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Two new species of African bubble-nesting *Microctenopoma* (Teleostei: Anabantidae) from Angola

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Two new species of the bubble-nesting anabantid genus *Microctenopoma* are identified and described from the watershed reaches of the Okavango, Zambezi, Cuanza, and Congo river systems in Angola. Poll (1967) pointed out that two forms of *Ctenopoma nanum* occurred in the southern tributaries of the Congo in Angola. Study of new material more recently collected in Angola and of material studied by Poll (1967) indicates that there are two new species, described here as *M. steveboyesi* and *M. stevenorrisi*. *Microctenopoma steveboyesi* occurs in the source reaches of the Cuanza, the Cuito-Okavango and the Zambezi. *Microctenopoma stevenorrisi* occurs in the source reaches of the Cuango and Cuilo-Casai, Congo system. These new species are members of the savannah cluster of the *Microctenopoma nanum* complex as determined by Norris (1995). Each is distinguished from the widespread southern African species *M. intermedium*, by shape and pigmentation as well as modally in meristic characters such as the number of dorsal-fin spines and vertebrae.

Introduction

Microctenopoma species are relatively small (<100 mm SL) bubble-nesting African anabantid fishes, that inhabit Afro-tropical swamps and bogs from Central West Africa through the Congo basin south to the Zambezi and, on the East coast, south to KwaZulu-Natal, South Africa (Skelton, 1988; Norris, 1995). *Microctenopoma* species are most closely related to African '*Ctenopoma*' [a clade of deep-bodied species that have a swimbladder with paired extensions] (Norris, 1995, 2007; Rüber et al., 2006; Wu et al., 2019). The generally larger males have extended finnage and display brighter nuptial coloration than females (Norris, 1995). Breeding males actively establish a territory, construct a bubble-nest, attract suitable mates, and, post-spawning, guard the eggs and embryos in the nest (Norris, 1995).

Currently, 12 *Microctenopoma* species are recognized, in at least two morphological groups, one of which was identified and named as the

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M. nanum (Günther 1896) complex (Norris & Douglas, 1991; Norris, 1995). Within this complex, Norris (1995) further identified a group of savannah species, including a northern isolate, *M. lineatum* (Nichols 1923) in the Lake Chad drainage and the Uele–Congo River, a north-eastern species, *M. uelense* Norris & Douglas 1995, also in the Uele drainage, and three species, *M. intermedium* (Pellegrin 1920), *M. nigricans* Norris 1995 and *M. ocellifer* (Nichols 1928), from the southern and south-eastern tributaries of the Congo. The distribution of *M. intermedium* extends further south into the Zambezi, Okavango, and south-east Africa (Skelton, 1988; Norris & Douglas, 1991). Norris (1995) noted that the pigmentation of the three southern species, all from savannah locales beyond the rain forest zone, are not as clearly barred as the forest zone species, e. g. *M. nanum*. He also recorded that the pectoral-fin rays of the three southern species are darkly pigmented, an unusual feature for anabantids.

Skelton (1988) revised the taxonomic identity of *Microctenopoma intermedium* (Fig. 1a) and indicated that its distribution extends into the upper and lower Zambezi, Okavango, Kafue, Lake St Lucia catchment (KwaZulu-Natal), as well as certain southern Congo tributaries. When Norris (1995) described *M. nigricans* from the eastern branches of the Casai basin, he also redescribed *M. ocellifer* from the upper Lualaba and Lake Upemba drainage, and refined the known distribution of *M. intermedium* in the Congo basin to include the Angolan Casai system (as recorded by Poll, 1967), and the upper Luapula-Chambeshi system (Van Steenberg et al., 2014).

On considering the species now regarded as *Microctenopoma intermedium* (then as *Ctenopoma nanum*) in Angola, Poll (1967: 317) made an important, but overlooked, observation that there were two distinct pigmentation patterns (Poll's "livrées") of the species, one with clear bars on the body (Poll's "linée") and the other with a marbled (Poll's "marbrée") pattern. Poll (1967) further observed that the distributions of the two forms were different. The barred form occurred in tributaries of the Luachimo (Casai-Congo) and tributaries of the upper Zambezi; the marbled form, in tributaries of the Cuango and the Cuilo (lower Casai-Congo). Norris examined Poll's marbled specimens as lodged in the Royal Museum for Central Africa, Tervuren (RMCA, see below) and indicated on labels with the samples that they represented an undescribed species. Recent collections of *Microctenopoma* lodged in the South African Institute for Aquatic Biodiversity (SAIAB), taken from the headwaters of the Cuito (Okavango drainage) and the Cueve (Cuando drainage) in Angola, have a marbled pigmentation that could also represent this undescribed species (Fig. 1b). The differences in marbled and barred forms are consistent within populations, and herein are regarded as indicative of separate species. Elsewhere within its range *M. intermedium* is characteristically barred (see e. g. Fig. 1a) and the marbled form (see e. g. Fig. 1b) is recognised as an undescribed species and is described herein. The inclusion of Poll's (1967) marbled specimens in this study also indicated that they are of a species that is distinct both from *M. intermedium* and a new species from the Cuito and Lungwebungwe tributary of the Zambezi.

Material and methods

Type material of the new species described is listed under the descriptions. Other material is given under separate heading. Institutional abbreviations: RMCA, Royal Museum for Central Africa, Tervuren; SAIAB, South African Institute for Aquatic Biodiversity, Makhanda (Grahamstown).

Measurements were taken according to Skelton (1988) [Fig. 2a–b] with digital Vernier callipers and recorded to 0.1 mm accuracy from the left side of the body unless it was damaged. The size of the specimens is reported as standard length (SL) in millimetres. Measurements and abbreviations are as follows: Standard Length (SL) defined and derived from the anterior tip of the head, considered as the anterior edge of the symphysis of the upper jaw, to the end of the hypural plates as determined by flexure of the caudal-fin rays. Head length (HL) was taken from the tip of the snout to the hind margin of the opercle. Snout length (SntL), from tip of snout to anterior edge of orbit. Orbit diameter (OD), direct horizontal internal diameter of the bony orbit. Orbit to preopercular groove (O-popL), horizontal distance between posterior orbit rim and the pre-opercular groove. Interorbit distance (IO), the least distance between the dorsal bony rims of the orbits. Post-orbit length (PoL), horizontal distance between posterior rim of orbit and the posterior edge of the opercle. Cheek depth (CkD), least distance between the orbit and the upper jaw groove. Length of upper jaw (JL), was taken from the mid-symphysis of the upper jaw

Fig. 1. Body form and life colours of *Microctenopoma* from the Okavango system: **a,** *M. intermedium*, SAIAB 205489, 40.0 mm SL; Okavango Delta, Botswana; **b,** *M. steveboyesi*, new species, SAIAB 202273, 36.5 mm SL; Cuito source lagoon outlet, Cuito-Okavango system, Angola.

to the distal edge of the premaxilla. Predorsal length (PdL), from the tip of the snout to the anterior base of the dorsal fin. Pre-pectoral length (PpecL), from the tip of the snout to the anterior base of the pectoral fin. Pre-pelvic length (PpelL), from the tip of the snout to the anterior base of the pelvic fin. Pre-anal length (PanL), from the tip of the snout to the anterior base of the anal fin. Caudal-peduncle length (Cpl), from the median point on the vertical from the posterior base of the anal fin to the median point on the flexure (end of the hypural plates) of the caudal fin. Caudal peduncle depth (Cpd) is the least depth through the vertical of the caudal peduncle. Body depth (BD), was measured at two places; (a) from the anterior base of the dorsal fin through the vertical to the ventral margin of the body (Bd1), and (b) from the anterior base of the anal fin through the vertical to the dorsal body margin (i.e. at the base of the dorsal fin, Bd2). Fin lengths were taken from the base of the first articulating spine or ray to either the base of the posterior most ray (dorsal and anal fin base lengths, DL; AL) or the fin extremity for the pectoral (PecL) and pelvic-fin lengths (PelvL). The caudal-fin length (Caudal L) was taken from the mid-point of the articulation as indicated by flexure of the fin to the extremity of the median rays.

Fin-ray counts were taken directly from specimens and from digital X-radiographs produced by an Inspex 20i Digital X-Ray Imaging System. Spines and rays are considered single elements when articulating from a single base. Vertebral counts were taken from X-radiographs and include all vertebrae with the compound ural centrum counted as one vertebra. Predorsal vertebrae include all vertebrae for which the neural spine precedes the anterior most pterygiophore of the dorsal fin. Abdominal vertebrae include all vertebrae without a haemal spine. Caudal vertebrae include all vertebrae with a haemal spine and the compound ural centrum. Preanal vertebrae include all vertebrae in advance of the intersection of the anterior most pterygiophore

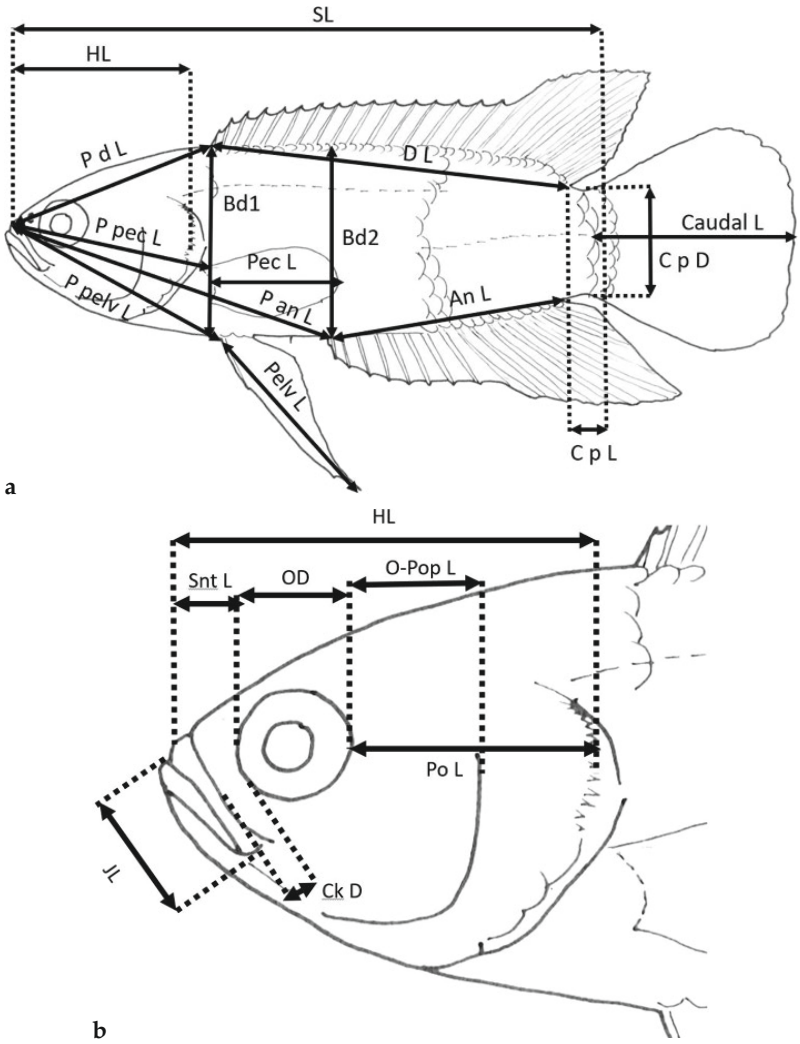

Fig. 2. Linear measurements taken of *Microctenopoma* specimens in this study: **a,** body and head measurements; **b,** head measurements. Abbreviations and measurements as given in text under Material and methods.

of the anal fin. Supraneural bones include all visible independent median elements between the neurocranium and the dorsal fin. Lateral line scales include all scales along the rows in which the lateral line pores occur, taken to the scale row at the flexure of the caudal fin. Dorsal to pelvic-fin scales are the number of scale rows crossing the line drawn from the origin of the dorsal fin to the origin of the pelvic fin. Caudal peduncle scales are all circum-peduncle scale rows crossing the line of least depth of the peduncle.

In order to determine taxonomic status, specimens were clustered according to general phenotypic identification and to geographic distribution into four lots for the analysis. These lots included (i) a set of comparative specimens of *Microctenopoma intermedium*, (ii) samples of *Microctenopoma* from the Cuito-Cueve River headwaters, (iii) the RMCA samples of Poll's (1967) marbled form of *Microctenopoma* from tributaries of the Congo River in Angola and labelled as a new species by Norris in 1996, and (iv) four specimens, of which two larger specimens were measured, of *Microctenopoma* from the Lungwebungwe River, a tributary of the upper Zambezi.

Data analysis. We examined the morphometric data using sheared Principal Component Analysis (SPCA), which factors the covariance matrix and restricts size variation to the first principle component (Humphries et al., 1981; Bookstein et al., 1985). This method ordinates factors independently of the main linear ordination (Reyment et al., 1984). Meristic data were analyzed using Principle Component Analysis (PCA), which factors the correlation matrix. Differences among species were illustrated by plotting the sheared second principle component (SPC 2) of the morphometric data against the first principle component (PC 1) of the meristic data (Stauffer & Hert, 1992). All data were analyzed using SAS software, version 9.4 (SAS Institute Inc., SAS 9.4 TS1M1).

Results

Taxonomy

Microctenopoma steveboyesi, new species

(Figs. 1b, 3a–c)

Holotype. SAIAB 203370, male, 39.7 mm SL; Calua Lagoon, tributary to Cuito River, Okavango system, Moxico Province, Angola, 12°44'11"S 18°23'34"E; A. Costa & B. C. W. van der Waal, 21 Feb 2016.

Paratypes. All from Angola, Moxico Province: SAIAB 209567 (ex 203370), 5, 22.8–32.4 mm SL; and RMCA 2020.008.P.0001–0003 (ex SAIAB 209567), 3, 24.6–32.3 mm SL; collected with the holotype. – SAIAB 202344, 1, 35.8 mm SL; Cuito source lake outlet, Okavango system, 12°42'43"S 18°29'26"E; P. H. Skelton, 23 May 2015. – SAIAB 204683, 2, 19.3–30.1 mm SL; Cueve sources, Cuanza River system, 12°40'11"S 18°21'07"E; P. H. Skelton, 14 April 2017. – SAIAB 204020, 4, 21.1–38.9 mm SL; Lungwebungwe near bridge, Upper Zambezi system, 12°34'54"S 18°40'26"E; B. C. W van der Waal & N. Mazungula, 20 Oct 2016.

Non-types. All from Angola, Moxico Province: SAIAB 202273, 3, 29.9–36.5 mm SL; SAIAB 202408, 1, 28.0 mm SL; and SAIAB 202391, 1, 27.0 mm SL; Cuito source lake, Cuito River, Okavango system. – SAIAB 203154, 22, 11.0–40.0 mm SL; and SAIAB 203370, 21, 12.0–39.0 mm SL; Calua lagoon, tributary Cuito River, Okavango system.

Diagnosis. *Microctenopoma steveboyesi* belongs to the genus *Microctenopoma* as defined by Norris (1995), and is most similar to southern savannah species of the *C. nanum* complex (sensu Norris, 1995) *M. intermedium*, *M. nigricans*, and *M. ocellifer*. It differs from *M. intermedium* in shape (a steeper more convex dorsal profile, more slender body, longer caudal peduncle, a rounded caudal fin vs. straight profile, deeper body, a shorter caudal peduncle, semi-truncated caudal fin), modally fewer dorsal-fin spines (XV vs. XVI), fewer vertebrae (25 vs. 26), particularly caudal vertebrae (16 vs. 17), in pigment pattern (a chequer pattern of light golden scales with dark grey to black scales over linear stripes vs. plain light brown background with dark brown bars) and male nuptial dress (head and body black, fins black with deep blue streaks on the dorsal and anal fins vs. head and body brown with dark brown and black bars, with metallic-turquoise highlights on cheeks, operculum, flanks and ventral body between bars and of turquoise or blue vermiculations on the pelvic, dorsal and anal fins). It differs from *M. milleri*, a species that also has a chequer-board pattern of pigmentation, in having underlying linear stripes (vs. no stripes), in body shape (shallow ellipsoid with round head profile vs. deeper somewhat fusiform body with straight head profile – see Norris & Douglas, 1991: 168, fig. 1) and in the number of dorsal (XV vs. XI) and anal-fin spines (VIII–IX vs. VI–VII). It differs from both, *M. nigricans* and *M. ocellifer*, in general pigmentation (underlying linear stripes and metallic golden fleck chequer board pattern vs. no linear stripes or chequer board pattern) and nuptial dress (dorsal and anal fins with blue streaks vs. fins without blue streaks). It differs further from *M. ocellifer* in having fewer anal-fin spines (VII–IX, modally VIII vs. IX–XI, modally X). It differs from *M. stevenorrisi*, new species, in the number of dorsal spines (XIV–XV mode XV vs. XV–XVII mode XVII, Table 2), number of vertebrae (25–26 mode 26 vs. 27–28 mode 27, Table 2) especially caudal vertebrae (16–17 mode 17 vs. 17–19 mode 18, Table 2) and the length of the caudal peduncle (9.0–15.1 vs. 5.7–11.0 % SL).

Description. Based on types. Anatomical measurements, meristic information and proportions given in Tables 1 and 2. Overall body shape slender, ellipsoid, depth declining gradually from behind head to caudal peduncle, three times in SL. Caudal peduncle short, length 40–50 % depth.

Fig. 3. *Microctenopoma steveboyesi*, new species, SAIAB 203370, holotype, 39.7 mm SL; Angola: Okavango system. **a,** lateral view; **b,** head dorsal view; **c,** head ventral view.

Head 3–3.2 times in SL, depth equal or subequal to length, obtusely rounded anteriorly, with steep (overall, 60° to the horizontal), gently convex predorsal profile. Snout short, less than ½ orbit diameter. Nares before orbit, anterior tubular, posterior a simple pit adjacent to antero-dorsal orbit rim. Eye large, orbit diameter 3–4 times in HL, antero-dorsal on head, below level of dorsal edge of operculum, closely behind and above the mouth. Interorbit equal to orbit diameter. Post-orbit twice orbit diameter. Orbit to pre-opercular groove equal to orbit diameter. Pre-opercular groove reaching to opposite anterior half of orbit. Mouth small, supraterminal, jaws steeply inclined at about 45° to horizontal, reaching to below anterior half of orbit. Upper jaw with outer row of recurved, caniniform teeth along entire length and with inner row of smaller conical teeth. Dentary with short anterior outer row of 4 large recurved caniniform teeth, and 2–3 inner rows of smaller recurved conical teeth. Gular space weakly bulbous anteriorly and narrow posteriorly (Fig. 3c). Medial pores on lower jaw closely adjacent to symphysis, or confluent into single median pore. Operculum with postero-dorsal notch, armed with short series of spines above and below the notch.

Vomer with 2–3 minute conical teeth. Parasphenoid with slender bi-lateral transverse pharyngeal process set with small teeth and 3–4 large, curved conical teeth on posterior plate.

Gill-rakers on anterior branchial arch widely spaced, short and blunt. Suprabranchial chamber shallow, epibranchial organ simple.

Dorsal-fin origin close behind head, above base of pectoral fin. Dorsal fin base long, extending to caudal peduncle, with sheath of 1–2 rows of small scales along soft-ray section. Anterior dorsal-fin spines short, subsequent spines even in length, soft dorsal-fin rays extended and pointed behind in males. Anal-fin origin slightly closer to mid-caudal-fin base than to tip of snout, first spine short, subsequent spines even, soft anal-fin rays extended and pointed in males. Pectoral fin ventrolateral on flank, base almost vertically aligned, shape acutely rounded to pointed in mature males, with rays 6–8 extended. Pelvic fin

Fig. 4. Habitats at the collecting sites for *Microctenopoma steveboyesi*: **a,** Cuito source lake marsh, April 2016; **b,** Cuito source lake outlet marsh and stream, April 2016; **c,** type locality – Calua source marsh, April 2017; **d,** Calua outlet stream marsh, April 2017; Photos P. H. Skelton.

ventral, origin posterior to pectoral base, with short leading spine, fin-rays extending to origin of anal fin (females) or, in mature breeding males, forming filament reaching well beyond origin of anal fin (Fig. 3a). Caudal fin broad and rounded.

Entire body and most of head with well-developed, mostly ctenoid, scales, cycloid scales over predorsum and over chest and ventral body cavity. Scales on entire head surface except snout and dentary section of lower jaw. In holotype and several paratypes a distinct scale present over exposed angulo-articular section of lower jaw (Fig. 3c); such scale absent in other specimens. Three or four rows of scales across cheek below and posterior to orbit to pre-opercular groove, 3–4 rows across operculum, all ctenoid in mature males. Single bilateral row of large scales from articulation of lower jaw along exposed margin of gill cover (interopercle and subopercle) to opercle. Three interorbital scales at anterior edge of squamation. Squamation regular and even along body, with bilateral sheath of 1–2 small scales along posterior base of dorsal and anal fins. Bi-lateral sheath of small scales over caudal-fin base extending as series of tiny scales proximally onto fin-rays.

Lateral line in two sections, anterior section from immediately above operculum arches dorsad and posteriad to below last of dorsal-fin spines, spaced one full scale row below dorsal-fin base. Posterior section separated one scale row below anterior section, along mid-lateral scale row to end of caudal peduncle. Lateral-line pores and canals irregular and generally obscure.

Colour in life. Juvenile specimens with irregular, poorly defined brown to dark brown bars and markings on body. Sub-adults and adults (Figs. 1b, 3a) mesh of brown to dark brown or black with lighter, bright golden, flecks on head and body producing 8–10 indistinct and irregular bars; head of adults meshed dark and light brown-black

above, eye with pupil black and iris brown and reddish, cheeks and post-orbit with three indefinite, dark semi-parallel bars with bright golden flecks, branchiostegal membranes clear; black mid-caudal peduncle 'eye' spot with golden rim present in most specimens. A series of concentric parallel brown stripes along intersection of scale rows from behind head to caudal peduncle. Dorsal and anal-fin membranes mostly black or very dark brown with short gold or blue proximal streaks. Pectoral fin clear (hyaline) with brown rays. Pelvic fin of juveniles and females with whitish inner and outer edges and black middle rays, mature males entirely dark brown or black. Caudal fin essentially uniform dark brown to black, faint lighter flecks sometimes evident over proximal parts. Nuptial colouration of male intense black with blue streaks on dorsal and anal fins.

Colour in preservation. Holotype (Fig. 3a–c) entirely dark brown nearly black, with slightly lighter ventral aspects and light patches on cheeks;

Table 1. Morphometric measures of *Microctenopoma* species as determined in this study. *M. steveboyesi*, SAIAB 202344 (n = 1), SAIAB 203370 (n = 1), SAIAB 209567 (n = 5), and RMCA 2020.008.P.0001–0003 (n = 3); *M. stevenorrisi*, RMCA 164142–164144 (n = 3), RMCA 164148–164172 (n = 24), and SAIAB 202273 (n = 3); *M. intermedium*, SAIAB 101079 (n = 3), SAIAB 193581 (n = 9), SAIAB 200817 (n = 1), and SAIAB 205461 (n = 4). SD, standard deviation.

	M. steveboyesi, new species (n = 11)			*M. stevenorrisi*, new species (n = 30)			*M. intermedium* (n = 18)		
	mean	SD	range	mean	SD	range	mean	SD	range
Standard Length (mm)	31.8	–	24.4–39.7	35.3	–	27.5–46.5	34.3	–	25.6–47.5
As % SL									
Predorsal length	36.1	2.6	32.0–39.5	36.9	2.2	32.1–41.5	37.4	2.4	33.0–42.9
Head length	30.6	1.5	27.6–32.5	32.0	1.6	29.2–35.3	33.0	1.3	31.0–36.3
Prepectoral	34.1	1.3	32.0–36.6	35.0	1.8	31.7–39.5	36.4	1.5	34.6–40.5
Prepelvic	37.8	2.8	32.6–41.9	40.9	2.8	36.6–48.6	40.8	2.0	36.7–44.5
Preanal	56.9	3.3	52.9–63.4	58.1	3.0	53.3–64.2	56.7	2.5	53.3–62.2
Pelvic to anal base	19.2	1.5	17.3–21.8	18.3	1.5	14.8–20.9	16.8	1.5	14.7–19.4
Caudal peduncle length	12.7	1.7	9.0–15.1	8.2	1.2	5.7–11.0	9.2	1.0	7.2–10.5
Body depth at dorsal-fin origin	30.0	2.9	26.7–38.1	30.3	1.1	28.6–32.6	30.4	1.8	27.8–35.1
Body depth at anal-fin origin	28.0	1.8	26.2–31.0	29.6	1.3	27.8–32.7	30.0	1.4	27.2–33.1
Body width	17.3	0.8	15.6–18.4	17.6	1.0	15.4–19.5	16.8	0.7	15.2–19.1
Dorsal fin base length	57.2	2.6	52.7–60.9	59.7	2.6	54.9–64.3	59.9	3.1	51.0–63.6
Anal fin base length	35.3	2.3	32.1–39.5	36.2	2.0	32.4–40.9	39.4	3.2	32.3–45.7
Pectoral fin length	24.6	2.2	20.5–28.7	23.8	1.5	19.8–27.3	24.0	2.3	19.5–31.1
Pelvic fin length	31.1	9.7	19.1–50.6	20.7	3.6	15.1–29.7	22.0	4.0	17.3–29.9
Caudal fin length	27.5	2.6	22.0–30.1	27.8	1.7	24.2–31.6	29.1	2.4	24.7–33.0
As % HL									
Head depth	80.2	4.4	71.8–88.8	78.2	3.6	73.0–84.8	77.9	3.9	72.3–84.8
Head width	55.3	2.6	50.8–59.8	55.2	3.3	48.8–61.9	56.5	2.2	52.3–59.8
Snout length	18.4	1.4	15.5–20.8	17.6	1.8	12.9–21.9	18.9	1.2	16.7–20.6
Orbit diameter	26.5	1.9	22.9–29.0	24.8	1.7	22.4–29.2	25.2	1.9	22.8–28.6
Orbit – Pre-opercle	28.1	1.9	25.0–30.5	26.1	1.9	21.0–29.9	24.6	1.6	20.2–27.2
Post-orbit distance	56.5	3.7	51.5–66.3	56.7	2.7	52.3–62.0	53.2	2.5	47.3–57.0
Interorbit distance	22.5	1.1	21.3–25.2	20.6	1.4	18.3–24.2	21.9	1.3	19.3–25.0
Cheek depth	7.1	1.0	5.8–8.9	6.5	0.6	5.4–8.0	7.1	0.8	5.4–8.4
Upper jaw length	29.6	1.7	27.0–32.7	28.5	5.0	24.0–33.3	29.1	1.5	26.2–31.7
As %									
Caudal peduncle length/depth	62.5	10.4	38.8–75.0	52.1	7.8	36.7–66.7	58.6	7.1	45.2–67.3
Body width/head width	91.1	3.4	85.5–96.4	96.6	5.2	83.1–107.8	90.2	3.1	84.7–94.1

fins black. Dark parallel lateral stripes evident. Other specimens, not in nuptial state, patterned irregularly in shades of brown and dark brown as in Figure 1b.

Biology. *Microctenopoma steveboyesi* inhabits the dense vegetation of up-land peat-bog marshes (Fig. 4). Other fishes collected in these habitats include mormyrids (*Pollimyrus* sp., *Marcusenius* sp.), smiliogastrine minnows (*Enteromius chicapaensis*, *Enteromius brevidorsalis)*, an anguilliform clariid, blotched catfish (*Clarias stappersii*), the Zambezi grunter (*Parauchenoglanis ngamensis*), small cichlids (*Pseudocrenilabrus philander*, *Tilapia sparrmanii*) and the procatopodid topminnow *Lacustricola katangae*. As observed in an aquarium (PHS), breeding behaviour is typical for the genus: males construct small round floating bubble nests – less than about 10 cm diameter, evict the females and guard the fertilised ova and embryos. Territorial males are aggressive to other small fishes. In the aquarium they were mainly nocturnal.

Distribution. *Microctenopoma steveboyesi* has been recorded from source reaches and tributaries of the Cuito-Okavango, a source stream to the Cueve-Cuanza, and in the upper reaches of the Lungwebungwe, tributary to the Zambezi River, Moxico Province, Angola (Fig. 5a–b). The collection sites in the Cuito include the inflow and outflow marshes of the Cuito source lake, as well as marsh (bog) fringes and outlet to the source pan of the Calua, a left bank tributary to the Cuito (Fig. 5a–b).

Etymology. Named *steveboyesi* for Dr Rutledge Steven Boyes, an inspiring ornithologist, conservationist, and a National Geographic explorer. Dr Boyes is a founder of the Wild Bird Trust and the leader of the National Geographic Okavango Wilderness Project, on which expeditions in Angola the new species was discovered. The first name is spelt as Steve as that is how he is known to the first author.

Microctenopoma stevenorrisi, new species
(Fig. 6a–c)

Ctenopoma nanum (not Günther, 1896): Poll, 1967: 317–319, in part, marbled form (Poll, 1967; Exemplaires marbrés).

Holotype (Fig. 6a–c)**.** RMCA 164142, 1, 44.6 mm SL, Alto Chicapa, Luemba River, village Sá Mundji, approximately 10°50' S 19°10' E; Congo system, Angola, Museu do Dundo, 1–31 July 1954.

Table 2. Comparison of counts of *Microctenopoma* sample clusters in this study. Sample clusters: *M. steveboyesi*: SAIAB 202344 (n = 1), SAIAB 203370 (n = 1), SAIAB 209567 (n = 9); *M. steveboyesi* (Zambezi): SAIAB 204020 (n = 4); M. *stevenorrisi*: RMCA 164142–164144 (n = 3), RMCA 164148–164172 (n = 24); *M. intermedium*: SAIAB 101079 (n = 3), SAIAB 193581 (n = 9), SAIAB 205461(n = 4), SAIAB 200817 (n = 1). Abd, Abdominal; V, Vertebrae.

	Dorsal-fin spines					Dorsal-fin rays					Anal-fin spines				Anal-fin rays				
	14	15	16	17	18	6	7	8	9	10	7	8	9	10	7	8	9	10	11
M. steveboyesi (n = 11)	6	5						3	7	1		10	1				5	6	
M. steveboyesi (Zambezi, n = 4)	1	1	2					1	2	1	1	3					1	3	
M. stevenorrisi (n = 30)		1	12	16	1	1	1	11	3	2		7	8	3	2	10	4	1	
M. intermedium (n = 18)		5	13					4	13	1		9	9			1	6	7	4

	Total V				Abd V		Caudal V				Pre-Dorsal V		Pre-Anal V	
	25	26	27	28	9	10	16	17	18	19	1	2	9	10
M. steveboyesi (n = 11)	1	10			10	1	2	9			11		10	1
M. steveboyesi (Zambezi, n = 4)		4			3	1	1	3			4		3	1
M. stevenorrisi (n = 18)			14	4	14	4		2	15	1	15	3		18
M. intermedium (n = 17)	1	7	9		13	4	2	9	6		16	1	14	3

	Lateral line scales				Dorsal – pelvic scales				Caudal peduncle scales			
	26	27	28	29	10	11	12	13	14	15	16	
M. steveboyesi (n = 11)	3	8			4	6	1		1	1	9	
M. steveboyesi (Zambezi, n = 2)	1	1			1	1					2	
M. stevenorrisi (n = 30)	1	20	8	1	2	26	1	1	3	5	22	
M. intermedium (n = 18)	4	10	4			15	2	1	5	3	10	

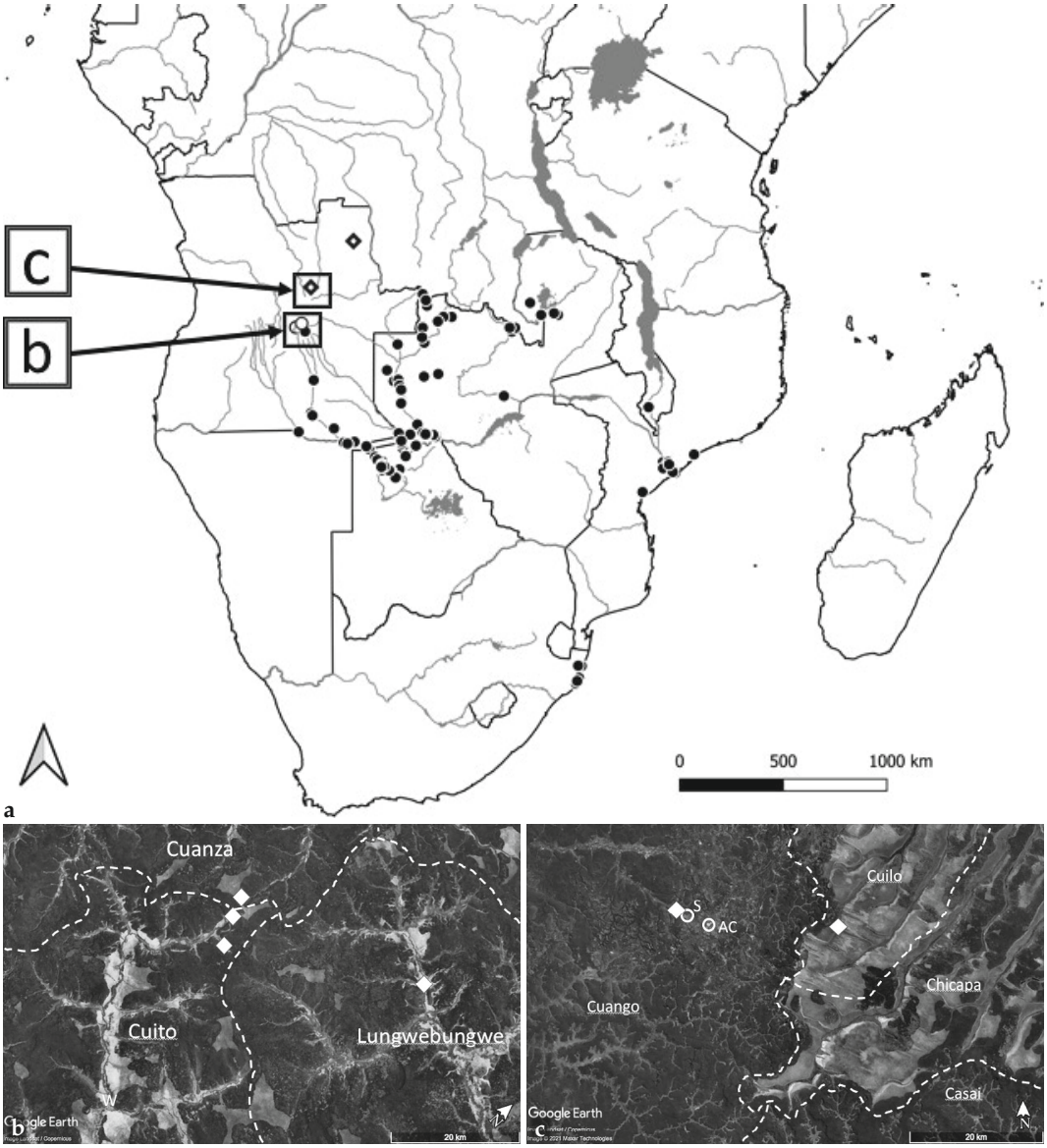

Fig. 5. a, Known distribution of *Microctenopoma steveboyesi* (○), *M. stevenorrisi* (open diamonds), and *M. intermedium* (●) in south-central Africa, based on records in SAIAB and the RMCA. **b,** Box B, Google Earth image indicating watersheds (dashed lines) and collecting locales of *M. steveboyesi* (◇). Drainages as named on the map; W, waterfall. **c**, Box C, Google Earth image indicating watersheds (dashed lines) and collecting locales of *M. stevenorrisi* (◇) as estimated from Poll (1967). Villages (○): AC, Alto Chicapa; S, Sá Mundji.

Paratypes. RMCA 164143, 164144, 164148, 7, 32.5–46.5 mm SL; and SAIAB 209783 (ex RMCA 164145–147), 3, 34.3–41.3 mm SL; collected with the holotype. – RMCA 164153–164159, 7, 32.9–41.7 mm SL; Alto Chicapa, Cachi River, (near village Sá Mundji), tributary to Luemba River, 10°55'54"S 19°04'35"E (label records as 7°32'S 21°22'E); Angola, Museu do Dundo, 20 Jul 1954. – RMCA 164160, 1, male, 40.0 mm SL; Alto Chicapa environs du sources du Cuilo, 10°52'S 19°24'E; Angola, Museu do Dundo (récolte indigène). – RMCA 164161-2, 2, 27.9–28.2 mm SL; sources

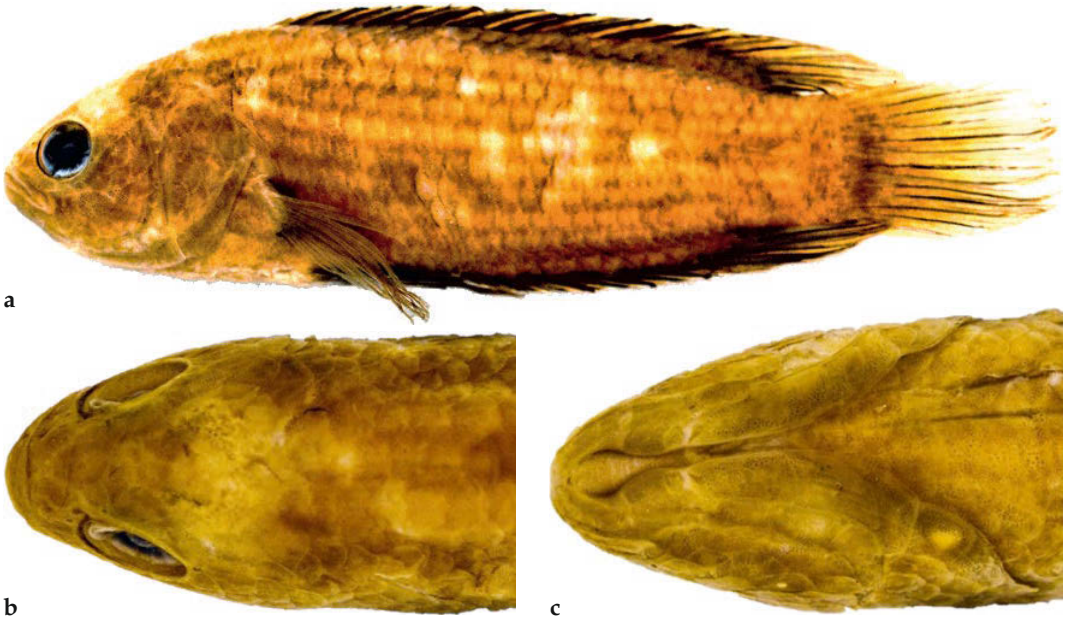

Fig. 6. *Microctenopoma stevenorrisi*, new species, RMCA 164142, holotype, 44.6 mm SL; Angola: Congo system. **a,** lateral view; **b,** head dorsal view; **c,** head ventral view.

du Cuilo, 10°52'S 19°24'E; Angola, Museu do Dundo (récolte indigène), 30 Aug 1954. – RMCA 164163–164172, 10, 27.5–36.1 mm SL; Lucoge River, approximately 8°50'S 21°03'E (label gives 7°33'S 20°27'E); Angola, Museu do Dundo, 1 Apr–30 Apr 1964.

Diagnosis. A species of *Microctenopoma* and part of the *M. nanum* complex as defined by Norris (1995). *Microctenopoma stevenorrisi* differs from *M. nanum* and *M. milleri* in head profile (rounded or convex with blunt snout vs. flat or straight with acute snout) and from *M. ocellifer* in the number of anal-fin spines (VIII–X, modally IX vs. IX–XI, modally X). It differs from *M. steveboyesi* in the number of dorsal spines (XV–XVII mode XVII vs. XIV–XV mode XV, Table 2), number of vertebrae (27–28 mode 27 vs. 25–26 mode 26) especially caudal vertebrae (17–19 mode 18 vs. 16–17 mode 17) and the length of the caudal peduncle 5.7–11.0 vs. 9.0–15.1 % SL. It differs from *M. intermedium* in pigmentation (marbled with underlying linear stripes vs. barred without underlying stripes), the shape of the caudal fin (rounded vs. emarginate), in having more pre-anal vertebrae (modally 10 vs. 9), and more dorsal spines (XV–XVII, modally XVII vs. XIV–XVI, modally XVI, Table 2).

Description. Based on types. Anatomical measurements, meristic information and proportions in Tables 1 and 2. Overall body shape obliquely ellipsoid, laterally compressed, widest and deepest at dorsal-fin origin with depth 3–3.5 times in SL, gently tapering to caudal peduncle. Caudal peduncle short, a half to two thirds its depth.

Head length 3–3.2 times in SL, depth sub-equal to length, obtusely pointed anteriorly (Fig. 6 a–c), with steep (60° to the horizontal) straight or marginally convex predorsal profile, ventral profile convex. Snout short, less than orbit diameter. Nares before orbit, anterior tubular, adjacent to maxillary groove, posterior a simple pit adjacent to anterior orbit rim. Eye large, orbit diameter 3.5–4 times in HL, antero-dorsal and forward on head, below level of dorsal edge of opercle. Interorbit sub-equal to orbit diameter, post-orbit twice orbit diameter; orbit to pre-opercular groove equal to orbit diameter. Pre-opercular groove reaching to opposite mid-orbit. Mouth small, supra-terminal, jaws inclined at about 45° to horizontal when closed, reaching to below anterior half of orbit. Upper jaw with row of recurved, caniniform teeth along entire length. Dentary with short anterior outer row of 4–5 larger recurved caniniform teeth, and 2–3 inner rows of smaller recurved conical

teeth. Gular space bulbous anteriorly, narrow posteriorly (Fig. 6c). Medial pores on lower jaw separated across symphysis (Fig. 6c). Operculum with postero-dorsal notch armed with short series of spines above and below notch.

Gill rakers on anterior branchial arch widely spaced, short and blunt. Suprabranchial chamber shallow, epibranchial organ simple.

Dorsal-fin origin close behind head, above base of pectoral fin. Base of dorsal fin long, extending to anterior base of caudal peduncle, with covering sheath of 1–2 rows of small scales over posterior two thirds. Anterior dorsal-fin spines short, subsequent spines even in length, soft-rayed section short, with pointed margin at hind extremity reaching to above basal caudal fin. Anal-fin origin closer to mid-caudal base than to tip of snout, first spine short, remaining spines even, soft-rayed section short, with pointed hind margin reaching to below proximal third of caudal fin. Pectoral-fin base steeply inclined to head, fin slender with rounded extremity. Pelvic fin with short leading spine, hind margin acute, extended to origin of anal fin in females or, in mature males, to beyond origin of anal fin. Caudal fin paddle-like, rounded.

Entire body and most of head with well-developed ctenoid scales or cycloid scales over predorsum, chest and ventral body cavity. Scales on entire head surface except snout and dentary section of lower jaw. Single scale over angular-articular ahead of lower jaw articulation (Fig. 6c). Three or four rows across cheek below orbit and post-orbit to pre-opercular groove, 3–4 rows across operculum, all ctenoid in mature males, cycloid in females and juveniles. Bilateral row of large scales along exposed margin of operculum (interopercle and subopercle) from the articulation of lower jaw to opercle. Three interorbital rows at anterior edge of squamation. Squamation regular and even along body. Scales all ctenoid along flanks, cycloid over pre-dorsum and ventrally from head to anus. Bilateral sheath of 1–2 small scales along two thirds of base of dorsal and anal fins. Bilateral sheath of small scales over caudal-fin base. Soft rays of dorsal, caudal and anal fins proximally covered with rows of tiny scales.

Lateral line in two sections, pores and canals generally obscure and irregular, anterior section from immediately above operculum, arched dorsad across three scale rows and extending along row spaced one full scale row below dorsal-fin base to below last of dorsal-fin spines. Posterior section in mid-lateral scale row to base of caudal fin.

Vertebrae 27–28 modally 27, with 9–10 abdominal and 17–19 modally 18 caudal vertebrae (Table 2). Usually only a single vertebra before dorsal fin, and 10 before anal fin. No clearly ossified supraneural bones visible in X-rays.

Colour in preservation. Pigmentation somewhat faded. Holotype and most paratypes light brown with deeper sub-parallel stripes along body and, in some, an eye spot at middle of caudal-fin base. Dorsal and anal fins dark brown (black), without indications of pattern. Head markings indistinct. Indications of marbling or irregular barring in addition to the stripes, evident in a few specimens.

Live colouration is not recorded. Poll (1967: 317) examined the specimens mostly over a decade after collection and described these specimens as "Brunâtre, marquée de bandes ou de marbrures transversales et d'une tache pédonculaire précaudale plus ou moins visibles. Nageoires noirâtres", translated as "brownish, marked with transverse bands or mottled and a more-or-less visible caudal peduncle spot. Blackish fins".

Distribution. Recorded from southern headwater tributary streams of the Congo basin in Angola, specifically the Cachi-Luembo-Cuango, the sources of the Cuilo-lower Casai in the Alto Chicapa district, as well as the Lucoge-Chiumbe-Casai, Lunda Sul Province, Angola (Poll, 1967) [Fig. 5a,c].

Etymology. The specific name is given to honour Dr Steven Norris, a leading researcher of African anabantids, who recognised the genus and described several species of *Microctenopoma*. Dr Norris examined the specimens of this species in the RMCA and recognised that they were of an undescribed species without formally describing it at the time. The first name is spelt as Steve as that is how he is known to the first author.

Morphometric and meristic data. Morphometric and meristic data are compared in Tables 1 and 2 respectively. The maximum polygon clusters formed by plotting the second sheared principal component of the morphometric data (SHRD PC2) against the first principal component of the meristic data (PC1) for *Microctenopoma intermedium*, *M. steveboyesi* and *M. stevenorrisi* (Fig. 7) were significantly different from each other

($p < 0.05$) along both the PC 1 and the SHRD PC 2 axes. Size (SHRD PC 1) accounted for 78.1 % of the observed variance and the sheared second principal component accounted for 9.6 %. The second SHRD PC 2 is independent of size, thus we plotted the second SHRD PC 2 against the first principal component of the meristic data. Variables with the highest loadings on the sheared second principal component were body width (0.16), prepelvic length (0.13), and dorsal fin base length (0.13). The PC 1 accounted for 55.7 % of the total variance. Variables with the highest loadings on the PC 1 were number of vertebrae (0.42), number of dorsal-fin spines (0.38), and number of caudal vertebrae (0.38).

Discussion

Pigmentation was the initial character that drew attention in the field suggesting a difference in the *Microctenopoma steveboyesi* from *M. intermedium* (Fig. 1a–b). The specimens highlighted by Poll (1967) as marbled date from the 1950's or early 1960's and now are faded to a certain extent largely obscuring superficial pigmentation (Fig. 6a). The predominant pattern seen in these specimens is a series of gently curved parallel lines or stripes along the body, formed by darker pigmentation at the dorsal and ventral corners of the exposed sections of the scales. A prominent caudal spot is evident in several specimens. The dorsal and anal fins are darker than the body but show no distinct patterns. Similarly underlying parallel stripes are also characteristic of *M. steveboyesi* (Fig. 1b) but are not present in *M. intermedium* (Fig. 1a). *Microctenopoma steveboyesi* specimens have a (overlying) pigment layer of irregular barring that gives it a flecked or chequered appearance in life (Fig. 1b). The *Microctenopoma* specimens from the Lungwebungwe tributary of the upper Zambezi (SAIAB 204020) appear as for *M. steveboyesi*.

The conclusion drawn from pigmentation is that the underlying parallel stripes of specimens from both the Cuito-Cueve and the Congo drainage are similar, and that both differ from *M. intermedium* which lacks longitudinal stripes. The taxonomic status of Poll's (1967) specimens therefore rests on the difference exhibited in the number of dorsal spines and the number of vertebrae (especially caudal vertebrae) and, to a lesser extent, the number of anal spines. The separation of clusters as depicted in Figure 7 supports taxonomic recognition of three separate species, *Microctenopoma intermedium*, and the two described herein as *M. steveboyesi* and *M. stevenorrisi*.

There is no overlap in the number of vertebrae of the *Microctenopoma steveboyesi* (25–26, modally 26) and *M. stevenorrisi* (27–28, modally 28, Table 2). This is primarily a difference in caudal vertebrae (16–17, modally 17 vs. 17–19, modally 18, Table 2). These taxa further differ in the number of dorsal-fin spines: XIV–XV, (modally XV) for *M. steveboyesi* vs. XV–XVII (modally XVI-XVII) for *M. stevenorrisi*. Only one of the 30 specimens examined of *M. stevenorrisi* specimens had XV spines. Modal differences also occur in the number of anal-fin spines. *Microctenopoma steveboyesi* has a mode of XVIII anal-fin spines, whereas both for *M. stevenorrisi* and *M. intermedium* specimens have a mode of VIII or IX for this character (Table 2).

Microctenopoma steveboyesi differs from *M. stevenorrisi* and *M. intermedium* in pelvic fin length and caudal peduncle length, although there is some marginal overlap in these characters among the species. It is also the most slender of the species (Table 1). As *M. stevenorrisi* tends to increase in body width with size, at larger sizes (above 35 mm SL) this discriminates the species relative to *M. steveboyesi*. The overlap in other morphometric characters reduces their taxonomic utility. The specimens from the Lungwebungwe conform morphometrically and to a large extent in meristic characters with *M. steveboyesi*.

The close similarity among these southern savannah *Microctenopoma* species (sensu Norris, 1995) suggests not only a similar lifestyle and habits but also that they may have only recently been isolated from each other. Further exploration of headwater streams along the watershed is desirable. The fact that *M. intermedium* occurs in the Casai (Poll, 1967; Norris, 1995) and that it is a widespread species in the upper Zambezi (Fig. 5a), is consistent with hydrographic interchange between these two systems (Bell-Cross, 1965). The presence of *M. steveboyesi* in the source reaches of Cuito (Okavango), the Cueve (Cuanza) and the Lungwebungwe River, a Zambezi tributary, supports the idea of interconnection of these systems (Fig. 5b). In addition it is noted that the fish fauna of source streams of the Cuito River is isolated from downstream interactions by an 8 m vertical waterfall (personal observations), and that *M. intermedium* does occur downstream of the waterfall (Fig. 5a).

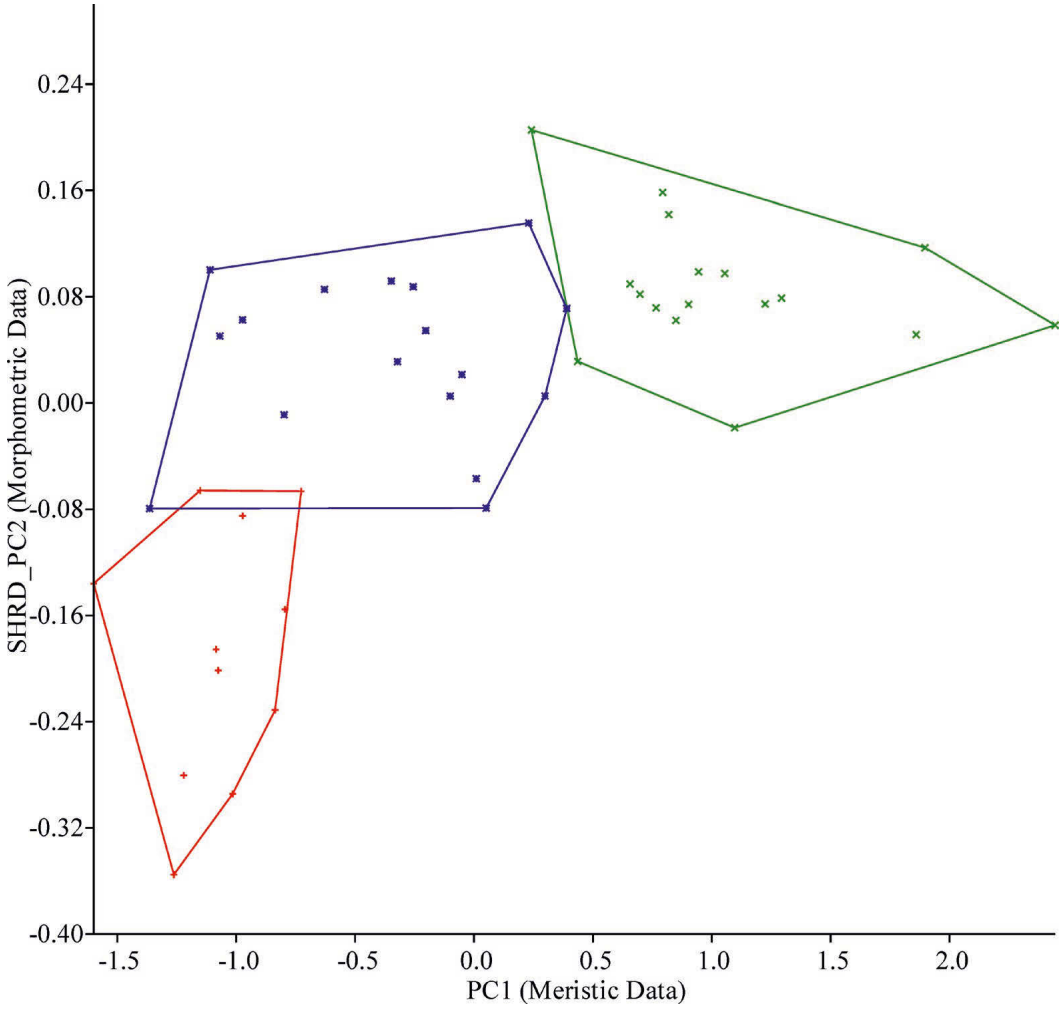

Fig. 7. Sheared second principal component (SHRD PC2 Morphometric Data) plotted against the first principal component (PC 1 Meristic Data) of studied specimens of *Microctenopoma steveboyesi* (+), *M. intermedium* (✱) and *M. stevenorrisi* (×).

Phylogenetic interrelationships of the new species have not been advanced at this stage. The distinction drawn between the forest and savannah species of *Microctenopoma* by Norris & Douglas (1991) and Norris (1995) points to an ecological dichotomy that may also be reflected in phylogeny. On-going research may clarify this issue. Such studies will also inform the complexity of the hydrographic evolution of the Congo and adjacent river systems. There is little doubt that multiple cross-watershed faunal exchanges have occurred over time (e. g. Bell-Cross, 1965) and that these include exchanges between major tributaries of both the Congo and the Zambezi River systems, such as the Casai River on the Congo side, likely leaving tell-tale genetic signatures.

The freshwater fish fauna of Angola is, as yet, incompletely explored (Skelton, 2019). This is true of many river systems, particularly in the northern parts of the country and in remote areas of the interior around the Congo-Zambezi-Okavango watersheds. Opportunities to explore and collect fishes in some of these remote areas have been provided to the lead author by the Wild Bird Trust's National Geographic Okavango Wilderness Project. Not only are the source lakes

and streams of the watershed reaches remote and difficult to explore, but the aquatic habitats are distinct, and frequently low gradient, with sandy and porous substrates and a high seasonal rainfall provide circumstances favourable to the formation of peat marshes. This zone of close headwater drainages on Kalahari Sand deposits that are easily scoured through slump erosional processes provides opportunities for frequent faunal exchanges across adjacent systems. These systems connect a vast and far-reaching network of rivers, including the Cuanza (Atlantic), southern Congo tributaries Cuango, Cuilo, Chicapa, Chiumbe and the Casai (Atlantic), Zambezi (Western Indian Ocean), Cuando (Zambezi), Okavango (Central Kalahari), and slightly further south and west on the watershed also the Cunene (Atlantic). A number of different fish species are shared across these drainages along the watershed to reflect connections both recent and past.

Currently the known and possibly restricted distributions of the new species do raise conservation concerns. There is evidence of environmental changes in the area resulting from direct human actions including deforestation, agriculture and infrastructural developments (Huntley et al., 2019). Actions to ensure environmental protection in this region that are being promoted by the National Geographic Okavango Wilderness Project in conjunction with the provincial and Angolan Government are commendable and need to be encouraged. Ongoing and future surveys will help to provide further understanding of the distribution ranges and ecological attributes of these newly described species.

Material examined. Type specimens of the new species are listed under the respective descriptions.

Microctenopoma intermedium. SAIAB 101079, 3, 26.0–37.0 mm SL, Jamba Camp site 2, Cuando River, Angola. – SAIAB 193581, 34, 22.0–39.0 mm SL, Pans, Liuwa Plains National Park, Upper Zambezi River, Zambia. – SAIAB 200817, 1, 49.0 mm SL, Floodplain, Kalembesa Road, Upper Zambezi, Namibia. – SAIAB 203663, 4, 21.0–36.0 mm SL, Samununga Village, N'Dala River, Lungwebungwe tributary, Upper Zambezi, Angola. – SAIAB 205461, 4, 27.0–36.0 mm SL, Mopiri Camp, Okavango Delta, Botswana. – SAIAB 205489, 2, 31.0–40.0 mm SL Mopiri Drift, Okavango Delta, Botswana.

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