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Four new species of *Serranochromis* (Teleostei: Cichlidae) from the Cuanza and Okavango river systems in Angola, including a preliminary key for the genus

JAY R. STAUFFER, JR.[1,2*], ROGER BILLS[2,4] & PAUL H. SKELTON[2,3,5]
[1]*Penn State University, 432 Forest Resources Building, University Park, Pennsylvania 16802, USA.,* [2]*Honorary Research Associate, South African Institute for Aquatic Biodiversity, Makhanda, RSA.*
[2]*South African Institute for Aquatic Biodiversity, Private Bag 1015, Makhanda, 6140, RSA*
[3]*National Geographic Okavango Wilderness Project, Wild Bird Trust.*
[4] *https://orcid.org/0000-0001-6034-4196*
[5] *https://orcid.org/0000-0001-9587-2802*
[*]*Corresponding author.* *vc5@psu.edu;* *https://orcid.org/0000-0001-9653-942X*

Abstract

The present study describes *Serranochromis alvum* **n. sp.**, *Serranochromis swartzi* **n. sp.**, *Serranochromis cuanza* **n. sp.**, and *Serranochromis cacuchi* **n. sp.** from Angolan tributaries of the Cuanza and Okavango systems in Angola. The presence of four or five scale rows between the posterior margin of the orbit and the ascending arm of the preoperculum, the presence of widely set unicuspid teeth on the jaws, widely separated gill rakers, and anal fins with egg ocelli place these four species in *Serranochromis*. The *Serranochromis* described herein are distinguishable based on a combination of morphological and meristic characters, as well as pigmentation patterns. The interorbital width (14.3–15.9 % HL) of *S. alvum* is narrower than that of *S. swartzi* (17.6–19.8), *S. cuanza* (16.3–18.0), and *S. cacuchi* (20.0–21.7). Moreover, the interorbital width of *S. cacuchi* is greater than the other three described species. *Serranochromis swartzi* has a smaller preorbital depth (16.2–18.9 % HL) and snout length (29.6–31.9 % HL) than *Serranochromis cuanza* (PD 19.1–22.2, SNL 35.2–39.6 % HL). *Serranochromis alvum* is known only from the type locality at Cuito-Cuanavale at the junction of the Cuito and Cuanavale rivers, tributary to the Okavango River in Angola. *Serranochromis swartzi* is known only from the type locality in the Cuanza River, Angola. *Serranochromis cuanza* is restricted to the Cuanza River, below Capanda Dam, Angola, while *S. cacuchi* is known only from the Cacuchi River, a tributary of the Cuchi-Cubango River in Angola. The limited distribution of all four species and the absence of many congeners suggest, that in addition to previous studies that invoked a lacustrine speciation model, vicariance through drainage isolation seems to have played an important role in driving speciation in this group. The minimum polygon clusters that are formed when the first principal components of the meristic data are plotted against the second sheared principal components of the morphometric data show separation of the four new species.

Key words: Blue-Headed Largemouth Bream, Red-flanked Largemouth Bream, Black-finned Largemouth Bream, Cacuchi Largemouth Bream, taxonomy

Introduction

Joyce *et al.* (2005) hypothesized that the riverine haplochromine cichlids (Cichlidae: Pseudocrenilabrinae: Haplochromini) of the upper Zambezian waters originally diversified in a large lake that existed north of the Kalahari Desert in the Holocene. The remnants of this paleolake are represented by the present-day Okavango Delta, Caprivi-Zambezi floodplains, and joining systems in southern Africa (Moore & Larkin 2001). The haplochromine cichlids thought to have arisen from this period are scattered throughout southern Africa.

Regan (1920) described the genus *Serranochromis* in a footnote and designated *Chromis thumbergi* Castelnau as the type species. Trewavas (1964) revised the genus, which comprised five previously described species and four new descriptions. She noted that previous authors had placed *Serranochromis* spp. in *Chromys* (*Chromis*), *Hemichromis*, *Paratilapia*, and *Pelmatochromis*. She further suggested that *Serranochromis* arose from two distinct haplochromine lineages with *Chetia, Serranochromis robustus* (Günther) and *S. thumbergi* forming one group and

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Chetia welwitschi (Boulenger) and the remaining *Serranochromis* spp. the other. Greenwood (1979) re-diagnosed *Serranochromis* based on the high number of abdominal vertebrae (16–18), gill-rakers on the outer arch of the ceratobranchial (9–15), and the high number of branched fin rays in the dorsal fin. He further described two subgenera, *Serranochromis* and *Sargochromis*. In 1993, Greenwood (1993) redefined the genus based on several key morphological features and elevated the *Sargochromis* to genus. Greenwood's (1993) serranochromines consisted of the following genera: *Pharyngochromis*, *Chetia*, *Sargochromis,* and *Serranochromis*. It should be noted that Greenwood (1993) considered the serranochromines a group of convenience, because monophyly could not be established. Subsequently, Schwarzer *et al.* (2012) proposed a phylogeny based on mtDNA and AFLP data and concluded that *Pharyngochromis acuticeps* (Steindachner) is imbedded within several *Serranochromis* spp. and undescribed *Serranochromis* spp. were closely related to *Orthochromis* spp. Strict consensus trees showed groupings that included *Pharyngochromis acuticeps* (Steindachner) with *Sargochromis giardi* (Pellegrin), *Sargochromis coulteri* (Bell-Cross)*, Sargochromis mellandi* (Boulenger)*, Sargochromis carlottae* (Boulenger)*, Chetia brevicauda* Bills and Weyl*,* and *Serranochromis macrocephalus* (Boulenger); while other populations of *S. coulteri* are aligned with *Serranochromis angusticeps* (Boulenger), *Serranochromis altus* Winemiller and Kelso-Winemiller, and *Chetia brevis* Jubb. Moreover, *S. thumbergi, S. angusticeps,* and *Serranochromis stappersi* (Trewavas) formed a separate cluster (Koblmüller *et al.* 2008). The polyphyly/paraphyly of the serranochromines has been attributed to hybridization coupled with introgression and river captures (Schwarzer *et al.* 2012).

Despite the lack of clear separation based on genetic data, there are consistent morphological, meristic, and colour pattern differences that readily separate these genera. The key diagnostic characters for the genus *Serranochromis* include the possession of coarse, widely set unicuspid teeth on the jaws, four or five scale rows between the posterior margin of the orbit and the ascending arm of the preoperculum (Trewavas 1964, Greenwood 1993), two or more scales between the eye and the pre-opercular groove (Greenwood 1993), high number of gill rakers (Greenwood 1979), large mouths (Skelton 2001), and a high number of branched dorsal-fin rays (Greenwood 1979). The genus currently contains 11 described species in southern Africa (Skelton, 2001). Most of these species were described in the early 1900s except *S. altus* and *Serranochromis meridianus* Jubb (Skelton 2001). Over the past two decades, there has been a surge in biodiversity exploration in the Upper Zambezi and adjacent river systems.

Since 2005, teams from the South African Institute for Aquatic Biodiversity (SAIAB) have explored and collected fishes in the Angolan tributaries of the Cuanza, Okavango, Cuando, and Zambezi systems. The SAIAB in partnership with the Instituto Nacional de Investigação Pesqueira (INIP) in Luanda mounted several expeditions to the Cuanza River from 2005 to 2009. Multi-disciplinary expeditions were undertaken in 2012 and 2013 to the Okavango and Cuando systems under the Southern African Regional Environmental Program (SAREP). Various expeditions of the Wild Bird Trust-National Geographic Okavango Wilderness Project (WBT-NGOWP) were made to the hitherto unexplored reaches of the Cuito, Cuanavale, and Cuando rivers, source reaches of the Lungwebungu, and Luanginga tributaries of the upper Zambezi, as well as to previously explored reaches of the Cubango and delta of the Okavango system, from 2015 through 2019.

These expeditions returned several serranochromines that morphological and/or molecular data indicate are new to science. Tissues from two of the unidentified serranochromines of the Cuanza (Kwanza) River were included by Schwarzer *et al.* (2012) and are described herein. The purpose of this paper is to describe four species, which we are placing in *Serranochromis* based on morphological criteria.

Methods

A variety of collection methods were used including electro-fishing, a 3m seine net, a throw net, a large D-shaped hand net, fyke and gill nets, and angling. Some specimens were purchased from local fishermen who typically used gill nets and traps. Some sampling gears were used in combination such as typically electro-fishing down channels into a seine net. Gill and fyke nets were all set overnight and seine nets were used both day and night.

Animal ethics procedures were followed according to SAIAB's ethics standard operating procedures for the ethical killing and preservation of animals. Permission for the research collections was granted for this work (research proposal 2012/06 granted 16.03.12).

Counts and measurements follow Stauffer (1994) and Konings & Stauffer (2006). All counts and measurements were taken from the left side of the body except for gill-raker counts, which were taken on the right side.

Morphometric data were analyzed using a sheared principal component analysis, which factors the covariance matrix and restricts size variation to the first principal component (Humphries *et al.* 1981; Bookstein *et al.* 1985). Meristic data were analyzed using a principal component analysis in which the correlation matrix was factored. Differences among species were illustrated by plotting the sheared second principal components (SPC2) of the morphometric data against the first principal components (PC1) of the meristic data (Stauffer & Hert 1992).

Other Material Examined

Serranochromis macrocephalus SAIAB 72887 (6), 56.06–141.52 mm SL, collected from Zambezi River above Senanga System.

Comparative material. Ocelli in breeding males of *S. robustus* and *Serranochromis jallae* (Boulenger) are restricted to the posterior 4–5 membranes of the anal fin (Stauffer *et al.* 2020). *Serranochromis stappersi* and *S. altus* possess small teeth that are buried in the lips (Trewavas 1964, Winemiller & Kelso-Winemiller 1991). *Serranochromis macrocephalus* (SAIAB 72887)*, Serranochromis janus* (Trewavas), and S. *angusticeps* possess rounded caudal fins (Trewavas 1964). *Serranochromis spei* Trewavas has an extended lower jaw (53.5–57.2 % HL; Trewavas 1964). *Serranochromis thumbergi* has more than 39 lateral-line scales (Trewavas 1964). An acute angle of the cleft of the mouth (50–60º of horizontal) is present in *S. meridianus* (Jubb 1967). Finally, long, dark pectoral fins that when extended upward reach to past the middle of the dorsal fin are present in *Serranochromis longimanus* (Boulenger) (Trewavas 1964).

Results

Fishes were obtained from SAIAB at the areas indicated in Fig. 1. When colour descriptions were provided with the field notes, a live colour description is provided. When these were not available markings on preserved specimens are given.

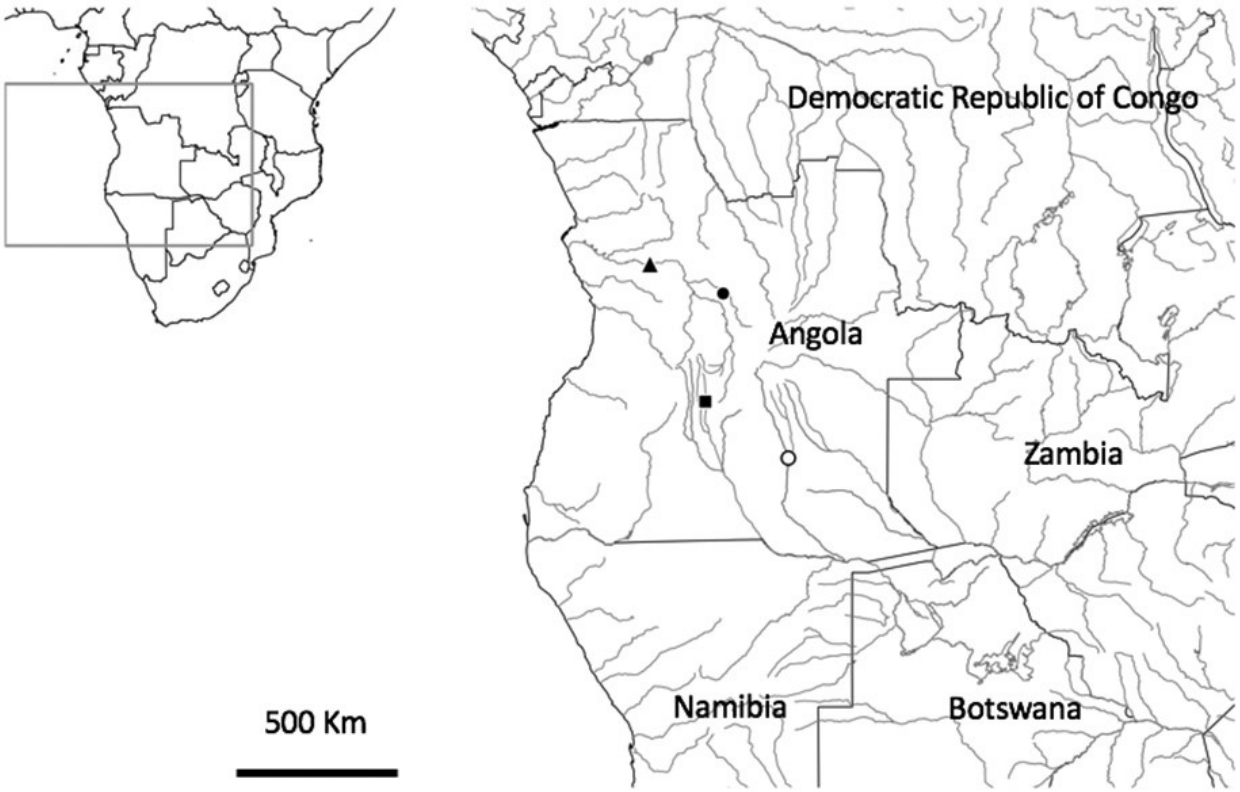

FIGURE 1. Locations of the type locality for *Serranochromis alvum* (open circle), *Serranochromis cacuchi* (solid square), *Serranochromis swartzi* (solid circle), *Serranochromis cuanza* (solid triangle).

***Serranochromis alvum* new species**
Suggested common name: Blue-Headed Largemouth Bream
(Fig. 2).

Holotype. SAIAB 186842, 151.8 mm SL (male), collected from Cuito-Cuanavale bridge, Cuito River, Okavango River system, Angola; 15º10'16.4" S, 19º11'39.3" E. Collected by R. Bills, P. H. Skelton, F. de Almedia, 18 May 2012. Collected with gill and seine nets.

Paratypes. SAIAB 205219 (5), 71.5–114.5 mm SL, data as for holotype.

Diagnosis. The presence of ocelli throughout the anal fin of breeding males distinguishes *S. alvum* from *S. robustus* and *Serranochromis jallae* (Boulenger) in which the ocelli in breeding males are restricted to the posterior 4–5 membranes of the anal fin. The exposed teeth of *S. alvum* differs from those of *S. stappersi* and *S. altus*, which possess small teeth that are buried in the lips. *Serranochromis alvum* has an emarginate caudal fin, while *S. macrocephalus*, *S. janus* (Trewavas), and *S. angusticeps* have rounded caudal fins. The shorter jaw of *S. alvum* (43.4–53.5 % HL) separates it from *Serranochromis spei* (Trewavas) (53.5–57.2 % HL). *Serranochromis alvum* has 34–36 lateral-line scales, while *S. thumbergi* possesses greater than 39 lateral-line scales. The acute angle of the cleft of the mouth (50–60º of horizontal) of *S. meridianus* delimits it from the 30º angle of *S. alvum*. The long dark pectoral fins which reach past the middle of the dorsal fin separates *S. longimanus* from *S. alvum.* The interorbital width (14.3–15.9 % HL) of *S. alvum* is narrower than that of *Serranochromis swartzi* **n. sp.** (17.6–19.8), *Serranochromis cuanza* **n. sp.** (16.3–18.0), and *Serranochromis cacuchi* **n. sp.** (20.0–21.7).

Description. Morphometric ratios and meristic data in Table 1. Body shape and pigment patterns in Fig 2.

Body slender, fusiform, and compressed, deepest at origin of dorsal fin. Dorsal-fin origin at vertical through posterior edge of operculum, dorsal-fin spines to maximum length over 5–6 spines, spine lappets prominent. Soft dorsal rounded behind, extending to base of caudal fin. Caudal peduncle short (13–18 % SL) 7.5 times in SL, slightly longer than deep (CPL/CPD 1.1–1.2). Caudal fin broad, relatively short (little more than half the head length), rectangular and truncate. Anal-fin origin closer to caudal-fin base than tip of snout, below vertical through first dorsal soft-ray; soft-rayed section with bluntly rounded hind edge, extending to caudal-fin base. Pectoral fin close behind gill slit, ventral on flanks, base sub-vertical, short, not extending beyond pelvic fins, postero-ventral margin bluntly rounded. Pelvic fins ventral, origin narrowly behind base of pectoral fin, short, not reaching origin to the anal fin, strong leading spine 2/3 length of fin. Scales small, in 15 even rows across flanks from dorsal-fin origin to anal-fin origin, 16 rows of scales around caudal peduncle, 34–36 in lateral line; upper lateral line gently curved, lower lateral line straight through mid-caudal peduncle; five scale rows between anterior dorsal and lateral line, two scale rows between soft dorsal and posterior end of upper lateral line, nape and chest scales reduced.

FIGURE 2. *Serranochromis alvum*, Holotype SAIAB 186842, 151.8 mm SL, collected from Cuito Canavale bridge, Angola; 15º10'16.4"S 19º11'39.3"E, 18 May 2012.

TABLE 1. Morphometric and meristic values of *Serranochromis alvum* (n=6). The mean, standard deviation and range include holotype and paratypes.

Variable	Holotype	Mean	SD	Range
Standard length, mm	151.8	103.27	29.0	71.5-151.8
Head length, mm	57.9	39.07	11.0	28-57.9
Percent of standard length				
Head length	38.1	37.8	0.68	37–39.0
Body depth	33.6	31.7	1.39	30.1–33.6
Snout to dorsal-fin origin	40.2	39.5	0.93	38–40.4
Snout to pelvic-fin origin	43.5	42.4	1.30	40.2–43.6
Dorsal fin base length	54.1	53.4	0.83	52.4–54.2
Anterior dorsal to anterior anal	48.0	46.1	1.3	44.4–48
Anterior dorsal to posterior anal	57.9	57.3	0.67	56.4–58.1
Posterior dorsal to posterior anal	14.4	14.5	0.89	13.4–15.9
Posterior dorsal to anterior anal	27.9	28.4	0.41	27.9–28.9
Posterior dorsal ventral caudal	18.4	18.8	1.2	17.1–20.2
Posterior anal to dorsal caudal	20.1	20.6	1.0	19.4–22.4
Posterior dorsal to pelvic-fin origin	53.1	51.9	1.2	50.6–53.4
Anterior dorsal to pelvic-fin origin	35.2	32.8	1.7	30.7–35.2
Caudal peduncle length	15.0	15.8	1.7	13–18
Least caudal peduncle depth	12.3	11.7	0.67	10.5–12.3
Percent of head length				
Snout length	34.9	32.4	1.69	30.3–34.9
Postorbital head length	45.0	43.2	1.49	41.1–45.0
Horizontal eye diameter	23.4	25.0	2.30	21–26.7
Vertical eye diameter	21.3	23.4	2.06	21.2–25.7
Interorbital width	15.3	15.1	0.54	14.3–15.9
Head depth	70.0	70.8	5.1	63.3–78
Pre-orbital depth	19.7	17.1	1.52	15.2–19.7
Cheek depth	27.6	25.7	1.97	23.5–28.1
Lower jaw length	51.4	48.7	3.73	43.4–53.5
Counts				
Dorsal-fin spines	15	15	83.3	14-15
Dorsal-fin rays	14	14	50	13–15
Anal-fin spines	3	3	100	
Anal-fin rays	10	10	83.3	9–10
Pelvic-fin rays	5	5	100	
Pectoral-fin rays	15	15	50	13–15
Lateral line scales	35	35	66.7	34–36
Pored scales posterior to LL	2	2	100	
Cheek scales	9	8	50	7–10
Gill rakers on first epibranchial	3	3/4	50	3–4
Gill rakers on first ceratobranchial	11	9	50	9–11
Teeth outer row of left lower jaw	2	8	50	7–12
Teeth rows on upper jaw	11	2	100	
Teeth rows on lower jaw	2	2	100	

Head elongate 2.5–2.7 times in SL (37–39%SL), length greater than body depth, pointed with straight predorsal profile extending 20˚ above horizontal. Eyes large (HED 21–26.7%HL; VED 21.2–25.7% HL), dorso-lateral in anterior half of head, entirely above level of the mouth and before the dorsal edge of the operculum. Interorbit narrow, less than half orbit diameter. Snout relatively long, greater than orbit diameter, nares in mid-snout before orbits. Lachrymal (pre-orbit) depth equal to orbit diameter. Cheek below and behind orbits deep with 7–10 rows of scales. Post orbit half-length of head, interorbit 14.3–5.9% HL. Mouth terminal, large, protrusible; angle of closed jaw of holotype 30˚ below horizontal, posterior premaxilla to below anterior orbit, lips well developed, even. Teeth caniniform, exposed, widely spaced in 2 series on upper and lower jaws. First branchial arch with 3–4-1-9–11 gill-rakers. Gill-slit large, extending from upper flank opposite dorsal orbit rim in smooth arch to mid-ventral below orbits.

Coloration. Preserved specimens yellowish-brown with darker greyish brown interorbital and body bars, ventral surfaces yellow-brown. Fins light yellowish with grey markings; head with broad greyish band across lachrymal through eye to upper operculum and opercular spot. Body with two lateral black pigment bands and six broad dark brown bars to caudal-fin base reaching from dorsal fin to lower flanks, dark brown spots at base of scales. Live males with broad black bar from lachrymal through lower eye across post-orbit to large opercular spot; iridescent pale blue and white patches on cheeks and above post-orbital bar, white lower cheeks and gular, opercle dusted with grey and black below dorsal black bar, pale blue opercular membrane. Body bluish-black above, prominent black bars on body with white infused with blue interspaces between bars, below pectoral fins, and on lower flanks and ventral side. Dorsal fin with grey-black blotched membranes between anterior spines; dark grey to black blotches with light blocks on membranes between posterior 5–6 spines; soft dorsal with dark grey-black blotches and clear spots on membranes, edges grey. Caudal fin with elongate dark grey-black rectangles and white spots on membranes, a lighter creamish brown submarginal band and greyish black marginal band. Anal fin with 3– 4 rows of deep greyish-red spots between pale yellow bands. Pectoral fins with grey rays and translucent hyaline membranes. Pelvic fins with clear rays and a sooty dust over rays.

Habitat. Collected in gill nets set along the fringing *Phragmites* reed bed in the main Cuito channel at the Cuito-Cuanavale main road bridge (Fig. 3). Water depths were approximately 1.5–2m. The riverbed was mostly sand substrate with occasional marginal aquatic weed beds and fringing emergent beds of *Phragmites*.

FIGURE 3. The main Cuito channel at the Cuito-Cuanavale main road bridge, where *Serranochromis alvum* was collected.

Distribution. Currently known only from the type locality at Cuito-Cuanavale at the junction of the Cuito and Cuanavale rivers, tributary to the Okavango River in Angola**.**

Etymology. The specific name, *alvum,* a noun in apposition, is derived from the Latin, which means blotches and refers to the prominent lateral pigmentation.

***Serranochromis swartzi* new species**

Suggested common name: Red-flanked Largemouth Bream

(Fig. 4)

Holotype. SAIAB 85174, 135.8 mm SL (male); at bridge between Cimanga and Capunda, Cuanza River, Angola; 10º38'26" S, 17º25'6" E; collected by Ernst Swartz, 23 August 2008.

Paratypes. SAIAB 204368 (13), 106.8–139.5 mm SL; data as for holotype.

Diagnosis. The presence of ocelli throughout the anal fin of breeding males distinguishes *S. swartzi* from *S robustus* and *S. jallae* in which the ocelli in breeding males are restricted to the posterior 4–5 membranes of the anal fin. The exposed teeth of *S. swartzi* differs from those of *S. stappersi* and *S. altus*, which possess small teeth that are buried in the lips. *Serranochromis swartzi* has an emarginate caudal fin, while *S. macrocephalus*, *S. janus*, and *S. angusticeps* have rounded caudal fins. The shorter jaw of *S. swartzi* (44.4–52.0 % HL) separates it from *S. spei* (53.5–57.2 % HL). *Serranochromis swartzi* has 34–37 lateral-line scales, while *S. thumbergi* possesses greater than 39 lateral-line scales. The acute angle of the cleft of the mouth (50–60º of horizontal) of *S. meridianus* delimits it from the 25º angle of *S. swartzi*. The long dark pectoral fins which reach past the middle of the dorsal fin separates *S. longimanus* from *S. swartzi.* The interorbital width (14.3–15.9 % HL) of *S. alvum* is narrower than that of *S. swartzi* (17.6–19.8). *Serranochromis swartzi* has a smaller preorbital depth (16.2–18.9 % HL) and snout length (29.6–31.9 % HL) than *Serranochromis cuanza* (PD 19.1–22.2, SNL 35.2–39.6 % HL). The greater preorbital depth (19.1–22.2 % HL) of *S. swartzi* distinguishes it from *S. cacuchi*, which has a smaller preorbital depth (11.3–15.5 % HL).

Description. Morphometric ratios and meristic data in Table 2. Body shape and pigment patterns in Figure 4.

Body fusiform and compressed, deepest at origin of dorsal fin. Dorsal-fin origin at vertical through posterior edge of operculum, dorsal fin with XVI-XVII + 12 spines and rays, spines to maximum length over 5–6 spines, dorsal-spine lappets prominent. Soft dorsal deep and pointed behind, not to beyond base of caudal fin. Caudal peduncle long, 16–19% SL, length 1.4–1.6 times depth. Caudal fin broad, relatively short (little more than half the head length), emarginate. Anal fin with III+10 rays, origin closer to caudal-fin base than tip of snout, below vertical through base of penultimate dorsal spine, soft-rayed section with pointed hind edge, not to hind margin of caudal peduncle. Pectoral fin with 13–15 rays, close behind gill slit, ventro-lateral on flanks, base near vertical, pointed, short not beyond pelvic fins. Pelvic fins ventral with strong leading spine 2/3 length of fin, origin narrowly behind vertical through base of pectoral fins, reaching to anus and anterior base of anal fin. Scales small, around 15–18 rows across flanks, dorsal and ventral rows tend to become irregular; 16 rows around the caudal peduncle, 34–37 in lateral line; upper lateral line slightly curved, lower lateral line short but straight; five or six irregular scale rows between anterior dorsal and lateral line, two scale rows between soft dorsal and posterior end of upper lateral line. Chest scales small reduced and irregular.

Head elongate (34.8–38.1 % SL), 2.6–2.8 times in SL, length greater than body depth, acute and pointed with straight predorsal profile extending 35˚ above horizontal. Eyes large (HED 22.3–38.1 % HL; VED 21.1–25.6% HL), dorso-lateral in anterior half of head, entirely above level of the mouth and below the dorsal edge of the operculum. Snout relatively long, greater than orbit diameter, nares in mid-snout before orbits. Lachrymal (preorbit) width equal to orbit diameter. Cheek below and behind orbits deep with 5-6 rows of scales. Post-orbit less than half length of head, interorbit 14.3–15.9 % HL. Mouth terminal, large, protractile; angle of closed jaw of holotype 25˚ below horizontal, posterior premaxilla to below anterior orbit, lips well developed, even along jaws. Teeth caniniform, exposed, narrowly spaced in two to three rows on upper and lower jaws. First branchial arch with 3–4-1-9–12 gill-rakers. Gill opening large, arched from above level of the eye to a vertical below the eye on the ventral side.

TABLE 2.. Morphometric and meristic values of *Serranochromis swartzi* (n=14). The mean, standard deviation and range include holotype and paratypes.

Variable	Holotype	Mean	SD	Range
Standard length, mm	135.8	123.9	10.09	106.8–139.5
Head length, mm	51.0	46.0	4.12	39.4–52.2
Percent of standard length				
Head length	37.6	37.1	0.85	34.8-38.1
Body depth	34.0	33.6	2.08	27.1–35.8
Snout to dorsal-fin origin	39.9	39.2	1.25	36.7–40.8
Snout to pelvic-fin origin	42.4	42.5	1.61	40–44.7
Dorsal fin base length	55.9	53.3	1.66	50.8–56.9
Anterior dorsal to anterior anal	46.8	47.0	3.15	44.7–57.5
Anterior dorsal to posterior anal	56.8	56.9	1.16	55.2–59.3
Posterior dorsal to posterior anal	15.5	14.7	0.87	13.4–16.4
Posterior dorsal to anterior anal	30.7	29.0	1.15	27.4–31.1
Posterior dorsal ventral caudal	17.1	18.3	0.93	16–19.5
Posterior anal to dorsal caudal	20.7	21.6	0.84	20–22.7
Posterior dorsal to pelvic-fin origin	51.5	51.0	0.86	49–52.6
Anterior dorsal to pelvic-fin origin	35.5	35.16	0.86	33.3–36.3
Caudal peduncle length	16.0	17.6	0.75	16–19
Least caudal peduncle depth	12.0	12.0	0.33	11.5–12.6
Percent of head length				
Snout length	29.6	30.9	0.74	29.6–31.9
Postorbital head length	46.2	44.3	0.90	43.1–46.2
Horizontal eye diameter	23.9	24.4	1.29	22.3–26.2
Vertical eye diameter	21.7	23.0	1.13	21.1–25.5
Interorbital width	19.3	18.3	0.69	17.6–19.8
Head depth	71.3	72.9	3.46	67.8–78.7
Pre-orbital depth	17.4	17.5	0.90	16.2–18.9
Cheek depth	24.0	24.9	2.81	20.2–31.2
Lower jaw length	48.2	48.2	2.15	44.4–52
Counts				
Dorsal-fin spines	15	15	85.7	14–15
Dorsal-fin rays	14	14	64.3	13–15
Anal-fin spines	3	3	100	
Anal-fin rays	10	10	100	
Pelvic-fin rays	5	5	100	
Pectoral-fin rays	14	13/14	42.9	13-15
Lateral line scales	36	35/36	35.7	34–37
Pored scales posterior to LL	3	2	50	1–3
Cheek Scales	8	7	85.7	7–8
Gill rakers on first epibranchial	3	3	92.9	3–4
Gill rakers on first ceratobranchial	12	11	50	9–12
Teeth outer row of left lower jaw	17	18	28.6	10–23
Teeth rows on upper jaw	2	2	92.9	2–3
Teeth rows on lower jaw	2	2	92.9	2–3

Coloration. Preserved specimens brown on flanks, darker on dorsal side, light yellowish brown ventrally. Head with dark interorbital and yellowish gular; broad grey bar on pre-opercle. Single thin lateral band and 8–9 grey vertical bars on body. Dorsal fin with plain brown membranes between anterior seven spines; posterior spinous and rayed membranes with grey blotches. Caudal fin with elongate dark rectangles on membranes and lighter submarginal band. Anal fin with brown membranes and 3–4 irregularly spaced grey blotches. Pelvic and pectoral fins plain brown. Live colours not recorded.

Distribution. Known only from the type locality on the Cuanza River in Angola.

Etymology The specific name *swartzi* is named after the primary collector Dr. Ernst Swartz - ichthyologist at SAIAB and primary explorer on the Cuanza River programme (2005-2009).

FIGURE 4. *Serranochromis swartzi*, SAIAB 85174, 135.8 mm SL; collected from bridge between Cimanga and Capunda, Cuanza River, Angola; 10º38'26" S 17º25'6"E; collected by Ernst Swartz, 23 August 2008.

Serranochromis cuanza **new species**

Suggested common name: Black-finned Largemouth Bream

(Fig. 5)

Holotype. SAIAB 84888, 181.0 mm SL (male); collected from Posto 5 on the Cuanza River, Angola, 09º48'23" S, 15º24'30" E collected by Ernst Swartz, 31 October 2007.

Paratypes. SAIAB 84791, 7, 49.6–123.4 mm SL; data as for holotype.

Diagnosis. The presence of ocelli throughout the anal fin of breeding males distinguishes *S. cuanza* from *S. robustus* and *S. jallae* in which the ocelli in breeding males are restricted to the posterior 4–5 membranes of the anal fin. The exposed teeth of *S. cuanza* differs from those of *S. stappersi* and *S. altus*, which possess small teeth that are buried in the lips. *Serranochromis cuanza* has an emarginate caudal fin, while *S. macrocephalus*, *S. janus*, and *S. angusticeps* have rounded caudal fins. The shorter jaw of *S. cuanza* (44.3–52.8 % HL) separates it from *S. spei* (53.5–57.2 % HL). *Serranochromis cuanza* has 36–37 lateral-line scales, while *S. thumbergi* possesses greater than 39 lateral-line scales. The acute angle of the cleft of the mouth (50–60º of horizontal) of *S. meridianus* delimits it from the 25º angle of *S. cuanza*. The long dark pectoral fins which reach past the middle of the dorsal fin separates *S. longimanus* from *S. cuanza.* The interorbital width of *S. cuanza* (16.3–18.0% HL) is narrower than that of *S. cacuchi* (20–21.7 % HL). *Serranochromis cuanza* has a greater preorbital depth (19.1–22.2% HL) and snout length (SNL 35.2–39.6% HL) than *S. swartzi* (PD 16.2.1–18.9, SNL 29.6–31.9% HL). The interorbital width of *S. cuanza* (16.3–18.0) is wider than that of *S. alvum* (14.3–15.9 % HL).

Description. Description. Morphometric ratios and meristic data in Table 3. Body shape and pigmentation patterns in Fig 5.

TABLE 3. Morphometric and meristic values of *Serranochromis cuanza* (n=8). The mean, standard deviation and range include holotype and paratypes.

Variable	Holotype	Mean	SD	Range
Standard length, mm	181.0	103.3	41.7	49.6–181.0
Head length, mm	67.2	39.3	15.7	19.2–67.2
Percent of standard length				
Head length	37.1	38.0	0.97	36.4–39.5
Body depth	35.7	31.1	2.5	27.7–35.7
Snout to dorsal-fin origin	39.4	39.2	1.39	38.0–41.8
Snout to pelvic-fin origin	42.6	42.2	1.26	40.6–44.3
Dorsal fin base length	54.1	53.0	0.78	51.6–54.1
Anterior dorsal to anterior anal	46.9	43.1	2.26	40.2–46.9
Anterior dorsal to posterior anal	57.2	54.2	2.5	49.4–57.2
Posterior dorsal to posterior anal	15.3	14.1	0.89	13.0–15.3
Posterior dorsal to anterior anal	31.7	27.9	1.89	26–28.7
Posterior dorsal ventral caudal	20.1	19.4	1.82	17.3–22.6
Posterior anal to dorsal caudal	22.4	21.8	1.24	20.7–24.5
Posterior dorsal to pelvic-fin origin	50.4	49.4	1.25	27.1–36.1
Anterior dorsal to pelvic-fin origin	36.1	31.6	2.91	27.1–36.1
Caudal peduncle length	17.0	19.1	2.70	17.0–25.0
Least caudal peduncle depth	12.0	11.0	0.97	9.6–12.0
Percent of head length				
Snout length	34.7	29.7	2.82	26.9–34.7
Postorbital head length	44.9	43.7	1.18	41.7–44.9
Horizontal eye diameter	21.3	27.5	3.24	21.3–30.9
Vertical eye diameter	20.1	25.9	3.02	20.1–30.4
Interorbital width	20.6	18.0	1.23	16.3–20.6
Head depth	74.7	67.2	7.04	55.2–75.32
Pre-orbital depth	19.7	15.6	2.41	11.3–19.7
Cheek depth	29.1	21.7	3.67	17.2–29.1
Lower jaw length	52.8	48.3	3.27	44.3–52.8
Counts		**Mode**	**Freq**	**Range**
Dorsal-fin spines	15	15	100	
Dorsal-fin rays	12	14	50	12–14
Anal-fin spines	3	3	100	
Anal-fin rays	10	10	75	9–11
Pelvic-fin rays	5	5	100	
Pectoral-fin rays	14	14	75	12–14
Lateral line scales	37	36/37	50	36–37
Pored scales posterior to LL	2	½	50	1–2
Cheek Scales	8	7	62.5	7–8
Gill rakers on first epibranchial	2	3	75	2–4
Gill rakers on first ceratobranchial	10	9/10/11/12	25	9–12
Teeth outer row of left lower jaw	19	19	37.5	18–21
Teeth rows on upper jaw		3	60	2–3
Teeth rows on lower jaw		2	80	2–3

FIGURE 5. *Serranochromis cuanza*, SAIAB 84888, 181.0 mm SL; collected from Posto 5 09º48'23"S 15º24'30"E collected by Ernst Swartz, 31 October 2007.

Body fusiform and compressed, deepest at origin of dorsal fin. Dorsal-fin origin at vertical through posterior edge of operculum; dorsal fin with XV + 12–14 spines and rays; dorsal spines increase to maximum length over 5–6 spines, lappets prominent. Soft dorsal deep and obtusely pointed behind, extending to base of caudal fin. Caudal peduncle long, 5.3–6.3 times in SL (16–19% SL), length 1.3–1.5 times depth. Caudal fin broad, relatively short rectangular (little more than half the head length), emarginate. Anal fin with III+10 rays, origin behind mid body, closer to caudal-fin base than tip of snout, below vertical through base of ultimate dorsal spine, soft-rayed section with pointed hind edge, extending to base of caudal fin. Pectoral fin with 12–14 soft rays, close behind gill slit, ventro-lateral on flanks, base near vertical, pointed paddle-shaped, not beyond pelvic fins. Pelvic fins ventral with strong leading spine 2/3 length of fin, origin narrowly behind vertical through base of pectoral fins, reaching to anus and anterior base of anal fin. Scales small, with 18–20 regular rows across flanks from dorsal-fin origin to anal-fin origin; 16 scale rows around the caudal peduncle, 36–37 in lateral line, pores complete; upper lateral line nearly straight, slightly curved, lower lateral line straight through mid-caudal peduncle; five or six scale rows between anterior dorsal and lateral line, two scale rows between soft dorsal and posterior end of upper lateral line. Chest scales small reduced and irregular.

Head triangulate, length slighter greater than body depth, 2.5–2.7 times in SL (36.4–39.5% SL); predorsal profile straight, angle 30˚. Eyes large (HED 21.3–30.9 % HL; VED 20.1–30.4 % HL) dorso-lateral in anterior half of head, entirely above level of the mouth and below the dorsal edge of the operculum. Snout relatively long, greater than orbit-diameter, nares in mid-snout before orbits. Lachrymal (preorbit) width equal to orbit diameter. Cheek below and behind orbits deep with 5–6 rows of scales. Post-orbit less than half length of head, interorbit subequal to orbit diameter, 14.3–15.9% HL. Mouth terminal, large, protractile, angle of closed jaw of holotype 25˚ below horizontal, posterior premaxilla to below anterior orbit, lips well developed. Teeth caniniform, exposed, narrowly spaced in two to three rows on upper and lower jaws. First branchial arch with 3–4-1-9–12 gill-rakers. Gill opening large, curved from above level of eye to mid-ventrally through a vertical below eye.

Coloration. Head and body brown in preserved specimens. Laterally with single thin mid-lateral band and 8–9 regular bars from dorsum to lower flank. Dorsal fin with greyish brown membranes, rayed membranes with proximal dark spots and distal streaks. Caudal fin brown. Anal fin brown with light indications of egg spots. Pectoral and pelvic fins plain light brown. In life, metallic silvery on sides from head to caudal peduncle, dorsum mixed coppery-olive, white ventral surface; iris a deep purple-charcoal to reddish around the black pupil; upper operculum with metallic golden tinge; opercular spot grey, metallic light blue over exposed maxilla; inter-spinous membranes of

dorsal fin light grey with darker grey posterior edges, lappets tinged with red, soft rayed membranes with light and dark blocks proximally, plain greyish distally; caudal fin with light rays and pale grey membranes forming blocks proximally; anal fin an overall yellow cast with greyish infusion, 4–5 scattered greyish egg spots with lighter margins on medial and posterior membranes; pectoral-fins colourless off-white; pelvic-fins yellow infused with grey, spines dusted sooty grey.

Distribution. Known only from the collection locality Posto 5 on the Cuanza River, below Capanda Dam, Angola.

Etymology. The specific name *cuanza*, a noun in apposition, refers to the Cuanza River, spelt as generally done in Angola. The species is most likely endemic to the Cuanza River system.

Serranochromis cacuchi new species

Suggested common name: Cacuchi Largemouth Bream
Fig. 6.

Holotype. SAIAB 186684, 181.9 (male) mm SL; collected from the Cacuchi River, approximately 15 km south west of Chitembo Village at the bridge on the main road north from Menongue, tributary of Cuchi, Cubango (Okavango) River system, Angola; 13º35'39.6" S, 16º52'49.8" E. Collected by R. Bills, P. H. Skelton, F. de Almeida, 11 May 2012.

Paratypes. SAIAB 186674, (4) 132.7–191.5 mm; data as for holotype

Diagnosis. The presence of ocelli throughout the anal fin of breeding males distinguishes *S. cacuchi* from from *S. robustus* and *S. jallae* in which the ocelli in breeding males are restricted to the posterior 4–5 membranes of the anal fin. The exposed teeth of *S. cacuchi* differs from those of *S. stappersi* and *S. altus*, which possess small teeth that are buried in the lips. *Serranochromis cacuchi* has an emarginate caudal fin, while *S. macrocephalus*, *S. janus*, and *S. angusticeps* have rounded caudal fins. The shorter jaw of *S. cacuchi* (47.8–52.3 % HL) separates it from *S. spei* (53.5–57.2 % HL). *Serranochromis cacuchi* has 32–33 lateral-line scales, while *S. thumbergi* possesses greater than 39 lateral-line scales. The acute angle of the cleft of the mouth (50–60º of horizontal) of *S. meridianus* delimits it from the 25º angle of *S. cacuchi*. The long dark pectoral fins which reach past the middle of the dorsal fin separates *S. longimanus* from *S. cacuchi.* The interorbital width (20.0–21.7 % HL) delimits *S. cacuchi* from *S. alvum* (14.3–15.9 % HL).The snout length of *S. cacuchi* (35.2–39.6 % HL) is longer than that of *S. alvum* (30.3–34.9 % HL) and *S. cuanza* (26.9–34.7 % HL). The larger preorbital depth of *S. cacuchi* (19.1–22.2 % HL) distinguishes it from *S. swartzi* (16.2–18.9 % HL).

Description. Morphometric ratios and meristic data in Table 4. Body shape and pigment patterns in Fig 6.

FIGURE 6. *Serranochromis cacuchi*, SAIAB 186684, 181.9 mm SL; collected from Bridge of 1000 mines north of Mambue 13º35'39.6"S 16º52'49.8"E. Collected by R. Bills, P. Skelton, F. de Almeida, 11 May 2012.

TABLE 4. Morphometric and meristic values of *Serranochromis cacuchi* (n=5). The mean, standard deviation and range include holotype and paratypes.

Variable	Holotype	Mean	SD	Range
Standard length, mm	181.9	156.0	28.36	132.7–191.5
Head length, mm	67.2	57.8	10.33	48.6–70.6
Percent of standard length				
Head length	36.9	37.0	0.34	36.6–37.5
Body depth	32.4	31.6	0.95	30.4–32.7
Snout to dorsal-fin origin	38.4	38.4	0.81	37.3–39.6
Snout to pelvic-fin origin	42.6	42.3	0.54	41.6–42.8
Dorsal fin base length	54.4	52.5	1.54	50.7–54.4
Anterior dorsal to anterior anal	46.5	45.3	0.79	44.4–46.5
Anterior dorsal to posterior anal	57.0	55.5	1.27	53.7–57.0
Posterior dorsal to posterior anal	13.6	14.1	0.74	13.1–14.9
Posterior dorsal to anterior anal	27.8	25.5	1.02	26.0–28.7
Posterior dorsal ventral caudal	19.5	19.0	0.74	17.7–19.5
Posterior anal to dorsal caudal	21.2	20.9	0.75	20.0–22.0
Posterior dorsal to pelvic-fin origin	51.8	51.0	1.10	49.3–52.1
Anterior dorsal to pelvic-fin origin	33.2	32.1	1.00	30.8–33.2
Caudal peduncle length	16.0	17.4	1.67	16.0–20.0
Least caudal peduncle depth	11.1	10.8	0.40	10.3–11.1
Percent of head length				
Snout length	39.6	37.4	1.90	35.2–39.6
Postorbital head length	42.2	43.8	0.81	42.6–44.8
Horizontal eye diameter	18.5	21.5	2.18	18.5–24.5
Vertical eye diameter	17.7	19.8	1.74	17.7–22.3
Interorbital width	21.7	20.6	0.67	20.0–21.7
Head depth	75.4	72.5	2.95	67.9–75.4
Pre-orbital depth	22.2	20.54	1.31	19.1–22.2
Cheek depth	30.2	27.7	1.48	26.3–30.2
Lower jaw length	52.3	50.1	2.02	47.8–52.3
Counts				
Dorsal-fin spines	15	15	60	14–15
Dorsal-fin rays	12	12	80	12–13
Anal-fin spines	3	3	100	
Anal-fin rays	9	9	100	
Pelvic-fin rays	5	5	100	
Pectoral-fin rays	13	13	60	12–14
Lateral line scales	33	33	60	32–33
Pored scales posterior to LL	1	2	80	1–2
Cheek Scales	6	6	80	5–6
Gill rakers on first epibranchial	4	3	80	5–6
Gill rakers on first ceratobranchial	10	10	80	10–11
Teeth outer row of left lower jaw	18	18	60	13–19
Teeth rows on upper jaw	2	3	60	2–3
Teeth rows on lower jaw	2	2	80	2–3

Body slender, fusiform, and compressed, deepest at origin of dorsal fin. Predorsal profile straight at 30˚ to horizontal, with shallow kink at interorbit and gentle curve towards dorsal fin. Dorsal-fin origin at vertical through posterior edge of operculum, dorsal fin with XIV-XV + 12–13 spines and rays, spines increase to maximum length over 5–6 spines, spine lappets prominent. Soft dorsal pointed behind, not beyond base of caudal fin. Caudal peduncle moderately long, 16–20 % SL, length 1.4–1.8 times depth. Caudal fin broad, relatively short (around half the head length), emarginate. Anal fin with III+9 spines and rays, origin well behind midline and closer to caudal-fin base than tip of snout, below vertical through base of ultimate dorsal spine, soft-rayed section with pointed hind edge, not extending to below base of caudal fin. Pectoral fin close behind gill slit, base inclined ventro-lateral on flanks, obtusely pointed, to pelvic extremity. Pelvic fins ventral, with strong spine half a length of fin, origin narrowly behind base of pectoral fins, not reaching to anus and anterior base of anal fin. Scales small, with around 14 regular rows across flanks; 16 rows around the caudal peduncle, 32–33 in lateral line; upper lateral line gently curved, lower lateral line short but straight; three scale rows between anterior dorsal and lateral line, two scale rows between soft dorsal and posterior end of upper lateral line. Chest scales small, reduced, and irregular.

Head elongate 2.7 times in SL (36.6–37.5 % SL), length greater than body depth, acute and pointed with marginally kinked predorsal profile, extending 30–35˚ above horizontal. Eyes large (HED 18.5–24.5 % HL; VED 17.7–22.3 % HL), dorso-lateral in anterior half of head, entirely above level of the mouth and at level of dorsal edge of the operculum. Snout relatively long, 2–3 times orbit diameter (35.2–39.6 % HL), nares in mid-snout before orbits. Preorbital depth (lachrymal) 1.5 times orbit diameter. Cheek below and behind orbits deep with 4–5 rows of scales. Post-orbit less than half length of head, interorbit sub-equal to orbit diameter (20.0–21.7 % HL). Mouth terminal, large (lower jaw 47.8–52.3 % HL), protractile, angle of closed jaw of holotype 25˚ below horizontal, posterior premaxilla to below anterior orbit, lips well developed, even along jaws. Teeth caniniform, exposed, narrowly spaced in two rows on upper and 2–3 rows on lower jaws. First branchial arch with 3–4-1-10–11 gill-rakers. Gill opening large, curved from level of eye to midventral below vertical through eye.

Coloration. Preserved holotype shades of brown and grey as in Fig 6. In life, head with dark interorbital, dark bar from orbit to posterior maxilla and white gular; green-blue highlights and small orange-red spots on cheek, opercle and preopercle; dark opercular spot. Ventral head, throat to base of pectorals and belly white. Laterally dark grey patch above pectoral base, lower flanks yellow to light green, whitish ventrally, dark olive-grey across dorsum, with single thin lateral band and 8–9 short bars; dark orange-red spots in centre of each scale forming 8–10 rows, green-blue highlights between spots. Dorsal fin with membranes between anterior 7–9 spines olive proximally to grey distally; posterior spinous and rayed membranes light olive yellow with rows of dark grey spots, lappets and dorsal edge to tip of soft-rayed bright red with narrow pale blue submarginal band. Caudal fin light olive-yellow with dark spots scattered throughout membranes and forming bars, broad light grey margin. Anal fin with yellow cast and rows of 2–5 red egg spots along membranes including distal single egg spots over spines, thin charcoal dusted margin along ventral edge. Pelvic and pectoral fins clear with feint yellow cast.

Habitat. The Cacuchi River at the collection site is a fast-flowing rocky substrate river (Fig. 7). There were several channels with only one flowing at the time of sampling. Specimens were caught in the margins of the main rocky channel with electric fishing and large hand D-nets. They came from deep rock boulder crevices. Water depths were between 0.5–1.0m.

Distribution. Currently known only from the type locality on the Cacuchi River, tributary of the Cuchi-Cubango River in Angola, approximately 15 km south west of Chitembo Village at the bridge on the main road north from Menongue.

Etymology. The specific name *cacuchi* a noun in apposition refers to the Cacuchi River where this species was collected and is most likely narrowly endemic.

Remarks

When the morphometric and meristic data for all four species were analysed, the first principal component (size variable) of the morphometric data explained 96.7% of the observed variance, and the sheared second principal component explained 27% of the remaining. Variables that had the highest loadings on the sheared second principal components of the morphometric data were caudal peduncle length (-0.44), interorbital width (-0.40), and snout length (-0.38). The first principal component of the meristic data explained 46% of the variance. Variables with

the highest loadings on the first principal components of the meristic data were dorsal-fin rays (0.28), anal-fin rays (0.27), and number of lateral-line scales (0.24). A plot of the first principal component of the meristic data versus the second sheared principal component of the morphometric data shows that *S. cacuchi* was clearly separated from the other three species (Fig 8).

FIGURE 7. The Cacuchi River at the collection site of *Serranochromis cacuchi.*

The data were analyzed again without the morphometric and meristic data of *S. cacuchi*. The first principal component (size variable) of the morphometric data explained 96.9% of the observed variance, and the sheared second principal component explained 31.9% of the remaining. Variables that had the highest loadings on the sheared second principal components of the morphometric data were caudal peduncle length (0.54), cheek depth (-0.52), and interorbital width (0.49). The first principal component of the meristic data explained 49% of the variance. Variables with the highest loadings on the first principal components of the meristic data were lateral-line scales (0.41), rows of teeth on the upper jaw (0.36), and number of pored scales posterior to the hypural plate (-0.36). A plot of the first principal component of the meristic data versus the second sheared principal component of the morphometric data showed that *S. alvum* was clearly separated from the other two species (Fig 9). An ANOVA in conjunction with a Duncans Multiple Range test showed that the minimum polygons formed by *S. swartzi* and *S. cacuchi* were significantly different ($p<0.05$). Thus, a multivariate analysis of meristic and morphometric data supported the fact that these four forms are heterospecific.

Discussion

Four species of *Serranochromis* are described bringing the number of species of *Serranochromis* to 15. These distinctive relatively large riverine predators constitute a remarkable African cichlid radiation that has been proposed to have roots in a mega-palaeo-lake that existed in the Kalahari during the Pleistocene (Joyce *et al.* 2005, Burrough *et al.* 2009).

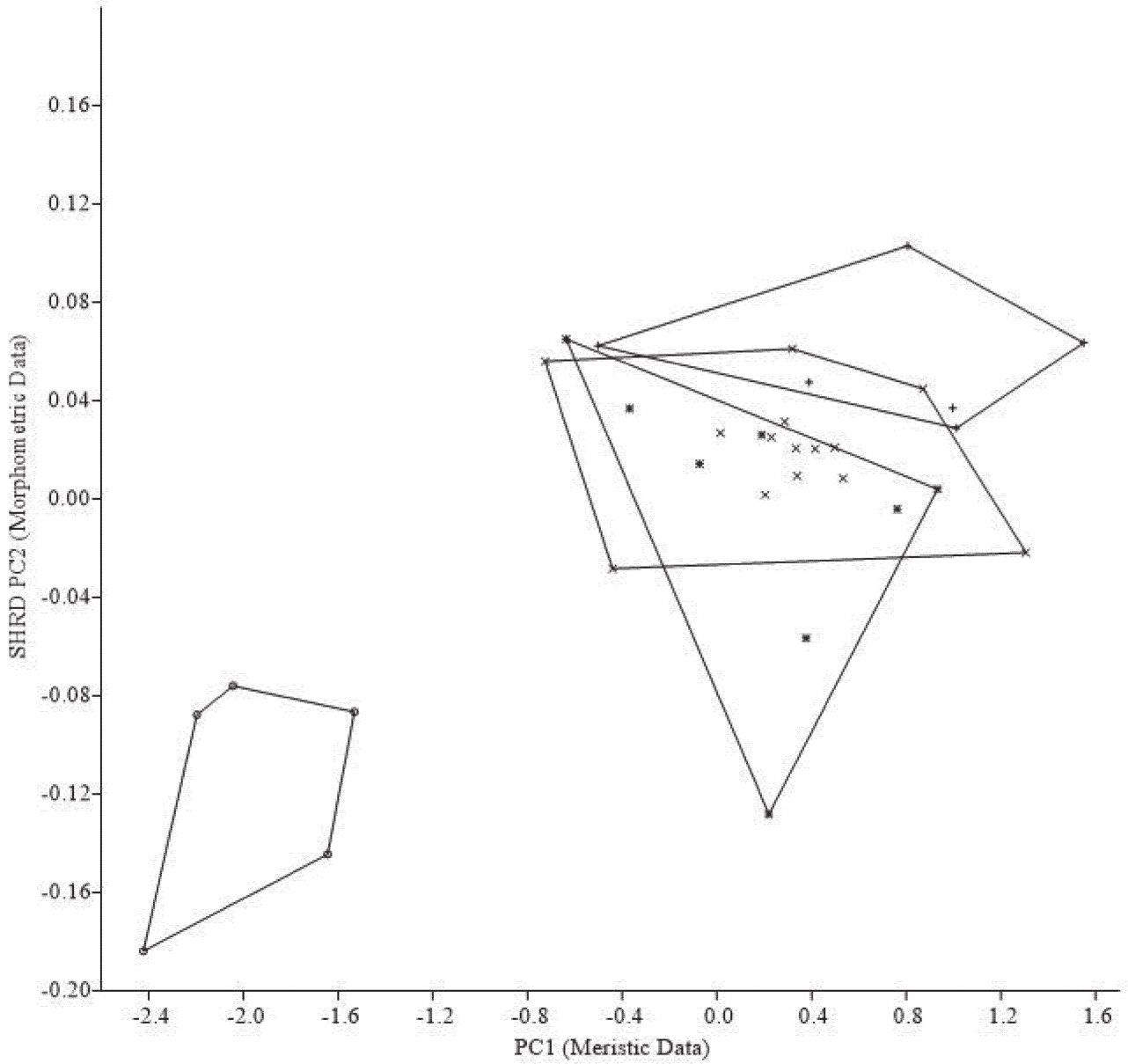

FIGURE 8. First principal components (meristic data) plotted against the sheared second principal components (morphometric data) of *Serranocromis alvum* (+), *Serranochromis swartzi* (x), *Serranochromis cuanza* (*), and *Serranochromis cacuchi* (o).

Schwarzer *et al.* (2012) included the Cuanza species described herein in their study of trans-watershed hybridization of haplochromines that featured several *Serranochromis*. The Cacuchi river flows south from a watershed with the headwaters of the Cuquema River, tributary to the Cuanza that, and after initially flowing due south, abruptly swings to the north and clearly represents a river capture. Musilova *et al.* (2013) demonstrated close molecular relationships between the cichlid species *Tilapia sparrmanii* Smith and *Serranochromis macrocephalus* across this watershed.

Finally, it seems obvious that the southern Congo region with the abundant lakes and long systems running largely in parallel north will harbour other new species. *Serranochromis alvum* is known only from the type locality at Cuito-Cuanavale at the junction of the Cuito and Cuanavale rivers, tributary to the Okavango River in Angola. It is possible that *S. altus, S. angusticeps, S. jallae, S. thumbergi,* and *S. macrocephalus* might be present there. *Serranochromis swartzi* is known only from the type locality in the Cuanza River, Angola, and *S. macrocephalus* might be sympatric. *Serranochromis cuanza* is restricted to the Cuanza River, below Capanda Dam, Angola, and again *S. macrocephalus* might occur there. *Serranocrhomis cacuchi* is known only from the Cacuchi River, a tributary of the Cuchi-Cacuchi River in Angola and was the only *Serranochromis* collected at this locality. The limited

distribution of these four described species along with the previously described isolates (e.g., *S. spei, S. janus,* and *S. stappersi)* and with the exception of *S. alvum* the species described herein are not sympatric with more than one other *Serranochromis* suggest, in addition to previous studies that invoked a lacustrine speciation model, vicariance through drainage isolation seemed to have played an important role in driving speciation in this group. Certainly, our understanding of these species' distributions and the presence of new taxa needs exploration.

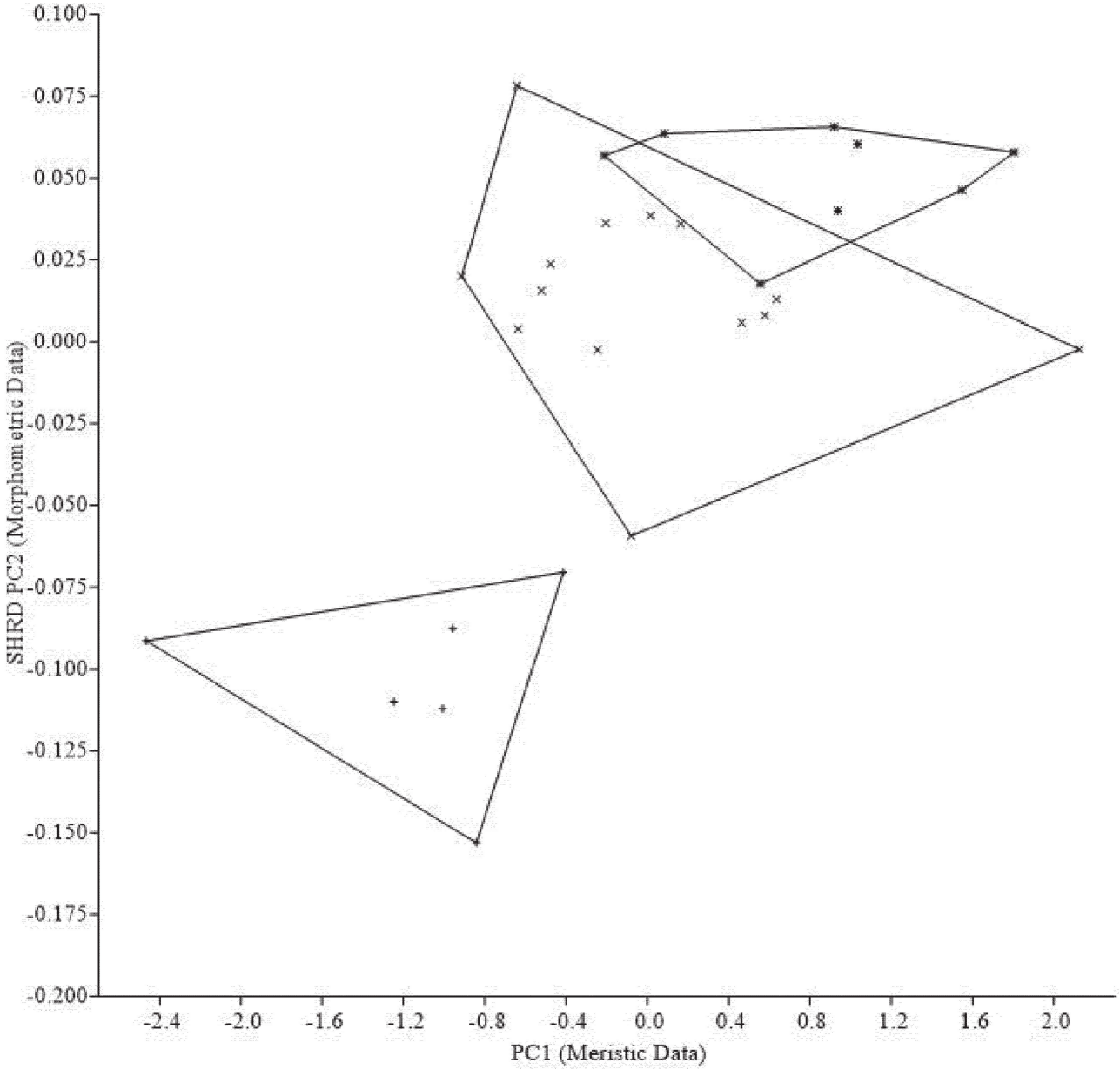

FIGURE 9. First principal components (meristic data) plotted against the sheared second principal components (morphometric data) of *Serranocromis alvum* (+), *Serranochromis swartzi* (x), and *Serranochromis cuanza* (*).

Artificial key to the species of *Serranochromis*

1a.	Teeth embedded in lips	2
1b.	Teeth exposed	3
2a.	Body depth less than 40% SL	*Serranochromis altus*
2b.	Body depth greater than 40% SL; found in Luapula River, Congo system	*Serranochromis stappersi*
3a.	Series of blotches along flanks	4
3b	No distinct blotches along flanks	5
4a	Length of pectoral fin greater than 33% SL; males with silver/white ground colour	*Serranochromis longimanus*

4b Length of pectoral fin less than 33% SL; males with blueish head . . . . . *Serranochromis alvum*
5a Caudal fin rounded 6
5b Caudal fin emarginated or rectangular 10
6a Ocelli in breeding males restricted to 4–5 posterior membranes 7
6b Ocelli in breeding males throughout anal fin 8
7a. In fish greater than 100 mm SL, least caudal peduncle depth less than 12.8% SL; males blue/green laterally with a narrow yellow marginal band on the dorsal fin; native endemic to Lake Malaŵi ; introduced elsewhere (e.g., Sand River Dam in Swaziland,, Komati River system in South Africa). . . . . *Serranochromis robustus*
7b. In fish greater than 100 mm SL least caudal peduncle depth greater than 13%; males yellow/green laterally with a bright orange marginal band on the dorsal fin in fish from the Okavango River system, but creamy yellow bands in fish from the Upper Zambezi River system; endemic to upper Zambezi Region, introduced into Zimbabwe . . . . . *Serranochromis jallae*
8a. Premaxillary pedicel greater than 40% of HL . . . . . *Serranochromis angusticeps*
8b. Premaxillary pedicel less than 39% of HL 9
9a. Teeth in outer series of upper jaw 30–52; horizontal eye diameter 22–29 % HL . . . . . *Serranochromis macrocephalus*
9b. Teeth in outer series of upper jaw 54–74; horizontal eye diameter 16–20 % HL . . . . . *Serranochromis janus*
10a. Lateral-line scales greater than 39; dorsal-fin spines 17–18 . . . . . *Serranochromis thumbergi*
10b. Lateral-line scales less than 38; dorsal-fin spines less than 17 11
11a. Lateral-line scales less than 34 . . . . . *Serranochromis cacuchi*
11b. Lateral-line scales 34 or more 12
12a. Snout length greater than 37% HL; endemic to southern Limpopo and Incomatic systems in . . . . . South Africa and Mozambique . . . . . *Serranochromis meridianus*
12b. Snout length less than 36% HL 13
13a. Lower jaw length greater than 53% HL; endemic to the Kwanza system in Angola . . . . . *Serranochromis spei*
13b. Lower jaw length less than 53% HL . . . . . *Serranochromis swartzi*

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