire; and Ogoja, Kaduna, and Bendel State, Nigeria). In other specimens (Poko, Zaire; Fernando Po, and Luali, Angola) the anterolateral margin is completely smooth. In specimens from Oban, Nigeria, the anterolateral margin is smooth except for the epibranchial tooth (which is the size of a large granule), followed by two smaller granules. It is possible that the above variations of the anterolateral margin are due to changes associated with growth. For example, the adult male (CW 53.5 mm) from Juba, Sudan (FMC) was the only one in which the anterolateral margin was smooth out of 25 specimens of all sizes. This margin was toothed or serrated in all the other specimens which measured CW 48 mm or less. A similar observation was made in the series of specimens from Cameroon (RCM 53.389), where the anterolateral margin of a large male (CW 60.4 mm) was completely smooth, but that of smaller specimens was granulated. Some specimens from Juba, Sudan, had serrations on the dorsal surface of the dactylus of the cheliped while other specimens from Juba, and from Nepoko, Zaire, lacked these serrations.

ECOLOGICAL NOTES

Sudanonautes floweri is a common species of fresh-water crab widely distributed in Nigeria and Central Africa. It is found in the moister regions of the woodland and guinea savanna zones from central Nigeria to southern Sudan. This species is also found in the humid tropical rain forest habitats in south-east Nigeria, south Cameroon, Bioko, Central African Republic, Zaire, Congo, and Gabon. In Nigeria, *S. floweri* occurs in the drainage basins of the lower Niger, Benue and Cross rivers. Specimens collected from Yankari Game Reserve, Bauchi State, Nigeria were dug from holes at the base of tufts of tall grass clumps in a marsh at the confluence of rivers Yashi and Gaji, an area heavily trampled by big game, especially elephants. Many specimens of *S. floweri* were caught on land during heavy tropical rain.

In Sudan, *S. floweri* lives both in the Yei river basin (a tributary of the Nile), in the mountainous watershed between the Nile and the Zaire rivers, and in the level papyrus swamps (Flower, 1931). In Zaire, *S. floweri* has been reported from the lower and middle reaches of the Zaire river, and in the Ubangi and Uele rivers (Rathbun, 1921). The habitat of *S. floweri* in Zaire has also been described by Rathbun (1921), who summarised the field notes of Herbert Lang. *S. floweri* was often found in heaps of rotting vegetation in water courses, and Lang speculated that this habit may carry the crabs downstream, explaining (at least in part) the wide distribution of this species. Predators of *S. floweri* in the rain forests of Zaire include crocodiles, monitor lizards (*Varanus niloticus*), insectivorous otter shrews (*Potamogale velox*) and several small carnivores, chiefly species of mongooses and the African civet (*Viverra civetta*).

Sudanonautes floweri is common in shallow streams, rivers,

and ponds, and digs burrows near waterways. This species is also found on land either next to water or some distance away, since it is capable of breathing air, and functions well for long periods out of water. The widened and highly arched carapace, and the lack of teeth on the anterolateral margins of the carapace of *S. floweri* are features often associated with air-breathing and burrow-living. This body shape contrasts with the more flattened, deep-grooved, and spiny carapace of the more aquatic river-living species such *S. faradjensis* (Rathbun, 1921).

TAXONOMIC REMARKS

The difficulties in distinguishing between *S. aubryi* and *S. floweri* date back to the work of Rathbun (1904, 1905). Although Rathbun (1905) described *S. floweri* and *S. aubryi* as separate species, her description of *P. (P.) aubryi* was based largely on specimens of *S. floweri*. Specimens from Cabinda (MNHN B5048) and Zaire (BP 5049) used by Rathbun (1905) to describe *S. aubryi* have been examined in the present study and found to be *S. floweri*. This opinion is supported by the photographs of the specimens from Zaire and Gabon provided by Rathbun (1904: TVI, plate IX, figs 5, 8) which closely resemble *S. floweri*, and which are clearly different from the photograph of the female type of *S. aubryi* (Rathbun, 1904: TVI, plate IX, fig. 3). Unfortunately, Rathbun's (1905) ideas were accepted by later workers with the result that the descriptions of *S. aubryi* in Balss (1914, 1929), Capart (1954), Bott (1955) and Monod (1977, 1980) all refer to *S. floweri* rather than to *S. aubryi sensu* H. Milne Edwards (1853).

COMPARISONS. Six species of *Sudanonautes* are sympatric with *S. floweri* in Nigeria and Central Africa, viz. *S. granulatus* (Balss, 1929), *S. kagoroensis* Cumberlidge, 1991, *S. orthostylis* Bott, 1955, *S. monodi* (Balss, 1929), *S. aubryi*, and *S. africanus*. These taxa can be distinguished from *S. floweri* as follows. The small hard flap on the mandibular palp at the junction between the two segments (Fig. 2 a-c), and the conspicuous raised ridges on the sternum at the points where the chelipeds insert (Fig. 1 c), distinguish *S. floweri* from all other species of *Sudanonautes*, which lack these features.

In addition, the raised lobe on the cephalic part of the terminal segment of gonopod 1, separated from the caudal part by a conspicuous longitudinal groove in *S. floweri* (Fig. 2 d,f) is also shared, in varying degrees, by *S. monodi*, *S. kagoroensis* and *S. granulatus*. These three species can be further distinguished from *S. floweri* by the following characters. The raised lobe on the cephalic part of the terminal segment of gonopod 1 of *S. monodi* (Cumberlidge, 1991) is considerably higher than that of *S. floweri*. In addition, the carapace of *S. monodi* is significantly ($P < 0.001$) flatter (CH/CL *S. monodi* = 0.52, *S. floweri* = 0.61), and less wide (CW/CL *S. monodi* = 1.37, *S. floweri* = 1.51) than that of *S. floweri* (Table 1). *Sudanonautes monodi* has patches of granules on the anterior corners of the carapace behind the postfrontal crest, while *S. floweri* lacks these granules. Finally, *S. monodi* is found in dry sudan savanna from Nigeria to Sudan, while *S. floweri* is absent from this region; and *S. monodi* is absent from woodland savanna and rain forest where *S. floweri* is abundant.

Sudanonautes kagoroensis was described by Cumberlidge

(1991), and can be distinguished from *S. floweri* by examination of gonopod 1: the raised lobe on the cephalic part of the terminal segment in *S. kagoroensis* is lower than that in *S. floweri*, and the outer margin of the subterminal segment of gonopod 1 is slim, while that of *S. floweri* is conspicuously broadened (Fig. 2 d, e). Furthermore, the carapace of *S. kagoroensis* is significantly ($P < 0.001$) flatter (CH/CL = 0.44) than that of *S. floweri* (CH/CL = 0.61).

Sudanonautes granulatus was redescribed by Cumberlidge (1993a) and can be distinguished from *S. floweri* as follows. The carapace of *S. granulatus* is significantly ($P < 0.001$) flatter (CH/CL *S. granulatus* = 0.51, *S. floweri* = 0.61), and less widened (CW/CL *S. granulatus* = 1.41, *S. floweri* = 1.51) than that of *S. floweri* (Table 1). In addition, the dactylus of the major cheliped of the adult male of *S. granulatus* is dramatically arched, while that of *S. floweri* is only moderately arched; the major cheliped of adult male *S. granulatus* is as long as, or longer, than the carapace width (Cumberlidge, 1993a), whereas that of *S. floweri* is shorter (Fig 1 f) than the carapace width (Fig. 1 a, b).

Three other species, *S. aubryi*, *S. africanus*, and *S. orthostylis*, differ from *S. floweri* in that the terminal segments of gonopod 1 of these species lack both a raised cephalic lobe, and a distinct longitudinal groove in the caudal view. These three taxa can be further distinguished from *S. floweri* as follows. The carapace of *S. aubryi* is significantly ($P < 0.001$) flatter (CH/CL *S. aubryi* = 0.52, *S. floweri* = 0.61), and less wide (CW/CL *S. aubryi* = 1.37, *S. floweri* = 1.51) than that of *S. floweri* (Table 1). In addition, the carapace and post-frontal crest of *S. aubryi* are a green-brown colour, whereas these parts of *S. floweri* are uniformly red-brown with a contrasting yellow postfrontal crest.

The terminal segment of gonopod 1 of *S. africanus* is thin and needle-like, while that of *S. floweri* (Fig. 2 d) is wider and has a distinct groove in the caudal view. The carapace of *S. africanus* is significantly ($P < 0.001$) flatter (CH/CL *S. africanus* = 0.43, *S. floweri* = 0.61) and less wide (CW/CL *S. africanus* = 1.38, *S. floweri* = 1.51) than that of *S. floweri* (Table 1). The carapace of *S. africanus* has patches of raised warts, while that of *S. aubryi* is completely smooth. Finally, the pollex of the propodus of the major cheliped of *S. africanus* has a large and conspicuously flattened tooth, which is lacking in adult *S. floweri*.

Sudanonautes orthostylis was redescribed by Cumberlidge (1993b), and can be distinguished from *S. floweri* as follows. The terminal segment of gonopod 1 of *S. orthostylis* is straight, lacks a visible groove, and curves outwards sharply only at the tip, while that of *S. floweri* bears a longitudinal groove and curves from the mid point (Fig. 2 d). The carapace of *S. orthostylis* is significantly ($P < 0.001$) flatter (CH/CL *S. orthostylis* = 0.51, *S. floweri* = 0.61), and less wide (CW/CL *S. orthostylis* = 1.44, *S. floweri* = 1.51) than that of *S. floweri* (Table 1). The frontal margin of *S. orthostylis* is significantly ($P < 0.001$) wider than that of *S. floweri* (FW/CL *S. orthostylis* = 0.46, *S. floweri* = 0.38, Table 1). The dactylus of the major cheliped of *S. orthostylis* is broad and flat, while that of *S. floweri* is narrow. Finally, *S. orthostylis* is a much smaller species, maturing at CW 22 mm, compared to maturity between CW 33–42 mm in *S. floweri*.

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