AMERICAN MUSEUM NOVITATES

Number 3992, 16 pp. November 15, 2022

Systematic review and cranial osteology of *Petersius* with redescription of *P. conserialis* (Teleostei: Alestidae) from the Rufiji and Ruvu rivers of Tanzania

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ABSTRACT

We review the systematics of the monotypic alestid genus *Petersius* and provide a taxonomic redescription of *P. conserialis* from eastern Tanzania. Morphological investigation includes direct observation and examination of radiographed and μCT-scanned data from type and non-type specimens. We delimit the taxon's geographic distribution along the lowland regions of the Rufiji and Ruvu river basins in Tanzania and provide information on ecology, sexual dimorphism, and ontogenetic variation. *Petersius* is herein diagnosed by the possession of a unique cuspidation patterning of the inner-row premaxillary dentition and a distinctively shaped anterodorsal margin of the supraoccipital crest. It shares with some species of *Phenacogrammus* a sigmoid-shaped process on the dorsal margin of the second infraorbital, a feature lacking in other alestid taxa. Additional features of potential utility for ongoing investigation of relationships among alestid genera include the possession of contralateral premaxillae separated by the anteromedial process of the mesethmoid and without interdigitations connecting the medial surfaces of the premaxillae; four, occasionally five or six, small outer-row premaxillary teeth implanted alternately with those of the inner row; a dentary lacking a pair of conical inner-row teeth proximal to the symphysis; a dorsal posttemporal fossa that is smaller than the ventral fossa; a median third posttemporal fossa located entirely within the epioccipital; a truncate dorsomedial cranial fontanel; and a complete circumorbital series forming an uninterrupted ring around the orbit in adult specimens.

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 ISSN 0003-0082

INTRODUCTION

The characiform family Alestidae, popularly known as African tetras, robbers, and tigerfishes, are present throughout tropical sub-Saharan Africa with notable species richness in the Congo basin and West Africa (Zanata and Vari, 2005; Stiassny et al., 2011). Morphological disparity within the family is noteworthy with species ranging in size from miniature forms such as *Lepidarchus* (max. size 2.1 cm standard length, SL) to the giant tigerfish *Hydrocynus goliath* (1.3 m SL). Currently 118 species are allocated in 19 recognized genera: *Alestes* (7 species), *Alestopetersius* (10), *Arnoldichthys* (1), *Bathyaethiops* (6), *Brachypetersius* (6), *Brycinus* (29), *Bryconaethiops* (5), *Bryconalestes* (5), *Clupeocharax* (1), *Hemigrammopetersius* (2), *Hydrocynus* (5), *Ladigesia* (1), *Lepidarchus* (1), *Micralestes* (16), *Nannopetersius* (3), *Petersius* (1), *Phenacogrammus* (11), *Rhabdalestes* (7), and *Tricuspidalestes* (1).

Despite considerable progress toward resolving inter- and intrageneric relationships within Alestidae, much uncertainty remains (Murray and Stewart, 2002; Hubert et al., 2005; Zanata and Vari, 2005; Schaefer, 2007; Arroyave and Stiassny, 2011; Melo et al., 2022). One taxon of particular interest is the monotypic genus *Petersius*, the nominate genus of a large grouping of dwarf alestids designated as Petersiini (Poll, 1967). Recent phylogenetic studies using anatomical and/or genetic data indicated the paraphyly of Petersiini with small-sized species variously placed across the tree of Alestidae (Murray and Stewart, 2002; Calcagnotto et al., 2005; Zanata and Vari, 2005; Arroyave and Stiassny, 2011) suggesting uncertainty for the phylogenetic placement of *Petersius*.

Petersius conserialis was originally described from specimens collected during expeditions of the German naturalist Franz Stuhlmann in East Africa (Hilgendorf, 1894). The species was based on five syntypes deposited at the Museum für Naturkunde, Berlin (ZMB), and later at the Carnegie Museum of Natural History, Pittsburgh, and the Field Museum of Natural History, Chicago (FMNH) (Zarske, 2011; Fricke et al., 2022). The original description was brief with little information on morphological features of the taxon, and although some subsequent publications included morphometric and meristic data for the syntypes (Boulenger, 1909; Poll, 1967; Zarske, 2011), they added little to our knowledge of morphological attributes of the species. Based on examination of syntypes, Zanata and Vari (2005) included *Petersius* in their morphology-based study of Alestidae, but a limited number of available specimens and the lack of cleared and stained material resulted in 25% noncoded characters for the taxon in their matrix. Consequently, their placement of *Petersius* as an early-diverging genus, and sister to all African genera except *Hydrocynus* and *Arnoldichthys*, relies on limited externally visible features and radiographs of the type material. Additionally, there remains a lack of information on the distribution, ontogeny, coloration, sexual dimorphism, and much potentially phylogenetically informative morphological character data.

Our redescription is based on direct examination of one syntype, photographs of the other syntypes, and examination of 20 nontype juvenile and adult specimens from the Canadian Museum of Nature, Ottawa (CMN). We employed a combination of morphometrics, meristics, radiographs, and μCT-scan images to redescribe *P. conserialis* and investigate key anatomical features potentially relevant to its phylogenetic placement within the

Alestidae. We also provide information on sexually dimorphic characters, elucidate the exact type locality, and provide the known geographic distribution of *P. conserialis* across eastern Tanzania.

MATERIALS AND METHODS

Morphometrics and meristic counts follow Stiassny et al. (2021) with the following additions: dorsal-fin origin to hypural flexion, dorsal-fin origin to anal-fin origin, dorsal-fin origin to pelvic-fin origin, dorsal-fin origin to pectoral-fin origin, longest pectoral-fin length, longest pelvic-fin length, longest dorsal-fin length, postorbital length, and minimum interorbital width. Measurements were rounded to the nearest 0.1 mm and presented as percentages of standard length (SL) or head length (HL). Frequency values are in parentheses after each respective count; asterisks denote values of the syntype FMNH 54287. Counts of vertebrae, unbranched-fin rays and other skeletal features were taken from radiographs. Three specimens ranging from juvenile to adult were μCT scanned: CMN-FI 1981.0177.4 (39.7 mm SL), CMN-FI 1981.196.7 (70.0 mm SL), and syntype FMNH 54287 (99.0 mm SL). Scans were made at the Microscopy and Imaging Facility at AMNH using a GE Phoenix v|tome|x with a 240 kV Nano Tube (General Electric, Fairfield, CT). Scan resolution ranged from 15.7 to 25.2 μm, with beam energy set at 110 kV and 166 mA. Scans were reconstructed using Phoenix datos|x (General Electric, Wunstorf, Germany) and rendered using VGStudio Max 3.5.1 (Volume Graphics, Heidelberg, Germany). Database for the topography map is *TessaDEM* (https://tessadem.com/) based on *Copernicus DEM* (https://spacedata.copernicus.eu/web/cscda/dataset-details?articleId=394198), *NASADEM* (https://lpdaac.usgs.gov/documents/1318/NASADEM_User_Guide_V12.pdf) and *MERIT DEM* (Yamazaki et al. 2017; https://agupubs.onlinelibrary.wiley.com/doi/full/10.1002/2017GL072874). Museum abbreviations: AMNH: American Museum of Natural History, New York; CMN-FI: Canadian Museum of Nature, Ottawa; FMNH, Field Museum of Natural History, Chicago; ZMB: Museum für Naturkunde, Berlin.

Petersius Hilgendorf, 1894

Type species: *Petersius conserialis* Hilgendorf, 1894. Type by monotypy.

Diagnosis: *Petersius* is diagnosed by a unique cuspidation pattern of the inner row premaxillary dentition with the cusps of the cutting-edge oriented buccally (vs. lingually oriented in all other alestids), and the possession of a distinctively shaped margin of the supraoccipital with a steep anterodorsal convexity at the junction of the parietals followed by a dorsomedial concavity on the surface of the supraoccipital.

Description. Corresponds to the description of the type species *Petersius conserialis* Hilgendorf, 1894.

Etymology. In naming *Petersius* Hilgendorf (1894) honored the naturalist and curator Wilhelm C.H. Peters of the Museum für Naturkunde, Berlin.

Petersius conserialis Hilgendorf, 1894

Figures 1–4, table 1

Petersius conserialis Hilgendorf, 1894: 173 [original type locality: "Kinganiflusse in Deutsch-Ostafrika" (= Kingani River in German East Africa), Tanzania].
Pfeffer, 1896: 44 [short description].
Boulenger, 1909: 233–234 [morphometrics; meristic, data from types].
Myers, 1929: 5 [key to genera; notes; restriction of genus *Petersius*].
Hoedeman, 1951: 5 [key to genera and species].
Poll, 1967: 28 [description; morphometrics; meristic data; distribution; figures of specimen and dentition].
Matthes, 1975: 171 [key to freshwater fishes; Tanzania].
Géry, 1977: 50 [remarks].
Paugy, 1984: 140–183 [synonym list, genus, species]
Ibarra and Stewart, 1987: 64 [catalog of types, FMNH].
Géry, 1995: 40 [key, comments on cranial fontanel].
Murray and Stewart, 2002: 1892 [osteology; phylogeny].
Zanata and Vari, 2005: 100, 117 [character description; morphological phylogeny].
Zarske, 2011: 64 [catalog of types; description of ZMB types of *Petersius*].
Dueck, 2020: 55–99 [ontogeny; osteology].

Diagnosis: As for *Petersius*.

Description: Morphometric data summarized in table 1. Medium-sized species (maximum observed size 137.0 mm SL), with general appearance as in figure 1. Body moderately elongate, dorsal head profile concave from snout to supraoccipital, convex to dorsal-fin origin, slightly convex along dorsal-fin base to adipose fin, and slightly concave from adipose fin to origin of caudal fin. Ventral body profile convex from anterior tip of lower jaw to end of anal-fin base, slightly concave to caudal fin. Caudal peduncle longer than deep. Adipose eyelid weakly developed, restricted to thin band immediately anterior to orbit. Snout shorter than orbital diameter. Nostrils closely aligned, anterior nostril circular, posterior nostril semi lunate.

Lower jaw slightly prognathous, mouth superior, horizontally aligned with dorsal margin of pupil. Teeth in both jaws pluricuspid and incisiform with reduced buccal shelves. Dentary with 4* (21) outer row teeth, median tooth frequently with five cusps, second and third teeth with seven cusps, fourth tooth markedly smaller than adjacent tooth. Inner row of conical teeth proximate to dentary symphysis absent in all specimens (fig. 2E). Contralateral premaxillae separated by anteromedial process of mesethmoid and without interdigitations connecting medial surfaces (fig. 3C). Premaxilla with two rows of pluricuspid teeth. Outer premaxillary row usually with 2* (13) tricuspid teeth, but number variable 0 (2), 1 (3), or 3 (3), even variable contralaterally in a few specimens. Regardless of number, outer row premaxillary teeth always implanted above and between inner row teeth (i.e., alternating). Inner premaxillary row with 4* (21) teeth, each with 7 cusps. Series of cutting-edge cusps of inner row premaxillary teeth located along buccal (vs. lingual) face of each tooth (fig. 3C, see also Discussion). Four replace-

FIGURE 1. *Petersius conserialis*: **A**. FMNH 54287, syntype, 99.0 mm SL, male, Kingani River (= Ruvu River), Dunda, Tanzania. **B**. CMN-FI 1981.0201.1, nontype, female, 109.5 mm SL, Rufiji River, Lake Ruwe, Tanzania. Profile of anal fin indicated by dotted lines. Scale bar = 1 cm.

ment teeth in both premaxillary and dentary replacement trenches. Maxilla edentulous, ascending process elongate and pointed, without terminal bifurcation (fig. 2F).

Distal margin of dorsal fin straight, second unbranched and first branched fin rays longest. Dorsal-fin rays ii,8* (21), first unbranched ray very short. Distal margin of pectoral fin straight or slightly rounded. Adpressed pectoral fin reaching or surpassing pelvic-fin origin. Pectoral-fin rays ii,13 (10), ii,14 (8), or ii,15* (3). Pelvic fin pointed, adpressed pelvic fin reaching two to four scales short of anal-fin origin. Pelvic-fin rays ii,7 (1), ii,8 (6), ii,9* (13), or ii,10 (1). Caudal fin forked. Adipose fin present, tall with narrow base. Anal fin emarginate, anteriormost branched rays more than twice length of ultimate ray. Anal-fin rays iii,18* (9), iii,19 (11), or iii,20 (1), first unbranched ray very short.

Lateral line scales from supracleithrum to hypural joint 30 (3), 31* (6), 32 (5), or 33 (7). Anteriormost 6 scales of lateral line descending steeply to below midlateral line. Last 3–4 pored scales slightly ascending to midlateral body plane. Scales posterior to hypural joint 2 (10) or 3* (11). Scales in transverse series from lateral line to dorsal-fin origin 6.5 (9) or 7.5* (12). Scales in transverse series from lateral line to pelvic-fin origin 2* (10) or 2.5 (11). Middorsal series from supraoccipital tip to dorsal-fin origin 13 (1), 14 (8), 15* (8), 16 (2), or 17 (1). Circumpeduncular scales 10* (20) or 11 (1). Axial scale present, extending over basal third of pelvic fin. First gill arch with 11* (20) or 12 (1) epibranchial rakers and 18 (1), 19 (1), 20* (6), 21 (12), or 23 (1) rakers on ceratobranchial and hypobranchial arches. Total vertebrae 36 (1) or 37 (21). Supraneurals 8 (12), first supraneural associated with fourth vertebra.

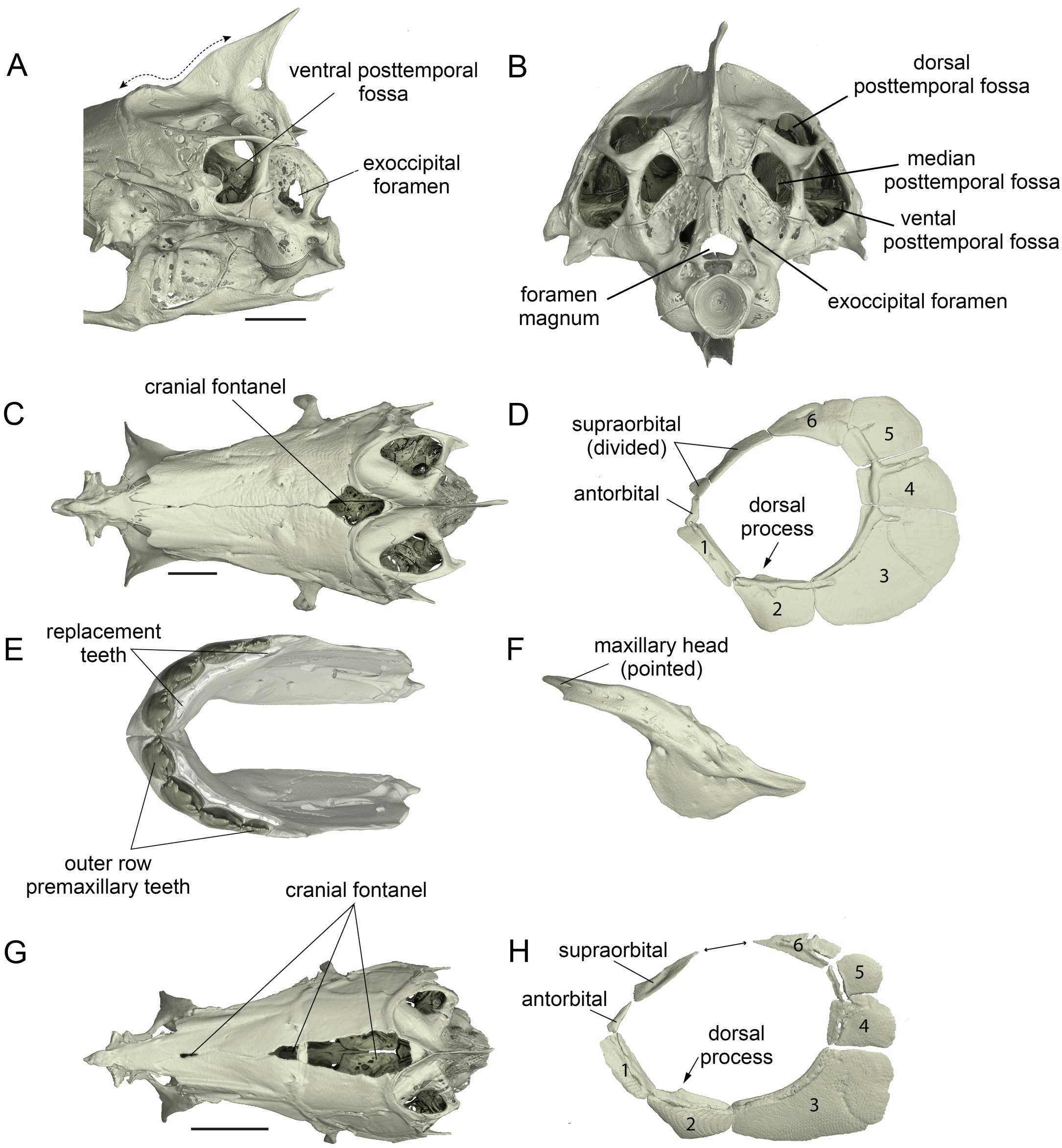

FIGURE 2. *Petersius conserialis*, FMNH 54287, 99.0 mm SL: **A**. Posterolateral portion of neurocranium; **B**. posterior view of neurocranium; **C**. dorsal view of neurocranium; **D**. circumorbital series; **E**. lower jaws in dorsal view; **F**. isolated maxilla in lateral view. CMN-FI 1981.0177.4, 39.7 mm SL: **G**. Dorsal view of neurocranium; **H**. circumorbital series. Scale bars: A, C = 2.5 mm; G = 2 mm.

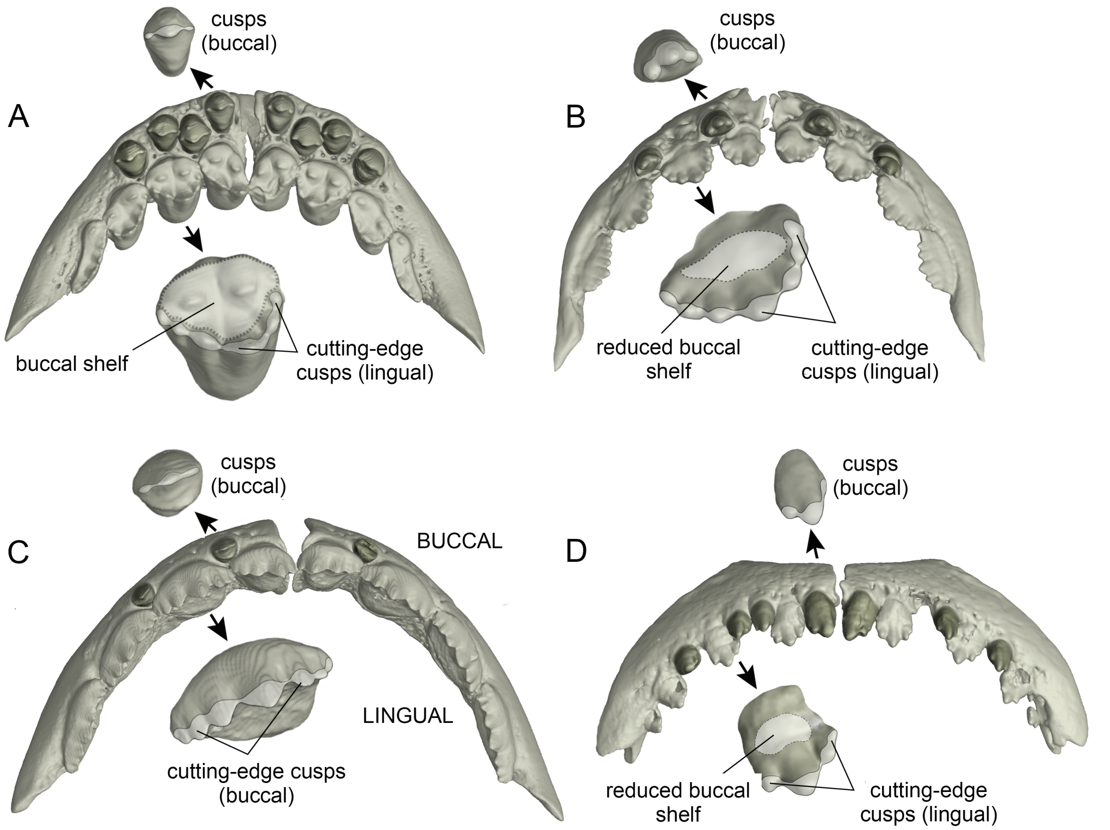

FIGURE 3. Premaxillae and dentition in ventral view. **A**. *Brycinus nurse*, AMNH 215629; **B**. *Nannopetersius ansorgii*, AMNH 263093; **C**. *Petersius conserialis*, FMNH 54287; **D**. *Arnoldichthys spilopterus*, AMNH 216017. Outer row teeth darkened.

Additional Osteological Features: Supraoccipital distinctively shaped with steep anterodorsal convexity at junction of parietals and supraoccipital followed by dorsomedial concavity on surface of the crest (fig. 2A). Three pairs of posttemporal fossae present (fig. 2 A, B). Median posttemporal fossae located entirely within epioccipital. Dorsal posttemporal fossae (bounded by the supraoccipital, parietals, and epioccipitals) somewhat smaller than ventral posttemporal fossae (bounded by the epioccipitals and pterotics). Exoccipital foramen well developed. Dorsomedial cranial fontanel present, size correlated with developmental stage. In juveniles smaller than 60 mm SL, fontanel extends anteriorly from posterior region of frontal to anterior margin of supraoccipital. In larger specimens, fontanel is restricted to a small, ovoid opening extending just in front of frontoparietal ridge to anterior margin of supraoccipital (fig. 2C, G). Circumorbital series complete, in adults forming an uninterrupted ring around orbit, in juveniles (ca. 40–60 mm SL) supraorbital separated from 6th infraorbital by wide gap (fig. 2D, H). Supraorbital elongate, slightly sigmoid, and without ventral process. Syntype FMNH 54287 with supraorbital segmented into two elements (fig. 2D). Anterior element in contact with antorbital, posterior element contacts 6th infraorbital. All other examined specimens with

FIGURE 4. *Petersius conserialis*, female, live photograph, not preserved, Lake Nzerakera, flooded area at rainy season, Rufiji River, Tanzania, 4 January 2018. Photography: Fraser Gear.

a single ossification of supraorbital. Whether a bipartite supraorbital represents an autapomorphy of an isolated lineage from Ruvu River or is an individual anomaly cannot be determined without detailed examination of remaining syntypes. Second infraorbital with a pronounced, sigmoid-shaped process on the dorsal margin (fig. 2D, H see also Discussion).

Coloration: In preservation, overall body coloration brownish yellow, darker dorsally than ventrally, often with overlay of silver iridescence (fig. 1). Small, vertically elongated humeral blotch of pigmentation around fourth and fifth scale of midlateral surface of body, faint in most specimens but more evident in larger individuals. Faint deep-lying longitudinal stripe along midlateral surface from supracleithrum to anterior margin of caudal peduncle. Posterior region of caudal peduncle with blotch of dark pigmentation, circular to ovoid in shape extending to proximal margin of middle caudal-fin rays. Distal caudal-fin lobes with dark margins. Adipose fin outlined by small dark chromatophores, more so on dorsal margin.

In life overall body coloration iridescent silver, darker dorsally (fig. 4). Humeral and caudal blotch visible but overlain by silver iridescence. Dorsal, caudal, and anal fins yellowish to dark orange, distal margin of caudal fin darker. Adipose fin yellowish. Pectoral and pelvic fins hyaline; first unbranched pectoral-fin ray slightly darker.

Sexual dimorphism: Specimen FMNH 54287 was the single male analyzed, clearly identified by the pronounced sexual dimorphism typical of many alestids. The specimen has the fifth through ninth rays of the anal fin expanded and forming a distinct median anal-fin lobe (fig. 1A). Females have straight-edged anal fin with no median lobe (figs. 1B, 4).

Ecology: *Petersius conserialis* has been collected in sandy river courses and floodplain lakes with bushy shorelines with forested or grassy margins. The species was found recently (2018) in a seasonally flooded area of the Rufiji River in shallow water with submerged vegetation (Fraser Gear, personal commun.). *Petersius conserialis* appears to be endemic to lowland

TABLE 1. Morphometric data for *Petersius conserialis.* Range includes syntype FMNH 54287 and 20 non-type specimens. SD = standard deviation.

	Syntype	n	Mean	Range	SD
Standard length (mm)	99.0	21		37.0–137.0	–
% SL					
Greatest body depth	30.3	21	31.7	29.1–37.3	2.5
Snout to dorsal-fin origin	55.3	21	56.3	55.1–57.9	0.8
Snout to pectoral-fin origin	28.6	21	30.3	27.5–32.6	1.4
Snout to pelvic-fin origin	51.3	21	52.5	50.8–54.7	1.2
Snout to anal-fin origin	75.4	21	75.2	73.5–78.0	1.1
Dorsal-fin origin to hypural joint	47.3	21	47.2	45.0–49.8	1.2
Dorsal-fin origin to anal-fin origin	33.8	21	35.4	32.6–40.3	2.2
Dorsal-fin origin to pelvic-fin origin	30.3	21	31.3	27.7–37.4	2.9
Dorsal-fin origin to pectoral-fin origin	41.1	21	39.4	36.2–44.2	2.2
Caudal-peduncle depth	11.0	21	10.7	9.8–11.7	0.5
Pectoral-fin length	24.1	21	24.2	23.0–25.7	0.8
Pelvic-fin length	20.4	21	20.6	17.8–25.0	1.4
Dorsal-fin length	25.8	21	25.4	22.3–26.9	1.2
Head length	28.7	21	29.7	25.9–32.1	1.8
% head length					
Snout length	21.9	21	20.8	18.4–23.4	1.4
Orbital diameter	31.4	21	35.5	31.4–39.7	2.3
Postorbital length	49.0	21	44.5	39.7–49.8	2.8
Interorbital width	26.1	21	24.1	21.0–26.6	1.6

regions, with the highest elevation point at Mkalinzu sands of the Rufiji River at approximately 95–100 m asl (CMN-FI 1981-0174.4). The lowest altitudinal record (5 m asl) is at the type locality of Mtoni Fort approximately 10 km from the Ruvu River mouth in the Indian Ocean. The alestids *Alestes stuhlmannii*, *Brycinus affinis*, *B. imberi*, *B. lateralis*, *Hemigrammopetersius barnardi*, and *Hydrocynus vittatus* were collected in sympatry in the Rufiji River basin (CMN-FI records; www.fishnet2.net).

Distribution and Conservation: Hilgendorf (1894) described *Petersius conserialis* based on five specimens collected in eastern Tanzania. The original description mentioned "Kinganiflusse in Deutsch-Ostrafrika," and subsequent authors indicated the type locality as the Kingani River at Dunda (Boulenger, 1909; Poll, 1967; Zarske, 2011). The Kingani River is an alternative name for the southern Ruvu River, with annotations of Stuhmann's 1890 expedition indicating Dunda near the current Mtoni Fort, west of Bagamoyo, eastern Tanzania (Turner et al., 2021). Thus, we herein consider the type locality of *Petersius con-*

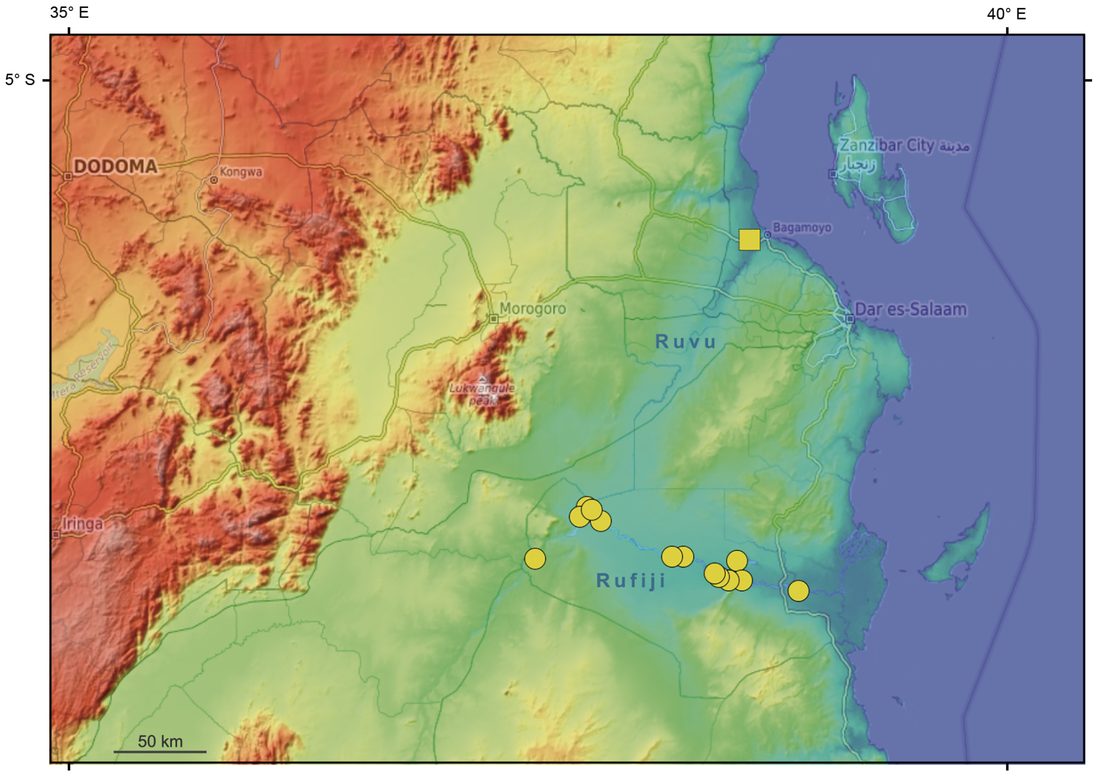

FIGURE 5. Map of eastern Tanzania showing museum records of *Petersius conserialis* (yellow circles) in the Rufiji and Ruvu river basins. Yellow square denotes type locality in the lower Ruvu River.

serialis as the Ruvu River near Mtoni Fort, approximately 06° 28′ 04.8″S 38° 50′ 31.2″E, Magomeni, Tanzania.

Petersius conserialis is seemingly endemic to lowland regions of the Rufiji and Ruvu rivers in the Pwani Region of eastern Tanzania (fig. 5). Within the Rufiji basin the species has been reported from lakes Lugongwe, Chemchem, Siwandu, Ruwe, Tagalala, and Nzerakera. Although the Ruvu River is apparently in good condition, the Rufiji basin has been affected by loss of hydrological connectivity, sediment trapping, and construction of hydropower dams (Hamerlynck et al., 2011; Duvail et al., 2014), which are likely to impact some populations of *P. conserialis*.

Taxonomic Remarks: Following the ICZN Recommendation 74G, lectotypes should not be designated for curatorial convenience. Therefore, we do not designate lectotype and paralectotypes keeping the syntype series unaltered. Noteworthy, one of the syntypes from ZMB 13535 was sent to Carnegie Museum in 1910, and posteriorly to FMNH 54287.

Materials examined: *Petersius conserialis*, all from Pwani Region, Tanzania: FMNH 54287, syntype of *Petersius conserialis*, 99.0 mm SL, Kingani at Dunda, Stuhlmann (approximate locality: Ruvu River, Magomeni, 06° 28′ 04.8″S 38° 50′ 31.2″E), 1µCT scan. – CMN-FI 1981-0177.4, 9, 37.0–49.4 mm SL, Lake Siwandu (Nzerakera), northwest corner, internal delta region of upper Rufiji River floodplain, Mwaseni, 7° 40′ 00″S 38° 07′ 00″E, 17 Jul 1979, Hopson et al., 1µCT scan. – CMN-FI 1981-0194.4, 1, 55.0 mm SL, Rufiji River, north shore, at Ndundu ferry landing,

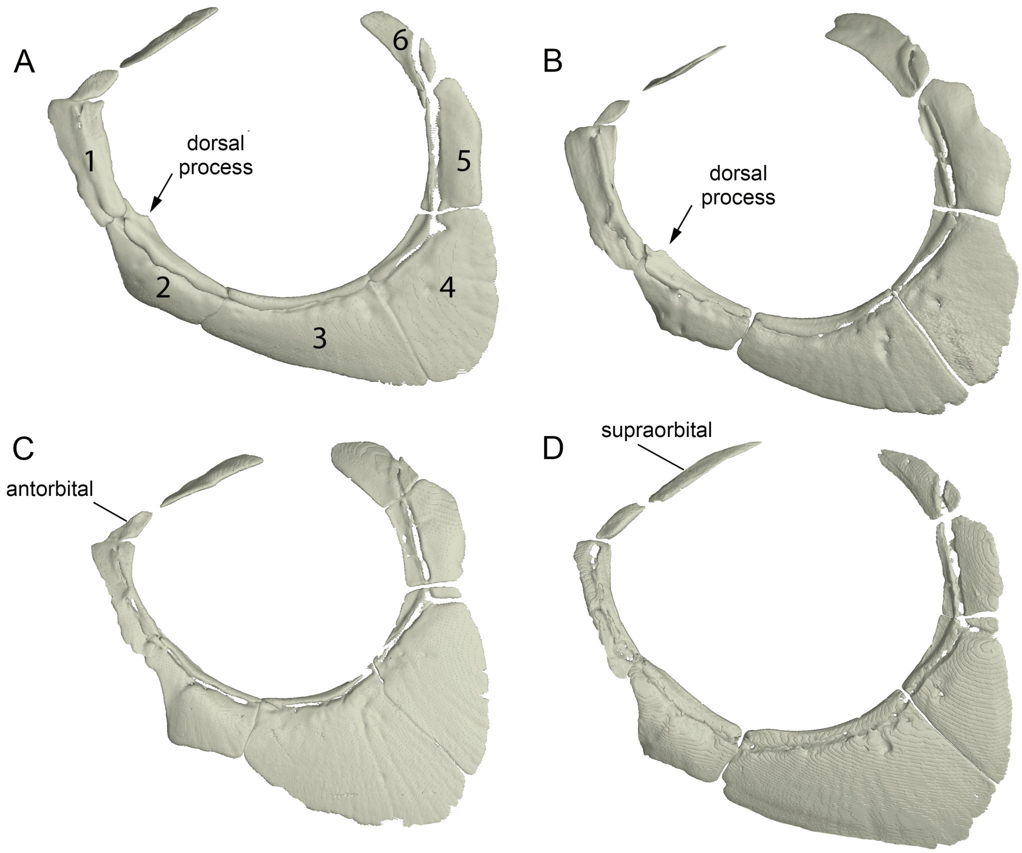

FIGURE 6. Circumorbital series of **A**. *Phenacogrammus deheyni* AMNH 252208, **B**. *P. aurantiacus* AMNH 274780, **C**. *P. major* AMNH 236514, **D**. *P. urotaenia* AMNH 253971.

Ikwiriri, 08° 02′ 00″S 39° 02′ 00″E, 31 Jul 1979, Hopson et al. – CMN-FI 1981-0196.7, 6, 51.1–70.0 mm SL, Rufiji River, south bank near Utete, muddy creek below Rubada camp and courthouse, Utete, 07° 58′ 00″S 38° 47′ 00″E, 01 Aug 1979, Hopson et al., 1µCT scan. – CMN-FI 1981-0201.1, 4, 106.0–137.0 mm SL, Lake Ruwe, 2 km southeast of Mkongo, south shore, northern Rufiji River floodplain, Mkongo, 07° 53′ 00″S 38° 46′ 00″E, 28 Jul 1979, Bernacsek et al.

Comparative materials examined: *Alestes macrophthalmus*: AMNH 217360, Malagarazi River, Tanzania. – AMNH 245441, 1µCT scan, Sangha River at Senga Bato, Republic of Congo. – *Alestopeterius dentex*: AMNH 226449, 1C&S, Niger River, Benin. – *Alestopetersius caudalis*: AMNH 263304, Congo River, Boma, Democratic Republic of Congo. – *Alestopetersius hilgendorfi*: AMNH 244114, 1µCT scan, Yenge River at Boyenga, Democratic Republic of Congo. – *Arnoldichthys spilopterus*: AMNH 233398, Lower Niger River, Nigeria. – AMNH 216017, 1µCT scan, New Calabar River, Nigeria. – *Bathyaethiops atercrinis*: AMNH 253502, 2C&S, 1µCT scan, Lekoumou River, Republic of Congo. – *Bathyaethiops greeni*: AMNH 252261, Salonga National Park, Democratic Republic of Congo. – *Bathyaethiops breuseghemi*: AMNH 269023, 1μCT scan, Lulua River, Democratic Republic of Congo. – *Brachypetersius altus*: AMNH 252504, Kwilu River, Democratic Republic of Congo. – AMNH 259243, 2μCT scan, Mai Ndombe River, Democratic Republic of Congo. – *Brachypetersius notospilus*: AMNH 253967, 1μCT scan, Lebayi River, Republic of Congo. – *Brycinus macrolepidotus*: AMNH 239507, 1C&S, Congo River, Brazzaville, Republic of Congo. – AMNH 270775, 1μCT scan, Niger River at Mafou, Guinea. – *Brycinus nurse*: AMNH 227279, Gambella, Ethiopia. – AMNH 230623, Ouandja River, Central African Republic. – AMNH 215629, 1μCT scan, Bahr El Ghazal, Sudan. – *Brycinus taeniurus*: AMNH 262981, 2μCT scan Gniabale River, Gabon. – *Bryconaethiops microstoma*: AMNH 238290, 2C&S, Malebo Pool, Brazzaville, Republic of Congo. – AMNH 263324, Boma, Congo River, Democratic Republic of Congo. – AMNH 253823, 1μCT scan, Kwilu River, Democratic Republic of Congo. – *Bryconaethiops boulengeri*: AMNH 240415, 1μCT scan, Odzala National Forest, Republic of Congo. – *Bryconalestes longipinnis*: AMNH 258383, Noumbi River, Republic of Congo. – AMNH 59626, 1μCT scan, Gola north forest reserve, Sierra Leone. – *Bryconalestes. tholloni*: AMNH 253925, 1 μCT scan, Kouilou-Niari at Loudima, Republic of Congo. – *Clupeocharax schoutedeni*: AMNH, 242487, 1μCT scan, Lac Ndekengelo, Bandudu, Democratic Republic of Congo. – AMNH 242485, 1μCT scan, Lac Ikenge, Democratic Republic of Congo. – *Hemigrammopetersius barnardi*: AMNH 50825, Tanzania. – *Hydrocynus forskahlii*: AMNH 238308, Kasai River, Bandundu, Democratic Republic of Congo. – AMNH 238305, 1μCT scan, Kasai River, Democratic Republic of Congo. – *Hydrocynus vittatus*: AMNH 238297, 1C&S, Fimi River, Bandundu, Democratic Republic of Congo. – *Ladigesia roloffi:* AMNH 50886, Sierra Leone. – AMNH 233394, 2μCT scan, Aquarium material. – *Lepidarchus adonis*: AMNH 261317, 2μCT scan, Guinea. – *Micralestes humilis*: AMNH 245464 , Lengoue River, Sangha, Republic of the Congo. – AMNH 240814, 1μCT scan, Luilaka River, Democratic Republic of Congo,. – *M. holargyreus*: AMNH 263359, 1μCT scan, Congo River at Boma, Democratic Republic of Congo. – *M. pabrensis*: AMNH 57427, 2C&S, Volta River, Ghana. – AMNH 50831, 2μCT scan, no locality data. – *Nannopetersius ansorgii*: AMNH 258095, Kouilou, Republic of the Congo. – AMNH 263093, 2μCT scan, Lake Tchibanji, Republic of Congo. – *Nannopetersius lamberti*: AMNH 238370, 1μCT scan, Foulakari River, Republic of Congo. – *Phenacogrammus aurantiacus*: AMNH 274780, 2μCT scan, Ndzaa River, Democratic Republic of Congo. – *Phenocogrammus concolor*: AMNH 276321, 2μCT scan, Ndzaa River, Democratic Republic of Congo. – *Phenacogrammus deheyni:* AMNH 252208, 1μCT scan, Bionga Bionga, Democratic Republic of Congo. – *Phenacogrammus flexus*: AMNH 276320, 2μCT scan, Ndzaa River, Democratic Republic of Congo. – *Phenacogrammus interruptus*: AMNH 239467, 2C&S, Congo River, Brazzaville, Republic of the Congo. – AMNH 256217, Kwilu River, Democratic Republic of Congo. – AMNH 274784, 2μCT scan, Lomomo River, Democratic Republic of Congo. – *Phenacogrammus major*: AMNH 236514, 1μCT scan, Pont So'o, Cameroon. – *Phenacogrammus polli*: AMNH 240818, 1C&S, Salonga National Park, Democratic Republic of Congo. – AMNH 240816, 1μCT scan, Luilaka River, Democratic Republic of Congo. – *Phenacogrammus urotaenia*: AMNH 253971, 2μCT scan, Lebayi River, Republic of Congo. – *Rhabdalestes aeratis*: AMNH 242479, 2μCT scan, Lac Besako, Democratic Republic of Congo. – *Rhabdalestes septentrionalis*: AMNH 275205, Kodiwol, Gaoual, Guinea. – AMNH

254042, 1µCT scan, Liberia. – *Rhabdalestes yokai*: AMNH 274862, 2µCT scan, Kouyou River, Republic of Congo. – *Tricuspidalestes caeruleus*: AMNH 252193, 1µCT scan, Ta'Simon a Bouagui, Democratic Republic of Congo.

DISCUSSION

During this study, we have identified two features assessed to be diagnostic for *Petersius*. The first is the possession of a distinctively shaped supraoccipital crest with a steep anterodorsal convexity at the junction of the parietals and supraoccipital followed by a dorsomedial concavity on the surface of the crest (fig. 2A). This characteristic sculpting of the supraoccipital crest is present in juveniles and adults and appears to be unique to *Petersius* among alestids. The second apomorphy, premaxillary inner row teeth with cutting-edge cusps located along the buccal versus lingual face of each tooth merits further discussion.

Features of morphology and implantation patterning of jaw teeth have long been recognized as taxonomically and ontogenetically important features within Alestidae (Hoedeman, 1951; Poll, 1967; Paugy, 1986; Murray and Stewart, 2002; Murray, 2004; Zanata and Vari, 2005; Paugy and Schaefer, 2007). With the exceptions of *Hydrocynus*, *Lepidarchus*, and *Clupeocharax* where both upper and lower jaw teeth are unicuspid and arrayed in single rows, most alestids have pluricuspid teeth with two (or three in the case of *Bryconaethiops*) rows on each premaxilla, and one on each dentary (numerous taxa also have an inner row pair of conical teeth located either side of the dental symphysis). Among pluricuspid alestids two types of inner row premaxillary dentition have been recognized: the "molariform" type (fig. 3A) and the "non-molariform" type (sometimes referred as incisiform teeth; fig. 3B–D), and in traditional classifications these have been used to recognize two main tribes; the Alestini (molariform premaxillary dentition) and Petersiini (incisiform premaxillary dentition; see, e.g., Poll, 1967; Paugy and Schaefer, 2007).

To interpret the morphology of premaxillary teeth in *Petersius* and to provide a more detailed description of dental variation we undertook a survey of tooth form across the family. Our results are briefly summarized, utilizing exemplars of the range of variation observed (fig. 3). Here we can see that molariform teeth (e.g., *Brycinus*, fig. 3A) are characterized by a wide buccal shelf bearing robust rounded cusps (variously developed in different taxa), and with a series of cutting-edge cusps aligned along the lingual face of each tooth. In typical incisiform teeth (e.g., *Nannopetersius*, fig. 3B), while the buccal shelf is greatly reduced or absent, the location of cutting-edge cusps remains along the lingual face of the tooth (in a "palm up" configuration). A clearly lingual orientation of cutting-edge cusps is found across the alestid radiation, including in the early diverging *Arnoldichthys* (fig. 3D). *Petersius*, however, is an exception as in this taxon the buccal shelf is reduced, as in the incisiform tooth type, but the cutting-edge cusps are arrayed along the buccal face of each tooth (in a "palm down" configuration, fig. 3C). This unusual configuration mirrors the orientation of cusps in both outer row premaxillary and dentary teeth in all pluricuspid alestids. This observation, in addition to providing an apomorphic and diagnostic feature for *Petersius*, provides a helpful guide to the location and number of outer row premaxillary teeth across Alestidae, which can often be difficult to determine. The example of *Arnoldichthys* (fig. 3D) is illustrative as outer and inner row teeth are somewhat randomly arrayed and difficult to distinguish based on implantation. However, as we determine that all outer row premaxillary teeth have cusps arrayed buccally, differentiating between inner (lingual cusps) and outer (buccal cusps) row teeth becomes readily apparent. While the phylogenetic significance of the distribution of molariform and incisiform inner row premaxillary teeth among alestid lineages remains to be determined, the presence of buccally oriented cutting row cusps in *Petersius* represents an intriguing outlier within Alestidae.

An additional osteological feature observed in this study is the presence in *Petersius* of a small dorsally oriented process on the upper margin of second infraorbital (fig. 2D, H). A similar dorsally oriented process was reported in *Phenacogrammus major* by Zanata and Vari (2005) who considered it autapomorphic for that taxon. However, our examination of μCT scans of *Phenacogrammus* species contradicts Zanata and Vari's observation as we found that the second infraorbital of both *Ph. major* (fig. 6C) and *Ph. urotaenia* (fig. 6D), in common with most other alestids, lack a dorsal process. A process of varying size is present in *Ph. deheyni* (fig. 6A), *Ph. aurantiacus* (fig. 6B), *Ph. flexus*, *Ph. interruptus*, *Ph. polli*, and *Ph. concolor.* The phylogenetic significance of this, and other osteological features highlighted in this study remain to be determined, but ongoing investigation using genomic data will allow us to establish a framework for understanding character evolution within Alestidae and close relatives. Currently, tissues from preserved *Petersius* have been assembled and next steps will involve the inclusion of *Petersius* in a densely sampled molecular phylogeny through analysis of historical DNA (hDNA) to better understand the phylogenetic placement and morphological evolution of this enigmatic alestid lineage.

ACKNOWLEDGMENTS

We are extremely grateful to Katriina Ilves and Stéphanie Tessier (CMN) and Caleb McMahan (FMNH) for specimen loans, and Peter Bartsch and Edda Aßel (ZMB) for sending photographs of syntypes. We also thank Fraser Gear for permission to reproduce his field photograph of *Petersius*, and for providing habitat information. This project was funded by CNPq Research Grant #200159/2020-8 (BFM) and AMNH Axelrod Research Curatorship (BFM and MLJS).

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