

A critical revision of the churchill snoutfish, genus *Petrocephalus* Marcusen, 1854 (Actinopterygii: Teleostei: Mormyridae), from southern and eastern Africa, with the recognition of *Petrocephalus tanensis*, and the description of five new species

Bernd Kramer^{a*}, Roger Bills^b, Paul Skelton^b and Michael Wink^c

^aZoological Institute, University of Regensburg, D-93040 Regensburg, Germany; ^bSouth African Institute for Aquatic Biodiversity, Private Bag 1015, Grahamstown 6140, South Africa; ^cInstitut für Pharmazie und Molekulare Biotechnologie, Universität Heidelberg, D-69120 Heidelberg, Germany

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We morphologically and genetically studied the southern African electric fish *Petrocephalus catostoma*, or churchill, and its six nominal species, five of which by synonymization (three valid subspecies). We reinstate the synonymized species, and recognize *Petrocephalus tanensis* (Whitehead and Greenwood, 1959) from the Tana River in Kenya, also using electric organ discharges. The Okavango delta (Botswana) is inhabited by *Petrocephalus okavangensis* **sp. nov.** and *Petrocephalus magnitrunci* **sp. nov.**, and the Namibian Cunene River by *Petrocephalus magnoculis* **sp. nov.** We recognize *Petrocephalus petersi* **sp. nov.** for the Lower Zambezi River (Mozambique), and *Petrocephalus longicapitis* **sp. nov.** for the Upper Zambezi River (Namibia). The Lufubu River in Northern Zambia is inhabited by *Petrocephalus longianalis* **sp. nov.** For the southern churchill, *Petrocephalus wesselsi* Kramer and Van der Bank, 2000, we confirm intraspecific and interspecific differentiation. Sequence data from mitochondrial DNA confirm differentiation of two new western and two eastern species, forming mutual sister groups.

Keywords: systematics; morphometrics; electric organ discharges; molecular genetics; allopatric speciation

Introduction

The African snoutfish genus *Petrocephalus* Marcusen, 1854 is defined on characteristic skeletal features (Taverne 1969), certain characters of external morphology, such as a pair of narrowly spaced nostrils the posterior one of which is closely apposed to the eye (Bigorne and Paugy 1991), and molecular DNA studies (Lavoué et al. 2000; Sullivan et al. 2000). About 25 species are distributed throughout the more tropical regions of Africa, two in southern Africa. The type locality for the widely distributed *Petrocephalus catostoma* (Günther, 1866), or churchill, is the Rovuma River that arises in the highlands east of Lake Malawi (Livingstone Mountains), whence it flows eastward into the Indian Ocean (Figure 1, no. 1). The Rovuma (also Ruvuma) forms the border between Tanzania and Mozambique for about 600 km at 11° S. Whitehead and Greenwood (1959) reviewed the status of “three closely related species of *Petrocephalus* . . . recorded from East Africa; these are *P. degeni*

*Corresponding author. Email: bernd.kramer@biologie.uni-regensburg.de

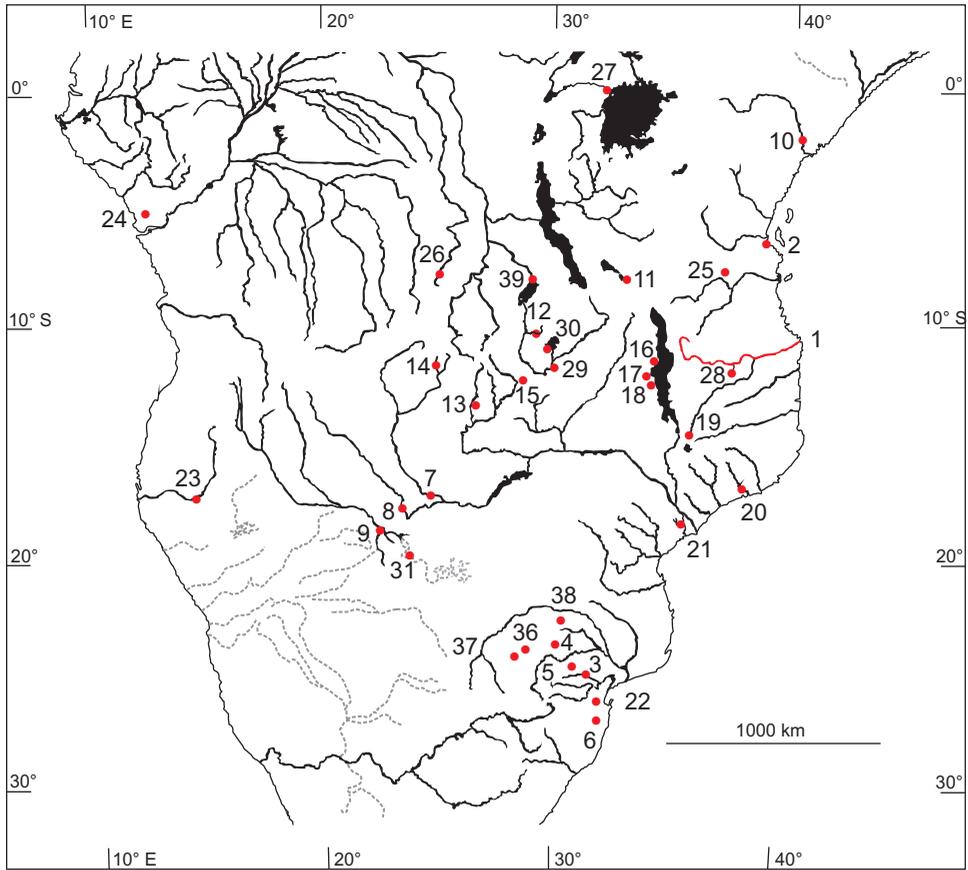


Figure 1. Map of southern Africa indicating the origin of samples of the *Petrocephalus* species studied. (1) Rovuma (Ruvuma) River, type locality for *P. catostoma* (Günther 1866) [BMNH 1863.10.12.4]; (2) Ruvu (Kingani) River, type locality for *P. stuhlmanni* Boulenger 1909 [BMNH 1907.12.3.1]; (3) Sabie River, type locality for *P. wesselsi* Kramer and Van der Bank 2000 [ZSM 28554 to ZSM 28566, SAIAB 054449]; (4) Groot Letaba River, Limpopo System [SAIAB 85920]; (5) Blyde River, Limpopo System [SAIAB 85923]; (6) Pongola River [SAIAB 85919]; (7) Upper Zambezi River near Katima Mulilo, type locality for *P. longicapitis* sp. nov. [SAIAB 85916]; (8) Kwando River [ZSM 38658]; (9) Okavango Delta, Nguma Lagoon, type locality for *P. okavangensis* sp. nov. [SAIAB 030046]; (10) Tana River, type locality for *P. catostoma tanensis* Whitehead and Greenwood, 1959, here recognized as *P. tanensis* (Whitehead and Greenwood, 1959) [SAIAB 85907]; (11) Lake Rukwa [SAIAB 059515]; (12) Lufubu River, Luapula River system, *P. longianalis* sp. nov. [SAIAB 76758]; (13) East Lungu River, Kafue/Zambezi River system [SAIAB 040074]; (14) East Lumwana River, Zambezi system [SAIAB 041208]; (15) Mwekera Stream, Kafue/Zambezi River system [SAIAB 042559]; (16) Kapesha River, Lake Malawi [SAIAB 039328]; (17) Dwangwa River, Lake Malawi [specimen SAIAB 050065]; (18) Kaombe River, Lake Malawi [SAIAB 050155]; (19) Lake Chiuta [SAIAB 039264]; (20) Mulela River [SAIAB 055875]; (21) Zambezi River Delta, type locality for *P. petersi* sp. nov. [SAIAB 060846]; (22) Mbuluzi River, Swaziland [SAIAB 067228]; (23) Cunene River, type locality for *P. magnoculis* sp. nov. [SAIAB 78788]; (24) Lukula River, type locality for *P. haullevillii* Boulenger 1912 [BMNH 1912.4.1.186-188]; (25) Rufiji basin, type locality for *P. steindachneri* Fowler 1958 [NMW 551181]; (26) Mukishi on Lomami River (Congo River basin), type locality for

BLGR. 1906, *P. stuhlmanni* BLGR. 1909 and *P. catostoma* GÜNTHER, 1866". These authors concluded ". . . it became clear that size discrepancies and paucity of material could explain why three 'species' had been recognised." Therefore, they united all three species as members of a single, widespread species, *P. catostoma*. To the list of synonyms they added *P. stuhlmanni congicus* David and Poll, 1937 and *P. haullevillii* Boulenger, 1912 from the distant and unconnected upper and lower Congo basins, respectively, while recognizing that the "Congo form of this species clearly differs from the eastern and southern subspecies . . .", and that "the two Congoan forms may yet have to be united". In consequence, *P. steindachneri* Fowler, 1958 of East Africa became the sixth nominal species referred to *P. catostoma* (Seegers 1996). *Petrocephalus catostoma* defined in this way ranged from the Katonga River, Lake Victoria, in Uganda in the north to the Pongola River in South Africa (a distance of 3000 km); from the Atlantic Congo and Cunene Rivers in the west to the Indian Ocean in the east (Whitehead and Greenwood 1959; Gosse 1984; Seegers 1996; Eschmeyer 2011) (Figure 2).

A critical comparison among a few allopatric samples from southern localities revealed that South African churchills represented a different species from *P. catostoma* (Kramer and Van der Bank 2000). The southern churchill, *P. wesselsi* Kramer and Van der Bank, 2000, as it is now called, also differed genetically from the *Petrocephalus* sampled from the Upper Zambezi (Van der Bank 1996). Additional species diversity within *Petrocephalus* has similarly been discovered in other regions of sub-Saharan Africa: in Gabon in Central Africa where a new (fourth) species of *Petrocephalus*, *P. sullivanii* Lavoué, Hopkins and Kamdem Toham, 2004, was recognized on the basis of anatomical and electrical characters (Lavoué et al. 2004). Five more species [supported by molecular genetics and electric organ discharge (EOD) comparisons] have been found in a small region in the northwest of the Republic of Congo (Lavoué et al. 2008, 2010; Lavoué 2011); one more species in the upper reaches of the Congo basin in northern Zambia (Lavoué Forthcoming 2012). For a full revision of only *P. catostoma* as traditionally understood (including all the nominal species), all local populations need to be sampled and critically compared. Given the huge distribution and the prevailing sparseness of museum specimens, especially type material, this goal appeared difficult to achieve.

We took the opportunity to sample additional rivers, among them the Tana River, type locality for *P. c. tanensis* Whitehead and Greenwood, 1959, for more material to extend our comparisons of allopatric churchills (Figure 1). We compared anatomical

P. stuhlmanni congicus David and Poll 1937 [MRAC 30.807–30.808]; (27) Katonga River, Lake Victoria (Uganda), type locality for *P. degeni* Boulenger 1906 [BMNH 1906.5.30]; (28) approximate location for our type region material for *P. catostoma* (SAIAB 73802, 73808, 73887, 73894); (29) Luapula River [SAIAB 76582]; (30) Bangweulu Lake [SAIAB 76859 and SAIAB 76825]; (31) Okavango delta, Boro River, type locality for *P. magnitrunci* sp. nov. [SAIAB 67069]. (36) Lepalala River, tributary of Limpopo [SAIAB 96537]; (37) Mokolo River, tributary of Limpopo [SAIAB 95989]; (38) Nwanedzi River, tributary of Limpopo [SAIAB 58157]; (39) "Ruisseau affluent de la Lukinda", close to Lake Moero, type locality of *P. squalostoma* (Boulenger, 1915) [BMNH 1920.5.26.1]. Some rivers and lakes are too small to be shown at the scale used.

data and, where possible, also EODs and molecular genetics to test the hypothesis of a *P. catostoma* species complex for the whole of southern and eastern Africa. We attempted to reconstruct the systematics and phylogeography in what has traditionally been considered to represent a single species, the churchill (*P. catostoma*) of subcontinental distribution, and to identify some of the local adaptations both for morphology and the electric communication signal.

Material and methods

Electrical and morphological studies

A total of 566 specimens was examined morphologically and at least 16 measurements and at least three meristic characters were recorded. Measurements are illustrated in Figure 3 and were made using vernier calliper readings to 0.1 mm. The following abbreviations were used: PDL, predorsal length: distance tip of snout to dorsal fin origin; PAL, preanal length: distance tip of snout to anal fin origin; LD, dorsal fin length; LA, anal fin length; pD, distance dorsal fin origin to end of caudal peduncle; CPL, length of caudal peduncle: end of anal fin base to midbase caudal fin; CPD, depth of caudal peduncle: the least vertical distance across the caudal peduncle; LSo, length of snout: distance tip of snout to posterior orbital rim of eye; LSc, length of snout: distance tip of snout to centre of eye; HL, head length: distance tip of the snout to furthest bony edge of the operculum; Na, distance between the pair of nares of one side (from centre to centre); OD, eye diameter: defined by orbital rims; LPF, length of pectoral fins: from anterior base to tip; PPF, distance between anterior base of pectoral fin to anterior base of pelvic fin; BD, body depth: the greatest vertical distance across the body; SL, standard length: distance tip of snout to midbase caudal fin; nD, number of dorsal fin rays; nA, number of anal fin rays; SPC, number of scales around caudal peduncle; SLS, number of scales in linear series along the lateral line row, as detailed in Skelton (2001: 67); SLS range of accuracy, ± 2 counts.

Abbreviations used to represent institutions and collections follow Leviton et al. (1985) and Fricke and Eschmeyer (2011). Specimens collected during the course of the present study are permanently stored at the South African

Figure 2(A–D). Photographs of members of southern and eastern African *Petrocephalus* species studied (numbers refer to localities given in Figures 1, 6 and 9). (1) *P. catostoma* (Günther, 1866), Lectotype, BMNH 1863.10.12.4, right side, SL 4.7 cm. (2) *P. stuhlmanni* Boulenger, 1909, holotype, BMNH 1907.12.3.1, SL 7.9 cm. (3) *P. wesselsi* Kramer and Van der Bank, 2000, right side, SL 9.7 cm, SAIAB 85922 (R1). (7) *P. longicapitis* sp. nov., SMF 28265 (R1), SL 9 cm. (9) *P. okavangensis* sp. nov., holotype, SAIAB 030046, right side, SL 6.1 cm. (10) *P. catostoma tanensis* Whitehead and Greenwood, 1959, holotype, BMNH 1963.11.29.1, right side, SL 6.7 cm. (10a) *P. tanensis*, field no. Ta05na, SL 8.7 cm, SAIAB 85907. (12) *P. longianalis* sp. nov., holotype, SL 8.2 cm, right side, SAIAB 76758. (21) *P. petersi* sp. nov., holotype, SAIAB 060846, right side, SL 6.4 cm. (23) *P. magnoculis* sp. nov., SL 8.9 cm, ZSM 38659. (24) *P. haullevillii* Boulenger, 1912, BMNH 1912.4.1.186–188 (R1), right side, SL 5.7 cm. (25) *P. steindachneri* Fowler 1958, syntype, NMW 55118:3, right side, SL 6.4 cm. (26) *P. stuhlmanni conigicus* David and Poll, 1937, syntype, MRAC 30807–30808, SL 7.8 cm. (27) *P. degeni* Boulenger, 1906, BMNH 1906.5.30.84, right side, SL 8.12 cm. (28) *P. catostoma*, SAIAB 73894 (R1), right side, SL 6.4 cm. (31) *P. magnitrunci* sp. nov., SL 8.5 cm, SAIAB 67069 (R5, right side), see map Figure 6. Scale bar, 1 cm.

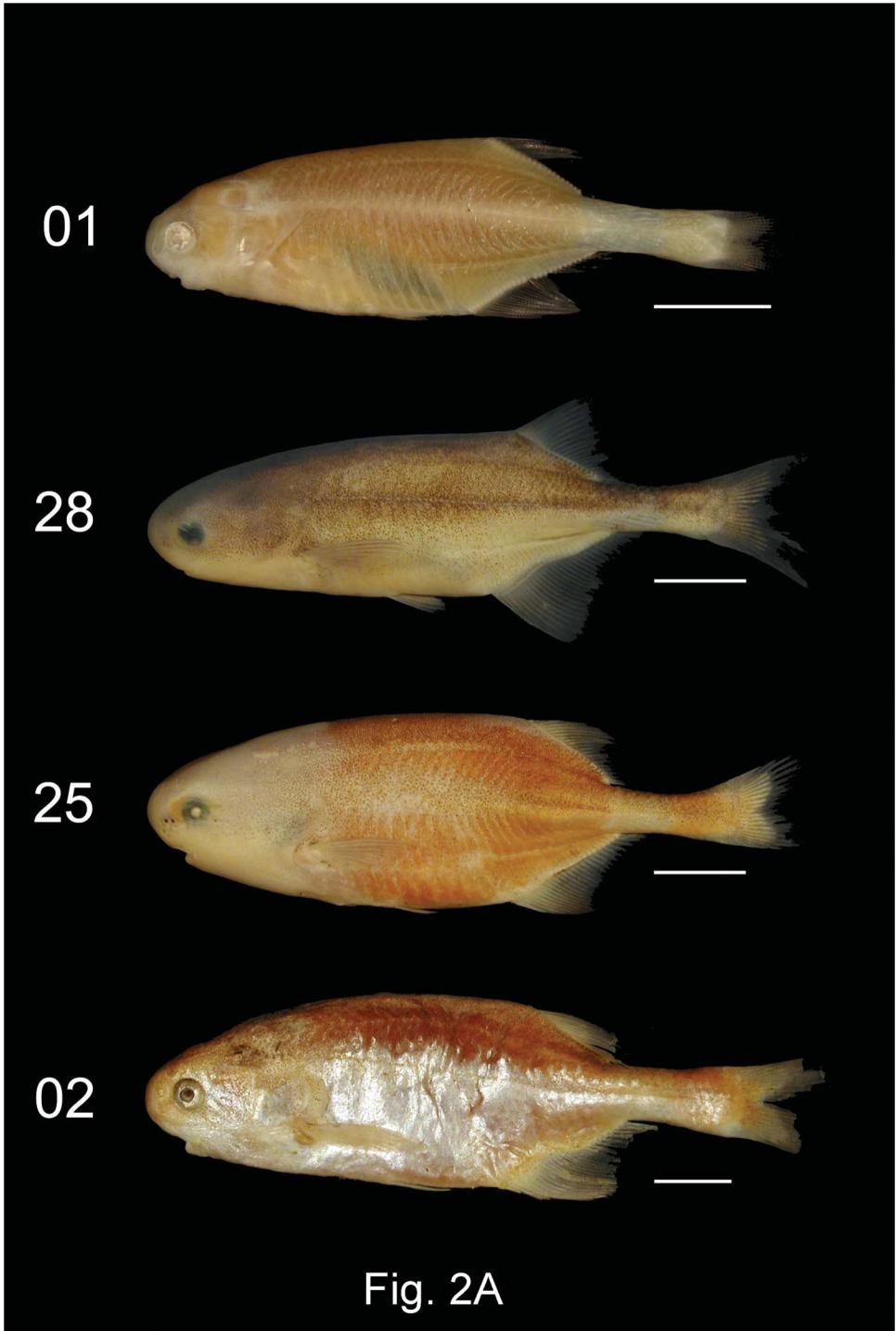




Figure 2(A–D). (Continued)

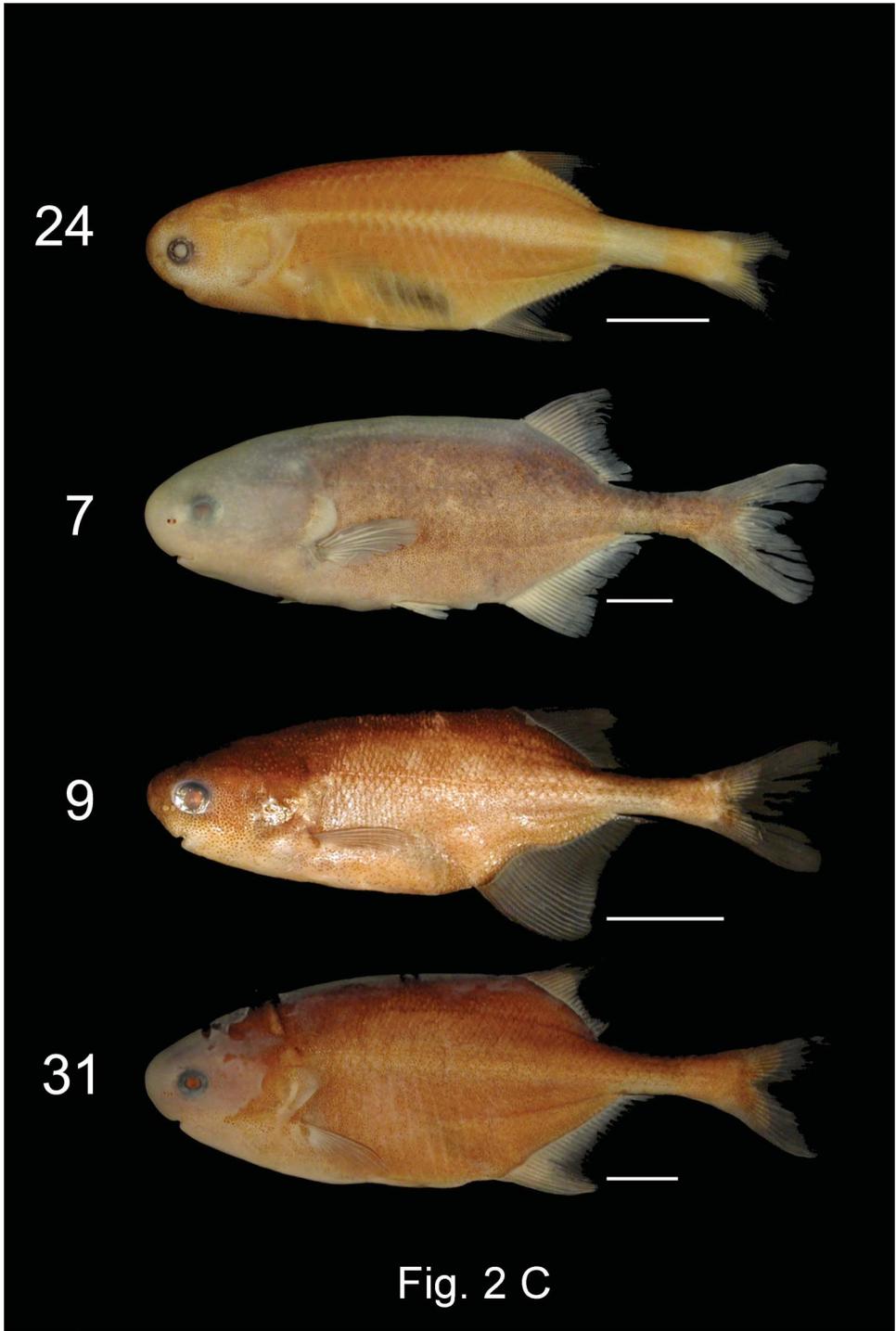


Figure 2(A–D). (Continued)



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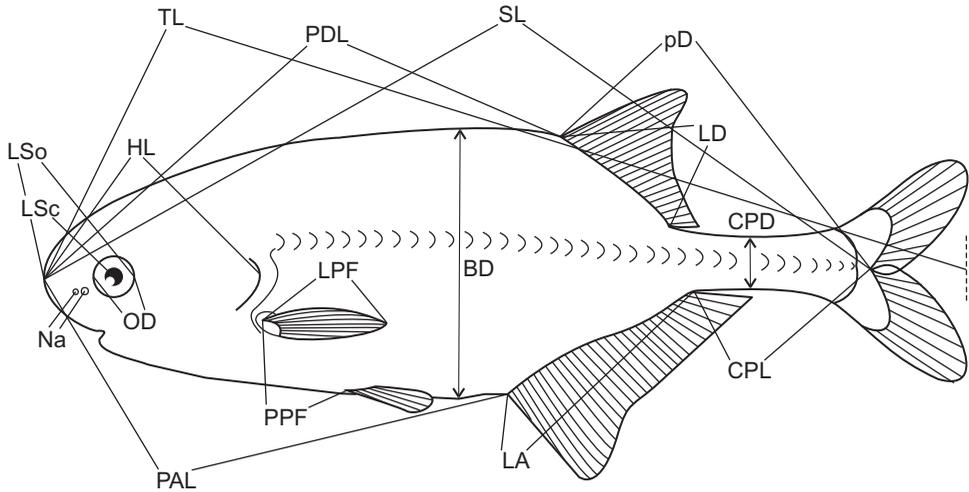


Figure 3. Schematic sketch of how measurements were taken on *Petrocephalus* sp. For abbreviations, see Material and methods.

Institute for Aquatic Biodiversity, Grahamstown, South Africa (SAIAB); at the Zoologische Staatssammlung, München, Germany (ZSM); and at the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Frankfurt am Main, Germany (SFM). Specimens studied were initially identified using dichotomous keys in Bell-Cross and Minshull (1988) and Skelton (1993, 2001).

Fish sampled from the field were transferred into a 37-litre plastic aquarium filled with river water where the fish were collected for recording their EODs with minimum delay. Conductivity ($\pm 1 \mu\text{S}/\text{cm}$) and temperature ($\pm 0.1 \text{ }^\circ\text{C}$) were monitored using an electronic meter (LF92 by Wissenschaftlich-Technische Werkstätten WTW, 82362 Weilheim, Germany). Conductivity changes possibly affecting EOD waveform (Bell et al. 1976; Bratton and Kramer 1988; Kramer and Kuhn 1993) were excluded.

Methods for capturing and analysing EODs are as described in Kramer and Van der Bank (2000). The three phases to an EOD pulse were head-positive, head-negative, head-positive (P1, N, P2). Before analysis, EODs were temperature-corrected to 25°C using a Q_{10} of 1.5 (Kramer and Westby 1985), and normalized in amplitude (by setting the peak amplitude of the P1 phase, measured from baseline, equal to 1). Abbreviations of EOD parameters: P1amp, P2amp, Namp, peak amplitudes from baseline for the P1, the P2 and the N phases, respectively; P1dur, P2dur, Ndur, durations of the P1, P2 and N phases, respectively, with P1 and P2 phases slightly shortened by using an amplitude criterion of $\pm 2\%$ of P1amp for estimating start or termination, respectively; P1Nsep, P1P2sep, NP2sep, separation (or interval) between the peaks of the P1 and N phases, the peaks of the P1 and P2 phases, and the peaks of the N and P2 phases, respectively; P1area, P2area, Narea, areas under the P1, the P2, or the N phase curves measured from $\pm 2\%$ P1amp of the baseline.

Statistical analyses as indicated in the Results section; *P* values are two-tailed unless otherwise stated. For a Principal Components Analysis (PCA) on correlations among anatomical characters we estimated eigenvalues, eigenvectors

and, for interpreting the principal components in terms of the anatomical characters, the component loadings, i.e. the principal component structure (see McGarigal et al. 2000). For assessing the significance of loadings we followed Tabachnick and Fidell (2007). These authors recognize five levels of significance: loadings > 0.32 or < -0.32 are poor, > 0.45 or < -0.45 fair, > 0.55 or < -0.55 good, > 0.63 or < -0.63 very good, and > 0.71 or < -0.71 excellent. These benchmarks account for 10%, 20%, 30%, 40% and 50% of the variance in the component, respectively. The software used was STATVIEW v. 5 and JMP v. 7.0.2 to 9 (SAS Institute, Cary, NC, USA, 2007).

Genetic studies

DNA isolation

DNA was isolated from muscle or scale tissue, which was preserved in ethanol, using a standard phenol/chloroform protocol (Sambrook et al. 1989). The mitochondrial cytochrome *b* (cyt *b*) gene was amplified using the published mitochondrial DNA primers (Kramer et al. 2007).

The PCR amplifications were performed with 50- μ l reaction volumes containing 1 \times PCR buffer (Bioron, Ludwigshafen, Germany), 100 μ M dNTPs, 0.2 units of *Taq* DNA polymerase (Bioron, Ludwigshafen, Germany), 200 ng DNA and 5 pmol primers. Thermal cycling was performed under the following conditions: (1) an initial denaturing step at 94°C for 5 min; (2) 35 cycles: 1 min at 94°C, 1 min at 52°C and 1 min at 72°C; and (3) a final 5-min extension at 72°C. The PCR products were precipitated with 4 M NH_4Ac and ethanol (1:6) and centrifuged for 15 min (15 550 \times g). Sequencing was carried out on an ABI 3730 automated capillary sequencer (Applied Biosystems, 64293 Darmstadt, Germany) with the ABI Prism Big Dye Terminator Cycle Sequencing Ready Reaction Kit 3.1 by STARSEQ GmbH (Mainz, Germany).

Phylogenetic analyses

The tree reconstruction was performed using the maximum likelihood method with the substitution model Tamura–Nei and the Nearest-Neighbour-Interchange algorithm. Bootstrap was carried out with 600 replications and the mean pairwise p-distances were calculated following Nei (1987). All of these analyses were conducted with MEGA version 5.0 (Tamura et al. 2011).

Genetic samples examined

(IPBM collection nos = Institut für Pharmazie und Molekulare Biotechnologie, Heidelberg University, Germany).

Petrocephalus magnoculis sp. nov. ($n = 6$), Namibia: Cunene River: just below Ruacana Falls, coll. B. Kramer and E. Swartz, 17°24'24" S, 14°13'01" E: IPBM 43982 = ZSM38659#A278, 19 August 2006; IPBM 43983 = SAIAB78788#A288, 20 August 2006; IPBM 43984 = SAIAB79480#A302, 20 August 2006; IPBM 43987 = ZSM38660#A309, 20 August 2006, IPBM 43991 = SAIAB78790#A364, 22 August 2006; IPBM 43992 = SAIAB78788#A280, 22 August 2007, released.

Petrocephalus longicapitis sp. nov. ($n = 4$), Namibia: East Caprivi: Upper Zambezi: Katima Mulilo, 17°29'30" S, 24°16'18" E, coll. H. van der Bank August 1994, scale

taken from live fish on 9 February 2009: IPBM 51428, #32, IPBM 51429, #33, IPBM 51430, #34, IPBM 51431, #35.

Petrocephalus catostoma ($n = 2$), Mozambique: Rovuma System: Lucombe River, coll. R. Bills: IPBM 35836 = SAIAB73891#N303, 26 August 2003, 12.0839° S, 37.5619° E; IPBM 35837 = SAIAB73889#N317, 22 August 2003, 12.0875° S, 37.5606° E.

Petrocephalus wesselsi ($n = 4$), South Africa: Limpopo System: Mogol (Mokolo) River at Hermanusdorings, 24°06.823' S, 27°48.153' E, coll. A. Hoffman and B. Kramer, 20 October 2008, IPBM 50695, IPBM 50696, IPBM 50698, IPBM 50699, released.

Marcusenius altisambesi ($n = 2$), IPBM 57467, #9, Namibia: Cunene River Mouth, coll. F.H. Van der Bank, 15 December 2009, 17°15.606' S, 11°45.892' E; IPBM 50679, #15, Namibia: Upper Zambezi River: Kalimbeza, 17°32'27.3" S, 24°31'26.2" E, coll. F.H. Van der Bank and B. Kramer, 21 August 1999, tissue sample live fish taken on 10 October 2008.

Material examined

Petrocephalus catostoma (Günther, 1866) and its previous synonyms and subspecies

Mormyrus catostoma Günther, 1866. Lectotype BMNH 1863.10.12.4, 4.7 cm SL, and four paralectotypes BMNH 1863.10.12.5-6(4), 4.1–4.4 cm SL, for *Petrocephalus catostoma catostoma* (Günther, 1866),

BMNH 1906.5.30.84, *Petrocephalus degeni* Boulenger, 1906, holotype (unique), 8.1 cm SL, Katonga River, Lake Victoria (Uganda),

BMNH 1907.12.3.1 *Petrocephalus stuhlmanni* Boulenger, 1909, holotype (unique), 7.8 cm SL,

BMNH 1912.4.1.181-185, *Petrocephalus haullevillii* Boulenger, 1912, syntypes (5), 3.9–5.9 cm SL, Angola, Portuguese Congo, Lundo, Luali River,

MRAC 1496-1501, *Petrocephalus haullevillii* Boulenger, 1912, syntypes (6), 4.6–6.4 cm SL, Angola, Portuguese Congo, Lundo,

BMNH 1912.4.1.186-188, *Petrocephalus haullevillii* Boulenger, 1912, syntypes (3), 5.7–6.5 cm SL, Democratic Republic of the Congo (Belgian Congo), Lukula River,

NMW 55118(3), -117 (half of a fish), *Petrocephalus steindachneri* Fowler, 1958, syntypes (1+3), 6.4–6.6 cm SL, Tanzania, Ulanga, Kiperege, Msola-stream,

MRAC 30807–30808, *Petrocephalus stuhlmanni congicus* David and Poll, 1937, syntypes (2), 7.2–7.8 cm SL, Zaire, Congo River basin, Mukishi (Lomami River), 08°30' S, 24°44' E,

SAIAB 73887(9), 3.7–4.5 cm SL, Mbatamila-Matondovela Rd, Litungulu stream near Matondovelo 18 August 2003, Mozambique, Niassa Reserve, Litungulu Rovuma, 12°05'27" S, 37°19'40" E, coll. R. Bills,

SAIAB 73802(10), *Petrocephalus catostoma*, 3.8–4.4 cm SL, Mbatamila-Matondovela Rd, third river crossing, 14 August 2003, Mozambique, Niassa Reserve, Rovuma, 12°08'05" S, 37°24'18" E, coll. R. Bills,

SAIAB 73808(10), *Petrocephalus catostoma* 3.8–4.6 cm SL, Mbatamila-Matondovela Road, third river crossing, 18 August 2003, Mozambique, Niassa Reserve, Rovuma, 12°08'05" S, 37°24'18" E, coll. R. Bills,

- SAIAB 73894(6), *Petrocephalus catostoma* 3.8–6.4 cm SL, Mbatamila-Mussoma Rd, Nkupo stream near Mussoma bridge, 22 August 2003, Mozambique, Niassa Reserve, Nkupo, Lugenda River (confluence of Rovuma R), 12°26'42" S, 37°40'44" E, coll. R. Bills,
- SAIAB 050155(2), *Petrocephalus cf. catostoma*, 3.8–4.7 cm SL, Malawi, Nkhotakota, Malenga Chanzi, Pool in stream bed above Lake Chiku, Shire River system, Kaombe River, 12°58' S, 34°13' E, 25 July 1995, coll. D. Tweddle,
- SAIAB 050065(2), *Petrocephalus cf. catostoma*, 4.8–5.7 cm SL, Malawi, Nkhotakota, Kanyenda, Below main dam for sugar estate tak, Shire River system, Dwangwa River, 12°31' S, 34°07' E, 20 July 1995, coll. D. Tweddle,
- SAIAB 039328(1), *Petrocephalus cf. catostoma*, 6.1 cm SL, Malawi, South of Chinteche, Lake Malawi, Kapesha River, 11°54' S, 34°09' E, 5 July 1992, coll. D. Tweddle.

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- SAIAB 76825(3), 6.1–7.4 cm SL, Zambia Province: Luapula System: Lake Bangweulu shoreline at rocky point near Samfya Ferry dock, 11°21'19.44" S, 29°33'47.52" E, coll: R. Bills, A. Chilala, J. Friel, 25. September 2005, field no. JPF-05-014,
- SAIAB 76859(1), 5.6 cm SL, Zambia Province: Luapula System: Lake Bangweulu shoreline at rocky point near Samfya Zambian Fisheries building, 11°22'20.64" S, 29°33'53.64" E, coll: R. Bills, A. Chilala, J. Friel, 25 September 2005, field no. JPF-05-015,

Petrocephalus longianalis sp. nov.

- SAIAB 76758, holotype, specimen R9, 8.2 cm SL, Zambia Province: Luapula System: Luongo River: Lufubu River, Lufubu River Falls below bridge at Chipili on Mensa-Mununga road, 10°43'46.92" S, 29°05'36.96" E, coll: R. Bills, A. Chilala, J. Friel, 2 October 2005, field no. JPF-05-025,
- SAIAB 186060(48), paratypes, 3.8–8.2 cm SL, Zambia Province: Luapula System: Luongo River: Lufubu River, Lufubu River Falls below bridge at Chipili on Mensa-Mununga road, 10°43'46.92" S, 29°05'36.96" E, coll: R. Bills, A. Chilala, J. Friel, 2 October 2005, field no. JPF-05-025,
- Non-types: SAIAB 76582(5), 7.0–7.3 cm SL, Zambia Province: Central System: Luapula River: Luapula, Luapula River Bridge, 12°06'56.16" S, 29°50'49.92" E, coll: R. Bills, A. Chilala, J. Friel, 22 September 2005, field no. JPF-05-006,
- SAIAB 76733(2), 10.1–11.9 cm SL, Zambia Province: Luapula System: Luongo River at bridge on Kashiba-Mwenda road, 10°28'12.72" S, 29°01'28.2" E, coll: R. Bills, A. Chilala, J. Friel, 1 October 2005, field no. JPF-05-023.

Petrocephalus longicapitis sp. nov.

- SAIAB 85916 Holotype, 19fish, 8.4 cm SL, Upper Zambezi River at Katima Mulilo, East Caprivi, Namibia, rocks in middle of river (opposite boat landing), approx. 17°29'30" S, 24°16'18" E, 10 September 1993, coll. F.H. Van der Bank and B. Kramer,

- Paratypes: SMF 28265(27), 3.8–9.0 cm SL (one of which 2.8 cm SL); SAIAB 85911(2), 25fish, 26fish, 8.4–8.5 cm SL; SAIAB 85917(2), 14fish, 16fish, 8.0–8.4 cm SL; SAIAB 85918(3), 37fish, 38fish, 43fish, 7.6–7.9 cm SL; all from same location, 10–13 September 1993, water conductivity and temperature, 81 $\mu\text{S}/\text{cm}$, 21.8°C, SL from 28–105 mm, coll. F.H. Van der Bank and B. Kramer,
- Non-types: ZSM 38657(1), L29isi, 10.3 cm SL, Lisikili backwater of Zambezi downstream of Katima Mulilo, 17°29' S, 24°26' E, 6 March 1994, 56.1 $\mu\text{S}/\text{cm}$ and 26.8°C, gravid female, coll. F.H. Van der Bank and B. Kramer,
- Non-types: ZSM 38658(1), N53ak, 9.5 cm SL, specimen from Kwando River, Nakatwa, 18°06' S, 23°23' E, 9 March 1994, 130 $\mu\text{S}/\text{cm}$ and 24.9°C, gravid female, coll. F.H. Van der Bank and B. Kramer,
- Non-types: SAIAB 85909(3), Ven02, Ven03, Ven09, 8.1–9.1 cm SL, from Zambezi rapids at Wenela just upstream of Katima Mulilo (border post to Zambia; 17°29'21.5" S, 24°15'33" E, 9 September 1997, coll. F.H. Van der Bank and B. Kramer,
- Non-types: SAIAB 041208(5), 6.1–7.3 cm SL, Zambia, North West Province, E Lumwana, confluence of Mwambeshi and East Lumwana Rivers (Upper Kabompo/Zambezi system), off Mwinilunga-Solwezi road, 12°15' S, 25°40' E, 31 July 1983, coll. R. Bills,
- Non-types: SAIAB 041025(1), 3.6 cm SL, Zambia, North West Province, Off Solwezi-Mwinilunga Road, Zambezi River system, Kabompo River, Lumwana River, 12°15' S, 25°40' E, 31 July 1983, coll. R. Bills,
- Non-types: SAIAB 042559(18), 4.1–10.4 cm SL, specimens of *Petrocephalus* from Zambia, below dam and fish ladder, Kafue/Zambezi River system, Mwekera Stream, 12°40' S, 28°30' E, 1 July 1983, coll. R. Bills,
- Non-types: SAIAB 41224(4), 10.2–11.0 cm SL, specimens of *Petrocephalus* from Zambia, Kafue System, Mwekera Stream pool below waterfalls, 12°40'00" S, 28°30'00" E, 4 July 1983, coll. R. Bills,
- Non-types: SAIAB 040074(1), 7.7 cm SL, *Petrocephalus*, Zambia, East Lunga River, Kafue/Zambezi River system, Lunga River, 14°00' S, 26°30' E, 17 April 1983, coll. R. Bills.

Petrocephalus magnitrunci sp. nov.

- SAIAB 67069, holotype, specimen R2, 8.8 cm SL, Botswana, Okavango Delta, southeast of Chief's Island, Boro River, 19°31'57" S, 023°05'21" E, 20 June 2000, coll. D. Tweddle and B.C.W. van der Waal,
- SAIAB 186057(10), paratypes, 7.7–8.8 cm SL, Botswana, Okavango Delta, southeast of Chief's Island, Boro River, 19°31'57" S, 023°05'21" E, 20 June 2000, coll. D. Tweddle and B.C.W. Van der Waal.

Petrocephalus magnoculis sp. nov.

- SAIAB 78788, holotype, specimen Ruac06, 9.6 cm SL, from Cunene River, Ruacana Falls, Hippo Pool Campsite, just below the Falls, 17°24'24" S, 14°13'01" E, about 800 m altitude; from 19 August 2006, coll. B. Kramer and E. Swartz,
- ZSM 38659(1), paratype, Ruac07, 8.9 cm SL, from Cunene River, Ruacana Falls, Hippo Pool Campsite, just below the Falls, 17°24'24" S, 14°13'01" E, about 800 m altitude; 19 August 2006, coll. B. Kramer and E. Swartz,

- SAIAB 186053(1), paratype, Ruac09, 10.5 cm SL, from Cunene River, Ruacana Falls, Hippo Pool Campsite, just below the Falls, 17°24'24" S, 14°13'01" E, about 800 m altitude; 20 August 2006, coll. B. Kramer and E. Swartz,
- SAIAB 79480(1), paratype, Ruac10, 9.4 cm SL, from Cunene River, Ruacana Falls, Hippo Pool Campsite, just below the Falls, 17°24'24" S, 14°13'01" E, about 800 m altitude; 19 August 2006, coll. B. Kramer and E. Swartz,
- ZSM 38660(1), paratype, Ruac13, 9.1 cm SL, from Cunene River, Ruacana Falls, Hippo Pool Campsite, just below the Falls, 17°24'24" S, 14°13'01" E, about 800 m altitude; 21 August 2006, coll. B. Kramer and E. Swartz,
- SAIAB 78790(1), paratype, Ruac17, 9.6 cm SL, from Cunene River, Ruacana Falls, Hippo Pool Campsite, just below the Falls, 17°24'24" S, 14°13'01" E, about 800 m altitude; from 22 August 2006, coll. B. Kramer and E. Swartz,
- SAIAB 028120(3), non-types, 9.1–10.5 cm SL, *Petrocephalus* sp., Namibia, "Hippo Pool", Ruacana Falls, Cunene River system, Cunene River, 17°24' S, 14°12' E, 5 October 1986, coll. B. van Zyl.

Petrocephalus okavangensis sp. nov.

- SAIAB 030046, holotype, specimen R22, 6.1 cm SL, Botswana, Okavango, Thoage River, Nguma (Guma) Lagoon, 18°56'60" S, 22°22'59.99" E, 3 January 1987, coll. G. Merron,
- SAIAB 186062(41), paratypes, 4.2–7.8 cm SL, Botswana, Okavango, Thoage River, Nguma (Guma) Lagoon, 18°56'60" S, 22°22'59.99" E, 3 January 1987, coll. G. Merron,
- Non-types: ZSM 38665(3), 8.0–8.1 cm SL, Botswana, Okavango, Thoage River, Guma Lagoon, 18°57'46.6" S, 22°22'25.3" E, 10 August 2004, coll. F. H. Van der Bank and B. Kramer,
- one specimen for EOD only, Botswana, Okavango, Thoage River, 19°03'45.3" S, 22°23'24.3" E, 23 March 2002, 26°C water temperature, 50 µS/cm, EOD recorded 7 March 2003 Regensburg,
- one specimen for EOD only, Botswana, Okavango, Thoage River, Guma Lagoon, 18°57'46.6" S, 22°22'25.3" E, 17.1°C water temperature, 38 µS/cm, EOD recorded 12 August 2004,
- SAIAB 36841(24), 3.7–6.6 cm SL, Namibia, Okavango River, Popa Rapids, 18°06'00" S, 21°36'00" E, 15 July 1986, coll. P. Skelton,
- SAIAB 36823(12), 3.6–7.8 cm SL, same location, second island, 14 July 1986, coll. T. Andrew, G. Merron, P. Skelton,
- SAIAB 19769(21), 4.5–8.3 cm SL, Botswana, Okavango Delta, Moanachira River, Gadikwe Lagoon, mid island 19°10'00" S, 23°14'00" E, 3 November 1983, coll. G. Merron,
- SAIAB 19705(11), 5.6–9.5 cm SL, Botswana, Okavango Delta, Moremi Game Reserve, Xakanixa Channel, opposite Safari Lodge, upper swamp 19°10'00" S, 23°24'00" E, 2 November 1983, coll. G. Merron,
- SAIAB 21271(38), 3.6–9.3 cm SL, Botswana, Okavango Delta, Moremi Game Reserve, Xakanixa River, 19°15'00" S, 23°15'00" E, 24 June 1984, coll. G. Merron and G. May.

Petrocephalus petersi sp. nov.

- SAIAB 060846, holotype, specimen R1, 6.4 cm SL, Mozambique, stream near campsite 1, edge of wet Zambezi River System, Zambezi River, 18°33'54" S, 35°39'46" E, 1 August 1999, coll. R. Bills,
SAIAB 186054(10), paratypes, 4.1–6.1 cm SL, Mozambique, stream near campsite 1, edge of wet Zambezi River System, Zambezi River, 18°33'54" S, 35°39'46" E, 1 August 1999, coll. R. Bills,
SAIAB 055875(4), non-types, 7.1–7.3 cm SL, Mozambique, Zambesia, Mulela Village, Mulela River, Mulalae, 16°53'42" S, 38°17'27" E, 20 July 1997, coll. R. Bills.

Petrocephalus tanensis (Whitehead and Greenwood, 1959), elevated to species rank

- Holotype BMNH 1963.11.29.1, *Petrocephalus catostoma tanensis* Whitehead and Greenwood, 1959, 6.7 cm SL, Lower Tana River, Garsen, Kenya; BMNH 1963.11.29.2-8, 8 paratypes, 3.0–4.5 cm SL, same locality,
Non-types: NMK nos 24102, 24108, 24109, 24111, 24112, 24126, 24143, 24144, 24151, 24159, 23902, 23903, 23905, 23906, 23910, 23911, 23912, 23913, 239NotLegible, 23915, 6371, 6372, 6373, 6375, 6378, 63713, 63714, 63715, 63717, 29 specimens of "*Petrocephalus catostoma tanensis*", 5.6–8.1 cm SL, Kenya, Lower Tana River, Garsen,
ZSM 38661(3), Ta01na, Ta04na, Ta09na, 8.0–8.2 cm SL; ZSM 38662(3), Ta15na, Ta17na, Ta26na, 8.3–9.7 cm SL; ZSM 38663(1), Ta06na, 9.6 cm SL; ZSM 38664(2), Ta39na, Ta44na, 6.6–6.7 cm SL; SAIAB 85906(8), Ta35na, Ta36na, Ta37na, Ta38na, Ta40na, Ta41na, Ta42na, Ta43na, 5.8–8.5 cm SL; SAIAB 8907(5), Ta02na, Ta03na, Ta05na, Ta07na, Ta08na, 8.3–8.8 cm SL, SAIAB 85908(5), SinEOD2, SinEOD3, SinEOD6, R1, R2, 6.4–9.8 cm SL; Lower Tana River at Tana Primate Research Reserve near village Wenje, east of road B8, 1°52'38.1" S, 40°8'22.5" E, 48 m above sea level, 3–6 September 2001, coll. L. De Vos and B. Kramer, 23 specimens for EOD, 186 µS/cm and 25.7°C

Petrocephalus wesselsi Kramer and Van der Bank, 2000

- ZSM 28556, holotype, 10.8 cm SL; ZSM 28554–ZSM 28555, ZSM 28557–ZSM 28566 (12 paratypes, 5.6–10.1 cm SL), SMF 28266 (13 paratypes, 5.7–8.9 cm SL), SAIAB 054449 (13 paratypes, 5.4–8.4 cm SL), all from Sabie River, Kruger National Park, South Africa, bridge near Lower Sabie tourist camp (25°07' S, 31°55' E), 29–30 March 1996, coll. F.H. Van der Bank and B. Kramer, 139 µS/cm and 25.1°C,
Non-types: SAIAB 85922(5), 2.0–3.0 cm SL, same time and place etc. as previous paragraph,
SAIAB 58157(9), SL 4.7–9.8 cm, Nwanedzi River (Limpopo system) at Nwanedi, Northern Province, South Africa, below dams, 22°37'45" S, 30°23'52" E, 25 March 1997, coll. B. van der Waal,
SAIAB 85920(2), 4.8–5.7 cm SL, Groot Letaba River (Olifants System, Limpopo drainage) just below Tzaneen Dam, Northern Province, South Africa, 23°49'00" S, 30°10'00" E, 22 September 1998, coll. W. Vlok and B. Kramer, 114 µS/cm and 21.4°C,

- SAIAB 85923(6), 3.8–9.0 cm SL, Blyde River (Olifants System, Limpopo drainage) just below Blydepoortriviers Dam, Mpumalanga, South Africa, 24°32'00" S, 30°47'05" E, 25/26 September 1998, coll. J. Engelbrecht and B. Kramer, 154 μ S/cm and 16.7°C, 82–90 mm SL,
- SAIAB 85919(1), 7.2 cm SL, Pongola River, KwaZulu-Natal, South Africa, at bridge on road from Ndumo to Kosibay, 27°01'15" S, 32°18' E, 14 August 1999, coll. J. Engelbrecht and B. Kramer, 600 μ S/cm and 22°C,
- SAIAB 068279(2), 4.6–8.8 cm SL, Mnjoli Dam Wall, Mbuluzi River, Swaziland, 26°09'41" S, 31°40'14" E, 29 January 2003, coll. R.C. Boycott,
- SAIAB 067228(1), 8.9 cm SL, Mnjoli Dam Wall, Mbuluzi River, Swaziland, 26°09'41" S, 31°40'14" E, 14 August 2002, coll. R.C. Boycott,
- SAIAB 066355(1), 9.8 cm SL, Mnjoli Dam Wall, Mbuluzi River, Swaziland, 26°09'26" S, 31°40'10" E, 19 July 2002, coll. R.C. Boycott,
- SAIAB 95989(30), 3.7–6.0 cm SL, specimens: Mogol05–Mogol14, Mogol17, Mogol20, Mogol21, Mogol30, Mogol31a, Mogol31b, Mogol39–Mogol51; and ZSM 39537(8), 4.5–5.9 cm SL, specimens: Mogol52–Mogol56, Mogol58–Mogol60; and ZSM 39538 (10), 4.3–5.4 cm SL, specimens: Mogol61–Mogol66, MogolDead1–MogolDead3, ohne Fish-ID; Limpopo System: Mokolo River, 24°06.823' S, 27°48.153' E, altitude 932 m, near Hermanusdorings, 20 October 2008, coll. A. Hoffman and B. Kramer,
- SAIAB 96537(2), 4.8 cm SL, specimens Palala04, Palala05, Limpopo System: Lepalala River, 23°59.049' S, 28°24.281' E, 1144 m altitude, near Melkrivier, 22 October 2008, coll. A. Hoffman and Bernd Kramer.

Other material examined, of uncertain status

- SAIAB 059515(1), 8.5 cm SL, *Petrocephalus* sp., Tanzania, Lake Rukwa at mouth of Luika River, Lake Rukwa, Luika, 8°24'5" S, 32°54'20" E, 19 November 1995, coll. P. Skelton,
- SAIAB 039264(1), 7.7 cm SL, *Petrocephalus* sp., Malawi, Zikanyeka Beach, Lake Chiuta, 14°43' S, 35°51' E, 13 July 1992, coll. D. Tweddle.

Results

Morphological comparisons

Comparisons between nominal species

Our first concern was to investigate whether or not our own sample from the type region represented *P. catostoma*. David Livingstone collected the five type specimens from the lower reaches of the Rovuma River in 1859, but the exact type locality is unknown (no. 1, Figure 1; Livingstone 1865). The fresh material from locality no. 28 (Figure 1; $n = 35$) corresponds very well to the type material. The medians for the meristic characters were identical, and the mensural characters similar, with the bigger sample usually showing a wider range that is overlapping the smaller. We conclude that our fresh specimens from the Rovuma drainage represent the species *P. catostoma*, and will use them for comparisons with nominal species and statistical comparisons with allopatric populations (Table 1).

Petrocephalus stuhlmanni congicus David and Poll, 1937 ($n = 2$; locality 26, Figure 1). Whitehead and Greenwood (1959) had seen differentiation from “the eastern and southern subspecies, particularly in its lower modal number of dorsal fin

Table 1. Morphometrics of the southern and eastern African *Petrocephalus* species.

	PDL/SL	PAL/SL	LD/SL	LA/SL	pD/SL	CPL/SL	CPD/CPL	LSc/HL	LSo/HL	HL/SL	HL/Na	BD/SL	nD	nA	SPc	SLS	OD/HL	LPF/HL	PPF/SL	SL (cm)	
<i>P. catostoma</i> - Types																					
Lecto-, BMNH	0.631	0.56	0.175	0.229	0.441	0.237	0.318	0.318	0.441	0.249	18.47	0.292	21	29	12					4.74	
1863.10.12.4																					
Mean/Median*	0.628	0.581	0.167	0.227	0.423	0.22	0.338	0.319	0.436	0.259	18.82	0.289	20	27	14					4.32	
SE/SIQ*	0.001	0.006	0.004	0.008	0.007	0.006	0.008	0.003	0.005	0.004	0.21	0.002	0.5	1	0.25					0.12	
Min	0.625	0.56	0.159	0.196	0.41	0.207	0.318	0.309	0.422	0.249	18.47	0.283	20	27	12					4.1	
Max	0.631	0.593	0.18	0.244	0.441	0.237	0.356	0.33	0.45	0.274	19.64	0.293	21	29	14					4.74	
n	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5					5	
Rovuma System																					
Mean/Median*	0.625	0.578	0.174	0.233	0.411	0.21	0.331	0.326	0.423	0.277	17.433	0.274	20	27	14					4.2	
SE/SIQ*	0.002	0.002	0.001	0.001	0.002	0.002	0.003	0.003	0.002	0.001	0.21	0.002	0.75	0.5	0.75					0.08	
Min	0.602	0.549	0.16	0.219	0.383	0.195	0.296	0.287	0.398	0.259	16.07	0.252	18	25	12					3.7	
Max	0.656	0.602	0.188	0.252	0.434	0.238	0.385	0.356	0.454	0.291	23.21	0.306	22	28	16					6.4	
n	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35					35	
Lake Malawi confluences																					
Mean/Median*	0.637	0.584	0.174	0.239	0.421	0.21	0.341	0.337	0.451	0.267	19.58	0.292	21	26	16					5	
SE/SIQ*	0.005	0.004	0.002	0.002	0.007	0.005	0.016	0.003	0.006	0.003	1.43	0.007	0.125	0.5	2					0.39	
Min	0.627	0.57	0.167	0.233	0.393	0.201	0.289	0.328	0.44	0.256	16	0.266	20	26	12					3.9	
Max	0.652	0.596	0.179	0.246	0.435	0.228	0.386	0.347	0.473	0.276	24.81	0.305	21	27	16					6.1	
n	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5					5	
<i>P. steindachneri</i> - Types																					
1 of 3 synt., NMW	0.623	0.61	0.206	0.252	0.425	0.204	0.299	0.312	0.437	0.273	27.77	0.294	26	31	12					6.5	
55118.1																					
Mean/Median*	0.632	0.609	0.193	0.238	0.42	0.204	0.3	0.322	0.436	0.273	26.25	0.308	24.5	30	12					6.5	
SE/SIQ*	0.005	0.004	0.01	0.009	0.009	0.004	0.006	0.011	0.001	0.001	2.72	0.01	2	1.75	0					0.054	
Min	0.623	0.601	0.173	0.222	0.402	0.195	0.285	0.311	0.434	0.272	20.98	0.294	22	26	12					6.4	
Max	0.641	0.616	0.206	0.252	0.432	0.211	0.313	0.343	0.438	0.274	30	0.328	27	31	12					6.6	
n	3	3	3	3	3	3	4	3	3	3	3	3	4	4	4					3	
<i>P. stuhlmanni</i> - Type																					
BMNH 1907.12.3.1	0.643	0.596	0.152	0.239	0.398	0.216	0.389	0.288	0.382	0.276	25.83	0.301	21	27	12					7.86	
(n = 1)																					
<i>P. catostoma tanensis</i> - Types																					
Holo-, BMNH	0.598	0.594	0.205	0.247	0.449	0.217	0.343	0.325	0.407	0.294	31.13	0.318	25	28	16					6.7	
1963.11.29.1																					

(Continued)

Table 1. (Continued).

	PDL/SL	PAL/SL	LD/SL	LA/SL	pD/SL	CPL/SL	CPD/CPL	LS _c /HL	LS _o /HL	HL/SL	HL/Na	BD/SL	nD	nA	SPc	SLS	OD/HL	LPF/HL	PPF/SL	SL _c (μ m)	
Mean/Median*	0.598	0.562	0.198	0.246	0.453	0.215	0.386	0.328	0.43	0.283	23.94	0.305	25	28	14					4.1	
SE/SIQ*	0.003	0.006	0.002	0.003	0.001	0.002	0.007	0.005	0.006	0.003	1.06	0.003	0	0.5	0					0.35	
Min	0.589	0.545	0.189	0.234	0.449	0.207	0.343	0.305	0.407	0.269	19.51	0.281	24	26	12					3	
Max	0.619	0.594	0.205	0.257	0.462	0.225	0.413	0.354	0.458	0.301	31.13	0.318	25	28	16					6.7	
<i>n</i>	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9					9	
Tana River																					
Mean/Median*	0.612	0.583	0.192	0.239	0.448	0.223	0.346	0.327	0.424	0.266	32.85	0.299	24	28	12	37	0.232	0.742	0.164	7.4	
SE/SIQ*	0.002	0.002	0.001	0.001	0.001	0.001	0.004	0.002	0.002	0.001	0.46	0.003	0.625	0.5	1	0.5	0.003	0.015	0.002	0.15	
Min	0.574	0.554	0.167	0.214	0.427	0.193	0.291	0.297	0.399	0.237	27.31	0.257	22	26	12	36	0.206	0.507	0.143	5.6	
Max	0.645	0.618	0.222	0.257	0.472	0.247	0.439	0.382	0.457	0.282	42.83	0.356	27	29	14	38	0.276	0.862	0.180	9.8	
<i>n</i>	54	54	54	54	54	54	54	54	54	54	54	54	53	54	54	27	27	27	27	54	
<i>P. degeni</i> - Type, BMNH																					
1906.5.30.84 (<i>n</i> = 1)	0.634	0.641	0.155	0.221	0.427	0.202	0.369	0.258	0.411	0.261	20.59	0.29	19	27	12					8.12	
<i>P. stuhlmanni congicus</i> - Syntypes (<i>n</i> = 2)																					
MRAC 30807-30808	0.635	0.535	0.166	0.241	0.438	0.237	0.297	0.343	0.429	0.231	18.87	0.3	19	27	12					7.2	
MRAC 30808-30808	0.618	0.578	0.155	0.234	0.417	0.228	0.296	0.326	0.408	0.238	21.32	0.286	18	28	12					7.8	
<i>P. haulevittii</i> - Syntypes (<i>n</i> = 5) BMNH																					
1912.4.1.181-185	0.607	0.549	0.177	0.258	0.44	0.228	0.306	0.292	0.4	0.226	21.71	0.266	18	27	12					5.9	
Mean/Median*	0.618	0.564	0.168	0.254	0.421	0.22	0.326	0.322	0.429	0.24	20.03	0.283	19	27	12					5.41	
SE/SIQ*	0.003	0.003	0.002	0.002	0.003	0.002	0.008	0.005	0.006	0.002	0.21	0.005	0.5	0	0					0.23	
Min	0.605	0.542	0.154	0.24	0.401	0.209	0.277	0.292	0.4	0.225	18.86	0.24	18	26	12					3.9	
Max	0.641	0.586	0.177	0.269	0.44	0.231	0.365	0.362	0.484	0.248	21.71	0.312	21	28	12					6.5	
<i>n</i>	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14					14	
Lower Zambezi - <i>P. petersi</i> sp. nov.																					
Holo-, SAIAB 060846	0.656	0.625	0.166	0.235	0.406	0.197	0.378	0.355	0.449	0.268	22.96	0.323	18	26	16					6.4	
Mean/Median*	0.642	0.616	0.166	0.228	0.409	0.197	0.356	0.364	0.462	0.278	21.87	0.299	20	26	16					5	
SE/SIQ*	0.003	0.004	0.002	0.002	0.003	0.002	0.006	0.003	0.004	0.002	0.52	0.003	0.5	0.5	1					0.2	
Min	0.623	0.595	0.151	0.215	0.391	0.185	0.324	0.345	0.442	0.268	20.15	0.287	18	25	12					4.1	
Max	0.658	0.637	0.182	0.242	0.425	0.208	0.339	0.383	0.479	0.288	26.35	0.323	20	26	16					6.4	
<i>n</i>	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11					11	

(Continued)

Table 1. (Continued).

	PDI/SL	PAL/SL	LD/SL	LA/SL	pD/SL	CPL/SL	CPD/CPL	LSc/HL	LSO/HL	HL/SL	HL/Na	BD/SL	nD	nA	SFc	SLS	OD/HL	LPF/HL	PPF/SL	SL (cm)
Kafue System: Mwekera Stream																				
Mean/Median*	0.636	0.593	0.182	0.23	0.422	0.202	0.367	0.343	0.465	0.273	25.52	0.287	23	28	12	38.5	0.245	0.703	0.169	6.9
SE/SIQ*	0.002	0.002	0.001	0.002	0.002	0.002	0.006	0.003	0.003	0.002	1.05	0.004	0.5	0	0	0.75	0.004	0.016	0.004	0.54
Min	0.622	0.577	0.171	0.202	0.402	0.184	0.314	0.315	0.44	0.257	18.79	0.267	21	27	12	38	0.236	0.669	0.16	4.1
Max	0.658	0.628	0.193	0.243	0.439	0.215	0.439	0.368	0.483	0.29	36.74	0.328	25	30	14	40	0.252	0.743	0.176	11
n	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	4	4	4	4	22
Kafue S: Lunga R (= 1)	0.6573	0.6158	0.1625	0.2491	0.4278	0.2104	0.3665	0.3465	0.4798	0.2653	28.14	0.3191	21	30	12					7.64
Okavango River, <i>P. okavangensis</i> sp. nov.																				
Holo-, SAIAB 030046	0.64	0.587	0.177	0.275	0.408	0.189	0.333	0.277	0.408	0.264	21.48	0.303	22	30	12	37	0.253	0.685	0.163	6.1
Guma L - Mean/Median*	0.623	0.576	0.17	0.264	0.426	0.207	0.311	0.309	0.439	0.25	19.68	0.291	22	30	12	37	0.253	0.685	0.163	5.6
SE/SIQ*	0.002	0.002	0.001	0.001	0.002	0.001	0.003	0.004	0.003	0.001	0.51	0.003	1	0.5	0	0.375	0.014	—	0.001	0.14
Min	0.589	0.538	0.145	0.247	0.403	0.182	0.264	0.261	0.385	0.232	15.11	0.261	20	27	12	37	0.229	0.641	0.161	4.2
Max	0.66	0.619	0.195	0.286	0.454	0.23	0.349	0.372	0.478	0.274	28.97	0.348	24	32	12	38	0.277	0.728	0.165	8.1
n	45	45	45	45	45	45	45	45	45	45	45	45	45	45	45	3	3	2	3	45
Gadikwe L - Mean/Median*	0.614	0.578	0.171	0.256	0.426	0.211	0.295	0.355	0.466	0.261	20.54	0.3	22	30	12	38	0.256	0.729	0.146	5.7
SE/SIQ*	0.002	0.004	0.002	0.002	0.002	0.002	0.004	0.002	0.003	0.002	0.57	0.002	1	0.125	0	0.5	0.003	0.007	0.001	0.2
Min	0.595	0.553	0.153	0.242	0.404	0.191	0.276	0.334	0.434	0.247	16.89	0.279	20	29	11	36	0.234	0.675	0.135	4.5
Max	0.636	0.626	0.192	0.272	0.444	0.226	0.333	0.376	0.494	0.296	27.54	0.322	26	32	14	39	0.285	0.786	0.161	8.3
n	21	21	21	21	21	21	21	21	21	21	21	21	21	21	21	21	21	21	21	21
Popa Rap - Mean/Median*	0.618	0.576	0.181	0.252	0.428	0.207	0.306	0.364	0.479	0.271	19.72	0.29	23	29	12	37	0.265	0.703	0.148	4.9
SE/SIQ*	0.003	0.002	0.001	0.002	0.002	0.002	0.004	0.002	0.002	0.003	0.49	0.002	0.75	0.75	0	1	0.002	0.008	0.001	0.16
Min	0.58	0.554	0.165	0.229	0.399	0.191	0.252	0.347	0.454	0.247	15.22	0.259	22	27	12	35	0.242	0.6	0.132	3.7
Max	0.658	0.619	0.195	0.275	0.457	0.229	0.352	0.387	0.509	0.32	25.9	0.329	25	32	12	39	0.289	0.799	0.170	7.8
n	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36
Xakanixa Ch - Mean/Med*	0.624	0.586	0.172	0.255	0.418	0.204	0.317	0.342	0.456	0.262	20.96	0.307	22	29	12	37	0.241	0.69	0.151	6.5
SE/SIQ*	0.004	0.007	0.002	0.004	0.005	0.004	0.009	0.003	0.004	0.004	1.18	0.006	0.75	0.5	0	0.875	0.003	0.007	0.004	0.35
Min	0.604	0.556	0.159	0.234	0.386	0.183	0.282	0.322	0.431	0.243	17.72	0.265	20	27	12	36	0.228	0.650	0.137	5.6
Max	0.652	0.624	0.179	0.284	0.437	0.221	0.359	0.360	0.481	0.290	30.96	0.351	23	32	12	38	0.258	0.721	0.176	9.5
n	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11

(Continued)

Table 1. (Continued).

Xakanixa R - Mean/Med*	0.615	0.575	0.182	0.259	0.433	0.211	0.302	0.341	0.459	0.255	19.48	0.291	22	30	12	37	0.256	0.697	0.144	6.4
SE/SIQ*	0.003	0.004	0.001	0.002	0.002	0.002	0.007	0.003	0.003	0.002	0.5	0.003	0.5	1	0	0.5	0.002	0.006	0.003	0.25
Min	0.585	0.537	0.168	0.214	0.397	0.178	0.216	0.310	0.425	0.239	15.1	0.254	21	27	12	36	0.226	0.618	0.122	3.6
Max	0.655	0.64	0.199	0.278	0.458	0.233	0.382	0.381	0.5	0.281	26.6	0.346	25	32	12	39	0.289	0.778	0.183	9.3
n	38	38	38	38	38	38	38	38	38	38	38	38	38	38	38	38	38	38	38	38
Okavango delta: Boro R., <i>P. magnitrunci</i> sp. nov.																				
Holotype, SAIAB 67069	0.641	0.597	0.178	0.27	0.429	0.194	0.34	0.358	0.467	0.248	24.1	0.345	21	31	12	40	0.25	0.671	0.171	8.9
Boro R - Mean/Median*	0.643	0.607	0.172	0.254	0.413	0.192	0.337	0.358	0.464	0.25	21.19	0.344	21	29	12	40	0.232	0.658	0.173	8.3
SE/SIQ*	0.004	0.003	0.002	0.003	0.003	0.003	0.008	0.002	0.003	0.002	0.68	0.004	0.5	1.25	0	0.875	0.002	0.008	0.002	0.12
Min	0.621	0.59	0.162	0.235	0.396	0.176	0.296	0.346	0.449	0.239	17.61	0.327	19	27	11	39	0.218	0.609	0.160	7.7
Max	0.658	0.626	0.178	0.27	0.43	0.215	0.376	0.369	0.481	0.258	24.1	0.368	22	31	12	41	0.250	0.698	0.185	8.9
n	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11
Cunene River, <i>P. magnitrunci</i> sp. nov.																				
Holo-, SAIAB 78788	0.617	0.607	0.179	0.238	0.427	0.201	0.354	0.391	0.47	0.256	24.34	0.314	22	29	13	38	0.292	0.685	0.173	9.6
Mean/Median*	0.632	0.611	0.18	0.234	0.423	0.199	0.327	0.37	0.485	0.258	27.89	0.312	23	29	12	40	0.294	0.706	0.167	9.7
SE/SIQ*	0.005	0.005	0.003	0.004	0.003	0.003	0.008	0.005	0.005	0.003	0.83	0.006	1	1	0	1	0.01	0.013	0.003	0.22
Min	0.612	0.59	0.17	0.215	0.408	0.184	0.283	0.352	0.47	0.25	24.34	0.283	20	26	11	38	0.259	0.662	0.158	8.9
Max	0.661	0.628	0.194	0.256	0.433	0.218	0.354	0.391	0.514	0.277	31.09	0.34	24	31	13	42	0.329	0.746	0.179	10.9
n	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	6	6	6	6	9
<i>P. wevelsi</i> (Sabie River)																				
Holotype, ZSM 28556	0.621	0.595	0.178	0.248	0.43	0.199	0.42	0.296	0.382	0.26	24.09	0.307	20	26	16	16	0.292	0.685	0.173	10.8
Mean/Median*	0.634	0.593	0.171	0.238	0.417	0.212	0.381	0.34	0.432	0.271	21.71	0.318	20	26	16	37	0.212	0.709	0.167	6.8
SE/SIQ*	0.002	0.001	0.001	0.001	0.002	0.001	0.003	0.002	0.003	0.001	0.32	0.002	0.5	0.5	0	0.625	0.006	0.021	0.001	0.2
Min	0.611	0.572	0.156	0.225	0.392	0.197	0.342	0.296	0.382	0.253	19.08	0.283	18	25	16	35	0.2	0.643	0.164	5.4
Max	0.655	0.61	0.183	0.251	0.444	0.226	0.42	0.375	0.461	0.289	27.34	0.343	21	28	16	37	0.233	0.754	0.169	10.8
n	44	44	44	44	44	44	44	44	44	44	44	44	44	44	44	5	5	5	5	44
<i>P. wevelsi</i> (Mbuluzi River)																				
Mean/Median*	0.628	0.599	0.161	0.231	0.416	0.21	0.367	0.354	0.452	0.264	22.83	0.293	19	26	16	16	0.293	0.709	0.167	8
SE/SIQ*	0.002	0.009	0.001	0.008	0.006	0.006	0.019	0.006	0.007	0.005	1.89	0.009	0.5	0.5	0	0	0.006	0.021	0.001	1.17
Min	0.624	0.576	0.158	0.21	0.406	0.199	0.329	0.342	0.436	0.251	18.63	0.27	18	24	16	16	0.2	0.643	0.164	4.6
Max	0.632	0.62	0.162	0.244	0.432	0.226	0.408	0.368	0.47	0.272	26.72	0.309	20	26	16	16	0.233	0.754	0.169	9.8
n	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4

(Continued)

Table 1. (Continued).

	PDL/SL	PAL/SL	LD/SL	LA/SL	pD/SL	CPL/SL	CPD/CPL	LSc/HL	LS ₀ /HL	HL/SL	HL/Na	BD/SL	nD	nA	SPc	SLS	OD/HL	LPF/HL	PPF/SL	SL (cm)	
Limpopo System																					
<i>P. wesselsi</i> (Blyde River)																					
Mean/Median*	0.620	0.589	0.167	0.24	0.423	0.209	0.361	0.316	0.395	0.264	22.97	0.291	20	27	16	35	0.218	0.699	0.165	8.1	
SE/SIQ*	0.002	0.004	0.003	0.004	0.004	0.002	0.005	0.003	0.004	0.002	0.35	0.004	0.75	0.625	0	0.25	0.009	0.008	0.003	0.26	
Min	0.617	0.578	0.161	0.225	0.408	0.204	0.349	0.307	0.385	0.259	21.93	0.28	18	26	16	34	0.19	0.669	0.158	7.6	
Max	0.627	0.602	0.177	0.249	0.432	0.213	0.374	0.325	0.405	0.271	24.08	0.303	21	28	16	36	0.238	0.715	0.173	9.0	
n	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	
<i>P. wesselsi</i> (Groot Letaba River)																					
Mean/Median*	0.626	0.587	0.168	0.225	0.418	0.216	0.348	0.305	0.389	0.276	19.05	0.28	20	26	16	34	0.253	0.741	0.161	5.2	
Min	0.626	0.585	0.165	0.221	0.405	0.214	0.347	0.303	0.382	0.27	18.93	0.279	20	25	16	34	0.245	0.729	0.159	4.8	
Max	0.627	0.589	0.172	0.228	0.431	0.219	0.349	0.306	0.396	0.282	19.18	0.28	20	27	16	34	0.261	0.753	0.164	5.7	
n	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>P. wesselsi</i> (Nwanedzi River)																					
Mean/Median*	0.625	0.6	0.17	0.23	0.422	0.212	0.34	0.371	0.474	0.265	21.42	0.293	21	27	16	37	0.231	0.655	0.158	6.7	
SE/SIQ*	0.003	0.005	0.002	0.003	0.004	0.002	0.013	0.005	0.006	0.003	0.78	0.006	0.625	1	0.25	0.5	0.004	0.015	0.005	0.55	
Min	0.612	0.582	0.158	0.222	0.409	0.203	0.285	0.345	0.451	0.25	18.06	0.266	19	26	16	36	0.214	0.591	0.14	4.7	
Max	0.642	0.622	0.179	0.248	0.453	0.22	0.399	0.389	0.496	0.276	24.29	0.313	22	28	18	38	0.252	0.731	0.19	9.8	
n	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	
<i>P. wesselsi</i> (Mokoto River)																					
Mean/Median*	0.627	0.587	0.167	0.226	0.417	0.208	0.311	0.361	0.494	0.269	21.2	0.258	20	26	16	38	0.276	0.727	0.154	5.1	
SE/SIQ*	0.001	0.001	0.001	0.001	0.002	0.002	0.004	0.003	0.003	0.001	0.63	0.002	0.5	0.5	0	1	0.003	0.007	0.001	0.07	
Min	0.606	0.564	0.155	0.209	0.393	0.188	0.252	0.302	0.445	0.257	14.87	0.236	19	25	16	36	0.221	0.633	0.136	3.7	
Max	0.648	0.617	0.183	0.239	0.451	0.228	0.37	0.4	0.531	0.285	31.11	0.29	21	28	17	40	0.323	0.794	0.171	6	
n	48	48	48	48	48	48	48	48	48	48	48	48	48	48	48	48	48	47	48	48	
<i>P. wesselsi</i> (Lepalala River)																					
Mean/Median*	0.62	0.587	0.18	0.238	0.413	0.195	0.321	0.326	0.476	0.273	19.26	0.254	20.5	26.5	16	37.5	0.245	0.677	0.162	4.8	
Min	0.618	0.562	0.177	0.231	0.413	0.188	0.285	0.316	0.45	0.262	18.32	0.243	20	26	16	37	0.206	0.632	0.156	4.8	
Max	0.621	0.612	0.183	0.246	0.413	0.202	0.357	0.336	0.5	0.283	20.19	0.264	21	27	16	38	0.285	0.722	0.168	4.8	
n	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
<i>P. wesselsi</i> (Pongola)																					
Mean/Median*	0.61	0.576	0.172	0.243	0.431	0.213	0.387	0.315	0.438	0.273	23.52	0.294	21	27	16	37	0.238	0.742	0.156	7.2	

(n = 1)

(Continued)

Table 1. (Continued).

<i>P. squalostoma</i> - <i>Synstictes</i> (<i>n</i> = 2)																			
<i>BMNH 1920.5.26.1</i>	0.667	0.603	0.174	0.241	0.412	0.184	0.388	0.304	0.441	0.263	19.12	0.329	21	30	12	0.257	0.689	0.198	6.8
(R1)																			
<i>BMNH 1920.5.26.1</i>	0.673	0.599	0.160	0.250	0.406	0.192	0.346	0.259	0.409	0.280	27.6	0.335	18	30	12	0.223	0.638	0.208	6.6
(R2)																			
<i>P. longianalis</i> sp. nov. (Luftubu River)																			
Holotype SAIAB 76758	0.636	0.579	0.175	0.268	0.401	0.192	0.291	0.334	0.455	0.243	24.15	0.274	22	31	12	0.213	0.694	0.164	8.2
Mean/Median*	0.622	0.569	0.178	0.261	0.417	0.194	0.298	0.337	0.464	0.268	18.8	0.267	24	33	12	0.248	0.664	0.152	4.8
SE/SIQ*	0.002	0.002	0.001	0.001	0.001	0.001	0.002	0.002	0.003	0.001	0.234	0.002	0.5	0.5	0	0.002	0.005	0.001	0.1
Min	0.592	0.543	0.162	0.244	0.402	0.172	0.269	0.29	0.407	0.243	15.93	0.225	22	30	11	0.213	0.599	0.128	3.8
Max	0.64	0.59	0.191	0.278	0.444	0.215	0.331	0.362	0.496	0.279	24.15	0.293	26	35	12	0.273	0.789	0.169	8.2
<i>n</i>	49	49	49	49	49	49	49	49	49	49	49	49	49	49	49	49	49	49	49
Luongo River																			
Mean/Median*	0.627	0.572	0.184	0.287	0.415	0.179	0.298	0.346	0.447	0.237	25.96	0.294	24	33.5	12	0.223	0.698	0.152	11
SE/SIQ*	0.006	0.007	0.004	0.004	0.008	0.003	0.004	0.005	0.005	0.003	0.276	0.003	0.75	0.625	0	0.007	0.014	0.005	0.12
Min	0.611	0.546	0.168	0.257	0.408	0.184	0.284	0.344	0.448	0.244	20.13	0.288	21	31	12	0.235	0.631	0.138	6.6
Max	0.638	0.585	0.19	0.278	0.455	0.199	0.305	0.369	0.479	0.259	21.82	0.304	24	33	12	0.27	0.718	0.166	7.3
<i>n</i>	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5
Luapula River																			
Mean/Median*	0.627	0.569	0.176	0.27	0.431	0.193	0.295	0.357	0.462	0.25	20.88	0.298	23	32	12	0.255	0.665	0.15	7.0
SE/SIQ*	0.006	0.007	0.004	0.004	0.008	0.003	0.004	0.005	0.005	0.003	0.276	0.003	0.75	0.625	0	0.007	0.014	0.005	0.12
Min	0.611	0.546	0.168	0.257	0.408	0.184	0.284	0.344	0.448	0.244	20.13	0.288	21	31	12	0.235	0.631	0.138	6.6
Max	0.638	0.585	0.19	0.278	0.455	0.199	0.305	0.369	0.479	0.259	21.82	0.304	24	33	12	0.27	0.718	0.166	7.3
<i>n</i>	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5
<i>P. frieli</i> (Lake Bangweulu)																			
Mean/Median*	0.614	0.567	0.208	0.268	0.436	0.201	0.29	0.36	0.494	0.265	23.78	0.317	26	30	12	0.283	0.728	0.148	6.6
SE/SIQ*	0.001	0.005	0.004	0.004	0.004	0.006	0.012	0.007	0.009	0.001	0.843	0.008	0.5	0.25	0	0.008	0.01	0.002	0.42
Min	0.612	0.557	0.201	0.261	0.429	0.185	0.264	0.339	0.48	0.261	21.89	0.3	25	30	12	0.259	0.712	0.141	5.6
Max	0.618	0.579	0.216	0.281	0.446	0.209	0.322	0.372	0.519	0.267	25.69	0.338	27	31	12	0.297	0.755	0.152	7.4
<i>n</i>	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4

*Median and SIQ, semi-interquartile range, for meristic data. Abbreviations of anatomical characters, see Material and Methods.
 Fish from "Rovuma System": SAIAB 73887(9), SAIAB 73802(10), SAIAB 73808(10), SAIAB 73894(6). "Upper Zambezi System": "Katima": SMF 28265(26), SAIAB 85909(3), 85911(2), 85916(1), 85917(2), 85918(3), ZSM 38657(1), "East Lumwana River": SAIAB 041208(5), and SAIAB 041025(1); "Wayama Lagoon": SAIAB 72670(1) pooled with Kama Lagoon, SAIAB 71792(1); "Kwando River": ZSM 38658(1), "Lake Malawi confluences": SAIAB 039328(1), SAIAB 050065(2), SAIAB 050155(2). "Kafue System: Mwekera Stream": SAIAB 042559(18), SAIAB 41224(4). "Luongo River": SAIAB 040074(1). "Okavango River": "Guma Lagoon": SAIAB 030046(1), SAIAB 186062(41), ZSM 38665(3); "Boro River": SAIAB 67069(1), SAIAB 186057(10); "Gadikwe Lagoon": SAIAB 19769(21); "Popa Rapids": SAIAB 36841(24), SAIAB 36823(12); "Xakanixa Channel": SAIAB 19705(11); "Xakanixa River": SAIAB 21271(38). "Cunene River": SAIAB 028120(3), SAIAB 186053(1), SAIAB 79480(1), SAIAB 78790(1), ZSM 38659(1), ZSM 38660(1). *P. longianalis* sp. nov. from "Luftubu River": SAIAB 76758(1), SAIAB 186060(48); *P. longianalis* sp. nov. from "Luongo River": SAIAB 76733(2); *P. longianalis* sp. nov. from "Luapula River": SAIAB 76582(5); *P. frieli* from "Lake Bangweulu": SAIAB 76825(3) and SAIAB 76859(1). *P. wesselsi* from "Sabie River": SAIAB 05449(13), ZSM 28554 to 28566(13), SMF 28266(13), SAIAB 85922(5); "Mbuluzi River": SAIAB 067228(1), SAIAB 066355(1), SAIAB 068279(2). *P. wesselsi* from "Limpopo System": Blyde River": SAIAB 85923(5); Groot Letaba River": SAIAB 85920(2); Nwanedzi River: SAIAB 58157(9). *P. wesselsi* from "Pongola" River: SAIAB 85919(1).

rays (19 in the Congo subspecies cf. 21 for *P. catostoma* and 24 for *P. tanensis*)” and recognized it as a subspecies of *P. catostoma*. *Petrocephalus stuhlmanni conigicus* appears clearly more differentiated from *P. catostoma* than that by its extremely short HL, short LD, CPD, long CPL and low number of SPc and nD. Furthermore, its inferior mouth position even behind the centre of the eye (rare: Bigorne 2003: 158–159) and its reduced dorsal fin that originates far behind the origin of the anal fin set it apart from *P. catostoma*. Species status is more appropriate than its present subspecific designation.

Petrocephalus stuhlmanni Boulenger, 1909 ($n = 1$) cannot be referred to *P. catostoma* because of its low LD, LSo (also LSc), SPc, Na and high CPD and BD (locality 2, Figure 1). The synonymization appears unjustified. Whitehead and Greenwood’s (1959) synonymization with *P. catostoma*, that was not commented upon, again seems mainly based on the similar number of dorsal fin rays: 19–20–21 in *P. stuhlmanni* ($n = 9$) vs 19–22–23 in *P. catostoma* ($n = 17$).

Petrocephalus haullevillii Boulenger, 1912 ($n = 14$; locality 24, Figure 1), a valid subspecies, is differentiated from *P. catostoma*: its low SPc, HL and Na, and high LA and its very inferior mouth also set it clearly apart from *P. catostoma*. [Whitehead and Greenwood’s (1959) comment on the status of *P. stuhlmanni conigicus* (cited above) applies also for *P. haullevillii*.] The hypothesis of no difference (from Rovuma specimens) among 13 anatomical characters (the ones listed on Table 2) was rejected by multivariate analysis of variance (MANOVA; $F_{13,35} = 47.76$, $P < 0.0001$ for all four test variables, Wilks’ Lambda, Roy’s Greatest Root, Hotelling–Lawley Trace and Pillai Trace). Subsequent univariate ANOVAs identified PAL, LD, LA, pD, CPL, HL, nD, nA and SPc as sources of the difference ($F_{1,47} \geq 5.516$, $P \leq 0.0231$). PCA on the same set of 13 anatomical characters revealed complete separation of populations already for principal components PC1 and PC2 (not shown). The synonymization appears unjustified (locality 24, Figure 1).

With extreme values for PAL (highest), LSc and LD lowest among all nominal species, the lowest possible number of 12 for SPc, and with CPD and Na in the extreme range for the species, *P. degeni* Boulenger, 1906 ($n = 1$) clearly does not represent *P. catostoma*, and the synonymization appears mistaken (locality 27, Figure 1). Whitehead and Greenwood’s (1959) reasons for full synonymization of *P. degeni* with *P. catostoma* (not a subspecies) are not explained *expressis verbis*, but the near identity of their dorsal fin ray counts (19–21–22) with that for *P. catostoma* (19–22–23) may have played a role.

Petrocephalus steindachneri Fowler, 1958 ($n = 3$) is well differentiated from *P. catostoma* by its high nD, LD, nA, PAL, BD, and low SPc, CPD and Na (locality 25, Figure 1). The synonymization with *P. catostoma* cannot be supported. Given Whitehead and Greenwood’s (1959) synonymization of all eastern African *Petrocephalus* species with *P. catostoma*, including even two Congoan forms such as *P. haullevillii* from near the Atlantic coast, Seegers (1996) logically united the East African species *P. steindachneri* with *P. catostoma*.

Petrocephalus catostoma tanensis Whitehead and Greenwood, 1959 ($n = 9$) was recognized as a subspecies when discovered (locality 10, Figure 1). With very high values for LD, nD, pD, high BD, LA, CPD and low PDL and Na there is a marked degree of differentiation present in the type material when compared with *P. catostoma*; subspecies status appears inadequate and species status more appropriate. This is supported by statistical comparisons using fresh samples from the Tana River (below).

Table 2. Comparison of anatomical characters in allopatric *Petrocephalus* species from southern and eastern Africa; multivariate analysis of variance (MANOVA) followed by univariate ANOVAs.

	PDL/SL	PAL/SL	LD/SL	LA/SL	pD/SL	CPL/SL	CPD/CPPL	LSc/HL	HL/SL	BD/SL	nD	nA	SPc
MANOVA													
ANOVA	<10 ⁻⁴												
Post tests													
Rovuma, Tana	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Rovuma, U Zambezi	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Rovuma, Okavango													
Rovuma, Kafue	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Rovuma, <i>P.wesselsi</i> *	<0.01	<0.01	<0.01	0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Tana, U Zambezi	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Tana, Okavango	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Tana, Kafue	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Tana, <i>P.wesselsi</i> *	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
U Zambezi, Okvgo	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
U Zambezi, Kafue													
U Zambezi,	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
<i>P.wesselsi</i> *													
Okavango, Kafue	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Okavango, <i>P.wesselsi</i> *	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Kafue, <i>P.wesselsi</i> *													
Lufubu, Tana	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Lufubu, Kafue	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Lufubu, U Zambezi	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Lufubu, <i>P.wesselsi</i> *	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Lufubu, Okavango													
Lufubu, Rovuma	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01

P values in the body of the table not shown when *P* > 0.01. For sample sizes, see footnote to Table 1.

Abbreviations of anatomical characters, see Material and methods. U Zambezi, Upper Zambezi. MANOVA $F_{\geq 13,277} \geq 33.51$, depending on procedure; MANOVA *P* value: same for Wilks' Lambda, Roy's Greatest Root, Hotelling–Lawley Trace, and Pillai Trace tests. ANOVA $F_{6,284} \geq 16.55$. Post tests followed the Games/Howell procedure.

**Petrocephalus wesselsi* from Incomati River system; Kafue sample, *n* = 22.

Comparisons between allopatric populations referred to P. catostoma

Whereas firm conclusions for the relationships among most of the above nominal species and *P. catostoma* can only be drawn with caution because of the general dearth of material, multivariate statistics can be used to characterize the differences among the allopatric populations we have sampled. The first three principal components (PC1–PC3) on correlations accounted for almost two-thirds (65%; Appendix 1) of the morphological variation in the data set. This shows that there was considerable redundancy, and PCA was quite successful. Therefore, in order not to overestimate differentiation when examining the hypothesis of no morphological difference between fish from different origins by inferential statistics, a MANOVA was required (McGarigal et al. 2000).

Included in both MANOVA and PCA were specimens from (1) the Rovuma region ($n = 35$, representing the type species in the present study), (2) Tana River ($n = 54$), (3) Upper Zambezi River ($n = 44$), (4) Okavango River, Guma Lagoon ($n = 45$), (5) Kafue River ($n = 22$), (6) the Luapula System, Lufubu River ($n = 49$), and (7) *P. wesselsi* from the Sabie River ($n = 44$). Characters excluded from both PCA and MANOVA were LSo (for its high degree of redundancy with LSc) and Na (because of the danger of measurement error of this very small measure); thus, 13 anatomical characters (the dependent variables) were compared by PCA and MANOVA/ANOVA, using group (origin) as an independent variable in the latter two. (Additional samples and characters were included in certain instances, as indicated where appropriate.)

The null hypothesis of no difference among the seven allopatric groups was clearly rejected by MANOVA ($P < 0.0001$, Table 2). Subsequent univariate ANOVAs identified all 13 anatomical characters included in the analysis as contributing to the differentiation ($P < 0.0001$ for each). The PCA identified the main characters responsible for this differentiation. PC1 captured 32.9% of the variation in the data set and was correlated with positive and negative loadings (Appendix 1). Characters loading strongest on PC1 (“excellent”, in that order) were PAL, PDL and nA, the loading by CPD was “very good”, the loadings by LA, SPc, nD and pD “good”, the ones by HL and BD “fair”, and the one by LSc “poor”. PC1 therefore represented a gradient for “length and depth of anterior trunk and depth of caudal peduncle vs length of rear section, especially of anal fin”, signifying that a long PAL and PDL and high CPD were associated with a short anal fin, small number of rays and short pD (and vice versa). PC2 captured an additional 17.5% of the variation, representing a gradient for characteristics of “caudal peduncle and peduncle-to-dorsalis length vs anal fin and anterior body length”. “Excellent” was the loading by CPL, “good” those by pD and nA, “fair” the ones by LA and PDL, and “poor” the one by SPc. PC3 captured an additional 14.7% of the variation, and was strongly loaded by LD and nD (“excellent”), but only “poorly” by PAL, HL and SPc. PC3 seemed to represent a gradient for the dorsal fin, and also head and trunk, being long when SPc was small (or vice versa). LSc was the only character loading no more than “poorly” on any one of the first three (and even four) PCs, but loaded strongly on PC5 (“excellent”). PC5 accounted for only 6.8% of the variation, and LSc does not seem to contribute significantly to any dominant morphological trait in the present data sample set.

Pairwise post-hoc tests showed significant differentiation between Rovuma specimens and each one of the other populations in 7–11 characters ($P < 0.01$, Games/Howell procedure; Table 2); that is, none of the latter represents *P. catostoma*. Furthermore, all possible pairwise comparisons among the six allopatric

populations yielded significant differences in 6–11 characters, except for the pair Upper Zambezi–Kafue that differed significantly only in LSc (PCA had identified LSc as the trait explaining least of the variation; see above). That is, with the exception of the latter pair, all allopatric populations studied are well differentiated from each other.

We compared the small Lower Zambezi sample ($n = 11$) to its neighbouring populations only, to keep the number of pairwise comparisons manageable (and the result meaningful). MANOVA rejected the null hypothesis of no difference among 13 anatomical characters when comparing Rovuma, Lower Zambezi, Upper Zambezi, Kafue and Sabie (*P. wesselsi*) samples with one another. Subsequent ANOVAs showed that each one of the 13 characters contributed significantly to this result. Lower Zambezi samples differed from the standard, Rovuma samples, in seven characters, from Kafue samples also in seven, from Upper Zambezi samples in six (among them the three meristic characters), and from Sabie samples (*P. wesselsi*) in seven characters (Table 3).

Plots of the principal component axes PC1 vs PC2 confirmed differentiation from the Rovuma samples by a separation of clouds of points for samples from (1) the Tana River (Figure 4A), the Upper Zambezi River (Figure 4B), the Okavango River (Guma Lagoon; Figure 4C), the Lower Zambezi delta (Figure 4D), the Lufubu River (Figure 4E), the Sabie (*P. wesselsi*, Figure 4F), the Cunene River (Figure 4G), and the Boro River (Okavango delta; Figure 4H). (Where an individual point fell into the region of the other sample, as in Figures 4A and 4F, tilting the graph slightly by the third dimension PC3 revealed complete separation in separate spaces; not shown for economy of presentation.) The samples from the Cunene River also proved differentiated from another neighbouring population, those of the Upper Zambezi (Figure 4I).

The two systems neighbouring the Okavango River, with sporadically interconnected waterways, are the Upper Zambezi and the Cunene rivers. Samples of the latter two were differentiated from the two samples of the Okavango River proper: Guma and Popa. This is shown by non-overlapping ranges in PC1–PC3 coordinates, independent of whether the Okavango River was represented by the Guma Lagoon sample (Figure 5A, B) or the Popa Rapids sample (Figure 5C, D).

Despite the small Cunene sample size, MANOVA/ANOVA analysis (Table 4) confirmed differentiation from Rovuma specimens (in eight characters), from Lower Zambezi specimens in seven characters, from Upper Zambezi specimens in four characters, and from Okavango (Guma) specimens in three characters. Cunene samples differed from Guma samples by their greater PAL and LSo, and smaller LA; additional differentiation is present in HL/Na ($P < 0.001$, $t = 6.836$), and SLS and OD (not testable at present for insufficient sample size). In conclusion, we recognize morphological differentiation on the species level for the samples from (1) the Tana River, (2) the Lower Zambezi delta, (3) the Upper Zambezi River (including Kafue), (4) the Okavango (Guma), (5) the Lufubu River, and (6) the Cunene River, and confirm such differentiation for Sabie River samples (i.e. *P. wesselsi*). (A further species for the Okavango, Boro River, is recognized below).

Comparisons of putative new species with nominal species for P. catostoma

Tana sample. The geographically closest nominal species, *P. stuhlmanni* (type, $n = 1$), showed values below the lowest of our large Tana sample for the characters LD,

Table 3. Comparison of anatomical characters in allopatric *Petrocephalus* species focussing on the Lower Zambezi sample; multivariate analysis of variance (MANOVA) followed by univariate ANOVAS.

	PDL/SL	PAL/SL	LD/SL	LA/SL	pD/SL	CPL/SL	CPD/CPL	LSc/HL	HL/SL	BD/SL	nD	nA	SPc
MANOVA	<10 ⁻⁴												
ANOVA	<10 ⁻⁴												
Post tests													
Rovuma, L Zambezi	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Rovuma, Kafue	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Rovuma, U Zambezi	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
L Zambezi, Kafue	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
L Zambezi,	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
U Zambezi													
Kafue, U Zambezi				<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
L Zambezi, <i>P.wesselsi</i> *		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01

P values in the body of the table not shown when $P > 0.01$. For sample sizes, see footnote to Table 1.

Abbreviations of anatomical characters, see Material and methods. U Zambezi, Upper Zambezi; L Zambezi, Lower Zambezi. MANOVA $F_{13,138}$ to $F_{52,552} \geq 19.8$, depending on procedure; MANOVA *P* value: same for Wilks' Lambda, Roy's Greatest Root, Hotelling-Lawley Trace, and Pillai Trace tests. ANOVA $F_{4,147} \geq 6.14$. Post tests followed the Games/Howell procedure.

* *Petrocephalus wesselsi* from Incomati River system; Kafue sample, $n = 18$.

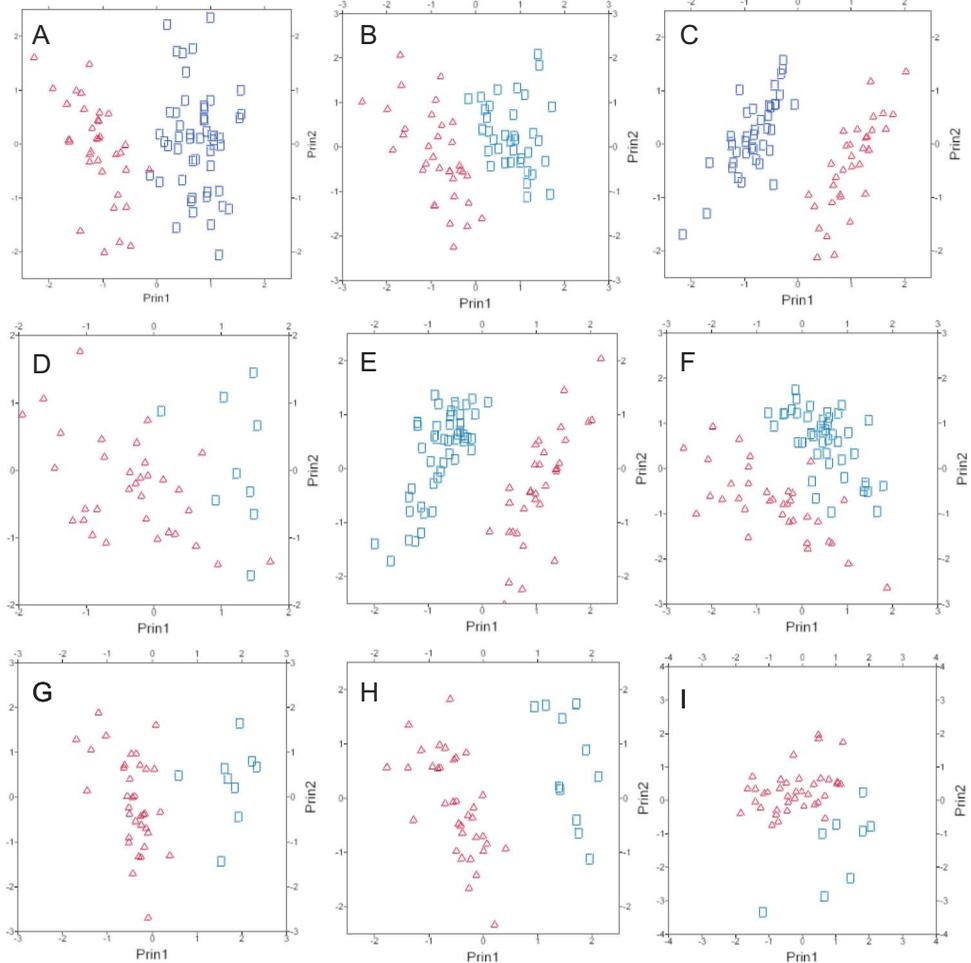


Figure 4(A–H). Principal component analysis for 13 anatomical characters of *Petrocephalus catostoma* from Rovuma System (red triangles; $n = 35$) compared (one by one) with various allopatric *Petrocephalus* populations (blue squares): (A) with *P. tanensis* from Tana River ($n = 52$); (B) *P. longicapitis* sp. nov. from Upper Zambezi River ($n = 38$); (C) *P. okavangensis* sp. nov. from Guma Lagoon, Okavango ($n = 45$); (D) *P. petersi* sp. nov. from Lower Zambezi River ($n = 11$); (E) *P. longianalis* sp. nov. from Lufubu River ($n = 49$); (F) *P. wesselsi* from Incomati System ($n = 44$); (G) *P. magnoculis* sp. nov. from Cunene River ($n = 9$); (H) *P. magnitrunci* sp. nov. from Boro River ($n = 11$). (I) compares *P. longicapitis* sp. nov. from Upper Zambezi River ($n = 38$, red triangles) with *P. magnoculis* sp. nov. from the Cunene River ($n = 9$, blue squares). Prin1, Prin2, for Principal Components 1 and 2.

pD, LSc, LSo, nD, and greater than (or greater than the 90th percentile) the highest Tana values for PDL, CPD and Na. Therefore, the Tana samples do not represent *P. stuhlmanni*.

Petrocephalus degeni (type, $n = 1$) of Lake Victoria, also in East Africa, is the next closest nominal species. However, the measurements for its anatomical characters were below the lowest of the Tana samples for LD, LA, pD, CPL, LSc, Na, nD and

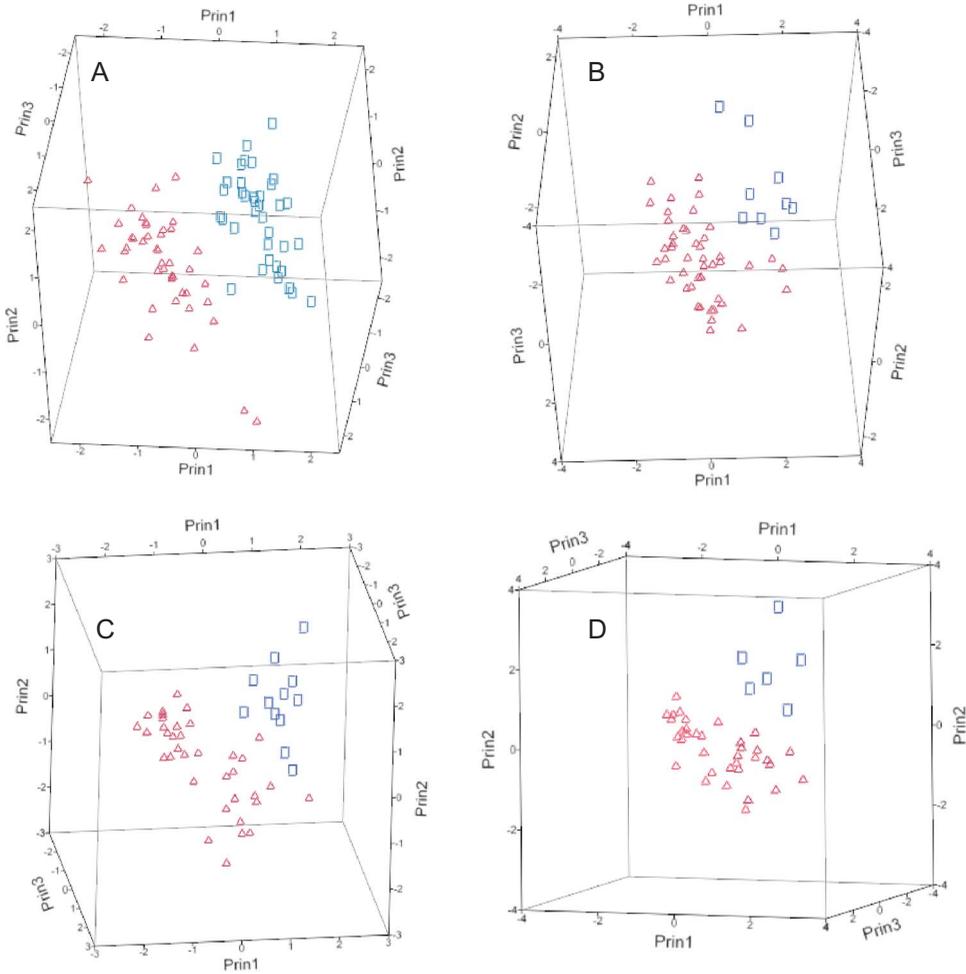


Figure 5. Principal component analysis for anatomy of *Petrocephalus okavangensis* sp. nov. (red triangles) from (A, B) Guma Lagoon ($n = 45$) and (C, D) Popa Rapids ($n = 36$), compared with (A, C) *P. longicapitis* sp. nov. from Upper Zambezi River (blue squares) and (B, D) *P. magnoculis* sp. nov. (blue squares). Upper panels, analyses on 13 characters (see Table 3), lower panels, analyses on 17 characters (see Table 1, with HL/Na and LSc/HL excluded). Prin1–Prin3, for Principal Components 1–3.

greater than the Tana sample's upper range for PAL and PDL (PDL, 90th percentile). Therefore, the Tana samples do not represent *P. degeni*.

From geography an unlikely species to associate with the Tana samples is *P. steindachneri* (types, $n = 3$) because the origin of *P. stuhlmanni* is between the two (all three inhabiting independent rivers draining into the Indian Ocean, with 600 km between the mouths of the Tana River and the Rufiji River inhabited by *P. steindachneri*). Anatomical measures below the 90th percentile of our large Tana samples' ranges were pD and CPD, and above, PAL (all characters loading strongest on PC1). Given these differences, the Tana samples cannot be conspecific with *P. steindachneri*.

Table 4. Comparison of anatomical characters in allopatric *Petrocephalus* species focusing on the Cunene River sample; multivariate analysis of variance (MANOVA) followed by univariate ANOVAs.

	PDL/SL	PAL/SL	LD/SL	LA/SL	pD/SL	CPL/SL	CPD/CPL	LSc/HL	HL/SL	BD/SL	nD	nA	SPc
MANOVA													
ANOVA	<10 ⁻⁴												
Post tests													
Rovuma, L Zambezi	<0.01	<0.01	<0.05		<0.05	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Cunene, L Zambezi			<0.05					<0.05	<0.01		<0.01	<0.01	<0.01
L Zambezi, Okavango	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01		<0.01	<0.01	<0.01
L Zambezi, U Zambezi	<0.01	<0.01	<0.01	<0.05				<0.01			<0.01	<0.01	<0.01
Rovuma, Cunene					<0.05			<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Rovuma, Okavango				<0.01	<0.01		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Rovuma, U Zambezi	<0.01	<0.01	<0.01			<0.01	<0.01			<0.01	<0.01	<0.01	<0.01
Cunene, Okavango				<0.01				<0.01					
Cunene, U Zambezi					<0.05		<0.05	<0.01	<0.01				
Okavango, U Zambezi	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01

P values in the body of the table not shown when *P* > 0.05. For sample sizes, see footnote to Table 1.

Abbreviations of anatomical characters, see Material and methods. U Zambezi, Upper Zambezi; L Zambezi, Lower Zambezi. MANOVA $F_{\geq 13,124} \geq 13.4$; MANOVA *P* value: same for Wilks' Lambda, Roy's Greatest Root, Hotelling-Lawley Trace, and Pillai Trace tests. ANOVA $F_{4,133} \geq 9.33$. Post tests followed the Games/Howell procedure.

The remaining two nominal species, *P. stuhlmanni congicus* (types, $n = 2$) and *P. haullevillii* (types, $n = 14$), inhabit distant basins draining into the Atlantic Ocean, with no connections to East Africa. For the closer of the two species, *P. s. congicus* from the Congo River basin, values lower than the Tana samples' lowest ranges were found for HL, Na and nD, with in addition both LD and CPD below the 90th Tana percentile. Regarding *P. haullevillii* from near the Atlantic coast and north of the Congo River, the hypothesis of no anatomical difference from Tana samples ($n = 53$) was rejected by MANOVA ($F_{13,52} = 47.24$, $P < 0.0001$ for all four multivariate test procedures). Subsequent univariate ANOVAs identified PAL, LD, LA, pD, CPD, HL, nD, nA and SPc as sources of the difference ($F_{1,64} \geq 5.259$, $P \leq 0.0251$). The Tana samples represent neither of these two nominal species, nor any other, except, of course, *P. c. tanensis* Whitehead and Greenwood, 1959, which we elevate to species rank, *P. tanensis* (Whitehead and Greenwood, 1959), in Systematics (below).

Upper Zambezi sample. The origins of the nominal species are all far off the origin of the present Upper Zambezi sample, the closest geographical association probably being with the Congo basin. Anatomical character measures for *P. s. congicus* were above those for the Upper Zambezi sample for CPL, and below for LD, CPD, HL, nD and PAL (PAL, 90th percentile). Therefore, the Upper Zambezi sample does not represent *P. s. congicus*.

Nor are the Upper Zambezi samples representing *P. haullevillii*. The hypothesis of no difference from Upper Zambezi samples when considering all anatomical characters together (as in Table 2) was rejected by MANOVA ($F_{12,45} = 45.16$; $P < 0.0001$ for all four multivariate test procedures). Subsequent univariate ANOVAs identified all anatomical characters except LSc and SPc as sources of the difference ($F_{1,56} \geq 7.741$, $P \leq 0.0073$).

The remaining nominal species are all in distant and isolated basins in East Africa. The *P. steindachneri* sample of three specimens overlaps with Upper Zambezi samples in most characters, except for its very low CPD, which is even below outliers of the Upper Zambezi sample, and among the characters loading strongest on PC1. Given its provenance even further from the Upper Zambezi than *P. catostoma*, we conclude that *P. steindachneri* is not conspecific with the Upper Zambezi samples.

Petrocephalus stuhlmanni differs from the Upper Zambezi sample by low LD and LSo values, and high CPL values beyond the range of Upper Zambezi sample outliers. In addition, its values for pD, LSc, nD and nA are below and CPD above the 90th Upper Zambezi sample percentile.

Petrocephalus geni from tropical Lake Victoria cannot be associated with the Upper Zambezi sample because of its low values for LD, LSc, nD and high PAL (all beyond the range of outliers of the Upper Zambezi sample), with in addition an HL below and a pD measure above the 90th Upper Zambezi percentile. Its short dorsal fin originates above (and not behind) its anal fin.

We conclude that the Upper Zambezi sample cannot be conspecific with any of the nominal species previously referred to *P. catostoma*, and recognize it as *P. longicapitis* sp. nov. in Systematics (below).

Guma Lagoon sample (Okavango). Among the morphological measurements of *P. s. congicus*, LA and nD are below the outlier range of the Guma sample, with in addition HL and nA below the lower 90th percentile and CPL greater than the upper 90th percentile. *P. s. congicus* is quite clearly not the species we find in Guma Lagoon.

Regarding *P. haullevillii*, the null hypothesis of no difference from Guma samples in anatomy (as represented by 13 characters) is rejected by MANOVA ($F_{12,46} = 21.13$, $P < 0.0001$ for all four test procedures). Subsequent univariate ANOVAs identified CPD, CPL, LA, PAL, HL, nA and nD as sources of the difference ($F_{1,57} \geq 4.123$, $P \leq 0.047$), and the Guma sample is considered a different species.

Petrocephalus steindachneri features an LA shorter than the lower 90th percentile of the Guma sample, and PAL and HL longer than the upper 90th percentile. *Petrocephalus steindachneri* is not the species we find in the Guma Lagoon.

The same holds for *P. stuhlmanni*. LA, pD, LSo were smaller than, and CPD and HL greater than the Okavango sample range. With in addition LD, nD and Na smaller than or equal to, and PDL and PAL greater than the lower or upper 90th percentiles, respectively. The Guma sample is well differentiated from *P. stuhlmanni*.

Petrocephalus degeni is not a possibility for the Guma sample. Its LA, LSc and nD were smaller, and its PAL and CPD greater than the most extreme values observed in the Guma sample. In addition, LD and nA were smaller than, and HL greater than the lower and upper 90th percentile, respectively. The origins of the dorsal fin differ: above anal fin in *P. degeni*, more posterior in the Guma sample of specimens.

We conclude that the Guma Lagoon sample has no close affinities with any of the nominal species referred to *P. catostoma*, and we recognize *P. okavangensis* sp. nov. in Systematics (below).

Boro River sample (Okavango). Samples from the Boro River in the Okavango delta were clearly differentiated from all other Okavango samples. This discovery raises the question of differentiation from nominal species also here. *Petrocephalus s. congicus* did not overlap with the Boro River sample's greater values for PAL, LSo, HL and BD, whereas for CPL its range of values was below that of *P. s. congicus*. Therefore, *P. s. congicus* is not the species found in the Boro River.

Petrocephalus haullevillii and the Boro River sample were drawn from clearly differentiated populations, as shown by MANOVA ($F_{13,11} = 26.58$, $P < 0.0001$). This result was brought about by significantly different distributions for PDL, PAL, CPL, LSo, HL, BD, nD and nA (ANOVA, $F_{1,23} \geq 8.56$, $P < 0.01$).

Comparing the Boro River sample with *P. steindachneri* yielded four non-overlapping characters (LSc, LSo and BD smaller, HL greater in *P. steindachneri*), in addition to further marked differences (nD, CPD). We therefore do not refer the Boro River sample to *P. steindachneri*.

The Boro River sample is quite clearly not referable to *P. stuhlmanni* whose LD, LSc, LSo and BD are all smaller, and CPD and HL greater than the most extreme values found in the Boro River sample.

The comparison of the Boro River sample with *P. degeni* shows clear differentiation in the characters (1) LD, LA, LSc, LSo and BD, and (2) PAL and HL, the distributions of which do not overlap. The first group of characters are all smaller, the second greater in *P. degeni*. The position of the dorsal fin origin with respect to that of the anal fin differs between the two species.

We conclude there are no close affinities with any of the nominal species, and we therefore recognize *P. magnitrunci* sp. nov. for the Boro River sample in Systematics.

Lower Zambezi sample. The most relevant nominal species for comparison with type-locality *P. catostoma* are those from rivers also discharging into the Indian Ocean. The Lower Zambezi sample proved to be anatomically well differentiated from

P. steindachneri, the geographically closest *P. catostoma* synonym. *Petrocephalus steindachneri*'s CPD, LSc and LSo were lower, and nD and nA higher than the most extreme values observed in the Lower Zambezi sample (that also differed by a median SPc of 16 vs 12 as observed in *P. steindachneri*). In addition, *P. steindachneri*'s LD was greater than the 90th LD percentile of the Lower Zambezi sample.

Similarly, the Lower Zambezi sample cannot be associated with *P. stuhlmanni*. The *P. stuhlmanni*'s LD, LSc and LSo were lower, and its CPL, nD and nA were higher than the most extreme observed in the Lower Zambezi sample. An SPc of a median count of 16 in the latter also contrasts with 12 in the former. Beyond the 90th percentiles of the Lower Zambezi sample were PAL and Na (low end of the distribution), LA and CPD (high end) in *P. stuhlmanni*.

The Lower Zambezi sample is clearly differentiated from *P. catostoma tanensis* (represented by a sample of $n = 54$). The hypothesis of no anatomical overall difference is rejected by MANOVA ($F_{13,49} = 41.285$, $P < 0.0001$ for all four test procedures). Subsequent univariate ANOVAs identified PDL, PAL, LD, LA, pD, CPL, LSc, HL, nD, nA and SPc as sources of the difference ($F_{1,61} \geq 15.67$, $P \leq 0.0002$).

Petrocephalus degeni of Lake Victoria is also not the species we find in the Lower Zambezi. With LSc, LSo and HL below, and PAL, pD and nA above the range observed in the Lower Zambezi sample, and an SPc of 12 vs a median 16, *P. degeni* and the Lower Zambezi species have little in common. In addition, *P. degeni*'s LD was below the 90th LD percentile of the Lower Zambezi sample.

Petrocephalus stuhlmanni congicus is clearly differentiated from the Lower Zambezi sample by anatomical character measures more extreme than the range of the latter in: PAL, CPD, LSc, LSo, HL (lower), and CPL and nA (higher); in addition, by SPc (12 vs a median 16 in the Lower Zambezi sample).

The hypothesis of no anatomical differences between *P. haullevillii* and the Lower Zambezi sample is rejected by MANOVA ($F_{13,11} = 45$, $P < 0.0001$ for all four multivariate test procedures; for the characters included, see Table 2). As shown by subsequent univariate ANOVAs, characters significantly contributing to this difference were PDL, PAL, LA, pD, CPL, CPD, LSc, HL, BD, nA and SPc ($F_{1,23} \geq 5.732$, $P \leq 0.0252$).

We conclude that the Lower Zambezi sample is not represented by any of the nominal species of *P. catostoma*, and recognize *P. petersi* sp. nov. in Systematics (below).

Lufubu sample. Samples from the Lufubu River are clearly differentiated from *P. s. congicus* even though both occur in the same river system, the Congo. The two samples show non-overlapping ranges in LA, CPL, LSo, HL, nD and nA.

A similarly clear differentiation was found for *P. degeni*: the Lufubu samples' ranges were below or above the values for this species in PAL, LD, LA, LSc, nD and nA.

Petrocephalus steindachneri from East Africa cannot be associated with the Lufubu samples for their non-overlapping ranges in PAL and BD, characters loading significantly on PC1. The 90th percentile ranges for LA, LSo and nA did not overlap with those for *P. steindachneri*.

Petrocephalus stuhlmanni. There was no overlap with Lufubu samples in any character except in SPc, that is, no affinity whatsoever.

Petrocephalus haullevillii. The hypothesis of no morphological difference between *P. haullevillii* ($n = 14$) and the Lufubu sample ($n = 49$) is rejected by MANOVA ($F_{13,49} = 54.45$; $P < 0.0001$). Significant differences were apparent in LD, CPL, CPD, HL, nD, LA and LSc (ANOVA, $F_{1,61} \geq 8.85$; $P < 0.01$); that is, the Lufubu sample is well differentiated.

The Lufubu sample is also clearly differentiated from *P. c. tanensis* ($n = 54$). Among the 13 anatomical characters included in MANOVA/ANOVAs, 11 proved to be significantly different ($P < 0.01$; Table 2). We conclude the Lufubu sample cannot be associated with any of the nominal species of *P. catostoma*.

However, there is another hypothesis to test. *Petrocephalus squalostoma* (Boulenger, 1915) resembles churchills and was recorded from a small tributary of Lake Moero, that is, from a region further downstream the Luapula River system compared with the Lufubu (Figure 1, no. 39). Therefore, we compared the Lufubu sample with two syntypes of *P. squalostoma*.

Petrocephalus squalostoma ($n = 2$) features the most extreme PDL/SL and PPF/SL values of all the samples studied in the present paper, with no overlap with Lufubu samples, including outliers ($n = 49$; Table 1). With no overlap, PAL/SL, CPD/CPL and BD/SL were all greater, and nD and nA smaller in the Types than in the Lufubu sample (nA: a single outlier of the Lufubu sample also had only 30 rays). LA/SL was longer in Lufubu samples than in Types that did not reach the lower 90th percentile of Lufubu samples. LSo/HL values in Types were below the lower 90th percentile of the Lufubu sample. Given these differences, we recognize the Lufubu samples as representing the new species *P. longianalis* sp. nov. in Systematics (below).

Cunene sample. The closest affinities of samples from the isolated Cunene River may be expected with the Guma Lagoon or Boro samples (however, Figures 5B,D, 8F confirmed differentiation), and with the Upper Zambezi sample (Figure 4I, also showing differentiation), whereas all other origins are so far away and unconnected that close affinities are unlikely (e.g. Figure 4G).

Comparison of other samples with nominal or putative new species

Petrocephalus catostoma of the type region. The specimens from Lake Malawi confluences (SAIAB 050155, 050065, 039328; localities 16–18, Figure 1) do not present clear differentiation in any anatomical character (Table 1), and are regarded as representing *P. catostoma*. However, SAIAB 039264, a specimen from Lake Chiuta (Malawi, locality 19), appears not to represent *P. catostoma* for its higher pD and SPc, smaller Na, as well as measures more extreme than the 90th percentile range for LA and HL. Considering the close association of Lake Chiuta with the Rovuma system through the Lugenda River, this degree of differentiation should be confirmed by more material.

Lower Zambezi samples. Specimens from Mulela (SAIAB 055875, $n = 4$) and Lower Zambezi (SAIAB 060846, $n = 11$) were mostly similar to each other, except for HL and Na being smaller, and CPD (90th percentile of Lower Zambezi) greater in the Mulela than Lower Zambezi sample. Mulela specimens appear rather well differentiated from *P. catostoma* (PAL and Na more extreme than the range of *P. catostoma*, CPD and BD equal to an outlier, and several characters as extreme or more than the

90th percentile range: LSc, LSo, CPL, Spc). Therefore, Mulela specimens are regarded as representing the Lower Zambezi species (*P. petersi* sp. nov.). The specimen from Lake Chiuta (SAIAB 039264) is well differentiated from both Lower Zambezi and Mulela specimens by nine and 12 anatomical measures at least at the 90th percentile level, respectively.

Lake Rukwa specimen. The specimen from Lake Rukwa (SAIAB 059515, locality 11, Figure 1) is well differentiated from *P. catostoma* (as well as from any other nominal species in a huge perimeter: *P. steindachneri*, *P. stuhlmanni*, the Tana sample, *P. s. con-gicus*, *P. degeni*) in all anatomical characters listed on Table 1 but BD, CPD and CPL. The Rukwa specimen's anatomical measurements or counts are also below or above the ranges of any one of the Luapula System samples for 11 characters; that is, there are no affinities with a new species (designated in Systematics). If confirmed by more material, a new species is suggested for Lake Rukwa.

Upper Zambezi sample. Kafue system churchills (locality 13, SAIAB 042559, 18 specimens; and locality 15, SAIAB 040074, one specimen) appear closely associated with Upper Zambezi churchills (only a single difference identified by MANOVA/ANOVA analysis, in LSc, see Table 2), despite geography from which one would expect affinities with the sample from the Lower rather than the Upper Zambezi (the Kafue River joins the Zambezi River below Victoria Falls and Lake Kariba). The specimen from the Kwando River differs from the Upper Zambezi specimens, particularly so from the Guma Lagoon (Okavango) specimens. Compared with both species' anatomical character ranges, the Kwando specimen was above range for PAL and CPD, below range for LSo; compared with the Guma sample, in addition below range for LA and pD. Compared with the 90th percentile ranges of both species, the Kwando specimen was also more extreme in CPL, LSc and Na. When exclusively compared with Guma samples, additional differences at or beyond the 90th percentile ranges occurred for nA, BD, LD, whereas when compared with Upper Zambezi samples, only HL was added to the list. The Kwando churchill therefore is closer to the Upper Zambezi churchill but may, with more material, prove to be differentiated.

Okavango samples. Churchills from six locations on the Okavango or its delta (Figure 6) are clearly differentiated among each other, as confirmed by MANOVA on 13 anatomical characters (Tables 4, 5). Subsequent ANOVAs eliminated only SPc as a source for this differentiation. The Boro River population from deep down the delta appeared strongly differentiated from all other, more northern or peripheral populations by significantly different mensural or meristic characters (compared to Gadikwe fish, six characters; Guma, five characters; Popa, seven characters; Xakanixa River, seven characters; all $P < 0.01$, Table 5). Some tendency for segregation in terms of PCA coordinates was obvious in all pairwise comparisons with Guma specimens, but only the Boro population approached separation from the Guma population, despite its low sample size and only 13 characters analysed (Figure 7E). When replacing the Guma by the more northern (more distant) Popa population from the Okavango River, the separation from Boro in 13 characters was complete (Figure 7F).

The characters in Boro River fish that differed most consistently from those of the other Okavango populations were PDL, PAL, BD, nD and SLS. A PCA-based comparison of Boro fish with all other Okavango samples in pairwise comparisons

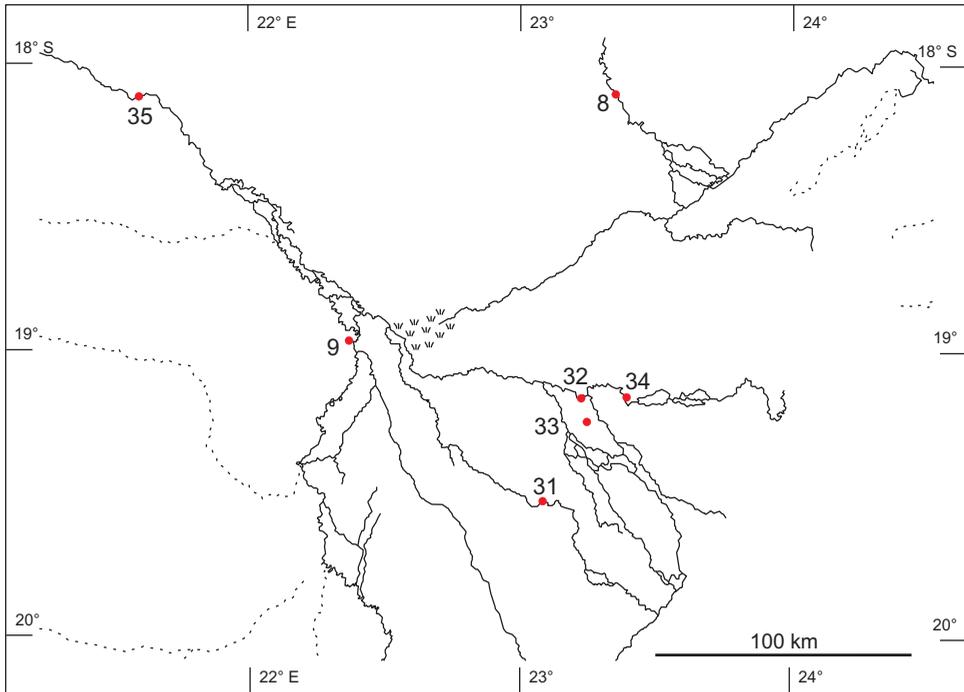


Figure 6. As Figure 1, but area of *Petrocephalus okavangensis* sp. nov. and location from where samples were taken shown at better resolution. (9) Nguma (Guma) Lagoon. (31) Boro River. (32) Gadikwe Lagoon. (33) Xakanixa River. (34) Xakanixa Channel. (35) Popa Rapids. (8) unique specimen from Kwando River.

confirmed strong differentiation and complete separation (Figure 8A–D), including the two neighbouring populations from further east (Upper Zambezi, Figure 8E) and west (Cunene River, Figure 8F). Also remarkable was the differentiation between fish from the Popa Rapids and Guma Lagoon in five characters, which we regard as infrasubspecific because of the considerable overlap in terms of PCA coordinates (Figure 7A, marked degree of overlap confirmed in three dimensions).

Whereas the Popa Rapids represent the Okavango River proper in our data set, Guma Lagoon in its southeast connects in addition to all major waterways of the delta, including the partly seasonal channel to the Upper Zambezi system (Magwegqana). In spite of much similarity with the Guma population, the Kwando specimen differs markedly from it in CPD, LSc and LSo. More specimens are needed before any conclusions can be drawn.

The differentiation presented here is based on a vastly incomplete picture of the variability within the Okavango and its delta. The six populations represent the Okavango River, the panhandle of its delta, and points on the northeastern edge of the delta, whereas central, western and southern regions are poorly represented or not at all. Furthermore, EOD and DNA samples are largely lacking. We still feel that the Boro population surpasses subspecific variation and recognize *P. magnitrunci* sp. nov. in Systematics.

Tana sample. No neighbouring samples present in our material.

Table 5. Comparison of anatomical characters in different populations of *Petrocephalus* species from the Okavango River or delta: multivariate analysis of variance (MANOVA) followed by univariate ANOVAs.

	PDL/SL	PAL/SL	LD/SL	LA/SL	pD/SL	CPL/SL	CPD/CPL	LS ₀ /HL	HL/SL	BD/SL	nD	nA	SPc
MANOVA	<10 ⁻⁴	<10 ⁻⁴	<10 ⁻⁴	0.011	0.0002	<10 ⁻⁴	<0.0001	<10 ⁻⁴	<10 ⁻⁴	<10 ⁻⁴	<10 ⁻⁴	<10 ⁻⁴	0.0102
ANOVA							0.0038						
Post tests													
Boro, Gadikwe	<0.01	<0.01	<0.01			<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Boro, Guma	<0.01	<0.01	<0.01					<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Boro, Popa	<0.01	<0.01	<0.01					<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Boro, Xakanixa													<0.01
Channel													
Boro, Xakanixa River	<0.01	<0.01	<0.01		<0.01	<0.01		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Gadikwe, Guma													
Gadikwe, Popa													
Gadikwe, Xakanixa													
Channel													
Gadikwe, Xakanixa													
River													
Guma, Popa				<0.01				<0.01	<0.01	<0.01	<0.01		<0.01
Guma, Xakanixa													
Channel													
Guma, Xakanixa			<0.01					<0.01					<0.01
River													
Popa, Xakanixa			<0.01					<0.01	<0.01	<0.01			<0.01
Channel													
Popa, Xakanixa River													
Xakanixa Ch,													
Xakanixa River			<0.01					<0.01					<0.01

P values in the body of the table not shown when *P* > 0.01. For sample sizes, see footnote of Table 1. Abbreviations of anatomical characters, see Material and methods. MANOVA $F_{1,3,148}$ to $F_{65,740} \geq 7.357$, depending on procedure; MANOVA *P* value: same for Wilks' Lambda, Roy's Greatest Root, Hotelling-Lawley Trace, and Pillai Trace tests. ANOVA $F_{5,156} = 3.128$ for *P* = 0.0102. Post tests followed the Games/Howell procedure.

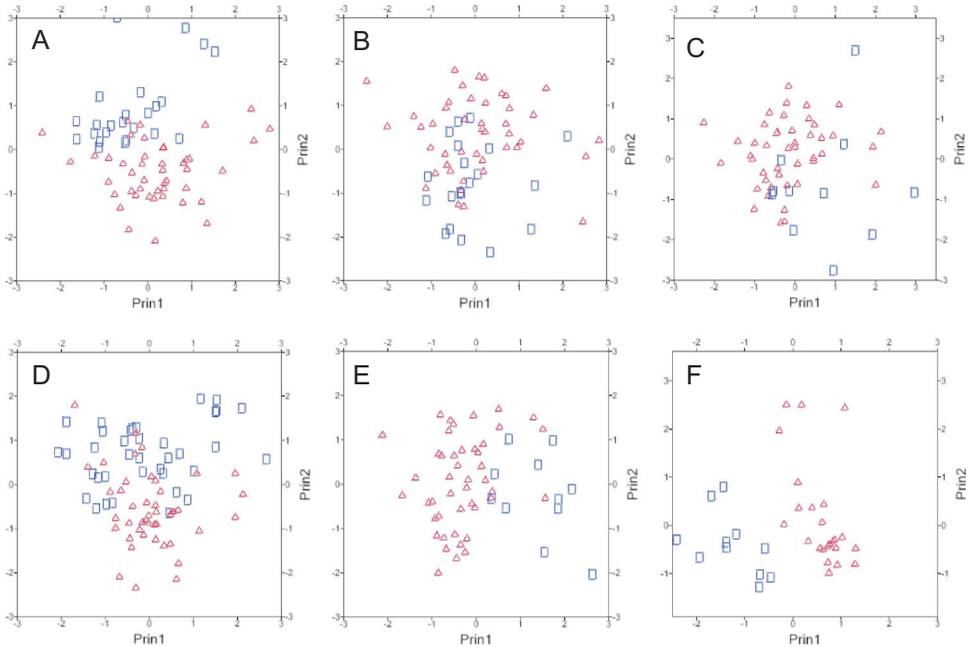


Figure 7(A–E). Principal component analysis on the 13 anatomical characters of Table 3, for six Okavango populations, focusing on the Guma Lagoon sample (*Petrocephalus okavangensis* sp. nov., red triangles). (A) Guma/Popa Falls (blue squares). (B) Guma/Gadikwe (blue squares). (C) Guma/Xakanixa Channel (blue squares). (D) Guma/Xakanixa River (blue squares). (E) Guma/Boro River (blue squares). (F) Popa Falls (red triangles)/Boro River (blue squares).

Lufubu sample. In addition to SAIAB 76758 from the Lufubu River, there were three small samples from (1) the close-by Luongo River (SAIAB 76733), (2) from a location considerably further upstream the Luapula River (SAIAB 76582), and (3) from Lake Bangweulu (SAIAB 76825 and 76859), all forming part of the Luapula drainage in the north of Zambia. Specimens from the closest location, the Luongo River, differed from the Lufubu sample in the characters LA, HL, HL/Na and BD (no overlap), and CPL (90th percentile), whereas Luapula River samples differed by BD at the 90th percentile level. Lake Bangweulu specimens were more markedly different by their LD and BD presenting no overlap, and pD, HL/Na, nD and nA differing at the 90th percentile level. The latter sample represents *P. frieli* Lavoué, 2012 (Lavoué Forthcoming 2012), whereas the former samples seem to demonstrate a rather large degree of intraspecific variation within the new species *P. longianalis* sp. nov. designated in Systematics (below)

Petrocephalus wesselsi. There is morphological differentiation among some of the eight *P. wesselsi* samples from different origins within South Africa and Swaziland (Table 1; geography, Figure 9). As demonstrated by PCA on correlations for anatomical characters of four of these samples [from Sabie River ($n = 45$), Blyde River ($n = 5$), Nwanedzi River ($n = 9$) and Mokolo River ($n = 48$)], PC1 captured 36.4% of the variation in the data set (33.6% when *P. longicapitis* sp. nov. from Namibia was included as shown

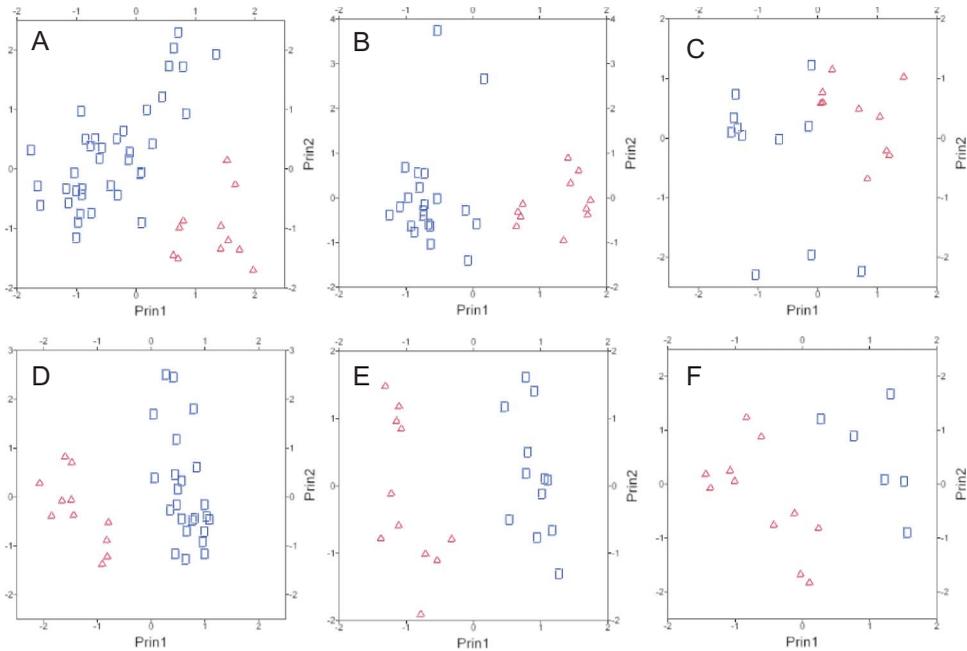


Figure 8. Principal component analysis on 17 anatomical characters (see Table 1), for six Okavango samples, focusing on that of the Boro River (*Petrocephalus magnitrunci* sp. nov., red triangles). (A) Boro/Xakanixa River (blue squares); (B) Boro/Gadikwe Lagoon (blue squares); (C) Boro/Xakanixa Channel (blue squares); (D) Boro/Popa Rapids (blue squares); (E) Boro/Upper Zambezi River (blue squares); (F) Boro/Cunene River (blue squares). The 17 characters included in the analysis were: PDL/SL, PAL/SL, LD/SL, LA/SL, pD/SL, CPL/SL, CPD/CPL, Lso/HL, HL/SL, BD/SL, nD, nA, SPc, SLS, OD/HL, LPF/HL, PPF/SL. Characters of Table 1 that were excluded: HL/Na, LSc/HL.

in Figure 10A). Positively loading on PC1 were LD, nD, nA (all “excellent”), CPD (“good”), LA, BD, HL (“fair”) and PDL (“poor”). Negatively loading on PC1 were SPc (“excellent”), LSc (“very good”) and CPL (“good”). PC1 seems to represent a gradient mainly for characteristics of the unpaired fins vs characteristics of the caudal peduncle, such as its length and SPc. PC2 captured an additional 15.7% of the variation, and characters loading positively on PC2 were PDL (“excellent”), PAL (“good”), BD (“fair”) and CPD (“poor”). Negatively loading on PC2 were LD, pD, nD, nA (all “poor”). PC2 therefore is mainly a gradient for trunk length and height vs unpaired fin development. PC3 captured a further 14.7% of the variation, however, none of the characters loading on PC3 did so better than “good” (LA, pD, BD), “fair” (CPD) or even “poor” (CPL, PDL, the latter being the only negatively loading character). The characters loading on PC1 had by far the greatest weight and separated the populations best.

The differentiation of populations seems to follow a north–south transect, with almost total separation of the two populations farthest apart (Sabie vs Mokolo River; Figure 10A). On the graph they are connected by the two populations that are also geographically intermediate (Blyde River, Nwanedzi River). Discriminant Analysis on the same data set confirms a very marked differentiation between Sabie and Mokolo,

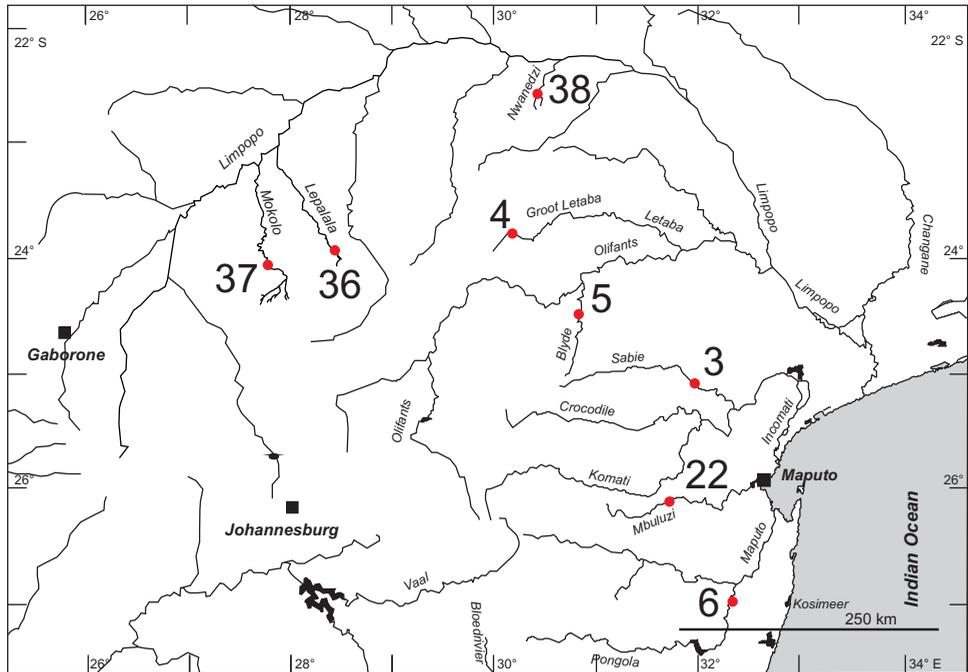


Figure 9. As Figure 1, but area of *Petrocephalus wesselsi* is shown at better resolution. (3) Incomati System: Sabie River. (4) Groot Letaba River (5) Blyde River, (36) Lepalala River, (37) Mokolo River, (38) Nwanedzi River, all Limpopo System. (6) Pongola River. (22) Swaziland: Mbuluzi River.

with Nwanedzi specimens again at an intermediate position (Figure 10B). However, compared with the differentiation from *P. longicapitis* sp. nov., the differentiation within South Africa is perhaps best regarded as indicating intraspecific variation, possibly in the form of a geographical cline).

Electric organ discharge comparisons

Allopatric churchill species

For *P. tanensis*, *P. longicapitis* sp. nov., *P. wesselsi*, *P. okavangensis* sp. nov. and *P. magnoculis* sp. nov. we confirm a degree of similarity of electric organ discharge waveforms among each other. In all species, a head-positive P1 phase is followed, in turn, by a strong head-negative N phase and a weaker positive P2 phase (Figure 11). Unsupported by references and without further comment, such triphasic EODs with head-negative main phase have been termed “atypical” for *Petrocephalus* by Lavoué et al. (2000), but Lavoué et al. (2004, 2008) show *Petrocephalus* EODs from more tropical species very similar to ours (acknowledged by Lavoué et al. 2004). It seems that the more tropical the sampling origin, the briefer the pulse. It is only by quantitative analysis of samples that a considerable degree of differentiation is revealed.

For reasons of sample size, the following statistical comparisons focus on *P. tanensis*, *P. longicapitis* sp. nov. and *P. wesselsi* ($n \geq 22$). We considered only adult

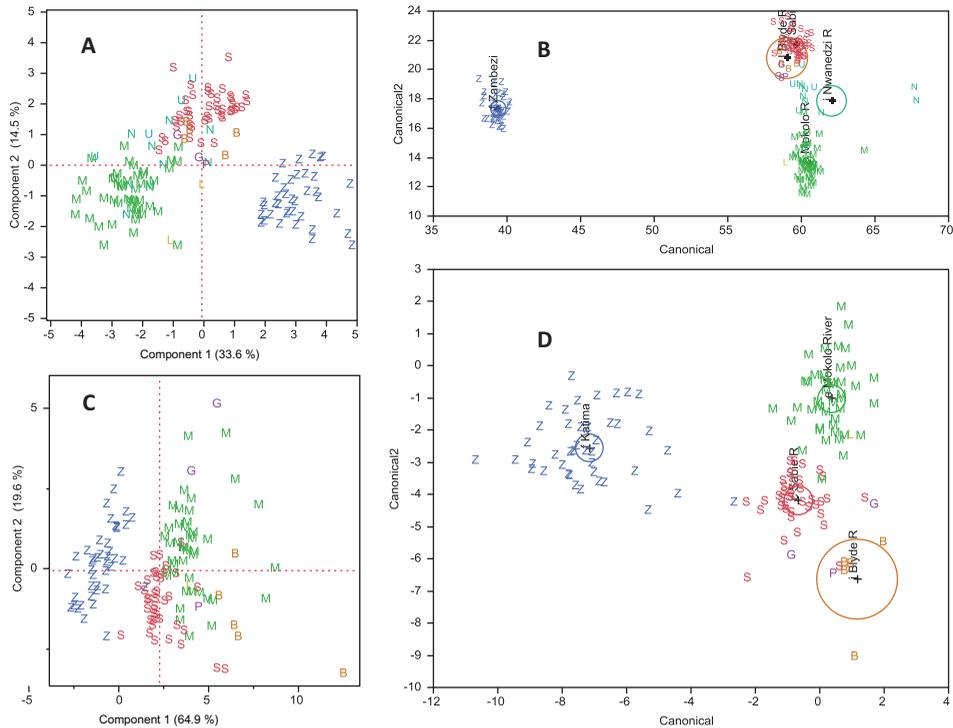


Figure 10. Differentiation within *Petrocephalus wesselsi* of different South African origins, studied using Principal Component (PCA) and Discriminant (DA) Analyses, as compared with another species (*P. longicapitis* sp. nov., Namibia, Upper Zambezi). Circles in DA, 95% confidence circles to contain true mean of group. (A) PCA and (B) DA on correlations among anatomical characters. (C) PCA and (D) DA same as (A) and (B), respectively, but for analyses on characters of Electric Organ Discharges (EODs). Green M symbols, specimens from Mokolo (Mogol) River ($n = 48$; 43, i.e. 48 for anatomy and 43 for EOD); blue-green N symbols, Nwanedzi River ($n = 9$; 0); orange B symbols, Blyde River ($n = 5$; 5); red S symbols, Sabie River ($n = 44$; 39); blue Z symbols, *P. longicapitis* sp. nov. from the Upper Zambezi (type locality Katima Mulilo; $n = 38$; 42); bluer shade of blue-green coloured U symbols, specimens from Mbuluzi River, Swaziland ($n = 4$; 0). Excluded from DA but shown on DA graphs: lilac G symbols, Groot Letaba River ($n = 2$; 2); sand-coloured L symbols, Lepalala River ($n = 2$; 1); redder shade of lilac P symbol, Pongola River ($n = 1$; 1). The 15 anatomical characters included in the anatomical analyses were: PDL/SL, PAL/SL, LD/SL, LA/SL, pD/SL, CPL/SL, CPD/CPL, LSc/HL, LSo/HL, HL/Na, HL/SL, BD/SL, nD, nA, SPc. The characters used in the EOD analyses were: Namp, P2amp, P1dur, Ndur, P2dur, P1Nsep, P1P2sep, NP2sep, P1area, Narea, P2 area.

fish (that is, $SL \geq 5.2$ cm, or 40% of the maximum species size; see Kramer 1997 for discussion). Except for P1dur, *P. tanensis* EODs differed between the sexes for all characters studied [$P \leq 0.0223$, analysis of covariance (ANCOVA); Table 6]. An ANCOVA with sex as a factor and SL as a covariate was chosen to control for any dependencies of EOD characters on size (SL). Such dependencies were found in all samples of sufficient size at least for P2amp (Table 6, underlined; for details, see Appendix 2).

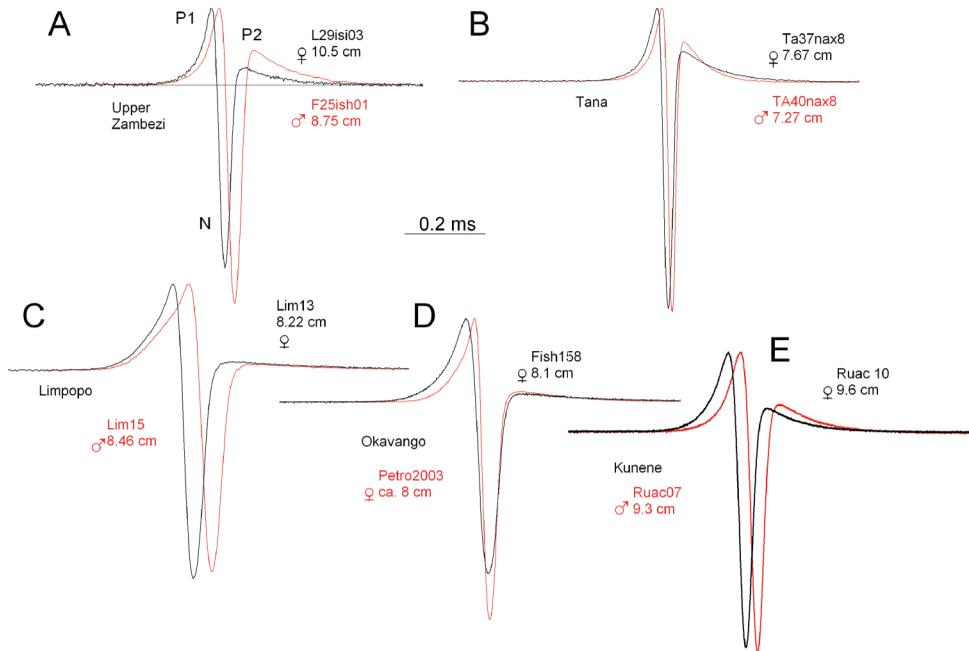


Figure 11. Oscilloscope traces of Electric Organ Discharges (EODs) of members of southern and eastern African *Petrocephalus* species. (A) *P. longicapitis* sp. nov. (B) *P. tanensis*, (C) *P. wesselsi*, (D) *P. okavangensis* sp. nov. Ordinate, voltage, with head-positivity upwards from baseline: shown in (A). Abscissa, time (see time bar); same scale everywhere. EOD amplitude scaled to first head-positive phase P1 = 1; P2, second head-positive phase; N, head-negative phase. EODs superimposed with temporal offset to better show differences among individuals: differences between the sexes statistically significant in (A) and (B).

The numerous differences between the sexes observed in *P. tanensis* EODs were in contrast with *P. longicapitis* sp. nov. and *P. wesselsi* EODs with their sex difference in the P2 phase, affecting characters such as P2amp and P2area (confirming Kramer and Van der Bank 2000 for both species). We also investigated whether EOD characters depended on origin and chose MANCOVA to control for any dependencies on SL (origin as a factor, SL as a covariate). Because of the above differences between the sexes we compared males and females of different origins separately.

In males, an overall MANCOVA P value of $<10^{-4}$ rejected the null hypothesis of no difference between EODs of different origins for nine EOD characters analysed together (Table 7). For all of these, subsequent univariate ANCOVAs confirmed this result by significant P values (≤ 0.0012). Post-hoc tests showed that *P. tanensis* male EODs differed from *P. wesselsi* male EODs in all nine characters, whereas the number of significant differences was six for the comparison of *P. tanensis* with *P. longicapitis* sp. nov. EODs. No surprise were the many significant differences between *P. longicapitis* sp. nov. and *P. wesselsi* male EODs.

For the four female EOD characters without significant interaction term (see below) the overall MANCOVA P value of $<10^{-4}$ showed that also female EODs depended on origin, a result that was confirmed by univariate ANCOVAs for all four characters (Table 7). Post-hoc tests showed that *P. tanensis* differed from *P. wesselsi*

Table 6. Electric organ discharges (EOD) waveform comparisons in allopatric *Petrocephalus* species.

	Namp (V)	P2amp (V)	P1dur (μs)	Ndur (μs)	P2dur (μs)	P1Nsep (μs)	PIP2sep (μs)	NP2sep (μs)	P1area (V×μs)	Narea (V×μs)	P2area (V×μs)	SL (cm)
<i>P. tanensis</i>												
Mean (n = 22)*	-3.132	0.442	126.5	40	262.83	28.8	70.3	41.49	40.19	73.21	41.34	8.31
SE	0.063	0.033	3.7	2	27.1	0.67	3.6	3	1.1	4.15	1.64	0.23
mean (F,15)	-3.238	<u>0.399</u>	<u>129.65</u>	43	309.3	29.83	76.1	46.29	41.79	80.55	44.15	8.4
SE	0.072	<u>0.042</u>	<u>4.98</u>	2.45	33.25	0.76	4.46	3.79	1.41	4.96	1.78	0.27
mean (M,7)	-2.904	0.534	119.8	33.36	163.26	26.61	57.79	31.2	36.77	57.47	35.33	8.21
SE	0.07	0.033	3.6	1.1	10.93	0.92	2.1	1.23	0.97	2.4	2.22	0.46
ANCOVA P(F,M)	0.0123	0.0223	0.0129	0.0068	0.0176	0.0085	0.0093	0.0114	0.0057	0.0079	0.0079	
F ratio	7.6530	6.1910	7.5290	9.2130	6.76	8.6180	8.3870	7.8370	9.7	8.8260	8.8260	
<i>P. longicapitis</i> sp.n.												
Mean (n = 43)	-2.766	0.419	131.5	49.14	206.6	36.83	82.85	46	46	80.1	34.5	7.04
SE	0.038	0.014	2.45	0.95	11.48	0.71	1.61	1	0.82	2	1.25	0.3
mean (F,17)	-2.733	<u>0.382</u>	<u>129.87</u>	47.49	200.58	35.56	80.46	44.91	43.93	76.38	<u>31.59</u>	7.86
SE	0.054	<u>0.022</u>	<u>3.14</u>	1.24	16.5	1.15	2.22	1.46	0.98	2.57	<u>2.27</u>	0.412
mean (M,15)	-2.693	<u>0.466</u>	<u>123.23</u>	48.8	181.82	36.38	81.81	45.43	44.25	79.07	<u>36.79</u>	8.02
SE	0.06	<u>0.016</u>	<u>3.27</u>	1.79	8.97	1.17	3	1.89	1.01	3.5	<u>1.89</u>	0.16
mean (J,11)	-2.91	0.412	145.34	52.21	249.74	39.39	87.94	48.53	51.61	87.34	35.96	4.42
SE	0.09	0.028	4.99	1.87	32.59	1.19	3.06	2.04	1.59	4.56	1.93	0.2
ANCOVA P(F,M)	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0462	
F ratio	19.5120	19.5120	19.5120	19.5120	19.5120	19.5120	19.5120	19.5120	19.5120	19.5120	4.3370	
<i>P. wesselsi</i> : Sabie R												
Mean (n = 39)	-2.48	0.132	174.75	66.71	353.21	40.98	121.62	80.65	58.27	90.33	24.12	7.3
SE	0.043	0.0041	1.62	1.65	6.75	0.827	3.22	2.595	0.8595	1.275	0.8	0.23
mean (F,31)	-2.514	<u>0.135</u>	<u>173.6</u>	<u>65.54</u>	<u>357.6</u>	<u>40.75</u>	<u>119.65</u>	<u>78.91</u>	<u>57.44</u>	<u>90.28</u>	<u>24.85</u>	7.0
SE	<u>0.048</u>	<u>0.004</u>	<u>1.56</u>	<u>1.52</u>	<u>6.44</u>	<u>0.864</u>	<u>2.6</u>	<u>2.03</u>	<u>0.772</u>	<u>1.31</u>	<u>0.8</u>	0.22
mean (M,8)	-2.349	0.1205	179.32	71.28	336.2	41.89	129.26	87.4	61.46	90.52	21.27	8.4
SE	<u>0.09</u>	<u>0.0096</u>	<u>5.01</u>	<u>5.45</u>	<u>21.57</u>	<u>2.36</u>	<u>12.26</u>	<u>10.08</u>	<u>2.8</u>	<u>3.815</u>	<u>2.25</u>	0.56
<i>P. wesselsi</i> : Mokolo R												
Mean (n = 43)	-2.56	0.162	178.96	84.76	475.78	48.76	148.54	99.77	61.78	115.54	37.61	5.4
SE	0.046	0.0057	2.36	2.1	10.89	1.25	3.43	2.41	0.95	2.02	1.5	0.09

(Continued)

Table 6. (Continued).

	mean (F,1,30)	-2.631	0.174	178.1	85.2	497.7	49.42	150.48	101.06	61.72	119.15	41.06	5.9
	SE	0.054	0.006	2.8	2.9	12.24	1.73	4.67	3.2	1.25	2.41	1.55	0.09
	mean (M,13)	-2.396	0.1343	180.93	83.74	425.19	47.25	144.06	96.82	61.91	107.21	29.66	6.0
	SE	0.069	0.009	4.48	1.925	15.17	1.07	3.51	2.98	1.31	2.57	2.2	0.09
			0.0151			0.0038	0.0494					0.0015	
	F ratio	6.447		9.468		4.109						11.64	
<i>P. wesselii</i> :	Lepalala R	-2.48	0.114	173.7	81.12	456.28	42.47	152.44	110	80.6	105.36	27.34	5.26
<i>P. wesselii</i> :	Blyde R	-2.143	0.08	220.86	108.94	447.36	66.86	194.84	128.02	82.96	115.72	18.36	8.7
	SE	0.035	0.0113	6.78	15.16	118.25	8.61	25.72	17.77	4.46	4.36	4.03	0.28
	mean (F,3)	-2.231	0.093	210.83	93.73	566.63	57.93	170.23	112.33	75.93	110.9	23.73	8.5
	SE	0.116	0.01	3.28	5.17	169.7	4.2	7.44	8.65	1.19	1.81	4.01	0.24
	mean (M,2)	-2.011	0.059	235.9	131.75	268.45	80.25	231.75	151.55	93.5	122.95	10.3	9.1
	Min	-1.69	0.0437	228.8	95.0	259.4	60.5	167.1	106.7	90.4	113.3	7.8	8.5
Max		-2.331	0.074	243.0	168.5	277.5	100.0	296.4	196.4	96.6	132.6	12.8	9.7
<i>P. wesselii</i> :	Groot	-3.545	0.208	207.05	73.8	651.6	50.15	129.6	79.45	82.45	141.65	48.5	5.7
Letaba R		-3.626	0.201	214.1	76.2	865.0	47.8	133.2	85.4	84.3	148.6	54.9	5.3
	(M,1)	-3.464	0.214	200.0	71.4	438.1	52.5	125.9	73.5	80.6	134.7	42.1	6.1
<i>P. wesselii</i> :	Pongola R	-2.414	0.114	210	78.8	319.7	50.4	136.8	86.4	76.5	105.6	19.5	7.9
<i>P. okavangensis</i> sp.n.		-2.317	0.117	181.83	73.9	318.4	47.1	134.05	86.95	62.67	93.04	19.61	ca.8
<i>P. magnoculis</i> sp.n.		-2.654	0.3	158	59.65	225.85	44.93	102.6	57.63	58.1	88.35	30.61	9.94
	SE	0.082	0.034	2.83	3.3	26.42	0.93	5.1	4.32	1.17	4.91	1.45	0.34
	mean (F, 3)	-2.615	0.283	158.8	61.1	227.7	45.7	104.6	59	59.1	89.3	29.4	10.1
	(M, 1)	-2.77	0.349	155.7	55.4	220.4	42.7	96.3	53.7	55	85.4	34.3	9.3

Means, standard errors and sample sizes for M = males, F = females, and J = juveniles.

Sex determined from presence (M, male) or absence (F, female) of a kink in the anal fin base; J = juveniles are specimens with SL < 5.2 cm.

*One additional female excluded for atypical EOD waveform. Boxes: difference between sexes significant at $P < 0.05$ (ANCOVA, with associated F ratio). Single underline, least-squares linear regression of waveform variable with SL significant at $P < 0.05$; double underline, $P < 0.01$. Abbreviations EOD variables, see Material and methods.

Table 7. MANCOVA study on electric organ discharge (EOD) characteristics in allopatric *Petrocephalus* species from southern and eastern Africa, testing the hypothesis of no difference (with geographical origin as the independent variable, and standard length, SL, as a covariate).

	Namp (V)	P1dur (μ s)	Ndur (μ s)	P1Nsep (μ s)	Males					Females										
					PIP2sep (μ s)	NP2sep (μ s)	P1area (V $\times\mu$ s)	Narea (V $\times\mu$ s)	P2area (V $\times\mu$ s)	P2dur (μ s)	PIP2sep (μ s)	P1area (V $\times\mu$ s)	Narea (V $\times\mu$ s)							
MANCOVA	<i>P</i>																			
ANCOVA	<i>P</i>	0.0012	<10 ⁻⁴	<10 ⁻⁴	0.004	<10 ⁻⁴	<10 ⁻⁴	<10 ⁻⁴	<10 ⁻⁴	<10 ⁻⁴	<10 ⁻⁴	<10 ⁻⁴	<10 ⁻⁴	<10 ⁻⁴	<10 ⁻⁴	<10 ⁻⁴	<10 ⁻⁴	<10 ⁻⁴	<10 ⁻⁴	<10 ⁻⁴
	<i>F</i>	8.54	59.687	18.282	10.421	19.584	24.13	36.552	19.599	19.133	11.839	44.718	39.93	7.138						
Post tests	Tana, UZ			<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.05									
	Tana, SA	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
	UZ, SA	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01

Tana, *P. tamensis* ♀♀, ♂♂ (*n* = 15, 7); UZ, *P. longicapitis* sp. nov. ♀♀, ♂♂ (*n* = 17, 15); SA, *P. wesselii* ♀♀, ♂♂ (*n* = 23, 12) of >5.2 cm SL (Sabie River sample). MANCOVA *P*: same for Wilks' Lambda, Roy's Greatest Root, Hotelling-Lawley Trace, Pillai Trace. Post tests: Games/Howell. Abbreviations of EOD parameters, see Material and methods.

female EODs in two out of four characters ($P < 0.01$; Table 7), and in one from *P. longicapitis* sp. nov. EODs, whereas all four characters were significantly different between *P. longicapitis* sp. nov. and *P. wesselsi* females ($P < 0.01$).

EOD characters such as P2dur and P2amp in males, and all characters except four in females, had to be excluded from MANCOVA and ANCOVA studies because of significant ($P < 0.05$) interaction of the factor origin with the covariate SL (which indicates non-parallel regression lines). For example, whereas in *P. longicapitis* sp. nov. and *P. wesselsi* P2amp fell with SL in both sexes, in *P. tanensis* females the opposite relationship held true (Figure 12; males, not significant). Therefore, in these EOD characters we looked for differences between regression line slopes rather than Y-intercepts (as done by (M)ANCOVA).

In male EODs, the simultaneous comparison of the three species' regression line slopes for P2amp and P2dur both yielded significant ($P < 0.05$) differences between species (Table 8). When samples of different origin were compared pairwise, regression line slopes differed significantly between *P. tanensis* and *P. longicapitis* sp. nov. males for P2amp, and between *P. tanensis* and *P. wesselsi* males for P2dur. Between *P. longicapitis* sp. nov. and *P. wesselsi* males both EOD characters differed significantly.

Also in female EODs, significant differences between samples emerged for each EOD character studied in this way. *Petrocephalus tanensis* differed from *P. longicapitis* sp. nov. female EODs in P2 phase properties (P2 amp and P2 area), but P1dur and NP2sep were also involved. Except for P1Nsep, *P. tanensis* female EODs differed from those of *P. wesselsi* in all characters of Table 8.

Small sample sizes excluded *P. okavangensis* sp. nov. ($n = 2$) and the Cunene churchill ($n = 4$) from the above statistical comparisons. From the field recordings made it is, however, clear that the EODs of *P. okavangensis* sp. nov. that lacked a clear P2 phase contrast sharply with those of its nearest neighbours, *P. longicapitis* sp. nov. in the east and the Cunene churchill in the west, both of which displayed well-developed P2 phases. The EOD of *P. okavangensis* sp. nov. was more similar to that of the distant South African *P. wesselsi*, despite the marked anatomical differences between the two, and the absence of any contact zones.

The similarity between the EODs of *P. longicapitis* sp. nov. and the Cunene churchill seemed limited to both fish's well-developed P2 phases, and the observation that the single Cunene male's P2 phase was also stronger than that of the opposite sex ($n = 3$). The Cunene churchill's EOD pulse was clearly of longer duration (a mean 448 μ s) than that of *P. longicapitis* sp. nov. (379 μ s, both based on females; males slightly shorter in both cases). This difference follows from a longer P1dur and greater P1area, longer Ndur, P1Nsep, P1P2sep and NP2sep for the Cunene churchill (Table 6).

The southern churchill, P. wesselsi

The *P. wesselsi* specimens included in a PCA of EOD characters showed a clear tendency for differentiation. Especially the Sabie and the Mokolo River samples were quite well differentiated along PC1 and PC2. However, with *P. longicapitis* sp. nov.

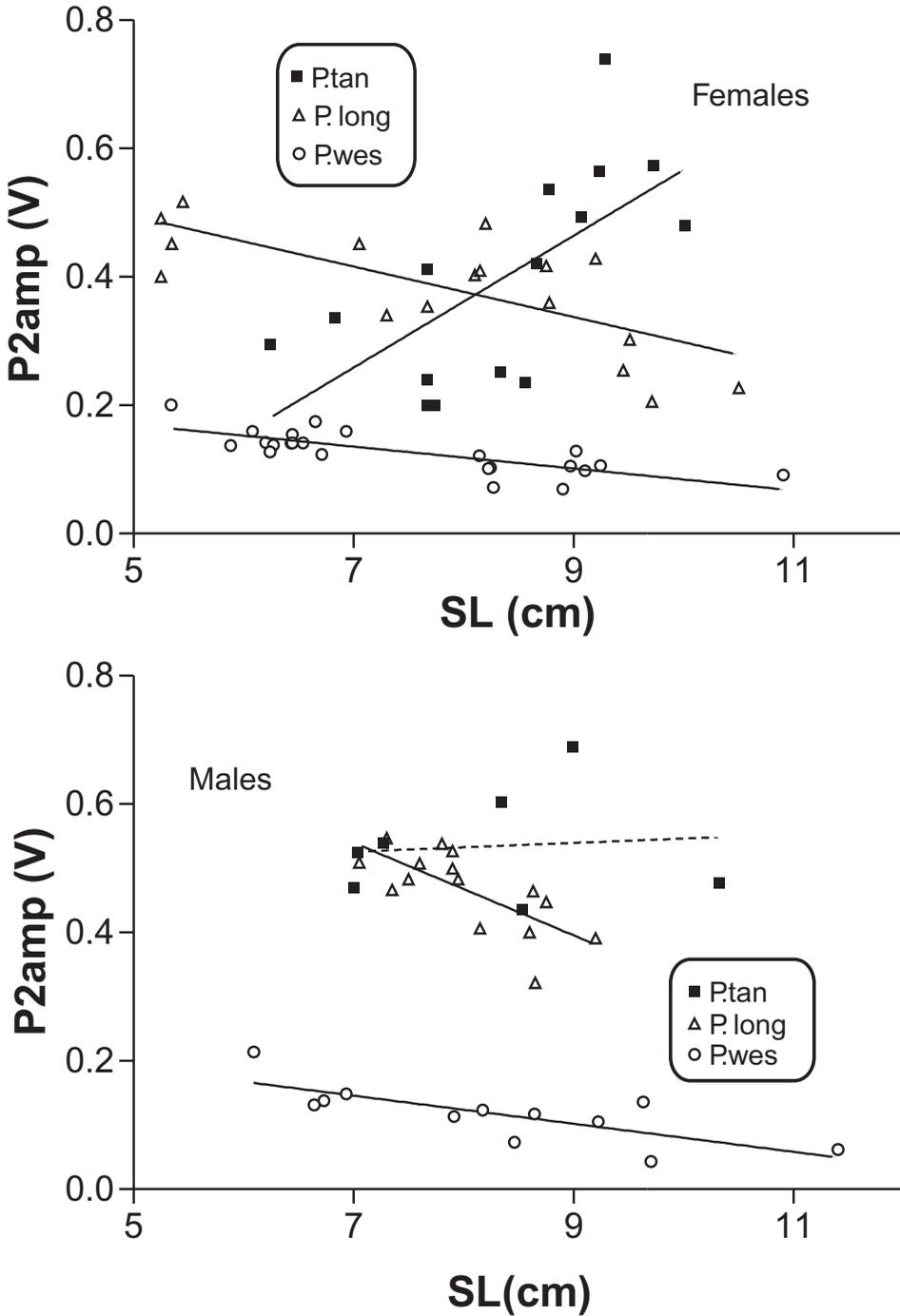


Figure 12. Least-squares regression of the EOD character P2amp with SL in southern and eastern African *Petrocephalus* species. Top, females, bottom, males. In *P. longicapitis* sp. nov. and *P. wesselsi* regression line slopes fall with SL and are about equal in contrast to their y-intercepts, which differ significantly. *Petrocephalus tanensis* differs from the other two species in showing no falling slope or even a steep rise (females). Stippled line, regression not significant ($P > 0.05$).

Table 8. Least-squares regression of electric organ discharge (EOD) characteristics with standard length, SL, in females (left) and males (right): test of the hypothesis of no difference among allopatric *Petrocephalus* species from different southern and eastern African origins. *P* values and *F* ratios are given in the body of the Table, as indicated.

	<i>P</i>	<i>F</i>	Namp (V)	P2amp (V)	P1dur (μs)	Ndur (μs)	P1Nsep (μs)	NP2sep (μs)	P2area (V × μs)	P2amp (V)	P2dur (μs)	
			Females						Males			
3 Slopes≠?	0.001	< 0.0001	0.04432	0.008	0.0158	0.048	0.00187	0.04049	0.0174			
	8.367	20.669	3.323	5.344	4.523	3.233	7.16	3.604	4.703			
<i>P</i> value	Tana,UZ	< 0.0001	0.04554	0.2571	0.55	0.0478	0.00317	0.035	0.645			
	Tana,SA	< 0.0001	0.0228	0.0233	0.131	0.0362	0.0003	0.24	0.0341			
	UZ, SA	0.001	0.02433	0.3215	0.0139	0.2277	0.665	0.013	0.026			

Tana, *P. tanensis* ♂♂ (*n* = 7); UZ, *P. longicapitis* sp. nov. ♂♂ (*n* = 15); SA, *P. wesselsi* ♂♂ (*n* = 12) all of > 5.2 cm SL (Sabie population).

Pairwise regression comparisons, *F*_{*n,d*}, *n* = 1 and *d* = 15 to 23 in males, *n* = 1 and *d* = 28 to 36 in females. Abbreviations of EOD characteristics, see Material and methods.

Comparison of three regression lines: *F*_{*n,d*}, *n* = 2 and *d* = 28 in males, *n* = 2 and *d* = 49 in females.

from the Upper Zambezi included the three South African samples appeared to form one group that was well differentiated from that species (Figure 10C).

PC1 alone captured 64.9% of the variation in the data set, showing the high degree of correlation of interdependent EOD characters. All EOD characters except P2area were loading on PC1, and their significance was “excellent” except for Namp (“fair”). The sign of all these component loadings was positive but for P2amp, which was negative (and “excellent”). PC1 therefore represents a gradient for all “early” characteristics of a churchill EOD to be high versus its latter sections, especially the terminal P2 phase, to be small (or vice versa). Positively loading on PC2, that captured an additional 19.6% of the variation in the data set, were P2area (“excellent”), Narea (“fair”), and P2dur and P2amp (“poor”). Negatively loading was Namp (“excellent”). PC2 therefore appears to represent mainly a gradient of P2 phase development or importance versus Namp, that is, PC2 mainly represents the latter part of an EOD.

Discriminant analysis confirmed rather marked differentiation within South African samples (again very clear between Mokolo and Sabie; Figure 10D; the positions only of samples with $n \leq 2$ from three further origins added). However, the inclusion of *P. longicapitis* sp. nov. from Namibia reveals that the differentiation among the South African samples may perhaps represent no more than intraspecific geographic variation.

Genetic studies

DNA sequencing of southern African electric fishes does not involve all the species mentioned, because it was not possible to recover intact DNA from some species. For four species the phylogenetic relationships could be reconstructed. Neighbour joining, maximum parsimony and maximum likelihood produced identical trees, of which the maximum likelihood tree is shown in Figure 13. Two sister clades of *Petrocephalus* are apparent: *P. catostoma* forms a sister species to *P. wesselsi* (Mokolo form) and *P. longicapitis* sp. nov. to *P. magnoculis* sp. nov. The genetic distances between clades ranged between 0.8% and 4.2% (p-distance; Table 9), supporting the findings from morphology and electrophysiology, that these taxa are distinct species.

Systematics

For *Material examined*, see Material and methods section.

Genus *Petrocephalus* Marcusen, 1854

*Diagnosis*¹

(Translated from Taverne 1969, reproduced with permission granted from the author.)

“Fairly short body; eye medium to large; snout much shorter than the postorbital portion of the skull and rounded; mouth underslung and located below the eye; nostrils slightly closer to the eye than to the end of the snout; caudal peduncle 2.5 to 3 times as long as high; 19 to 33 rays on the dorsal fin; two initial unbranched spines on the dorsal fin instead of one like the other Mormyridae; 25–39 rays on the anal fin; 9 or rarely 10 rays on the pectoral fin; 6 rays on the ventral fin; 39–44 rays on the caudal fin;

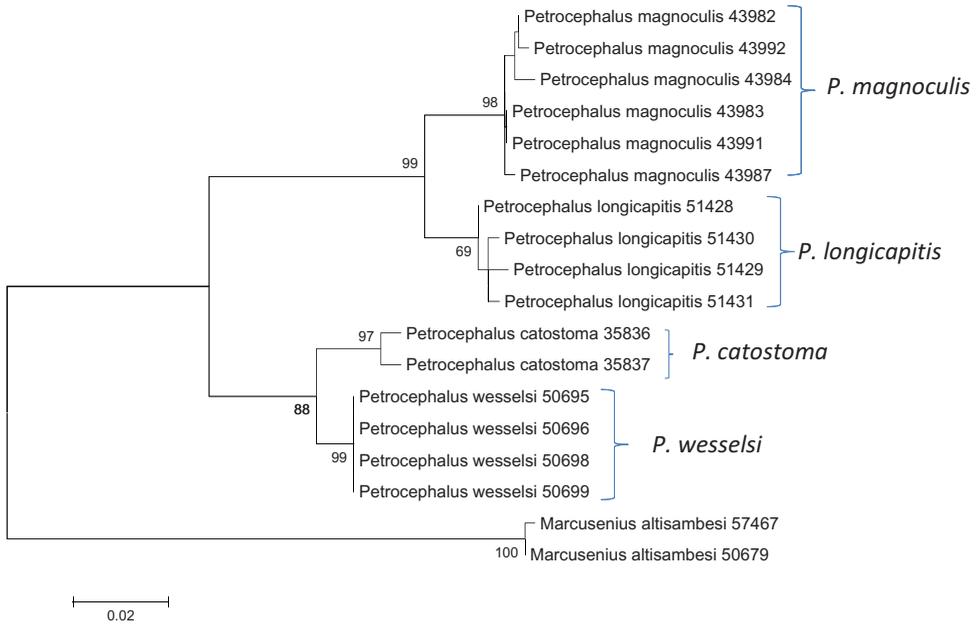


Figure 13. Molecular phylogenetic analysis for *Petrocephalus catostoma* and three allopatric *Petrocephalus* species by Maximum Likelihood method. The evolutionary history was inferred by using the Maximum Likelihood method based on the Tamura–Nei model (Tamura and Nei 1993). The tree with the highest log likelihood (−1811.6564) is shown. The percentage of trees in which the associated taxa clustered together is shown next to the branches. Initial tree(s) for the heuristic search were obtained automatically as follows. When the number of common sites was <100 or less than one-quarter of the total number of sites, the maximum parsimony method was used; otherwise BIONJ method with the maximum composite likelihood distance matrix was used. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 23 nucleotide sequences. Codon positions included were 1st+2nd+3rd+Noncoding. There was a total of 477 positions in the final dataset. Evolutionary analyses were conducted in MEGA5 (Tamura et al. 2011).

pelvic fins a bit closer to the pectorals than to the anal fin; scales more or less round and 90–105% as wide as they are long; 35–50 scales in lateral series; 6–15/11–15 scales in a transverse line on the body; 7–14/8–16 scales in a transverse line between the dorsal and anal fins; 8–16 scales around the caudal peduncle; jaws have 7–24/15–36 bicuspid teeth (10–26/16–36 according to Boulenger); the height of the skull (from the basi-occipital bone to the top of the supra-occipital bone) measures 85–95% of the width of the skull (from one ex-occipital to the other); a lateral ethmoid is present; massive median ethmoid, vertically orientated, more or less bulging dorsally and measuring about 50% of the length of the frontal bone; 6 circumorbital bones with the dermosphenotic attached to the sphenotic, and antorbital and the first infraorbital separately ossified; massive dentition with short and wide branches, no rudimentary third branch and with the dental portion of the sensory mandibular canal very enlarged and open all along its course; uneven orbitosphenoid with 2 lateral branches that join to form a single septum which rests on the parasphenoid; olfactory nerve (I) passes through

Table 9. Estimates of evolutionary divergence between sequences.

	[1]	[2]	[3]	[4]	[5]	[6]	[7]	[8]	[9]	[10]	[11]	[12]	[13]	[14]	[15]	[16]	[17]	[18]
[1] M.a._57467		0.002	0.195	0.193	0.201	0.193	0.193	0.193	0.190	0.193	0.189	0.192	0.179	0.174	0.171	0.171	0.171	0.171
[2] M.a._50679			0.193	0.190	0.198	0.190	0.190	0.190	0.187	0.190	0.186	0.189	0.176	0.171	0.169	0.169	0.169	0.169
[3] P.m._43982				0.002	0.004	0.004	0.002	0.002	0.030	0.037	0.038	0.036	0.096	0.096	0.087	0.087	0.087	0.087
[4] P.m._43983					0.006	0.002	0.000	0.004	0.028	0.034	0.035	0.034	0.096	0.096	0.087	0.087	0.087	0.087
[5] P.m._43984						0.008	0.006	0.006	0.034	0.041	0.042	0.041	0.096	0.096	0.087	0.087	0.087	0.087
[6] P.m._43987							0.002	0.006	0.028	0.034	0.035	0.034	0.096	0.096	0.087	0.087	0.087	0.087
[7] P.m._43991								0.004	0.028	0.034	0.035	0.034	0.096	0.096	0.087	0.087	0.087	0.087
[8] P.m._43992									0.028	0.034	0.035	0.034	0.094	0.094	0.084	0.084	0.084	0.084
[9] P.l._51428										0.006	0.005	0.005	0.087	0.087	0.080	0.080	0.080	0.080
[10] P.l._51429											0.007	0.007	0.089	0.089	0.082	0.082	0.082	0.082
[11] P.l._51430												0.002	0.085	0.080	0.082	0.082	0.082	0.082
[12] P.l._51431													0.085	0.079	0.082	0.082	0.082	0.082
[13] P.c._35836														0.008	0.026	0.026	0.026	0.026
[14] P.c._35837															0.026	0.026	0.026	0.026
[15] P.w._50695																0.000	0.000	0.000
[16] P.w._50696																	0.000	0.000
[17] P.w._50698																		0.000

The number of base substitutions per site from between sequences are shown. Analyses were conducted using the Jukes–Cantor model (Jukes and Cantor 1969). The analysis involved 18 nucleotide sequences. Codon positions included were 1st+2nd+3rd+ Noncoding. All ambiguous positions were removed for each sequence pair. There was a total of 477 positions in the final dataset. Evolutionary analyses were conducted using MEGA5 (Tamura et al. 2011). IPBM collection sample codes: [1] #Marcusenius_altisambesi_57467; [2] #Marcusenius_altisambesi_50679; [3] #Petrocephalus_magnoculis_43982; [4] #Petrocephalus_magnoculis_43983; [5] #Petrocephalus_magnoculis_43984; [6] #Petrocephalus_magnoculis_43987; [7] #Petrocephalus_magnoculis_43991; [8] #Petrocephalus_magnoculis_43992; [9] #Petrocephalus_longicapitis_51428; [10] #Petrocephalus_longicapitis_51429; [11] #Petrocephalus_longicapitis_51430; [12] #Petrocephalus_longicapitis_51431; [13] #Petrocephalus_catostoma_35836; [14] #Petrocephalus_catostoma_35837; [15] #Petrocephalus_wesselsi_50695; [16] #Petrocephalus_wesselsi_50696; [17] #Petrocephalus_wesselsi_50698; [18] #Petrocephalus_wesselsi_50699.

the orbitosphenoid, bulging into a nerve centre below the lateral ethmoid and passing into the olfactory sac between the median and lateral ethmoids; a single foramen for the left and right optical nerves (II) between the orbito-sphenoid and the basi-sphenoid bones; a single foramen between the pleurosphenoids and the pro-otics for the rami palatini of the left and right facial nerves (VII); basi-pterygoid process of the parasphenoid present; anterior portion of the parasphenoid is very high and only interlaces by means of 2 posterior extensions (instead of four) in the basi-occipital; the length of the toothed area of the parasphenoid measures 25–44% of the total length of this bone; the basi-occipital bone has a pair of tapering lateral processes touching the auditory diverticula of the swim bladder; very wide ectopterygoids which articulate with the lateral wings of the vomer; horizontal ventral median extension of the basi-occipital is longer than the lateral extensions; the angular does not extend into a thick point beyond the square; supra-occipital crest massive, already beginning to develop on the parietals and largely bypassing the posterior level of the skull; there is a basi-sphenoid; the crests of the epiotics extend very clearly on to the parietals; the frontal portion of the supra-orbital sensory canal opens into a large groove towards the front, only spanned by a bony bridge (vestigial remains of the dorsal vault of the canal) and foramen linking the supra-orbital canal to the interior of the skull, visible on the exterior plane of the frontal bone; a small vomer with lateral wings which are not ventrally fused and which are linked in the ectopterygoids; 2 toothed supra-basihyalic plates both bearing a few well developed conical teeth, the first of these plates does not extend towards the front beyond the level of the basihyal; indeterminate element (hypohyal bone?) of the hyoid skeleton; eight branchiostegal rays on each side of the skull; foramen of the scapular girdle pierced through in the hypercoracoid or between the hypercoracoid and hypocoracoid bones; the anterior end of the hypocoracoid almost reaches the anterior extremity of the cleithrum; 37–43 vertebrae (42–44 according to Boulenger); 13–17 supraneurals; 8 or 9 pairs of dorsal ribs; 7–9 pairs of ventral ribs directly attached to the vertebral centre; 2–5 pairs of ventral ribs resting against the hemapophyses; each pair has well-developed Gemmingerian bones and a central fusing plate between the two bones of each pair; caudal skeleton with four hypural bones.

¹⁾ The figures pertaining to the proportions of the body and the number of rays and scales are taken from Boulenger's works." (End of quotation from Taverne 1969.)

[Note: Taverne's 1969 diagnosis of the genus *Petrocephalus* is based on one specimen each of 10 species: *Petrocephalus bane* (Lacépède 1803), *P. balayi* Sauvage 1883 (spelled *ballayi* by Taverne), *P. grandoculis* Boulenger 1920, *P. microphthalmus* Pellegrin 1908, *P. sauvagii* (Boulenger 1887) (spelled *sauvagei* by Taverne), *P. schoutedeni* Poll 1954, *P. christyi* Boulenger 1920, *P. haullevillii* Boulenger 1912 (spelled *haullevillei* by Taverne), *P. simus* Sauvage 1879, *P. bovei* (Valenciennes 1847) (authority given as "Cuv. et Val." without year by Taverne). This diagnosis includes the most salient aspects of the diagnosis given by Orts (1967). Whereas Taverne's main focus was on skeletal features, Orts studied the anatomy of the soft tissues.]

Additional elements to a Diagnosis by present authors. Waveform of EOD with three phases (strong P1, very strong N, weak P2 phase), short duration (250–1200 μ s at "2% of P1 amplitude criterion" and 25°C). Strength of P2 phase dependent on body size. Diurnal activity in aquarium more prominent than in other mormyrid genera.

Type species: *Petrocephalus bane* (Lacépède, 1803)

Included species (valid unless otherwise stated)

- affinis*, *Petrocephalus* Sauvage, 1879. Current status: synonym of *Stomatorhinus walkeri* (Günther, 1867).
- amblystoma*, *Mormyrus* Günther, 1896. Current status: synonym of *Petrocephalus balayi* Sauvage, 1883.
- ansorgii*, *Petrocephalus* Boulenger, 1903.
- anterodorsalis*, *Petrocephalus* David and Poll, 1937. Current status: synonym of *Pollimyrus tumifrons* (Boulenger, 1902).
- balayi*, *Petrocephalus* Sauvage, 1883.
- ballayi*, *Petrocephalus* Bertin 1940. Current status: synonym of *Petrocephalus balayi* Sauvage, 1883.
- balteatus*, *Petrocephalus* Rochebrune, 1885. “Loanda, Gabon; Bathurst, Gambia, western Africa Museo Bouvieri, whereabouts unknown” (Eschmeyer 2011).
- bane*, *Mormyrus* Lacépède, 1803. Current status: valid as *Petrocephalus bane* (Lacépède, 1803).
- binotatus*, *Petrocephalus* Pellegrin, 1924.
- bovei*, *Mormyrus* Valenciennes, 1847. Current status: valid as *Petrocephalus bovei* (Valenciennes, 1847).
- brevipedunculatus*, *Petrocephalus* Svensson, 1933. Current status: synonym of *Petrocephalus bovei* (Valenciennes, 1847).
- catostoma*, *Mormyrus* Günther, 1866. Current status: valid as *Petrocephalus catostoma* (Günther, 1866)
- christyi*, *Petrocephalus* Boulenger, 1920.
- comoensis*, *Petrocephalus bane* de Merona, 1979. Current status: synonym of *Petrocephalus bane* (Lacépède, 1803).
- congicus*, *Petrocephalus stuhlmanni* David and Poll, 1937. Current status: *Petrocephalus congicus* (David and Poll, 1937).
- cunganus*, *Petrocephalus* Boulenger, 1910.
- degeni*, *Petrocephalus* Boulenger, 1906. Current status: *Petrocephalus degeni* Boulenger, 1906.
- dequesne*, *Mormyrus* Valenciennes, 1847. Current status: synonym of *Petrocephalus bane* (Lacépède, 1803).
- ehrenbergii*, *Mormyrus* Valenciennes 1847. Current status: synonym of *Petrocephalus bane* (Lacépède, 1803).
- frieli*, *Petrocephalus* Lavoué, 2012.
- gliroides*, *Mormyrus* Vinciguerra, 1897. Current status: valid as *Petrocephalus gliroides* (Vinciguerra, 1897)
- grandoculis*, *Petrocephalus* Boulenger, 1920.
- guineensis*, *Petrocephalus bovei* Reizer, Mattei and Chevalier, 1973. Current status: synonym of *Petrocephalus bovei* (Valenciennes, 1847).
- guttatus*, *Petrocephalus* Fowler, 1936.
- haullevillii*, *Petrocephalus* Boulenger, 1912. Current status: *Petrocephalus haullevillii* Boulenger, 1912.
- hutereaui*, *Marcusenius* Boulenger, 1913. Current status: valid as *Petrocephalus hutereaui* (Boulenger, 1913).
- joannisii*, *Mormyrus* Valenciennes, 1847. Current status: synonym of *Petrocephalus bane* (Lacépède, 1803).

- keatingii*, *Petrocephalus* Boulenger, 1901.
levequei, *Petrocephalus* Bigorne and Paugy, 1990.
longicapitis, *Petrocephalus* Kramer, Bills, Skelton and Wink, 2012.
magnitrunci, *Petrocephalus* Kramer, Bills, Skelton and Wink, 2012.
magnoculis, *Petrocephalus* Kramer, Bills, Skelton and Wink, 2012.
longianalis, *Petrocephalus* Kramer, Bills, Skelton and Wink, 2012.
marchei, *Petrocephalus* Sauvage, 1879. Current status: valid as *Ivindomyrus marchei* (Sauvage, 1879).
marchii, *Petrocephalus* Boulenger, 1899. Current status: synonym of *Ivindomyrus marchei* (Sauvage, 1879).
microphthalmus, *Petrocephalus* Pellegrin, 1908.
okavangensis, *Petrocephalus* Kramer, Bills, Skelton and Wink, 2012.
pallidomaculatus, *Petrocephalus* Bigorne and Paugy, 1990.
pellegrini, *Petrocephalus* Poll, 1941.
petersi, *Petrocephalus* Kramer, Bills, Skelton and Wink, 2012.
pictus, *Petrocephalus* Marcusen, 1864. Current status: valid as *Hippopotamyus pictus* (Marcusen, 1864).
sauvagii, *Mormyrus* (*Petrocephalus*) Boulenger, 1887. Current status: valid as *Petrocephalus sauvagii* (Boulenger, 1887).
schoutedeni, *Petrocephalus* Poll, 1954.
simus, *Petrocephalus* Sauvage, 1879.
soudanensis, *Petrocephalus* Bigorne and Paugy, 1990.
squalostoma, *Marcusenius* Boulenger, 1915. Current status: valid as *Petrocephalus squalostoma* (Boulenger, 1915).
steindachneri, *Petrocephalus* Fowler, 1958.
stuhlmanni, *Petrocephalus* Boulenger, 1909.
sullivanii, *Petrocephalus* Lavoué, Hopkins and Kamdem Toham, 2004.
tanensis, *Petrocephalus catostoma* Whitehead and Greenwood, 1959. Current status: *Petrocephalus catostoma tanensis* (Whitehead and Greenwood, 1959)
tchadensis, *Petrocephalus bane* Blache and Miton, 1961. Current status: synonym of *Petrocephalus bane* (Lacépède, 1803).
tenuicauda, *Mormyrus* Steindachner, 1894. Current status: valid as *Petrocephalus tenuicauda* (Steindachner, 1894).
vanderbilti, *Petrocephalus* Fowler, 1936. Current status: synonym of *Pollimyrus isidori* (Valenciennes, 1847).
wesselsi, *Petrocephalus* Kramer and Van der Bank, 2000.

Petrocephalus catostoma (Günther, 1866)
(Figure 2, nos 1, 28; online Figure 1)

Mormyrus catostoma Günther, 1866: 222.

Petrocephalus catostoma: Boulenger 1898: 790.

Petrocephalus catostoma catostoma: Whitehead and Greenwood 1959: 284.

Type specimens. BMNH 1863.10.12.4 (lectotype) and four paralectotypes BMNH 1863.10.12.5-6 (4) (studied)

Type locality. Rovuma (Ruvuma) River, Tanzania/Mozambique (lower reaches, place unspecified).

Diagnosis. Preanal length, PAL, mean 0.625 (range 0.602–0.656) of SL; length of snout to posterior orbital rim of eye, LSo, mean 0.423 (range 0.398–0.454) of head length, HL; head length, HL, mean 17.43 (range 16.07–23.21) times Na, distance between the pair of nares of one side; body depth, BD, mean 0.274 (range 0.252–0.306) of SL; number of dorsal fin rays, nD, median 20 (range 18–22); number of anal fin rays, nA, median 27 (range 25–29); head length, HL, mean 0.277 (range 0.249–0.291) of SL; number of scales around caudal peduncle, SPc, median 14 (range 12–16).

Description. Body oval shape (Figure 2, nos 1 and 28). Head broadly rounded with a small ventrally positioned subterminal mouth, situated ventral to the eye; head and body dorsolaterally compressed. Dorsal fin (a) origin situated about two-thirds of standard length from snout, (b) obliquely orientated, anteriorly higher and posteriorly lower, (c) distal margin crescentic with anterior two or three rays longer than posterior rays, and (d) number of rays 18 ($n = 1$), 19 ($n = 8$), 20 ($n = 17$), 21 ($n = 8$), 22 ($n = 1$). Anal fin (a) longer than dorsal fin, (b) opposite dorsal fin with slightly more anterior origin, (c) obliquely orientated, anteriorly lower and posteriorly higher, (d) anterior 10 or so rays longer than posterior ones, especially in males where they also appear stronger, (e) margin broadly rounded, (f) rays posterior to first 10 with distal margin straight, (g) number of rays 25 ($n = 3$), 26 ($n = 14$), 27 ($n = 15$), 28 ($n = 3$). Forked tail fin with rounded lobes. Scales cycloid with reticulate striae, scales extending anteriorly to operculum and pectoral fins (beyond pelvics). Scales on caudal peduncle circumference, 11 ($n = 1$), 14 ($n = 25$), 16 ($n = 9$). Caudal peduncle slender, subcylindrical entire length, usually 21% (19.5–23.85%) of SL (Table 1). Males with kink in anal fin base which is absent in juveniles and females where the anal fin base is straight.

Colour in preservation. Light brown, back darker, underside fair.

Colour in life. Grey-silver, underside lighter, paired fins light and transparent, gold-brownish hue on back and tail section.

Ecology. The species is common and widespread throughout upper catchments within the Niassa Reserve. Occurs in aquatic weed beds, marginal vegetation and root-stocks of bank vegetation in headwater streams through to floodplain margins. Water conductivities ranging from 104 to 268 $\mu\text{S}/\text{cm}$ in August 2003, probably reflecting human impact (Bills 2004; personal observation). Online Figures 2–5.

Distribution. Rovuma System including Niassa Reserve (no. 28 on Figure 1), also western confluences to Lake Malawi (nos 16–18), but probably not Lake Chiuta (no. 19).

Remarks. Compared with the other species, *P. catostoma* is distinguished by its very low range for PAL, LSo, HL/Na, BD, nD, nA, but long HL, and an SPc median of 14 intermediate between the extremes.

Petrocephalus congicus David and Poll, 1937 (resurrected and elevated to species rank)
(Figure 2, no. 26)

Petrocephalus stuhlmanni congicus David and Poll, 1937: 199. Whitehead and Greenwood 1959: 286 (synonymy with *Petrocephalus catostoma congicus*).

Type specimens. Syntypes: MRAC 30807-30808 (2) (studied)

Type locality. Mukishi River at Lumami, Congo River basin, Democratic Republic of Congo (08°30' S, 24°44' E).

Diagnosis. Predorsal length, PDL, mean 0.627 (range 0.618–0.635) of SL; preanal length, PAL, mean 0.556 (range 0.535–0.578) of SL; dorsal fin length, LD, mean 0.16 (range 0.155–0.166) of SL; anal fin length, LA, mean 0.237 (range 0.234–0.241) of SL; distance dorsal fin origin to end of caudal peduncle, pD, mean 0.427 (range 0.417–0.438) of SL; length of caudal peduncle, CPL, mean 0.232 (range 0.228–0.237) of SL; depth of caudal peduncle, CPD, mean 0.2965 (range 0.296–0.297) of CPL, length of caudal peduncle; length of snout to centre of eye, LSc, mean 0.334 (range 0.326–0.343) of HL; length of snout to posterior orbital rim of eye, LSo, mean 0.419 (range 0.408–0.429) of HL; head length, HL, mean 0.234 (range 0.231–0.238) of SL; distance between the pair of nares of one side, Na, mean 20.1 (range 18.87–21.32) times in HL, head length; body depth, BD, mean 0.293 (range 0.286–0.3) of SL; dorsal fin ray number, nD, median 18.5 (range 18–19); anal fin ray number, nA, median 27.5 (range 27–28); number of scales around caudal peduncle, SPc, median 12 (range, 12–12).

Remarks. “Judging from the known range of variation within *P. c. catostoma* it seems possible that the two Congoan forms [i.e. *haullevillii* and *congicus*] may yet have to be united” (Whitehead and Greenwood 1959: 286). *Petrocephalus stuhlmanni congicus* is distinguished from other *Petrocephalus* by one of the shortest values for head length, HL, in combination with dorsal fin ray number, nD, in the lowest range. This leaves only *P. haullevillii* as an alternative. *Petrocephalus stuhlmanni congicus* differs from *P. haullevillii* by a rosette of electroreceptor organs (above the eye, Augenrosette; Harder 1968), absent in *P. haullevillii* that has no such rosette (S. Lavoué, personal communication). Among other differences, *P. congicus* and *P. stuhlmanni* differ markedly in their values for caudal peduncle depth (CPD) and head length (HL); these characters are among the greatest in the former and smallest in the latter species in the present assemblage of *Petrocephalus*.

Petrocephalus degeni Boulenger, 1906 (resurrected species)
(Figure 2, no. 27)

Petrocephalus degeni Boulenger, 1906: 434; Whitehead and Greenwood 1959: 284 (synonymy with *Petrocephalus catostoma catostoma*).

Type specimens. Holotype (unique): BMNH 1906.5.30.84 (studied).

Type locality. Mouth of Katonga River, Lake Victoria (Uganda).

Diagnosis. Preanal length, PAL 0.641 of SL; predorsal length, PDL 0.634 of SL; dorsal fin length, LD 0.155 of SL; anal fin length, LA 0.221 of SL; distance dorsal fin origin to end of caudal peduncle, pD 0.427 of SL; length of caudal peduncle, CPL 0.202 of SL; depth of caudal peduncle, CPD 0.369 of CPL; length of snout to centre of eye, LSc 0.258 of HL; length of snout to posterior orbital rim of eye, LSo 0.411 of HL; head length, HL 0.261 of SL; dorsal fin ray number, nD 19; anal fin ray number, nA 27; number of scales around caudal peduncle, SPc 12.

Etymology. See title of Boulenger (1906): "... new Fishes discovered by Mr. E. Degen . . .".

Remarks. "Easily distinguished from its congeners in the short dorsal fin originating above the first ray of the anal" (Boulenger 1906: 434). Distinguished from all other species by highest PAL/SL and lowest LSc/HL, in combination with low LD/SL, low LA/SL, rather high pD/SL.

Petrocephalus haullevillii Boulenger, 1912 (resurrected species)
(Figure 2, nos 24, 26)

Petrocephalus haullevillii Boulenger, 1912: 5.

Petrocephalus stuhlmanni haullevillii: David and Poll 1937: 200 (spelt *haullevillei*).

Petrocephalus catostoma haullevillii: Whitehead and Greenwood 1959: 286.

Type specimens. Syntypes: BMNH 1912.4.1.181–183 (3), BMNH 1912.4.1.184–185 (2), BMNH 1912.4.1.186–188 (3), MRAC 1496–1501 (6) (all studied); ZMB 18795 (1), ANSP 38586–88 (3) (not studied).

Type locality. "Chiloanga [River] at Mayili, Luali [River] at Lundo and in the Luculla [River]", Lower Congo.

Diagnosis. Predorsal length, PDL, mean 0.618 (range 0.605–0.641) of SL; preanal length, PAL, mean 0.564 (range 0.542–0.586) of SL; dorsal fin length, LD, mean 0.168 (range 0.154–0.177) of SL; anal fin length, LA, mean 0.254 (range 0.24–0.269) of SL; distance dorsal fin origin to end of caudal peduncle, pD, mean 0.421 (range 0.401–0.44) of SL; length of caudal peduncle, CPL, mean 0.22 (range 0.209–0.231) of SL; depth of caudal peduncle, CPD, mean 0.326 (range 0.277–0.365) of CPL, length of caudal peduncle; length of snout to centre of eye, LSc, mean 0.322 (range 0.292–0.362) of HL; length of snout to posterior orbital rim of eye, LSo, mean 0.429 (range 0.4–0.484) of HL; head length, HL, mean 0.24 (range 0.225–0.248) of SL; distance between the pair of nares of one side, Na, mean 20.03 (range 18.86–21.71) times in HL, head length; body depth, BD, mean 0.283 (range 0.24–0.312) of SL; dorsal fin ray number, nD, median 19 (range 18–21); anal fin ray number, nA, median 27 (range 26–28); number of scales around caudal peduncle, SPc, median 12 (range, 12–12).

Remarks. *Petrocephalus haullevillii* is distinguished from other *Petrocephalus* species by one of the shortest values for head length, HL, in combination with dorsal fin ray number, nD, in the lowest range. This leaves only *P. stuhlmanni congicus* as an alternative that differs, however, categorically in possessing a rosette of electroreceptor organs above the eye (Augenrosette; Harder 1968), in contrast to *haullevillii* that possesses none (S. Lavoué, personal communication)

***Petrocephalus longianalis* sp. nov.**

(Figure 2, no. 12)

Type specimens. Holotype: SAIAB 76758 (specimen R9) from Zambia Province: Luapula System: Luongo River: Lufubu River. Paratypes: SAIAB 186060 (48 specimens).

Type locality. Zambia, Zambia Province, Luapula System, Luongo River, Lufubu River, Lufubu River Falls below bridge at Chipili on Mensa-Mununga road 10.7297° S, 29.0936° E.

Diagnosis. Number of anal fin rays, nA, median 33 (range 30–35); anal fin length, LA, mean 0.261 (range 0.244–0.278) of SL; preanal length, PAL, mean 0.569 (range 0.543–0.59) of SL; depth of caudal peduncle, CPD, mean 0.298 (range 0.269–0.331) of CPL, length of caudal peduncle; body depth, BD, mean 0.267 (range 0.225–0.293) of SL; number of dorsal fin rays, nD, median 24 (range 22–26); number of scales in lateral line row, SLS, median 40 (range 39–42); distance between anterior base of pectoral fin to anterior base of pelvic fin, PPF, mean 0.152 (range 0.128–0.169) of SL.

Description. Body long-oval shape (Figure 2, no. 12). Head broadly rounded with a small ventrally positioned subterminal mouth, situated ventral to the eye; head and body dorsolaterally compressed. Dorsal fin (a) origin situated about two-thirds of standard length from snout, (b) obliquely orientated, anteriorly higher and posteriorly lower, (c) distal margin crescentic with anterior two or three rays longer than posterior rays, and (d) number of rays 22 ($n = 8$), 23 ($n = 20$), 24 ($n = 18$), 25 ($n = 3$), (e) dark spot below fin origin (lacking in samples from Luapula River bridge, SAIAB 76582). Anal fin (a) longer than dorsal fin, (b) opposite dorsal fin with slightly more anterior origin, (c) obliquely orientated, anteriorly lower and posteriorly higher, (d) anterior 10 or so rays longer than posterior ones, especially in males where they also appear stronger, (e) margin broadly rounded, (f) rays posterior to first 10 with distal margin straight, (g) number of rays 30 ($n = 2$), 31 ($n = 6$), 32 ($n = 16$), 33 ($n = 17$), 34 ($n = 6$), 35 ($n = 2$). Forked tail fin with rounded lobes. Scales cycloid with reticulate striae, scales extending anteriorly to operculum and pectoral fins (beyond pelvics). Scales in lateral series, 39 ($n = 9$), 40 ($n = 17$), 41 ($n = 21$), 42 ($n = 2$). Scales on caudal peduncle circumference, 11 ($n = 2$), 12 ($n = 47$). Caudal peduncle slender, subcylindrical entire length, usually 19.3% (18.4–19.9%) of SL (Table 1). Males with kink in anal fin base, which is absent in juveniles and females where the anal fin base is straight.

Colour in preservation. Body brown, back only slightly darker, breast and belly fair, fins rather unpigmented and transparent, anal and dorsal fin bases emphasized as dark

lines. Well-circumscribed dark spot below dorsal fin origin (except for specimens from Luapula River bridge, SAIAB 76582).

Ecology. The Lufubu River just above a 3–4 m falls is a braided rocky channel with dense riparian forest. Water flow was rapid in section but there were also deeper pools with large rocks providing slacker flow areas. The substrate was rocky but with considerable amounts of leaf litter. In some sections there were mats of aquatic water ferns and mosses and filamentous algae. Fishes were collected with rotenone. Altitude, approximately 1200 m. Online Figure 6.

Remarks. A median of $nA = 33$ is highest and distinctive among the *Petrocephalus* species of the present study. Except for samples from Luapula River bridge (SAIAB 76582), all other samples referable to *P. longianalis* sp. nov. with dark spot below dorsal fin origin, usually round, small and distinct.

***Petrocephalus longicapitis* sp. nov.**
(Figure 2, no. 7; online Figure 7)

Type specimens. Holotype: SAIAB 85916 (specimen 19fish) from Upper Zambezi River at Katima Mulilo, East Caprivi, Namibia. Paratypes: SMF 28265 (27 specimens), plus SAIAB 85917 (specimens 14fish, 16fish), SAIAB 85911 (25fish, 26fish), SAIAB 85918 (37fish, 38fish, 43fish).

Type locality. Upper Zambezi River at Katima Mulilo, East Caprivi, Namibia, approx. 17°29'30" S, 24°16'18" E.

Diagnosis. Head length, HL, mean 0.279 (range 0.258–0.296) of SL; predorsal length, PDL, mean 0.635 (range 0.619–0.657) of SL; preanal length, PAL, mean 0.596 (range 0.575–0.617) of SL; depth of caudal peduncle, CPD, mean 0.36 (range 0.334–0.398) of CPL, length of caudal peduncle; number of scales around caudal peduncle, SPC, median 12 (range 12–12); eye diameter as defined by orbital rims, OD, mean 0.261 (range 0.249–0.281) of HL, head length; body depth, BD, mean 0.295 (range 0.277–0.315) of SL; length of anal fin, LA, mean 0.237 (range 0.221–0.252) of SL; length of snout to posterior orbital rim of eye, LSo, mean 0.431 (range 0.389–0.458) of HL, head length; number of dorsal fin rays, nD, median 23 (range 21–25); number of scales in lateral line row, SLS, median 38 (range 37–39). EOD characteristics at 25°C and “2% threshold criterion” (see Material and methods): peak amplitude of P2 phase, P2amp, in males, mean 0.466 (range 0.321–0.547) of P1amp, peak amplitude of P1 phase; in females, mean 0.382 (range 0.206–0.517) of P1amp; duration of P2 phase, P2dur, mean 207 μ s (range 113–477 μ s); duration of P1 phase, P1dur, mean 131 μ s (range 101–169 μ s); duration of N phase, Ndur, mean 49 μ s (range 36–62 μ s); negative peak amplitude (absolute value) of N phase, Namp, mean – 2.77 (range – 2.291 to – 3.468) of P1amp, peak amplitude of P1 phase.

Description. Body oval shape (Figure 2, no. 7). Head broadly rounded with a small ventrally positioned subterminal mouth, situated ventral to the eye; head and body dorsolaterally compressed. Dorsal fin (a) origin situated about two-thirds of standard

length from snout, (b) obliquely orientated, anteriorly higher and posteriorly lower, (c) distal margin crescentic with anterior two or three rays longer than posterior rays, and (d) number of rays 21 ($n = 2$), 22 ($n = 10$), 23 ($n = 21$), 24 ($n = 3$), 25 ($n = 2$). Anal fin (a) longer than dorsal fin, (b) opposite dorsal fin with slightly more anterior origin, (c) obliquely orientated, anteriorly lower and posteriorly higher, (d) anterior 10 or so rays longer than posterior ones, especially in males where they also appear stronger, (e) margin broadly rounded, (f) rays posterior to first 10 with distal margin straight, (g) number of rays 26 ($n = 1$), 27 ($n = 1$), 28 ($n = 23$), 29 ($n = 11$), 30 ($n = 2$). Forked tail fin with rounded lobes. Scales cycloid with reticulate striae, scales extending anteriorly to operculum and pectoral fins (beyond pelvics). Scales in lateral series, 37 ($n = 3$), 38 ($n = 8$), 39 ($n = 1$). Scales on caudal peduncle circumference, 12 ($n = 38$). Caudal peduncle slender, subcylindrical entire length, usually 19.9% (18–21.5%) of SL (Table 1). Electric organ discharge, triphasic pulse with strong head-positive phase P1 followed by head-negative main phase N, and weaker head-positive P2 phase (Figure 10); P2 phase stronger in males than in females of same size. Pulse duration short [mean 379 μ s (range 298–642) in females ($n = 19$) and 354 μ s (253–473) in males ($n = 15$), respectively; 25°C, 2% threshold criterion]. Males with kink in anal fin base, which is absent in juveniles and females where the anal fin base is straight.

Colour in preservation. Light brown.

Colour in life. Colour in life: grey-silver, underside lighter, paired fins light and transparent.

Ecology. Appears to prefer quiet reaches of oxbow lakes or arms with dense vegetation on borders. Both sexes are territorial during the day but combine to schools at night (Scheffel and Kramer 2006). Van der Waal and Skelton (1984) studied the fishes of Caprivi, and found *P. longicapitis* sp. nov. to be abundant in the Zambezi River and common in the Eastern Floodplain, in the Chobe and in Lake Liambezi (which has since dried up), but rare in the Kwando River. The species was common in the shallow water of swamps and flood plains, but rare in streams with sandy or rocky substrate, and also rare in pools beneath *Salvinia molesta* mats. Where it occurs in the main river channel, sand and gravel substrate mainly with occasional rocky rapids. Marginal roots stocks of riparian trees and patches of aquatic vegetation beds. During the day *P. longicapitis* sp. nov. is associated with marginal cover in holes in banks, root stocks and aquatic weed beds.

Distribution. Presently known only from the lower and the upper reaches of the Upper Zambezi River: East Caprivi, Namibia, and Lumwana River, Zambia.

Etymology. The species name *longicapitis* sp. nov. refers to this species' long head (*longus*, long and *caput*, head).

Remarks. *Petrocephalus longicapitis* sp. nov. is characterized by a long HL, PDL, PAL, CPD and low SPc. The EOD shows a strong P2 phase of short duration, short P1dur, short Ndur, and weaker Namp than *P. tanensis*.

Petrocephalus magnitrunci sp. nov.

(Figure 2, no. 31)

Type specimens. Holotype: SAIAB 67069 (specimen R2) from Botswana, Okavango Delta, southeast of Chief's Island, Boro River. Paratypes: SAIAB 186057 ($n = 10$).

Type locality. Botswana, Okavango Delta, southeast of Chief's Island, Boro River, 19°31'57" S, 23°05'21" E.

Diagnosis. Number of scales in lateral line row, SLS, median 40 (range 39–41); body depth, BD, mean 0.344 (range 0.327–0.368) of SL; eye diameter as defined by orbital rims, OD, mean 0.232 (range 0.218–0.250) of HL, head length; number of dorsal fin rays, nD, median 21 (range 19–22); anal fin length, LA, mean 0.254 (range 0.235–0.27) of SL; length of snout to posterior orbital rim of eye, LSo, mean 0.464 (range 0.449–0.481) of HL; head length, HL, mean 21.2 (range 17.6–24.1) times Na, distance between the pair of nares of one side.

Description. Rounded-oval body of egg-like shape (Figure 2, no. 31). Rounded head with a small ventrally positioned subterminal mouth, situated ventral to the eye; head and body dorsolaterally compressed. Dorsal fin (a) origin situated about two-thirds of standard length from snout, (b) obliquely orientated, anteriorly higher and posteriorly lower, (c) distal margin crescentic with anterior two or three rays longer than posterior rays, and (d) number of rays 19 ($n = 2$), 20 ($n = 3$), 21 ($n = 5$), 22 ($n = 1$); no spot below dorsal fin origin. Anal fin (a) longer than dorsal fin, (b) opposite dorsal fin with slightly more anterior origin, (c) obliquely orientated, anteriorly lower and posteriorly higher, (d) anterior 10 or so rays longer than posterior ones, especially in males where they also appear stronger, (e) margin broadly rounded, (f) rays posterior to first 10 with distal margin straight, (g) number of rays 27 ($n = 1$), 28 ($n = 2$), 29 ($n = 3$), 30 ($n = 2$), 31 ($n = 3$). Forked tail fin with rounded lobes. Scales cycloid with reticulate striae, scales extending anteriorly to operculum and pectoral fins (beyond pelvics). Scales in lateral series, 39 ($n = 5$), 40 ($n = 3$), 41 ($n = 3$). Scales on caudal peduncle circumference, 11 ($n = 1$), 12 ($n = 10$). Caudal peduncle slender, subcylindrical entire length, usually 19.2% (17.6–21.5%) of SL (Table 1). Males with kink in anal fin base, which is absent in juveniles and females where the anal fin base is straight.

Colour in preservation. Intense brown, with dark back, breast and belly lighter.

Ecology. The site where types were collected was a shallow floodplain lagoon on the edges of the Boro River channel and Chief's Island. The substrate was mud and the vegetation was dense emergent grasses and water lilies (*Nymphaea* sp.), water depth was up to 2 m. Collection methods included daytime D-netting in the shallower margins and overnight gill-netting of the deeper sections. The lagoon was flooded during the winter flood cycle and would be dry during the low water period.

Distribution. At present, only known from the Boro River in the central part of the Okavango Delta, west of the southern tip of Chief's Island. Note that the comments of Skelton et al. (1985) on distribution, cited in the section on *P. okavangensis* sp. nov., may embrace *P. magnitrunci* sp. nov.

Etymology. Species name refers to *magnus*, great and *truncus*, trunk (such as of the body).

Remarks. *Petrocephalus magnitrunci* sp. nov. compared with *P. okavangensis* sp. nov. is characterized by a greater SLS and higher BD/SL, and an apparently obligatory lack of black spot below the dorsal fin origin. Compared with both *P. magnoculis* sp. nov. and *P. longicapitis* sp. nov., distinctly smaller OD/HL, lower nD, greater BD and greater LA in *P. magnitrunci* sp. nov. Compared with *P. longicapitis* sp. nov.: in addition to the above, greater no. of SLS, smaller HL and longer LSo in *P. magnitrunci* sp. nov. Compared with *P. magnoculis* sp. nov.: in addition to the above, shorter LSo and greater Na in *P. magnitrunci* sp. nov.

***Petrocephalus magnoculis* sp. nov.**

(Figure 2, no. 23; online Figure 8)

Type specimens. Holotype: SAIAB 78788 (specimen Ruac06) from Cunene River, just below Ruacana Falls. Paratypes: SAIAB 186053 (specimen Ruac09), SAIAB 79480 (specimen Ruac10), SAIAB 78790 (specimen Ruac17), ZSM 38659 (specimen Ruac07), ZSM 38660 (specimen Ruac13).

Type locality. Namibia: Cunene River: just below the Ruacana Falls, Hippo Pool Campsite, 17°24'24" S, 14°13'01" E, about 800 m altitude.

Diagnosis. Eye diameter defined by orbital rims, OD, mean 0.294 (range 0.259–0.329) of HL, head length; number of scales in lateral line row, SLS, median 40 (range 38–42); length of snout to posterior orbital rim of eye, LSo, mean 0.485 (range 0.47–0.514) of HL, head length; length of snout to centre of eye, LSc, mean 0.37 (range 0.352–0.391) of HL; head length, HL, mean 0.258 (range 0.25–0.277) of SL; preanal length, PAL, mean 0.611 (range 0.59–0.628) of SL; anal fin length, LA, mean 0.234 (range 0.215–0.256) of SL; number of dorsal fin rays, nD, median 23 (range 20–24); body depth, BD, mean 0.312 (range 0.283–0.34) of SL; distance between the pair of nares of one side, Na, mean 27.9 (range 24.3–31.1) times in HL, head length.

Description. Body oval shape (Figure 2, no. 23). Head with rounded nose, small ventrally positioned subterminal mouth, situated ventral to the eye; head and body dorsolaterally compressed. Dorsal fin (a) origin situated about two-thirds of standard length from snout, (b) obliquely orientated, anteriorly higher and posteriorly lower, (c) distal margin crescentic with anterior two or three rays longer than posterior rays, and (d) number of rays 20 ($n = 1$), 21 ($n = 0$), 22 ($n = 2$), 23 ($n = 2$), 24 ($n = 4$). Anal fin (a) longer than dorsal fin, (b) opposite dorsal fin with slightly more anterior origin, (c) obliquely orientated, anteriorly lower and posteriorly higher, (d) anterior 10 or so rays longer than posterior ones, especially in males where they also appear stronger, (e) margin broadly rounded, (f) rays posterior to first 10 with distal margin straight, (g) number of rays 26 ($n = 1$), 27 ($n = 0$), 28 ($n = 2$), 29 ($n = 2$), 30 ($n = 3$), 31 ($n = 1$). Forked tail fin with rounded lobes. Scales cycloid with reticulate striae, scales extending anteriorly to operculum and pectoral fins (beyond pelvics). Scales in lateral series,

38 ($n = 1$), 39 ($n = 1$), 40 ($n = 2$), 42 ($n = 1$). Scales on caudal peduncle circumference, 11 ($n = 1$), 12 ($n = 7$), 13 ($n = 1$). Caudal peduncle slender, subcylindrical entire length, usually 19.9% (18.4–21.8%) of SL (Table 1). Electric organ discharge a triphasic pulse with strong head-positive phase P1 followed by head-negative main phase N, and head-positive P2 phase of 30% amplitude re: P1 phase (Figure 10). Pulse duration mean 443 (394–536) μs ($n = 4$); 25 °C, 2% threshold criterion). Males with kink in anal fin base which is absent in juveniles and females where the anal fin base is straight.

Colour in preservation. Light beige, back darker and grey, but brown where mormyrid skin gone.

Colour in life. Grey-silver, underside lighter, paired fins light and transparent.

Ecology. The Cunene River is dammed for hydroelectric power generation just above Ruacana Falls in Angola. Even in the dry season when the Falls proper were completely dry the water level just below the Falls was regulated rather high, and the current rather strong. Dicotyledonous trees, extensive reed beds and semiaquatic bushes dominated the river banks. River banks were rocky or sandy, depending on whether they were on the inside or outside bank. Crocodiles were seen, and hippopotamus are reported for the area but were not seen. At 800 m sea level marked diurnal temperature differences with chilling nights. Online Figure 9.

Distribution. Presently known only from just below the Ruacana Falls; downstream limit perhaps at Epupa Falls. Nothing is known about whether *P. magnoculis* sp. nov. is also found upstream of Ruacana Falls.

Etymology. Species name derived from *magnus*, great, and *oculus*, eye.

Remarks. In *P. magnoculis* sp. nov., Eye diameter and SLS are in the top range compared with the other species, also LSo, LSc, HL and PAL, whereas LA is in the lower range.

***Petrocephalus okavangensis* sp. nov.**
(Figure 2, no. 9; online Figure 10)

A brief overview of records of Churchills from the Okavango is given in Skelton et al. (1985: 5), including a review of the discussions about their identity. Based on their own ‘preliminary observations’, these authors retained the name *P. catostoma*, ‘pending further analysis of the problem’.

Type specimens. Holotype: SAIAB 030046 (specimen R22) from Botswana, Okavango, Thoage River, Nguma (Guma) Lagoon. Paratypes: SAIAB 186062 (41 specimens).

Type locality. Botswana, Okavango, Thoage River, Nguma (Guma) Lagoon, 18°57'43.2" S, 22°22'26.1" E.

Diagnosis. Length of anal fin, LA, mean 0.264 (range 0.247–0.286) of SL; number of anal fin rays, nA, median 30 (range 27–32); head length, HL, mean 0.25

(range 0.232–0.274) of SL; depth of caudal peduncle, CPD, mean 0.311 (range 0.264–0.349) of CPL, length of caudal peduncle; preanal length, PAL, mean 0.576 (range 0.538–0.619) of SL; dorsal fin length, LD, mean 0.17 (range 0.145–0.195) of SL; number of scales around caudal peduncle, SPc, median 12 (range 12–12); body depth, BD, mean 0.291 (range 0.261–0.348) of SL; number of scales in lateral line row, SLS, median 37 (range 37–38). EOD characteristics at 25°C and “2% threshold criterion” (see Material and methods) for $n = 2$: peak amplitude of P2 phase, P2amp < 0.13 of P1amp, peak amplitude of P1 phase; duration of P1 phase, P1dur, range 161–202 μ s; duration of N phase, Ndur, range 65–83 μ s; duration of P2 phase, P2dur, range 294–343 μ s.

Description. Body oval shape (Figure 2, no. 9). Head with distinctly pointed nose in most specimens, with a small ventrally positioned subterminal mouth, situated ventral to the eye; head and body dorsolaterally compressed. Dorsal fin (a) origin situated about two-thirds of standard length from snout, (b) obliquely orientated, anteriorly higher and posteriorly lower, (c) distal margin crescentic with anterior two or three rays longer than posterior rays, and (d) number of rays 20 ($n = 3$), 21 ($n = 13$), 22 ($n = 15$), 23 ($n = 8$), 24 ($n = 6$). Anal fin (a) longer than dorsal fin, (b) opposite dorsal fin with slightly more anterior origin, (c) obliquely orientated, anteriorly lower and posteriorly higher, (d) anterior 10 or so rays longer than posterior ones, especially in males where they also appear stronger, (e) margin broadly rounded, (f) rays posterior to first 10 with distal margin straight, (g) number of rays 27 ($n = 1$), 28 ($n = 1$), 29 ($n = 6$), 30 ($n = 21$), 31 ($n = 12$), 32 ($n = 4$). Forked tail fin with rounded lobes. Scales cycloid with reticulate striae, scales extending anteriorly to operculum and pectoral fins (beyond pelvic fins). Scales in lateral series, 37 ($n = 2$), 38 ($n = 1$). Scales on caudal peduncle circumference, 12 ($n = 45$). Caudal peduncle slender, subcylindrical entire length, usually 20.7% (18.2–23%) of SL (Table 1). Electric organ discharge a triphasic pulse with strong head-positive phase P1 followed by head-negative main phase N, and very weak head-positive P2 phase (Figure 10). Pulse duration mean 574 (520–628) μ s in females ($n = 2$); 25°C, 2% threshold criterion). Males with kink in anal fin base which is absent in juveniles and females where the anal fin base is straight.

Colour in preservation. Between ochre and light brown. Some preserved specimens' dark spot below dorsal fin origin seems to have faded. Present at least in some individuals in all samples referable to *P. okavangensis* sp. nov., even when sampled in 1983.

Colour in life. Grey-silver or brownish-silver, then with gold-olive hue, anal fin base emphasized by black line, less distinct for dorsal fin base, first few rays of unpaired fins darker, irregular shaped dark spot under dorsal fin origin, sometimes visible only on one body side, throat and belly very fair, back dark, paired fins light and transparent.

Ecology. Guma Lagoon is a large (approximately 1 km²) lagoon at the edge of the floodplain at the lower Okavango panhandle. It is on the Thoage channel, which is a thin, deep meandering channel off the main Okavango River. Although the lagoon has an inflow channel there is no obvious outflow point with water seeping out along the southeastern edge. Water flows within the lagoon are effectively nil. The majority of the lagoon is fringed with papyrus and varied emergent vegetation. *Petrocephalus* were

collected under papyrus root stocks. According to Skelton et al. (1985) “*P. catostoma* (or a form thereof)” is a fairly hardy and eurytopic species, common in both swamp and river.

Distribution. The species is presently known from Popa Falls in Caprivi/Namibia, and from the point where the Okavango River fans out to form the delta (Botswana), and also from the northeastern sections of the delta, such as Gadikwe Lagoon and Xakanixa (Xakanaxa). According to Skelton et al. (1985), this species (or forms thereof) ranges much more widely (from north to south): it is present in Angolan headwaters of the Okavango, in the Namibian Okavango, in riverine floodplains of the Okavango (Botswana), in its permanent swamps, in the delta’s southern drainage rivers, in Lake Ngami in the southwest of the delta, and, following the course of the Botletli River, even in the distant southeast of the delta, Lake Xau/Mopipi Dam (Makgadikgadi Salt Pan region).

Etymology. The species name *okavangensis* refers to the Okavango River.

Remarks. *Petrocephalus okavangensis* sp. nov. in comparison with the other species is characterized by a very long LA, high nA, short HL, low CPD, shorter PAL and LD than *P. longicapitis* sp. nov., low SPc. EOD with weak P2amp (<13% of P1amp), long P1dur (161–202 μ s) and Ndur (65–83 μ s), all different from *P. longicapitis* sp. nov. and *P. tanensis*, and more similar to *P. wesselsi*. If present, dark spot below dorsal fin origin seems to be distinctive with regard to *P. magnitrunci* sp. nov. that lacks a spot.

***Petrocephalus petersi* sp. nov.**

(Figure 2, no. 21)

Type specimens. Holotype: SAIAB 060846 (specimen R1), Mozambique, stream near campsite 1, edge of wet Zambezi River System, Zambezi River. Paratypes: SAIAB 186055 (10 specimens).

Type locality. Mozambique, stream near campsite 1, edge of wet Zambezi River System, Zambezi River, 18°33′54″ S, 35°39′46″ E.

Diagnosis. Preanal length, PAL, mean 0.616 (range 0.595–0.637) of SL; predorsal length, PDL, mean 0.642 (range 0.623–0.658) of SL; length of snout to centre of eye, LSc, mean 0.364 (range 0.345–0.383) of HL, head length; length of snout to posterior orbital rim of eye, LSo, mean 0.462 (range 0.442–0.479) of HL, head length; body depth, BD, mean 0.299 (range 0.287–0.323) of SL; number of scales around caudal peduncle, SPc, median 16 (range 12–16).

Description. Body round-oval shape (Figure 2, no. 21). Head broadly rounded with a small ventrally positioned subterminal mouth, situated ventral to the eye; head and body dorsolaterally compressed. Dorsal fin (a) origin situated about two-thirds of standard length from snout, (b) obliquely orientated, anteriorly higher and posteriorly lower, (c) distal margin crescentic with anterior two or three rays longer than posterior rays, and (d) number of rays 18 ($n = 2$), 19 ($n = 2$), 20 ($n = 7$). Anal fin (a) longer

than dorsal fin, (b) opposite dorsal fin with slightly more anterior origin, (c) obliquely orientated, anteriorly lower and posteriorly higher, (d) anterior 10 or so rays longer than posterior ones, especially in males where they also appear stronger, (e) margin broadly rounded, (f) rays posterior to first 10 with distal margin straight, (g) number of rays 25 ($n = 4$), 26 ($n = 7$). Forked tail fin with rounded lobes. Scales cycloid with reticulate striae, scales extending anteriorly to operculum and pectoral fins (beyond pelvics). Scales on caudal peduncle circumference, 12 ($n = 1$), 13 ($n = 1$), 14 ($n = 2$), 15 ($n = 1$), 16 ($n = 6$). Caudal peduncle slender, subcylindrical entire length, usually 19.7% (18.5–20.8%) of SL (Table 1). Males with kink in anal fin base, which is absent in juveniles and females where the anal fin base is straight.

Colour in preservation. Light beige.

Ecology. Only collected at one site near camp 1 where local fisherwomen had poisoned a small stream. One of two mormyrids present there and it accounted for less than 4% of the population. The habitat was a medium-sized stream, sand substrate with lots of leaf litter and marginal grass. *Petrocephalus petersi* sp. nov. is regarded as rare, and prefers freshwater (<1% salinity). Online Figure 11.

Distribution. Presently only known from the Zambezi delta region.

Etymology. The species name *petersi* is given in honour of the German herpetologist Wilhelm C. H. Peters who, until recently, during his *Naturwissenschaftliche Reise nach Mossambique 1842–1848*, had carried out the only major fish survey of the lower Zambezi region, and discovered many of the endemics and other more widespread species (Peters 1868; Bills 2000).

Remarks. In comparison, *P. petersi* sp. nov. is characterized by a very long PAL, long PDL, long LSc and LSo, quite high BD, and a usually high SPc.

***Petrocephalus squalostoma* (Boulenger, 1915)**
(Online Figure 12)

Marcusenius squalostoma Boulenger, 1915: 162.

Petrocephalus squalostoma (Boulenger, 1915): Taverne 1972: 162. Current status: valid as *Petrocephalus squalostoma* (Boulenger, 1915).

Type specimens. Syntypes: (5) BMNH 1920.5.26.1(2) studied, MRAC 14352-54 (3), not studied.

Type locality. Tributary of Lukinda River, a tributary of Moero Lake, Democratic Republic of Congo, estimated at 8.51° S, 28.96° E (coordinates cited from Lavoué Forthcoming 2012).

Diagnosis. Number of dorsal fin rays, nD, 18–21; of anal fin rays, nA, 29–31; predorsal length, PDL, 0.6671–0.673 of SL; preanal length, PAL, 0.598–0.603 of SL; body depth, BD, 0.329–0.335 of SL; caudal peduncle depth, CPD, 0.346–0.388 of CPL, caudal peduncle length; length of snout to posterior orbital rim of eye, LSo, 0.409–0.441 of

head length, HL; distance anterior base of pectoral fin to anterior base of pelvic fin, PPF, 0.198–0.208 of SL; length of dorsal fin, LD, 0.160–0.174 of SL.

Description. Body asymmetrically oval shape with long, prominent, arched back and deep body. Head broadly rounded, with very short snout to posterior orbital rim, LSo, 0.409–0.441 of head length, HL. HL 0.263–0.280 of SL. Eye diameter, OD, 0.223–0.257 of HL. Small mouth ventrally located under the eye; head and body dorso-laterally compressed. Dorsal fin set far back, at about two-thirds of standard length from snout, starting above the fourth or fifth ray of the anal fin. Predorsal length, PDL, 0.667–0.673, preanal length, PAL, 0.599–0.603. Number of dorsal fin rays, nD 18–21, of anal fin rays, nA 29–31. Anal fin, LA, with 0.241–0.250 of SL longer than and opposite dorsal fin, with length, LD, 0.160–0.174 of SL. Forked tail fin with rounded, slightly pointed lobes on slender, subcylindrical caudal peduncle the depth of which, CPD, is 0.346–0.388 its length, CPL. Length of pectoral fins, LPF, 0.638–0.689 of HL. Length of caudal peduncle, CPL, 0.184–0.192 of SL. Scales extending anteriorly to operculum and pectoral fins. The number of circumpeduncular scales, SPc, 12. Body depth, BD, 0.329–0.335 of standard length. Pectoral to pelvic fin distance, PPF, 0.198–0.208 of SL.

Colour in preservation. Homogeneously brown.

Ecology. Unknown.

Remarks. Values for PDL, PPF and BD that are either highest or in the uppermost range among the present assemblage of *Petrocephalus* species are distinctive of *P. squalostoma*.

Etymology. Perhaps from Latin *squalidus*, without ornament, and Greek *stoma*, mouth.

Petrocephalus steindachneri Fowler, 1958 (resurrected species)
(Figure 2, no. 25)

Petrocephalus steindachneri Fowler, 1958: 8; *nomen novum* for *Petrocephalus affinis* sp. nov.? Steindachner, 1914: 536–537, more fully described by Steindachner 1916: 62–63, which is preoccupied by *Mormyrus (Petrocephalus) affinis* Sauvage, 1879. Synonym of *Petrocephalus catostoma* (Günther 1866): Seegers 1996:82.

Type specimens. Syntypes: NMW 55.118:1–3 (3), NMW 55117(1), studied.

Type locality. Msola Brook, near Kiperege, Ulanga River system, Rufiji basin, Tanzania.

Diagnosis (n = 3). Predorsal length, PDL, mean 0.632 (range 0.623–0.641) of SL; preanal length, PAL, mean 0.609 (range 0.601–0.616) of SL; dorsal fin length, LD, mean 0.193 (range 0.173–0.206) of SL; anal fin length, LA, mean 0.238 (range 0.222–0.252) of SL; distance dorsal fin origin to end of caudal peduncle, pD, mean

0.42 (range 0.402–0.432) of SL; length of caudal peduncle, CPL, mean 0.204 (range 0.195–0.211) of SL; depth of caudal peduncle, CPD, mean 0.3 (range 0.285–0.313) of CPL; length of snout to centre of eye, LSc, mean 0.322 (range 0.311–0.343) of HL; length of snout to posterior orbital rim of eye, LSo, mean 0.436 (range 0.434–0.438) of HL; head length, HL, mean 0.273 (range 0.272–0.274) of SL; distance between the pair of nares of one side, Na, mean 26.25 (range 21–30) times in HL, head length; body depth, BD, mean 0.308 (range 0.294–0.328) of SL; dorsal fin ray number, nD, median 24.5 (range 22–27); anal fin ray number, nA, median 30 (range 26–31).

Remarks. The most useful characters to distinguish *P. steindachneri* from other *Petrocephalus*, especially eastern and northern ones, are: dorsal fin ray number (nD) and length of dorsal fin (LD/SL) high, long head (HL/SL), slender caudal peduncle (CPD/CPL low).

Petrocephalus stuhlmanni Boulenger, 1909 (resurrected species)
(Figure 2, no. 2)

Petrocephalus stuhlmanni Boulenger, 1909: 56. Whitehead and Greenwood 1959: 286 (synonymy with *Petrocephalus catostoma catostoma*).

Type specimens. Holotype (unique): BMNH 1907.12.3.1 (studied).

Type locality. Kingani River, Tanzania.

Diagnosis. Dorsal fin length, LD 0.152 of SL; length of snout to posterior orbital rim of eye, LSo 0.382 of HL; number of scales around caudal peduncle, SPc 12; distance between the pair of nares of one side, Na 25.8 times in HL, head length; depth of caudal peduncle, CPD 0.389 of CPL, caudal peduncle length; body depth, BD 0.301 of SL; predorsal length, PDL 0.643 of SL; preanal length, PAL 0.596 of SL; anal fin length, LA 0.239 of SL; distance dorsal fin origin to end of caudal peduncle, pD 0.398 of SL; length of snout to centre of eye, LSc 0.288 of HL; head length, HL 0.276 of SL; dorsal fin ray number, nD, range₁ 20–22, range₂ 19–21 ($n = 9$); anal fin ray number, nA, range₁ 25–29, range₂ 25–29 ($n = 9$); number of lateral line scales, SLS, range₁ 35–38 (range₁: Boulenger 1909: 56–57, with n unknown; range₂: Whitehead and Greenwood 1959: 294).

Remarks. *Petrocephalus stuhlmanni* is distinguished from all other *Petrocephalus* by the combination of a very short dorsal fin (LD/SL) that originates well behind the anal fin, a very low snout length (LSo/HL) and a great head length (HL/SL). “Head slightly longer than deep; with convex upper profile” (Boulenger 1909: 56).

Petrocephalus tanensis (Whitehead and Greenwood, 1959), elevated to species rank
(Figure 2, nos 10, 10a; online Figure 13)

Petrocephalus catostoma tanensis Whitehead and Greenwood, 1959: 286. Tana-churchill, Seegers et al. 2003: 29.

Type specimens. Holotype: BMNH 1963.11.29.1 collected at Kenya, Lower Tana River, Garsen (a settlement in Kenya's Coast Province). Paratypes: BMNH 1963.11.29.2–8 (eight specimens). Studied.

Type locality. Garsen, Tana River, Kenya.

Diagnosis. Distance dorsal fin origin to end of caudal peduncle, pD, mean 0.448 (range 0.427–0.472) of SL; dorsal fin length, LD, mean 0.192 (range 0.167–0.222) of SL; number of dorsal fin rays, nD, median 24 (range 22–27); body depth, BD, mean 0.299 (range 0.257–0.356 of SL; anal fin length, LA, mean 0.239 (range 0.214–0.257) of SL; depth of caudal peduncle, CPD, mean 0.346 (range 0.291–0.439) of CPL, length of caudal peduncle; predorsal length, PDL, mean 0.612 (range 0.574–0.645) of SL; head length, HL, mean 32.9 (range 27.3–42.8) times Na, distance between the pair of nares of one side. EOD characteristics at 25°C and “2% threshold criterion” (see Material and methods): peak amplitude of P2 phase, P2amp, in males, mean 0.534 (range 0.435–0.69) of P1amp, peak amplitude of P1 phase; in females, mean 0.375 (range 0.021–0.74) of P1amp; duration of P2 phase, P2dur, mean 256 μ s (range 105–510 μ s); duration of P1 phase, P1dur, mean 130 μ s (range 95–198 μ s); duration of N phase, Ndur, 46 μ s (range 31–191 μ s), negative peak amplitude (absolute value) of N phase, Namp, mean –3.1 (range –2.382 to –3.748) of P1amp.

Description. Body oval shape, dorsally deep and rounded, ventrally rather flat (Figure 2, no. 10). Head broadly rounded with a small ventrally positioned subterminal mouth, situated ventral to the eye; head and body dorsolaterally compressed. Dorsal fin (a) origin situated almost two-thirds of standard length from snout, (b) obliquely orientated, anteriorly higher and posteriorly lower, (c) distal margin crescentic with anterior two or three rays longer than posterior rays, and (d) number of rays 22 ($n = 1$), 23 ($n = 12$), 24 ($n = 19$), 25 ($n = 18$), 26 ($n = 2$). Anal fin (a) longer than dorsal fin, (b) opposite dorsal fin with slightly more anterior origin, (c) obliquely orientated, anteriorly lower and posteriorly higher, (d) anterior 10 or so rays longer than posterior ones, especially in males where they also appear stronger, (e) margin broadly rounded, (f) rays posterior to first 10 with distal margin straight, (g) number of rays 26 ($n = 1$), 27 ($n = 16$), 28 ($n = 24$), 29 ($n = 13$). Forked tail fin with rounded lobes. Scales cycloid with reticulate striae, scales extending anteriorly to operculum and pectoral fins (beyond pelvics). Scales in lateral series, 36 ($n = 12$), 37 ($n = 14$), 38 ($n = 1$). Scales on caudal peduncle circumference, 12 ($n = 37$), 13 ($n = 2$), 14 ($n = 14$). Caudal peduncle slender, subcylindrical entire length, usually 22.3% (19.3–24.7%) of SL (Table 1). Electric organ discharge a triphasic pulse with strong head-positive phase P1 followed by head-negative main phase N, and weaker head-positive P2 phase (Figure 10); P2 phase stronger in males than in females of same size. Pulse duration, median 403 (312–735) μ s in females ($n = 15$), and shorter median, 307 (276–391) μ s, in males ($n = 15$); 25°C, 2% threshold criterion. Males with kink in anal fin base which is absent in juveniles and females where the anal fin base is straight.

Colour in preservation. Light ochre.

Colour in life. Grey-silver, underside lighter, paired fins light and transparent.

Ecology. Despite the dry season, the terminal section of the Tana River was a strong-flowing river with steep and high borders accompanied by gallery forest. The water was muddy brown. Riparian reed vegetation not very prominent.

Distribution. “From Hola, Wema and Garsen, Tana River. Confined to the Tana River and probably not occurring above Garissa (600 feet above sea level)” (Whitehead and Greenwood 1959); “apparently missing from the Athi” (Whitehead 1962). Garissa is about 250 km from the Indian Ocean, and the other localities within 130 km or less.

Etymology. Not explained by Whitehead and Greenwood (1959) but clearly thought to be an endemic species to the Tana River.

Remarks. Longest pD among all samples, very long LD, very high nD, and high values for BD, LA, CPD while those for PDL and Na low. EOD distinguished by very strong Namp (modal 3.17 times P1amp), strong P2amp (modal 0.47 times P1amp), and very short Ndur (modal 37 μ s at 25°C). EOD with strongest Namp in spite of shortest Ndur and smallest Narea, short P1dur, P1Nsep shortest, P1P2 shortest, NP2 shortest.

Petrocephalus wesselsi Kramer and Van der Bank, 2000
(Figure 2, no. 3; online Figure 14)

Type specimens. Holotype: ZSM 28556 (one specimen) from Sabie River, Kruger National Park, South Africa. Paratypes: ZSM 28554 - ZSM 28565 (12 specimens); SMF 28266 (13 specimens), SAIAB (RUSI) 054449 (13 specimens). Studied.

Type locality. Sabie River, Kruger National Park, bridge near Lower Sabie tourist camp, South Africa, 25°07' S, 31°55' E.

Discussion

Following a multitude of new species descriptions by the early explorers of Africa's freshwater ichthyofauna, there has been a strong tendency to synonymize younger names. Some of these synonymizations no longer appear justified, especially those that were not based on a critical comparison of populations, even when samples were taken from separate and distant river systems. Today, a mere similarity to the eye between two forms of fish, that were sometimes represented by very few specimens, is regarded as insufficient; we seek to decide systematic questions on the basis of a sufficient sample size and statistical comparisons of quantitative characters. Among other techniques, multivariate procedures greatly aid in establishing whether or not differentiation is present. In recent years Africa's freshwater bodies have proven to be far more species rich than thought previously. This has been observed in several genera, such as *Petrocephalus* (Bigorne and Paugy 1991; Kramer and Van der Bank 2000; Lavoué et al. 2004, 2010), *Marcusenius* (Bigorne and Paugy 1990; Boden et al. 1997; Kramer et al. 2007), *Hippopotamyrus* (Lévêque and Bigorne 1985; Kramer et al. 2004, Kramer and Swartz 2010), *Pollimyrus* (Kramer et al. 2003), *Cyphomyrus* (Kramer and Van der Bank 2011), *Campylomormyrus* (Feulner et al. 2006, 2007), and *Paramormyrops* (Sullivan et al. 2004).

For example, in the present study several new *Petrocephalus* species are recognized for an area that still is or has formed part of the Okavango–Makgadikgadi system in the past (Moore and Larkin 2001). The Makgadikgadi is a salt pan today but was a huge lake as recently as 2000 years ago. This system is thought to have represented a centre for explosive speciation for haplochromine cichlids, from where several adjacent river systems were seeded with the species we find today (Joyce et al. 2005). The presence of five rather than a single *Petrocephalus* species (*P. okavangensis* sp. nov., *P. magnitrunci* sp. nov., *P. magnoculis* sp. nov., *P. longicapitis* sp. nov. and *P. wesselsi*) in rivers that are or have been associated with the Okavango–Makgadikgadi system supports this notion.

The present study shows that the past tendency for a clean-up of the genus *Petrocephalus* by synonymizations has gone too far. This is especially clear for tropical–Atlantic forms such as the Congoan species *haullevillii* and *stuhlmanni congicus*. Even when only including southern African forms, the hypothesis of a *Petrocephalus catostoma* species complex, that is, closely related sibling species or subspecies, cannot be maintained in the present form. As shown by DNA sequence analysis (Figure 13 and Table 9), the two eastern species (*P. catostoma* and *P. wesselsi* from near the Indian Ocean) form a sister clade to the two western species (*P. longicapitis* sp. nov. and *P. magnoculis* sp. nov. from the Upper Zambezi/Cunene Rivers). The two latter species do not form part of a *P. catostoma* species complex. It is a widely established observation that the Victoria Falls separate a western from an eastern fish fauna in southern Africa (e.g. Skelton 2001; Kramer and Van der Bank 2011).

We based our study mainly on a comparison of external morphology, using among other techniques PCA, which allows comparison of fish shape. We conclude that the first three principal components readily account for consistent morphological gradients in churchill fish. They seem to suggest that geographical differentiation in morphology reflects adaptations for different life styles. There is a clear gradient for setting back the unpaired fins to increased trunk length and depth, with caudal peduncle depth also increasing (for example, Sabie churchills, *P. wesselsi*). This seems to be a trend for increasing swimming speed and acceleration, which is adaptive for overcoming strong currents as found in short rivers arising from high mountains (such as the South African escarpment, the habitat of *P. wesselsi*). The converse is increased length of unpaired fins with shorter trunk (*P. longianalis* sp. nov. from the tropical Luapula system), probably for increased manoeuvrability and adroit swimming while feeding. A similar differentiation of body shape is seen in the allopatric southern African bulldog species, *Marcusenius macrolepidotus/altisambesi/pongolensis* (Kramer et al. 2007).

Independent of anatomy was the study of EODs, which are characteristic of all mormyrids; however, pulse waveform, pulse duration and the sequence of interpulse intervals differ widely in a species-characteristic fashion (reviews: Kramer 1990, 1996, 2009; Moller 1995). In species with a sizable P2 phase to their EOD the males show a stronger P2amp than their respective females (*P. longicapitis* sp. nov., *P. tanensis*, and the Cunene churchill, but not *P. wesselsi* nor *P. okavangensis* sp. nov., if the two individuals of the latter species studied are typical). As hypothesized by Bratton and Kramer (1988) for the West African *Pollimyrus adspersus* with a similar, triphasic EOD waveform (and a similar, statistically significant sex difference with wide overlap), a stronger P2 phase in male EODs may be a result of a higher testosterone titre. Testosterone is well-known for fostering the build-up of stronger vertebrate muscle, the tissue of

which mormyrid electric organs are made. By this hypothesis, the head-negative, electrically evoked N phase would be triggered earlier by (and relative to) a stronger male P phase potential that is split into two by the much shorter N phase potential, resulting in a stronger P2amp. These ideas are compatible with the most recent review on the morphology and physiology of *Petrocephalus* species EODs by Lavoué et al. (2004), and have been mathematically modelled in species with a similar discharge by Westby (1984) and Markowski et al. (2008).

Evidence for a role of a sex difference in P1amp/P2amp ratio in assortative mating, or sexual selection, as suggested by Westby and Kirschbaum (1982) and Crawford (1992), is lacking. Neither in *Pollimyrus adspersus* (Bratton and Kramer 1989; Crawford 1991), nor in *Petrocephalus longicapitis* sp. nov. (Eglhuber and Kramer, unpublished results) have observational and experimental studies been successful in demonstrating such an effect. [*Pollimyrus adspersus*' identity has often been confused with that of *Pollimyrus isidori* in much of the literature from the 'electric fish community' before Crawford (1997).] *Petrocephalus longicapitis* sp. nov. (and certainly other mormyrids as well) may signal sexual identity either by behaviour or by acoustic signals (Lamml and Kramer 2008).

However, even minute changes in P1amp/P2amp ratio (due to a phase shift of only 2 μ s) are detected by trained, food-rewarded *P. adspersus*, and seem to be the basis for species and individual identification, as suggested by Graff and Kramer (1992) and demonstrated by Paintner and Kramer (2003). Therefore, the differentiation of this character among the *Petrocephalus* species flock studied in the present paper is clearly of taxonomic significance.

It is also clear that many species, especially the wide-ranging ones, show considerable intraspecific variation. This may occur in the form of a geographic cline, as in *Cyphomyrus discorhynchus* for both anatomical and electrical characters (Kramer and Van der Bank 2011), or in a geographically more complex pattern. For example, both anatomical and "electrical" analyses demonstrated a marked degree of differentiation in *P. wesselsi* of different South African origins. PCA and discriminant analyses of both electrical and anatomical characters yielded congruent results, confirming the usefulness of EOD as a systematic tool. The inclusion of *P. longicapitis* sp. nov. in the analysis suggested that we are probably dealing with intraspecific variation in South Africa. *Petrocephalus longicapitis* sp. nov. was chosen because the Limpopo valley was once the Zambezi's outlet to the Indian Ocean, hence the Upper Zambezi may have seeded South Africa with churchills (however, this hypothesis is not supported by the present DNA sequence analysis, which shows two sister clades; Figure 13). There is probably still a common water divide, for example, at the level of the sources of the Shashe River and other Limpopo tributaries to the East. An alternative scenario of how South Africa was invaded by churchills is by "river hopping" along the the Indian Ocean coast line, with *P. petersi* sp. nov. as nearest northern neighbour. The strong differentiation of *P. wesselsi* from their northern relatives may be the result of the more extreme temperature variation in South Africa that includes occasional freezing, more rain in the coastal ranges, and steep gorges with strong current.

What remains to be done is to sample more material, especially (but not only) for the resurrected species, some of which are represented by no more than their (unique) holotype, for morphological, DNA, EOD and behavioural studies. This is certainly true for most of the Indian Ocean-orientated origins, including Mozambique, Malawi, Tanzania and beyond (Kenya, Somalia), but also tropical and more central areas

(such as northern Zambia, Lake Moero, the Congo, Lake Rukwa, Lake Victoria). The Upper Zambezi/Kwando/Okavango/Cunene systems also need more extensive exploration, as does the whole of largely unknown Angola. Only then will it be possible to reconstruct the phylogeography of the southern and eastern African *Petrocephalus* species in a satisfactory fashion.

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Appendix 1: Principal components analysis on morphology

For a principal component analysis on correlations among anatomical characters, we used the original data sample set from which Table 1 had been computed, excluding 42 specimens. Excluded were all local samples with $n < 3$, and also Type material for which we had better preserved, more numerous samples.

Principal Components on correlations. Southern and eastern *Petrocephalus* species, anatomical characters. All allopatric populations with $n \geq 3$ specimens* included.

Eigenvalue	4.274	2.274	1.906	1.286	0.881	0.728	0.471
Percent	32.876	17.493	14.664	9.891	6.774	5.597	3.62
Cumulative %	32.876	50.37	65.033	74.924	81.698	87.295	90.915
PCA structure (component loadings)							
PDL/SL	0.7393	-0.4815	0.1183	0.0186	-0.1379	-0.1820	0.1667
PAL/SL	0.7711	-0.1557	0.3687	0.1220	-0.0869	-0.2608	-0.1358
LD/SL	-0.2766	0.3084	0.7841	0.0508	-0.0800	0.2575	0.0458
LA/SL	-0.6286	-0.4886	-0.1727	0.3733	-0.1587	0.2832	0.1761
pD/SL	-0.553	0.6263	0.2357	0.3319	0.0933	-0.0384	-0.0153
CPL/SL	-0.1639	0.8314	-0.252	0.1174	0.0201	-0.3050	0.2052
CPD/CPL	0.7078	0.2263	0.2383	0.1080	-0.3032	0.3494	-0.2669
LSc/HL	0.3425	-0.2364	0.2022	0.3112	0.8144	0.0490	-0.0852
HL/SL	0.4890	0.1062	0.4107	-0.6093	0.1205	0.0743	0.3785
BD/SL	0.5101	-0.0370	0.236	0.7178	-0.1551	-0.1047	0.2817
nDges	-0.5830	0.0282	0.7279	-0.0768	0.0072	-0.0625	-0.0305
nAges	-0.7143	-0.5844	0.1401	-0.0162	0.0284	0.0839	0.1381
SPc	0.6004	0.3722	-0.3483	0.0599	0.1372	0.4833	0.1667

*Data set of $n = 402$ specimens, 42 of which excluded: (a) Types: *P. degeni* ($n = 1$), *P. stuhlmanni* ($n = 1$), *P. catostoma* ($n = 5$), *P. steindachneri* ($n = 1$), *P. s. congicus* ($n = 2$), *P. c. tanensis* ($n = 9$); (b) allopatric populations: Kwando ($n = 1$), all specimens from Malawi Lake region ($n = 5$), Chiuta ($n = 1$), Luongo ($n = 2$), Lunga ($n = 1$), Rukwa ($n = 1$), and all *P. wesselsi* specimens except those from Sabie (type locality), that is, Pongola ($n = 1$), Limpopo ($n = 7$), Mbuluzi River ($n = 4$).

Variables excluded from PCA were LSo and Na/HL. Outliers not excluded.

Appendix 2: Comparison of EODs in females and males of southern and eastern African *Petrocephalus* species for samples from different origins. Least-squares regression of EOD waveform characters with fish standard length (only specimens with SL > 5.2 cm). Abbreviations of EOD characters, see Methods.

	Namp (V)	P2amp (V)	Pldur (μ s)	Ndur (μ s)	P2dur (μ s)	PlNsep (μ s)	Plarea ($V \times \mu$ s)	Narea ($V \times \mu$ s)	P2area ($V \times \mu$ s)
Tana									
$r^2(\sigma^2)$	0.164	0.009	0.438	0.001	0.013	0.026	0.313	0.049	0.015
$r^2(\Omega)$	0.035	0.438	0.392	0.146	0.105	0.084	0.315	0.057	0.386
slope(σ^2) \pm SE	0.061 \pm 0.062	0.007 \pm 0.032	-5.236 \pm 2.65	0.066 \pm 1.062	-2.656 \pm 10.539	-0.321 \pm 0.879	-1.181 \pm 0.782	-1.156 \pm 2.275	-0.589 \pm 2.137
slope(Ω) \pm SE	-0.05 \pm 0.072	0.103 \pm 0.0323	-11.43 \pm 3.945	-3.439 \pm 2.305	-39.49 \pm 31.97	-0.8031 \pm 0.7367	-2.905 \pm 1.188	-4.347 \pm 4.900	4.049 \pm 1.416
Y-icpt (σ^2) \pm SE	-3.409 \pm 0.514	0.478 \pm 0.265	162.84 \pm 21.97	32.816 \pm 8.806	185.1 \pm 87.36	29.254 \pm 7.287	46.473 \pm 6.483	66.693 \pm 18.858	40.163 \pm 17.713
Y-icpt (Ω) \pm SE	-2.824 \pm 0.609	-0.461 \pm 0.272	225.2 \pm 33.23	71.79 \pm 19.42	639.57 \pm 269.35	36.54 \pm 6.206	66.08 \pm 10.01	116.91 \pm 41.28	10.29 \pm 11.93
$P_{\text{slope}} \sigma^2$	0.367	0.84	0.1051	0.953	0.811	0.7296	0.1913	0.633	0.794
$P_{\text{slope}} \Omega$	0.5052	0.0072	0.0125	0.1595	0.2386	0.2955	0.0295	0.3911	0.0134
$t(\sigma^2)$	0.992	0.212	-1.976	0.062	-0.252	-0.366	-1.511	-0.508	-0.275
$t(\Omega)$	-0.685	3.186	-2.897	-1.492	-1.235	-1.090	-2.445	-0.887	2.86
Upper Zambezi									
$r^2(\sigma^2)$	0.00005	0.512	0.008	0.009	0.012	0.092	0.074	0.011	0.134
$r^2(\Omega)$	0.002	0.523	0.142	0.111	0.003	0.27	0.303	0.086	0.252
slope(σ^2) \pm SE	0.003 \pm 0.096	-0.072 \pm 0.02	1.854 \pm 5.585	-1.08 \pm 3.061	6.162 \pm 15.299	-2.185 \pm 1.909	-1.699 \pm 1.668	-2.293 \pm 5.968	-4.276 \pm 3.01
slope(Ω) \pm SE	-0.006 \pm 0.034	-0.039 \pm 0.01	-2.871 \pm 1.825	-1.002 \pm 0.732	-2.016 \pm 10.337	-1.448 \pm 0.614	-1.305 \pm 0.511	-1.834 \pm 1.542	-2.767 \pm 1.233
Y-icpt (σ^2) \pm SE	-2.714 \pm 0.772	1.044 \pm 0.157	108.35 \pm 44.93	57.433 \pm 24.625	132.39 \pm 123.08	53.906 \pm 15.357	57.873 \pm 13.421	97.462 \pm 48.013	71.092 \pm 24.211
Y-icpt (Ω) \pm SE	-2.682 \pm 0.27	0.691 \pm 0.078	152.445 \pm 14.664	55.375 \pm 5.881	184.733 \pm 83.043	46.949 \pm 4.936	54.197 \pm 4.106	90.803 \pm 12.39	53.349 \pm 9.903
$P_{\text{slope}} \sigma^2$	0.979	0.0027	0.7452	0.7298	0.6937	0.2731	0.3272	0.707	0.179
$P_{\text{slope}} \Omega$	0.8512	0.001	0.1366	0.1911	0.848	0.0325	0.0221	0.2529	0.0403
$t(\sigma^2)$	0.027	-3.692	0.332	-0.353	0.403	-1.144	-1.018	-0.384	-1.421
$t(\Omega)$	-0.191	-4.059	-1.573	-1.369	0.195	-2.356	-2.533	-1.189	-2.245
$r^2(\sigma^2)$	0.573	0.578	1.4×10^{-7}	0.215	0.695	0.094	0.008	0.027	0.72
P_{nesszisi} (Sabie River)									
$r^2(\Omega)$	0.525	0.598	0.001	0.215	0.006	0.135	0.006	0.042	0.371
slope(σ^2) \pm SE	0.214 \pm 0.058	-0.022 \pm 0.006	-0.006 \pm 5.15	9.18 \pm 5.54	-34.71 \pm 7.262	3.511 \pm 3.437	0.842 \pm 2.934	-2.028 \pm 3.833	-5.14 \pm 1.014
slope(Ω) \pm SE	0.188 \pm 0.039	-0.017 \pm 0.003	0.438 \pm 2.632	4.413 \pm 1.84	-8.56 \pm 23.42	2.088 \pm 1.152	0.48 \pm 1.386	-2.213 \pm 2.3	-3.441 \pm 0.978
Y-icpt (σ^2) \pm SE	-4.167 \pm 0.492	0.299 \pm 0.05	193.08 \pm 43.4	5.862 \pm 46.68	619.91 \pm 61.189	20.753 \pm 28.961	62.665 \pm 24.721	117.684 \pm 32.297	63.644 \pm 8.546
Y-icpt (Ω) \pm SE	-3.912 \pm 0.296	0.255 \pm 0.023	176.68 \pm 19.94	37.01 \pm 13.935	467.7 \pm 177.37	27.595 \pm 8.724	57.276 \pm 10.495	111.696 \pm 17.42	50.979 \pm 7.405
$P_{\text{slope}} \sigma^2$	0.0043	0.0041	0.9991	0.1285	0.0007	0.3311	0.7799	0.6083	0.0005
$P_{\text{slope}} \Omega$	< 10^{-4}	< 10^{-4}	0.8693	0.0258	0.7184	0.0842	0.7325	0.347	0.002
$t(\sigma^2)$	3.665	-3.701	-0.001	1.657	-4.779	1.022	0.287	-0.529	-5.068
$t(\Omega)$	4.816	-5.591	0.167	2.398	-0.365	1.813	0.346	-0.962	-3.52

No significant regression for PIP2sep, NP2sep with SL anywhere.