

Article



A new species of *Petrocephalus* Marcusen 1854 (Osteoglossomorpha: Mormyridae) from the Sanaga River basin, Cameroon

SÉBASTIEN LAVOUÉ

Institute of Oceanography, National Taiwan University, Roosevelt Road, Taipei 10617, Taiwan, E-mail: microceb@hotmail.com

Abstract

Petrocephalus similis n. sp. is described from the Djerem River, upper Sanaga basin, in Cameroon. It can be distinguished from all other Petrocephalus from West and Central Africa by an unique combination of morphological characters including: body without melanin mark, 22–24 branched rays in the dorsal fin and 28 or 29 branched rays in the anal fin, mouth commissure under the posterior half of the eye. Petrocephalus similis mostly resembles Petrocephalus sullivani. Yet, P. similis has proportionally a larger mouth and a wider head, and reaches a longer maximum standard length. The electric organ discharge waveform of this species is not known. Molecular comparisons based on cytochrome b nucleotide sequences are congruent with morphological comparisons in independently supporting the distinctiveness of this species from 17 other species of *Petrocephalus*. Within the genus *Petrocephalus*, *P. similis* belongs to a group that is almost exclusively composed of endemic species of Central Africa, pointing out its likely origin from this region. Additional examinations of museum specimens from the Sanaga River basin demonstrate the occurrence of at least two other species of Petrocephalus: Petrocephalus microphthalmus, and a second species which is conservatively assigned to Petrocephalus cf. christyi, pending additional evidence.

Key words: electric fish, Central Africa, molecular phylogeny, cytochrome b, integrative taxonomy

Résumé

Petrocephalus similis n. sp. est décrite de la rivière Djerem, bassin de la Haute Sanaga, au Cameroun. Elle se distingue de toutes les autres espèces de Petrocephalus de la Basse Guinée et des régions limitrophes par la combinaison des caractères suivants : patron de coloration sans marque noirâtre ; 22-24 rayons branchus à la nageoire dorsale et 28 ou 29 rayons branchus à la nageoire anale ; commissures de la bouche situées sous la moitié postérieure de l'œil. Petrocephalus similis ressemble le plus à *Petrocephalus sullivani*. Elle s'en distingue néanmoins par une bouche et une tête proportionnellement plus larges, et elle atteint une plus grande longueur standard. La forme de la décharge électrique n'est pas connue. Les comparaisons moléculaires fondées sur des séquences complètes du cytochrome b confirment les résultats morphologiques obtenus en soutenant la distinction de cette nouvelle espèce par rapport à 17 autres espèces de Petrocephalus. Au sein du genre Petrocephalus, P. similis appartient à un groupe constitué pratiquement uniquement d'espèces endémiques d'Afrique Centrale, soulignant l'origine de cette espèce à partir de cette région. Des observations complémentaires sur des spécimens du bassin de la Sanaga montrent qu'il y coexiste au moins deux autres espèces de Petrocephalus : Petrocephalus microphthalmus et une seconde espèce qui est provisoirement identifiée comme Petrocephalus cf. christyi, en attendant d'avoir plus de données.

Introduction

The Sanaga River is the main drainage in Cameroon (~900 km long, average flow of 2,072 m³/sec), with its basin covering about 140,000 km² of the central region of the country (Fig. 1). The geographic position of the Sanaga River makes its fish fauna particularly interesting. The entire Sanaga basin is placed within the Lower Guinea ichthyo-province (Lévêque 1997; Roberts 1975; Stiassny et al. 2007). Yet the western and northern parts of the upper Sanaga basin are respectively bordered by the Benue River, a tributary of the Niger basin, and the Lake Chad basin,

both from the Nilo-Sudanian province and the eastern part is bordered by the Dja River, a tributary of the Congo basin. Consequently, the origin of the fish fauna of the Sanaga basin is composite (Daget 1979; Daget & Depierre 1980).

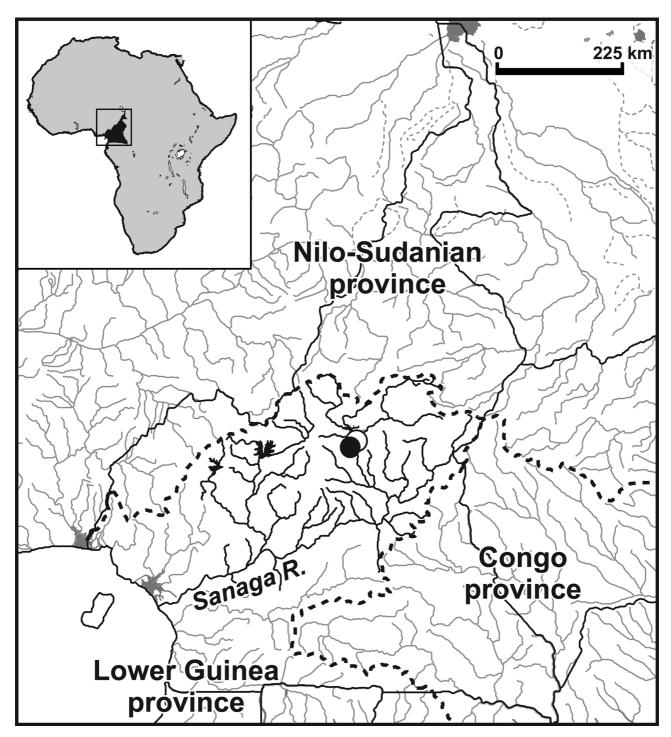


FIGURE 1. Map of the hydrographic system of Cameroon (top-left inset showing the location of Cameroon in Africa). The Sanaga River basin is highlighted with deep grey lines. The boundaries among the faunal regions are indicated with black dashed lines. The filled black circle indicates the type locality of *Petrocephalus similis* **n. sp.** and the open circle indicates the second known locality.

The current knowledge on the ichthyofauna of the Sanaga River is still imperfect. No large ichthyofauna survey has been undertaken since the collections made by Daniel Depierre, more than 30 years ago (Daget 1979; Daget & Depierre 1980) and more recently by Guy Teugels and collaborators (in the mid 1990's), yielding to the descriptions of new taxa (Boden *et al.* 1997; Van den Bergh & Teugels 1998). The most recent account by Brum-

TERMS OF USE This pdf is provided by Magnolia Press for private/research use. Commercial sale or deposition in a public library or website is prohibited.

met and Teugels (2004) reported only about 120 species from the Sanaga River that probably represents an underestimation of the total species number.

Daget and Depierre (1980) listed only two species of *Petrocephalus* Marcusen 1854 they identified as *Petrocephalus microphthalmus* Pellegrin 1908 and *Petrocephalus simus* Sauvage 1879. Lavoué *et al.* (2004) and Hopkins *et al.* (2007) reexamined the *Petrocephalus* material collected by Daniel Depierre and others; they confirmed the presence of *P. microphthalmus* but not *P. simus*. Hopkins *et al.* (2007) concluded the specimens previously identified as *P. simus* belong probably to two or more different species, although they were unable to unambiguously diagnose them. Thus, these authors decided to conservatively place all these specimens under the species name *Petrocephalus christyi* Boulenger 1920, awaiting additional material.

Here, a new species of *Petrocephalus* from the Sanaga River, Cameroon, is described that was previously misidentified as *P. simus* (Daget & Depierre 1980). This description is now possible because of the availability of material recently collected by Duncan T. Reid. As an independent line of evidence to assess the distinctiveness of this new species, the complete cytochrome *b* nucleotide sequences for six specimens of this species were phylogenetically analyzed within an existing dataset of 17 *Petrocephalus* species, including *P. simus* and *Petrocephalus* sullivani Lavoué *et al.* 2004.

Material and methods

Specimen sampling. All specimens of the new species examined in this study were collected from the Djerem River, upper Sanaga basin, downstream to the Mbakaou (Tibati) Reservoir, Adamaoua region, Cameroon (Fig. 1). Comparative material from the Sanaga basin is listed herein, and a complete list of all *Petrocephalus* material examined is listed in Lavoué *et al.* (2004; 2010). It includes type specimens from all valid species from the Lower Guinea and the Congo provinces. From the Nilo-Sudanian province, the original species descriptions and the taxonomic revision of Bigorne and Paugy (1991) were consulted. Nucleotide sequences of the complete cytochrome *b* gene (1,140 base pairs) for the holotype and five paratypes of this new species were determined, as well as a partial cytochrome *b* sequence (852 base pairs from the 3' end) of a specimen of *Petrocephalus balayi* Sauvage 1883 from a coastal stream on a logging road nearby Doumvou and the lagoon Banio [3.36° S, 10.74° E], southern Gabon [CU 83327, EOD and morphology reported in Lavoué *et al.* (2004)].

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) and 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.

The presence or absence of three dense clusters of Knollenorgan-type electroreceptors [i.e., the Augenrosettes, Nackenrosettes and Kehlrosettes (Harder, 1968)] on the head of some *Petrocephalus* species is a diagnostic character in the taxonomy of the genus *Petrocephalus* (Lavoué *et al.* 2010). Their definitions follow those given by Harder (1968).

The sex of specimens was determined by examining the body profile along the base of the anal fin (Pezzanite & Moller 1998). Sexually mature males exhibit a strongly indented anal fin base whereas "sex undetermined" specimens (i.e., juveniles and mature females) exhibit a nearly straight anal fin base.

Museum abbreviations: CUMV, Cornell University Museum of Vertebrates, Ithaca, New York; MNHN, Muséum National d'Histoire Naturelle, Paris; MRAC, Musée Royal de l'Afrique Centrale, Tervuren.

DNA sequencing and molecular phylogenetic methods. DNA was extracted from 95% ethanol-preserved fin clips. PCR amplification and sequencing of the complete cytochrome *b* gene were as described by Sullivan *et al.* (2000) using the *Petrocephalus*-specific primers designed by Lavoué *et al.* (2008). Cytochrome *b* sequences generated in this study have been deposited in Genbank database under accession numbers JF438960 to JF438966.

New cytochrome *b* sequences were included and aligned manually to the dataset published in Lavoué *et al.* (2010). The alignment does not require any indels. Cytochrome *b* sequences of the following three species of the subfamily Mormyrinae are used 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 graphical interface raxmlGUI (Silvestro & Michalak 2010). All positions and types of substitution

TERMS OF USE This pdf is provided by Magnolia Press for private/research use. Commercial sale or deposition in a public library or website is prohibited.

were equally considered. Thorough bootstrap searches (1,000 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 ($GTR+\Gamma$) as outlined in the RAxML 7.0.4 manual.

Petrocephalus similis **n. sp.** (Fig. 2, Table 1)

Holotype. CU 95318 (107.9 mm SL male), Cameroon, Adamaoua Province, Sanaga River basin, Djerem River near Mbakaou Village, (6.21° N, 12.75° E), D.T. Reid, July 2006.

Paratypes. CU 93218, 4 spec. (108.9 mm SL sex undetermined, 104.9 mm SL sex undetermined, 101.3 mm SL male, 103.8 mm SL male), same collection data as holotype. — CU 93219, 3 spec. (104.6 mm SL male, 91.8 mm SL male, 97.9 mm SL male), same collection data as holotype. — CU 93221, 4 spec. (118.5 mm SL male, 106.1 mm SL male, 106.1 mm SL sex undetermined, 106.2 mm SL male), same collection data as holotype. — MNHN 1978-0720, 1 spec. (110.4 mm SL sex undetermined). Cameroon, Adamaoua Province, Sanaga River basin, Djerem River, just downstream of Lake Tibati (=Mbakaou Reservoir), ~6.3° N, 12.8° E, D. Depierre.

Diagnosis. *Petrocephalus similis* is distinguished from all other *Petrocephalus* species of Central Africa (i.e., Lower Guinea and Congo provinces) by the following combination of characteristics: body coloration gold/silverwhite without melanin mark; 22–24 branched rays in the dorsal fin and 28 or 29 branched rays in the anal fin. *Petrocephalus similis* can be further distinguished from *P. simus* by its mouth opening under the posterior half of the eye (*vs.* the anterior half of the eye in *P. simus*); its relatively deep caudal peduncle (CPL/CPD = 2.2–2.6, mean = 2.4; holotype = 2.3 *vs.* 2.8 in *P. simus*) and its greater number of scale rows between the anterior base of the anal fin and the lateral line (16 or 17 versus 12 in *P. simus*). *Petrocephalus similis* can be further distinguished from *P. sullivani*, by its proportionally larger mouth (HL/mouth width = 3.9–4.5, mean = 4.2, holotype = 4.4 *vs.* 4.8 in *P. sullivani*, wider head (HL/head width = 1.6–1.9, mean = 1.8, holotype = 1.7 *vs.* 2.0 in *P. sullivani*), and its shorter caudal peduncle (SL/CPL = 6.3–7.5, mean = 6.8, holotype = 7.1 *vs.* 6.3 in *P. sullivani*).

From the six Nilo-Sudanian species occurring in the Niger and Chad basins bordering the upper Sanaga, *P. similis* is easily distinguished from *Petrocephalus pallidomaculatus* Bigorne & Paugy in Lévêque *et al.* 1990, *Petrocephalus soudanensis* Bigorne & Paugy in Lévêque *et al.* 1990 and *Petrocephalus ansorgii* Boulenger 1903 by its complete absence of large melanin sub-dorsal spot, from *Petrocephalus bane* (Lacepède 1803) and *Petrocephalus sauvagii* (Boulenger 1887), by its smaller mouth and fewer branched rays in the dorsal and anal fins, and from *Petrocephalus bovei* Valenciennes in Cuvier & Valenciennes 1847, by its fewer branched rays in the dorsal and anal fins and its larger maximum standard length (Bigorne & Paugy 1991).

Description. Morphometric ratios and meristic data for the holotype and paratypes are presented in Table 1. Petrocephalus similis is a relatively large sized species within the genus (maximum observed SL = 118.6 mm; holotype = 107.9 mm). Body ovoid, 2.9–3.3 times longer than high (paratype average = 3.0, holotype = 2.9) and laterally compressed. Head length 3.8–4.2 times in SL (paratype average = 4.0, holotype = 3.9). Snout short $(4.3 \le$ $HL/SNL \le 5.8$, paratype average = 5.0, holotype = 5.3) and round. Mouth small (3.9 $\le HL/MW \le 4.5$, paratype average = 4.2, holotype = 4.4), sub-terminal, opening under the posterior half of the eye. Teeth small and bicuspid, 8-11 in a single row in the upper jaw (paratype median = 10, holotype = 9), 19-23 in a single row in the lower jaw (paratype median = 21, holotype = 21). Dorsal and anal fins originate in the posterior half of the body $(1.5 \le SL/$ PDD \leq 1.6 and 1.6 \leq SL/PAD \leq 1.7, respectively). Pre-dorsal distance slightly greater than the pre-anal distance $(1.0 \le PDD/PAD \le 1.1)$. Dorsal fin with 22–24 branched rays (paratype median = 23, holotype = 24). Anal fin with 28 or 29 branched rays (paratype median = 29, holotype = 29). Scales cover the body, except for the head. Lateral line visible and complete with 36–40 (paratype median = 39, holotype = 38) pored scales along its length. Twelve scales around the caudal peduncle. Fifteen to 17 scales (paratype average = 16, holotype = 17) between the anterior base of the anal fin and the lateral line. Caudal peduncle thin $(2.2 \le CPL/CPD \le 2.6, paratype average = 2.4, holo$ type = 2.3). Twelve scales around the caudal peduncle. Skin on head thick, turning opaque with formalin fixation. Knollenorgans visible, clustered into the three distinct rosettes of Harder (1968).

Live coloration (Fig. 2A). Body background color gold/silver-white with metallic reflection on the head, darker dorsally from the midline. No large melanin spot or mark on side below dorsal fin and at the base of the pectoral fins and the caudal fin. All fins whitish-yellowish, mostly translucent.

TABLE 1. Morphometric measurements and meristic counts for the holotype (CU 95318) and 12 paratypes (CU 93218(4), CU 93219(3), CU 93221(4), MNHN 1978-0720(1)) of *Petrocephalus similis* **n. sp.**

	Holotype	Paratypes (n=12)		
		Range	Mean	Std. Dev.
Standard length (mm)	107.9	91.8–118.6	105.1	6.6
Head length (mm)	37.7	29.6–39.8	35.1	2.6
Ratio of standard length (SL):				
SL/body height (H)	2.9	2.9–3.3	3.0	0.1
SL/head length (HL)	3.9	3.8-4.2	4.0	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)	4.3	4.3-4.6	4.4	0.1
SL/anal-fin length (AFL)	3.3	3.3-3.7	3.4	0.1
SL/caudal peduncle length (CPL)	7.1	6.3–7.5	6.8	0.4
SL/mouth width (MW)	17.4	15.4–17.7	16.5	0.8
Ratio of head length (HL):				
HL/snout length (SNL)	5.3	4.3–5.8	5.0	0.4
HL/mouth width (MW)	4.4	3.9-4.5	4.2	0.2
HL/eye diameter (ED)	3.6	3.5–3.8	3.7	0.1
HL/interorbital width (IOW)	2.8	2.4-3.1	2.8	0.2
HL/head width (HW)	1.7	1.6-1.9	1.8	0.1
HL/mouth position (MP)	3.6	2.9–3.6	3.1	0.2
Ratio of caudal peduncle length (CPL):				
CPL/caudal peduncle depth (CPD)	2.3	2.2–2.6	2.4	0.1
		Range	Median	
Meristic counts:				
Dorsal-fin branched rays (DR)	24	22 or 23	23	
Anal-fin branched rays (AR)	29	28 or 29	29	
Lateral-line scales (SLL)	38	36–40	39	
Scale rows between the anterior base of the anal fin and the lateral line (SDL)	17	15–17	16	
Number of upper jaw teeth (TUJ)	9	8–11	10	
Number of lower jaw teeth (TLJ)	21	19–23	21	

Distribution (Fig. 1). Endemic to the upper Sanaga basin. *Petrocephalus similis* is known from two adjacent localities along the course of the Djerem River (upper Sanaga basin), slightly downstream of the Mbakaou (Tibati) Reservoir.

Electric organ discharge. Unknown. Electrocyte anatomy not studied; all *Petrocephalus* species examined to date have electric organ of type "NPp" (i.e., the electrocytes have non-penetrating cellular stalks arising from their posterior face (Bass 1986; Lavoué *et al.* 2010; Sullivan *et al.* 2000)).

Remarks. Based on identity of museum records from the Sanaga River basin, *P. similis* has probably been confused several times with *P. simus*, due to the conspicuous absence of a large melanin spot on the side beneath the dorsal fin, the overall similarity of the body, with few distinctive characteristics. *Petrocephalus simus* is endemic to the lower part of the Lower Guinea province; its occurrence is restricted to the following rivers (from north to south): Ntem, Woleu, Ogooué, Nyanga and Kouilou-Niari (Hopkins *et al.* 2007).

Etymology. The specific epithet "similis" is given in reference to the resemblance between this new species and *P. sullivani*.

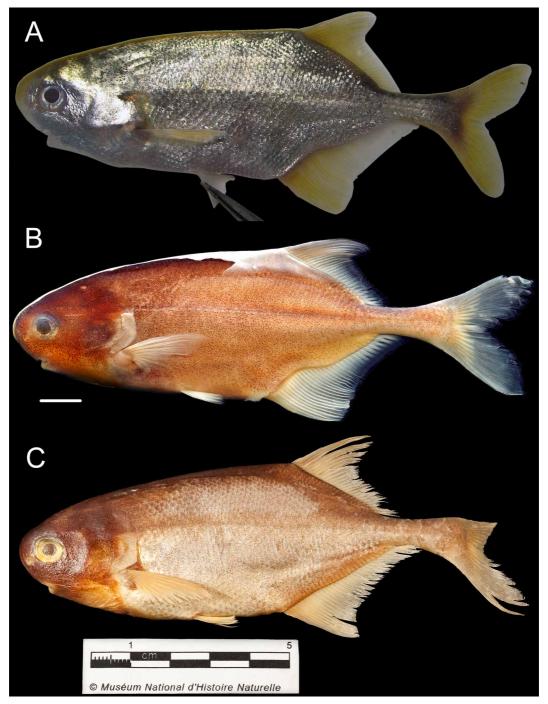


FIGURE 2. *Petrocephalus similis* **n. sp.** from Djerem River near the village of Mbakaou, Adamoua province, Cameroon. A. Photograph of a live specimen ~100 mm SL showing coloration in life (CU 93219), photo by Duncan T Reid. B. Photograph of the preserved holotype (CU 95318, scale bar = 1.0 cm), photo by John P. Sullivan. C. Photograph of a preserved paratype (MNHN 1978-0720), photo by Claude Ferrara.

Discussion

The comparative study of the external morphology shows *P. similis* to be a new species, even in the absence of an electric organ discharge recording. This species has been previously confused with *P. simus* (Daget & Depierre 1980), although it most closely resembles *P. sullivani*. In addition to its morphological distinctiveness, *P. similis*

and *P. sullivani* are genetically distinct from each other and they are not sister species (Fig. 3). The two species are allopatrically distributed in the Lower Guinea province, *P. sullivani* occurring only in the Ogooué and Ntem basins. Examination of additional specimens from the region situated between the Sanaga basin and the Ntem basin might better establish the distribution of *P. similis* relative to *P. sullivani* and other possible cryptic morphotypes.

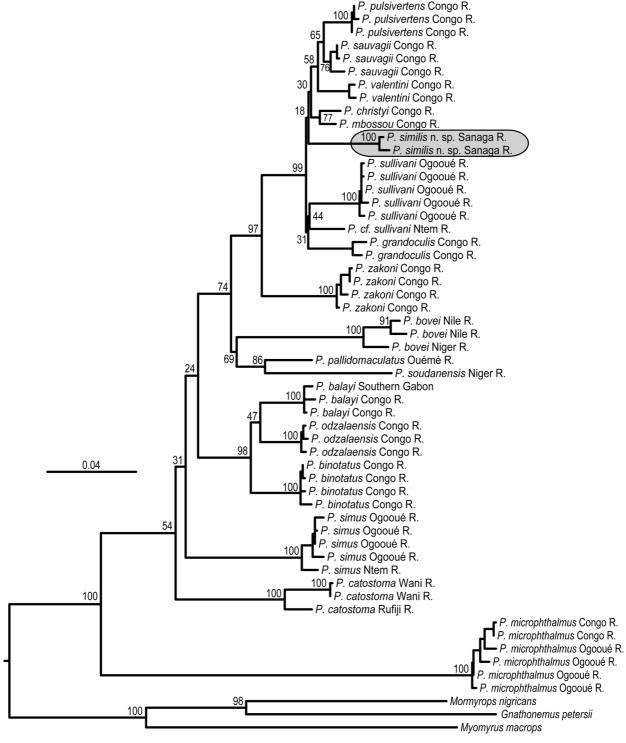


FIGURE 3. Petrocephalus phylogenetic tree (18 species, 56 haplotypes, 66 specimens) estimated by maximum likelihood using complete cytochrome b sequences (see text for details on the tree reconstruction method). Cytochrome b sequences of Gnathonemus petersii, Mormyrops nigricans and Myomyrus macrops were used to root the tree. Numbers at nodes are bootstrap proportions represented as percentages. Bootstrap proportions are not shown for intraspecific relationships. The position of Petrocephalus similis **n. sp.** is indicated within grey ovoid. Scale bar corresponds to 0.04 substitutions per site. Specimen origins are indicated after their species names.

TERMS OF USE This pdf is provided by Magnolia Press for private/research use. Commercial sale or deposition in a public library or website is prohibited.

According to Daget and Depierre (1980) and Brummet and Teugels (2004), the ichthyofauna of the Sanaga basin shows mixed origins, with some species having affinities with the Nilo-Sudanian region and others with the Central Africa region. Phylogenetic analysis based on the cytochrome *b* reveals that *P. similis* is nested within a clade composed of nine other *Petrocephalus* species, all but one strictly endemic to Central Africa (Fig. 3). Only *P. sauvagii* has a distinct population outside this region (*i.e.*, in the lower Niger basin). Furthermore, this clade is the sister group of another Central African species, *Petrocephalus zakoni* Lavoué *et al.* 2010. This result highlights the likely Central African origin of *P. similis*.

Of the two species listed in Daget and Depierre (1980), it appears that the specimens identified as *P. simus* belong to at least two different species, neither of them being *P. simus*. The first one is *P. similis*, herein described; the second species is diagnosed by the presence of a distinct subdorsal blackish mark, similar to that of *P. christyi*. Yet, the examination of other morphological characters suggests some differences with the type series and other specimens of *P. christyi* from the Congo basin. The second species is herein conservatively assigned to *P. cf. christyi* even if it most likely represents a distinct and undescribed species. Molecular and/or electrophysiological examination of new material is needed to confirm and prepare its formal description.

Petrocephalus similis is the sixth species of Petrocephalus currently known from the Lower Guinea province (excluding the Cross River); the other five are P. simus, P. balayi, P. microphthalmus, P. sullivani and Petrocephalus haullevillii Boulenger 1912. Petrocephalus guttatus Fowler 1936 was recently transferred into the genus Pollimyrus (Lavoué et al. 2010). Further ichthyological surveys in the Cameroonian basins of Lower Guinea are likely to uncover additional species of Petrocephalus.

Comparative material examined from the Sanaga Basin: MNHN 1979-0245, Petrocephalus microphthalmus, 2 spec. (63.3 and 64.3 mm SL males), Cameroon, Sanaga River basin, near Velabo, 50 km south to the confluence of Lom and Djerem Rivers, where Sanaga changes from a north-east to an east-west course, D. Depierre. — MNHN 1978-0445, Petrocephalus cf. christyi, 5 spec. (64.9–98.3 mm SL), region of Nanga-Eboko, Sanaga basin, D. Depierre. — MNHN 1978-0446, Petrocephalus cf. christyi, 1 spec. (100.5 mm SL male), slightly upstream of the Nachtingal Falls, Sanaga basin, D. Depierre. — MNHN 1978-0447, Petrocephalus cf. christyi, 1 spec. (85.4 mm SL sex undetermined), Lom River, between Bétaré-oya and the confluence with the Djerem River, D. Depierre. — MRAC 73-2-P-24-29, Petrocephalus cf. christyi, 4 spec. (99.6–114.0 mm SL), Edéa près du pont Cameroun, D.F.E. Thys van den Audenaerde, 16 November 1986. — MNHN 1979-0203, Petrocephalus cf. christyi, 1 spec. (73.3 mm SL sex undetermined), Lake Ossa downstream to Edea, T. Monod, June 1927. — MNHN 1979-0204, Petrocephalus cf. christyi, 1 spec. (66.6 mm SL sex undetermined), Lake Ossa downstream to Edea, T. Monod, June 1927.

Acknowledgments

I am particularly grateful to Duncan T. Reid for collecting *Petrocephalus* specimens during his stay in the Djerem region, Cameroon. I also thank John P. Friel and Charles Dardia (Cornell University Museum of Vertebrates, Ithaca, NY, USA), Jos Snoeks, Emmanuel Vreven and Miguël Parrent (Royal Museum for Central Africa, Tervuren, Belgium) and Romain Causse and Patrice Pruvost (Muséum National d'Histoire Naturelle, Paris, France) for access to the collection under their care. The photographs were taken by Duncan T. Reid, John P. Sullivan, and Claude Ferrara.

References

Bass, A.H. (1986) Electric organs revisited: evolution of a vertebrate communication and orientation organ. *In:* Bullock, T.H. & Heiligenberg, W. (Eds.) *Electroreception*. John Wiley and Sons, New York, pp. 13–70.

Bigorne, R. & Paugy, D. (1991) Note sur la systématique des *Petrocephalus* (Teleostei, Mormyridae) d'Afrique de l'Ouest. *Ich-thyological Exploration Freshwaters*, 2, 1–30.

Boden, G., Teugels, G.G. & Hopkins, C.D. (1997) A systematic revision of the large-scaled *Marcusenius* with description of a new species from Cameroon (Teleostei; Osteoglossomorpha; Mormyridae). *Journal of Natural History*, *31*, 1645–1682.

Boulenger, G.A. (1887) On new fishes from the lower Congo. Annals and Magazine of Natural History, 19, 148-149.

Boulenger, G.A. (1899) Poissons nouveaux du Congo. Quatrième Partie. Polyptères, Clupes, Mormyres, Characins. Matériaux pour la faune du Congo. Zoologie--Série I. *Annales du Musée du Congo, Zoologie, 1,* 59–96.

TERMS OF USE

This pdf is provided by Magnolia Press for private/research use. Commercial sale or deposition in a public library or website is prohibited.

- Boulenger, G.A. (1903) Second account of the fishes collected by Dr. W. J. Ansorge in the Niger Delta. *Proceedings of the General Meetings for Scientific Business of the Zoological Society of London*, 2, 324–330.
- Boulenger, G.A. (1912) Poissons recueillis dans la région du Bas-Congo par le Dr. W. J. Ansorge. *Annales du Musée du Congo, Zoologie*, 2, 1–25.
- Boulenger, G.A. (1914) Descriptions of three new fishes from South Cameroon. *Annals and Magazine of Natural History*, 14, 383–385.
- Boulenger, G.A. (1920) Poissons recueillis au Congo Belge par l'expédition du Dr C. Christy. Matériaux pour la faune du Congo. *Annales du Musée du Congo, Zoologie*, 2, 1–38.
- Cuvier, G. & Valenciennes, A. (1847) Histoire Naturelle des Poissons. Tome dix-neuvième. Pitois, Paris, 544 pp.
- Brummet, R.E. & Teugels, G.G. (2004) Rivers of the Lower Guinean rainforest: Biogeography and sustainable exploitation. *In:* R. L. Welcomme & T. Petr (Eds), *Proceedings of the second international symposium on the management of large rivers for fisheries.* FAO Regional Office for Asia and the Pacific, Bangkok, Thailand, pp. 149–171.
- Daget, J. (1979) Contribution à la faune de la République Unie du Cameroun. Poissons de l'Ayina, du Dja et du Bas Sanaga. *Cybium*, 3, 55–64.
- Daget, J. & Depierre, D. (1980) Contribution à la faune de la République Unie du Cameroun. Poissons du Sanaga Moyen et Supérieur. *Cybium*, 3, 53–65.
- Fowler, H.W. (1936) Zoological Results of the George Vanderbilt African Expedition of 1934. Part III,— The Fresh Water Fishes. *Proceedings of The Academy of Natural Sciences of Philadelphia*, 88, 243–335.
- Günther, A. (1862) Eine neue art von Mormyrus. Archiv für Naturgeschichte, 28, 64.
- Harder, W. (1968) Zum Aufbau der epidermalen Sinnesorgane der Mormyridae (Mormyriformes, Teleostei). Zeitschrift für Zellforschung, 89, 212–224.
- Hopkins, C.D., Lavoué, S. & Sullivan, J.P. (2007) Mormyridae. *In:* M.L.J. Stiassny, G.G. Teugels & C.D. Hopkins (Eds), *Faune des poissons d'eaux douces et saumâtres de l'Ouest de l'Afrique Centrale (Cameroun, Guinée Equatoriale, Gabon, Congo Brazzaville).* IRD, Paris, pp. 219–334.
- Lacepède, B.G.E. (1803) Histoire Naturelle des Poissons. Tome cinquième. Saugrain, Paris, 803 pp.
- Lavoué, S., Arnegard, M.E., Sullivan, J.P. & Hopkins, C.D. (2008) *Petrocephalus* of Odzala offer insights into evolutionary patterns of signal diversification in the Mormyridae, a family of weakly electrogenic fishes from Africa. *Journal of Physiology-Paris*, 102, 322–339.
- Lavoué, S., Hopkins, C.D. & Kamdem Toham, A. (2004) The *Petrocephalus* (Pisces, Osteoglossomorpha, Mormyridae) of Gabon, Central Africa, with the description of a new species. *Zoosystema*, 26, 511–535.
- Lavoué, S., Sullivan, J.P. & Arnegard, M.E. (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*, 2600, 1–52.
- Lévêque, C. (1997) *Biodiversity dynamics and conservation: the freshwater fish of tropical Africa*. Cambridge: Cambridge University Press, 438 pp.
- Lévêque, C., Paugy, D. & Teugels, G.G. (1990) Faune des poissons d'eaux douces et saumâtres de l'Afrique de l'Ouest. MRAC, ORSTOM, Tervuren, Paris, 384 pp.
- Marcusen, J. (1854) Vorläufige Mittheilung aus einer Abhandlung über die Familie des Mormyren. *Bulletin de l'Académie des Sciences de St. Petersbourg*, *12*, 1–14.
- Pellegrin, J. (1908) Sur une seconde collection de poissons recueillis par M. E. Haug à Ngomo. *Bulletin de la Société Philomatique de Paris, 11*, 184–190.
- Pezzanite, B. & Moller, P. (1998) A sexually dimorphic basal anal-fin ray expansion in the weakly discharging electric fish *Gnathonemus petersii*. *Journal of Fish Biology*, 53, 638–644.
- Roberts, T.R. (1975) Geographical distribution of African freshwater fishes. *Zoological Journal of the Linnean Society*, 57, 249–319.
- Sauvage, H.E. (1879) Notice sur la faune ichthyologique de l'Ogooué. *Bulletin de la Société Philomatique de Paris*, 7, 90–103. Sauvage, H.E. (1883) Descriptions de quelques poissons de la collection du Muséum d'Histoire Naturelle. *Bulletin de la Société Philomatique de Paris*, 7, 156–161.
- Silvestro, D. & Michalak, I. (2010) raxmlGUI: a graphical front-end for RAxML. available from: http://sourceforge.net/projects/raxmlgui/ (December 2010).
- Stamatakis, A. (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690.
- Stiassny, M.L.J., Teugels, G.G. & Hopkins, C.D. (2007) Faune des poissons d'eaux douces et saumâtres de l'Ouest de l'Afrique Centrale (Cameroun, Guinée Equatoriale, Gabon, Congo Brazzaville). IRD, Publication Scientifique du Muséum, MRAC, Paris, 800 pp.
- Sullivan, J.P., Lavoué, S. & Hopkins, C.D. (2000) Molecular systematics of the African electric fishes (Mormyroidea: Teleostei) and a model for the evolution of their electric organs. *Journal of Experimental Biology*, 203, 665–683.
- Van den Bergh, E.C. & Teugels, G.G. (1998) Description of new small-sized *Barbus* species from the Sanaga Basin in Cameroon. Comments on *B. jae* and on the taxonomic status of *B. condei* (Ostariophysi; Cyprinidae). *Journal of Natural History*, 32, 1367–1401.