Journal of Natural History
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tnah20

Petrocephalus Marcusen, 1854 (Osteoglossomorpha: Mormyridae) of the Bangweulu-Mweru ecoregion (Luapula River system, Congo basin), with the description of a new species

Sébastien Lavoué [a]

[a] Institute of Oceanography, National Taiwan University, Roosevelt Road, Taipei, 10617, Taiwan

Version of record first published: 10 Sep 2012.

Journal of Natural History
Vol. 46, Nos. 35–36, September 2012, 2159–2178

Taylor & Francis
Taylor & Francis Group

Petrocephalus Marcusen, 1854 (Osteoglossomorpha: Mormyridae) of the Bangweulu-Mweru ecoregion (Luapula River system, Congo basin), with the description of a new species

Sébastien Lavoué*

Institute of Oceanography, National Taiwan University, Roosevelt Road, Taipei 10617, Taiwan

(*Received 2 September 2011; final version received 22 March 2012; printed 20 September 2012*)

A recent collection of African electric fish of the genus *Petrocephalus* from the Bangweulu-Mweru ecoregion of the Congo basin comprises two endemic species, *Petrocephalus squalostoma* (Boulenger, 1915), which was previously known only from its type specimens and another specimen, and a new species described herein as *Petrocephalus frieli* **sp. nov.** An exclusive set of morphological characters distinguishes *P. frieli* sp. nov. from *P. squalostoma* and all other species of *Petrocephalus* from the Congo basin. *Petrocephalus frieli* sp. nov. can further be distinguished from the East African *Petrocephalus catostoma catostoma* (Günther, 1866) in having only 12 circumpenduncular scales (versus 15/16 in *P. c. catostoma*). A molecular phylogenetic analysis confirms the distinctiveness of *P. squalostoma* and *P. frieli* sp. nov. among a sampling of 18 species of *Petrocephalus*. Previous reports of *Petrocephalus simus* Sauvage, 1879 from the Bangweulu-Mweru ecoregion probably represent misidentifications and the occurrence of *P. c. catostoma* is not confirmed.

Keywords: *Petrocephalus*; Mormyridae; Africa; lac Moéro; lac Bangouéolo; integrative taxonomy; cytochrome *b*

Introduction

The vast basin of the Congo River covers ∼ 4 million km^2 of Central Africa, and it represents a complex hydrographical system (Runge 2007). Whereas the whole Congo basin is recognized as a distinct biogeographic entity because of its overall faunal homogeneity (Roberts 1975; Lévêque 1997), a recent work aiming to establish the world's ecoregions for conservation purposes recognized 16 ecoregions within this basin, each based upon expert knowledge of freshwater species distribution and level of endemism (Thieme et al. 2005; Abell et al. 2008). These ecoregions are not only useful for developing conservation management strategies, but they allow investigation of local taxonomic diversity of otherwise widespread groups of organisms. Herein, the diversity and taxonomy of the African electric fish genus *Petrocephalus* Marcusen, 1854 (Osteoglossomorpha: Mormyridae) is examined in the Bangweulu-Mweru ecoregion, lying in the southeastern-most part of the Congo basin (Figure 1).

The only genus of the subfamily Petrocephalinae, *Petrocephalus* has a widespread distribution in the freshwaters of subtropical and tropical regions of Africa, and currently comprises 30 valid species (Eschmeyer and Fricke 2011). The genus

*Email: microceb@hotmail.com

ISSN 0022-2933 print/ISSN 1464-5262 online

http://dx.doi.org/10.1080/00222933.2012.708449
http://www.tandfonline.com

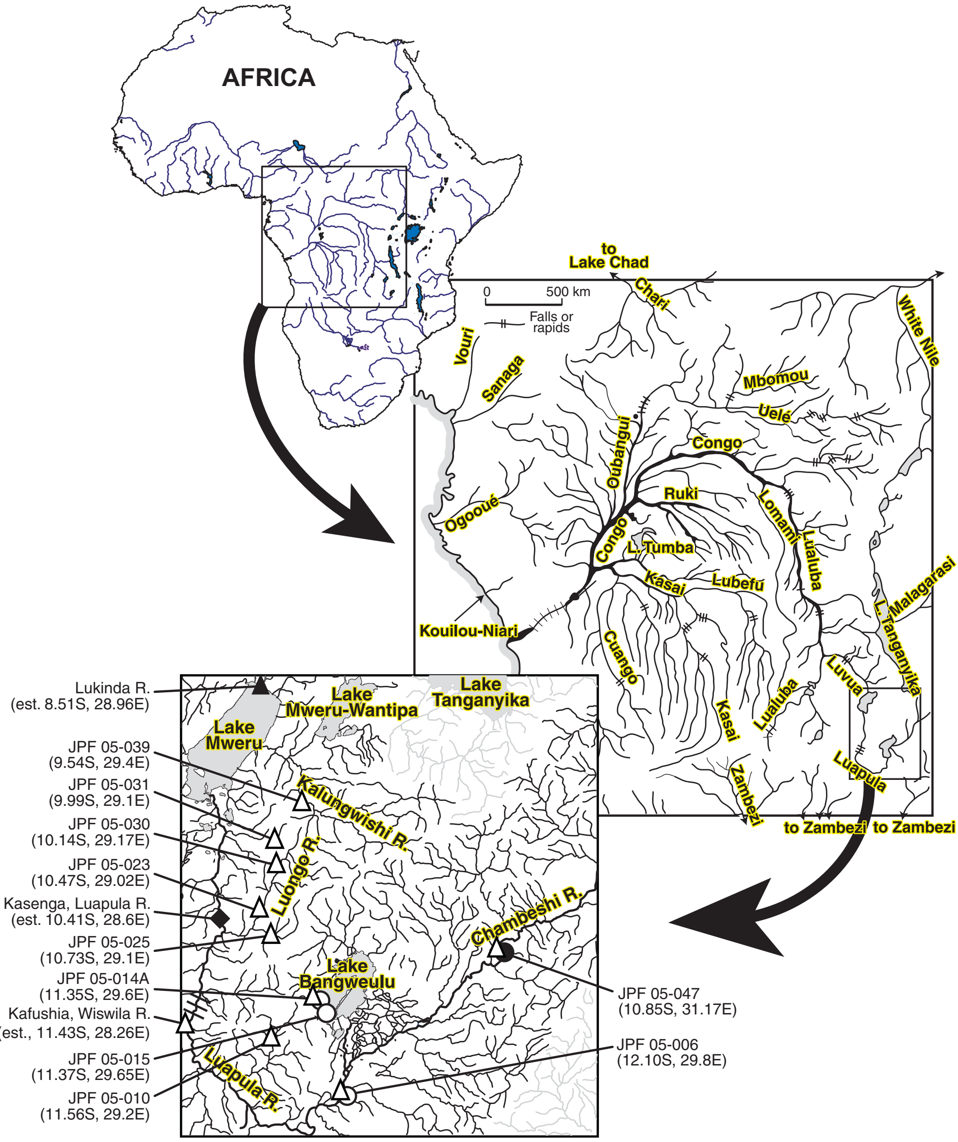

Figure 1. Map of Africa (top right) showing the location of the Congo basin. The first inset at centre details the topography of the Congo River and its main tributaries and rapids/falls sections. The second inset (bottom left) provides a detailed map of the Bangweulu-Mweru ecoregion (comprising the Luapula River basin), located in the southeastern-most part of the Congo River basin. The filled circle indicates the type locality of the new species *Petrocephalus frieli* sp. nov.; open circles indicate additional localities. The filled triangle indicates the type locality of *Petrocephalus squalostoma*; open circles indicate additional localities. Filled diamond marks the estimated location of the first specimen identified as *Petrocephalus simus* by Boulenger (1920) (identification uncertain, see text for details).

Petrocephalus is monophyletic and the sister group of the remaining Mormyridae (i.e. the subfamily Mormyrinae) from which it can easily be distinguished by several unique morphological characteristics; the most salient are the presence of an orbitosphenoid, a basisphenoid, two single unsegmented and unbranched rays at the origin of the dorsal fin and two nostrils closely apposed with the posterior one very close to the eye (Taverne 1969). Moreover, the electric organ discharge waveforms of *Petrocephalus* are always of short duration (Lavoué et al. 2008; Moritz et al. 2009; Kramer et al. 2012). *Petrocephalus* are small fish (typically < 11 cm in standard length), that can form large schools, and are mostly active at night. They may be locally abundant and diverse, as recently found in the Odzala National Park (northwest Congo basin) with 11 sympatric species (Lavoué et al. 2008, 2010). Currently 16 species of *Petrocephalus* have been reported from the Congo basin, with 10 of them being considered endemic (Lavoué et al. 2010). Among these 16 species, the non-endemic polytypic *Petrocephalus catostoma* (Günther, 1866) is represented by two subspecies in this basin: *Petrocephalus catostoma haullevillii* (Boulenger, 1912) and *Petrocephalus catostoma congicus* (David and Poll, 1937). Since the creation of the genus *Petrocephalus* by Marcusen (1854), there has been no taxonomic revision of the Congolese species and subspecies, and the identifications of several of them are still tentative and their distributions are poorly documented.

The Bangweulu-Mweru ecoregion comprises the entire Luapula River system (Thieme et al. 2005; Abell et al. 2008). It is formed by several large lakes along with large floodplains and swampy areas, all interconnected through channels and rivers with rapid and fall sections (Figure 1). From the southeastern-most part, flowing southwest, the Chambeshi River is considered as the source of the Congo River. It flows into Lake Bangweulu through a large papyrus swampy delta area. Then, Lake Bangweulu flows into the Luapula River through again an extensive swampy area. The Luapula River makes a curve, running first south, then west and finally north until Lake Mweru. There are several rapid sections on the course of the Luapula River, the best known being the Mambilima Falls. The Luongo River, the main right tributary of the Luapula River, flows into the Luapula River between two of these rapid sections. Lake Mweru, the largest lake of this ecoregion, receives the waters of the Luapula River at its southern end, and supplies the Luvua River at its northern end. Finally, the Luvua River marks the limit of this region with the rest of the Congo basin when it merges with the Lualaba River, 300 km downstream, after a series of rapids and falls, isolating this region from the rest of the Congo basin. Lying to the east, between Lakes Mweru and Tanganyika, is the Lake Mweru-Wantipa system. This system is connected to Lake Mweru through one of its tributaries, the Kalungwishi River.

This region is recognized for the uniqueness of its fish fauna because of different climatic and ecological conditions coupled with physical isolation from other drainages and the rest of the Congo basin, and its complex geology (Banister 1986; Moore and Larkin 2001; Abell et al. 2008). Historically, the most southeastern part of the Bangweulu-Mweru ecoregion flowed into the Zambezi basin via past connections between this basin and the upper Chambeshi River (Moore and Larkin 2001; Stankiewicz and de Wit 2006). Evidence for these past connections is provided by geological data together with the presence of several fish species of Zambezi origin that have invaded this region. Banister (1986) pointed out that of about 150 species recorded in this region, 18 species are exclusively shared with the Zambezi system.

Other possible connections during heavy rainfall periods could have occurred in the watershed plain lying between both basins (Bell-Cross 1965; Banister 1986).

Previous reports in the Bangweulu-Mweru region mentioned the presence of three species of *Petrocephalus*. First, Boulenger (1915) described *Marcusenius squalostoma* Boulenger, 1915 from a small northern tributary of Lake Mweru, named Lukinda (sometimes Lunchinda R.) (Figure 1). Taverne (1972) moved this species into the genus *Petrocephalus*. *Petrocephalus squalostoma* is a species that was only known from the type series (five syntypes) along with an additional specimen housed in the MRAC collection, identified by Max Poll in 1948 and collected from the same region at the locality of Kafushia, Wiswila River, Luapula River (estimated 11.43° S, 28.26° E) (Figure 1). Five years later, Boulenger (1920) listed a second species of *Petrocephalus* for this region (actually the first one known at this time, because *P. squalostoma* was still placed within the genus *Marcusenius* by the same author) from the locality Kasenga on the Upper Luapula River (estimated 10.41° S, 28.6° E) that he identified as *Petrocephalus simus* Sauvage, 1879, a species described from the Ogooué River in Gabon (Lower Guinea province). Later reports, such as those of Worthington (1933), Ricardo-Bertram (1943), Jackson (1961) or De Kimpe (1964), also mentioned the presence of *P. simus* with or without *P. squalostoma*. In their exploration of the Luongo River basin, Balon and Stewart (1983) reported the presence of *P. simus* at two specific localities. Imai (1985, 1987) in two fisheries reports on the Bangweulu Swamps region reported the occurrence of two species of *Petrocephalus* in fisheries statistics, *P. simus* and, more abundant, *P. catostoma*, which represented the first mention of the second species in this region. Subsequently, Ticheler et al. (1998) also reported the occurrence of *P. catostoma* from the Bangweulu Swamps. Jackson (1989) did not report any *Petrocephalus* from Lake Mweru-Wantipa; he hypothesized that it was the result of periodic severe droughts affecting this area. Museum records and distribution of the *Petrocephalus* species of this region are summarized in *Faunafri* (Paugy et al. 2008) and a comprehensive list of references is provided in CLOFFA (Daget et al. 1984).

The examination of a recent collection of *Petrocephalus* from 10 localities within the Bangweulu-Mweru region, made by Roger Bills, Alex D. Chilala and John P. Friel, reveals the presence of two species of *Petrocephalus*, one of them is new and described here. This study is part of a larger taxonomic revision of the *Petrocephalus* of the Congo basin that is currently in progress.

Material and methods

Specimen sampling

The collection of *Petrocephalus* specimens examined in this study is made from 10 Zambian localities within the Luapula River basin, the upper reaches of the Congo basin (Figure 1): one locality is on the Chambeshi River, two localities are on Lake Bangweulu, two localities are on the upper part of the Luapula River system, downstream of Lake Bangweulu, four localities are on the Luongo River basin, and one locality is on the Kalungwishi River, a tributary of the Lake Mweru system. Given that most of the species of *Petrocephalus* have restricted distributions (Bigorne and Paugy 1991; Hopkins et al. 2007; Lavoué et al. 2010; Kramer et al. 2012), the taxonomic comparisons are mostly limited to species of *Petrocephalus* occurring nearby the Bangweulu-Mweru region (i.e. Congolese and East African species). They include type specimens from all nominal species from Central Africa (Congo and Lower Guinea provinces). Comparative specimens are listed in Lavoué et al. (2004, 2010). Because of the proximity of this region to the Zambezi River basin and their past connections, the original description of *P. catostoma* was consulted (Günther 1866) as well as the recent taxonomic work of Kramer and van der Bank (2000) on *Petrocephalus* spp. of South Africa. Nucleotide sequences of the partial cytochrome *b* gene (590 base pairs from the 3' end) were determined for 10 specimens of *P. squalostoma* from seven localities and for two specimens of the new species from two localities.

Morphology

Methods for making counts and measurements and abbreviations and definitions for each of these counts and measurements follow those given by Boden et al. (1997) as slightly modified by Lavoué et al. (2004). Numbers of dorsal fin rays (DR) and anal fin rays (AR) exclude all unbranched rays; number of scales between the origin of the anal fin and the lateral line (SDL) excludes the pored scale itself.

In some *Petrocephalus* species, up to three dense clusters of Knollenorgan-type electroreceptors [i.e. the Augenrosettes, Nackenrosettes and Kehlrosettes (Harder 1968)] are present in the head. Their presence and their size are two valuable diagnostic characters in the taxonomy of the genus *Petrocephalus* (Lavoué et al. 2010). Their definitions follow those given by Harder (1968).

The sex of each preserved specimen was determined into two categories by examining the body profile along the base of the anal fin (Pezzanite and Moller 1998): "sexually mature males" exhibit a strongly indented anal fin base and "sex undetermined individuals" exhibit a nearly straight anal fin base.

Museum abbreviations: CUMV, Cornell University Museum of Vertebrates, Ithaca, NY; BMNH, Natural History Museum, London; MRAC, Musée Royal de l'Afrique Centrale, Tervuren; SAIAB, South African Institute for Aquatic Biodiversity, Grahamstown.

DNA sequencing and molecular phylogenetic methods

Fin clips were preserved in 95% ethanol in the field and DNA was extracted from them with a standard procedure. Polymerase chain reaction amplification and sequencing conditions of the partial cytochrome *b* gene were as described by Sullivan et al. (2000) using the following *Petrocephalus*-specific primers combination: L15213_MOR (5′-CTA ACC CGA TTC TTT GCC TTC CAC TTC CT-3′) and H15913_MOR (5′-TCG ATC TCC GGA TTA CAA GAC CG-3′). Cytochrome *b* sequences generated in this study have been deposited in the GenBank database under accession numbers JQ435085 to JQ435096.

Twelve new partial cytochrome *b* sequences were included and aligned manually to the dataset published in Lavoué (2011). The alignment does not require any indels and missing data at the 5′-end were coded with question marks. The cytochrome *b* sequences of the following three species of the subfamily Mormyrinae are used together to root the phylogenetic tree: *Myomyrus macrops* Boulenger, 1914, *Mormyrops nigricans* Boulenger, 1899 and *Gnathonemus petersii* (Günther, 1862).

The best maximum likelihood phylogenetic tree with bootstrap proportions at the internal branches was calculated using the software RAxML (Stamatakis 2006) and the graphic interface RAXMLGUI (Silvestro and Michalak forthcoming). All positions and types of substitution were equally considered. Thorough bootstrap searches (1000 replicates) and heuristic phylogenetic searches (100 replicates) were performed under the general time reversible model of nucleotide substitution with rate heterogeneity following a discrete gamma distribution (GTR+Γ) (consult the RAxML v.7.0.4 manual for further details).

Taxonomy

Petrocephalus squalostoma (Boulenger, 1915)
(Figures 2A–C; 3C)

Marcusenius squalostoma Boulenger, 1915: 163.

Pollimyrus squalostoma (Boulenger, 1915): Taverne (1971): 105. (Revised definitions and contents of several mormyrid genera, including *Marcusenius*, with the creation of two genera, *Pollimyrus* and *Brienomyrus*)

Petrocephalus squalostoma (Boulenger, 1915): Taverne (1972): 162. (Descriptive work on the osteology of several mormyrid genera followed by comments on the evolution of the Mormyridae with a revised classification)

Type specimens

Syntypes. BMNH 1920.5.26.1 (two syntypes, two examined), MRAC 14352–54 (three syntypes, one examined); Zambia, Congo basin, Lake Mweru, a tributary of the Lukinda River (currently known as the Lunchinda River), a tributary of Lake Mweru (estimated 8.51° S, 28.96° E, see Figure 1); coll. L. Stappers and M.G. Dhont-De Bie.

Diagnosis

Petrocephalus squalostoma is distinguished from all other *Petrocephalus* species of the Congo province by the following combination of characteristics: body coloration pattern without intense melanin mark, sometimes a faded subdorsal roundish mark present; short dorsal fin with 15–22 branched rays (median 20) and 27–32 branched rays in the anal fin (median 29); more than 13 scale rows between the anterior base of the anal fin and the lateral line; three distinct electroreceptive rosettes in the head.

Description

Morphometric ratios and meristic data for three syntypes and 23 non-type specimens are detailed in Table 1. *Petrocephalus squalostoma* is a medium-sized species within the genus (maximum SL observed = 121.7 mm). Body ovoid, longer than high (mean SL/H = 3.3) and laterally compressed. Head length 3.9 times (mean) in standard length. Snout short (mean HL/SNL = 6.4) and round. Mouth relatively small

Table 1. Principal morphometric ratios and meristic counts for three syntypes [BMNH 1920.5.26 (2), MRAC 14352-54 (one specimen examined)] and 23 non type specimens [CU 91147 (2), CU 91149 (2), CU 91150 (1), CU 91151 (1), CU 91142 (1), CU 95316 (5), CU 91145 (1), CU 91141 (5), CU 91148 (5)] of *Petrocephalus squalostoma* (Boulenger, 1915).

	Syntypes ($n = 3$) (o, o, m)	Syntypes + non-types ($n = 26$)		
		Min–Max	Mean	SD
Standard length (in mm)	63.7, 64.6, 65.8	50.4 – 121.7	68.1	16.3
Head length (in mm)	16.6, 17.9, 18.0	13.6 – 28.6	17.4	3.5
Ratio of standard length (SL):				
SL/body height (H)	3.0, 3.1, 3.1	3.0 – 3.6	3.3	0.1
SL/head length (HL)	3.8, 3.6, 3.7	3.6 – 4.3	3.9	0.2
SL/pre-dorsal distance (PDD)	1.5, 1.5, 1.6	1.5 – 1.6	1.6	0.0
SL/pre-anal distance (PAD)	1.6, 1.7, 1.7	1.6 – 1.8	1.7	0.0
SL/dorsal fin length (DFL)	5.1, 5.5, 5.7	4.7 – 5.8	5.2	0.2
SL/anal fin length (AFL)	3.9, 4.0, 4.0	3.1 – 4.0	3.5	0.2
SL/caudal peduncle length (CPL)	5.6, 6.1, 6.6	5.6 – 7.0	6.2	0.4
SL/mouth width (MW)	15.2, 14.1, 15.1	13.9 – 18.0	15.6	0.9
Ratio of head length (HL):				
HL/snout length (SNL)	7.0, 6.0, 6.4	5.6 – 8.0	6.4	0.6
HL/mouth width (MW)	4.0, 3.9, 4.1	3.6 – 4.5	4.0	0.2
HL/eye diameter (ED)	4.1, 4.1, 4.3	4.1 – 5.0	4.5	0.3
HL/interorbital width (IOW)	2.4, 2.7, 3.0	2.4 – 3.4	3.0	0.2
HL/head width (HW)	1.6, 1.8, 1.9	1.6 – 2.0	1.9	0.1
HL/mouth position (MP)	3.9, 3.3, 3.5	3.2 – 4.2	3.7	0.3
Ratio of caudal peduncle length (CPL):				
CPL/caudal peduncle depth (CPD)	2.5, 2.0, 2.3	2.0 – 3.1	2.6	0.3
		Min–Max	Median	
Meristic counts:				
Dorsal fin branched rays (DR)	18, 15, 17	15–22	20	
Anal fin branched rays (AR)	27, 27, 27	27–32	29	
Number of scales in the lateral line (SLL)	38, 35, 36	35–42	40	
Number of scale rows between the anterior base of the anal fin and the lateral line (SDL)	16, 13, 13	13–17	15	
Number of teeth in the upper jaw (TUJ)	11, 10, 11	5–13	11	
Number of teeth in the lower jaw (TLJ)	16, 16, 17	16–23	19	

Abbreviations: o, other; m, male; SD, standard deviation; Min–Max, minimum–maximum.

(mean HL/MW = 4.0), sub-terminal, opening under the posterior half of the eye. Teeth small and bicuspid, a median of 11 teeth in a single row in the upper jaw, a median of 19 teeth in a single row in the lower jaw. Dorsal and anal fins originate in the posterior half of the body (mean SL/PDD = 1.6 and mean SL/PAD = 1.7). Pre-dorsal distance slightly greater than the pre-anal distance ($1.0 \leq$ PDD/PAD ≤ 1.1). Median dorsal fin branched rays of 20. Median anal fin branched rays of 29. Scales cover the body, except for the head. Lateral line visible and complete, a median count of 40 pored scales along its length. Median scales of 15 between the anterior base of the anal fin and the lateral line. Caudal peduncle thin (mean CPL/CPD = 2.6). Skin on head thick, turning opaque with formalin fixation, masking the eyes (see Figure 2A). Knollenorgans visible, clustered into the three distinct rosettes of Harder (1968).

Petrocephalus squalostoma differs from *Petrocephalus grandoculis* Boulenger, 1920 and *Petrocephalus sauvagii* (Boulenger, 1887) by its fewer number of branched rays

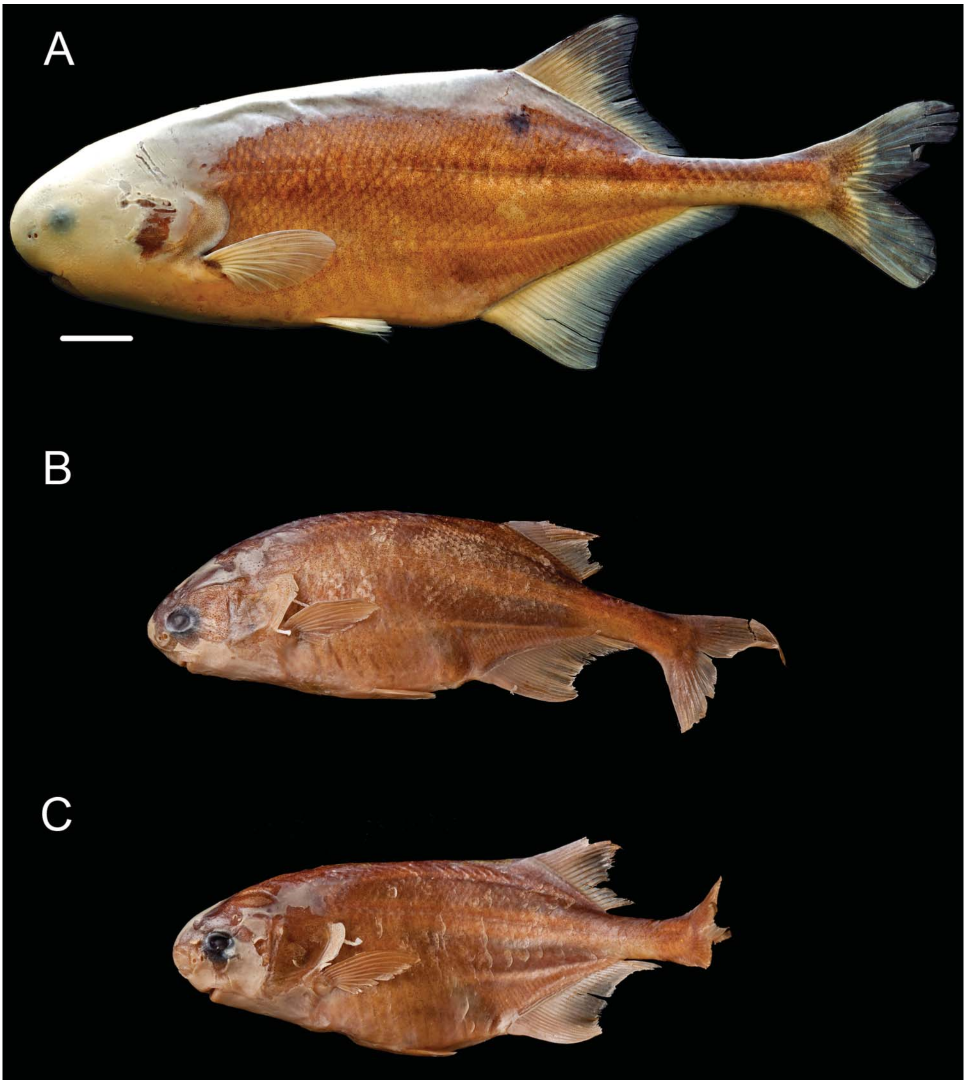

Figure 2. Photographs of preserved specimens of *Petrocephalus squalostoma* from the Bangweulu-Mweru ecoregion, Luapula River system, Congo basin. (A) Preserved specimen (CU 91141, scale bar 1.0 cm) (photo by John P. Sullivan, CUMV). (B, C) Two syntypes (BMNH 1920.5.26.1, same scale bar as in A) (© The Natural History Museum, London).

in the dorsal fin (median = 25, range 24–26 in *P. grandoculis* and median = 28, range 26–30 in *P. sauvagii*) and anal fins (median = 31, range 30–32 in *P. grandoculis* and median = 35, range 33–38 in *P. sauvagii*) but *Petrocephalus squalostoma* differs from *Petrocephalus hutereaui* (Boulenger, 1913) by more branched rays in the dorsal and anal fins (16 and 25 in *P. hutereaui*, respectively). *Petrocephalus squalostoma* differs from *P. c. haullevillii*, *P. c. congicus*, *Petrocephalus mbossou* Lavoué, Sullivan and Arnegard, 2010, *Petrocephalus microphthalmus* Pellegrin, 1908, *Petrocephalus schoutedeni* Poll, 1954, *Petrocephalus valentini* Lavoué, Sullivan and Arnegard, 2010, and *Petrocephalus zakoni* Lavoué, Sullivan and Arnegard, 2010 by the presence of three very distinct Knollenorgan-type clusters in the head. *Petrocephalus squalostoma* can be further distinguished from *P. simus* by its mouth opening under the posterior half of the eye (versus the anterior half of the eye in *P. simus*) and its relatively larger mouth (HL/MW = 4.0, range 3.6–4.5 versus 5.3, range 4.4–7.3 in *P. simus*). Finally, *P. squalostoma* can be further distinguished from *P. c. catostoma* by its number of scales around the caudal peduncle (12 versus 15/16 in *P. c. catostoma*) (Kramer and van der Bank 2000).

Live coloration

Body background mostly silver-white/gold with metallic reflections, darker dorsally from the snout to the caudal peduncle (Figure 3C). Absence of melanin mark in most specimens. In a few specimens presence of a pale subdorsal roundish mark lying below the anterior base of the dorsal fin, on each side of the body. All fins whitish-yellowish, mostly translucent with fine black pigmentation on the lepidotrichia.

Petrocephalus squalostoma differs from *Petrocephalus balayi* Sauvage, 1883, *Petrocephalus binotatus* Pellegrin, 1924, *Petrocephalus christyi* Boulenger, 1920, *P. mbossou*, *Petrocephalus odzalaensis* Lavoué, Sullivan and Arnegard, 2010, *Petrocephalus pulsivertens* Lavoué, Sullivan and Arnegard, 2010, and *P. zakoni* by the absence of any distinct black marking on the body.

Distribution

The five syntype specimens of *P. squalostoma* collected from a small northern tributary of Lake Mweru; the present collection extends the distribution of *P. squalostoma* to the Luongo River, the Upper Lualupa River downstream to Lake Bangweulu, Lake Bangweulu, and as far as the Chambeshi River (Figure 1).

Electric organ discharge

Unknown. Electrocyte anatomy not examined.

Remarks

The cytochrome *b* analysis reveals two distinct genetic groups of *P. squalostoma*: a "Chambeshi River/Lake Bangweulu" group and a "Luongo River/Kalungwishi River" group (Figure 4). No morphological differentiation was found to support this genetic differentiation. The type specimens from the Lukinda stream (Figure 1) are also notable in having comparatively few dorsal and anal fin rays compared with the other specimens (Table 1).

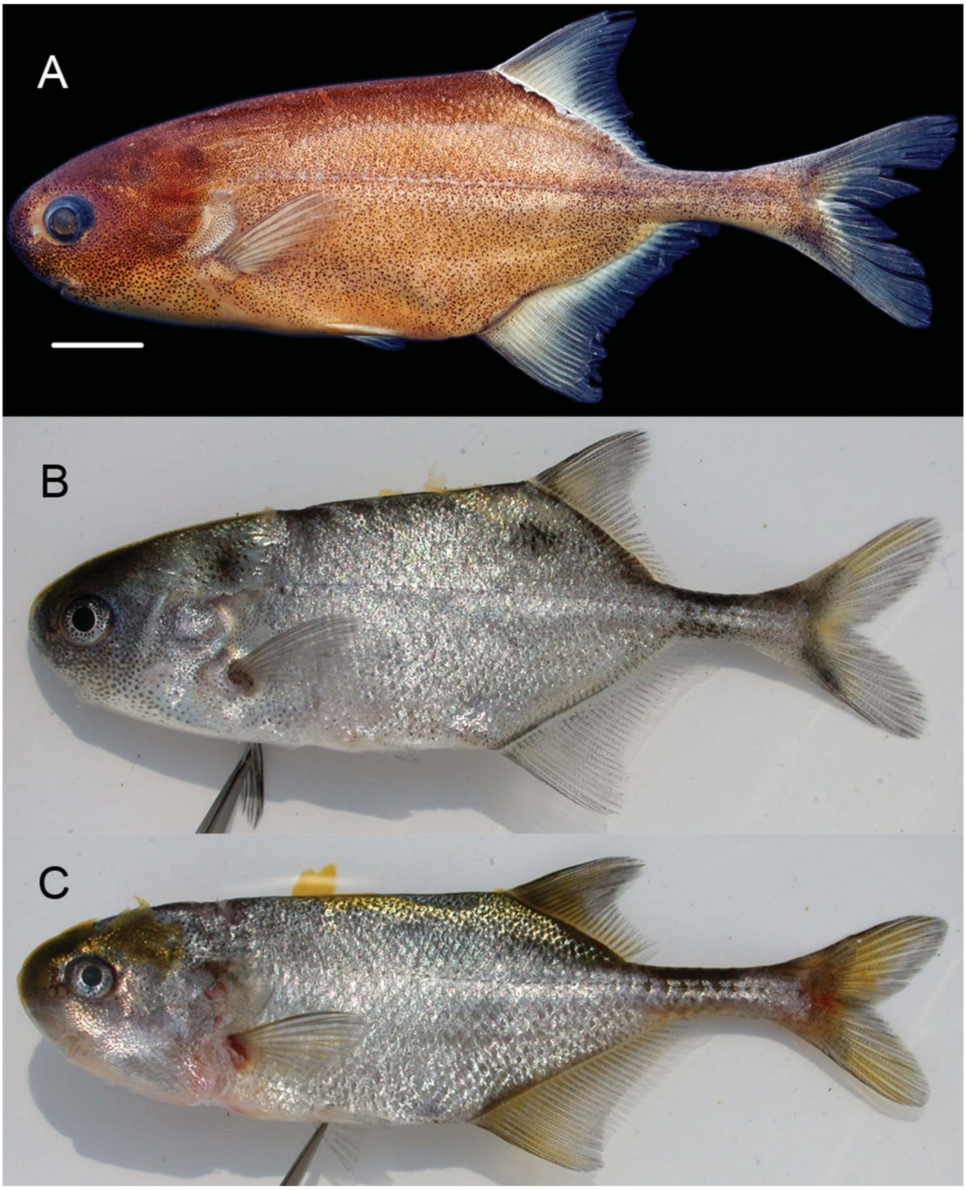

Figure 3. Photographs of *Petrocephalus frieli* sp. nov. and *Petrocephalus squalostoma* from the Bangweulu-Mweru ecoregion, Luapula River system, Congo basin. (A) Preserved holotype of *P. frieli* sp. nov. (CU 96866, scale bar 1.0 cm) (photograph by John P. Sullivan, CUMV). (B) Live specimen of *P. frieli* sp. nov. of about 8.0 cm [estimated] standard length (photograph by Roger Bills, SAIAB). (C) Live specimen of *P. squalostoma* of about 8.0 cm [estimated] standard length (photograph by Roger Bills, SAIAB).

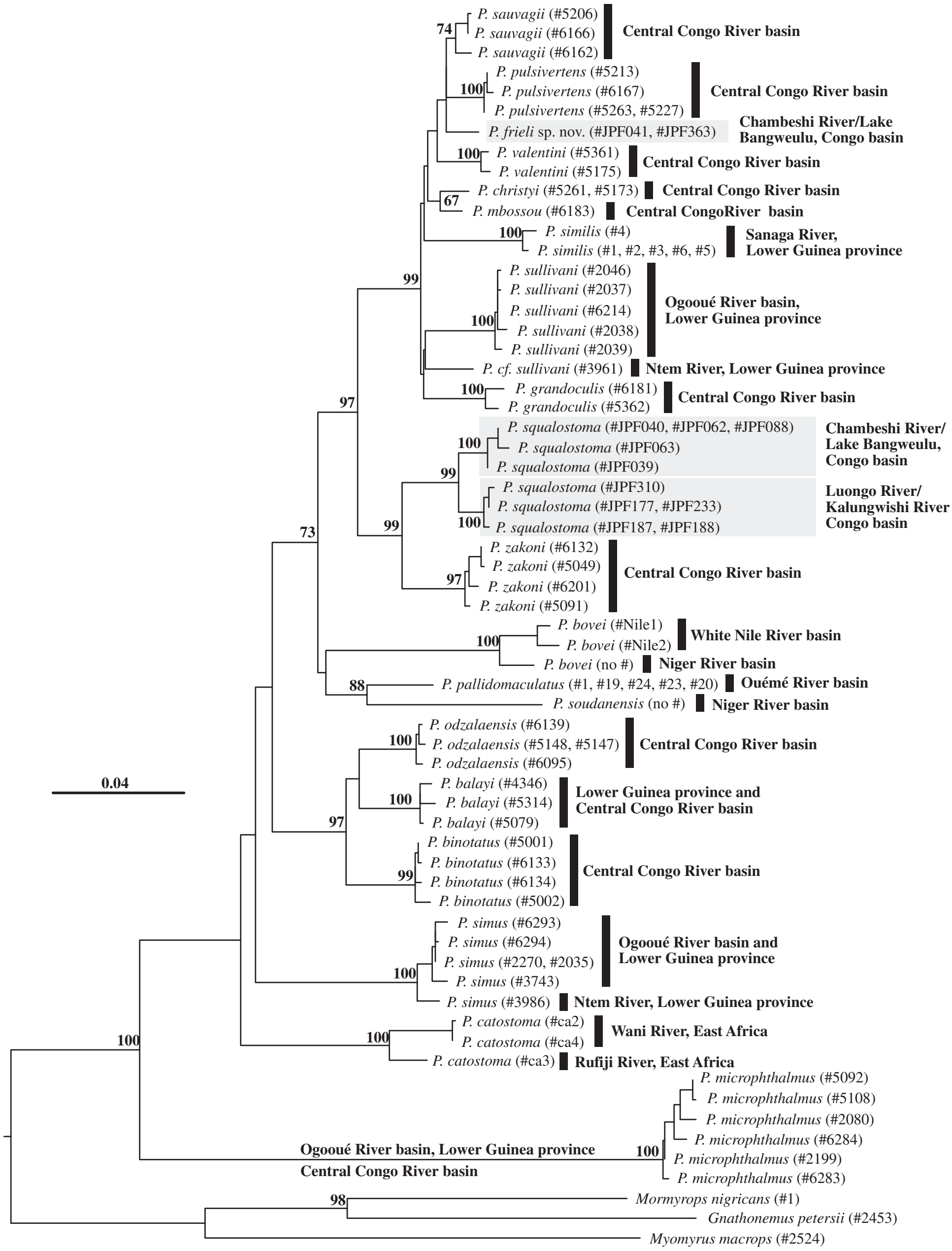

Figure 4. *Petrocephalus* phylogenetic tree (20 species, 60 haplotypes, 77 specimens, not considering the outgroups) estimated by maximum likelihood using cytochrome *b* sequences (see text for details on the phylogenetic reconstruction method). Cytochrome *b* sequences of three mormyrins species – *Gnathonemus petersii*, *Mormyrops nigricans* and *Myomyrus macrops* – were used to root the tree. Species names followed by specimen numbers. Numbers at nodes are bootstrap proportions (if > 50%) and are only shown for interspecific relationships. The positions of *Petrocephalus frieli* sp. nov. and *Petrocephalus squalostoma* are highlighted with grey-filled boxes. Geographical origins of the examined specimens are indicated on the right. The scale bar corresponds to 0.04 substitutions per site.

Other specimens examined

Zambia, Congo basin. CU 91141; Luapula River, Central Luapula River at Luapula River Bridge (12.11° S, 29.85° E) (station JPF 05-006); coll. Bills, Chilala and Friel, 22 September 2005 (five specimens including one sexually mature male, 65.3–74.0 mm SL) (CU DNA tissues: 40 and SAIAB DNA tissue: 39). CU 91142; Luapula River, Lwela River at bridge on road from Mansa to Kafwanka Lwela River (11.56° S, 29.17° E) (station JPF 05-010); coll. Bills, Chilala and Friel, 22 September 2005 (one sexually mature male, 68.5 mm SL) (CU DNA tissue 62 and SAIAB DNA tissue 63). CU 91145; Luapula River, Lake Bangweulu, Lake Bangweulu shoreline at rocky point near Samfya Ferry dock (11.35° S, 29.56° E) (station JPF 05-014A); coll. Bills, Chilala and Friel, 24 September 2005 (one sexually mature male, 56.3 mm SL) (CU DNA tissue 88). CU 91147; Luapula River, Luongo River at bridge on road from Kashiba to Mwenda (10.47° S, 29.02° E) (station JPF 05-023); coll. Bills, Chilala and Friel, 1 October 2005 (two specimens including one sexually mature male, 88.9 and 121.7 mm SL) (CU DNA tissue 177). CU 91148; Luapula River, Luongo River, Lufubu River Falls below bridge at Chipili on road from Mansa to Mununga (10.73° S, 29.09° E) (station JPF 05-025); coll. Bills, Chilala & Friel, 2 October 2005 (five specimens including two sexually mature males, 50.4–59.4 mm SL) (CU DNA tissue 187 and SAIAB DNA tissue 188). CU 91149; Luapula River, Luongo River, Luongo River at Mukonshi Bridge on road from Mwenda to Kawambwa (10.14° S, 29.16° E) (station JPF 05-030); coll. Bills, Chilala and Friel, 3 October 2005 (two sex undetermined specimens, 67.4 and 107.1 mm SL) (CU DNA tissue 233). CU 91150; Luapula River, Luongo River, Lubulafita Stream at bridge on road from Mwenda to Kawambwa (9.99° S, 29.11° E) (station JPF 05-031); coll. Bills, Chilala and Friel, 3 October 2005 (one sex undetermined specimen, 75.7 mm SL). CU 91151; Luapula River, Kalungwishi River, above Lumangwe Falls on Kalungwishi River (9.54° S, 29.39° E) (station JPF 05-039); coll. Bills, Chilala and Friel, 8 October 2005 (one sex undetermined specimen, 75.3 mm SL) (CU DNA tissue 310). CU 95316; (northern Zambia on label), Luapula River, Chambeshi River, Samfa Rapids at pontoon on Chambeshi River (10.85° S, 31.17° E) (station JPF 05-047); coll. Bills, Chilala and Friel, 11 October 2005 (eight sex undetermined specimens in total, five examined, 55.0–77.2 mm SL).

Petrocephalus frieli sp. nov.
(Figure 3A, B)

Type specimens

Holotype. CU 96866; Zambia (Northern province on label), Congo basin, Luapula River, Samfa Rapids at pontoon on Chambeshi River, Chambeshi River, (10.85° S, 31.17° E) (station JPF 05-047); coll. Bills, Chilala and Friel, 11 October 2005 (sexually mature male, 90.7 mm SL).

Paratypes (10). Zambia, Congo basin: CU 91152; *same locality, date and collectors as the holotype* (five specimens including one sexually mature male, 47.1–87.8 mm SL)

(CU DNA tissue 363). CU 91140; Luapula River, Central Luapula River at Luapula River Bridge (12.11° S, 29.85° E) (station JPF 05-006); coll. Bills, Chilala and Friel, 22 September 2005 (one sex undetermined specimen, 60.0 mm SL) (CU DNA tissue: 41). CU 91144; Luapula River, Lake Bangweulu shoreline at rocky point near Samfya Ferry dock (11.35° S, 29.56° E) (station JPF 05-014A); coll. Bills, Chilala and Friel, 24 September 2005 (three sex undetermined specimens, 52.9–66.7 mm SL). CU 91146; Luapula River, Lake Bangweulu shoreline at rocky point near Samfya Zambian Fisheries Offices (11.37° S, 29.65° E) (station JPF 05-015); coll. Bills, Chilala and Friel, 25 September 2005 (one sex undetermined specimen, 57.2 mm SL).

Diagnosis

Petrocephalus frieli sp. nov. is distinguished from all other *Petrocephalus* spp. of Central Africa (i.e. Lower Guinea and Congo provinces) by the following combination of characteristics: body coloration brownish without an intense subdorsal pigmentation mark; 21 to 24 branched rays in the dorsal fin (mean = 23) and 28–30 branched rays in the anal fin (mean = 29); more than 13 scale rows between the anterior base of the anal fin and the lateral line; three distinct electroreceptive rosettes on the head.

Description

Morphometric ratios and meristic data for the holotype and paratypes are presented in Table 2. Maximum SL observed = 90.7 mm (holotype). Body ovoid longer than high (mean SL/H = 2.9) and laterally compressed. Head length 3.6 times (mean) in standard length. Snout short (mean HL/SNL = 6.0) and round. Mouth small (mean HL/MW = 4.2), sub-terminal, opening under the posterior half of the eye. Teeth small and bicuspid, a median of 11 teeth in a single row in the upper jaw, a median of 20 teeth in a single row in the lower jaw. Dorsal and anal fins originate in the posterior half of the body (mean SL/PDD = 1.6 and mean SL/PAD = 1.7). Predorsal distance slightly greater than the pre-anal distance ($1.0 \leq$ PDD/PAD ≤ 1.1). Median dorsal fin branched rays of 23. Median anal fin branched rays of 29. Scales cover the body, except for the head. Lateral line visible and complete, with a median of 38 pored scales along its length. Twelve scales around the caudal peduncle. Median of 16 scales between the anterior base of the anal fin and the lateral line. Caudal peduncle thin (mean CPL/CPD = 2.7). Skin on head thick, turning opaque with formalin fixation. Knollenorgans visible, clustered into the three distinct rosettes of Harder (1968).

Petrocephalus frieli sp. nov. can be distinguished from the otherwise similar *P. squalostoma*, occurring in sympatry in the Lake Bangweulu region, by its number of branched rays in the dorsal fin (median = 23, range 21–24 versus median = 20, range 15–22 in *P. squalostoma*) – this results in a longer dorsal fin in *P. frieli* sp. nov. (Figure 3B, C) – and its deeper body (mean SL/H = 3.3, range 3.0–3.6 versus mean = 2.9, range 2.7–3.2 in *P. squalostoma*). *Petrocephalus frieli* sp. nov. differs from *P. c. haullevillii*, *P. c. congicus*, *P. mbossou*, *P. microphthalmus*, *P. schoutedeni*, *P. valentini* and *P. zakoni* by the presence of three very distinct Knollenorgan-type clusters in the head. *Petrocephalus frieli* sp. nov. also differs from *P. grandoculis* and *P. sauvagii* by the lower number of branched rays in the dorsal fin (median = 25, range 24–26 in *P. grandoculis* and median = 28, range 26–30 in *P. sauvagii*) and anal

Table 2. Principal morphometric ratios and meristic counts for the holotype [CU 96866] and 10 paratypes [CU 91152 (5), CU 91144 (3), CU 91140 (1), CU 91146 (1)] of *Petrocephalus frieli* sp. nov.

	Holotype (m)	Holotype + paratypes ($n = 11$)		
		Min–Max	Mean	SD
Standard length (in mm)	90.7	47.1 − 90.7	66.9	14.6
Head length (in mm)	24.0	13.9 − 24.6	18.5	3.7
Ratio of standard length (SL):				
SL/body height (H)	2.9	2.7 − 3.2	2.9	0.1
SL/head length (HL)	3.8	3.4 − 3.8	3.6	0.1
SL/pre-dorsal distance (PDD)	1.6	1.5 − 1.6	1.6	0.0
SL/pre-anal distance (PAD)	1.7	1.6 − 1.7	1.7	0.0
SL/dorsal fin length (DFL)	4.5	4.4 − 4.9	4.6	0.2
SL/anal fin length (AFL)	3.5	3.3 − 3.6	3.5	0.1
SL/caudal peduncle length (CPL)	5.9	5.4 − 6.4	5.8	0.3
SL/mouth width (MW)	14.2	13.2 − 17.0	15.1	1.0
Ratio of head length (HL):				
HL/snout length (SNL)	6.7	5.3 − 6.7	6.0	0.4
HL/mouth width (MW)	3.8	3.7 − 4.9	4.2	0.4
HL/eye diameter (ED)	3.5	3.5 − 4.4	3.8	0.2
HL/interorbital width (IOW)	3.1	3.0 − 3.6	3.3	0.2
HL/head width (HW)	1.9	1.9 − 2.0	2.0	0.1
HL/mouth position (MP)	3.3	3.1 − 4.2	3.4	0.3
Ratio of caudal peduncle length (CPL):				
CPL/caudal peduncle depth (CPD)	2.7	2.3 − 2.9	2.7	0.2
		Min–Max	Median	
Meristic counts:				
Dorsal fin branched rays (DR)	22	21–24	23	
Anal fin branched rays (AR)	28	28–30	29	
Number of scales in the lateral line (SLL)	37	37–40	38	
Number of scale rows between the anterior base of the anal fin and the lateral line (SDL)	17	15–17	16	
Number of teeth in the upper jaw (TUJ)	14	9–14	11	
Number of teeth in the lower jaw (TLJ)	22	18–22	20	

Abbreviations: m, male; SD, standard deviation; Min–Max, minimum–maximum.

fin (median = 31, range 30–32 in *P. grandoculis* and median = 35, range 33–38 in *P. sauvagii*). *Petrocephalus frieli* sp. nov. can be further distinguished from *P. simus* by its mouth opening under the posterior half of the eye (versus the anterior half of the eye in *P. simus*) and its relatively larger mouth (HL/MW = 4.2, range 3.7–4.9 versus 5.3, range 4.4–7.3 in *P. simus*). Finally, *P. frieli* sp. nov. can be further distinguished from *P. c. catostoma* by the number of scales around the caudal peduncle (12 versus 15/16 in *P. c. catostoma*) (Kramer and van der Bank 2000).

Live coloration

Body background colour silver-white with metallic reflection on the flanks, darker on the snout, forehead and along the dorsal edge until the caudal peduncle (Figure 3B). Presence of a very faded subdorsal spot below the anterior part of the dorsal fin only on the specimens from Lake Bangweulu. Not observed in the other specimens. Scattered melanophores over the body, denser and larger on the head. All fins whitish, translucent, with melanophores marking the lepidotrichia.

Petrocephalus frieli sp. nov. differs from *P. balayi*, *P. binotatus*, *P. christyi*, *P. mbossou*, *P. odzalaensis*, *P. pulsivertens* and *P. zakoni* by the absence of any distinct black marking, including the absence of a distinct subdorsal spot.

Distribution

Petrocephalus frieli sp. nov. is restricted to the southern part of the Bangweulu-Mweru ecoregion, from the Chambeshi River to Lake Bangweulu and the upper Luapula River, downstream to Lake Bangweulu (Figure 1).

Electric organ discharge

Unknown. Electrocyte anatomy not examined.

Remarks

The specimens of *P. frieli* sp. nov. from Lake Bangweulu differ from the riverine specimens from the Chambeshi River and the upper Luapula River in having a pale melanin pattern, with an attenuated subdorsal roundish mark, the first dorsal fin rays and the base of the pectoral fin blackish, a croissant-shaped mark centred at the base of the caudal fin, and the eyes circled with denser melanophores. They are otherwise indistinguishable; therefore I interpret this geographical difference in the marking pattern as of intra-specific level.

Etymology

Dedicated to Dr John P. Friel, curator at the Cornell University Museum of Vertebrates (CUMV), in recognition of his contribution to African ichthyology and for his care of the large collection of African electric fish deposited at CUMV. In addition, John P. Friel is one of the collectors of this new species.

Discussion

Petrocephalus ***species diversity of the Bangweulu-Mweru ecoregion***

Before this work, three species of *Petrocephalus* were mentioned from the Bangweulu-Mweru ecoregion: *P. squalostoma*, *P. simus* and *P. catostoma*. A small tributary (the Lukinda River) of Lake Mweru is the type locality of *P. squalostoma*, described by Boulenger (1915) as *Marcusenius squalostoma*. Since its description, only a single additional museum specimen was assigned to this species, from the locality Kafushia on the Wiswila stream, a left tributary of the Luapula River (MRAC P 85732). Based on the collection examined in this study, *P. squalostoma* is widely distributed in this region with its occurrence reported from nine additional localities (Figure 1).

Petrocephalus simus was mentioned in several fish species lists of this region and other fisheries research reports, e.g. Boulenger (1920), Imai (1985, 1987), or Ticheler et al. (1998). Although I did not examine specimens previously identified as *P. simus* from this region, and no published description or photograph is available for these specimens, I believe that *P. simus* does not occur in this region. *Petrocephalus simus*, once thought to be widespread in tropical Africa, has its distribution range restricted to the Lower Guinea province, a rainforest region that lies on the West coast of Central Africa, several thousand kilometres from the Bangweulu-Mweru region (Hopkins et al. 2007). Misidentifications could have been the result of the overall morphological similarity between *P. simus*, *P. frieli* sp. nov. and *P. squalostoma*. Yet, the comparative examination of several morphological characters allows the clear distinction of *P. simus* from *P. frieli* sp. nov. and *P. squalostoma*.

Although it seems unlikely that *P. simus* occurs in the Bangweulu-Mweru region, the occurrence of *P. catostoma* (Imai 1985, 1987; Ticheler et al. 1998) could not be excluded at this stage. However, the taxonomy of *P. catostoma* of East Africa is complex and it deserves further comment.

Petrocephalus catostoma was initially described based on a single specimen from the Rovuma River, a coastal stream of Tanzania (Günther 1866). *Petrocephalus catostoma* was at that time the only species of *Petrocephalus* known from East Africa (not considering the Nile basin). Then, several additional species of *Petrocephalus* were described from East Africa: *Petrocephalus gliroides* Vinciguerra, 1897 from the locality Ganana Lugh on the Webi Jubba River in Somalia, *Petrocephalus degeni* Boulenger, 1906 from the mouth of the Katongo River a tributary of Lake Victoria in Uganda, *Petrocephalus stuhlmanni* Boulenger, 1909 from the Kingani River (currently known as the Ruvu River) in Tanzania, *Petrocephalus affinis* Steindachner, 1914 – renamed as *Petrocephalus steindachneri* by Fowler (1958) because the name *P. affinis* was preoccupied – from Msola Brook, Kiperege, Ulanga, Rufiji River in Tanzania. Outside this region, David and Poll (1937) recognized two subspecies of *P. stuhlmanni*: *P. s. congicus* from the Congo basin and *P. s. haullevillii* previously described from the lower part of the Lower Guinea province and subsequently mentioned from the Congo basin (Pellegrin 1920).

Whitehead and Greenwood (1959) attempted to revise the taxonomy of the East African group of *Petrocephalus* in comparing their external morphology. These authors recognized only two valid species: *P. gliroides* known only from Somalia and *P. catostoma* which they further divided in four subspecies: *P. c. catostoma* widely distributed in East Africa, including the Zambezi basin and the Lake Tanganyika–Malagarasi River region; *P. c. tanensis* restricted to the Tana River in Kenya, *P. c. congicus* from the Congo basin and *P. c. haullevillii* from the Lower Guinea and Congo regions. Kramer and van der Bank (2000) added a third species of *Petrocephalus* that is very distinctive from *P. catostoma*, *Petrocephalus wesselsi* Kramer and van der Bank, 2000. *Petrocephalus wesselsi* is known from the Pongola River, Incomati River and Limpopo River basins in South Africa and Mozambique.

Kramer et al. (2012) in an extensive taxonomic revision of *P. catostoma* of South and East Africa based on morphological, electrophysiological and molecular evidence demonstrate that *P. catostoma* (as recognized since Whitehead and Greenwood 1959) is a complex of several species. Kramer et al. (2012) reinstate *P. steindachneri*, *P. degeni* and *P. stuhlmanni*, and they describe five new species as well. Furthermore, these authors provide evidence that the three subspecies of *P. catostoma* – *P. c. tanensis*, *P. c. haullevillii* and *P. c. congicus* – should not be considered as conspecific. From my current work on Central African species of *Petrocephalus* and the re-examination of the type specimens of *P. c. haullevillii* and *P. c. congicus*, I concur with the result of Kramer et al. (2012) that these two subspecies should be considered as valid species (i.e. *P. haullevillii* and *P. congicus*), distinct from *P. catostoma*. In addition to the distinctive morphological characteristics highlighted by Kramer et al. (2012), *P. catostoma* has three clearly distinct clusters (i.e. rosettes) of Knollenorgan-type electroreceptors in the head whereas *P. haullevillii* has no rosette and *P. congicus* has only a single clearly distinct cluster above the eye, on each side, the Augenrosette (Harder 1968).

Along with these previous considerations, unambiguous evidence supporting the presence of *P. catostoma* in the Bangweulu-Mweru region is still lacking. If the occurrence of *P. catostoma* in the Bangweulu-Mweru region is confirmed, it is likely that this population would be related to one of the three new species described from the Zambezi basin (Kramer et al. 2012) because of the proximity of the two regions. A relatively high degree of similarity between the fauna of the Bangweulu-Mweru region and the Zambezi basin has been noted for a long time, due to past connections (Banister 1986).

Species origin, population structure and species distribution within the Bangweulu-Mweru region

The phylogenetic analysis performed in this study demonstrates that *P. squalostoma* and *P. frieli* sp. nov. are more closely related to Congolese species occurring in the Central Congo basin than to *P. catostoma* occurring in East Africa (Figure 4). This result supports a Central Congo origin for these two species instead of a Zambezi origin (Banister 1986).

A latitudinal pattern of intraregional genetic structure between the Lake Mweru/Kalungwishi River/Luongo River and the Lake Bangweulu/Chambeshi River populations has previously been noted for two other fish taxa. Katongo et al. (2005) reported that the Lake Mweru population of the cichlid *Pseudocrenilabrus philander* is genetically and morphologically distinct from the Lake Bangweulu population. Later, Katongo et al. (2007) reported similar results within a serranochromine cichlid lineage, with mostly distinct populations or species between the Lake Mweru region and the Lake Bangweulu/Chambeshi River. In agreement with these previous results, this study provides evidence for two genetically distinct groups of *P. squalostoma*, a "Lake Bangweulu/Chambeshi River" group and a "Luongo River/Kalungwishi River" group. No tissue samples were available from specimens from the type locality of *P. squalostoma*, which is close to Lake Mweru. Furthermore, *P. frieli* sp. nov. is only found in the south part of the Bangweulu-Mweru ecoregion. Katongo et al. (2005, 2007) proposed that the Mambilima and Mumbatuta Falls on the Luapula River represent effective barriers of dispersal between the north and south in this region. Our results further extend the possibility that these falls play an important role in shaping the distribution and the genetic structure of *Petrocephalus* in this region.

Acknowledgements

Roger Bills, Alex D. Chilala and John P. Friel collected the *Petrocephalus* specimens in the Bangweulu-Mweru region with funding from The All Catfish Species Inventory (NSF DEB-0315963). I also thank John P. Friel and Charles Dardia (Cornell University Museum of Vertebrates, Ithaca, NY, USA) and Oliver Crimmen and James Maclaine (Natural History Museum, London, UK) for access to the collections under their care. The specimen photographs are credited to Roger Bills, John P. Sullivan, and © The Natural History Museum, London. I thank Bernd Kramer, Roger Bills, Paul Skelton and Michael Wink for providing a copy of their taxonomic revision of the *Petrocephalus* of East and South Africa, ahead of publication. This manuscript has greatly benefited from the comments of two anonymous reviewers and Louise Allcock (co-editor, *Journal of Natural History*). This work was completed while I was at the National Taiwan University, supported by a postdoctoral fellowship from the National Science Council of Taiwan (NSC100-2811-M-002-069).

References

Abell R, Thieme ML, Revenga C, Bryer M, Kottelat M, Bogutskaya N, Coad B, Mandrak N, Balderas SC, Bussing W, et al. 2008. Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. Bioscience 58(5): 403–414.

Balon EK, Stewart DJ. 1983. Fish assemblages in a river with unusual gradient (Luongo, Africa Zaire System), reflections on river zonation, and description of another new species. Env Biol Fish. 9(3–4):225–252.

Banister KE. 1986. Fish of the Zaire system. In: The ecology of river systems. Dordrecht, the Netherlands: Dr. W. Junk Publishers. p. 215–224.

Bell-Cross G. 1965. Movement of fish across the Congo-Zambezi watershed in the Mwinilunga District of Northern Rhodesia. In: Proceedings of the Central African Scientific and Medical Congress, Lusaka. Oxford, UK: Pergamon Press. p. 415–424.

Bigorne R, Paugy D. 1991. Note sur la systématique des *Petrocephalus* (Teleostei, Mormyridae) d'Afrique de l'Ouest. Ichthyol Explor Freshwaters. 2(1):1–30.

Boden G, Teugels GG, Hopkins CD. 1997. A systematic revision of the large-scaled *Marcusenius* with description of a new species from Cameroon (Teleostei; Osteoglossomorpha; Mormyridae). J Nat Hist. 31:1645–1682.

Boulenger GA. 1915. Mission Stappers au Tanganika-Moéro. Diagnoses de poissons nouveaux. II. Mormyrides, Kneriides, Characinides, Cyprinides, Silurides. Rev Zool Afr. 4:162–171.

Boulenger GA. 1920. Poissons de la mission Stappers, 1911–1913 pour l'exploration hydrographique et biologique des lacs Tanganika et Moéro. Rev Zool Afr. 8(1):1–57.

Daget J, Gosse JP, Thys van den Audenaerde DFE editors. 1984. Cloffa: check-list of the freshwater fishes of Africa. 1st ed. Paris, Tervuren: ORSTOM, MRAC.

David L, Poll M. 1937. Contribution à la faune ichthyologique du Congo belge. Ann Musée R Congo Belge, Zool. 3(5):189–294.

De Kimpe P. 1964. Contribution à l'étude hydrobiologique du Luapula-Moéro. Ann Musée R Afr Centr Sci Zool. 128:1–238.

Eschmeyer WN, Fricke R editors. Catalog of fishes [internet]. 2011. San Francisco (CA): California Academy of Sciences; [cited 2011 March 29]. Available from: http://research.calacademy.org/ichthyology/catalog/fishcatmain.asp.

Fowler HW. 1958. Some new taxonomic names of fishlike vertebrates. Notulae Naturae (Philadelphia). 310:1–16.

Günther A. 1866. Catalogue of the fishes of the British Museum. London: Taylor and Francis.

Harder W. 1968. Zum Aufbau der epidermalen Sinnesorgane der Mormyridae (Mormyriformes, Teleostei). Z Zellforsch. 89:212–224.

Hopkins CD, Lavoué S, Sullivan JP. 2007. Mormyridae. In: Faune des poissons d'eaux douces et saumâtres de l'Ouest de l'Afrique Centrale (Cameroun, Guinée Equatoriale, Gabon, Congo Brazzaville). Paris: IRD. p. 219–334.

Imai I. 1985. Fishing life in the Bangweulu Swamps: a socio-ecological study of the swamp fishermen in Zambia. Afr stud monogr. 1985 (Suppl. 4):49–88.

Imai I. 1987. Fishing life in the Bangweulu Swamps (2): An analysis of catch and seasonal emigration of the fishermen in Zambia. Afr stud monogr. 1987 (Suppl. 6):33–63.

Jackson PBN. 1961. The fishes of Northern Rhodesia: a checklist of indigenous species. Lusaka: Govt. Printer.

Jackson PBN. 1989. Prediction of regulation effects on natural biological rhythms in South-Central African freshwater fish. Regul Rivers: Res Manage. 3(1):205–220.

Katongo C, Koblmuller S, Duftner N, Makasa L, Sturmbauer C. 2005. Phylogeography and speciation in the *Pseudocrenilabrus philander* species complex in Zambian Rivers. Hydrobiologia 542:221–233.

Katongo C, Koblmuller S, Duftner N, Mumba L, Sturmbauer C. 2007. Evolutionary history and biogeographic affinities of the serranochromine cichlids in Zambian rivers. Mol Phylogenet Evol. 45(1):326–338.

Kramer B, Bills R, Skelton P, Wink M. 2012. A critical revision of the churchill snoutfish, genus *Petrocephalus*, from southern and eastern Africa, with the recognition of *P. tanensis*, and the description of five new species (Teleostei, Mormyridae). J Nat Hist. p. 2179–2258.

Kramer B, van der Bank FH. 2000. The southern churchill, *Petrocephalus wesselsi*, a new species of mormyrid from South Africa defined by electric organ discharges, genetics, and morphology. Env Biol Fish. 59:393–413.

Lavoué S. 2011. A new species of *Petrocephalus* Marcusen 1854 (Osteoglossomorpha: Mormyridae) from the Sanaga River basin, Cameroon. Zootaxa 2011(2934):20–28.

Lavoué S, Arnegard ME, Sullivan JP, Hopkins CD. 2008. *Petrocephalus* of Odzala offer insights into evolutionary patterns of signal diversification in the Mormyridae, a family of weakly electrogenic fishes from Africa. J Physiol Paris. 102(4–6):322–339.

Lavoué S, Hopkins CD, Kamdem Toham A. 2004. The *Petrocephalus* (Pisces, Osteoglossomorpha, Mormyridae) of Gabon, Central Africa, with the description of a new species. Zoosystema 26(3):511–535.

Lavoué S, Sullivan JP, Arnegard ME. 2010. African weakly electric fishes of the genus *Petrocephalus* (Osteoglossomorpha: Mormyridae) of Odzala National Park, Republic of the Congo (Lekoli River, Congo River basin) with description of five new species. Zootaxa 2010(2600):1–52.

Lévêque C. 1997. Biodiversity dynamics and conservation: the freshwater fish of tropical Africa. Cambridge: Cambridge University Press.

Marcusen J. 1854. Vorläufige Mittheilung aus einer Abhandlung über die Familie des Mormyren. Bull Acad Sci St Petersb. 12:1–14.

Moore AE, Larkin PA. 2001. Drainage evolution in south-central Africa since the breakup of Gondwana. S Afr J Geol. 104(1):47–68.

Moritz T, Engelmann J, Linsenmair KE, von der Emde G. 2009. The electric organ discharges of the *Petrocephalus* species (Teleostei: Mormyridae) of the Upper Volta System. J Fish Biol. 74(1):54–76.

Paugy, D, Zaiss, R, Troubat, JJ. Faunafri [internet]. 2008. Paris, IRD; [cited 2011 June]. Available from: http://www.ird.fr/poissons-afrique/faunafri

Pellegrin J. 1920. Poissons de l'Ouham et de l'Oubanghi recueillis par M. Baudon. Description de deux cyprinidés nouveaux. Bull Soc Zool Fr. 45:245–248.

Pezzanite B, Moller P. 1998. A sexually dimorphic basal anal-fin ray expansion in the weakly discharging electric fish *Gnathonemus petersii*. J Fish Biol. 53(3):638–644.

Ricardo-Bertram CK. 1943. The fishes of the Bangweulu region. J Linn Soc (Zool). 41(278):183–217.

Roberts TR. 1975. Geographical distribution of African freshwater fishes. Zool J Linn Soc. 57:249–319.

Runge J. 2007. The Congo River, Central Africa. In: Large rivers: geomorphology and management. Chichester, UK: John Wiley and Sons, Ltd. p.293–309.

Silvestro D, Michalak I. Forthcoming 2012. raxmlGUI: a graphical front-end for RAxML. Org Divers Evol.

Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22(21):2688–2690.

Stankiewicz J, de Wit MJ. 2006. A proposed drainage evolution model for Central Africa – Did the Congo flow east? J Afr Earth Sci. 44(1):75–84.

Sullivan JP, Lavoué S, Hopkins CD. 2000. Molecular systematics of the African electric fishes (Mormyroidea: Teleostei) and a model for the evolution of their electric organs. J Exp Biol. 203:665–683.

Taverne L. 1969. Etude ostéologique des genres *Boulengeromyrus* Taverne et Géry, *Genyomyrus* Boulenger, *Petrocephalus* Marcusen (Pisces Mormyriformes). Ann Mus R Afr Centr Sci Zool. 174:1–85.

Taverne L. 1971. Notes sur la systématique des poissons Mormyriformes. Le problème des genres *Gnathonemus* Gill, *Marcusenius* Gill, *Hippopotamyrus* Pappenheim, *Cyphomyrus* Myers et les nouveaux genres *Pollimyrus* et *Brienomyrus*. Rev Zool Bot Afr. 84:99–110.

Taverne L. 1972. Ostéologie des genres *Mormyrus* Linné, *Mormyrops* Müller, *Hyperopisus* Gill, *Myomyrus* Boulenger, *Stomatorhinus* Boulenger et *Gymnarchus* Cuvier. Considérations générales sur la systématique des poissons de l'ordre des Mormyriformes. Ann Mus R Afr Centr Sci Zool. 200:1–194.

Thieme ML, Abell R, Stiassny MLJ, Skelton P, Burgess N, Lehner B, Dinerstein E, Olson D, Teugels GG, Kamdem-Toham A. 2005. Freshwater ecoregions of Africa and Madagascar: a conservation assessment. Washington: Island Press.

Ticheler HJ, Kolding J, Chanda B. 1998. Participation of local fishermen in scientific fisheries data collection: a case study from the Bangweulu Swamps, Zambia. Fisheries Manag Ecol. 5:81–92.

Whitehead PJP, Greenwood PH. 1959. Mormyrid fishes of the genus *Petrocephalus* in Eastern Africa with a redescription of *Petrocephalus gliroides* (Vinciguerra). Rev Zool Bot Afr. 60(3–4):283–295.

Worthington EB. 1933. The fishes (other than cichlidae) of Lake Bangweulu and adjoining regions, including descriptions of three new species. Ann Mag Nat Hist. 10(12):34–52.