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Osteology and redescription of the miniature lampeye species of *Congopanchax* Poll, 1971 with an overview of miniature African freshwater fishes

(Teleostei, Cyprinodontiformes, Procatopodidae)

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The Congo endemic genus *Congopanchax* is distinguished from all other Procatopodidae by the presence of the following exclusive character states: presence of ventral cleft in the anguloarticular, absence of premaxilla posterior margin indentation, autopalatine anterior margin concave, parhypural not contacting or slightly overlapping the hypural plate, dorsal fin bilobate, with first two and last dorsal-fin rays filamentous, infraorbital bar present and longitudinal stripe on ventral midline reaching isthmus. *Congopanchax myersi* and *C. brichardi* are redescribed and distinguished from each other by colouration in life and morphometrics. An updated list of African freshwater miniature species containing a total of 58 species is presented, including information about their distribution, habitat and conservation status. The diversity of miniature fish species in Africa is probably underestimated, and the orders Cyprinodontiformes (36 %) and Cypriniformes (26 %) include the highest proportion of miniatures followed by the Characiformes (17 %) and the Siluriformes (15 %). In total, about half of the miniature species have not been evaluated (29 %) regarding their conservation status or are data deficient (19 %).

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Introduction

The extreme reduction of body size as a result of changes in the onset and end of growth timing, also known as miniaturization (Hanken & Wake 1993, Hanken 1993), is an exciting research field, with many morphological studies (Britz et al. 2009, Britz & Conway 2009, Britz et al. 2014, Britz & Conway 2016, Mattox et al. 2016, Conway et al. 2017, Marinho 2017, Cordero 2021), and more recently genomic approaches directed to understand the basis of miniaturization (Liu et al. 2012, Malmstrøm et al. 2018, Decena-Segarra et al. 2020). Among vertebrates, miniaturization has been reported in different taxonomic groups, being more common in amphibians, reptiles and fishes. Miniaturization is generally associated with three main effects: reduction and structural simplification of body morphology, increased morphological variability and the appearance of morphological novelties (Hanken 1993).

The reduction and loss of bones due to changes in the degree of mineralization or even non-ossification of cartilaginous precursors, and structural simplification are the most common effects of miniaturization in vertebrates (Hanken & Wake 1993, Johnson & Brothers 1993, Britz & Kottelat 2003). Myers (1958) was the first to report many cases of miniaturization in fishes leading, e. g., to the simplification of the latero-sensory system, to the reduction of the number of vertebrae, body scales and fin rays, or reduction in sculpturing on the surface bones of the head. Later, Weitzman & Vari (1988) published the first study directed at documenting the diversity and ecology of miniature fishes in the Neotropical region. In the same study, they defined two arbitrary thresholds to identify miniature species: (1) the maximum standard length should not surpass 26.0 mm of SL; (2) or the individuals of the species should reach sexual maturity under 20 mm SL.

Increased osteological variability in the adult skeleton frequently involves structures that appear relatively late in ontogeny and that have a precociously truncated development or an alteration of skeletal patterning in early development (Hanken & Wake 1993, Britz & Conway 2009, Britz et al. 2014, Britz & Conway 2016, Conway et al. 2017, Conway et al. 2021). These processes result in intraspecific and even intra-individual (right-left asymmetry) variation in bone shape, size, and in some cases, absence or presence of the bone (Hanken 1993). This intraspecific variation may obscure interspecific differences in adult morphology, making the morphological study of miniature taxa difficult (Hanken & Wake 1993). In developmentally truncated miniatures, the miniaturization process is often related to the evolution of morphological novelties and many examples are known, especially among Southeast Asian freshwater fishes of the order Cypriniformes (Kottelat et al. 2006, Britz & Conway 2009, Britz et al. 2009, Britz et al. 2014, Britz & Conway 2016).

Among the difficulties in studying miniaturized fishes, in addition to the small size and delicate morphology, is that the inclusion of miniature taxa in morphology-based phylogenetic analyses can be quite problematic. The occurrence of paedomorphic parallelism, when similar plesiomorphic character states appear in non-related derived taxa due to independent events of developmental truncation may often remain unnoticed and could potentially be interpreted incorrectly as evidence of a common origin and close relationship of miniature taxa (Weitzman & Vari 1987, Schaefer et al. 1989, Britz et al. 2014).

In the past decades there has been an increasing interest in the study of the ontogeny and morphology of miniature freshwater species (Roberts 2003, Britz & Moritz 2007, Mattox et al. 2016, Conway et al. 2017, Marinho 2017, Mattox et al. 2020, Mattox & Conway 2021), and their important ecological role as suggested by some studies (Leitão et al. 2016, Castro & Polaz 2020, Perkin et al. 2022). After the publication of the first list of miniature fishes from the Neotropical region by Weitzman & Vari (1988), the frequency of new miniature species descriptions from the Neotropics increased significantly as shown by the publication of subsequent updated lists (Costa & Le Bail 1999, Toledo-Piza et al. 2014). Similar miniature fish lists were published for other regions such as Southeast Asia (Kottelat & Vidthayanon 1993) and North America (Bennett & Conway 2010). Conway & Moritz (2006) published the only list for African freshwater miniature fishes, but several miniature taxa have been described since then (e. g. Eccles et al. 2011, Jerep & Vari 2013, Van der Zee et al. 2013, Moritz & Schliewen 2016, Roberts 2019, Bragança et al. 2020, Bragança et al. 2021). Thus, it is time for an updated list of the miniature freshwater fishes of Africa.

The miniature procatopodid species of *Congopanchax* Poll, 1971

The family Procatopodidae is a diverse assemblage of small oviparous killifishes with about 100 species occurring across the African continent (Bragança & Costa 2019). They are also known as lampeyes, a reference to the bright colouration on the dorsal portion of the eye (Brüning 1929). Despite its diversity, the family systematics and taxonomy remain largely unknown. Only few publications have approached procatopodid diversity, and most of the genera are still in need of an updated definition (Parenti 1981, Huber 1999, Ghedotti 2000).

The genus *Congopanchax* Poll, 1971, was erected to include two miniature procatopodids: *C. myersi* (Poll, 1952a) from Malebo Pool in the lower Congo River basin, and *C. brichardi* Poll, 1971 from the Tshuapa River drainage, a tributary of the central Congo River basin. Poll (1971) diagnosed *Congopanchax* by the presence of an extremely prognathous lower jaw, few scales over the base of the anal and dorsal fins, dorsal-fin overhanging the anal-fin, a low number of anal and dorsal-fin rays, anal, dorsal and pelvic fins of males with filamentous rays, and by the anterior supraorbital latero-sensory canal closed with two pores. In the same publication, the presence of contact organs, minute bony projections along the fin rays, in the pelvic and anal-fin rays of males of both species was recorded, and *C. myersi* and *C. brichardi* were distinguished on the basis of colour pattern differences of males and morphometric characters.

Following the genus description, few studies have addressed the morphology of the included species, and their phylogenetic placement (Parenti 1981, Ghedotti 2000). Despite the fact that *Congopanchax* species have been listed as examined material, they were not included in phylogenetic analyses, and no data related to their morphology and osteology were provided (Parenti 1981, Ghedotti 2000). Huber's (1999) phylogenetic analysis included both species of *Congopanchax*, but it was restricted mainly to morphometric and meristic characters as well as ecological/habitat related characters.

Although *Congopanchax* includes two of the smallest freshwater fish species in Africa, with a maximum standard length not surpassing 18.0 mm, few data are available for its intriguing morphology, distribution and diversity. Recently, Bragança & Costa's (2019) molecular phylogenetic analysis provided a first understanding on the evolution and diversification of the African lampeyes since their estimated origin in the late Oligocene. According to this study, the *Congopanchax* lineage likely originated in the middle Miocene, during the Miocene climatic optimum moist period, in which rainforests extended to the east and north of Africa in areas nowadays predominately characterized by savanna or Sahelian vegetation. Strangely, despite their relatively ancient origin when compared to most other procatopodid genera, *Congopanchax* diversified only during the Pleistocene. This recent diversification suggests that possibly the formation of the Malebo Pool and/or the repeated fragmentation of lowland rainforests in the Plio-Pleistocene have triggered their divergence (Bragança & Costa 2019).

In the present study, an updated list and overview of the miniature African freshwater species is presented, addressing their distribution, habitat and conservation status. An osteological description for *Congopanchax* is provided and the species *C. myersi* and *C. brichardi* are redescribed. Information relating to the distribution of *Congopanchax* is also presented.

Material and methods

The definition of miniature fishes used here follows that provided by Weitzman & Vari (1988). Data on life colour pattern are based on the original descriptions (Poll 1952a, Poll 1971) and photos taken from live specimens kept in aquarium and wild caught specimens. The colour pattern of preserved specimens was also analysed. Measurements and counts follow Costa (1988). Caudal-fin rays count includes both principal and procurrent rays, as it is commonly presented in Cyprinodontiformes studies. Measurements are presented as percentages of standard length (SL) except those related to head morphology, which are expressed as percentages of head length (HL). In the description section, holotype's meristic data are indicated by an asterisk. Osteological studies were made on cleared and stained specimens (c&s) prepared according to Taylor & Van Dyke (1985). The bone structures were drawn with a camera lucida mounted on a Leica MS5 microscope. Images of skeletal complexes taken from cleared and stained specimens of *Congopanchax myersi* (UFRJ 4153) are shown. Structures were photographed using an Android Xiaomi Mi11 Ultra phone adapted to the same microscope. The photographs were stacked using Zerene Stacker 1.04 Build free trial, and edited in Photoshop CC 2019. Osteological nomenclature follows Mattox et al. (2016). Nomenclature for frontal squamation follows Hoedeman (1958) and that for head sensory canals follows Gosline (1949), except for the pre-orbital canal, here called anterior infra-orbital canal.

The specimens are deposited in the following institutions: ISRNB, Institut des Sciences Naturelles de Belgique, Brussels; MNHN, Muséum National d'Histoire Naturelle, Paris; RMCA, Royal Museum for Central Africa, Tervuren; UFRJ, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro. The abbreviation currently in use for the RMCA fish collection is MRAC. Comparative specimens are listed in Supplementary file 1.

Results

Osteology

Considering that no variation was identified when comparing the osteology of *C. myersi* and *C. brichardi*, the osteological plate includes mainly illustrations of *C. myersi*, the genus type species, but illustrations of *C. brichardi* were included when these were clearer due to a better clearing and staining process.

Superficial dermal bones and neurocranium

(Fig. 1A, B, C, D, Fig. 2B, Fig. 3)

Nasal thin, drop-shaped. Lachrymal triangular and elongated, anterior tip present; dorsal margin with small indentation, ventral posterior process sharp and pointed. Vomer absent. Mesethmoid absent. Lateral ethmoid compact, medial margin not overlap-

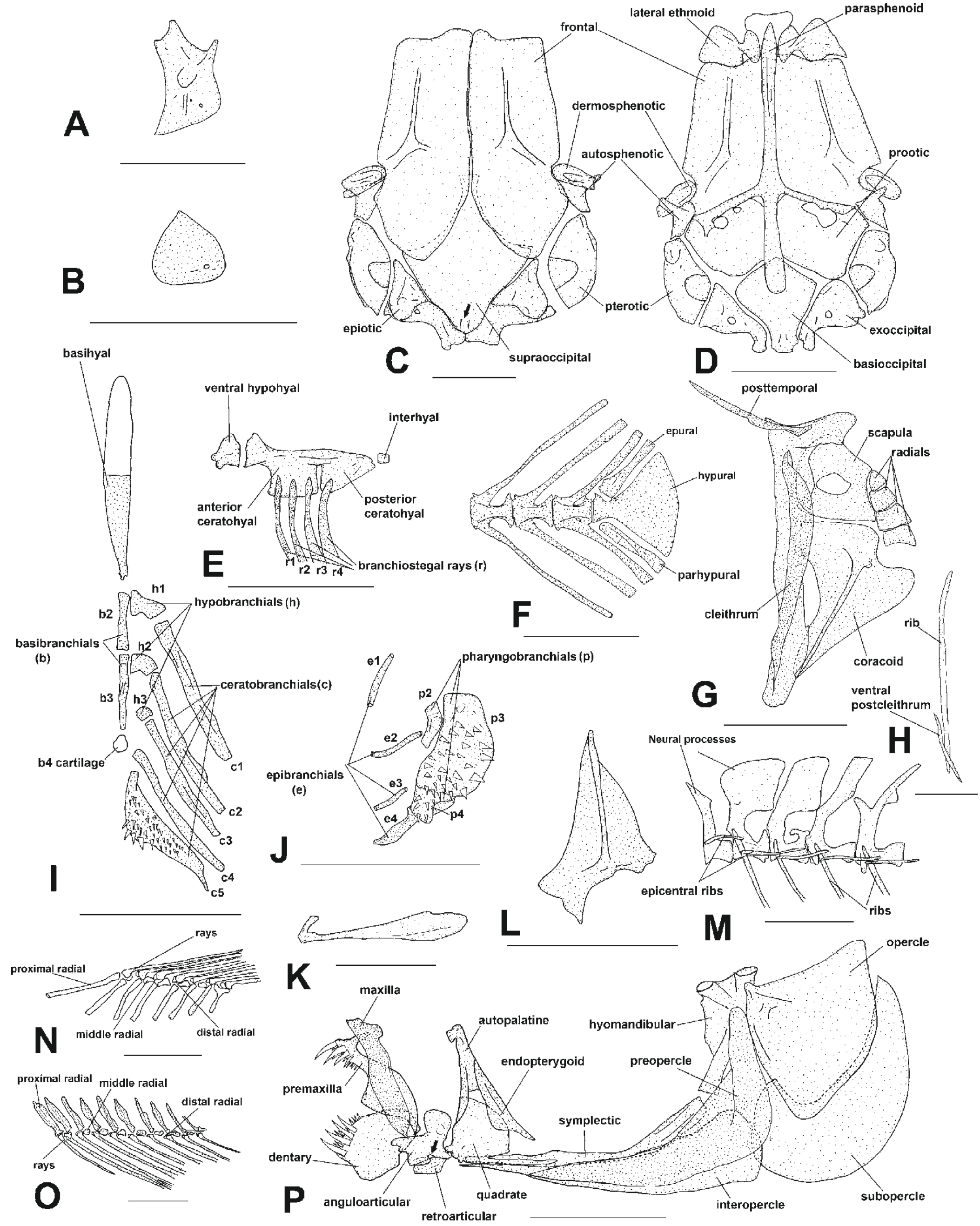

Fig. 1. Osteological features of *Congopanchax*: **A.** lachrymal; **B.** nasal; **C.** neurocranium, dorsal view; **D.** neurocranium ventral view; **E.** left hyoid bar, lateral view; **F.** caudal-fin skeleton, left lateral view; **G.** pectoral fin girdle, lateral view; **H.** ventral postcleithrum and adjacent first rib; **I.** left branchial arches ventral portion, ventral view; **J.** right dorsal portion of branchial arches, ventral view; **K.** urohyal, left lateral view; **L.** left basipterygium, dorsal view; **M.** anterior vertebrae, lateral view; **N.** dorsal-fin radials and proximal radials, left lateral view; **O.** anal-fin radials and proximal radials, left lateral view; **P.** left jaws, jaws suspensorium and opercular apparatus, lateral view. All illustrations were made based on *C. myersi* specimen (UFRJ 4153, 16.5 mm SL), except the anal fin, hypural structure, and first vertebrae which are from *C. brichardi* (RMCA 102543–102546, 14.9 mm SL). Scale bars: 1 mm.

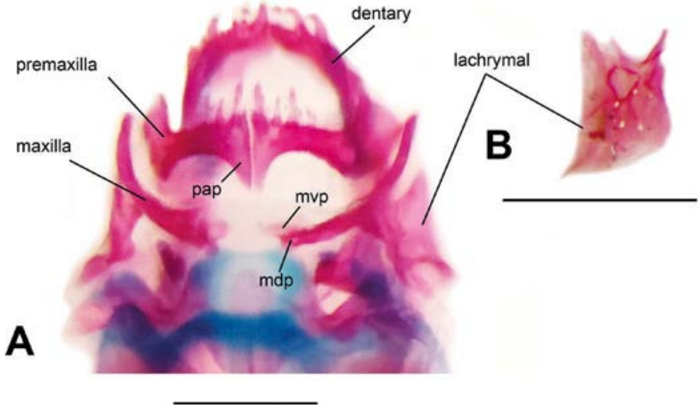

Fig. 2. *Congopanchax myersi*, c&s specimens. **A.** Anterior region of neurocranium and jaws, dorsal view (UFRJ 4153, 13.3 mm SL); **B.** lachrymal (UFRJ 4153, 16.5 mm SL). Cartilage blue. Abbreviations: mdp, maxilla dorsal process; mvp, maxilla ventral process; pap, premaxilla ascendent process. Cartilage blue. Scale bars: 1 mm.

ping anterior process of parasphenoid. Dermosphenotic thin, slightly elongated, its outer surface gently directed outwards. Autosphenotic with prominent narrow lateral process. Frontal trapezoidal and thin; anterior margin extending anteriorly between lateral ethmoids. Parietal absent. Supraoccipital with extremely short, paired posterior process, not surpassing supraoccipital posterior margin. Pterotic longitudinally elongated, anterior portion not overlapping with autosphenotic. Epiotic small, without dorsal process. Parasphenoid cross-shaped; distal portion of anterior process narrow and pointed; posterior process ventrally attached to basioccipital narrow. Prootic rounded to subrectangular with one or two large foramina just below parasphenoid lateral arm. Exoccipital curved, anterior portion directed to pterotic ventral portion. Basioccipital lozenge-shaped.

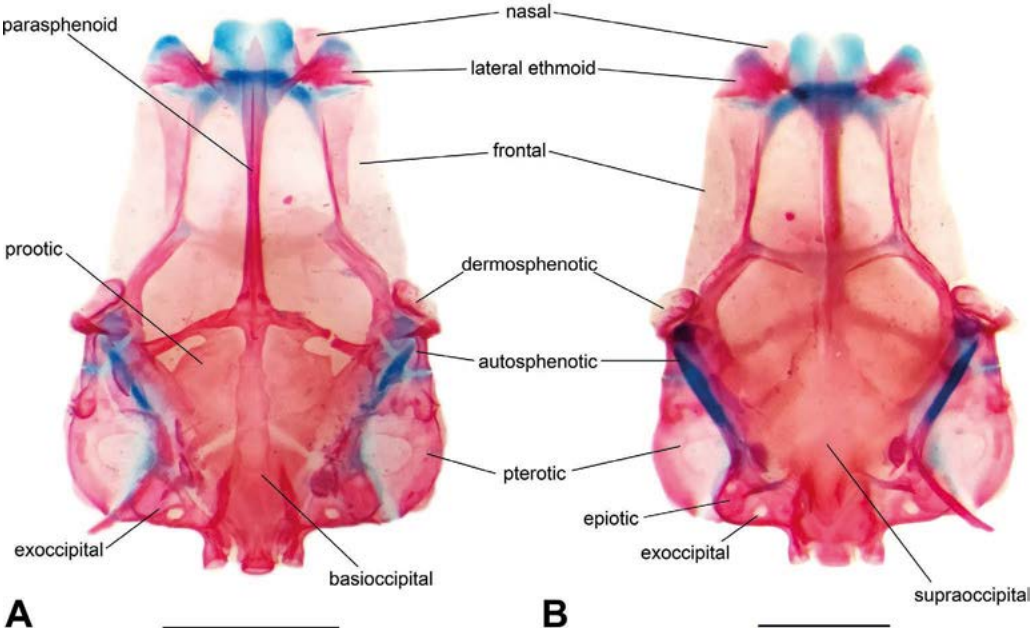

Fig. 3. *Congopanchax myersi* (UFRJ 4153), c&s specimen, 16.5 mm SL. Neurocranium: **A.** ventral view; **B.** dorsal view. Cartilage blue. Scale bars: 1 mm.

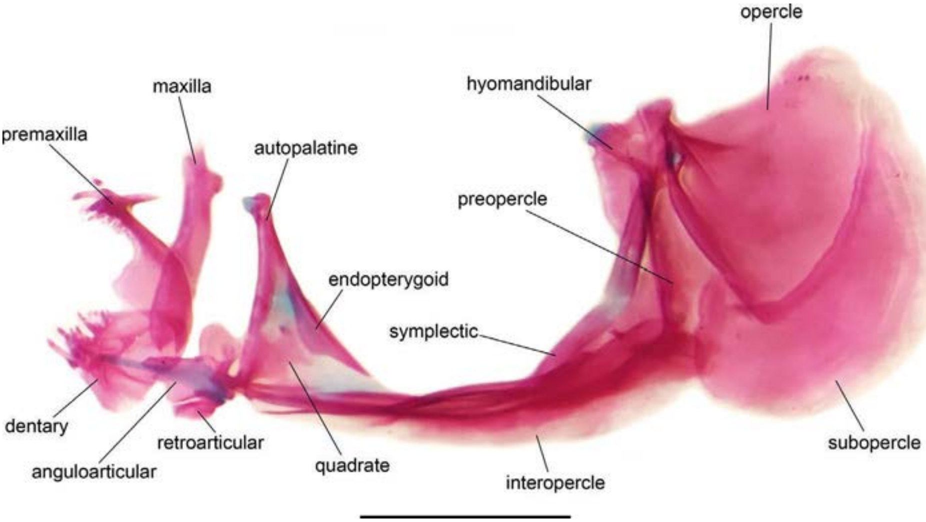

Fig. 4. *Congopanchax myersi* (UFRJ 4153), c&s specimen, 16.5 mm SL. Jaws, suspensorium and opercular apparatus, left side, lateral view. Cartilage blue. Scale bars: 1 mm.

Jaws, jaws suspensorium and opercular apparatus (Fig. 1P, Fig. 2A, Fig. 4)

Premaxilla with teeth restricted to its anterior portion; ascending process sharply pointed; ventral portion of anterior margin, forming a deep plate, dorsal margin convex, without a distinct tip. Maxilla subcylindrical, dorsal process extremely reduced, not reaching premaxilla ascending process; ventral process absent or extremely short. Rostral cartilage absent. Dentary compact, with teeth restricted to anterior region of its anterodorsal surface. Anguloarticular ventral process reduced; anterior process pointed and directed anteriorly; coronoid process constricted at its base; ventral margin with a distinct ventral cleft. Retroarticular wide and deep. Meckel's cartilage long. Premaxillary and dentary teeth conical, with slightly curved tip; teeth arranged in irregular rows, largest teeth on external most row. Autopalatine anterior margin slightly concave; distal head direct forward; ventral arm extending ventrally to the quadrate. Ectopterygoid absent. Endopterygoid thin and short, not reaching symplectic posteriorly. Ventral portion of endopterygoid overlapping dorsal portion of quadrate. Quadrate approximately triangular, anterior and ventral margins approximately straight, dorso-posterior margin convex; posterior process of quadrate subcylindrical, its dorsoposterior margin covering endopterygoid ventral portion. Symplectic slender and elongate. Metapterygoid absent. Hyomandibular narrow, Y-shaped; anterior margin of hyomandibular almost straight. Opercle subcircular, anterodorsal portion with a short process directed anteriorly. Subopercle anterodorsa margin with a small process as deep as the process base. Preopercle L-shaped, with distinct vertical lateral-line canal; dorsal and anterior ends rounded or slightly pointed.

Hyoid and branchial arches (Fig. 1E, I, J, K, Fig. 5)

Basihyal narrow, flattened; width about 15 % of length. Basihyal cartilage elliptical, about the same size as basihyal. Basibranchials 2–3 ossified; basibranchial 2 rectangular, slightly smaller than basibranchial 3, narrow and elongated in dorsal view; basibranchial 3, rectangular; basibranchial cartilage circular. Hypobranchial 1 anterior edge about straight, posterior margin concave; hypobranchial 2 squared or slightly arched with a concavity posteriorly directed; hypobranchial 3 rounded to squared shaped. Ceratobranchials 1–4 elongate, without teeth; ceratobranchial 5 with well-developed dentigerous plate containing conical, slightly curved teeth. Proximal tip of fourth ceratobranchial about the same width of proximal tip of ceratobranchials 1–3. Fifth ceratobranchial boomerang-shaped, anterior tip about the same width of proximal tip of adjacent fourth ceratobranchial. Pharyngobranchial 2 toothless. Pharyngobranchial 3 wide, with developed dentigerous plate containing large conical, slightly curved teeth. Pharyngobranchial 4 tooth plate with few small conical teeth. Epibranchials 1–2 about the same length, epibranchial 3 about half the length of epibranchials 1–2, epibranchial 4 longer and wider. Epibranchial 1 straight, not curved, proximal

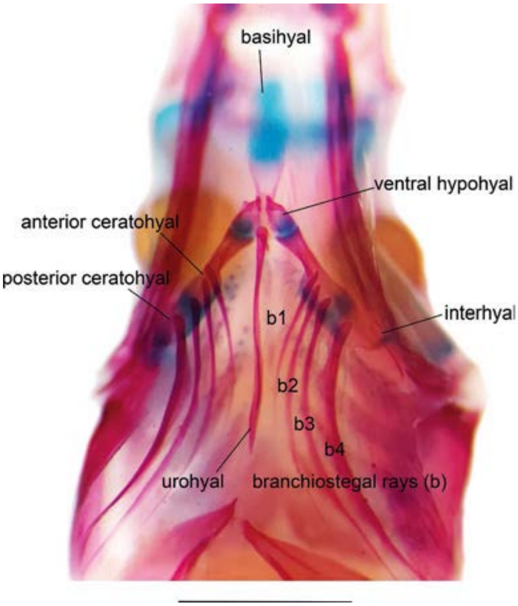

Fig. 5. *Congopanchax myersi* (UFRJ 4153), c&s specimen, 13.3 mm SL. Hyoid bar and urohyal, ventral view. Cartilage blue. Scale bars: 1 mm.

portion not widened. Epibranchial 3 not forked. Ventral hypohyal present. Dorsal hypohyal absent. Anterior process of anterior ceratohyal straight or slightly convex, narrowing posteriorly; anterior ceratohyal compressed and deep in its posterior portion, rectangular in lateral view. Anterior and posterior ceratohyals ventrally separated by cartilage, supporting four branchiostegal rays gradually becoming wider posteriorly. Posterior ceratohyal compressed, triangular. Interhyal present, reduced, attached to posterior end of posterior ceratohyal. Urohyal thin and slender, with short ventrolateral flap; anterodorsal process hook shaped.

Vertebrae and caudal-fin skeleton (Fig. 1F, M, Fig. 6)

Total vertebrae 27–29. Neural spine of first vertebra with long and narrow anterior extension, and without neural pre- and post-zygapophyses. Second and third neural spines wider and longer than first, with deep constriction at base. Vertebrae posterior to fourth or fifth with rod-like neural spines. Neural prezygapophyses of vertebrae 2 and 3 absent, neural postzygapophyses short. Ribs on all precaudal vertebrae except the first; epicentral bones narrow. Neural prezygapophyses of anterior caudal vertebrae short; neural postzygapophyses of caudal vertebrae short. Hemal spine of preural centrum 2 approximately as wide as hemal spines of anterior vertebrae. One short pointed process on dorsal surface of compound caudal centrum; one spinous process directed upwards on compound caudal centrum surface. Epural and parhypural similar in shape, laminar, with proximal portion not pointed. Parhypural not reaching compound caudal centrum. Hypurals ankylosed, forming a single plate. Accessory caudal cartilages present. Caudal-fin rays 18–24.

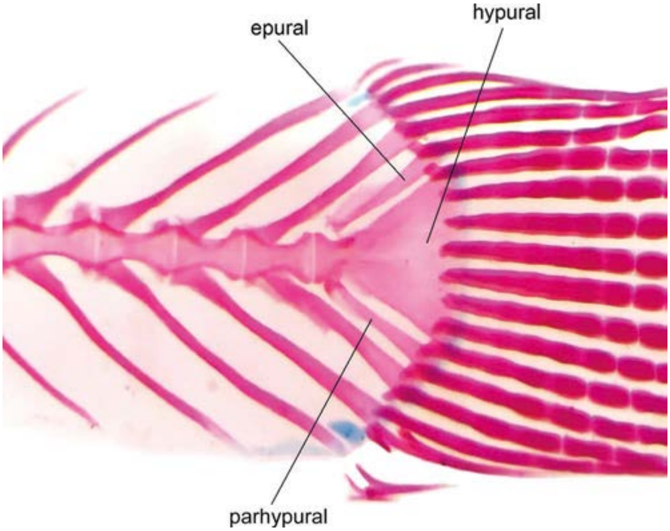

Fig. 6. *Congopanchax myersi* (UFRJ 4153), c&s specimen, 16.5 mm SL. Last caudal vertebrae, hypural plate, and caudal fin rays, left side, lateral view. Cartilage blue. Scale bars: 1 mm.

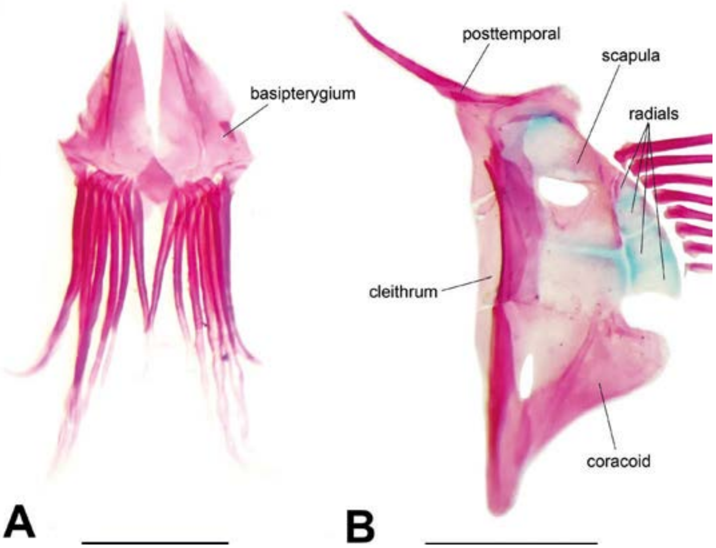

Fig. 7. *Congopanchax myersi* (UFRJ 4153), c&s specimen, 16.5 mm SL. Fins: **A.** left and right pelvic fins, dorsal view; **B.** left pectoral girdle, lateral view. Cartilages are in blue. Scale bars: 1 mm.

Pectoral and pelvic girdles (Fig. 1G, L, Fig. 7)

Pectoral-fin rays 9–11. Posttemporal straight or slightly convex, not forked. Supracleithrum absent. Dorsal portion of cleithrum slightly pointed, short, with reduced posterior flange. Ventral tip of cleithrum close to ventral tip of coracoid. Scapula roughly triangular in lateral view, coracoid scythe-shaped. Pectoral radials quadrangular, ventral most radial separated by interspace from coracoid. Dorsal postcleithrum absent. Ventral postcleithrum rod-like, about the same width of adjacent rib. Pelvic-fin rays 6. Basipterygium of pelvic girdle triangular; ischiatic process about the same length as lateral process; outer margin with small notch.

Dorsal and anal-fin support (Fig. 1N, O, Fig. 8)

Dorsal-fin rays 6–8. First dorsal-fin pterygiophore inserted between neural spines of vertebrae 9 and 10. Anal-fin rays 9–11. First anal-fin pterygiophore between ribs of vertebrae 9 and 10. One ray associated with first proximal radial of dorsal fin, and one associated with first proximal radial of anal fin. Proximal radials straight and narrow. Middle radials present. Distal radials small and poorly ossified, placed just before anterior portion of fin rays.

Reductive traits in *Congopanchax*

Here we list the reductive characters in *Congopanchax*, summarizing their distribution within the Procatopodidae:

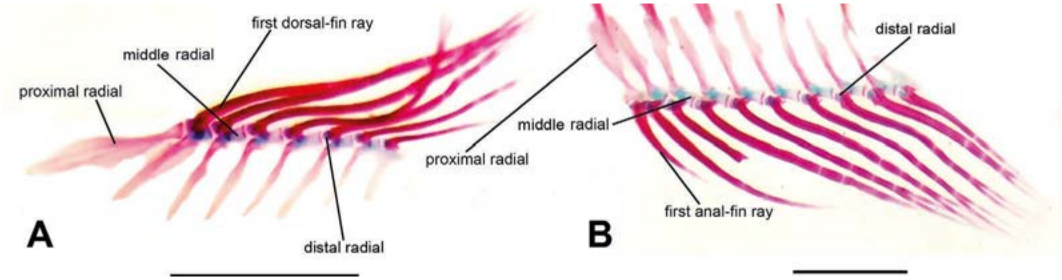

Fig. 8. *Congopanchax myersi* (UFRJ 4153), c&s specimen, 16.5 mm SL. Fins: **A.** dorsal-fin, left side, lateral view; **B.** anal-fin, left side, lateral view. Cartilages are in blue. Scale bars: 1 mm.

Mesethmoid absent

Parenti (1981) considered the absence of the mesethmoid (a cartilaginous mesethmoid sensu Parenti 1981) as diagnostic for the Procatopodidae, including *Aplocheilichtys spilauchen* (Duméril, 1859). Later, Ghedotti (2000) confirmed the absence of mesethmoid for all procatopodids except *A. spilauchen*. Here, we confirm the absence of this bone in *Congopanchax myersi* and *C. brichardi* and in all other taxa within the Procatopodidae except *A. spilauchen* and *Aapticheilichthys websteri* (Huber, 2007).

Vomer absent

Parenti (1981) was the first to report absence of the vomer in the procatopodids '*Lacustricola*' *johnstoni* (Günther, 1894), and in '*Hypsopanchax*' *zebra* (Pellegrin, 1929) and *Procatopus nototaenia* Boulenger, 1904. Later, Ghedotti (2000) confirmed the absence of this bone in '*Lacustricola*' *johnstoni*, *P. luxophthalmus* (Brüning, 1929), *Micropanchax pelagicus* (Worthington, 1932), *Rhexipanchax schioetzi* (Scheel, 1968), '*Hypsopanchax*' *zebra* and *Procatopus nototaenia*, and considered its absence polymorphic in *Micropanchax loati* (Boulenger, 1901). Here, we confirm that most procatopodid species don't have a vomer, which is only present in *Lamprichthys tanganicanus* (Boulenger, 1898), *Aapticheilichthys websteri*, and *Aplocheilichthys spilauchen*, and in species of *Plataplochilus*, *Hypsopanchax* , *H. platysternus* (Nichols & Griscom, 1917) and *H. modestus* (Pappenheim, 1914), *Lacustricola* Myers 1924, and of the southern Africa '*Lacustricola*' *katangae* species group (e. g. '*L.*' *katangae* (Boulenger, 1912), '*L.*' *mediolateralis* (Poll, 1967)). Here we report the presence of the vomer in *Procatopus similis* Ahl, 1924, its absence in *P. aberrans* Ahl, 1927, and a polymorphic condition of presence/absence in *P. nototaenia*.

Epiotic dorsal process absent

Ghedotti (2000) was the first to indicate the absence of an expanded epiotic process in all procatopodids, with the exception of *Aplocheilichthys spilauchen*. Herein we confirm for both *Congopanchax* species an epiotic bone lacking a dorsal process. Within the Procatopodidae, the dorsal epiotic process is only present in *Aplocheilichthys spilauchen*, *Aapticheilichthys websteri*, and in some *Plataplochilus* species (e. g. *P. cabindae* (Boulenger, 1911), *P. terveri* (Huber, 1980), *P. ngaensis* (Ahl, 1924)).

Supraoccipital posterior process reduced, not reaching first vertebra

In addition to *Congopanchax myersi* and *C. brichardi*, two other miniature species share a reduced posterior process of the supraoccipital bone, '*Micropanchax*' *camerunensis* (Radda, 1971) and *M. pfaffi* (Daget, 1974). In all other procatopodids, the posterior process reaches the first vertebra.

Ceratobranchial 4 teeth absent

Among cyprinodontoids most taxa present at least one row of conical teeth on the anterior portion of the fourth ceratobranchial (Ghedotti 2000). Here, the absence of teeth in the fourth ceratobranchial is reported for the first time in the Procatopodidae, in *Congopanchax myersi*, *C. brichardi*, and *Hylopanchax* aff. *ndeko* Van der Zee, Sonnenberg & Schliewen, 2013. All other examined *Hylopanchax* species have teeth in the fourth ceratobranchial. Costa (1996), mentioned the absence of teeth in the fourth ceratobranchial in the miniature Amazonian species of *Fluviphylax* (Fluviphylacidae).

Pharyngobranchial 2 teeth absent

The absence of teeth in pharyngobranchial 2 is only seen in *Congopanchax myersi* and *C. brichardi*, not being recorded in any other Procatopodidae.

Premaxilla, posterior margin indentation absent

Congopanchax myersi and *C. brichardi* are the only procatopodids with a non-indented posterior margin of the premaxilla.

Supracleithrum absent

Most Cyprinodontiformes have a rounded or slightly elongated supracleithrum (Ghedotti 2000). The bone is present in all Procatopodidae, except in *Congopanchax myersi*, *C. brichardi*, and species of *Poropanchax* (e. g. *P. rancureli* (Daget, 1965), *P. luxophthalmus*, *P. scheeli* (Roman, 1970), and *P. stigmatopygus* Wildekamp & Malumbres, 2004). Ghedotti (2000), differently from the present study, described the presence of a short, often disc-like supracleithrum in *P. luxophthalmus*. It is more likely that the structure present over the anterodorsal portion of the cleithrum in *Congopanchax* and *Poropanchax* is the posttemporal and not the supracleithrum, because in all procatopodids that have both structures, the supracleithrum is always much smaller than the posttemporal, and attached to its ventral portion. The posttemporal, on the other hand is much more elongated, generally rod-like or forked, with its anterior most tip connecting to the neurocranium. However, the correct identification of this bone as a supracleithrum or posttemporal needs further developmental studies. It will also allow us to understand if the supracleithrum is not developed, or it could be fused to the posttemporal bone in a latter developmental stage, a condition hypothesized for Aplocheiloidei

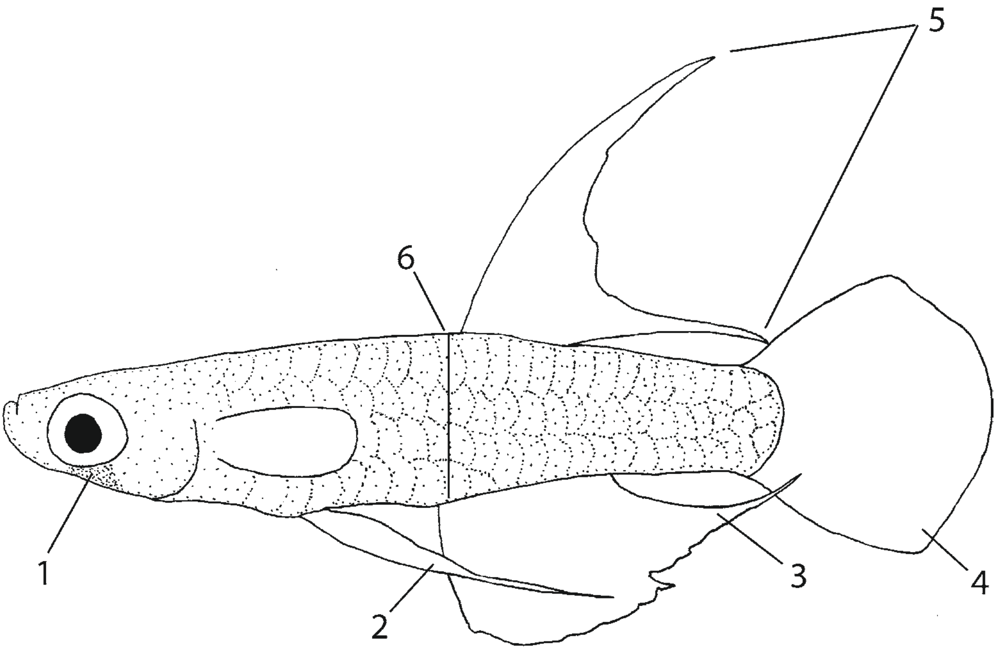

Fig. 9. Schematic illustration of male *Congopanchax brichardi* depicting the genus external morphology diagnostic/informative traits: 1, infraorbital bar; 2, filamentous pelvic fin; 3, filamentous anal fin; 4, fan-shaped caudal fin; 5, bifilamentous dorsal fin; 6, symmetrically arranged anal and dorsal fins.

based on their adult condition (Parenti 1981), but not present among the Cyprinodontoidei. Among Cyprinodontoidei, the supracleithrum was previously considered to be absent only in the poeciliid, *Tomeurus gracilis* Eigenmann, 1909 (Ghedotti 2000).

Parhypural, anterior portion not or slightly overlapping compound caudal centrum

Anterior portion of the parhypural not overlapping or slightly overlapping the caudal centrum is not commonly seen in cyprinodontoids (Costa 2012). Within the Procatopodidae a reduced anterior portion of the parhypural is only seen in *Congopanchax myersi* and *C. brichardi.*

Taxonomy accounts

Congopanchax Poll, 1971

Congopanchax Poll, 1971: 302 (type species *Aplocheilichthys myersi* Poll, 1952a by monotypy).

Diagnosis. *Congopanchax* is distinguished from all other Procatopodidae by: presence of a ventral cleft in the anguloarticular (Fig. 1P, indicated by an arrow); absence of an indentation in the posterior margin of the premaxilla (Fig. 1P); autopalatine anterior margin concave (Fig. 1P); parhypural not contacting or slightly contacting the compound caudal centrum (Fig. 1F); dorsal fin bifilamentous (Fig. 9); infraorbital bar present (Figs 9, 10B); and longitudinal stripe on ventral midline extending from caudal peduncle to head isthmus. Other characters not unique but useful to identify the genus *Congopanchax* are: eye extremely large; pelvic fin with long filament, reaching between the end of the anal-fin base to the caudal fin base; contact organs (small bony hooks) on anal and pelvic fins in males; posterior process of the supraoccipital reduced, not extending beyond supraoccipital bone (Fig. 1C, indicated by an arrow); second and fourth pharyngobranchials reduced (Fig. 1I); second pharyngobranchial teeth absent (Fig. 1J); fourth ceratobranchial teeth absent (Fig. 1I); four branchiostegal rays (Fig. 1E); supracleithrum absent (Fig. 1G); extremely reduced ventral process of maxilla (Fig. 1P); dentary compact (Fig. 1P); retroarticular deep (Fig. 1P); ascending process of premaxilla sharp and pointed (Fig. 1P); alveolar arm of premaxilla greatly modified in a deep bony plate (Fig. 1P); and hyoid arch short and compact (Fig. 1E); 6–8 dorsal-fin rays; 9–11 anal-fin rays.

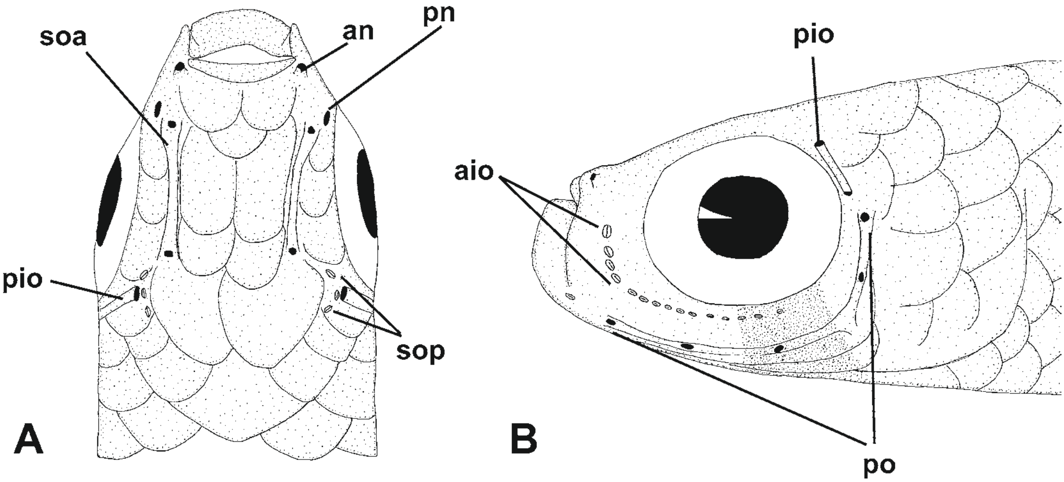

Fig. 10. Schematic illustration of the cephalic pores of *Congopanchax brichardi*: **A.** dorsal view; **B.** lateral view. Abbreviations: aio, anterior section of infraorbital canal; an, anterior nostril; pio, posterior section of infraorbital canal; pn, posterior nostril; po, preopercular canal; soa, anterior section of supraorbital canal; sop, posterior section of supraorbital canal.

Distribution. *Congopanchax* is endemic to the Congo River basin (Fig. 11) (Poll 1952a, Poll 1971, Wildekamp et al. 1986, Wildekamp 1995, Stiassny et al. 2011, Iyaba et al. 2013, Iyaba & Stiassny 2013, Schliewen 2014, Stiassny et al. 2021). Further information is provided below in the species redescriptions.

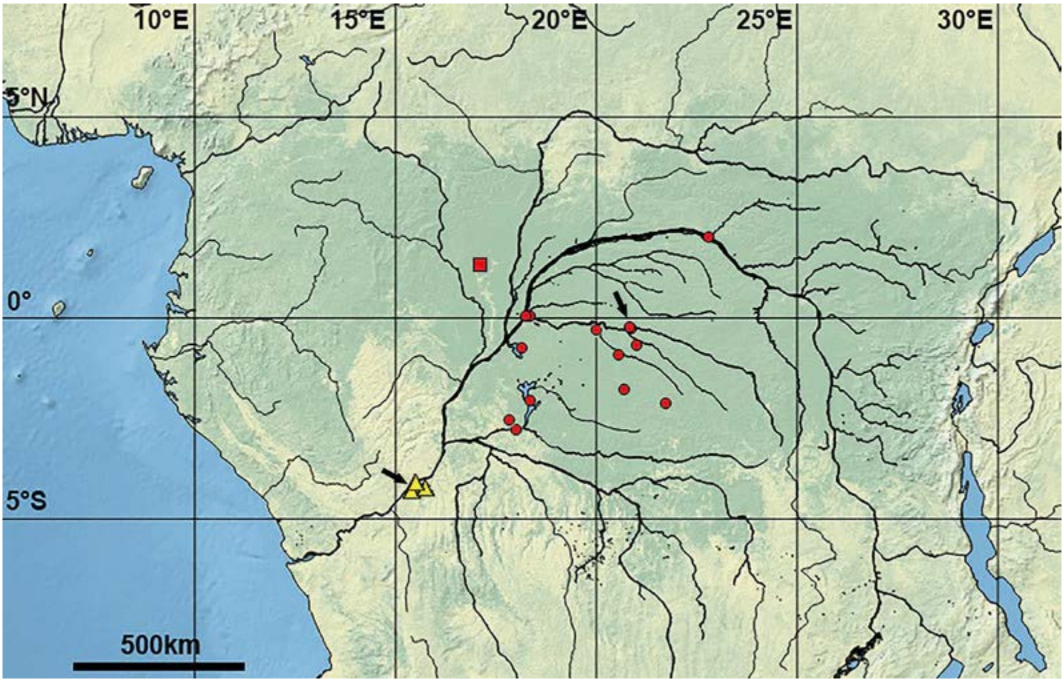

Fig. 11. Distribution of *Congopanchax* species: △, *C. myersi*; ●, *C. brichardi*; ■, *C.* cf. *brichardi*. The records were based on the examined specimens, photographs (for *C.* cf. *brichardi*) and localities listed in Iyaba & Stiassny (2013), Iyaba et al. (2013), and Stiassny et al. (2021). Type localities are indicated by an arrow. Each symbol may represent more than one locality.

Species: *Congopanchax myersi* and *C. brichardi*.

Congopanchax myersi (Poll, 1952a)

Fig. 12

Aplocheilichthys myersi Poll, 1952a: 302 (original description; Mbamu Island, Malebo Pool, Kinshasa, Democratic Republic of Congo)

Material examined. All from the Congo River basin. Democratic Republic of Congo: Kinshasa Province: MRAC 86801, 1 specimen (holotype), 16.5 mm SL; Mbamu Island former Ilê Atena, Malebo Pool (former Stanley Pool), Kinshasa (former Leopoldville), 04°19'S 15°19'E; A. Hulot, 9 Oct. 1948. – MRAC 77394, 1 specimen (paratype), 16.8 mm SL; Malebo Pool, near Kinshasa, 04°18'S 15°18'E; A. Dubois, 1951. – MRAC 86802, 1 specimen (paratype), 16.2 mm SL; Mbamu Island, Malebo Pool, Kinshasa, 04°19'S 15°19'E; A. Hulot, 19 Oct. 1948. – MRAC 118029, 1 specimen, 16.4 mm SL; Malebo Pool, 04°06'S 15°15'E; P. Brien, M. Poll, J. Bouillon, 3 Sep. 1957. – MRAC 117977–117989, 13 specimens, 11.3–17.3 mm SL; Malebo Pool, 04°06'S 15°15'E; P. Brien, M. Poll, J. Bouillon, 22 Apr. 1957. – MRAC 117990, 1 specimen, 15.2 mm SL; Malebo Pool, 04°06'S 15°15'E; P. Brien, M. Poll, J. Bouillon, 22 Apr. 1957. – MRAC 72507–72508, 2 specimens, 15.3–16.5 mm SL; swampy areas near Kinshasa, 04°18'S 15°18'E; Jardin Zoologique d'Anvers. – MRAC 103525–103532, 8 specimens, 11.2–14.7 mm SL; Malebo Pool, 04°06'S 15°15'E; A. Werner, Jun. 1955. – MRAC 117995–118022, 28 specimens, 14.5–17.9 mm SL; Malebo Pool, 04°06'S 15°15'E; P. Brien, M. Poll, J. Bouillon, 27 Sep. 1957. – MRAC 118023–118024, 2 specimens (c&s), 16.1–16.4 mm SL; Malebo Pool, 04°06'S 15°15'E; P. Brien, M. Poll, J. Bouillon, 27 Sep. 1957. – UFRJ 4152, 2 specimens, 17.2–17.8 mm SL; Malebo Pool, 04°06'S 15°15'E; P. Brien, M. Poll, J. Bouillon, 27 Sep. 1957. – UFRJ 4153, 2 specimens (c&s), 13.3–16.5 mm SL; Malebo Pool, 04°06'S 15°15'E; P. Brien, M. Poll, J. Bouillon, 27 Sep. 1957. – MNHN 1958-0125, 1 specimen, 14.0 mm SL; Malebo Pool, 04°06'S 15°15'E; P. Brien, M. Poll, J. Bouillon, 27 Sep. 1957. – MRAC 103533, 451 specimens (1 ex c&s), 7.5–13.8 mm SL; Malebo Pool, 04°06'S 15°15'E; A. Werner, Jun. 1955.

Diagnosis. *Congopanchax myersi* is distinguished from *C. brichardi* by: bright bluish green metallic colouration on side of body of males (Fig. 13A) (vs. bright blue metallic colouration; Fig. 15A); anal fin, dorsal fin and pelvic fin of males bright yellow (Fig. 13A) (vs. bright orange; Fig. 15A). It is further distinguished from *C. brichardi* by the presence of a shorter anal-fin base in females 7.6–10.5 % SL (vs. 10.9–11.4 % SL); longer pectoral fin in males 19.7–23.2 % SL (vs. 15–19.5 % SL); shorter pelvic fin in females 13.3–14.7 % SL (vs. 21.9–24.8 % SL); greater interorbital distance 43.1–48.8 % HL (vs. 33.8–36.1 % HL); longer snout in males 18.8–21.3 % (vs. 14.7–16.6 % HL); and a longer lower jaw 10.6–12.7 (vs. 4.7–8.5 HL) (Table 1).

Table 1. Morphometric data of *Congopanchax myersi* and *C. brichardi*.

	Congopanchax myersi		*Congopanchax brichardi*	
	males (n = 5)	females (n = 6)	males (n = 6)	females (n = 5)
Standard length (mm)	14.7–16.3	10.6–13.9	14.0–16.2	11.2–12.6
Percent of standard length				
Body depth	20.8–24.1	20.1–24.3	16.2–21.6	20.4–20.8
Caudal peduncle length	13.9–14.6	11.8–14.7	12.0–14.4	14.4–14.7
Pre-dorsal length	59.3–60.6	59.0–62.8	58.5–62.1	60.2–65.4
Pre-pelvic length	39.7–43.0	43.7–47.3	39.2–45.0	42.1–44.6
Length of dorsal-fin base	9.4–12.5	7.6–10.5	7.9–12.3	10.9–11.4
Length of anal-fin base	15.6–19.8	12.2–16.2	14.7–17.3	15.7–17.3
Caudal-fin length	27.0–28.6	25.0–30.0	24.5–29.7	25.1–28.1
Pectoral-fin length	19.7–23.2	15.8–21.4	15.0–19.5	16.8–18.5
Pelvic-fin length	34.0–38.4	13.3–14.7	29.4–37.4	21.9–24.8
Head length (mm)	4.0–4.4	4.0–4.4	3.9–4.3	3.8–4.2
Percent of head length				
Head depth	63.5–68.8	64.3–69.9	61.6–66.5	66.5–68.7
Head width	60.7–63.5	62.1–66.8	56.9–61.4	56.7–62.9
Snout length	18.8–21.3	16.9–21.7	14.7–16.6	14.2–17.9
Lower jaw length	10.6–12.5	10.9–12.7	4.7–8.5	5.4–5.5
Eye diameter	40.7–46.8	41.1–44.5	41.2–45.1	42.8–45.9
Interorbital diameter	43.1–47.4	43.4–48.9	33.8–35.8	34.6–36.1

Description

Morphometric data are presented in Table 1. Maximum size 17.9 mm SL. Dorsal profile of body approximately straight. Ventral profile slightly convex from lower jaw to pelvic-fin insertion, nearly straight between anal-fin origin and caudal peduncle. Anterior portion of body cylindrical, about as wide as deep, becoming laterally compressed posterior to anal-fin origin.

Dorsal fin filamentous in males, with first two and last two dorsal-fin rays filamentous; dorsal fin rounded in females, its origin at vertical through insertion of first or second anal-fin ray. Anal fin short and rounded in males, with penultimate anal-fin ray elongated; anal fin rounded in females. Caudal fin fan-shaped roughly truncate. Pectoral fin rounded, its posterior margin reaching vertical through point just posterior to pelvic-fin base. Pelvic fin elongated and filamentous in males, reaching end of anal-fin base; shorter in females reaching urogenital opening. Pelvic-fin bases separated medially by interspace broader than width of pelvic-fin base. Dorsal-fin rays 6*(9), 7(10), 8(1); anal-fin rays 9(1), 10(18), 11*(7); caudal-fin rays 18(6), 19(5), 20*(8), 21(4), 22(2); pectoral-fin rays 9*(17), 10(5); pelvic-fin rays 6.

Frontal squamation G-patterned. Cephalic lateral line system: anterior portion of supraorbital section closed in a long and straight canal with two pores, posterior portion an open groove, with three exposed neuromasts; anterior infra-orbital section an open shallow groove, with three or four neuromasts; middle infra-orbital section, just below orbit, with 10 to 11 minute neuromasts; posterior infra-orbital section, with two pores; preopercular canal with five pores; mandibular section represented by a single neuromast in vertical through corner of mouth. In juveniles, closed canals not completely formed and represented by shallow grooves instead (Fig. 10).

Longitudinal series of scales 24*(11), 25(4); transverse series of scales 6. Total vertebrae 27(1), 28(2), 29(2), 13–14 precaudal and 13–15 caudal vertebrae. First proximal radial of dorsal-fin between neural spine of vertebrae 9 and 10 or 10 and 11. First proximal radial of anal fin between pleural rib of vertebrae 9 and 10 or 10 and 11. Gill rakers on first branchial arch 8. Branchiostegal rays 4.

Colouration in alcohol (Fig. 12**).** Overall colouration of body pale yellowish brown, with a reticulate pattern due to concentration of small melanophores on scale border. Dorsum dark brown with melanophores concentrated on scale border. Melanophores on nape and along dorsal midline between nape and caudal-fin base. Melanophores forming a longitudinal stripe on ventral midline between isthmus and caudal-fin base. Dark brown chromatophores along whole mid-body line of flank, between pectoral-fin insertion and caudal peduncle. Head overall colouration pale yellowish brown. Dark brown melanophores on dorsal part of head. Infraorbital bar dark brown. Iris black, lighter close to pupil. All fins hyaline, with small melanophores arranged on fin membranes; in males, anal fin with melanophores concentrated on penultimate anal-fin ray and black spots regularly distributed on its base; in males, dorsal fin with melanophores concentrated on its margin and along filamentous dorsal-fin extensions; in males, melanophores concentrated on caudal-fin margin.

Colouration in life. Males (Fig. 13A). Side of body bright bluish green. Ventral region bright blue between head and caudal peduncle. Side of head bright blue, dorsal portion greenish brown; infraorbital bar black, extending to ventral portion of eye; mouth orange. Iris silver. Anal fin bright yellow with small black spots at its base; filament black. Dorsal fin bright yellow; distal margin black; filaments black. Caudal fin bright yellow; distal margin black. Pectoral fin hyaline. Pelvic fin bright yellow.

Females (Fig. 13B). Side of body light greyish brown; anterior region of flank bright silver between opercular aperture and anal-fin insertion. Dorsum light brown. All fins hyaline.

Distribution and habitat. *Congopanchax myersi* is known only from the swampy islands of Malebo Pool near Kinshasa and Brazaville, and from small tributaries that flow into Malebo Pool (Iyaba et al. 2013), in the lower Congo basin (Fig. 11). It is found in slow flowing water near the shore, generally associated with aquatic or riparian vegetation (Wildekamp 1995). According to the IUCN red list for Central Africa, *C. myersi* is considered an endangered species due to the urbanization process, sewage discharges and toxic substances such as oil from cars and boat traffic, all of which are intense at Malebo Pool (Stiassny et al. 2011).

Congopanchax brichardi Poll, 1971

Fig. 15

Congopanchax brichardi Poll, 1971: 304 (original description; Liyeke, isolated swamp near the margin of Tshuapa River, on the road between Boende–Watsi, 2 km from Boende, Democratic Republic of Congo).

Material examined. All from the Congo River basin. Democratic Republic of Congo: Equateur Province: MRAC 168566, 1 specimen (holotype), 16.0 mm SL; Liyeke, isolated swamp near the

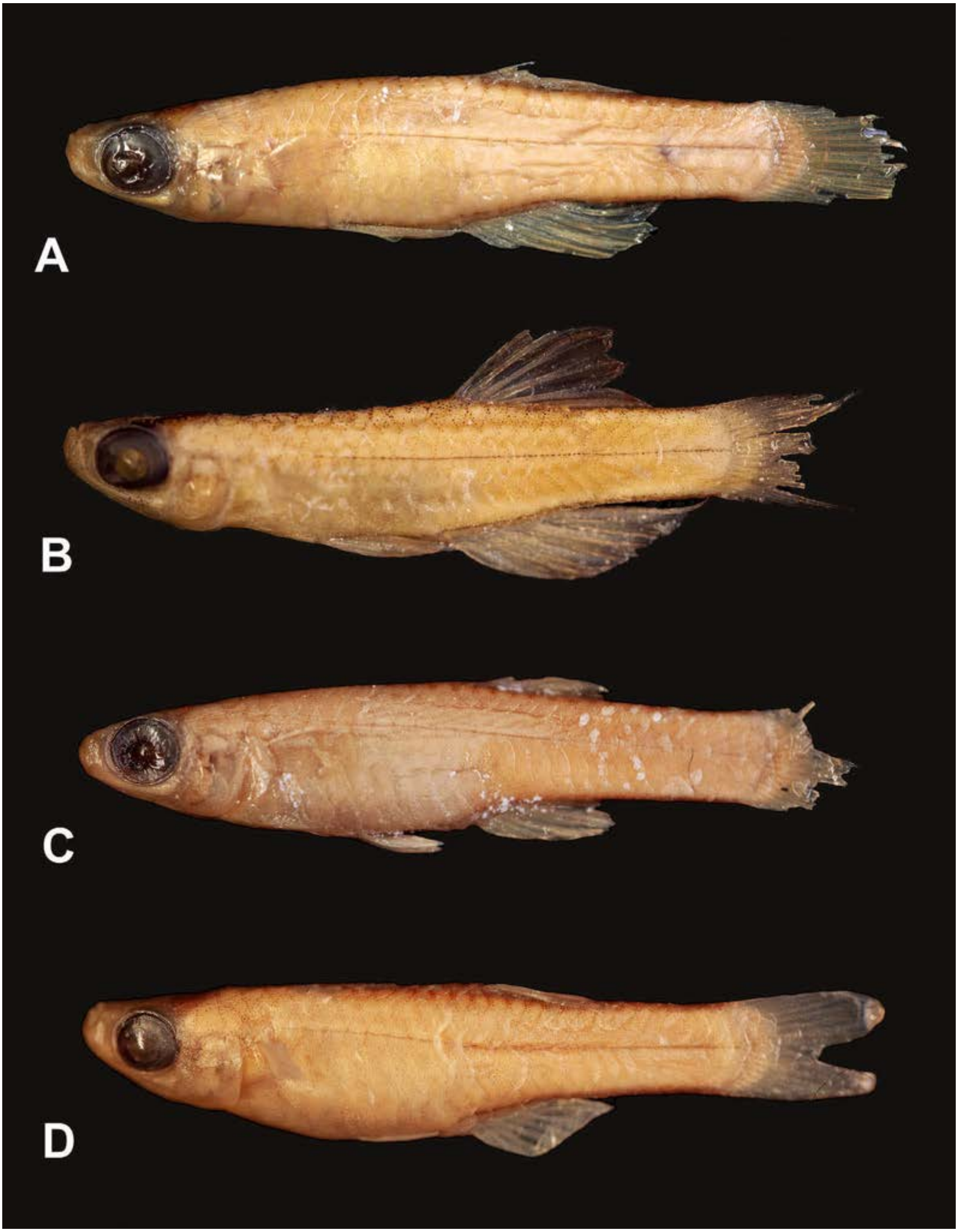

Fig. 12. *Congopanchax myersi*. **A.** MRAC 86801, male (holotype) 17.3 mm SL, Atena Island, Malebo Pool, Democratic Republic of Congo; **B.** MRAC 117977−117990, male, 15.5 mm SL, Malebo Pool, Democratic Republic of Congo; **C.** MRAC 86802, female (paratype) 16.6 mm SL, Atena Island, Malebo Pool, Democratic Republic of Congo; **D.** MRAC 117977−117990, female, 16.6 mm SL, Malebo Pool, Democratic Republic of Congo.

Fig. 13. Colouration in life of *Congopanchax myersi* (aquarium specimens): **A.** male; **B.** female. Photographs by John Stel.

margin of Tshuapa River, on the road between Boende-Watsi, 2 km from Boende, 00°14' S 20°52' E; P. Brichard, Feb. 1970. – MRAC 168567, 1 specimen (paratype), 14.9 mm SL; same as holotype. – MRAC 168568–168573, 6 specimens (paratypes), 14.3–16.1 mm SL; same as holotype. – MRAC 96684, 1 specimen, 16.3 mm SL; Bokuma, 00°06' S 18°41' E; P. Lootens, 1954. – MRAC 175803–175810, 8 specimens, 14.1–16.0 mm SL; Boende, 00°14' S 20°50' E; P. Lootens, 1–28 Feb. 1966. – MRAC 175811, 1 specimen, 13.0 mm SL; Boende, 00°14' S 20°50' E; P. Lootens, 1–28 Feb. 1966. – MRAC 99-078-P-0009–0012, 4 specimens, 12.7-18.4 mm SL; Mbandaka, 0°3'32'' N 18°15' 14'' E; M. Van Roten, 10 Aug. 1998. – MRAC 102437–102539, 98 specimens, 5.3–15.2 mm SL; Bwalanga, Esobe de Lolo lake, about 10 km from Bikoro, 00°54' S 18°06' E; G. Marlier, 30 Sep. 1955. – MRAC 102540–102542, 3 specimens, 13.6–15.2 mm SL; Bwalanga, Esobe de Lolo lake, about 10 km from Bikoro, 00°54' S 18°06' E; G. Marlier, 30 Sep. 1955. – MRAC 102543–102546, 4 specimens (c&s), 12.1–14.9 mm SL; Bwalanga, Esobe de Lolo lake, about 10 km from Bikoro, 00°54' S 18°06' E; G. Marlier, 30 Sep. 1955. – MRAC A9-024-P-0010–0011, 2 specimens, 12.5–15.5 mm SL; Lofofe River, 2°06'46'' S 21°43'54'' E; Danadu, J. Snoeks, alt: 334 m. – IRSNB 19475, 4 specimens, 12.4–13.6 mm SL; Mbandaka, on the margin of Congo River, 0°3'32'' N 18°15'14'' E; R. Kiss, Jul. 1979. – IRSNB 19191, 23 specimens (1 c&s), 13.3–18.8 mm SL; Eala, about 3 km from Ruki River mouth, 0°2'29'' N 18°20'08'' E; R. Kiss, Mar-May, 1978.

Diagnosis. *Congopanchax brichardi* is distinguished from *C. myersi* by: bright blue metallic colouration on side of body of males (Fig. 15A) (vs. bright bluish green metallic colouration; Fig. 13A); anal-fin base, dorsal-fin base and pelvic fin of males bright orange (Fig. 15A) (vs. bright yellow; Fig. 13A). It is further distinguished by: presence of a longer anal-fin base in females 10.9–11.4 % SL (vs. 7.6–10.5 % SL); shorter pectoral fin in males 15–19.5 % SL (vs. 19.7–23.2 % SL); longer pelvic fin in females 21.9–24.8 % SL (vs. 13.3–14.7 % SL); shorter interorbital distance 33.8–36.1 % HL (vs. 43.1–48.8 % HL); shorter snout in males 14.7–16.6 % HL (vs. 18.8–21.3 % HL); shorter lower jaw 4.7–8.5 % HL (vs. 10.6–12.7 % HL) (Table 1).

Description

Morphometric data are presented in Table 1. Maximum recorded adult size 18.8 mm SL. Dorsal profile of body approximately straight. Ventral profile slightly convex from lower jaw to pelvic-fin insertion, nearly straight between anal-fin origin and caudal peduncle. Anterior portion of body cylindrical, about as wide as deep, becoming laterally compressed posterior to anal-fin origin.

Dorsal fin filamentous in males, with first two and last dorsal-fin rays filamentous; dorsal fin rounded in females, dorsal-fin origin at vertical through insertion of first or second anal-fin ray. Anal fin short and rounded in males, with penultimate anal-fin ray elongated; anal fin rounded in females. Caudal fin fan-shaped roughly truncate. Pectoral fin rounded, its posterior margin reaching vertical through a point just posterior to pelvic-fin base. Pelvic fin elongated and filamentous in males, reaching the end of anal-fin base; shorter in females reaching between urogenital opening and base of first anal-fin ray. Pelvic-fin bases separated medially by interspace broader than width of each pelvic-fin base. Dorsal-fin rays 6* (5), 7 (17), 8 (3); anal-fin rays 9 (1), 10* (22), 11 (6); caudal-fin rays 19 (12), 20 (5), 21* (7), 22 (5), 23 (1), 24 (1); pectoral-fin rays 9* (12), 10 (16), 11 (3); pelvic-fin rays 6.

Frontal squamation G-patterned. Cephalic lateral line system: anterior portion of supraorbital section closed, in a long and straight canal with two pores, posterior portion an open groove, with three exposed neuromasts; anterior infra-orbital section an open shallow groove, with three or four neuromasts; middle infra-orbital section, just below orbit, with 8 to 10 minute neuromasts; posterior infra-orbital section, with two pores; preopercular canal with five pores; mandibular section represented by a single neuromast in vertical through corner of mouth. In juveniles, closed canals not completely formed and represented by shallow grooves instead (Fig. 10).

Longitudinal series of scales 24* (9), 25 (9); transverse series of scales 6. Total vertebrae 27 (1), 28 (4), 12–14 precaudal and 14–15 caudal vertebrae. First proximal radial of dorsal-fin between neural spine of vertebrae 9 and 10. First proximal radial of anal-fin between pleural rib of vertebrae 9 and 10 or 10 and 11. Gill rakers on first branchial arch 8. Branchiostegal rays 4.

Colouration in alcohol (Fig. 14)**.** Overall colouration of body pale yellowish brown, with reticulate pattern due to small melanophores concentration on scale border in males. Dorsum dark brown with melanophores concentrated on scale border. Melanophores on nape and along dorsal midline between nape and caudal-fin base. Melanophores forming longitudinal stripe on ventral midline between isthmus and caudal-fin base. Dark brown melanophores along whole mid-body line of flank, between pectoral-fin insertion and caudal peduncle. Head overall colouration pale yellowish brown. Dark brown melanophores on dorsal part of head. Infraorbital bar dark brown. Iris black, lighter close to pupil; dark pigment concentrated on external margin of eye. All fins hyaline, with small melanophores arranged on fin membranes; in males, anal fin with melanophores concentrated on penultimate anal fin ray and black spots regularly distributed on its base; in males, dorsal fin with melanophores concentrated on its margin and along filamentous dorsal-fin extensions; in males melanophores concentrated on caudal-fin margin.

Colouration in life. Males (Fig. 15A). Side of body bright metallic blue. Ventral region bright blue between head and caudal peduncle. Side of head bright blue, dorsal portion greenish brown; infraorbital bar black, extending to eye ventral portion; mouth orange. Iris silver. Anal-fin bright orange with small black spots at its base; filament orange. Dorsal-fin bright orange; distal margin and filaments in dominant males black, bright orange in non-dominant males. Caudal fin dark orange; distal margin black. Pectoral fin hyaline. Pelvic fin bright orange.

Females (Fig. 15B). Side of body light greyish brown; anterior region of flank bright silver between opercular aperture and anal fin insertion. Dorsum light brown. All fins hyaline.

Distribution, habitat and ecology. *Congopanchax brichardi* is known from the middle Congo River basin, along the Tshuapa River drainage and its main tributaries, the Salonga, Lofofe, and Luilaka river drainages (Poll 1971, Iyaba & Stiassny 2013). It is also known to occur in Mfimi River (Stiassny et al. 2021), Lake Tumba, Lake Mai-Ndombe (Matthes 1964, Schliewen 2014) and along the Congo River swampy margins between Lisala and Bumba (Fig. 11). It is usually seen in slow flowing blackwater rivers and lakes, near the margin associated with marginal vegetation, floating meadows but

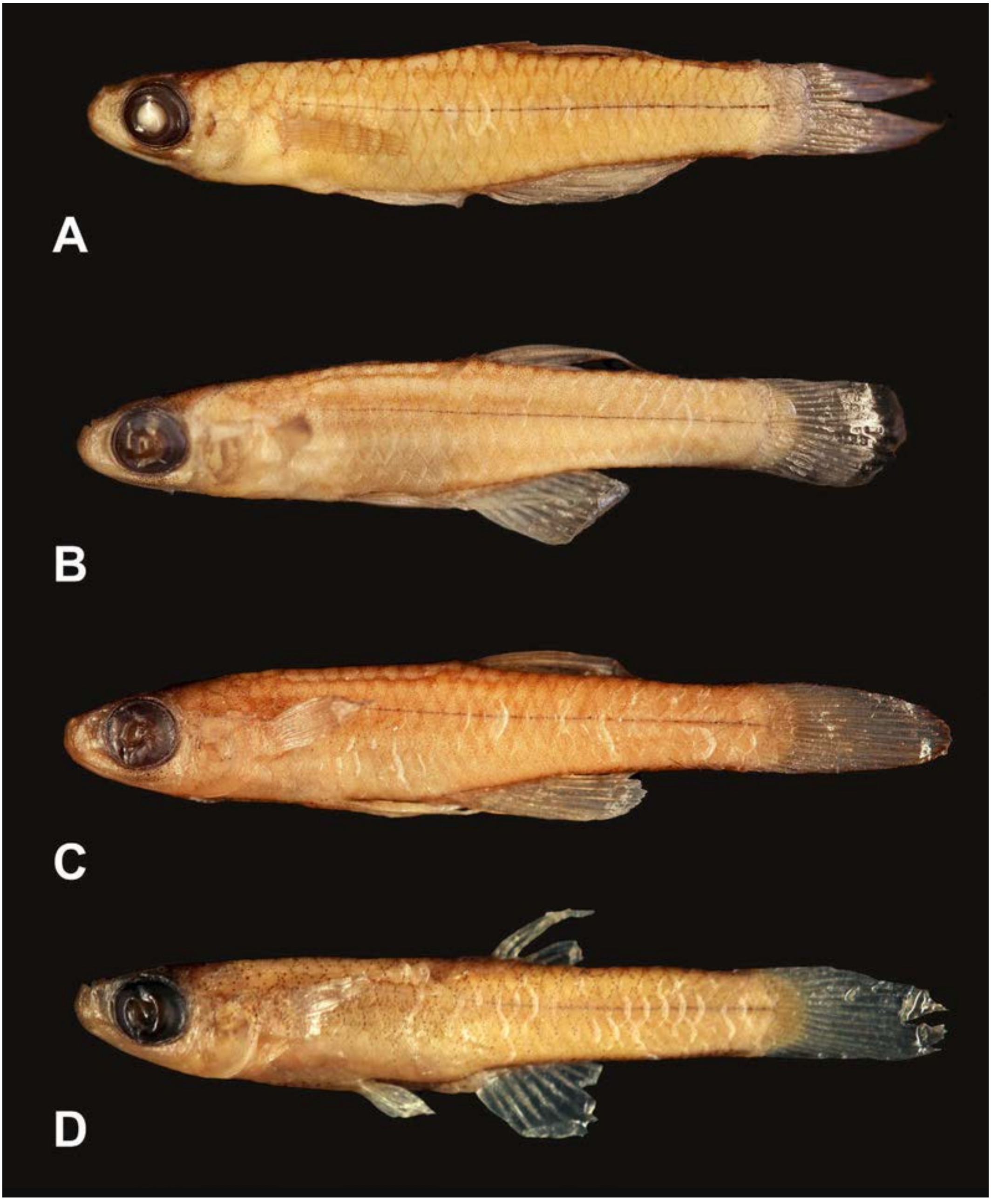

Fig. 14. *Congopanchax brichardi*: **A.** MRAC 102537–102546, 16.7 mm SL, Bwalanga mare de l'Esobe de Lolo, Democratic Republic of Congo; **B.** MRAC 168568–168573, male, 15.3 mm SL, Liyeke, 2 km from Boende, Democratic Republic of Congo; **C.** MRAC 176139–176159, male, 16.9 mm SL, Boende, Democratic Republic of Congo; **D.** MRAC 176139–176159, female, 15 mm SL, Boende, Democratic Republic of Congo.

also among lake shores with laterite rocks. Matthes (1964) reported a microphagous and planctophagous alimentary habit for *C. brichardi*, in which small Crustacea (Cladocera and Copepoda) and small insect larvae (Chironomidae and Ceratopogonidae) were the main items found in its stomach content.

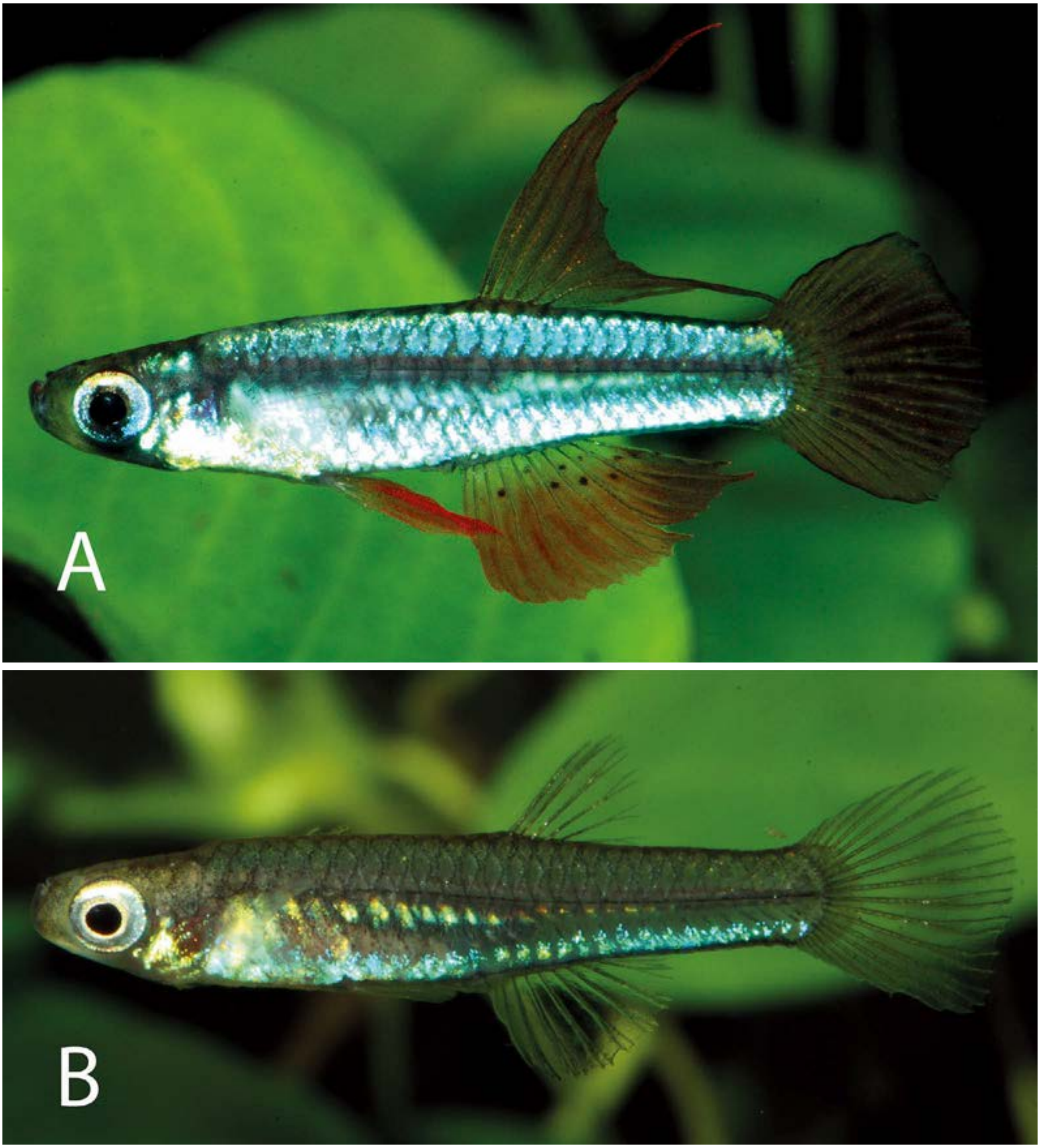

Fig. 15. Colouration in life of *Congopanchax brichardi* (aquarium specimens): **A.** male; **B.** female. Photographs by Heinz Ott.

Fig. 16. Miniature African freshwater fishes. Cypinodontiformes: **A.** *Congopanchax brichardi (*photo: H. Ott); **B.** *Poropanchax stigmatopygus* (photo: R. Tate); **C.** *Hylopanchax moke* (photo: T. Terceira); **D.** '*Lacustricola*' *pygmaeus* (photo: R. Bills); **E.** *Hylopanchax thysi* (photo: L. Chirio); **F.** *Foerschichthys nigeriensis* (photo: J. Stel); **G.** *Fenerbahce formosus* (photo: H. Ott); **H.** *Fenerbahce devosi* (photo: H. Ott); **I.** *Epiplatys duboisi* (photo: H. Ott). Cypriniformes: **J.** *Enteromius candens* (photo: J. Stel); **K**. *Enteromius sylvaticus* (photo: R. Allgayer); **L.** *Barboides* sp. (photo: J. Stel); **M.** *Enteromius hulstaerti* (photo: J. Van der Zee). Characiformes: **N.** *Dundocharax bidentatus* (photo: R. Tate); **O.** *Neolebias lozii* (photo: R. Bills); **P.** *Nannocharax rubensteini* (photo: J. Sullivan); **Q.** *Neolebias powelli* (photo: J. Stel); **R.** *Bathyaethiops baka* (photo: U. Schliewen); **S.** *Lepidarchus adonis* (photo: R. Tate). Siluriformes: **T.** *Zaireichthys kunenensis* (photo: P. Bragança); **U.** *Zaireichthys pallidus* (photo: R. Bills). Cichliformes: **V.** *Nanochromis minor* (photo: A. Lamboj).

▷

A

Congopanchax brichardi Poll, 1971

B

Poropanchax stigmatopygus Wildekamp & Malumbres 2004

C

Hylopanchax moke Van der Zee, Sonnenberg & Schliewen, 2013

D

'Lacustricola' pygmaeus Bragança, Skelton, Bills, Tweddle & Chakona, 2021

E

Hylopanchax thysi Bragança, Van der Zee, Sonnenberg & Vreven, 2020

F

Foerschichthys nigeriensis (Brüning, 1929)

G

Fenerbahce formosus (Huber, 1979)

H

Fenerbahce devosi Sonnenberg, Woeltjes & Van der Zee, 2011

I

Epiplatys duboisi Poll, 1952

J

Enteromius candens (Nichols & Griscom 1917)

K

Enteromius sylvaticus (Loiselle & Welcomme 1971)

L

Barboides britzi Conway & Moritz, 2006

M

Enteromius hulstaerti (Poll, 1945)

N

Dundocharax bidentatus Poll, 1967

O

Neolebias lozii Winemiller & Kelso-Winemiller 1993

P

Nannocharax rubensteini (Jerep & Vari 2013)

Q

Neolebias powelli Teugels & Roberts 1990

R

Bathyaethiops baka Moritz & Schliewen, 2016

S

Lepidarchus adonis Roberts, 1966

T

Zaireichthys kunenensis Eccles, Tweddle & Skelton, 2011

U

Zaireichthys pallidus Eccles, Tweddle & Skelton, 2011

V

Nanochromis minor Roberts & Stewart 1976

Table 2. Updated list of African freshwater miniature fishes. IUCN status abbreviations: CR, critically endangered; DD, data deficient; EN, endangered; LC, least concern; NE, not evaluated; VU, vulnerable.

Species	Size at maturity (mm)	Maximmum size (mm)	Conway & Moritz (2006)	This study
Clupeiformes				
Clupeidae				
Thrattidion noctivagus Roberts, 1972	?	21.4	x	
Gonorhychiformes				
Kneriidae				
Grasseichthys gabonensis Géry 1964	?	20.2	x	
Cypriniformes				
Cyprinidae				
Barboides britzi Conway & Moritz, 2006	12.6	12.9	x	
Barboides gracilis Brüning, 1929	13.7	22.5	x	
Enteromius candens (Nichols & Griscom, 1917)	?	26.0	x	
Enteromius erythrozonus (Poll & Lambert, 1959)	?	26.0	x	
Enteromius hulstaerti (Poll, 1945)	?	30.0*		x
Enteromius kissiensis (Daget, 1954)	?	16.5		x
Enteromius nigrifilis (Nichols, 1928)	?	22.0		x
Enteromius nigroluteus (Pellegrin, 1930)	?	26.0	x	
Enteromius papilio (Banister & Bailey, 1979)	?	20.7		x
Enteromius pumilus (Boulenger, 1901)	?	23.0	x	
Enteromius stigmatopygus (Boulenger, 1903)	?	24.0		x
Enteromius sylvaticus (Loiselle & Welcomme, 1971)	?	19.0	x	
Enteromius tongaensis (Rendahl, 1935)	?	25.0	x	
Garra lancrenonensis Blache & Miton, 1960	?	26.0	x	
Neobola nilotica Werner, 1919	?	20.0		x
Characiformes				
Alestidae				
Alestion rapax Roberts, 2019	?	16.8		x
Bathyaethiops baka Moritz & Schliewen, 2016	?	24.1		x
Lepidarchus adonis Roberts, 1966	?	21.0	x	
Virilia pabrensis (Roman, 1966)	18.8–19.7	29.5		x
Distichodontidae				
Dundocharax bidentatus Poll, 1967	?	19.0	x	
Neolebias ansorgii Boulenger, 1912	?	26.0	x	
Neolebias axelrodi Poll & Gosse, 1963	?	18.3	x	
Neolebias lozii Winemiller & Kelso-Winemiller, 1993	?	18.0		x
Neolebias powelli Teugels & Roberts, 1990	?	16.2	x	
Nannocharax rubensteini (Jerep & Vari, 2013)	?	25.8		x
Siluriformes				
Amphiliidae				
Zaireichthys kafuensis Eccles, Tweddle & Skelton, 2011	?	24.2		x
Zaireichthys kunenensis Eccles, Tweddle & Skelton, 2011	?	25.3		x
Zaireichthys lacustris Eccles, Tweddle & Skelton, 2011	17.0	22.1		x
Zaireichthys pallidus Eccles, Tweddle & Skelton, 2011	?	25.7		x
Zaireichthys wamiensis (Seegers, 1989)	?	25.0		x
Zaireichthys zonatus Roberts, 1968	?	24.5		x
Psammphiletria delicata Roberts, 2003	?	20.5		x
Psammphiletria nasuta Roberts, 2003	?	23.7		x
Tetracamphilius clandestinus Roberts, 2003	?	19.5		x

References	Environment	Ichthyofaunal Province	IUCN status
Roberts 1972a: 2	main river, lentic	Lower Guinea	DD
Géry 1964: 4806	rainforest streams	Lower Guinea, Congo basin	VU
Conway & Moritz 2006: 74	lowland/swamp forest	Upper Guinea	NE
Loiselle & Welcomme 1971: 13; Thys van de Audenaerde 1971: 139	lowland/swamp forest	Nilo-Sudanic, Lower Guinea	VU
Lévêque & Daget 1984: 237	lowland/swamp forest	Congo basin	LC
Lévêque & Daget 1984: 243	lowland/swamp forest	Congo basin	DD
Lévêque & Daget 1984: 250	lowland/swamp forest	Congo basin	LC
Lévêque & Daget 1984: 259	savanah river	Nilo-Sudanic	DD
Lévêque & Daget 1984: 274	savanah river	Congo basin	DD
Lévêque & Daget 1984: 274	lowland/swamp forest	Lower Guinea	EN
Banister & Bailey 1979: 221	lowland/swamp forest	Congo basin	DD
Lévêque 2003: 393	savanah river	Nilo-Sudanic	LC
De Weirdt et al. 2007: 484	savanah river	Nilo-Sudanic	LC
Loiselle & Welcomme 1971: 2,8	rainforest streams	Upper Guinea	VU
Lévêque & Daget 1984: 291	savanah river	Nilo-Sudanic	DD
Lévêque & Daget 1984: 303	savanah river	Nilo-Sudanic	DD
Werner 1919	savanah river	Nilo-Sudanic	DD
Roberts 2019: 84	rainforest stream	Congo basin	NE
Moritz & Schliewen 2016: 477	rainforest, margin	Congo basin	NE
Roberts 1966: 210	rainforest, margin	Upper Guinea	VU
Roberts 1967; Zanata & Vari 2005: 5	?	Upper Guinea	LC
Daget & Gosse 1984: 193	savanah swamp	Congo basin	DD
Gosse et al. 2003: 307	rainforest streams	Niger Delta, Lower Guinea, Congo basin	LC
Gosse et al. 2003: 311	rainforest streams	Upper Guinea	EN
Winemiller & Kelso-Winemiller 1993: 112	savanah swamp	Zambezi	CR
Gosse et al. 2003: 311	rainforest streams	Upper Guinea - Niger Delta	EN
Jerep & Vari 2013: 31	rainforest streams	Congo basin	NE
Eccles et al. 2011: 8	sandy/gravel substrate	Zambezi	NE
Eccles et al. 2011: 10	sandy/gravel substrate	Zambezi	NE
Eccles et al. 2011: 12	sandy/gravel substrate	Zambezi	LC
Eccles et al. 2011: 18	sandy/gravel substrate	Zambezi	NE
Eccles et al. 2011: 25	sandy/gravel substrate	East Africa	VU
Roberts 2003: 94	sandy/gravel substrate	Congo basin	DD
Roberts 2003: 102	sandy/gravel substrate	Congo basin	NE
Roberts 2003: 102	sandy/gravel substrate	Congo basin	NE
Roberts 2003: 106	sandy/gravel substrate	Congo basin	DD

Table 2 continued.

Species	Size at maturity (mm)	Maximmum size (mm)	Conway & Moritz (2006)	This study
Cyprinodontiformes				
Nothobranchidae				
Aphyosemion koungueense Sonnenberg, 2007	?	24.3		
Aphyosemion teugelsi Van der Zee & Sonnenberg, 2010	?	24.2		x
Epiplatys duboisi Poll, 1952b	?	30.0*		x
Fenerbahce devosi Sonnenberg, Woeltjes & Van der Zee, 2011	?	25.9		x
Fenerbahce formosus (Huber, 1979)	?	21.8		x
Foerschichthys nigeriensis (Brüning, 1929)	?	25.0		x
Procatopodidae				
Congopanchax brichardi Poll, 1971	?	18.0	x	
Congopanchax myersi (Poll, 1952a)	?	21.0	x	
Hylopanchax moke Van der Zee, Sonnenberg & Schliewen, 2013	?	21.1		x
Hylopanchax multisquamatus Bragança, Van der Zee, Sonnenberg & Vreven, 2020	?	22.6		x
Hylopanchax thysi Bragança, Van der Zee, Sonnenberg & Vreven, 2020	?	22.6		x
"*Lacustricola*" *chobensis* (Fowler, 1935)	?	25.9		x
"*Lacustricola*" *petnehazyi* (Nagy & Vreven, 2018)	?	19.1		x
"*Lacustricola*" *pygmaeus* Bragança, Skelton, Bills, Tweddle & Chakona, 2021	?	20.5		x
Lacustricola usanguensis (Wildekamp, 1977)	?	24.0		x
"*Micropanchax*" *camerunensis* (Radda, 1971)	?	22.5		x
Micropanchax keilhacki (Ahl, 1928)	?	22.3	x	
Micropanchax loati (Boulenger, 1901)	?	25.0		x
Micropanchax pfaffi (Daget, 1954)	?	22.5		x
Poropanchax scheeli (Roman, 1971)	?	23.3		x
Poropanchax stigmatopygus Wildekamp & Malumbres, 2004	?	24.3		x
Cichliformes				
Cichlidae				
Nanochromis minor Roberts & Stewart, 1976	?	23.8	x	

Updated list of miniature African freshwater fishes

Table 2 presents an updated list of African freshwater miniature fishes, which now includes 58 species. We also provide information about their geographical distributions, habitats and conservation status. Several miniature African freshwater fishes are illustrated in Figure 16 to show their diversity in life colouration which ranges from drab-coloured to highly colourful species.

Discussion

Since *Congopanchax* was erected by Poll (1971), subsequent taxonomic classifications for the genus were provided, in most cases, without justification. Parenti (1981) considered *Congopanchax* a subgenus of a more inclusive *Aplocheilichthys* Duméril, 1861, without providing detailed information on this miniaturized taxon. Huber (1999), considered *Congopanchax* a subgenus of *Poropanchax* Clausen, 1967 due to the presence of a distinct outer dark band on the caudal fin in males, filamentous pelvic fins, two bright metallic blue zones along the flank, a cylindrical body, small size, a narrow transversal profile of the mouth, a slender and elongated caudal fin and the head lateral line supraorbital system with 2–3 pores. However, a slender and elongated caudal fin is not present in *Congopanchax*, and despite the presence of a tubular supraorbital system in both genera, *Poropanchax* species have a wide supraorbital canal with large pores, while in *Congopanchax* the canal is narrow and straight, with small pores (Fig. 10). According to the present study, *Congopanchax* is distinguished from *Poropanchax* by the following characters, some of them probably

References	Environment	Ichthyofaunal Province	IUCN status
Sonnenberg 2007: 9	rainforest streams	Lower Guinea	NE
Van der Zee & Sonnenberg 2010: 61	rainforest streams	Congo basin	NE
Poll 1952: 299	lowland rainforest streams	Congo basin	LC
Sonnenberg et al. 2011: 5	lowland rainforest streams	Congo basin	NE
Sonnenberg et al. 2011: 5	lowland rainforest streams	Congo basin	LC
Romand 1990: 639	rainforest streams	Nilo-Sudanic, Upper Guinea	LC
Poll 1971: 307	lowland/swamp forest	Congo basin	EN
Poll 1971: 308	lowland/swamp forest	Congo basin	LC
Van der Zee et al. 2013: 46	lowland/swamp forest	Congo basin	NE
Bragança et al. 2020: 660	rainforest streams	Lower Guinea	NE
Bragança et al. 2020: 660	rainforest streams	Lower Guinea	NE
Bragança et al. 2021: 136	savanah swamp	Zambezi	NE
Nagy & Vreven 2018: 161	savanah swamp	Congo basin	NE
Bragança et al. 2021: 133	savanah swamp	Zambezi	NE
Wildekamp 1977: 107	savanah swamp	East Africa	VU
Radda 1971: 163	lowland/swamp forest	Lower Guinea/Congo basin	LC
Lederoun et al. 2018: 146	savanah swamp	Upper Guinea	LC
Sandon 1950: 52	savanah swamp	Nilo-Sudanic	LC
Daget 1954: 321	savanah swamp	Nilo-Sudanic	LC
Wildekamp & Malumbres 2004: 62	lowland/swamp forest	Lower Guinea	LC
Wildekamp & Malumbres 2004: 63	lowland/swamp forest	Lower Guinea	LC
Daget 1991: 271	river rapids	Congo basin	VU

reductions and losses linked to miniaturization: absence of teeth in the fourth ceratobranchial and second pharyngobranchial, size reduction in the second and fourth pharyngobranchial, presence of straight epibranchials, greatly reduced dorsal process of maxilla, short basipterygium ventral process, narrow cleithrum-coracoid foramen, closed preopercular latero-sensory canal with five pores, open infraorbital canal anterior portion, long and straight anterior section of supraorbital canal and dorsal and anal fins symmetrically arranged above each other. Previously, Bragança & Costa's (2019) molecular analysis recognized both genera as belonging to different and not related lineages.

Ghedotti (2000) considered *Congopanchax* a subgenus of *Micropanchax* Myers, 1924, the latter being diagnosed by the presence of a narrow and elongated retroarticular. However, this taxonomic decision was taken without confirmation of this diagnostic character in *Congopanchax*, since no specimen was prepared for osteological studies. In fact, both *C. myersi* and *C. brichardi* have a deep and robust retroarticular rather than a narrow and elongated one.

Congopanchax is herein corroborated as a valid genus diagnosed by the presence of eight exclusive character states (see comparative material in Supplementary file 1): presence of a ventral cleft in the anguloarticular, concave anterior margin of the autopalatine, bifilamentous dorsal-fin, infraorbital bar, elongated ventral midline longitudinal stripe reaching head isthmus, short anterior portion of parhypural bone not contacting or slightly overlapping the centrum hypural, and absence of indentation in the posterior margin of premaxilla. Among the aforementioned exclusive traits, a reduced supraoccipital posterior process, a short anterior portion of parhypural not reaching or slightly overlapping the compound caudal centrum, and the absence of indentation in the posterior margin of premaxilla are probably related to *Congopanchax* small size. These exclusive morphological character states support *Congopanchax* as a distinct evolutionary lineage of African lampeye as independently revealed by Bragança & Costa (2019) in their molecular analysis. Ongoing osteological studies also support the placement of *Congopanchax* as the sister group to a clade including the morphologically distinct *Lamprichthys tanganicanus* (Boulenger, 1898), the largest procatopodid species, and species of the genus *Lacustricola* Myers, 1924. However, this hypothesis of relationship, as well as an updated classification of the Procatopodidae is beyond the scope of this paper.

Despite their similar osteological structure, *Congopanchax myersi* and *C. brichardi* are herein recognized as valid species, and differentiated by the possession of distinct colouration pattern, meristic and morphometric characters (see species diagnosis). Poll (1971) pointed out that *C. myersi* can be distinguished from *C. brichardi* by having a slightly deeper body, a wider head, a longer pelvic fin and a wider interorbital space. All these morphometric differences were confirmed in the present study. In addition, *C. myersi* can also be distinguished from *C. brichardi* by the presence of a shorter anal-fin base length in females, a longer pectoral-fin length in males, a shorter pelvic-fin length in females, a longer snout length in males, and a longer lower jaw (see Table 1).

African freshwater miniature fishes

Following the criteria of Weitzman & Vari (1988), Conway & Moritz (2006), listed 24 miniature African freshwater fish species, distributed in seven orders and eight families. Thirty five additional species were included in the present list and one, the gobiid *Pandaka silvana* (Barnard, 1943), was removed because it does not occur in freshwaters (Penrith & Penrith 1972, Whitfield 1994), resulting in a total of 58 miniature freshwater species for the African continent (see Table 2 for references). One additional order, Siluriformes, was added to the list with nine miniature species in the Amphilidae belonging to three genera, *Psammphiletria* Roberts, 2003, *Tetracamphilius* Roberts, 2003, and *Zaireichthys* Roberts, 1968. The order with the largest increase in the number of miniature species, an additional 18 species, is the Cyprinodontiformes. Currently, with a total of 21 species, which corresponds to 36 % of all diversity of miniature African fishes, the order is the one including the most miniatures. It is followed by the Cypriniformes with 26 % of the African miniature fish diversity, and then by Characiformes with 17 % and Siluriformes, with 15 % of the African miniature fishes. The orders Clupeiformes, Cichliformes and Gonorynchiformes each have only one miniature species (Table 2).

Similar to the pattern seen in the African continent, Neotropical Characiformes (41.4 %), Cyprinodontiformes (28.8 %) and Siluriformes (24.2 %) include the highest proportion of miniature species, and the remaining three orders, Cichliformes, Gobiiformes and Clupeiformes together make up around 5 % of the miniatures (Toledo-Piza et al. 2014). The main contrast when comparing the diversity of miniatures in Africa and in the Neotropical region is in the total number of species and families with miniaturized taxa. On the African continent all 58 species are distributed across only nine families, whereas the 215 miniature Neotropical species are distributed across 21 families, some of them such as the Characidae and the Trichomycteridae with miniatures in different subfamilies. However, as it is herein suggested, the study of the diversity of miniatures in Africa has been neglected when compared to similar studies carried out in the Neotropics. We may therefore expect an increase in the number of miniature species to be described from the continent if the interest in miniature African freshwater fish species increases.

Most of the miniature African species occur in streams, rivers and lakes in tropical rainforests under dense forest cover, usually associated with clear black water slow flowing or lentic water bodies in the Lower Guinea (19 %) and Congo (43 %) ichthyogeographical provinces. One exception of this pattern is seen in the Amphiliidae, in which all the species occur in lotic environments and are associated with sandy/gravel substrate. Regarding the conservation status of the African freshwater miniature species, about half of the species have not been evaluated (29 %) or are data deficient (19 %) and 17 species (29 %) are considered to be of least concern (IUCN 2022). Within the threatened categories there are seven vulnerable (12 %), four endangered (7 %), and one critically endangered (2 %) species (IUCN 2022). The relatively high number of miniature species that have not been evaluated raises the concern about their conservation status, especially when considering the higher vulnerability of small sized species to potential threats (Olden et al. 2007, Ripple et al. 2017).

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