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Towards the phylogenetic placement of the enigmatic African genus *Prolabeops* Schultz, 1941

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Abstract

The small cyprinid genus *Prolabeops* Schultz, 1941 is restricted to the Nyong and Sanaga River systems in Cameroon. In the past, the genus had been suggested to be either a member of the Labeoninae, Torinae or the Smiliogastrinae mainly on the basis of morphological similarities, and it is nowadays considered as *incertae sedis* within the Cypriniformes. This study provides the first attempt to reveal the phylogenetic position of *Prolabeops* using molecular data. For this purpose, the authors sequenced a large fraction of the mitochondrial genome (*c.* 13,600 bp), including all mitochondrial protein coding genes, of two *Prolabeops melanhypopterus* specimens and an additional four *Enteromius* specimens. The large-scale phylogenetic analysis was based on an alignment including all mitochondrial protein coding genes of 902 specimens representing *c.* 899 cypriniform species. *Prolabeops* was clearly recovered within the African Smiliogastrinae, forming a weakly supported clade together with *Enteromius jae*, *Enteromius hulstaerti and Barboides gracilis*. The study data underline the urgent need of a thorough taxonomic revision of the small African barbs collectively placed in the genus *Enteromius*.

KEYWORDS
Cyprinidae, Cypriniformes, *Enteromius*, Smiliogastrinae

1 | INTRODUCTION

The order Cypriniformes (*i.e.*, suckers, loaches, algae eaters and carps) accounts for approximately one third of the entire freshwater fish diversity with *c.* 4724 described species (Fricke *et al.*, 2021; Stout *et al.*, 2016). Currently, 23 families are recognized within the order Cypriniformes which are classified into four different suborders: Gyrinocheiloidei, Catostomoidei, Cobitoidei and Cyprinoidei (Fricke *et al.*, 2021). The Cyprinoidei are divided into 12 families, including, among others, the family Cyprinidae *sensu stricto*, commonly referred to as carps and minnows, which are further subdivided into 11 subfamilies (Tan & Armbruster, 2018). Resolving the phylogenetic relationships and providing a robust taxonomic classification of the numerous cyprinid lineages has been subject of many studies (*i.e.*, Betancur *et al.*, 2017; He *et al.*, 2008; Mayden & Chen, 2010; Stout *et al.*, 2016; Yang *et al.*, 2015; Yang, Arunachalam, *et al.*, 2012; Yang, Hirt, *et al.*, 2012). Nevertheless, despite considerable progress in this regard, many cyprinid genera still remain *incertae sedis* as reviewed in Tan and Armbruster (2018). One of these genera is *Prolabeops* Schultz, 1941 which is endemic to Cameroon.

Currently, two species are assigned to the genus *Prolabeops*: *Prolabeops melanhypopterus* (Pellegrin, 1928) and *Prolabeops nyongensis* Daget, 1984. *P. melanhypopterus* is endemic to the Sanaga River system and was originally described as *Barbus melanhypopterus* Pellegrin, 1928

based on two specimens collected in "Lake Monoun" (Mbam River). Pellegrin (1928) suggested a close relationship of his new species with *Barbus* (*Enteromius*) *aboinensis* Boulenger, 1911 or *Barbus* (*Enteromius*) *dolichosoma* Nichols and Griscom, 1917 [later synonymized with *Barbus* (*Enteromius*) *humeralis* Boulenger (1902)], which have meanwhile been assigned to the genus *Enteromius* Cope, 1867. Several years later, Schultz (1941) described a new species for which he also introduced a new genus, *i.e.*, *Prolabeops cameroonensis* Schultz, 1941. The genus is diagnosed by a combination of morphological characters such as the presence of a characteristically formed fleshy pad underneath the lower jaw, a protractile premaxillary and a naked (scaleless) postoccipital area. Apparently not aware of the previously described *B. melanhypopterus*, Schultz (1941) compared his new genus with *Garra* Hamilton, 1822, *Labeobarbus* Rüppell, 1835 and *Labeo* Cuvier, 1816. Further, he suggested that *Prolabeo* Norman, 1932, a monotypic genus endemic to Sierra Leone, might be most closely related to *Prolabeops*.

More than two decades later, Thys van den Audenaerde (1965) sampled additional specimens of *P. cameroonensis* at two sites in the Sanaga River basin, of which one was in the Mbo River (or Mbo'o River) just above the Nachtigal Falls. Based on these new specimens he re-evaluated the relationships of this genus, concluding that *Prolabeops* is neither related to *Labeo* nor with *Prolabeo*. He rather suggested an intermediate phylogentic position between genera *Barbus* (*Labeobarbus*) and *Garra*. He based his hypothesis mainly on morphological similarities of the mouth region of that of *Prolabeops* and *Barbus* (*Labeobarbus*) and the combination of an overall similar body shape of *Prolabeops* and of *Garra* and a naked (scaleless) postoccipital area. In contrast, Poll (1957) had postulated a close similarity of both *Prolabeops* and *Prolabeo* with the genus *Labeo*, however, without providing a detailed argumentation. After additional collections conducted in the Sanaga drainage and the reinvestigation of the type material of *B. melanhypopterus*, Thys van den Audenaerde (1974) synonymized *P. cameroonensis* with *B. melanhypopterus* while retaining *Prolabeops* as a valid genus. Ten years later, a second species of this enigmatic genus, *P. nyongensis* from the Nyong River system was described by Daget (1984). In the same publication Daget (1984) raised doubts concerning a putative close relationship of *Prolabeops* and *Garra* as, in his view, both genera would not share any diagnostic characters. Instead, he argued for a closer relationship of *Prolabeops* with some of the small African barbs (most likely *Enteromius*), based on the scale morphology of *Prolabeops*. Further, he suggested that the naked (scaleless) postoccipital area as well as the fleshy pad underneath the lower jaw represents secondarily derived adaptions to the rheophilic ecology of the genus.

In their comprehensive morphological study on the genus *Garra*, Stiassny and Getahun (2007) provided an overview of labeonin relationships. They considered *Prolabeops* part of the Barbini (=Barbinae) and not Labeonini (=Labeoninae), which, in turn, contrasts with the tentative assignment of *Prolabeops* to Labeonini (=Labeoninae) by Yang, Arunachalam, *et al.* (2012), a view not followed by Tan and Armbruster (2018) as mentioned earlier. The most recent account on the possible relationships of *Prolabeops* was provided by Lavoue (2020), who based his inference mainly on the observations previously made by Daget (1984). According to him the genus is tentatively grouped with the "Afrotropical diploid small barbs" of the subfamily Smiliogastrinae, *i.e.*, the genera *Enteromius*, *Barboides* Brüning, 1929, *Barbopsis* Di Caporiacco, 1926, *Clypeobarbus* Fowler, 1936, *Caecobarbus* Boulenger, 1921 and *Pseudobarbus* Smith, 1841 (the latter being tetraploid).

To the best of the authors' knowledge no molecular phylogenetic study has so far included *Prolabeops* to clarify the taxonomic status of this genus. Therefore, taking advantage of a growing database of mitochondrial genomes for the order Cypriniformes they sequenced a large fraction of the mitochondrial genome of *P. melanhypopterus* to obtain first insights into its phylogenetic positioning.

2 | MATERIALS AND METHODS

2.1 | Taxon sampling and sampling procedures

To assess the phylogenetic affinities of *Prolabeops* the authors sequenced partial mitochondrial genomes of two specimens of *P. melanhypopterus* and an additional four specimens of *Enteromius*. Further, they included all available mitochondrial genomes of the order Cypriniformes from GenBank. In doing so, they aimed to comprehensively represent cypriniform diversity to account for the disputed phylogenetic placement of *Prolabeops* within Cypriniformes. For taxa with more than one mitochondrial genome available they randomly selected one sequence to be included in their data set. Further, they excluded some taxa obtained from GenBank after a first explorative maximum likelihood (ML) analysis because of the highly implausible phylogenetic positioning of the respective GenBank sequences (see Supporting Information Table S1 for further details). Finally, they excluded *Ellopostoma mystax* Tan and Lim, 2002 (family: Ellopostomatidae) and all species of the genus *Paedocypris* Kottelat *et al.*, 2006 (family: Paedocyprididae) from their further analysis. Both families are well-known "rogue taxa," *i.e.*, taxa that are phylogenetically unstable or hard to place (Sanderson & Shaffer, 2002), and, in addition, close phylogenetic relationships with *Prolabeops* are highly unlikely according to previous studies which had extensively explored their affinities (Bohlen & Šlechtová, 2009; Chen *et al.*, 2009; Malmstrøm *et al.*, 2018; Mayden & Chen, 2010; Rüber *et al.*, 2007; Stout *et al.*, 2016). In total, the authors included 902 specimens (*c.* 899 species-level taxa, see Supporting Information Table S1) in their final mitochondrial genome data set, including representatives of the suborders Gyrinocheiloidei ($N = 2$), Catostomoidei ($N = 17$), Cobitoidei ($N = 187$) and Cyprinoidei ($N = 695$) and one characiform species as an out-group.

Samples of *Prolabeops* and *Enteromius* sequenced in this study were collected on various field expeditions to Cameroon and Zambia (Supporting Information Table S1 for detailed sampling information, see Figure 1 for all published locations of *Prolabeops*). Only one *Enteromius* specimen could be identified to the species level, *Enteromius bifrenatus* (Fowler, 1935). As this species is known to be highly variable over its distribution range (see *i.e.*, Skelton, 2001) the authors herein refer to it as *E. bifrenatus* "Kalungwishi." The second sequenced

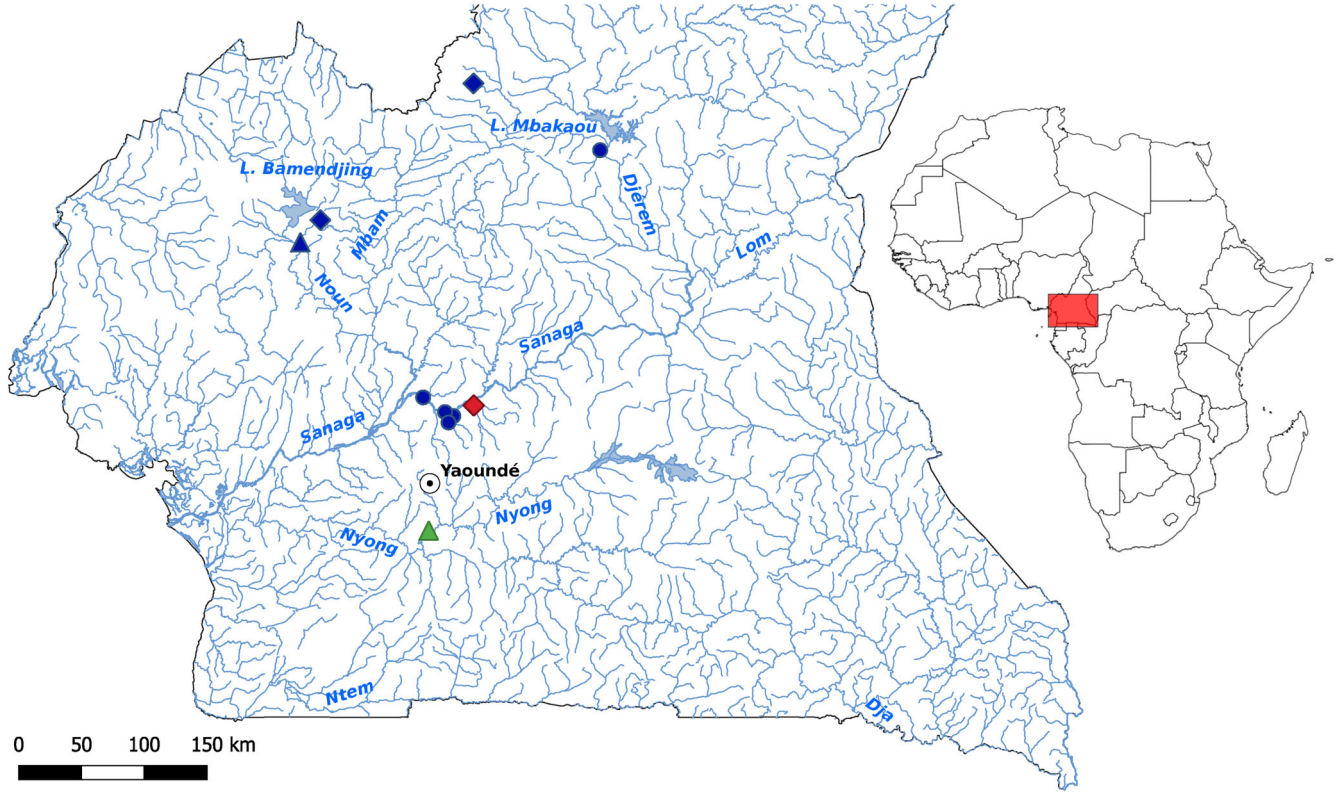

FIGURE 1 Map of Southern Cameroon depicting known sample locations of *Prolabeops*. Dark-blue triangle: type locality of *Prolabeops melanhypopterus*; dark-blue diamonds: paratype locality of *P. melanhypopterus*; dark-blue circles: additional sample locations of *P. melanhypopterus* from Thys van den Audenaerde (1965) and Thys van den Audenaerde (1974); red diamond: sample location of *P. melanhypopterus* sequenced for this study; green triangle: type locality of *Prolabeops nyongensis*. No explicit type location is known for *Prolabeops cameroonensis*. Baseline map is based on shapefiles obtained from DIVA-GIS (http:/diva-gis.org/Data)

Enteromius species could not be identified to species level and most likely represents a new species endemic to the Kalungwishi system.

Freshly caught fish (*i.e.*, using hand-nets, dip and gillnets) were killed by an overdose of an approved fish anaesthetic (*i.e.*, MS222) and photographed in a cuvette. Subsequently a fin clip was taken and fixed in 96% ethanol, and the corresponding specimen was fixed in formalin. The authors followed all applicable national laws and considered all relevant ethical standards for sample collection, which was conducted in accordance with the requirements of local authorities (see in Acknowledgements for more details on permit information).

2.2 | Molecular methods and phylogenetic analysis

Partial mitochondrial genomes were sequenced on an Illumina MiSeq platform (MiSeq Reagent Kit v2; 2X250, Illumina, San Diego, California, USA) by the Sequencing Service of the Ludwig Maximilian University of Munich. For this, genomic DNA was extracted from all samples following a custom CTAB DNA extraction protocol. DNA concentrations were quantified using a spectrophotometer (NanoDrop ND-1000, Thermo Scientific, Wilmington, USA) and adjusted to 25 ng μl^{-1}. Subsequently, the authors amplified a large fragment of the mitochondrial genome (*c.* 13,600 bp, including all mitochondrial protein coding genes) using the TaKaRa LA Taq DNA polymerase kit (TaKaRa Bio Inc., Shiga, Japan) and the primer pair L2508KAW: [5'-CTC GGC AAA CAT AAG CCT CGC CTG TTT.

ACC AAA AAC-3′; (Kawaguchi *et al*., 2001)] and H16461 [5'–CTT CGG ATT ACA AGA CC-3′; (Kisekelwa, 2019)]. For PCR, they adapted the temperature profile from Schedel *et al*. (2019): initial denaturation at 98°C (60 s), followed by 35 cycles of denaturation at 98°C (10 s), annealing at 50°C (60 s), elongation at 68°C (15 min) and a last extension step at 72°C (10 min) for the amplification reactions. The GeneJET Gel Extraction Kit (Thermo Fisher Scientific) was used to purify successfully amplified PCR products which were then adjusted to 0.21 ng μl^{-1}. Finally, library preparations were conducted using the Nextera XT DNA Sample Preparation Kit (Illumina) following the manufacture's protocol until the library normalization step, which was modified to pooling libraries equimolarly based on their fragment size distribution and DNA concentration. The final library pool was subsequently sequenced by the Sequencing Service of the Ludwig Maximilian University of Munich on an Illumina MiSeq platform. Adaptor trimming and quality control of demultiplexed sequencing reads were conducted using Geneious v.11.0.4 (Kearse *et al*., 2012) and the plugin BBDuk Trimmer. Using the "De Novo Assembly" function implemented in Geneious the reads were assembled and the resulting partial mitochondrial genomes were annotated using the mitochondrial

genome of the goldfish (*Carassius auratus*; GenBank accession number: KX505165) as reference. The newly sequenced partial mitochondrial genomes are available under the following GenBank accession numbers ON323515–ON323520 (data will be made available once published; see Supporting Information Table S1).

For the phylogenetic analysis the authors extracted the sequence information of all 13 mitochondrial protein coding genes of the cypriniform mitochondrial genomes obtained from GenBank ($N = 896$) and their six newly sequenced partial mitochondrial genomes. Sequences of individual genes were first aligned using the Geneious alignment tool (default settings) and individually checked for misalignments/ambiguities and trimmed to uniform lengths. Further, in the rare cases of missing or incomplete sequence information of individual genes for some specimens they inserted a multi-N string at the respective position of the corresponding alignment. Single-gene alignments were subsequently concatenated to their final working alignment, resulting in a total alignment of 10,713 bp with relative base frequencies of C = 27.1%, G = 16.5%, A = 27.8% and T = 28.6% and a percentage of missing data close to zero.

This alignment, referred in the following as "Cypriniform data set," was subsequently used to reconstruct an ML tree using the programme IQ-TREE 2.0-rc1 (Nguyen *et al*., 2015) with optimal substitution model (GY + F + R10) as calculated with ModelFinder (Chernomor *et al*., 2016; Kalyaanamoorthy *et al*., 2017) implemented in IQ-TREE and under the Bayesian information criterion (BIC). Further, the authors portioned the data set into first, second and third codon positions and ran 1000 ultrafast bootstrap (BS) replications (Hoang *et al*., 2018; Minh *et al*., 2013). The resulting consensus tree was visualized and edited with FigTree 1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/).

In addition to the global "Cypriniform data set," the authors created an "African Smiliogastrinae data subset" only including all the available species of the African Smiliogastrinae and of the Asian genus *Systomus* McClelland 1838 as an out-group as well as representative species of the genera *Pseudobarbus*, *Sedercypris* Skelton *et al*., 2018 and *Cheilobarbus* Smith, 1841 for which sequence information of at least two mitochondrial protein coding genes (*i.e.*, ATP 6, ATP 8 and cytochrome b) was available on GenBank (see Supporting Information Table S2). The authors incorporated the corresponding sequence data into the subsampled alignment, using the same strategy of concatenating individual gene alignments and filling missing sequence information with multi-N strings as outlined earlier. The resulting alignment included 30 specimens representing 23 species and had a total length of 10,713 bp with approximately 25% of missing data. Using IQ-TREE they conducted an ML analysis on the "African Smiliogastrinae data subset" analogous to the "Cypriniform data set," which allowed them to investigate additional candidate relationships of *Prolabeops* within the African Smiliogastrinae, *i.e.*, specifically with Southern African tetraploid cyprinids. In addition, they conducted a Bayesian Inference (BI) analysis for the sub-set using MrBayes 3.2.7a (Huelsenbeck & Ronquist, 2001; Ronquist *et al*., 2012). Two Markov Chain Monte Carlo (MCMC) runs were simultaneously run for 5 million generations, and tree and parameter sampling occurred every 1000th generation. Upon the completion of the two MCMC runs the authors discarded the first 1.25 million generations as burn-in and subsequently checked the estimated sample size (EES) values for all parameters. All ESS values were well above 200, and a consensus tree was calculated from the remaining trees.

3 | RESULTS

3.1 | Partial mitochondrial genomes

For each of the newly sequenced specimens (two *P. melanhypopterus* and four *Enteromius* spp.) the authors retrieved a single contig (=assembled consensus sequence of all reads covering the PCR-amplified fragment) ranging from 13,541 to 13,572 bp with an average coverage of 670. These contigs included all mitochondrial protein coding genes as well as 18 tRNA genes, but they were missing the sequence information of the two rRNAs (12S and 16S), four tRNAs (tRNA-Phe, tRNA-Pro, tRNA-Thr and tRNA-VAl) and that of the control region (D-loop).

3.2 | Cypriniform phylogenetic relationships based on partial mitochondrial genomes

The ML analysis based on the "Cypriniform data set" recovered the monophyly of all four cypriniform suborders with strong support: Gyrinocheiloidei, Catostomoidei and Cyprinoidei were very strongly supported (BS: 100) and Cobitoidei slightly less strongly supported (BS: 95; see Figure 2). Interrelationship of the four suborders was only moderately supported with Catostomoidei as the earliest-diverging clade of the Cypriniformes and Cobitoidei and Gyrinocheiloidei forming the sister group to the Cyprinoidei. All currently recognized families within Cyprinoidei were recovered as monophyletic with strong support (BS: 100), but interfamilial relationships were only partially resolved with good support. Likewise, the analysis recovered the monophyly of all cyprinid subfamilies with very strong support (BS: 100) except for "Poropuntiinae" (BS: 85) and Smiliogastrinae (BS: 85). Further, this analysis recovered the presence of three major clades within the Smiliogastrinae (see Figure 2, Supporting Information Figure S1). The earliest-diverging lineage (referred herein as Smiliogastrinae group I) encompasses the three tropical Asian genera *Oreichthys* Smith, 1933, *Chagunius* Smith, 1938 and *Eirmotus* Schultz, 1959, contrasting to the remaining two Smiliogastrinae clades with only moderate support (BS: 85). The second clade (Smiliogastrinae group II; BS: 96) encompasses all other included Asian genera of the Smiliogastrinae except for the genus *Systomus*. The latter genus, was recovered as sister group to all African Smiliogastrinae with strong support (BS: 100) as it was the case in previous studies (Ren *et al*., 2020; Ren & Mayden, 2016; Yang *et al*., 2015). Within the African Smiliogastrinae four major clades were recovered, of which three were moderately to strongly supported (BS: >94) and which corresponded to the three "*Enteromius/Barbus*" clades of Ren and

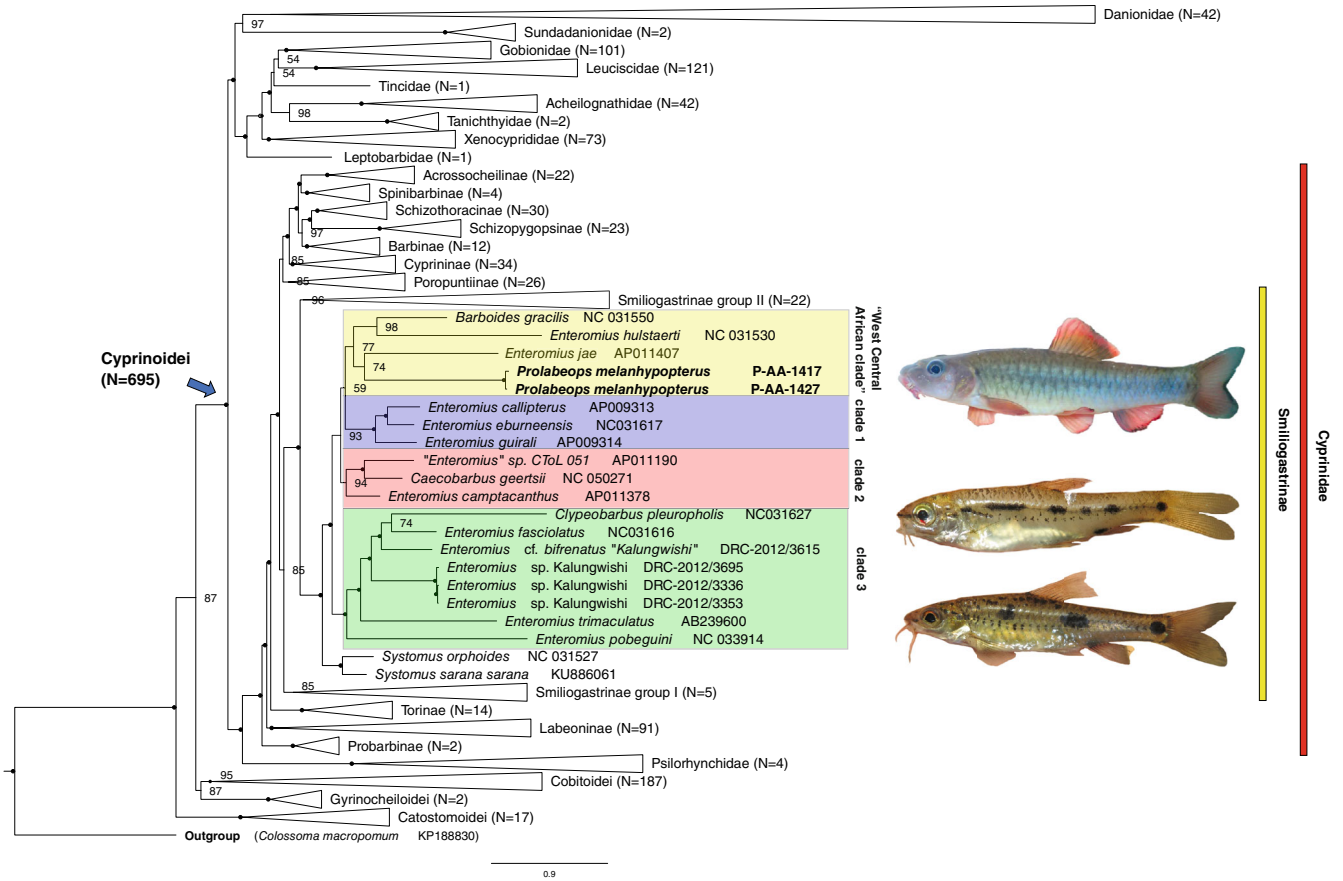

FIGURE 2 The phylogenetic position of the genus *Prolabeops* and the Smiliogastrinae family within the order Cypriniformes based on all mitochondrial protein coding genes (10,713 bp). Maximum-likelihood phylogeny was reconstructed with IQ-TREE, and the bootstrap values based on 1000 ultrafast bootstrap (BS) replicates are indicated at nodes by corresponding ultrafast BS values or by black dots (BS = 100). The suborders Catostomoidei, Cobitoidei, Gyrinocheiloidei as well as families and subfamilies within Cyprinoidei are collapsed, with the exception of the Smiliogastrinae clade containing *Prolabeops melanhypopterus*. Family and subfamily designation follows the latest classification by Tan and Armbruster (2018) for the order Cypriniformes. For a non-collapsed version of the ML-phylogeny see Supporting Information Figure S1. A representative specimen of *P. melanhypopterus* (individual: P-AA-1427) and of two *Enteromius* species (*Enteromius* cf. *bifrenatus*, individual: DRC-2012/3615 and *Enteromius* sp. Kalungwishi, individual: DRC-2012/3336) from the Kalungwishi River are depicted next to their corresponding position (Pictures by F.D.B. Schedel)

Mayden (2016). The fourth clade only including taxa from West Central Africa (*i.e.*, Lower Guinea ichthyoprovinces) such as *Prolabeops melanhypopterus*, *Enteromius jae* (Boulenger, 1903), *Enteromius hulstaerti* (Poll, 1945) and *Barboides gracilis* Brüning, 1929 among others, was only weakly supported (BS: 77). Within this "West Central African clade" *P. melanhypopterus* was recovered, albeit with comparatively low support (BS: 74), as sister group to *E. jae* a small barb known to occur in several drainage systems of Lower Guinea, including the Sanaga and Nyong River systems and which is currently under taxonomic revision (de Weirdt *et al.*, 2007; Hayes, 2020).

Both analyses (ML and BI, see Figure 3), based on the "African Smiliogastrinae data subset," recovered the three included tetraploid Southern African genera *Pseudobarbus*, *Sedercypris* and *Cheilobarbus* as an additional monophyletic clade within the African Smiliogastrinae, as it was the case in previous studies (Hayes & Armbruster, 2017; Yang *et al.*, 2015). Nonetheless, whereas the BI analysis recovered the tetraploid barbs of Southern Africa as sister group to the remaining African Smiliogastrinae (BPP: 1), the ML analysis recovered them as a sister group to a clade encompassing the *Enteromius* clades 1 and 2 (BS: 100). Likewise, there are topological differences concerning the phylogenetic placement of *P. melanhypopterus*. The BI analysis recovered *P. melanhypopterus* as a sister group to *E. jae* (BPP: 1), as it was the case for the ML analysis based on the "Cypriniform data set," whereas the ML analysis based on the "African Smiliogastrinae data subset" recovered it as a sister group to a clade encompassing *E. hulstaerti* and *B. gracilis* albeit with very low support (BS: 41).

The recovered interrelationships of cypriniform suborders, families, subfamilies as well as species-level relationship should be interpreted with caution as the "Cypriniform data set" of this study incorporated a large fraction of the cypriniform diversity (mined from GenBank) but was solely based on mitochondrial data and showed signatures of saturation (detected *via* IQ-TREE) which potentially influenced the ML analysis. Nonetheless, the goal was not to resolve higher-level relationships of cypriniforms but rather to explore phylogenetic affinities of *Prolabeops*.

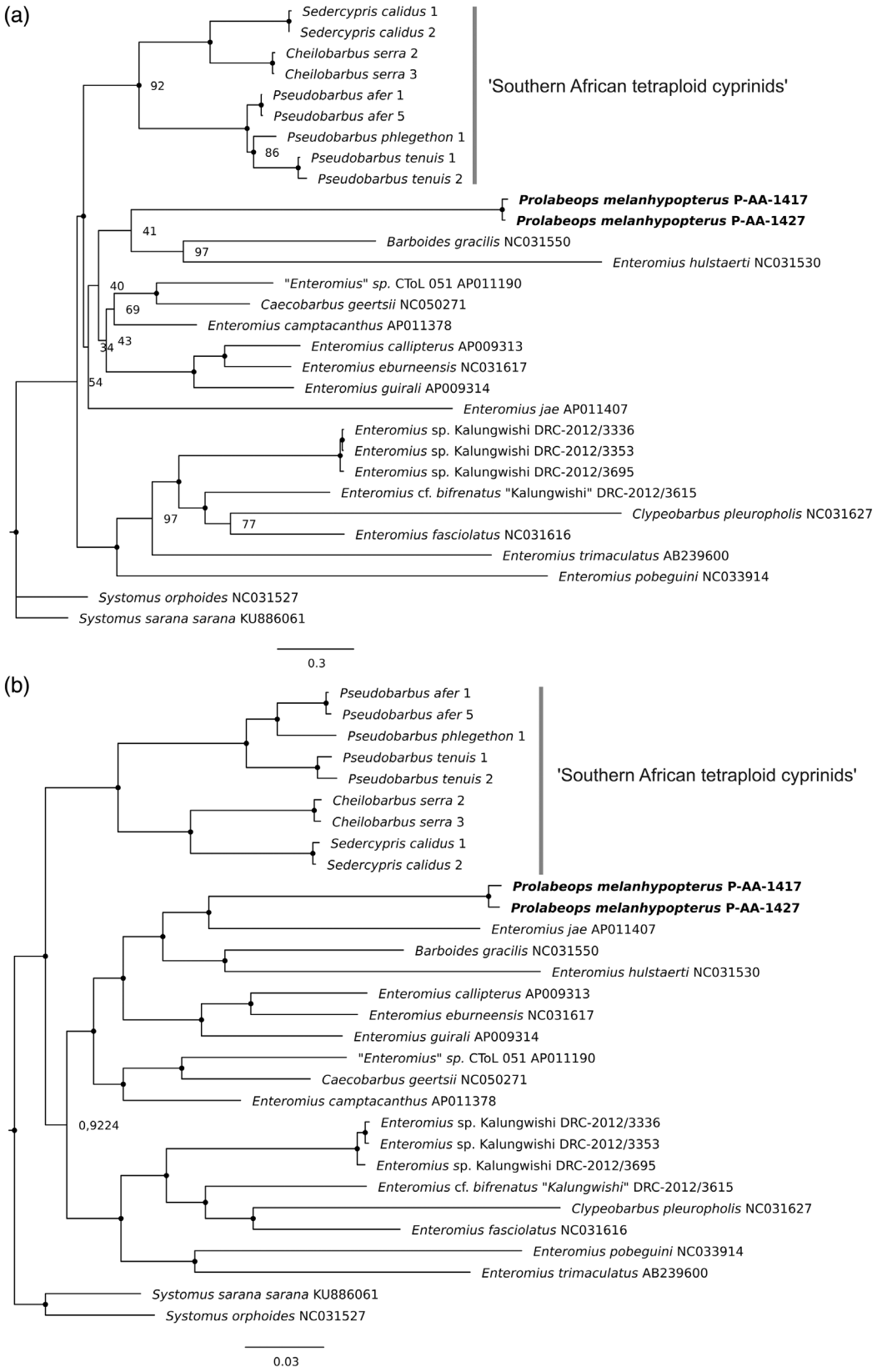

FIGURE 3 Phylogenetic trees based on the "African Smiliogastrinae data subset" on all mitochondrial protein coding genes (10,713 bp); for the included Southern African tetraploid cyprinids sequence information of at least two of three genes (ATP 6, ATP 8 and cytochrome b) is incorporated in the alignment. (a) Maximum-likelihood (ML)-phylogeny (IQ-TREE); bootstrap proportions based on 1000 ultrafast bootstrap (BS) replicates are indicated at nodes by corresponding ultrafast BS values or by black dots (BS = 100). (b) BI-phylogeny (MrBayes); Bayesian posterior probabilities (BPP) are indicated by numbers next to corresponding nodes or by black dots (BPP = 1)

TABLE 1 Overview of the genus composition of African Smiliogastrinae

Genus	Number of species	Remark
Amatolacypris Skelton *et al*., 2018	1	Southern African tetraploid cyprinids
Barboides Brüning, 1929	2	Nested within *Enteromius* ("West Central African clade")
Barbopsis Di Caporiacco, 1926	1	Phylogenetic placement pending, no genetic data available
Caecobarbus Boulenger, 1921	1	Nested within *Enteromius* clade 2 (*sensu* Ren & Mayden, 2016)
Cheilobarbus Smith, 1841	2	Southern African tetraploid cyprinids
Clypeobarbus Fowler, 1936	9	Nested within *Enteromius* clade 3 (*sensu* Ren & Mayden, 2016)
Enteromius Cope, 1867	220	Non-monophyletic
Namaquacypris Skelton *et al*., 2018	1	Southern African tetraploid cyprinids
Pseudobarbus Smith, 1841	11	Southern African tetraploid cyprinids
Sedercypris Skelton *et al*., 2018	2	Southern African tetraploid cyprinids
Prolabeops Schultz, 1941	2	Nested within *Enteromius* ("West Central African clade")

Note: Numbers of valid species for each of the genera were obtained from Fishbase (Froese & Pauly, 2021). Remarks on phylogenetic groups are based on results of this study as well as those of previous studies (*i.e.*, Hayes & Armbruster, 2017; Mullens *et al*., 2020; Ren & Mayden, 2016; Yang *et al*., 2015).

4 | DISCUSSION

4.1 | Phylogenetic placement of *Prolabeops* within the African Smiliogastrinae

The phylogenetic position of the enigmatic genus *Prolabeops* has long been considered as uncertain (Tan & Armbruster, 2018). The mitochondrial genome data of this study strongly suggest that *P. melanhypopterus* is a member of the African Smiliogastrinae, as tentatively suggested already by Lavoue (2020) based on certain putatively derived morphological characters. Nevertheless, within this lineage the phylogenetic affinities of *Prolabeops* remain vague, as it is the case for phylogenetic relationships of the major clades of the African Smiliogastrinae. One reason for this is the limited Smiliogastrinae taxon sampling used in this study because mitogenome data in public databases such as GenBank are scarce. Including the authors' 6 newly sequenced partial mitochondrial genomes there are currently only 19 mitochondrial genomes (representing 17 species) available for the entire African Smiliogastrinae. Moreover, there are no mitochondrial genomes available for the tetraploid barbs of Southern Africa (*i.e.*, *Pseudobarbus*, *Sedercypris*, *Cheilobarbus*, *Amatolacypris* Skelton *et al*., 2018, *Namaquacypris* Skelton *et al*., 2018) as well as for the monotypic genus *Barbopsis* Di Caporiacco, 1926. This leaves most of the species diversity of African Smiliogastrinae unsampled, as the current valid species count is approximately 250 by far the most belonging to the genus *Enteromius* (see Table 1).

As in all previous studies, this analyses recovered *Enteromius* to be paraphyletic with respect to the genera *Caecobarbus*, *Clypeobarbus*, *Barboides* (and *Prolabeops* is now added to this list of genera) nested within the different *Enteromius* clades (Hayes & Armbruster, 2017; Mullens *et al*., 2020; Ren & Mayden, 2016; Yang *et al*., 2015). Since the formal resurrection of the genus *Enteromius* by Yang *et al*. (2015) its application has been highly debated (*i.e.*, Conway *et al*., 2017; Schmidt *et al*., 2017; Schmidt & Bart, 2015; Stiassny & Sakharova, 2016) because *Enteromius* and allied genera are in need of extensive taxonomic revisions. Based on morphological observations Roberts (2010) suggested that the type species of the genus, *Enteromius potamogalis* Cope, 1867, is related to some of the West African *Enteromius* species among others *Enteromius ablabes* (Bleeker, 1863). This would translate into a grouping of the *Enteromius*-type species in the ("*Barbus*"/*Enteromius*) clade I of Ren and Mayden (2016) and Hayes and Armbruster (2017). Nonetheless, *E. potamogalis* has not yet been included in any molecular analysis, hampering further integrative taxonomic approaches for a revised classification (Englmaier *et al*., 2020; Mullens *et al*., 2020). This study suggests *P. melanhypopterus* to be related most likely to members of the "West Central African clade," which appear to be restricted to the Lower Guinea ichthyoprovince, but which most likely does not include *E. potamogalis* based on the observations of Roberts (2010). The authors therefore encourage us to include ideally both described species of *Prolabeops* in any upcoming taxonomic studies on the "West Central African clade" of *Enteromius*.

Nevertheless, this study is limited to mitochondrial data, and nuclear data might provide additional phylogenetic insights concerning the relationships of *Prolabeops*. Based on its phylogenetic position it is likely that *Prolabeops* is diploid as it generally assumed for other African Smiliogastrinae except for the Southern African tetraploid cyprinids (Berrebi *et al*., 1996; Hayes & Armbruster, 2017; Rab *et al*., 1995; Tsigenopoulos *et al*., 2002). Nonetheless, this assumption needs to be tested as, to the authors' knowledge, no karyotype data are available for any *Prolabeops* species nor for any other taxa of the "West Central African clade."

This study includes only samples of a single population of *P. melanhypopterus* from the middle section of the Sanaga, and it is missing *P. nyongensis*, the second species of the genus. For studying biogeography of *Prolabeops* it would be important to include *P. nyongensis*, as well as the other known populations of *P. melanhypopterus* which are widely distributed over the Sanaga drainage system, *i.e.*, in the Mbam and the Djerem drainage (see Figure 1). This is particularly important because Thys van den Audenaerde (1974) observed morphological variation between populations of *P. melanhypopterus*. Nonetheless, he did not consider these differences to be pronounced sufficiently to justify the

description of additional species. In the same study, based on similar scale counts he speculated that the type specimen of *P. cameroonensis*, for which no precise type location is known, might have originated from the middle Sanaga. This hypothesis possibly could be verified by sequencing the type of *P. cameroonensis* and other known populations *Prolabeops* in the future.

Last but not least the authors strongly suggest exploring the phylogenetic relationships of the yet-understudied *Prolabeo batesi* Norman, 1932. This enigmatic species is endemic to a small area in northern Sierra Leone and inspired Schultz (1941) in naming it after the phenotypically similar Prolabeops. Analogous to the present case the genus *Prolabeo* is still considered as *incertae sedis* (Tan & Armbruster, 2018).

5 | DISCLAIMER

Data on genetic material contained in this paper are published for non-commercial use only. Use by third parties for purposes other than non-commercial scientific research may infringe the conditions under which the genetic resources were originally accessed, and should not be undertaken without obtaining consent from the corresponding author of the paper and/or obtaining permission from the original provider of the genetic material.

AUTHOR CONTRIBUTIONS

F.D.B.S. designed and conducted the study and wrote the first draft of the manuscript after U.K.S. had conceived the idea of investigating the phylogenetic position of *Prolabeops* using mitogenome data. Z.M., A.I., A.R.B.-N. and F.D.B.S. collected the specimens and tissue samples analysed herein. F.D.B.S. performed the molecular work and conducted all phylogenetic analyses and prepared all figures. W.S. and U.K.S. contributed to the improvement of all versions of the manuscript. All authors read and approved the final version of the manuscript.

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SUPPORTING INFORMATION

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