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Revalidation and Redescription of "*Lacustricola*" *chobensis* (Fowler, 1935) and Description of a New Miniature Species of "*Lacustricola*" from Southern Africa (Cyprinodontiformes: Procatopodidae)

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The "*Lacustricola*" *hutereaui* species complex is herein defined by the possession of banded dorsal, anal, and caudal fins in males and also by the pointed premaxilla ascending process, in which the premaxilla medial surface is slightly convex. "*Lacustricola*" *pygmaeus*, new species, known from the Okavango, Cuando, and upper Zambezi Rivers, is distinguished from the other species belonging to the "*L.*" *hutereaui* species complex by the following exclusive character states: an inconspicuous reticulate pattern on scale margins (vs. conspicuous); banded anal, dorsal, and caudal fin in females (vs. hyaline); faint bands in the middle rays of caudal fin in males (vs. conspicuous bands); rounded caudal fin in males (vs. slender); bright green-blue color in some of the flank scales (vs. absent); quadrate posterior margin with a deep concavity (vs. convex or about straight); and first dorsal-fin ray inserted in a vertical to second and third anal-fin ray (vs. fourth to eighth). Additionally, other morphometric, meristic, and osteological characters in combination proved to be useful in distinguishing the new species. Through the analysis of type material and recently collected specimens, the little known species "*L.*" *chobensis* is considered as a valid species and redescribed. It is easily distinguished from the other species belonging to the "*L.*" *hutereaui* species complex by a combination of external morphology, osteology, and coloration pattern characters. Comprehensive information on the osteology and external morphology of topotypes of "*L.*" *hutereaui* are presented, and description of coloration in life is provided for specimens from the Ubangui River, in the Central African Republic.

THE Procatopodidae is a fish family with about 100 species widely distributed across the main freshwater water bodies of Africa, with a few species occurring in brackish water environments (Huber, 1999; Ghedotti, 2000; Bragança and Costa, 2019). Until recently, there have been no comprehensive studies that focused on resolving the internal relationships and evaluating the monophyly of the procatopodid genera. The discovery of hidden diversity at both the species and generic level from recent molecular studies that provided better resolution of the phylogenetic relationships within the Procatopodidae (Bragança and Costa, 2019) has stimulated renewed interest in the systematics and taxonomy of this group (Bragança et al., 2020).

In a molecular phylogeny, Bragança and Costa (2019) revealed evidence that the genus *Lacustricola* is polyphyletic, with included species occurring in two separate, geographically disjunct clades. The eastern African *Lacustricola* species group comprises species that are largely confined to coastal rivers and lakes in East Africa, including the type species of the genus *L. pumilus*, described from Lake Tanganyika. It was found to be more closely related to the monotypic genus *Lamprichthys*, which has a pelagic species endemic to the Lake Tanganyika, and to *Congopanchax*, a genus of miniature species from lowland swampy rainforest areas of the Congo basin (Bragança and Costa, 2019). The southern African "*Lacustricola*" species group represents an undescribed genus with highest diversity in southern Africa, from the Nseleni River system in South Africa to the upper reaches of southern Congo River tributaries draining savanna areas, though it is also present in the northern Congo River tributaries and in the adjacent Chad River basin (Bragança and Costa, 2019). The southern African "*Lacustricola*" species group was recovered as the sister clade to the broadly distributed genus *Micropanchax* which occurs from coastal rivers in west Africa to the Nile, a typical Nilo-Sudanic distribution, and extending south to eastern African rivers and lakes and to the upper Lualaba River, a main tributary of the Congo River. According to Bragança and Costa (2019), the southern African "*Lacustricola*" belongs to the arid-savanna clade, which originated in the late Miocene, and most of its diversification is probably related to the increase in aridity and climate instability during that period and in the Plio-Pleistocene.

"*Lacustricola*" *hutereaui* has been considered one of the most morphologically distinct species of the southern African species group, readily distinguished from its congeners by the presence of conspicuous bands on the dorsal, anal, and caudal fins in males and a distinct reticulate pigment pattern on the margins of flank scales in both sexes (Huber, 1999). Boulenger (1913) described "*L.*" *hutereaui* based on three syntypes that were collected from the Uele River, a tributary of the Ubangui River which is the major northern affluent of the Congo River system. Three other species possessing the aforementioned distinctive coloration pattern traits were subsequently described from other river systems in central and southern Africa. These species are: "*Lacustricola*" *baudoni*, which was described in 1924 by Myers based on specimens that were collected from the Chad River system, "*L.*" *chobensis*, which was described in 1935 by

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Fowler from the Chobe River, a tributary of the upper Zambezi River system, and "*L.*" *schalleri*, described in 1974 by Scheel and Radda, with a vague type locality in southern Mozambique that most likely corresponds to the region just to the south of the Save River mouth. However, Wildekamp et al. (1986) and Wildekamp (1995) treated the latter three species as junior synonyms of "*L.*" *hutereaui*, but there is no evidence that this decision was substantiated by detailed morphological examination of the type specimens. Acceptance of this decision by subsequent authors meant that "*L.*" *hutereaui* became one of the most widely distributed cyprinodontiform fishes in Africa, with a range extending from the Chad-Chiari catchment through the Congo, upper and lower Zambezi, and the Okavango to coastal drainages in southern Mozambique (Wildekamp et al., 1986; Wildekamp, 1995).

Recently, a fifth species, "*L.*" *petnehazyi* was described in 2018 by Nagy and Vreven from the Katanga region in the Democratic Republic of Congo. This newly described species is readily distinguished from "*L.*" *hutereaui* (including its three junior synonyms) by differences in meristic, morphometric, and coloration pattern. Nagy and Vreven (2018) also found meristic and morphometric differences that suggested that the three synonyms of "*L.*" *hutereaui* may represent distinct species. However, these authors did not make any taxonomic decisions, probably due to the small sample sizes that they had examined (Nagy and Vreven, 2018). Hereafter, the term "*L.*" *hutereaui* complex will be used to refer to "*L.*" *hutereaui* and its three putative synonyms.

The purpose of the present study is to provide information supporting the revalidation and redescription of "*L.*" *chobensis* by examining the types and substantial number of conspecific specimens collected in southern Africa. In addition, we present comprehensive morphometric, meristic, and osteological information from topotypes of "*L.*" *hutereaui* and provide a description of a new miniature species, "*L.*" *pygmaeus*, new species (previously referred to as pigmy topminnow in Skelton, 2001), known from swampy areas in the Okavango, Cuando, and upper Zambezi river systems. This study brings the number of valid species belonging to the "*L.*" *hutereaui* complex to four, and further discussion on miniaturization in "*Lacustricola*" and the status of the little known "*L.*" *schalleri* is provided.

MATERIALS AND METHODS

Specimens examined, preservation, and fixation.—The present study included specimens deposited in the National Collection Facility at the NRF-South African Institute for Aquatic Biodiversity (NRF-SAIAB). The fishes were sampled using various gear, including electrofishing, seine nets, traps, fyke nets, and dip nets. Captured fishes were anaesthetized with clove oil, digitally photographed, and a small piece of muscle tissue was dissected from the right side of each specimen and preserved in 95% ethanol in the field for future genetic analysis. Tissue samples were stored at –80°C at the South African Institute for Aquatic Biodiversity (NRF-SAIAB), Makhanda (former Grahamstown). Voucher specimens were fixed in 10% formalin in the field and were then transferred through 10% and 50% to 70% ethanol for long-term storage upon returning from the field. The aforementioned fish euthanasia and preservation methods followed the recommendations of the NRF-SAIAB animal ethics guidelines (see https://www.saiab.ac.za/saiab-animal-ethics-policy.htm).

Morphological study, osteological preparations, and species concept.—Meristic and morphometric data were taken from specimens fixed in formalin and transferred to 70% ethanol. Measurements were obtained using digital calipers under a dissecting microscope following Costa (1988). Body measurements are presented as percent of standard length (SL) and head measurements are expressed as percent of head length (HL). Osteological studies were made on cleared and stained (CS) specimens prepared according to Taylor and Van Dyke (1985). Nomenclature for bone structures followed Costa (2006). Most osteological illustrations were made on structures present in the left side, unless these were damaged. Nomenclature for frontal squamation follows Hoedeman (1956) and that for head sensory canals follows Gosline (1949), except for the preorbital and postorbital canals, here called the anterior and posterior infraorbital canal, respectively. The species concept followed in this study is the unified species concept, as proposed by De Queiroz (2007), which states that any property that provides evidence for lineage separation is relevant to infer boundaries and number of species; in our particular case, the evidence come from the presence/combination of different character states (diagnosability).

Classification remarks.—The genus name for the southern African lampeyes is provisionally presented as "*Lacustricola*" to distinguish them from the eastern African species which belong to the genus *Lacustricola* (Bragança and Costa, 2019). Bragança is working on a comprehensive study integrating molecular, morphological, and osteological data to revise the systematics of the Procatopodidae.

RESULTS

"*Lacustricola*" *chobensis* (Fowler, 1935)

Figures 1, 2; Table 1

Aplocheilus chobensis Fowler, 1935: 276 [original description: Chobe River, below rapids, 3 miles from Kasane, Botswana].

Aplocheilichthys schalleri Scheel and Radda, 1974: 160 [original description: about 180 kilometers south of Beira, Mozambique].

Diagnosis.—"*Lacustricola*" *chobensis* is distinguished from "*L.*" *centralis*, "*L*" *jobaerti*, "*L.*" *johnstoni*, "*L.*" *jubbi*, "*L.*" *katangae*, "*L.*" *macrurus*, "*L.*" *matthesi*, "*L.*" *mediolateralis*, "*L.*" *moeruensis*, "*L.*" *myaposae*, "*L.*" *nigrolateralis*, and "*L.*" *stiassnyae* by the possession of banded dorsal, anal, and caudal fins in males, a conspicuous reticulate pattern on scale margins, and also by the possession of a pointed premaxilla ascending process, in which the premaxilla medial surface is slightly convex (Fig. 3B, E). It is distinguished from "*L.*" *hutereaui* by the possession of 10–13 anal-fin rays (vs. 14–15); first dorsal-fin ray inserted in a vertical to the fourth or fifth anal-fin rays (vs. sixth anal-fin ray); first dorsal-fin proximal radial between 11th–12th vertebral neural spine (vs. 13th); absence of maxilla ventral sharp process (Fig. 3E, F; vs. presence, Fig. 3B, C); retroarticular about the same size as anguloarticular ventral process (Fig. 3F; vs. shorter, Fig. 3C); posteroventral

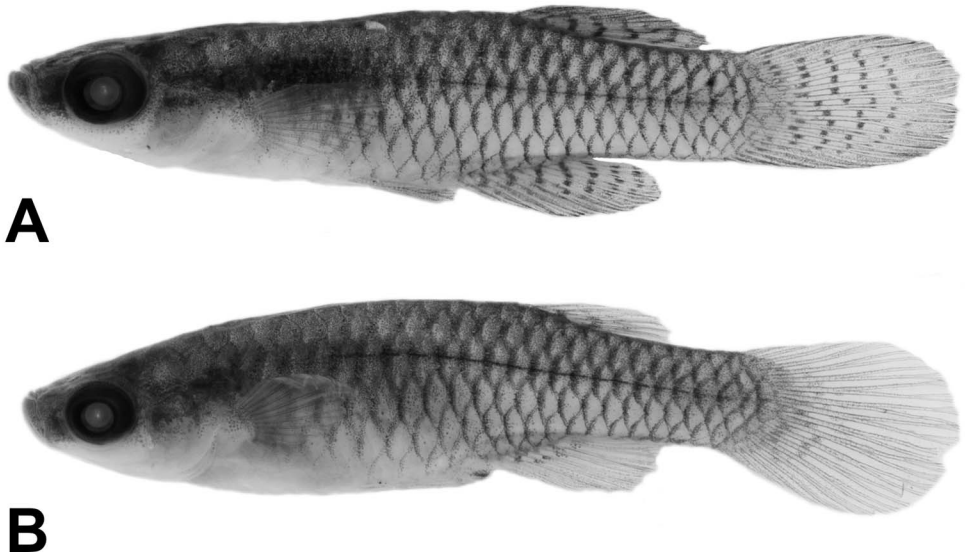

Fig. 1. "*Lacustricola*" *chobensis*, preserved specimens: (A) male SAIAB 101089, 22.6 mm SL, Boa Fé Lagoon, Okavango River basin, Angola; (B) female SAIAB 200797, 17.5 mm SL, Bwabwata National Park, Okavango River basin, Namibia.

extension on lachrymal (Fig. 3D; vs. rectangular, without posteroventral extension, Fig. 3A); infraorbital canal anterior portion open, with three neuromasts (Fig. 4B; vs. closed, with four pores, Fig. 4D); mandibular canal open, with two small neuromasts (Fig. 4B; vs. closed, with four pores, Fig. 4D); head neuromasts placed in shallow grooves or in the same level as head surface (Fig. 4A, B; vs. in deep grooves, Fig. 4C, D); posttemporal ventral arm not ossified (Fig. 5B; vs. ossified, Fig. 5A); cleithrum posterodorsal flap rounded (Fig. 5B; vs. sinuous, Fig. 5A); and by hypural plate completely fused (Fig. 5D; vs. with a small gap, rarely fused, Fig. 5C). "*Lacustricola*" *chobensis* is distinguished from "*L.*" *petnehazyi* by the presence of 10–12 anal-fin rays (vs. 14–16); first dorsal-fin ray inserted in a vertical to fourth or fifth anal-fin rays (vs.

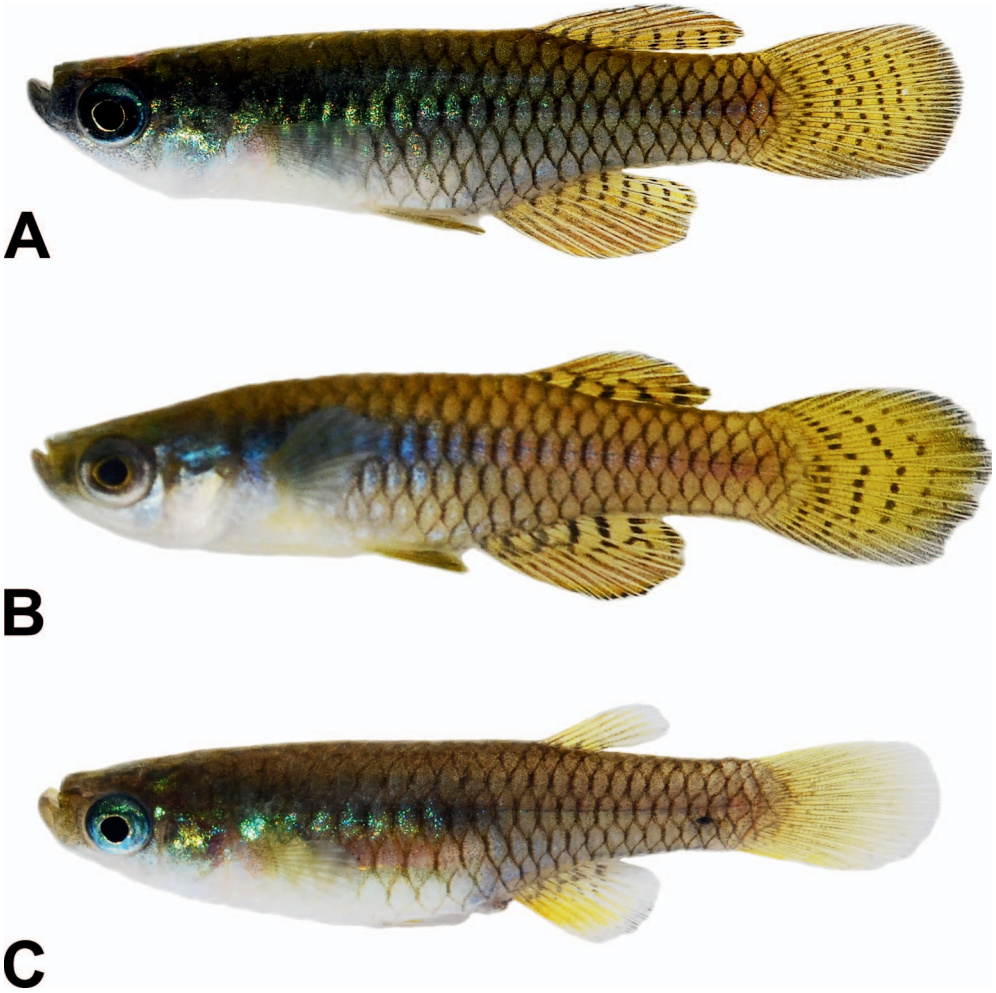

Fig. 2. Coloration of "*Lacustricola*" *chobensis* in life: (A) male SAIAB 200765, 24.0 mm SL, Bwabwata National Park, Okavango River basin, Namibia; (B) male uncatalogued, Kalimbeza swamps, Namibia; (C) female SAIAB 200765, 19.0 mm SL; same locality as specimen (A).

Table 1. Morphometric data of "*Lacustricola*" *chobensis*, "*L.*" *pygmaeus*, and "*L.*" *hutereaui*.

	"*Lacustricola*" *chobensis*			"*Lacustricola*" *pygmaeus*			"*Lacustricola*" *hutereaui*	
	Holotype (female)	Males ($n = 11$)	Females ($n = 15$)	Holotype (male)	Males ($n = 20$)	Females ($n = 14$)	Males ($n = 7$)	Females ($n = 3$)
Standard length (mm)	24.0	17.4–22.9	18.3–24.0	17.1	13.5–18.3	13.3–16.3	19.4–23.5	18.7–19.9
Percent of standard length								
Body depth	22.5	23.2–27.5	21.3–26.6	33.3	29.6–33.5	27.0–31.0	25.7–29.4	20.7–23.1
Caudal peduncle depth	15.0	14.2–17.1	12.6–15.2	18.1	15.9–20.0	14.3–17.4	16.8–18.7	13.8–14.6
Pre-dorsal length	69.6	63.5–70.7	65.0–73.4	67.2	65.7–68.4	66.9–70.4	67.3–71.1	70.0–70.4
Pre-pelvic length	49.6	44.9–49.7	45.0–50.0	51.5	45.9–52.8	46.8–53.6	42.5–47.9	46.5–48.2
Length of dorsal-fin base	9.2	8.8–13.5	7.9–10.3	22.8	17.4–22.8	14.0–18.4	10.6–12.3	9.6–10.0
Length of anal-fin base	12.9	13.2–19.6	11.8–14.1	21.0	19.2–22.0	14.7–17.8	18.9–20.1	16.6–17.5
Caudal-fin length	23.7	25.0–34.2	23.8–31.9	26.9	26.5–31.1	20.9–28.6	31.5–34.1	33.2–34.2
Pectoral-fin length	20.4	16.4–20.7	15.1–20.5	22.8	19.6–23.0	16.2–21.8	20.1–23.4	20.3–21.3
Pelvic-fin length	13.7	13.7–18.7	12.0–14.7	14.6	14.6–18.9	11.5–15.8	13.6–17.9	13.3–13.9
Head length (mm)	6.1	4.8–6.3	4.9–6.1	5.3	4.0–5.3	3.8–4.8	4.9–5.8	4.6–5.0
Percent of head length								
Head depth	63.9	53.7–63.5	53.1–63.9	69.8	61.0–72.7	59.1–69.0	70.9–79.3	62.5–69.6
Head width	65.6	58.5–67.3	59.6–67.2	66.0	65.0–71.4	65.9–71.4	63.6–69.4	65.2–68.0
Snout length	21.3	16.4–21.3	17.3–21.3	15.1	14.3–18.6	13.6–18.6	20.0–20.7	18.7–20.0
Lower jaw length	9.8	7.3–9.7	7.0–9.8	7.5	7.9–9.7	6.8–9.7	10.9–15.5	8.7–10.4
Eye diameter	37.7	36.5–43.7	36.8–41.1	37.7	35.8–40.5	38.1–41.5	39.6–43.4	40.0–43.5

sixth to eight anal-fin rays); 22–24 scales on longitudinal line, mode 23 (vs. 24–27, mode 26); 6–8 dorsal-fin rays, mode 7 (vs. 8–9 dorsal-fin rays, mode 9). It is distinguished from "*Lacustricola*" *pygmaeus*, new species, by the possession of 21–24 caudal-fin rays (vs. 26–30); an elliptical caudal fin in males (Figs. 1A, 2A, B; vs. rounded); chromatophores along whole mid-body line of flank, forming a conspicuous line (Fig. 1; vs. inconspicuous, Fig. 6); 6–8 dorsal-fin rays (vs. 10–12); first dorsal-fin ray inserted in a vertical to the fourth or fifth anal-fin rays (vs. second and third anal-fin ray); and by the absence of a concavity on quadrate posterior margin (Fig. 3C; vs. presence, Fig. 3F).

Description.—Morphometric data presented in Table 1. Maximum recorded adult size 24.0 mm SL. Dorsal profile of body slightly convex from snout tip to dorsal-fin origin; slightly concave from dorsal-fin origin to end of caudal peduncle. Ventral profile convex from lower jaw to end of anal-fin base; nearly straight on caudal peduncle. Anterior portion of body laterally compressed, becoming more compressed behind anal-fin origin.

In males, dorsal fin rounded and slightly more elongated than in females; its origin in vertical between 4th and 5th anal-fin rays; anal fin rounded and slightly elongated in males. Pelvic fin in males reaching between urogenital papilla aperture and base of first anal-fin ray. In females, pelvic fin shorter than in males, tip reaching region just before urogenital opening. Caudal fin elliptical in both sexes. Pectoral fin elliptical in both males and females, its posterior margin reaching vertical just behind pelvic-fin base. In both males and females, dorsal-fin rays 6(2), 7(36), or 8(10); anal-fin rays 10(11), 11(30), 12(6), or 13(1); caudal-fin rays 21(2), 22(1), 23(5), or 24(3); pectoral-fin rays 11(14), 12(32), or 14(2); pelvic-fin rays 6.

Frontal squamation G-patterned (Fig. 4A, B). Head neuromasts placed in shallow grooves or on same level as head surface. Cephalic lateral-line system: anterior portion of supraorbital sensory canal open, with three neuromasts, anteriormost one anteriorly displaced from other two; posterior portion open, with three exposed neuromasts; anterior infra-orbital canal open, with three exposed neuromasts; median portion of infra-orbital region with series of 9–11 minute neuromasts; posterior infra-orbital canal closed, with two pores; preopercular canal closed in both dorsal and ventral portions with 5–6 pores; mandibular canal represented by two neuromasts, one in vertical through corner of mouth and other anteriorly positioned in the lower jaw ventral portion. Longitudinal series of scales 22(15), 23(17), or 24(3); transverse series of scales 6; circumpeduncular scales 10; predorsal scales 12(2), 13(19), or 14(11).

Osteology.—Only informative characters illustrated. Mesethmoid and vomer absent. Frontal anterior margin slightly extends anteriorly between nasals. Parasphenoid medial process short, not contacting pterosphenoid; anterior margin rounded. Lateral ethmoid overlaps anterior portion of parasphenoid. Supraoccipital posterior process long, reaching first vertebra. Lachrymal with posteroventral extension (Fig. 3D). Premaxillary and dentary teeth well developed, conical; outer row with larger well-spaced teeth (Fig. 3E, F). Retroarticular triangular or subtriangular, about same depth and length to anguloarticular ventral arm (Fig. 3F). Dentary deep (Fig. 3F). Dorsal process of maxilla broad, overlapping premaxilla ascending process; ventral process greatly reduced, consisting of rounded ventromedial bulge (Fig. 3E, F). Ventral arm of maxilla broad, laterally expanded (Fig. 3F). Premaxilla ascending process medial surface with convex profile (Fig. 3E). Entopterygoid posterior portion and symplectic keel deep (Fig. 3F). Opercle triangular, anterodorsal process present (Fig. 3F). Anterior process of anterior ceratohyal not extending ventrally to ventral hypohyal. Urohyal ventral margin straight to slightly concave. First and second basibranchials lateral bone flanges unexpanded. Basihyal cartilaginous portion shorter than osseous portion.

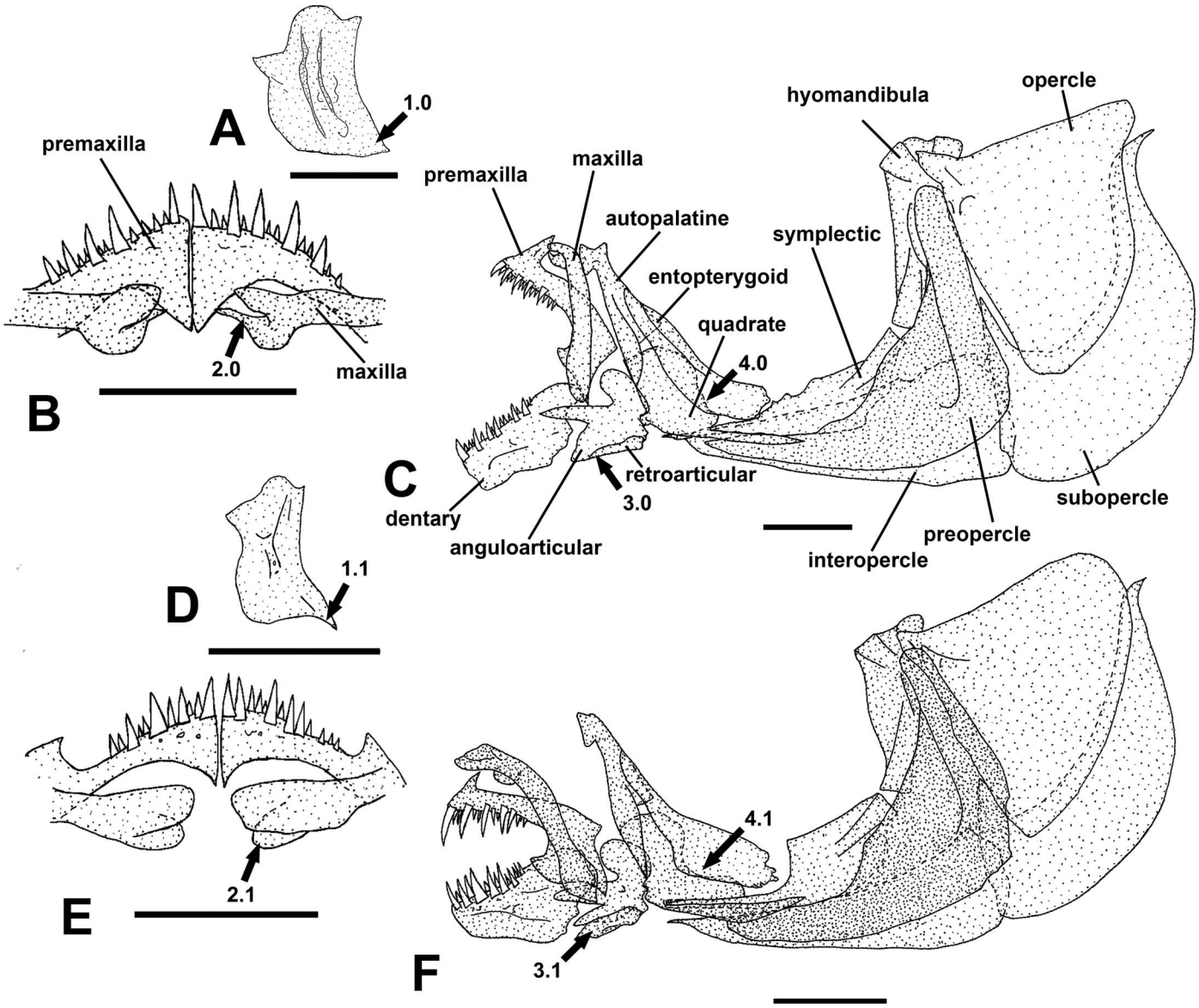

Fig. 3. Lachrymal, jaws, suspensorium, and opercular apparatus. "*Lacustricola*" *hutereaui* (MRAC P.182191–205): (A) lachrymal; (B) jaws, dorsal view; (C) jaws, suspensorium, and opercular apparatus, lateral view; "*Lacustricola*" *pygmaeus* (SAIAB 204087): (D) lachrymal; (E) jaws, dorsal view; (F) jaws, suspensorium, and opercular apparatus, lateral view. Arrows indicate informative traits: 1.0, posteroventral extension absent; 1.1, posteroventral extension present; 2.0, maxilla sharp ventral process; 2.1, maxilla ventral process greatly reduced, consisting of rounded ventromedial bulge; 3.0, retroarticular smaller than anguloarticular ventral arm; 3.1, retroarticular similar in depth and length to anguloarticular ventral arm; 4.0, quadrate posterior margin convex or about straight; 4.1, quadrate posterior margin with deep concavity. Scale bars = 1 mm.

Fourth ceratobranchial, anterior third portion with teeth. Second pharyngobranchial plate with teeth. Base of first epibranchial broad, more than three times width of anterior portion. Supracleithrum rounded (Fig. 5B). Posttemporal rod-like, ventral arm absent (Fig. 5B). Cleithrum bony flange not covering scapula foramen (Fig. 5B). Cleithrum posterodorsal flap rounded (Fig. 5C). Ventral postcleithrum slender, similar in width to adjacent first pleural rib. Basipterygium posterior process shorter than medial process. Anal-fin proximal radials about same length and parallel to each other. Hypurals completely fused (Fig. 5D). Parhypural proximal end overlapping preural centrum (Fig. 5D). Total vertebrae 24(2), 25(6), or 26(2), precaudal 10(1), 11(8), or 12(1) and caudal 13(2), 14(6), or 15(2). First proximal radial of dorsal fin between neural spine of vertebrae 11 and 12. First proximal radial of anal fin between pleural rib of vertebrae 9 and 11. Gillrakers on first branchial arch 7–9. Branchiostegal rays 5.

Coloration in alcohol.—Overall coloration of body pale yellowish brown with conspicuous dark brown reticulate pattern along margins of flank scales; anterior portion of flank darker (Fig. 1). Dorsal portion of body and anterior region of flank dark brown, densely pigmented; ventral surface scarcely pigmented. Brown chromatophores along whole mid-body line of flank, forming conspicuous line. Head overall coloration yellowish brown. Brown chromatophores on dorsum of head, lower jaw, and preorbital region,

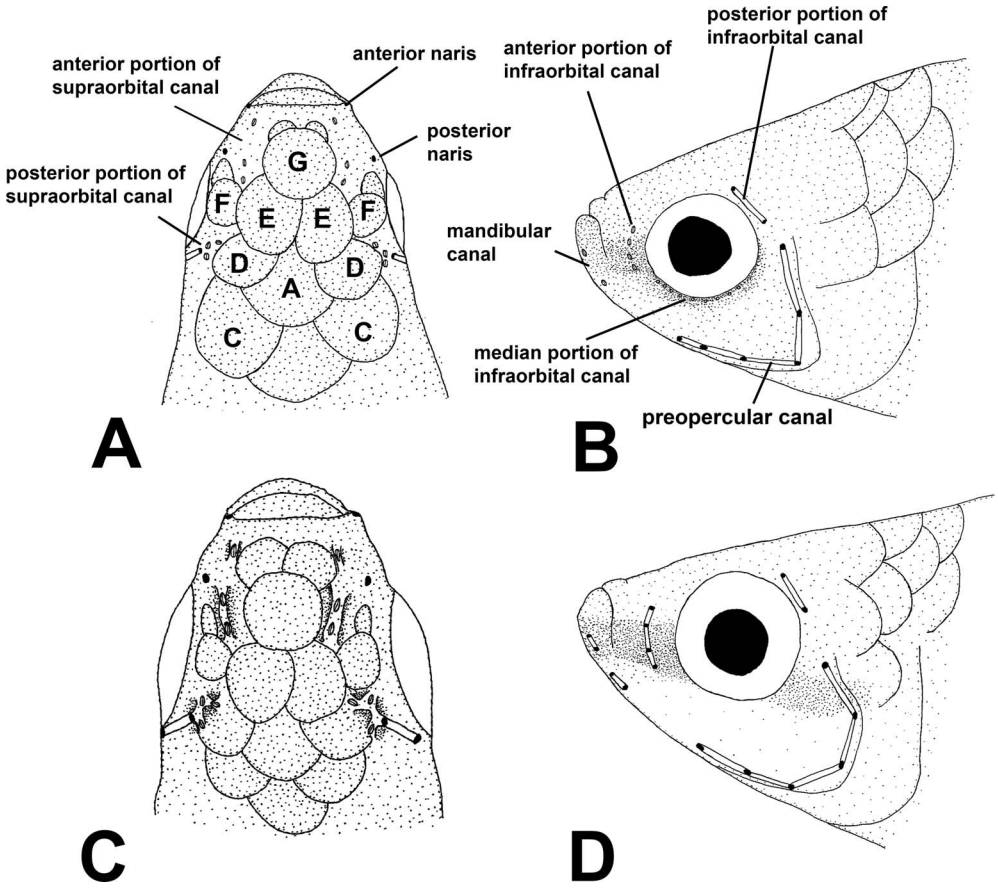

Fig. 4. Cephalic pores and head squamation pattern: (A–B) "*Lacustricola*" *pygmaeus* (same pattern is seen in "*L.*" *chobensis*); (C–D) "*L.*" *hutereaui*.

forming distinct darker region. Iris silver, darker close to pupil; dark pigment concentrated on dorsal margin of eye. All fins hyaline in females, with melanophores sparsely concentrated only on base of anal-, dorsal-, and caudal-fin membranes; melanophores forming conspicuous transversal bands on male dorsal and anal fins, and faint brown margin in both fins; caudal fin with three to five conspicuous vertical bands, and faint brown margin; pelvic fin with melanophores sparsely concentrated on fin membrane; pectoral fin hyaline. Female urogenital opening pocket scales with dark brown chromatophores.

Coloration in life.—Males (Fig. 2A, B). Side of body bright green, mainly in posterior head region and flank anterior region, with conspicuous dark brown reticulate pattern along scale margins, slightly thicker on each scale anterior margin. Dorsum yellowish green. Ventral surface white between head and region anterior to pelvic-fin origin; gray between pelvic fin and caudal peduncle. Side of head predominantly bluish green, dorsal portion yellowish brown, postorbital region with distinct bright green blotch. Iris dark gray, light yellow close to pupil. Eye bright bluish green on dorsal portion. Lower jaw and preorbital region dark brown-gray, forming distinct horizontal band. Pectoral fin hyaline; all other fins orange-yellow with dark brown dots arranged as distinct bands. Dorsal and anal fins with transverse bands; and caudal fin with three to five rows of transverse bands. Anal, dorsal, and caudal fins with dark brown to black marginal band, broader in caudal fin.

Females (Fig. 2C). Side of body pale gray, with conspicuous dark brown reticulate pattern along scale margins; anterior portion of flank darker. Bluish green iridescent blotch on region from pectoral-fin insertion into vertical to pelvic fin. Dorsum gray-brown. Venter white between head and region just anterior to urogenital opening; bright purple-blue between urogenital opening and end of anal-fin base; brownish gray from end of the anal-fin base to caudal peduncle. Scales around urogenital opening covered with dark chromatophores. Side of head predominantly dark brown, ventral portion white, dorsal portion dark brown, postorbital region with distinct light blue bright blotch. Iris dark gray, light yellow close to pupil. Eye bright silver-green on dorsal portion. Lower jaw and preorbital region dark brown-gray, forming distinct stripe. Pectoral and pelvic fins hyaline; dorsal fin orange, distal margin hyaline; anal fin hyaline, with distinct orange blotch on anterior portion; caudal fin hyaline with light orange coloration on ray insertions.

Distribution and habitat.—"*Lacustricola*" *chobensis* is a widespread species inhabiting swampy and riverine environments close to marginal vegetation (Fig. 7A, B) in the Okavango, Cuando, upper and lower Zambezi Rivers, a region comprising southern Angola, northern Botswana, northeastern Namibia, southern tip of Malawi, southern Mozambique, and northern Zambia (Fig. 8).

Remarks.—The holotype of "*Lacustricola*" *chobensis* (SAIAB 30007) is a female. This information is relevant as most procatopodid holotypes are males due to the presence of

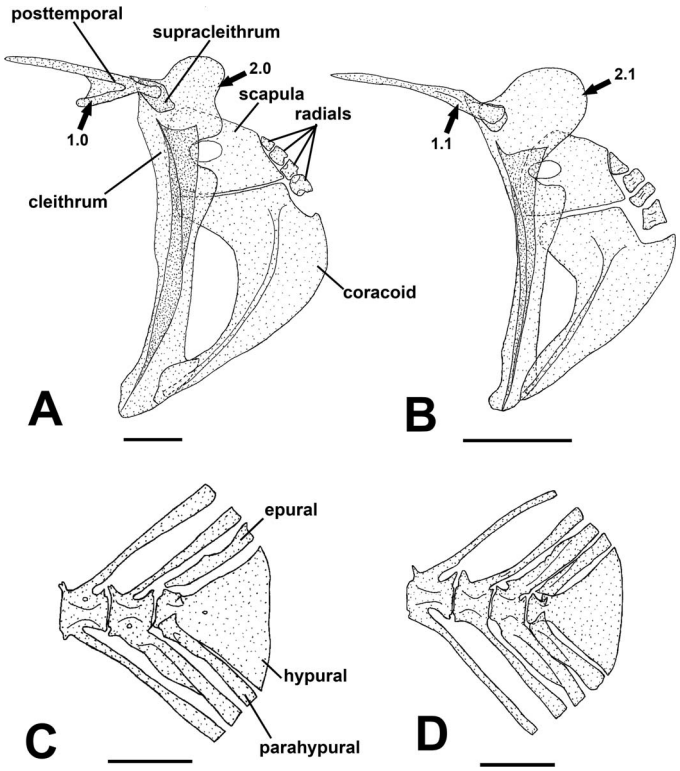

Fig. 5. Pectoral-fin girdle and caudal-fin skeleton, left lateral view: (A, C) "*Lacustricola*" *hutereaui* (MRAC P.182191–205); (B) "*L.*" *pygmaeus* (SAIAB 204242); (D) "*L.*" *chobensis* (SAIAB 66784). Arrows indicate informative traits: 1.0, posttemporal forked; 1.1, posttemporal rod-like; 2.0, cleithrum posterodorsal flap sinuous; 2.1, cleithrum posterodorsal flap rounded. Scale bars = 1 mm.

more diagnostic characters. After a few weeks in aquarium, wild-caught male specimens collected in the Cuando River presented a white submarginal band in the anal, dorsal, and in the lower lobe of the caudal fin, a trait not seen in specimens photographed just after collection (Heiko Karst, pers. comm.). We consider that this difference may be related either to the food available for the fish in aquarium, to a less stressful environment without predators, or to the mating coloration pattern.

Lacustricola pygmaeus, new species

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Figures 6, 9A; Table 1

Aplocheilichthys sp. 'pigmy topminnow,' Skelton (1993, 2001).

Micropanchax sp. 'pigmy,' Tweddle et al. (2014) and Skelton (2019).

Micropanchax sp. 'pygmy topminnow,' Tweddle at al. (2018).

Holotype.—SAIAB 204197, 17.1 mm SL, swamp near Cuanavale Lake, Okavango, Província do Moxico, Angola, 13°06′27.0″S, 18°51′39.2″E, R. Bills, 12 November 2016.

Paratypes.—SAIAB 209344, 6, 14.0–15.8 mm SL, same data as holotype; BMNH 2020.7.29.1–6, 6, 13.1–15.3 mm SL; MRAC 2020-001-P-004–006, 3, 14.0–15.6 mm SL; SAIAB 204073, 38, 7.8–17.4 mm SL; USNM 451063, 6, 12.0–15.8 mm SL, Cuando source lake, Cuando River, Província do Moxico, Angola, 13°04′05.9″S, 19°20′37.3″E, R. Bills, 14 November 2016; MRAC 2020-001-P-001-003, 3, 13.7–15.2 mm SL; SAIAB 204087, 9 (3 CS), 12.0–17.6 mm SL, Cangamba Road crossing, Okavango, Província do Moxico, Angola, 13°08′31.0″S, 19°26′42.1″E, R. Bills, 16 November 2016; SAIAB 204192, 6, 11.4–16.8 mm SL; UFRJ 12658, 3, 14.0–16.5 mm SL, swamp near Cuanavale source lake, Okavango, Província do Moxico, Angola, 13°06′27″S, 18°51′39.2″E, R. Bills, 12 November 2016; SAIAB 204242, 13 (5 CS), 10.6–17.0 mm SL; UFRJ 12659, 3, 12.9–14.6 mm SL, Salia Kuembo Lake, Okavango, Província do Moxico, Angola, 13°08′10″S, 19°02′42″E, R. Bills, 9 November 2016.

Additional non-type material.—SAIAB 35762, 2, 13.7–14.4 mm SL, road between Mongu and Senanga, upper Zambezi, Zambia, K. Winemiller, 29 August 1989; SAIAB 40758, 2, 14.2–16.9 mm SL, Cuando-Linyanti Sichika channel crossing

Fig. 6. "*Lacustricola*" *pygmaeus*, preserved specimens: (A) holotype, male, SAIAB 204087, 17.1 mm SL, Cuanavale Lake, Okavango River basin, Angola; (B) female, SAIAB 204242, 16.1 mm SL, Salia Kuembo Lake, Okavango River basin, Angola.

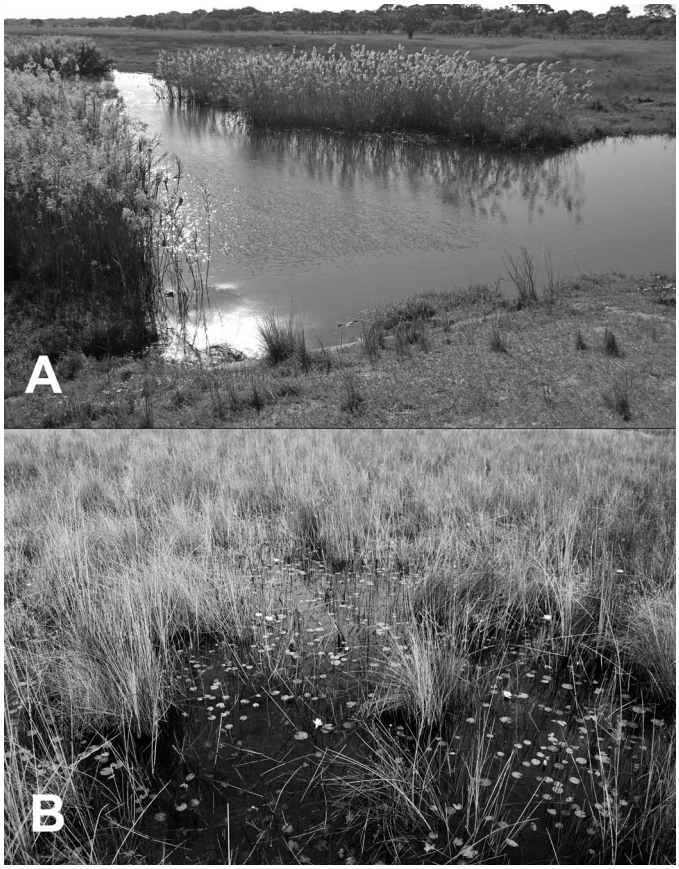

Fig. 7. (A) Riverine habitat of "*Lacustricola*" *chobensis* and "*L.*" *pygmaeus* in the Kataba River, upper Zambezi, Zambia (photo: D. Tweddle, 2015); (B) swampy habitat of "*Lacustricola*" *pygmaeus* in one of the source lakes of the upper Cuando River, Angola (photo: R. Bills, 2016).

Shibumu pool in Malimi National Park, Namibia, K. C. Hocutt and P. Johnson, 15 September 1992; SAIAB 49229, 1, 16.2 mm SL, Chobe River, Namibia, 17°47′60″S, 25°9′60″E, B. van Zyl, May 1997; SAIAB 66708, 1, 16.1 mm SL, Xakanaxa Lagoon, Okavango Delta, Botswana, 19°10′19″S, 23°23′40″E, D. Tweddle and B. van der Waal, 16 June 2000; SAIAB 66729, 1, 16.9 mm SL, Gadikwe HATB camp 11 (landing site), Maunachira River, Northwestern Moremi, Ngamiland, Botswana, 19°10′4″S, 23°14′42″E, B. van der Waal, D. Tweddle, S. Nengu, L. Mokunki et al., 14 June 2000; SAIAB 66771, 7, 11.6–15.4 mm SL, Xakanaxa Lagoon, Maunchira River, Northestern Moremi, Ngamiland, Botswana, 19°11′7″S, 23°23′42″E, D. Tweddle and B. van der Waal, 16 June 2000; SAIAB 66935, 1, 11.8 mm SL, Du Plessis's Camp, Sepopa, Okavango River, Northern Panhandle, Ngamiland, Botswana, 18°44′39″S, 22°11′47″E, R. Bills, P. Skelton, and B. Van der Waal, 10 June 2000; SAIAB 68426, 3, 14.1–15.8 mm SL, Maunachira Channel, Moremi Wildlife Park, Ngamiland, Botswana, 19°8′58″S, 23°16′14″E, J. Kolding, R. Bills, K. Mosepele, and K. Kuturo, 11 February 2003; SAIAB 68437, 2, 13.6–15.9 mm SL, Lagoon at top end of Thoage River east channel, Okavango River, Guma, Ngamiland, Botswana, 18°52′44″S, 22°23′28″E, J. Kolding, R. Bills, K. Mosepele, and K. Kuturo, 8 February 2003; SAIAB 68478, 1, 15.1 mm SL, Water Affairs, Guma, Guma Lagoon, Thaoge River, Okavango Delta, Ngamiland, Botswana, 18°57′22″S, 22°22′38″E, J. Kolding and R. Bills, 5 February 2003; SAIAB 68547, 1, 13.3 mm SL, Okavango Research Station, main channel of Boro River, Chief's Island Gunn's Camp, Ngamiland, Botswana, 19°32′30″S, 23°10′39″E, R. Bills, J. Kolding, K. Mosepele, and K. Kuturo, 16 February 2003; SAIAB 68633, 1, 15.4 mm SL, Gadiikwe Lagoon, Okavango Delta, Botswana, 19°9′45″S, 23°14′30″E, R. Bills, J. Kolding, and K. Mosepele, 11 February 2003; SAIAB 68647, 1, 14.9 mm SL, Xakanaxa Lagoon, Maunachira River, Okavango Delta, Botswana, 19°11′7″S, 23°23′42″E, J. Kolding, R. Bills, and K. Mosepele, 12 February

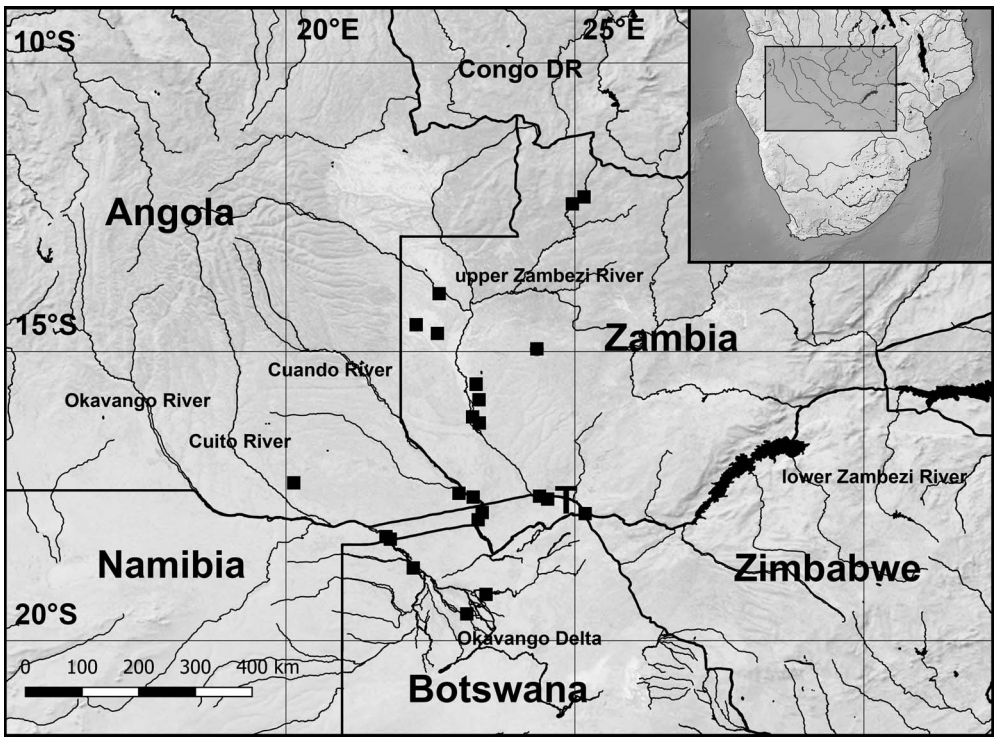

Fig. 8. Distribution of "*Lacustricola*" *chobensis* based on the SAIAB specimens examined in the present study. The letter (T) refers to type locality.

Fig. 9. Coloration in life. (A) "*Lacustricola*" *pygmaeus*, male, SAIAB 204242, 15.8 mm SL, from one of the source lakes of the Cuando River, Angola. "*Lacustricola*" *hutereaui*: (B) male, SAIAB 78314, 22.5 mm SL; (C) female, 19.4 mm SL; both from Ubangui River drainage, Central African Republic.

2003; SAIAB 68654, 28, 9.0–17.6 mm SL, Paradise lagoon hippo pool Makoro channel, Maunchira River, Okavango, Moremi Wildlife Park, Ngamiland, Botswana, 19°11′57″S, 23°27′36″E, R. Bills, J. Kolding ,and K. Mosepele, 10 February 2003; SAIAB 71023, 131 (7 CS), 9.6–19.3 mm SL, Musokwezi River, Kabompo River, upper Zambezi, Zambia, 13°11′15″S, 24°13′39″E, D. Tweddle and B. van der Waal, 23 October 2002; SAIAB 71057, 9, 15.6–17.8 mm SL, Sefula River, Kataba, upper Zambezi, Zambia, 15°22′29″S, 23°12′2″E, D. Tweddle and B. van der Waal, 25 October 2002; SAIAB 71071, 6, 15.8–17.9 mm SL, Sianda River, Kataba, upper Zambezi, Zambia, 15°34′49″S, 23°17′46″E, D. Tweddle and B. van der Waal, 25 October 2002; SAIAB 71285, 1, 13.3 mm SL, Kataba River, upper Zambezi, Zambia, 15°34′2″S, 23°17′0″E, D. Tweddle and B. van der Waal, 7 November 2002; SAIAB 71871, 12, 12.4–17.2 mm SL, Sefula River, upper Zambezi, Zambia, 15°22′29″S, 23°12′2″E, D. Tweddle and B. van der Waal, 27 April 2003; SAIAB 71902, 2, 9.1–12.4 mm SL, swampy dambo in forest, Zambia, 15°34′2″S, 23°17′0″E, D. Tweddle and B. van der Waal, 27 April 2003; SAIAB 71911, 2, 12.9–13.6 mm SL, Mukango Swamp, Kataba River, upper Zambezi, Zambia, 15°28′56″S, 23°25′14″E, D. Tweddle and B. van der Waal, 27 April 2003; SAIAB 71934, 3, 12.7–13.8 mm SL, Lipaa, Kataba River, upper Zambezi, Zambia, 15°27′26″S, 23°18′24″E, D. Tweddle and B. van der Waal, 28 April 2003; SAIAB 71961, 3, 10.0–11.1 mm SL, Sianda River, tributary of the Kataba River, upper Zambezi, Zambia, 15°34′49″S, 23°17′46″E, D. Tweddle and B. van der Waal, 29 April 2003; SAIAB 72173, 6, 13.4–

17.1 mm SL, Nalonga River, upper Zambezi, Zambia, 16°2′21″S, 23°19′44″E, D. Tweddle and B. van der Waal, 3 May 2003; SAIAB 72931, 33 (6 CS), 10.7–15.0 mm SL, Sianda River, Kataba, upper Zambezi, Zambia, 15°34′49″S, 23°17′42″E, D. Tweddle and B. van der Waal, 15 September 2003; SAIAB 72953, 21, 12.–15.9 mm SL, Kataba River, upper Zambezi, Zambia, 15°34′2″S, 23°17′0″E, D. Tweddle, B. van der Waal, and A. Chilala, 15 September 2003; SAIAB 73599, 14, 11.3–13.1 mm SL, Mayau River, upper Zambezi, Zambia, 12°44′55″S, 24°15′2″E, D. Tweddle and B. van der Waal, 6 October 2003; SAIAB 81094, 4, 10.5–18.2 mm SL, Limulanga, Kavombo River, upper Zambezi, Zambia, 15°6′21″S, 23°9′31″E, D. Tweddle and B. van der Waal, 26 April 2003; SAIAB 83387, 15, 9.9–17.4 mm SL, Paradise pools, Okavango River Delta, Okavango, Botswana, 19°12′13″S, 23°27′38″E, R. Bills, 15 June 2000; SAIAB 101049, 23, 9.6–13.3 mm SL, drifts through river at Maue village, Okavango, Província do Cuando e Cubango, Angola, 16°54′35.3″S, 19°18′27.7″E, R. Bills, N. Mazungula, M. Domingos, and F. de Almeida, 21 April 2013; SAIAB 186669, 12, 8.4–14.4 mm SL, flood plain below Soba Mathias, Menongue, Cubango, Angola, 14°26′20.8″S, 17°48′53.7″E, R. Bills, P. Skelton, F. de Almeida, and M. Domingos, 10 May 2012; SAIAB 186682, 18, 7.3–20.0 mm SL, swamp in a small dambo stream, Soba Mathias, Cubango, Província do Cuando-Cubango, Angola, 14°15′25.4″S, 17°46′42.7″E, R. Bills, P. Skelton, F. de Almeida and M. Domingos, 10 May 2012; SAIAB 186714, 1, 14.3 mm SL, bridge of 1000 mines, north of Mambue, Província do Bié, Angola, 13°35′39.6″S, 16°52′49.8″E, R. Bills, P. Skelton, F. de Almeida, and M. Domingos, 11 May 2012; SAIAB 190398, 1, 18.3 mm SL, Bukalo channel, Caprivi, Namibia, 17°43′25″S, 24°31′15″E, R. Peel, 26 March 2013; SAIAB 190407, 1, 13.3 mm SL, Kataba River, upper Zambezi, Western Province, Zambia, 15°34′02.6″S, 23°17′00″E, D. Tweddle, 26 May 2013; SAIAB 190588, 1, 11.5 mm SL, Rito campsite (upstream from Rito village), Província do Cuando e Cubango, Angola, 16°37′24.0″S, 19°3′12.8″E, R. Bills et al., 19 April 2013; SAIAB 193697, 8, 13.2–19.3 mm SL, Kataba River at main road culvert, upper Zambezi, Western Province, Zambia, 15°34′02.5″S, 23°17′00″E, D. Tweddle, 29 October 2013; SAIAB 202248, 1, 13.2 mm SL, Luasinga River bridge, Tribhonga tributary, Cuito River, Okavango, Província do Cuando, Angola, 14°35′23.4″S, 18°10′13.7″E, P. Skelton, 8 February 2016; SAIAB 202276, 5, 13.0–17.5 mm SL, Cuito source, Okavango River, Província do Bié, Angola, 12°41′22.06″S, 18°21′36.46″E, P. Skelton and B. van der Waal, 15 February 2016; SAIAB 203206, 2, 11.6–11.9 mm SL, Cuanavale source wetland, Cuanavale River, Okavango, Província do Moxico, Angola, 13°03′2.45″S, 18°53′51.1″E, A. Costa, 29 February 2016; SAIAB 203236, 1, 14.4 mm SL, Forest camp, Cuito River, Okavango, Província do Moxico, Angola, 13°53′50.6″S, 18°17′40.3″E, A. Costa, 21 June 2015; SAIAB 203249, 9, 9.5–16.1 mm SL, bubbling fountain, Cuanavale River, Okavango, Província do Moxico, Angola, B. van der Waal, 8 March 2016; SAIAB 203919, 6, 9.6–15.7 mm SL, Lussinga River, Província do Cuando, Angola, 14°35′22.92″S, 18°10′15.96″E, W. Conradie, 5 June 2015; SAIAB 204069, 23, 11.8–16.2 mm SL, Cuando source vlei, Cuando River, Província do Moxico, Angola, 13°00′13.8″S, 19°07′37.9″E, R. Bills, 13 November 2016; SAIAB 204142, 7, 10.6–16.2 mm SL, Cuanavale source lake, Okavango, Província do Moxico, Angola, 13°05′23.9″S, 018°53′38.0″E, N. Mazungula and B. van der Waal, 23 October 2016; SAIAB 204156, 9, 8.3–14.3 mm SL, Cuanavale near confluence, Okavango, Província do Moxico, Angola, 13°07′29.2″S, 018°54′00.6″E, N. Mazungula and B. van der Waal, 24 October 2016; SAIAB 204248, 13, 11.8–15.4 mm SL, pan near Cuanavale Camp, Seepage, Okavango River, Província do Moxico, Angola, 13°06′27.0″S, 18°51′39.2″E, R. Bills, 17 November 2016; SAIAB 204331, 5, 14.2–17.1 mm SL, Salia Kuembo Lake, Província do Moxico, Angola, 13°08′10″S, 19°02′42″E, R. Bills, 9 November 2016; SAIAB 204705, 14, 9.0–17.3 mm SL, Cuando source bog, Cuando River, Província do Moxico, Angola, 13°00′13.8″S, 19°07′37.9″E, P. Skelton, 17 April 2017; SAIAB 204723, 4, 12.9–16.0 mm SL, Cuanavale bog above lake, Cuanavale River, Okavango, Província do Moxico, Angola, 13°05′08.7″S, 18°53′31.75″E, P. Skelton and L. Mason, 18 April 2017; SAIAB 204292, 2, 12.8–14.7 mm SL, crossing maintrack SW Cambuta, Zambezi River, Província do Moxico, Angola, 13°26′48.4″S, 19°57′50.5″E, R. Bills, 20 November 2016; SAIAB 204685, 1, 17.2 mm SL, Calua Lagoon, Okavango, Província do Moxico, Angola, 12°44′23.6″S, 18°23′21.39″E, P. Skelton, 14 April 2017.

Diagnosis.—*"Lacustricola" pygmaeus* is distinguished from *"L." centralis*, *"L." jobaerti*, *"L." johnstoni*, *"L." jubbi*, *"L." katangae*, *"L." macrurus*, *"L." matthesi*, *"L." mediolateralis*, *"L." moeruensis*, *"L." myaposae*, *"L." nigrolateralis*, and *"L." stiassnyae* by the possession of banded dorsal, anal, and caudal fins in males and also by the possession of a pointed premaxilla ascending process, in which the premaxilla medial surface is slightly convex (Fig. 3B, E). It is further distinguished from *"L." hutereaui*, *"L." chobensis*, and *"L." petnehazyi* by an inconspicuous reticulate pattern on scale margins (Fig. 9A; vs. conspicuous, Fig. 1); banded anal, dorsal, and caudal fins in females (Fig. 6B; vs. hyaline, Figs. 1B, 2C); faint bands in the middle rays of caudal fin of male (Figs. 6A, 9A; vs. conspicuous bands, Figs. 1A, 2A, B); rounded caudal fin in males (Figs. 6A, 9A; vs. elliptical, Figs. 1A, 2A, B); bright green-blue color restricted to the area delimited by some of the flank scales (Fig. 9A; vs. bright green coloration not restricted to scale area in *"L." chobensis* and *"L." petnehazyi*, and absent in *"L." hutereaui*, Figs. 2, 9B, C); quadrate posterior margin with a deep concavity (Fig. 3F; vs. convex or about straight, Fig. 3C); first dorsal-fin ray inserted in a vertical to second and third anal-fin ray (vs. fourth to eighth). *"Lacustricola" pygmaeus* is further distinguished from *"L." hutereaui* by the absence of maxilla ventral sharp process (Fig. 3E, F; vs. presence, Fig. 3B, C); retroarticular about the same size as anguloarticular ventral process (Fig. 3F; vs. shorter, Fig. 3C); posteroventral extension on lachrymal (Fig. 3D; vs. rectangular, without posteroventral extension, Fig. 3A); infraorbital canal anterior portion open, with three to four neuromasts (Fig. 4B; vs closed, with four pores, Fig. 4D); mandibular canal open, with two small neuromasts (Fig. 4B; vs. closed, with four pores, Fig. 4D); head neuromasts placed in shallow grooves or on the same level as head surface (Fig. 4A, B; vs. on deep grooves, Fig. 4C, D); possession of chromatophores close to eye, along infraorbital region (Fig. 4B; vs. absence of chromatophores, Fig. 4D); posttemporal ventral arm not ossified (Fig. 5B; vs. ossified, Fig. 5A); and by a cleithrum posterodorsal bone flap rounded (Fig. 5B; vs. sinuous, Fig. 5A). *"Lacustricola" pygmaeus* is further distinguished from *"L." petnehazyi* by the possession of 20–22 scales on longitudinal series (vs. 24–27), and from *"L."*

chobensis by the possession of 26–30 caudal-fin rays (vs. 21–24); 10–12 dorsal-fin rays (vs. 6–8); and chromatophores along whole mid-body line of flank, forming an inconspicuous line (Figs. 6, 9A; vs. conspicuous, Figs. 1, 2).

Description.—Morphometric data presented in Table 1. Maximum recorded adult size 20.5 mm SL. Dorsal profile of body deeply convex from snout tip to end of dorsal-fin base; slightly concave to straight on caudal peduncle. Ventral profile convex from lower jaw to end of anal-fin base; nearly straight on caudal peduncle. Caudal peduncle slightly deeper in males. Anterior portion of body laterally compressed, becoming more compressed behind anal-fin origin.

Dorsal fin rounded and elongated in males, tip reaching caudal-fin base; its origin in vertical between 2nd and 3rd anal-fin rays (Fig. 6). Anal fin rounded and elongated in males, tip reaching region just before caudal-fin base. Dorsal and anal fins not elongated in females. Caudal fin rounded in males and elliptical in females. Pectoral fin elliptical, its posterior margin reaching vertical just behind pelvic-fin base. Pelvic-fin length in males longer than in females, reaching between urogenital papilla aperture and first anal-fin ray; short in females, tip reaching region just before urogenital opening. Pelvic-fin bases medially separated by interspace broader than width of each pelvic-fin base. Dorsal-fin rays 10(17), 11(31), or 12(4); anal-fin rays 12(2), 13(36), 14(14), or 15(1); caudal-fin rays 26(2), 27(6), 28(5), 29(6), or 30(2); pectoral-fin rays 12(7) or 13(36); pelvic-fin rays 6.

Frontal squamation G-patterned (Fig. 4A, B). Head neuromasts placed in shallow grooves or on same level as head surface. Cephalic lateral line system: anterior portion of supraorbital sensory canal open, with 3 neuromasts, anteriormost one anteriorly displaced from other 2; posterior portion open, with 3 exposed neuromasts; anterior infra-orbital canal open, with 3 exposed neuromasts; median portion of infra-orbital region with series of 7 to 9 minute neuromasts; posterior infra-orbital canal closed, with 2 pores; preopercular canal closed in both dorsal and ventral portions with 5 pores; mandibular canal represented by 2 neuromasts, 1 in vertical through corner of mouth and other anteriorly positioned in lower jaw ventral portion. Longitudinal series of scales 20(12), 21(17), or 22(3); transverse series of scales 6; circumpeduncular scales 10; predorsal scales 11(12), 12(14), or 13(4).

Osteology.—Only informative characters illustrated. Mesethmoid and vomer absent. Frontal, anterior margin slightly extends anteriorly between nasals. Parasphenoid medial process short, not contacting pterosphenoid; anterior margin rounded. Lateral ethmoid overlaps anterior portion of parasphenoid. Supraoccipital posterior process long, reaching first vertebra. Lachrymal with posteroventral extension (Fig. 3D). Premaxillary and dentary teeth well developed, conical; outer row with larger well-spaced teeth (Fig. 3D, F). Retroarticular triangular or subtriangular, about same depth and length of anguloarticular ventral arm (Fig. 3F). Dentary deep (Fig. 3F). Dorsal process of maxilla broad, overlapping premaxilla ascending process; ventral process greatly reduced, consisting of rounded ventromedial bulge (Fig. 3E, F). Ventral arm of maxilla broad, laterally expanded (Fig. 3D). Premaxilla ascending process medial surface with convex profile (Fig. 3E). Entopterygoid posterior portion and symplectic bone keel deep (Fig. 3F). Opercle triangular, anterodorsal process present (Fig. 3F). Quadrate posterior margin with deep concavity (Fig. 3F). Anterior process of anterior ceratohyal not extending ventrally to ventral hypohyal. Urohyal ventral margin straight to slightly concave. First and second basibranchial lateral bone flanges unexpanded. Basihyal cartilaginous portion shorter than osseous portion. Fourth ceratobranchial anterior third portion with teeth. Second pharyngobranchial plate with teeth. Base of first epibranchial broad, more than three times width of anterior portion. Supracleithrum rounded (Fig. 5B). Posttemporal rod-like, ventral arm absent (Fig. 5B). Cleithrum bony flange not covering scapula foramen (Fig. 5B). Cleithrum posterodorsal flap rounded (Fig. 5B). Ventral postcleithrum slender, width similar to adjacent first pleural rib. Basipterygium posterior process shorter than medial process. Anal-fin proximal radials similar in length and parallel to each other. Hypurals completely fused (Fig. 5D); small gap seen in only one specimen (Fig. 5C). Parhypural proximal end overlapping preural centrum (Fig. 7C). Total vertebrae 24(14), 25(6), or 26(1), precaudal 10(16) or 11(5); and caudal 14(18) or 15(3). First proximal radial of dorsal fin between neural spine of vertebrae 9 and 11. First proximal radial of anal fin between pleural rib of vertebrae 9 and 10. Gill rakers on first branchial arch 7–8. Branchiostegal rays 5.

Coloration in alcohol.—Overall coloration of body pale brown-yellow with inconspicuous light brown reticulate pattern along flank scale margins; anterior portion of scales with concentrated chromatophores (Fig. 6). Dorsal portion of body dark brown, densely pigmented; ventral surface scarcely pigmented. Pale brown chromatophores along whole mid-body line of flank, forming distinct inconspicuous line. Head overall coloration yellowish brown. Brown chromatophores on dorsum of head, lower jaw, and preorbital region, forming distinct darker region. Iris silver, darker close to pupil; dark pigment concentrated on dorsal margin of eye. Anal and dorsal fins with melanophores forming conspicuous transversal bands in both males and females. Gray zone in fin margin of males. Caudal fin with three to four inconspicuous bands in males, restricted to middle caudal-fin rays, margins gray with several small chromatophores; conspicuous in females extending from dorsal to ventral margin of fin; pelvic fin with melanophores sparsely concentrated on fin membrane in females; dark brown in males; pectoral fin hyaline. Female urogenital opening pocket scales with dark brown chromatophores.

Coloration in life.—Males (Fig. 9A). Side of body gray, with inconspicuous light brown reticulate pattern on flank scales, and bright blue coloration on some of flank scales; anterior portion of flank, just behind pectoral fin, with golden background coloration. Dorsum grayish brown. Ventral surface white between region just after lower jaw and pelvic-fin insertion; iridescent blue from pelvic-fin insertion to caudal peduncle. Side of head predominantly bluish silver, dorsal portion dark brown. Iris silver, light yellow close to pupil. Eye bright silver on dorsal portion. Lower jaw and preorbital region dark brown-gray, forming distinct horizontal stripe. Pectoral fin hyaline; pelvic fin brown with dark chromatophores; anal and dorsal fins with brown transverse bands, most anterior bands restricted to ray insertions, posteriorly bands in sequence extending along fin rays; distinct light brown to gray zone, between transversal bands

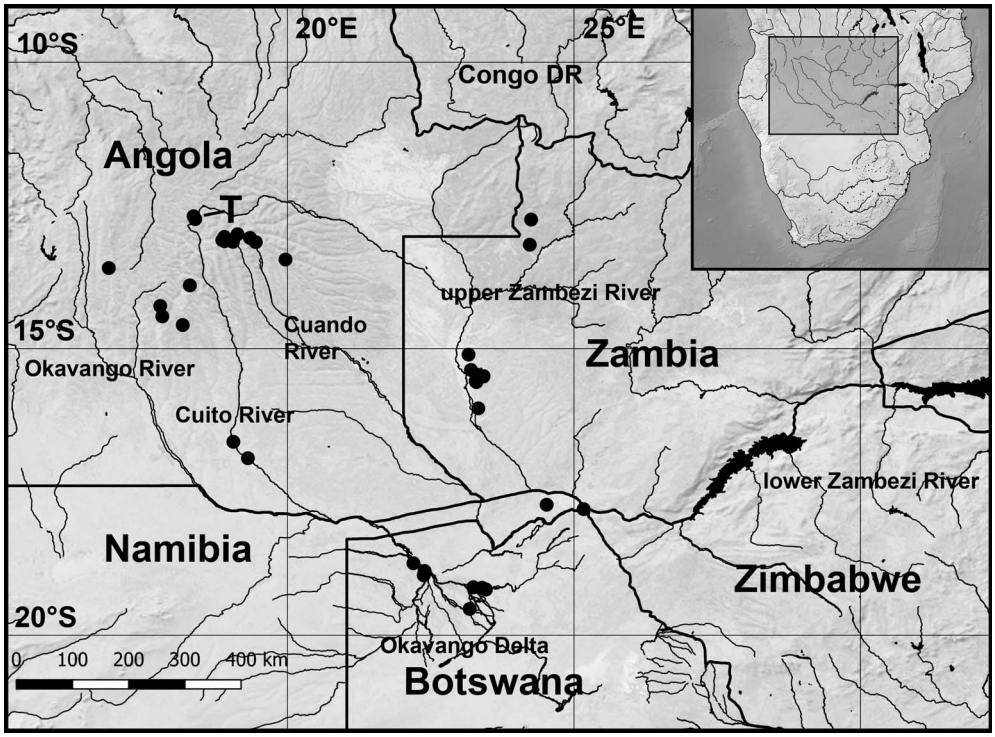

Fig. 10. Distribution of "*Lacustricola*" *pygmaeus* based on the SAIAB specimens examined in the present study. The letter (T) refers to type locality.

and fins border; caudal fin brownish gray with three to four vertical bands, melanophores forming light brown to gray zone close to fin margin.

Females. Side of body gray, with inconspicuous light brown reticulate pattern on flank scales, and bright blue coloration scattered on some of flank scales. Light yellowish brown blotch on region just posterior to pectoral-fin insertion. Dorsum yellowish brown. Ventral surface white between lower jaw and pelvic-fin insertion; iridescent blue from pelvic-fin insertion to end of caudal-fin base; and gray from end of caudal-fin base to caudal peduncle. Side of head predominantly bright bluish silver, ventral portion white, dorsal portion yellowish brown, postorbital region and opercle with distinct bright blue blotch. Iris bluish gray, light yellow close to pupil. Eye bright silver on dorsal portion. Lower jaw and preorbital region dark brown-gray, forming distinct horizontal stripe. Pectoral and pelvic fins hyaline; dorsal and anal fins light yellow-orange with transversal bands. Caudal fin light yellow with 3 to 5 vertical bands.

Distribution and habitat.—"*Lacustricola*" *pygmaeus* is a swamp-dwelling species that does not occur in riverine habitats (Fig. 7B). It is known from grassy patches in shallow swampy areas in the source of the Cuito, Cuanavale, and Okavango Rivers as well as in the source of the Cuando and small upper Zambezi tributaries draining the same Angola plateau region, in a region comprising Angola and Zambia (Fig. 10). The species is also known from lagoons and swamps in the Okavango Delta, Chobe River, in Botswana and Namibia and in swamps adjacent to and to the north of the Barotse floodplains in the upper Zambezi in Zambia, but has not been found on the floodplain itself. It has also been found in the Bukalo Channel in Namibia, which is an overflow channel from the Zambezi that connects to Lake Liambezi in high flood years and is reduced to isolated swampy pools at low water levels.

Etymology.—The epithet *pygmaeus*, from the Latin *pygmaei* (singular *pygmaeus*), is an allusion to the very small or miniature size of "*L.*" *pygmaeus*, the smallest species within the "*L.*" *hutereaui* complex.

***Information on osteology, cephalic pore system, and coloration pattern of* "L." hutereaui.**—Based on the osteological analysis of three cleared and stained specimens of "*L.*" *hutereaui* from Dungu, in the Uele River, a tributary of the Ubangui River, its type locality, and additional specimens from the Ubangui River in the Central African Republic, it was possible to identify informative characters that easily distinguish it from the other species belonging to the "*L.*" *hutereaui* complex. "*Lacustricola*" *hutereaui* is easily distinguished from "*L.*" *chobensis* and "*L.*" *pygmaeus* by the possession of a ventral arm in the posttemporal bone (Fig. 5A; vs. ventral arm absent, Fig. 5B), a sharp ventral process in the maxilla (Fig. 3B, C; vs. ventral process absent, Fig. 3E, F), retroarticular smaller than anguloarticular ventral arm (Fig. 3C; vs. about the same size, Fig. 3F), a lachrymal without a posteroventral extension (Fig. 3A; vs. posteroventral extension present, Fig. 3D), and by a sinuous cleithrum posterodorsal flap (Fig. 5A; vs. flap rounded, Fig. 5B).

The cephalic pore system also proved to be useful in distinguishing "*L.*" *hutereaui* from the other species in the "*L.*" *hutereaui* complex. "*Lacustricola*" *hutereaui* is the only species to present the anterior portion of the infraorbital canal closed, with four pores, the mandibular canal closed, with four pores, and the neuromasts placed in deep grooves (Fig. 4C, D). Based on photographs of live specimens of "*L.*" *hutereaui* from the Central African Republic, it is possible to note the lack of intense bluish green bright metallic coloration in the flank and the presence of an intense orange coloration in the anal, dorsal, and caudal fins (Fig. 9B, C).

DISCUSSION

Recently, morphometric and meristic information from "*L.*" *hutereaui* and its three putative synonyms were provided, suggesting that they could represent distinct species, but, probably due to the low sampling, no further taxonomic decision was made (Nagy and Vreven, 2018). Herein, based on extensive sampling from southern Africa, including the examination of types, the present study provides comprehensive morphological evidence supporting the revalidation of "*L.*" *chobensis*. The status of "*L.*" *schalleri*, until now considered a synonym of "*L.*" *hutereaui*, is revaluated, and a new species, "*L.*" *pygmaeus*, is described.

Despite the lack of specimens of "*L.*" *baudoni* and "*L.*" *schalleri* available for examination in this study, the revalidation of "*L.*" *chobensis*, along with information from Nagy and Vreven (2018) and from the original description of "*L.*" *schalleri* (Scheel and Radda, 1974), allows us to move "*L.*" *schalleri* from the synonymy of "*L.*" *hutereaui* and consider it a junior synonym of "*L.*" *chobensis*. The distinction between "*L.*" *schalleri* and "*L.*" *chobensis* is not evident when comparing the external morphology and coloration pattern, whereas both can be clearly differentiated from "*L.*" *hutereaui* (Nagy and Vreven, 2018). "*Lacustricola*" *schalleri* was described based on only two small specimens (not reaching over 20.0 mm SL) from a coastal river in Mozambique, and Nagy and Vreven (2018) examined no additional specimens. Thus, we consider that the morphometric ranges and meristic variations presented for this species are probably underestimated, and some of them need to be verified, such as the number of transversal scales and circumpeduncular scales that according to Nagy and Vreven (2018) distinguish "*L.*" *chobensis* from "*L.*" *schalleri*. They reported six transversal scales for "*L.*" *schalleri* and seven for "*L.*" *chobensis*, instead of six scales for "*L.*" *chobensis*, as found in this study. We did not have access to specimens of "*L.*" *schalleri* for examination, so it was not possible to check the counts of circumpeduncular scales, which according to Nagy and Vreven (2018) are 12 for "*L.*" *schalleri* and 10 for "*L.*" *chobensis*. With the exception of both aforementioned counts, all other meristics and morphometrics overlap (see Nagy and Vreven, 2018), and they share an identical cephalic lateral line system (see fig. 3 in Scheel and Radda, 1974). In addition, molecular data also support the presence of "*L.*" *chobensis* in a broad region in southern Africa, comprising the Okavango, upper Zambezi, and the Shire River, a lower Zambezi River tributary (Bragança et al., 2020), this later locality close to Mozambique coastal drainages. Thus, we consider "*L.*" *schalleri* a synonym of "*L.*" *chobensis* until populations from the lower Zambezi and Mozambique coastal drainages can be sampled and studied morphologically and molecularly.

For the first time, an osteological character diagnosing the "*L.*" *hutereaui* complex from the other southern African "*Lacustricola*" is presented. A pointed premaxilla ascending process, in which the premaxilla medial surface is slightly convex (Fig. 3B, E), is unique among the southern African "*Lacustricola*" that possess a concave medial surface of the premaxilla (see fig. 6n in Bragança et al., 2020). In addition, osteological information suggests a closer relationship between "*L.*" *chobensis* and "*L.*" *pygmaeus*, since they differ from "*L.*" *hutereaui* by having a retroarticular similar in size to the anguloartiular ventral process (Fig. 3F), a non-ossified ventral arm of the posttemporal (Fig. 5B), a rounded cleithrum posterodorsal bone flap (Fig. 5B), a posteroventral extension on lachrymal (Fig. 3D), and the absence of a ventral sharp process in the maxilla (Fig. 3E, F). The possession of a deep concavity in the quadrate posterior margin (Fig. 3F) is another character useful in distinguishing "*L.*" *pygmaeus* from "*L.*" *chobensis*.

The cephalic pore system was useful not only in distinguishing species from the "*L.*" *hutereaui* complex, but also in suggesting a close relationship between "*L.*" *chobensis*, "*L.*" *pygmaeus*, and "*L.*" *petnehazyi*. The anterior portion of the infraorbital canal is open, with three neuromasts in "*L.*" *chobensis*, "*L.*" *pygmaeus*, and "*L.*" *petnehazyi* (Fig. 4B), whereas it is closed, with four pores in "*L.*" *hutereaui* (Fig. 4D). The mandibular canal is open, with two small neuromasts in "*L.*" *chobensis*, "*L.*" *pygmaeus*, and "*L.*" *petnehazyi* (Fig. 4B) and closed, with four pores in "*L.*" *hutereaui* (Fig. 4D). Also, the neuromasts in "*L.*" *hutereaui* are placed in deep grooves (Fig. 4C, D), whereas in the aforementioned species the neuromasts are placed in shallow grooves or in the same level of head surface (Fig. 4A, B). Nagy and Vreven (2018) listed the presence of an open cephalic supraorbital canal formed by two short, discontinuous grooves with exposed neuromasts and a postorbital and preopercular sensory canal closed, with pores as diagnostic of the "*L.*" *hutereaui* complex. However, the aforementioned character states are present in other southern African species of "*Lacustricola*" (e.g., "*L.*" *johnstoni* and "*L.*" *myaposae*; Bragança et al., 2020). The coloration in life also suggests a close relationship between "*L.*" *chobensis*, "*L.*" *pygmaeus*, and "*L.*" *petnehazyi*, which share an intense bluish green bright metallic coloration in the flank, absent in "*L.*" *hutereaui* (Fig. 9B, C), that on the other hand can be readily distinguished from the first three species by an intense orange coloration in the anal, dorsal, and caudal fins.

Despite no mention of the presence of miniature species among the southern African "*Lacustricola*" before, all three species, "*L.*" *chobensis*, "*L.*" *pygmaeus*, and "*L.*" *petnehazyi* are considered to be the only miniature species in "*Lacustricola*," since the maximum adult size is below 26.0 mm SL, an arbitrary threshold first proposed to identify miniature fishes in the Neotropics (Weitzman and Vari, 1988). In addition, the non-ossified ventral arm of the posttemporal, the absence of a ventral sharp process in the maxilla, and the aforementioned simplification of the cephalic pore system support them as miniatures, since the loss and incomplete formation of bone structures as well as simplification in the pore systems are commonly associated with miniaturization in fishes (Weitzman and Vari, 1988; Costa and Le Bail, 1999). Here we tentatively consider that the body size reduction seen in all three species is the result of a single miniaturization event that probably happened in the putative common ancestor shared among them.

The description of a new species from the "*L.*" *hutereaui* complex and the revalidation of "*L.*" *chobensis*, both inhabiting southern Africa, indicate that diversification did occur in the region, opposing the idea of a widespread "*L.*" *hutereaui*. The recent multilocus phylogenetic analysis of the Procatopodidae (Bragança and Costa, 2019) and the haplotype phylogeny of the southern African "*Lacustricola*" (Bragança et al., 2020) indicate a basal position for the "*L.*" *hutereaui* clade, with its origin dating back to the late Miocene and early Pliocene (around 5.4 mya). Thus, considering all main palaeogeographic and climatic events during that period, there are probably other undescribed species in southern Africa and in the southern Congo

tributaries, such as the population from the upper Lualaba River, as shown in Bragança et al. (2020). However, a further, more comprehensive study including molecular information from the type locality of "*L.*" *hutereaui* is critical for investigating the diversity of the "*L.*" *hutereaui* complex, especially in the Congo River basin. It is likely that future studies of the "*L.*" *hutereaui* complex could contribute significantly to the understanding of the evolution of the southern African landscape.

MATERIAL EXAMINED

"*Lacustricola*" *chobensis*: SAIAB 30007, holotype (x-ray examined), 24.6 mm SL, Chobe River, below rapids, 3 miles from Kasane, Botswana, 17°49′0.12″S, 25°8′60.00″E; SAIAB 30008, 5 paratypes, 11.4–14.5 mm SL, same data as holotype; SAIAB 19536, 10, 16.0–21.3 mm SL, Boro River, approximately 200 meters above Nxaragha Lagoon, Okavango Delta, Botswana, 19°31′59.88″S, 23°7′59.88″E; SAIAB 21496, 1, 18.2 mm SL, Nxaragha Lagoon, Okavango Delta, Botswana, 19°31′59.88″S, 23°7′59.88″E; SAIAB 37348, 10, 16.0–16.9 mm SL, Kataba creek just south of Mongu, Barotse floodplain, West Province, Zambia, 15°50′0.78″S, 23°19′59.91″E; SAIAB 49229, 3, 15.9–18.4 mm SL, Chobe River, Namibia, 17°47′S, 25°9′E; SAIAB 66784, 14 (4 CS), 13.7–22.4 mm SL, Paradise Pools, Maunachira River, Moremi, Okavango, Ngamiland, Botswana, 19°12′15″S, 23°27′36″E; SAIAB 66934, 59, 9.7–25.9 mm SL, Sepopa, Du Plessis's Camp, Okavango Delta, Northern Panhandle, Ngamiland, Botswana, 18°44′39″S, 22°11′47″E; SAIAB 68657, 3, 12.2–15.5 mm SL, Paradise Lagoon, Hippo pool Makoro channel, Okavango Delta, Moremi Wildlife Park, Ngamiland, Botswana, 19°11′57″S, 23°27′36″E; SAIAB 71199, 14, 10.4–21.0 mm SL, drying pools near Wambeya Lagoon, upper Zambezi River, Zambia, 16°9′3″S, 23°17′17″E; SAIAB 72732, 80, 9.5–16.7 mm SL, upper Zambezi River, Zambia, 16°9′6″S, 23°17′40″E; SAIAB 72928, 7, 13.7–16.7 mm SL, Sianda River, upper Zambezi, Zambia, 15°34′49″S, 23°17′42″E; SAIAB 72950, 82, 11.9–16.2 mm SL, Kataba River, upper Zambezi, Zambia, 15°34′2″S, 23°17′0″E; SAIAB 73234, 19, 14.1–16.8 mm SL, area below road bridge, Luampa River, upper Zambezi, Zambia, 14°57′27″S, 24°20′22″E; SAIAB 101066, 3, 17.0–20.4 mm SL, Boa Fé Lagoon, Jamba, Okavango, Província do Cuando Cubango, Angola, 17°19′44.4″S, 20°8′2.6″E; SAIAB 101071, 18 (5 CS), 12.3–19.2 mm SL, Jamba camp site 2, Okavango, Província do Cuando Cubango, Angola, 17°32′4.4″S, 23°11′20.7″E; SAIAB 101089, 5, 18.8–22.6 mm SL, Boa Fé Flood plain, Jamba, Okavango, Província do Cuando Cubango, Angola, 17°28′3.0″S, 23°4′47.1″E; SAIAB 119161, 6, 16.0–18.1 mm SL, 500 m upstream of Chikwanda tributary confluence, North West, Zambia, 12°19′45.1″S, 25°08′23.5″E; SAIAB 189974, 6, 13.9–21.0 mm SL, Cuando River upstream of bridge, Namibia, 17°46′18.24″S, 23°20′24.94″E; SAIAB 190383, 1, 21.5 mm SL, Kalimbeza road, Caprivi, Namibia, 17°33′25″S, 24°30′24″E; SAIAB 190406, 1, 15.7 mm SL, Kataba River, upper Zambezi, Western Province, Zambia, 15°34′02.6″S, 23°17′00″E; SAIAB 193548, 6, 15.5–17.0 mm SL, E10 Nkomba, Zambia, 12°27′13.27″S, 24°56′38.61″E; SAIAB 193588, 78, 11.1–18.2 mm SL, Liuwa Plain National Park Pans, upper Zambezi, Zambia, 14°41′20″S, 22°36′55″E; SAIAB 193609, 1, 12.6 mm SL, lily pad backwaters and slow stream in large dambo, upper Zambezi, Zambia, 16°13′26.5″S, 23°20′26.5″E; SAIAB 193622, 2, 10.9–12.6 mm SL, Luanginga River, upper Zambezi, Zambia, 14°32′9.32″S, 22°15′3.87″E; SAIAB 193673, 2, 13.4–14.4 mm SL, Lungwebungu River, upper Zambezi, Zambia, 14°0′1.26″S, 22°38′59.31″E; SAIAB 194902, 7, 13.2–18.1 mm SL, Kalimbeza culverts, Caprivi, Namibia, 17°33′24″S, 24°31′05″E; SAIAB 200458, 3, 9.9–14.2 mm SL, Kalimbeza culverts, Caprivi, Namibia, 17°33′22″S, 24°31′08″E; SAIAB 200765, 5, 16.3–24.4 mm SL, edge of Okavango River downstream of Bwabwata National Park, Namibia, 18°13′20.6″S, 21°45′09.9″E; SAIAB 200774, 6, 16.3–22.4 mm SL, Okavango River, Giant Baobab site, Bwabwata National Park, Namibia, 18°12′24.4″S, 21°44′43.6″E; SAIAB 200797, 13, 11.8–18.0 mm SL, Pond/channel on Road from Nambwa camp, Bwabwata National Park, Namibia, 17°52′15.4″S, 23°18′49.3″E; SAIAB 200803, 11 (2 CS), 13.5–22.4 mm SL, Road to Kalimbeza, 20 km South of Katima, Namibia, 17°33′26.5″S, 24°27′19.2″E; SAIAB 200814, 4, 10.5–20.3 mm SL, farm in swamp area along the road to Kalimbeza, Namibia, 17°33′29.8″S, 24°27′29.0″E.

"*Lacustricola*" *hutereaui*: MRAC P.182191–205, 15 (3 CS), 18.6–23.1 mm SL, Gangala na Bodio, Dungu River, Uele drainage, Congo basin, Democratic Republic of Congo, 03°41′N, 29°08′E; SAIAB 78314, 30 (5 CS), 13.4–22.7 mm SL, Baketa stream, Bambari River, Ouaka, Central African Republic, 06°9′51″N, 20°42′52″E; SAIAB 78317, 20, 15.7–24.1 mm SL, Baketa stream, Bambari River, Ouaka, Central African Republic, 06°12′24″N, 20°41′17″E.

DATA ACCESSIBILITY

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