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Identification of *Sudanonautes aubryi* (H. Milne-Edwards, 1853) (Brachyura: Potamoidea: Potamonautidae) from West and Central Africa

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(With 3 figures)

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Introduction

Four species of freshwater crabs of the genus *Sudanonautes* (Bott, 1955) – *S. aubryi* (H. Milne-Edwards, 1853), *S. africanus* (A. Milne-Edwards, 1869), *S. floweri* (De Man, 1901), and *S. granulatus* (Balss, 1929) – serve as second intermediate hosts of the human lung fluke *Paragonimus* in Nigeria and Central Africa (VOELKER, SACHS, VOLKMER & BRABAND, 1975; VOELKER & SACHS, 1977; NOZAIS, DOUCET, DUNAN & N'DRI, 1980; CUMBERLIDGE, 1993a). However, distinguishing between these species is not easy, and specimens belonging to all four species have been wrongly identified in the literature.

The taxonomy of *S. aubryi*, the subject of the present work, has long been unstable, making identification of this species especially difficult. For example, in the last major revision of the freshwater crabs of Africa (BOTT, 1955), this species appeared as *S. (S.) d. decazei* (A. Milne-Edwards, 1886) with *Potamon (Potamonautes) pobeguini*, Rathbun, 1905, *Potamon decazei granulata*, Balss, 1929, and *P. (P.) regnieri*, Rathbun, 1905, listed as synonyms. In a later work, that author (BOTT, 1964) judged *S. (S.) d. decazei* itself to be a junior synonym of *S. (S.) p. pelii* (Herklots, 1861).

In the present study, *Thelphusa pelii*, *T. decazei*, and *P. (P.) pobeguini* are judged to be synonyms of *S. aubryi*, following examination of type material. This synonymization of *T. pelii* with *S. aubryi* represents a

return to the original concept of the species proposed by earlier workers (H. MILNE-EDWARDS, 1853; A. MILNE-EDWARDS, 1887; DE MAN, 1901).

Ambiguous descriptions of *S. aubryi* in the literature have led to the misidentification of specimens of *S. aubryi* as *S. floweri* (RATHBUN, 1905; CAPART, 1954; BOTT, 1955).

Furthermore, the present investigation has revealed that *S. aubryi* has also been wrongly identified as *S. africanus* in reports on taxonomy (BOTT, 1959; MONOD, 1977, 1980), salt and water balance (LUTZ, 1969), growth (EJIKE, 1972), ecology (BERTRAND, 1974), and parasitology (VOELKER, SACHS, VOLKMER & BRABAND, 1975; fig. 6).

Because the male type of *S. aubryi* from Gabon is preserved dry, the gonopods and mandible of the type of this species have never been described. These characters are described here from other specimens of *S. aubryi* from Nigeria preserved in alcohol, which were selected following detailed examination of the male and female types from Gabon. Gonopod 1 of *S. aubryi* was found to be distinct (Fig. 1 d - f). When considered in conjunction with other characters of the carapace (Fig. 2 a - c) and mandibles (Fig. 1 a - c), it can be used to identify the species unequivocally. The aim of the present study is to clarify the confused taxonomy of *S. aubryi*. This, in turn, will make it easier for other workers to identify the species, and will allow its distribution to be updated.

Methods

The carapace and cheliped features of the dried male and female types of *S. aubryi* from Gabon were noted. The species is completely redescribed here from a specimen from Nigeria (Figs. 1 a - g, 2 a - l). The left mandible and left gonopods 1 and 2 were illustrated following removal from the specimen in order to describe these structures under magnification (Fig. 1 a - g). Reference was also made to the types of *T. pelii, T. decazei, P. (P.) pobeguini, T. africanus, P. decazei granulata,* and *P. aubryi monodi* Balss, 1929. Photographs of the lectotype of *T. pelii* are available in BOTT (1964, plate 2, figs. 1 - 2), and photographs of the types of *T. decazei* and *P. (P.) pobeguini* are given in RATHBUN (1904, TVI, plate XVI, figs. 3, 8 respectively). *Sudanonautes granulatus* has been redescribed in detail by CUMBERLIDGE (1993a). Carapace length, carapace width, carapace height, and front width were recorded from 59 specimens 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). All geographical localities for *S. aubryi* given in the present study result from the direct examination of specimens, since distribution records in the literature are based mostly on unreliable identifications.

The following abbreviations are used: AMNH, American Museum of Natural History, New York, USA; IFAN, Institute Fondamental d'Afrique Noir, Dakar, Senegal; MCZ, Museum of Comparative Zoology, Harvard, MA, USA; MNHN,

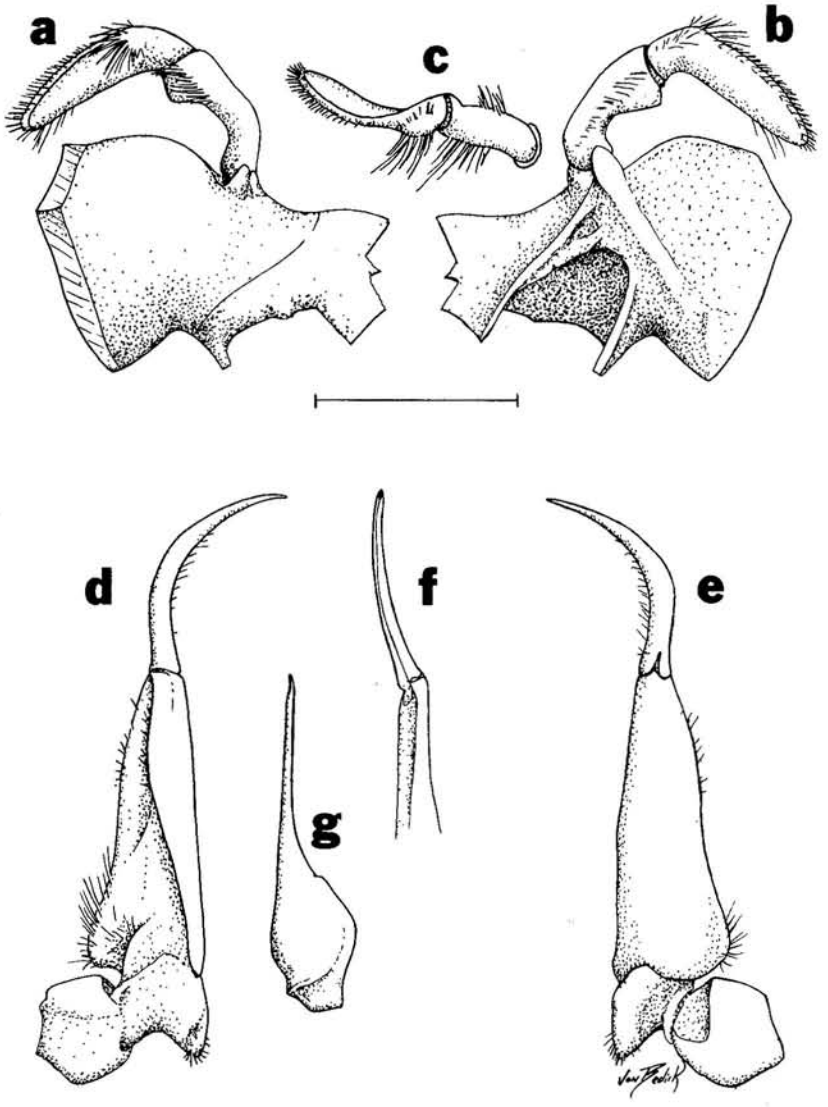

Fig. 1. *Sudanonautes aubryi*, adult male from Tiga Lake, Nigeria, (CW 66 mm), NMU 6.XI.1982. (a), left mandible anterior view; (b), left mandible posterior view; (c), left mandible superior view; (d), left gonopod 1, caudal view; (e), left gonopod 1, cephalic view; (f), left gonopod 1, superior view; (g), left gonopod 2, caudal view. Scale bar equals 5 mm (a - c); 7 mm (d - g).

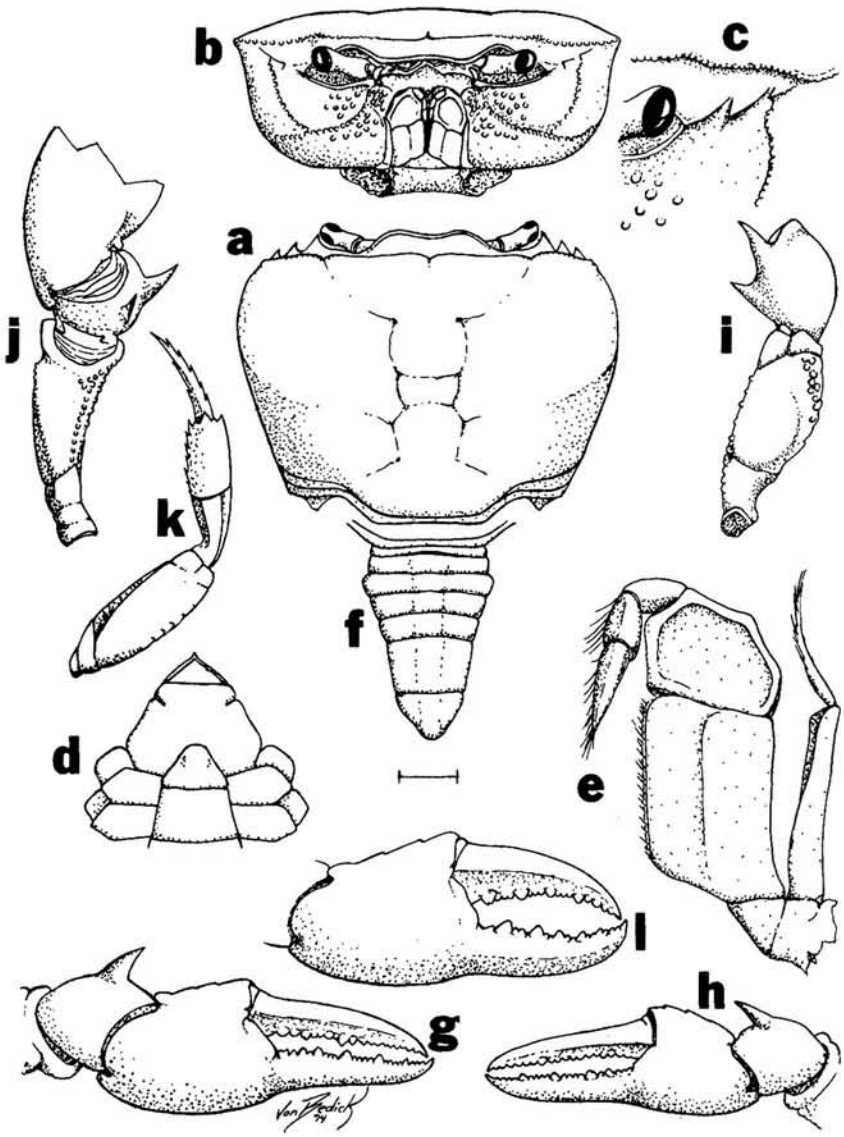

Fig. 2. *Sudanonautes aubryi*, adult male from Tiga Lake, Nigeria, (CW 66 mm), NMU 6.XI.1982. (a), whole animal, dorsal aspect; (b), carapace, frontal aspect; (c), carapace showing detail of epibranchial corner; (d), sternum; (e), left third maxilliped; (f), abdomen; (g), carpus, propodus, and dactylus of right cheliped, frontal view; (h), carpus, propodus, and dactylus of left cheliped, frontal view; (i), carpus, and merus of right cheliped, superior view; (j), carpus, and merus of right cheliped, inferior view; (k), left periopod 2; (l), *Thelphusa pelii* Herklots, 1861, NNH 322, lectotype, adult male from St. George d'Elmina, Ghana (CW 54 mm), propodus, and dactylus of right cheliped, frontal view. Scale bar equals 10 mm (a, b, d, f - l), 5 mm (c), and 2.5 mm (e).

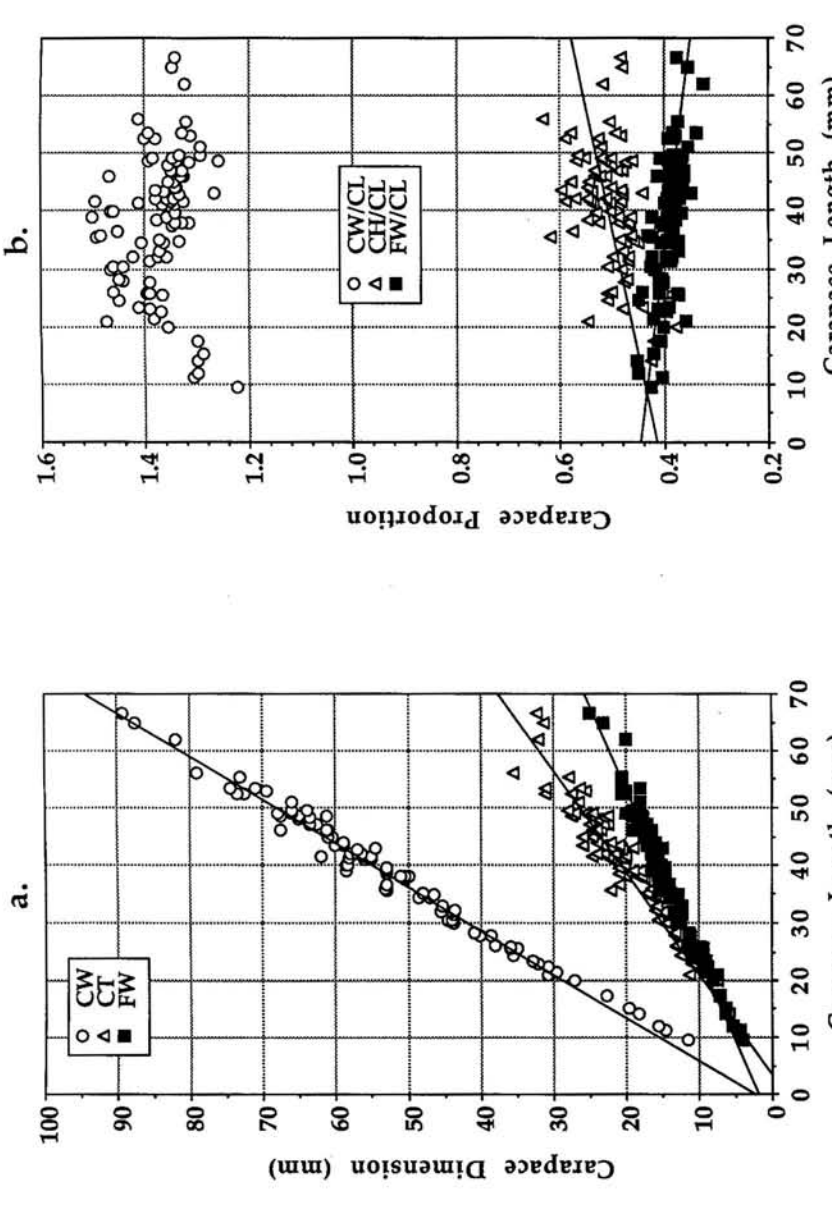

Fig. 3. Comparisons of 99 specimens of *Sudanonautes aubryi*. a, dimensions of the carapace (CW, CH, FW) compared to body size (CL), *r* values (all at $df = 98$) indicate a highly significant correlation ($P < 0.001$) between size classes. b, relative proportions of carapace width (CW/CL) compared to body size (CL), *r* value (at $df = 98$) indicates no significant correlation ($P > 0.05$) between size classes; relative proportions of carapace height (CH/CL) and front width (FW/CL), *r* values (both at $df = 98$) indicate a highly significant correlation ($P < 0.001$) between size classes.

Museum National d'Histoire Naturelle, Paris; NHM, The Natural History Museum, London, U.K.; NNH, Naturaal Historisches Museum, Leiden, The Netherlands; NMU, Northern Michigan University, Marquette, MI, USA; RCM, Royal Congo Museum, Tervuren, Belgium; SMF, Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt am Main, Germany; UZM, Universitetes Zoologiske Museum, Copenhagen, Denmark; USNM, The United States National Museum of Natural History, Smithsonian Institution, Washington DC.; 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, juv = juvenile.

Table 1

Means (± *SE*) of ratio of carapace width (CW), carapace height (CH), and front width (FW), to body size (CL) of adult *Sudanonautes aubryi* compared to the adults of four closely related species of *Sudanonautes* from Nigeria and Central Africa.

	CW/CL $X \pm SE$	CH/CL $X \pm SE$	FW/CL $X \pm SE$
Sudanonautes aubryi (n = 63)	1.37 ± 0.01	0.52 ± 0.01	0.38 ± 0.002
Sudanonautes floweri (n = 65)	1.52[a)] ± 0.01	0.61[a)] ± 0.01	0.38 ± 0.003
Sudanonautes africanus	1.38 ± 0.01 (n = 26)	0.43[a)] ± 0.003 (n = 14)	0.36[a)] ± 0.004 (n = 15)
Sudanonautes granulatus (n = 33)	1.42[a)] ± 0.01	0.51 ± 0.01	0.41 ± 0.01
Sudanonautes monodi (n = 23)	1.49[a)] ± 0.01	0.58[a)] ± 0.004	0.39 ± 0.004

[a)] = Proportion significantly different from that of *S. aubryi* at 95 % confidence limits.

Systematics

Sudanonautes aubryi, (H. Milne-Edwards, 1853).

Thelphusa aurantia, Herklots, 1851, p. 5, pl. 1, fig. 2.

Thelphusa aubryi, H. Milne-Edwards, 1853; A. Milne-Edwards, 1887; Aurivillus, 1899, p. 8 - 9.

Thelphusa pelii, Herklots, 1861, p. 13.

Thelphus decazei, A. Milne-Edwards, 1886, p. 150; 1887, p. 127, pl. 8, fig. 7.

Potamon (Potamonautes) pelii, (Herklots, 1861) – De Man, 1901, p. 99 - 100; Rathbun, 1905, p. 162, 191 - 193.

Potamon (Potamonautes) decazei, (A. Milne-Edwards, 1886) – Rathbun, 1900, p. 283; 1904, VI, pl. 16, Potamidae (VIII), fig. 3 (type, Franceville); 1905, p. 195; Sendler, 1912, p. 199; Balss, 1914a, p. 405 (ZIM K13556, CW 48.5 mm, K13557); Balss, 1914b, p. 104; 1929, part.

Potamon (Potamonautes) pobeguini, Rathbun, 1904, VI, pl. 16, Potamidae (VIII), fig. 8 (type, Batah); 1905, p. 195 - 197.

Potamon (Potamonautes) aubryi, (H. Milne-Edwards, 1853) – Rathbun, 1900, p. 283 (not p. 282); 1904, VI, pl. 17, Potamidae (IX), fig. 4 (type, Gabon); 1905 VII, p. 191, part, only the female from Gabon, not the specimens from Cabinda, Zaire, and Gabon; De Man, 1901, p. 94, 98 - 100; Balss, 1914a, p. 405 (ZIM K13557 only); Roux, 1927, p. 237.

Potamonautes decazei granulata, Balss, 1929, part.

Potamonautes pobeguini, (Rathbun, 1905) – Balss, 1914b, p. 104; 1929, part.

Potamon aubryi, H. Milne-Edwards, 1853) – Chace, 1942.

Potamon pobeguini, (Rathbun, 1905) – Chace, 1942.

Potamon decazei, (A. Milne-Edwards, 1886) – Chace, 1942; Capart, 1954, p. 830, figs. 12, 15.

Potamon pobeguini, (Rathbun, 1905) – Chace, 1942; Capart, 1954, p. 842 - 843, figs. 10, 39.

Sudanonautes (Convexonautes) aubryi aubryi, (H. Milne-Edwards, 1853) – Bott, 1955 (part, only type from Gabon, not specimens from Zaire).

Sudanonautes (Sudanonautes) pelii pelii, (Herklots, 1861) – Bott, 1964; Monod, 1977, p. 1217, figs. 98 - 101, 110 - 115; 1980.

Sudanonautes (Sudanonautes) africanus africanus, (A. Milne-Edwards, 1869) – Bott, 1959, p. 1004, part; Lutz, 1969; Ejike, 1972; Bertrand, 1974.

Sudanonautes pelii, (Herklots, 1861), Cumberlidge, 1991, 1993a, b.

Material

Types. – *Thelphusa aubryi,* H. Milne-Edwards, 1853, MNHN B3805, Gabon, 1m, adult, (CW 58, CL 40 mm), preserved dry, M. Aubry Lecomte, 31.v.1854, "C'est l'examplaire apellé *aubryi* par De Man, 1901, p. 94."; MNHN B3792, Gabon, 1f, (CW 36, CL 26 mm) preserved dry, M. Aubry Lecomte. *Thelphusa pelii,* Herklots, 1861, NNH, D322, St. George d'Elmina, Ghana, 1m, lectotype, (CW 64.0, CL 49.5), H. S. Pel. *Thelphusa decazei,* A. Milne-Edwards, 1886, USNM 30009, cotype, Alima river, at Franceville, Gabon, M. de Brazza. *Potamon (Potamonautes) pobeguini,* Rathbun, 1905, BP 278 (= B5278), Batah, Gabon, 1m, (CW 46.5, CL 33.0); USNM 30011, Batah, Gabon, 1m, cotype (CW 31, CL 23), ix.1890, M. Pobeguin. *Potamon (Potamonautes) floweri,* De Man, 1901, NHM 1901.8.26.2, syntype, Bahr el Gebel, Sudan, Capt. S. S. Flower. *Potamonautes aubryi monodi,* Balss, 1929, between Tschamba and Laro, Cameroon, T. Monod. *Potamon (Potamonautes) regnieri,* Rathbun, 1905, MNHN B5239, Basin de Sanga, 1f, ovigerous, (CW 35.0, CL 24.5), E. Regnier, 1899. *Thelphusa africana,* Milne-Edwards, 1869, Gabon, 1 juv, M. Aubryi Lecomte. *Potamon decazei granulata,* Balss, 1929, ZMB 11257, Misahohe, Togo, lectotype, 1f.

Other Material. – COTE D'IVOIRE. – MNHN B5002, B5007, B5008, Bandama river, reserve de Lamto, J.-Y. Bertrand, 1974. RCM 55.500, Bouaké, vi.1977, P. Elsen. GHANA. – ZMB 4427, Ungar. IFAN, Okone, on road to Suhum Adams College, 11.v.1950, Barringdale. NHM 1911.6.29.(5 - 7), Dr. G. Spurrell. NHM 1921.12.7.(1 - 2), Kofoudua, Gerald Dugeon. NHM 1938.6.28.1, Accra, F. R. Irvine. NHM 1938.7.4.(28 - 30), Ejura, Trustees of the Thomas Godman Fund. NHM 1972.30.3, block FXI, field of oil palms, Coco Research Institute, Tafo, east Ghana, Braun. NNH 28715, Volta region (7°12'N, 0°30'E), 6.vi.1972, W. F. Rodenburg, donated by M. S. Hoodmoed. SMF 2653, xii.1964, donated by IFAN, 1965. TOGO. – ZMB 8727, Bismarksburg, 1f, Büttner. ZMB 8981, Misahohe, 1f, 30.iii.1893, Baumann. ZMB 10353, Sokodi, 2m, Schroder. ZMB 20200, Kete Krashi, 2m, Mischlich. ZMB 21316, Misahohe, 1m, 1898 - 99, Smend, Deutsche Tiefsee-Expedition. IFAN, Klouto mountains, 500 - 800m, several specimens, 2-6.vi.1950, A. Villiers. RCM 53.088, Misahohe, river Kpemuta, 10 - 15 specimens, 6-7.viii.1969, F. Puylaert. RCM 52.963, Badou, 17.i.1968, W. Verheyen. RCM 52.966, Porto Seguro, Lac Togo, 29.vi.1968, W. Verheyen. RCM 53.089, Aledjo, 3 specimens, 20.vii.1969, F. Puylaert. RCM 53.096, Fazao, 20-21.viii.1969, F. Puylaert. RCM 51.101, Misahohe, 6.viii.69, F. Puylaert. RCM 53.105, Ebeva, 2 specimens, 13-17.viii.1969, F. Puylaert. RCM 53.106, Niamtougou, 3 specimens, 21-24.vii.1969, F. Puylaert. RCM 53.127, 10-15 specimens, EVUC Atakpeme, 28.ii.1969, Verenese. RCM 53.128, Evu (Atakpame), 28.ii.1969, Verenese. RCM 53.129, Kamina (Atakpame), 3 specimens, 20-23.x.1968, Verenese. NMU 22.IV.1980, downstream from Kpalime falls near Kpalime, southwest Togo, 1m, 1f, J. N. Raybould, donated by T. Williams. BENIN. – NMU vii.1991, near Cotonou, 2m, 1f, T. Kruppa, donated by R. Sachs. IFAN, Basilla, 2m, 3f, 20.vi.1950, Villiers. NIGERIA. – NHM 1908.10.12.1, Ogun river west province, A. E. Kitson. NHM 1911.3.20.(1), northern Nigeria, A. C. Francis. NHM 1913.10.27.2, Obubra district, Cross River State, W. A. C. Cockburn. NHM 1935.5.30.(7-10), Ibadan, 7 specimens, 30.V.1935, G. N. Herrington. NHM 1949.IX.30.(1), Ogun River, Lagos, 30.ix.1949, M. McLaren. NHM (no number), Ibadan, D. A. Priest, Nigerian College of Arts, Science, and Technology, Lagos. NHM 1959.4.16.1, Northern Nigeria, 16.iv.1959, P. W. Hanney. NHM 1966.10.17.5-6. NHM 1972.10.20, O. Tarnow. NMH 1966.10.17.5-6, C. Ejike. ZIM K30299, 16.iii.1973, J. Voelker. ZIM K30251, Okigwe, 3.iii.1973, J. Voelker. ZIM K30300, 1973, J. Voelker. UZM (no number), Oyo, West Bah Bag Laboratories, 1m, 1f, xii.1952, H. S. Clausen. ZIM K30301, Awgu, 8.iii.1973, J. Voelker. ZIM K30302, Amunu, 1962 - 63, J. Voelker. UZM (no number), Igbetti, northern part of Oyo province, northwest of Ilorin, 3m, 2f, 1955, H. S. Clausen. USNM (no number), stream bank, University of Ife, Ile-Ife, 27.vi.1975, A. O. Segun. ANHM (no number), stream bank, University of Ife, Ile-Ife, 3m, 2f, 27.vi.1975, A. O. Segun. NMU 16.XII.1981, Maska Dam Fish Farm near Funtua, Kano State, 4m, 8f, N. Cumberlidge. NMU 6.XI.1982, outflow from Tiga dam, Tiga lake, Kano State, 4m, 8f, N. Cumberlidge. NMU 1982, from main urban river in Jos, Plateau State, 2f, donated by University of Jos, i.1983. NMU 8.III.1983, Gwarzo, Kano State, 3m, 4f, N. Cumberlidge. NMU 1.VII.1983, Gwarzo, Kano State, 1m, Usman Abubakar. NMU 23.II.1984, Gwarzo, Kano State, 3m, 2f, N. Cumberlidge. NMU 1.III.1984, Rogo, Kano State, 1f, ovigerous, N. Cumberlidge. NMU 8.III.1984, Gwarzo, Kano State, 1f, ovigerous, found with *S. monodi*, Ali Garko. NMU 23.IV.1984, Osse River, tributary of Benin river, Owo, Ondo State, 7m, 12f, Monday Obanoyen Rotimi. NMU 13.IV.1984, Badeggi river, tributary of the Niger, 30km south of Badeggi, 37km east of Bida, Niger State, 1m, (found with *S. monodi*), N. Cumberlidge. NMU 13.IV.1984, Daguru, Niger State, 1m, N. Cumberlidge. NMU IV.1967, Oli river tributary from the west of river Niger, just south of Kainje, 4m,

F. Walsh, donated by T. Williams. CAMEROON. – NHM 1902.8.16.(3), Kribi river, Bates. NHM 1906.11.9.(1), Ja river. NHM 1907.7.1.(2-4), forest 26 miles east of Kribi. NHM 1907.7.1.2-5, south Cameroon. NHM 1910.11.1.1-2, Bitye. NHM 1912.6.22.2-7, Bitye, Ja river, G. L. Bates. NHM 1912.6.22.(8-9), Bitye, Ja river. ZIM K13556, Elephantensee (only CW 48.5 mm, not CW 55 mm), 3.ix.1904, Richard Rohde; ZIM K13557, Mukonje farm, 19.xi.1903, Richard Rohde. ZIM K30390, Kembong, Cross river, near Mamfe, 26.vii.1975, J. Voelker. ZIM K30391, Kembong, Mamfe, 26.iv.1975, J. Voelker. ZIM K30392, Mbabe, 8-9.iii.1975, J. Voelker. ZMB 9011, Yaounde, 3m, 1f, 1898 - 99, Zenker, Deutsche Tiersee Expedition. ZMB 11273, Longji, 5m, 1f, Paschen. ZMB 12413, Bipindihof, 2m, 12.iv.1907, Zenker. ZMB 13366, bush near Tabassi, 1m, 1f, 16.xi.1908, Riggenbach. ZMB 14823, river Manjou, Manengaba road, 1m, 15.xi.1910, E. Hintz. ZMB 15182, Bipindi, 1m, 1f, viii.1898, Zenker. ZMB 19360, Dr. Richnon. ZMB 20247, Ebolowa, 1m, Laasch. ZMB 21317, Bipindihof, 2m, 1f, 1904, Zenker. RCM 51.782, Makau River Koukoup, 2.x.1965, J. P. Omgba. RCM 53.388, Olounou, 2 specimens, 11-19.ix.1974, F. Puylaert. RCM 53.393, Olounou, 11-19.ix.1971, F. Puylaert. MCZ 9066, 1926, George Schwab. MCZ 9180, Sakbayeme, near Edea, George Schwab. SMF 9301, river Mfiende, near Enongal, 15.x.1977, Ripert. SMF 7271, Kembong, near Mamfe, 26.iv.1975, B. de Wilde-Duyfjes. MNHN B5006, stream in plantation of African Fruit Company, Tiko, Theodore Monod. NMU 4.V.1982, Rhumsiki, Kapsiki Mountains, northwest Cameroon, purchased from sorcerer's apprentice 1m, N. Cumberlidge & L. Bourgault. NMU II.1970, Mangasa, near Mamfe, 1f, R. H. L. Disney, donated by T. Williams. GABON. – NHM 1908.6.2.(26), Abanga river, Ogoué river.

Diagnosis. – Terminal segment of gonopod 1 robust, rounded, long ($^2/_3$ as long as penultimate segment), first half straight continuation of subterminal segment, second half curving outward, tapering to pointed tip, longitudinal groove present (Fig. 1f), but not visible from either cephalic or caudal views (Fig. 1d, e); subterminal segment of gonopod 1 slim (Fig. 1 d - f); terminal segment of gonopod 2 extremely short (Fig. 1g). Triangular intermediate tooth on anterolateral margin between exo-orbital and epibranchial teeth (Fig. 2 a - c); intermediate tooth almost as big as exorbital tooth; epibranchial tooth small. Vertical suture on flank meeting anterolateral margin at epibranchial tooth (Fig. 2 a - c). Postfrontal crest always meeting anterolateral margin at a point behind the epibranchial tooth; carapace moderately arched (CH/CL = 0.52). Arthrodial membrane of cheliped scarlet.

Description. – Carapace (Fig. 2 a - c). – Ovoid, widest in anterior third (CW/CL = 1.37), relatively high, with maximum height in anterior region (CH/CL = 0.52). Anterior margin of front slightly bilobed, curving under, relatively narrow, less than one-third carapace width (FW/CW = 0.29). Surface of carapace smooth with no deep grooves. Postfrontal crest spanning entire carpace, consisting of fused epigastric, postorbital crests, with notch on crest behind cornea; crest smooth in middle, slight crenulations at lateral ends, meeting anterolateral margin at a point behind the epibranchial tooth; midgroove broad, shallow. Exo-orbital tooth blunt, large, intermediate tooth almost as big as exo-orbital tooth, epibranchial tooth small, low. Anterolateral margin of carapace raised and granulated, curving inward in the hepatic region. Posterior margin about two-thirds as wide as carapace width.

Fields of conspicuous granules in suborbital regions. Each suborbital and subhepatic region with 2 sutures, 1 longitudinal, 1 vertical, dividing region into 3 parts (Fig. 2 b - c). Longitudinal suture dividing suborbital, subhepatic regions from pterygostomial region, beginning medially at margin of lower orbit, curving back-

ward across subhepatic region. Vertical suture short, dividing suborbital region from subhepatic region marked by row of small rounded granules (Fig. 2b, c); suture beginning just beneath epibranchial tooth, directed forward beneath intermediate tooth, then curving down to meet longitudinal suture. 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 (Fig. 2d). Third maxillipeds filling entire oral field, except for transversely oval efferent respiratory openings at superior lateral corners; long, plumose flagellum on exopod of third maxilliped (Fig. 2e); ishium of third maxilliped smooth, with faint vertical groove (Fig. 2e). Mandibular palp 2-segmented; terminal segment single, undivided, fringed with hairs, longest at junction between segments (Fig. 1 a - c). Segments 1 - 6 of abdomen four sided, last segment triangular, sides indented, rounded at distal margin (Fig. 2f); segment 3 broadest, segments 3 - 7 tapering inwards.

Chelipeds (Fig. 2 g - j, l). – Unequal, right longer, higher than left. Palm of propodus of major cheliped of adult male swollen; dactylus, pollex long and narrow, not arched, enclosing long thin interspace along their cutting edges when fingers closed. Fingers of right cheliped with 5 larger teeth on lower digit and 5 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 2 - 5 (pereiopods = P) slender (Fig. 2k), P4 longest, P5 shortest. Posterior margin of propodus of P2 - P5 serrated, dactyli of P2 - P5 tapering to point, each bearing rows of downward-pointing sharp bristles; dactylus of P5 shortest of the 4 legs (Fig. 2k).

Gonopods. – Terminal segment of gonopod 1 robust, rounded, long ($^2/_3$ as long as penultimate segment), first half straight continuation of subterminal segment, second half curving outward, tapering to pointed tip, faint longitudinal groove visible only from superior view (Fig. 1f). Subterminal segment of gonopod 1 slim (Fig. 1 d - f), with raised flap extending halfway across segment in distal part, flap 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. 1d). Gonopod 2 (Fig. 1g) shorter than gonopod 1 (reaching only to junction between last 2 segments of gonopod 1). 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 which supports 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 pereiopods 2 - 5. Segments of female abdomen 4 sided, becoming gradually longer distally, 1 - 5 becoming gradually wider; widest at groove separating segments 4, 5; segment 6, telson together forming near semicircle.

Growth (Fig. 3a, b, Table 1). – Carapace dimensions given in Fig. 3a, relative proportions in Fig. 3b, Table 1. Growth discussed by EJIKE (1972). 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 45 - 50 mm. Largest known specimen (male from Cameroon) CW 89.5 mm. Eggs produced in

March. Dimensions of carapace varying with age (Fig. 3a). Width of carapace (in relation to carapace length, CW/CL) not chaniging with age: CW/CL of juvenile and pubescent animals not significantly different ($P > 0.05$) from that of adults (Fig. 3b). Height of carapace (CH/CL) increasing with age: that of adult *S. aubryi* significantly higher ($P < 0.001$) than CH/CL of juvenile and pubescent animals. Width of frontal margin (FW/CL) decreasing with age: that of juvenile and pubescent animals significantly wider ($P < 0.001$) than that of adults (Fig. 3b).

Distribution. – Cote d'Ivoire, Ghana, Togo, Benin, Nigeria, Cameroon, Gabon. It is likely that *S. aubryi* is also present in Equatorial Guinea. BOTT (1955) and MONOD (1977, 1980) report *S. aubryi* from Togo to Zaire. The range of this species has been extended here westwards to include Cote d'Ivoire and Ghana, but there are no confirmed records of this species in the Republic of the Congo or in Zaire.

Colour. – (Living adults from Gwarzo, Nigeria): Dorsal carapace green-brown; postfrontal crest white-cream; flanks light green; eyestalks brown, cornea scarlet red; epistome brown orange "burnt" colour; edges of orbits and frontal margin white-cream; sternum and abdomen white-cream; arthrodial membranes between joints of chelipeds and pereiopods scarlet; dorsal surface of chelipeds and periopods dark green, ventral surface white-cream; ovigerous female with orange eggs. Specimens from Owo, Nigeria varied as follows: postfrontal crest green brown; flanks light brown becoming purple on lower margins; eyestalks brown, corneas black; abdomen, sternum, undersides of legs, and chelipeds, white-cream with pink-mauve wash.

Variation. – The height of the carapace (in relation to the carapace length) increases as crabs grow (Fig. 3b), and also varies with habitat. Thus, specimens from the rain forest regions (southern Nigeria, southern Cameroon and Gabon) have flatter carapaces than those from the savanna regions (Ghana, Togo, northern Nigeria, and northern Cameroon). Distinct patches of granulations on the flanks in the suborbital region are present in some specimens (Nigeria, Ejura, Ghana) while others (Bitye, Cameroon) have almost smooth flanks. The postfrontal crest is wavy in some specimens (Ja river, Bitye, Cameroon) and straight in others (Kribi river, Cameroon); the postfrontal crest is granulated in some specimens (Obubra district, Nigeria) and smooth in others (Ja river, Bitye, Cameroon); the postfrontal crest behind the intermediate tooth has a distinct notch in some specimens (Cote d'Ivoire, southern Nigeria, Edea, Cameroon) and is straight in others (Bitye, Kribi, Cameroon). The inner margin of the merus of the cheliped has granules on both edges (Ibaden, Nigeria) or on one edge only (Bitye, Cameroon). The specimen from Kribi River, Cameroon has only faint granules on the anterolateral margin, and the end of the anterolateral margin does not turn inward over the carapace in the hepatic region.

Ecology. – *Sudanonautes aubryi* is found in guinea and woodland savanna from Cote d'Ivoire to northern Cameroon, and in tropical rain forest from southeast Nigeria to Gabon. This large species inhabits streams, rivers, and ponds, and digs burrows near waterways. *Sudanonautes aubryi* is capable of breathing air, and is often found on land at night. The habitat of *S. aubryi* in wooded savanna fringing a forested area in Cote d'Ivoire has been described by BERTRAND (1974).

Comments

The present findings represent a return to the original concept of *S. aubryi* proposed by earlier workers (H. MILNE-EDWARDS, 1853; A. MILNE-EDWARDS, 1887; DE MAN, 1901) who based their descriptions on the types of *S. aubryi* from Gabon. The difficulties in distinguishing between *S. aubryi* and *S. floweri* date back to the work of RATHBUN (1904, 1905), in which specimens of *S. floweri* were substituted and described as *S. aubryi*.

Specimens from Cabinda (MNHN B5048) and Zaire (MNHN B5049) 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) opinions were accepted by later workers with the result that the descriptions of *S. aubryi* in BALSS (1914a, 1929), CAPART (1954), BOTT (1955), and MONOD (1977, 1980) all refer to *S. floweri*, rather than to *S. aubryi* sensu H. Milne-Edwards (1853). For example, it is likely that CAPART'S (1954) description of *Potamonautes aubryi* is actually *S. floweri*, since it is based on the same specimen from Cabinda (MNHN B5048), used by RATHBUN (1904, 1905). Similarly, the description of *S. (C.) a. aubryi* in Bott (1955: 304 - 305, figs. 65, 100, pl. XXVIII, figs. 2 a - d) is based on specimens of *S. floweri* from Zaire. Finally, the descriptions of *S. (C.) a. aubryi* in Monod (1977, 1980) probably also refer to *S. floweri*, since that author accepted the taxonomic opinions of BOTT (1955).

Sudanonautes aubryi sensu Bott (1955) was designated the type species of the subgenus *Convexonautes* Bott, 1955, and assigned two subspecies, *S. (C.) a. floweri*, and *S. (C.) a. monodi*. Comparison of the types of *Thelphusa aubryi* from Gabon, *Potamon (Potamonautes) floweri* from Sudan, and *Potamonautes aubryi monodi* from Cameroon in the present study indicates that these three taxa are all valid species. The present concept of *S. aubryi* creates inconsistencies in the use of the subgenera *Sudanonautes* Bott, 1955 and *Convexonautes*, and these categories are not recognised here.

BOTT'S (1955, 1964) works contributed further to the taxonomic confusion surrounding *S. aubryi* with his opinions concerning five other taxa. For example, *S. (S.) d. decazei* in BOTT (1955) was assigned three synonyms: *P. (P.) pobeguini*, *P. (P.) regnieri*, and *P. decazei granulata*. Later, BOTT (1964) considered *S (S.) d. decazei* to be a junior synonym of *S. (S.)*

p. pelii. Examination of the types of these five taxa in the present study indicates that *T. pelii, T. decazei,* and *P. (P.) pobeguini* are all synonyms of *S. aubryi*, but that *Potamon d. granulata* and *Potamon (P.) regnieri* are not. *Potamon d. granulata* was recently redescribed as *S. granulatus* by CUMBERLIDGE (1993a). The female type of *P. (P.) regnieri* lacks an intermediate tooth between the exo-orbital and epibranchial teeth, and so does not belong to *Sudanonautes;* most probably it is a species of *Potamonautes* MacLeay, 1838.

Because of the taxonomic difficulties outlined above, specimens belonging to all four species of freshwater crab that host the human lung fluke *(Paragonimus)* in Nigeria and Central Africa have been wrongly identified in the literature. For example, VOELKER, SACHS, VOLKMER & BRABAND (1975, fig. 6) misidentified *S. aubryi* (as *S. africanus)* and *S. floweri* (as *S. aubryi),* while VOELKER & SACHS (1977) misidentified *S. africanus* (as *S. aubryi*, fig. 1), *S. granulatus* (as *S. pelii,* fig. 3), and *S. floweri* (as *S. aubryi*, fig. 4).

Comparisons

Sudanonautes floweri, S. africanus, and *S. granulatus* are all sympatric with *S. aubryi*, and are all second intermediate hosts of *Paragonimus* in Nigeria and Central Africa. *Sudanonautes aubryi* can be distinguished from *S. floweri* by examination of the terminal segment of gonopod 1: that of *S. floweri* has a raised cephalic lobe, and a distinct longitudinal groove in the caudal view, while that of *S. aubryi* lacks these features (Fig. 1d). In addition, the outer margin of the subterminal segment of gonopod 1 of *S. floweri* is conspicuously broadened, while that of *S. aubryi* is slim (Fig. 1 d, e). The sternum of *S. floweri* has raised ridges at the points where the chelipeds insert, while *S. aubryi* lacks these sternal ridges. The carapace of *S. floweri* is significantly ($P < 0.001$) higher (CH/CL *S. floweri* = 0.61, *S. aubryi* = 0.52), and wider (CW/CL *S. floweri* = 1.51, *S. aubryi* = 1.37) than that of *S. aubryi* (Table 1). Finally, the carapace and postfrontal crest of *S. floweri* are uniformly red brown with a contrasting yellow postfrontal crest, while these features are green brown in *S. aubryi.*

Sudanonautes aubryi can be distinguished from *S. africanus* by examination of the terminal segment of gonopod 1: that of *S. africanus* is thin and needle-like, while that of *S. aubryi* (Fig. 1 d, e) is fatter and more curved. The carapace of *S. africanus* is significantly flatter ($P < 0.001$) than that of *S. aubryi* (CH/CL *S. africanus* = 0.43, *S. aubryi* = 0.52, Table 1). The postfrontal crest of *S. africanus* meets the anterolateral margin at, and not behind, the epibranchial tooth, and the carapace of

S. africanus has patches of raised warts, while that of *S. aubryi* is completely smooth. Finally, the proximal region of the pollex of the propodus of the major cheliped of *S. africanus* has a large, flattened, fused tooth, which is lacking in *S. aubryi*.

Sudanonautes aubryi can be distinguished from *S. granulatus* by examination of the terminal segment of gonopod 1: that of *S. granulatus* has a raised cephalic lobe, and a distinct longitudinal groove in the caudal view, while that of *S. aubryi* lacks these features (Fig. 1d). The carapace of *S. granulatus* is significantly ($P < 0.001$) wider than that of *S. aubryi* (CW/CL *S. granulatus* = 1.41, *S. aubryi* = 1.37, Table 1). Finally, the chelipeds of *S. granulatus* are brick red-yellow, and the arthrodial membranes are brown yellow, while the chelipeds of *S. aubryi* are green brown, and the arthrodial membranes crimson (CUMBERLIDGE, 1993a).

Sudanonautes aubryi can be distinguished from *S. monodi* by examination of the terminal segment of gonopod 1: that of *S. monodi* has a raised cephalic lobe, and a distinct longitudinal groove in the caudal view (CUMERLIDGE, 1991), while that of *S. aubryi* lacks these features (Fig. 1 d, e). The carapace of *S. monodi* is significantly ($P < 0.001$) higher (CH/CL *S. monodi* = 0.58, *S. aubryi* = 0.52) and wider (CW/CL *S. monodi* = 1.49, *S. aubryi* = 1.37) than that of *S. aubryi* (Table 1). Finally, the carapace and postfrontal crest of *S. monodi* are uniformly red brown with a contrasting yellow postfrontal crest, while the carapace and postfrontal crest of *S. aubryi* are green brown.

Summary

The freshwater crab *Sudanonautes aubryi*, one of the second intermediate hosts of the human lung fluke *(Paragonimus)* in Nigeria and Central Africa, is redescribed from type material and a large series of other specimens. *Sudanonautes aubryi* is recognised by a combination of characters of gonopod 1, and of the carapace. Three taxa *(S. pelii, S. decazei,* and *P. (P.) pobeguini)* are judged to be junior synonyms of *S. aubryi*. *Sudanonautes aubryi* is distinguished from similar species, including other freshwater crab hosts of *Paragonimus*. Two former subspecies of *S. aubryi* (*S. floweri* and *S. monodi*) are considered to be good species, and the subgenera *Sudanonautes* and *Convexonautes* are not recognised. The distribution of *S. aubryi* is revised to include guinea and woodland savanna from Cote d'Ivoire to northern Cameroon, and tropical rain forest from south-east Nigeria to Gabon; Congo and Zaire are excluded.

Zusammenfassung

Es wird eine Neubeschreibung der Süßwasserkrabbe *Sudanonautes aubryi*, einer der zweithäufigsten Zwischenwirte des menschlichen Lungenwurms *Paragonimus* in Nigeria und Zentralafrika, gegeben. *Sudanonautes aubryi* ist zu erken-

nen anhand einer Merkmalskombination von Gonopodium 1 und des Carapax. Drei Taxa *(S. pelii, S. decazei* und *P. (P.) pobeguini* werden als „Junior Synonyme" von *S. aubryi* angesehen. *S. aubryi* wird von ähnlichen Arten, einschließlich anderer Süßwasserkrabbenwirte von *Paragonimus*, unterschieden. Zwei frühere Subspezies von *S. aubryi (S. floweri* und *S. monodi)* werden als „wahre" Arten erkannt, die Subgenera *Sudanonautes* und *Convexonautes* werden nicht anerkannt. Die Verteilung von *Sudanonautes aubryi* wurde überarbeitet, sie schließt Guinea und die Waldland-Savanne von Elfenbeinküste bis Nord-Kamerun ein und den tropischen Regenwald von Südost-Nigeria bis Gabun; Kongo und Zaire sind ausgenommen.

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