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Evolutionary convergence in body shape obscures taxonomic diversity in species of the African *Labeo forskalii* group: Case study of *L. parvus* Boulenger 1902 and *L. ogunensis* Boulenger 1910

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Abstract

Labeo is the third most diverse genus of African cyprinids and is widely distributed across the continent. *Labeo parvus*, a small species originally described from the Congo basin, has been considered the only species of the *L. forskalii* group distributed across five African ichthyofaunal provinces (Nilo-Sudan, Congo, Cuanza, and Upper and Lower Guinea). However, morphological similarity between *L. parvus* and numerous congeners remains a central cause of taxonomic confusion within the genus. Here we employed a phylogenetic comparative approach to assess phenotypic convergence among species of the *L. forskalii* group, investigate the taxonomic status of *L. parvus sensu lato (sl)* in west Africa, and reevaluate the composition and distribution of *L. parvus sensu stricto (ss)*. Our phylogenetic analysis provides no support for a sister relationship between *L. parvus ss* and any of the west African *Labeo parvus*-like species. Geometric morphometric and molecular phylogenetic data indicate that *L. parvus ss* is a Congo basin endemic, and seemingly ecologically equivalent species found in west Africa are *L. ogunensis*, *L. obscurus* and other undescribed or previously synonymized species. We discuss our findings in terms of convergent evolution using phylomorphospace and tests for phylogenetic signal.

KEYWORDS
Africa, cryptic diversity, geometric morphometrics, *Labeo parvus*, repeated trait evolution

1 | INTRODUCTION

The dwarf African carp, *Labeo parvus*, was originally described by Boulenger (1902) from Mobayi-Mbongo (formerly Banziville) in the Ubangi (Congo basin) in the north central Democratic Republic of the Congo (DRC). Fifty-two years after its description, Daget (1954) reported the occurrence of *L. parvus* in the upper Niger basin and subsequently the species has been reported from coastal basins throughout western Africa (Jegu & Lévêque, 1984; Lévêque *et al*., 1990). Presently, *L. parvus* is recognized as a widespread species distributed from western Africa (Senegal River) to eastern Africa (Malagarasi River) via and across, central Africa (Congo and Cuanza basins) (Lalèyè *et al*., 2020; Lévêque *et al*., 1990; Montchowui *et al*., 2009; Paugy *et al*., 2003; Skelton, 2019). The taxon has also been reported as present in the Lake Chad system (Jegu & Lévêque, 1984; Paugy *et al*., 2003) and the Nile River (Yang *et al*., 2012), making *L. parvus sl* among the most widespread of African *Labeo*.

As currently recognized *L. parvus* is found in five African ichthyological provinces, each of which is generally considered to have a distinctive assemblage of fish taxa (Snoeks *et al*., 2011; Stiassny

et al., 2007). Considering the complex geological history of African drainages (Goudie, 2005; Stankiewicz & de Wit, 2006) and the several physical boundaries that exist between the Congo, Niger and Nile drainages, the presently recognized distribution of *L. parvus* is doubtful and likely represents multiple lineages. Reid (1985) questioned the distribution of *L. parvus* and proposed restricting *L. parvus ss* to the Congo basin, suggesting that the morphologically similar taxon found in western Africa is what he considered to be the closely related *L. ogunensis*.

The Ogun carp *Labeo ogunensis* was originally described by Boulenger (1910) from the Ogun River at Aro (Ilaro) in south-western Nigeria. According to Jegu and Lévêque (1984), *L. ogunensis* had also been reported in the Mono and Ouémé Rivers in Benin but on examination of specimens from these rivers, Jegu and Lévêque identified them instead as *L. parvus*. In 1985, Reid (1985) reported *L. parvus* (*sensu* Daget, 1954, 1961, 1962, Daget & Iltis, 1965 and *sensu* Jegu & Lévêque, 1984) in west Africa to be misidentification of *L. ogunensis* and considered several nominal west African *Labeo* species (*e.g*., *L. tibestii* Pellegrin, 1919 and *L. toboensis* Svensson, 1933) as synonyms, while recognizing *L. obscurus* Pellegrin, 1908 as valid. This latter taxon was considered by Boulenger (1910) and others as closely related to *L. ogunensis* (Lévêque *et al*., 1990; Reid, 1985). However, many of these proposals were ignored by subsequent authors (*e.g*., Lalèyè *et al*., 2004; Montchowui *et al*., 2009, 2011, 2012; Nwani *et al*., 2011; Paugy *et al*., 2003) who continued to recognize *L. parvus* in west Africa. Thus, as for *L. parvus*, the present status of *L. ogunensis* remains controversial, with some authors regarding the species as valid (Ayoade *et al*., 2004; Moritz, 2007) and others as a synonym of *L. parvus* (Fricke *et al*., 2022; Froese & Pauly, 2022; Paugy *et al*., 2003). Similarly, the status of *L. obscurus* considered valid by Reid is uncertain, with some authors considering it a synonym of *L. parvus* (Fricke *et al*., 2022; Froese & Pauly, 2022; Paugy *et al*., 2003) and others recognizing it as a valid species (Moritz & Neumann, 2017).

In central Africa (Congo and Lower Guinean provinces), Tshibwabwa (1997) considered *L. parvus* to be widespread in both the middle and upper Congo, but absent from the lower Congo and from Lower Guinea. However, some authors continue to report *L. parvus* from Lower Guinea (*e.g*., Nwani *et al*., 2011) likely following Teugels *et al*. (1992), who reported the presence of *L.* cf. *parvus* in the Cross River. Tshibwabwa (1997) proposed that *L. parvus* has affinities with several *Labeo* species in the Congo basin, including *L. dhonti*, *L. quadribarbis*, *L. lukulae* and *L. annectens*, all of which are currently considered members of the *L. forskalii* group of Reid (1985). After Tshibwabwa's revision of *Labeo* species of the Congo basin and Lower Guinean provinces, Lowenstein *et al*. (2011) were the first to use molecular data that highlighted discrepancies in the taxonomy of many Congo basin *Labeo*, including *L. parvus*. Similar observations were made by Decru *et al*. (2016) based on material from different localities within the Congo basin. To date no study has investigated the taxonomy and distribution of *L. parvus* and the numerous *L. parvus*-like species found throughout western and central Africa using the combined tools of molecular phylogenetics, geometric morphometrics and meristics.

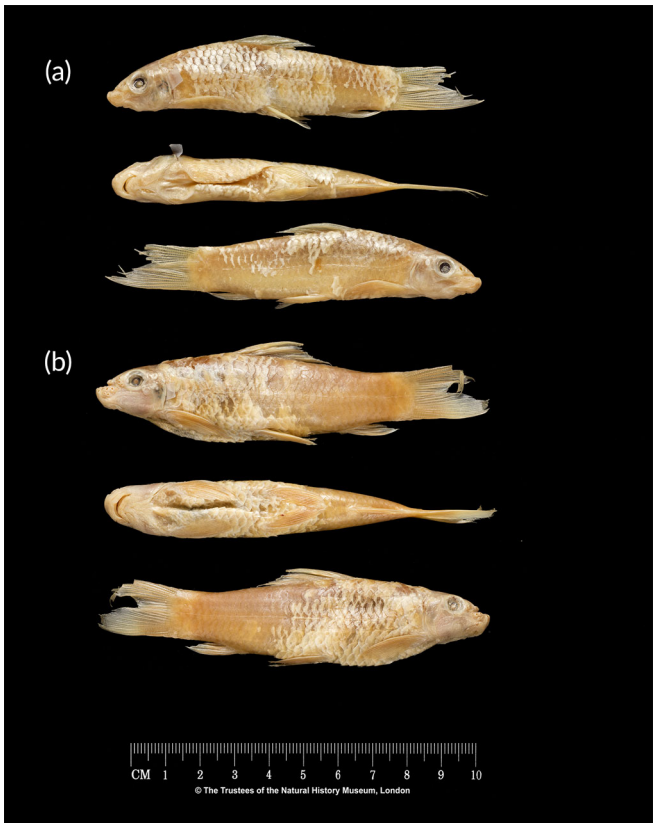


FIGURE 1 Type series of *Labeo parvus* in the Natural History Museum (London). (a and b) BMNH December 26, 1901.24–25, Syntypes from Ubangi river (Banziville, DRC)

Present organismal diversity has been shaped by past evolutionary mechanisms such as natural selection that adapt organisms to their environment, and organisms under similar selective regimes tend to produce similar characteristics (Adams & Nistri, 2010; Losos, 2011; Nosil, 2012). Such convergence is particularly widespread in aquatic habitats and often results in considerable hidden diversity (Mambo Baba *et al*., 2020; Arroyave *et al*., 2019; Alter *et al*., 2017; Goodier *et al*., 2011). Likely compounding taxonomic problems is the fact that the morphological features traditionally used to identify *Labeo* species may not be consistently discriminative (Van Steenberge *et al*., 2016). Lévêque *et al*. (1990), for example included within *L. parvus sl* in west Africa several west African species that were apparently identical based on the morphological criteria used but, as our study indicates, are phylogenetically only distantly related. An additional complicating issue is that Boulenger (1902) apparently included several species among his syntypical series of *L. parvus*, and two syntypes established as paralectotypes by Reid (1985) and used by Tshibwabwa (1997) in his description of *L. parvus* are clearly heterospecific (Figure 1). The absence of targeted taxonomic study to solve delineation problems among *L. parvus* and other *L. forskalii*-group species has impeded our understanding of the taxonomic composition and geographical distributions of a large and economically important lineage of fishes across large swaths of the continent.

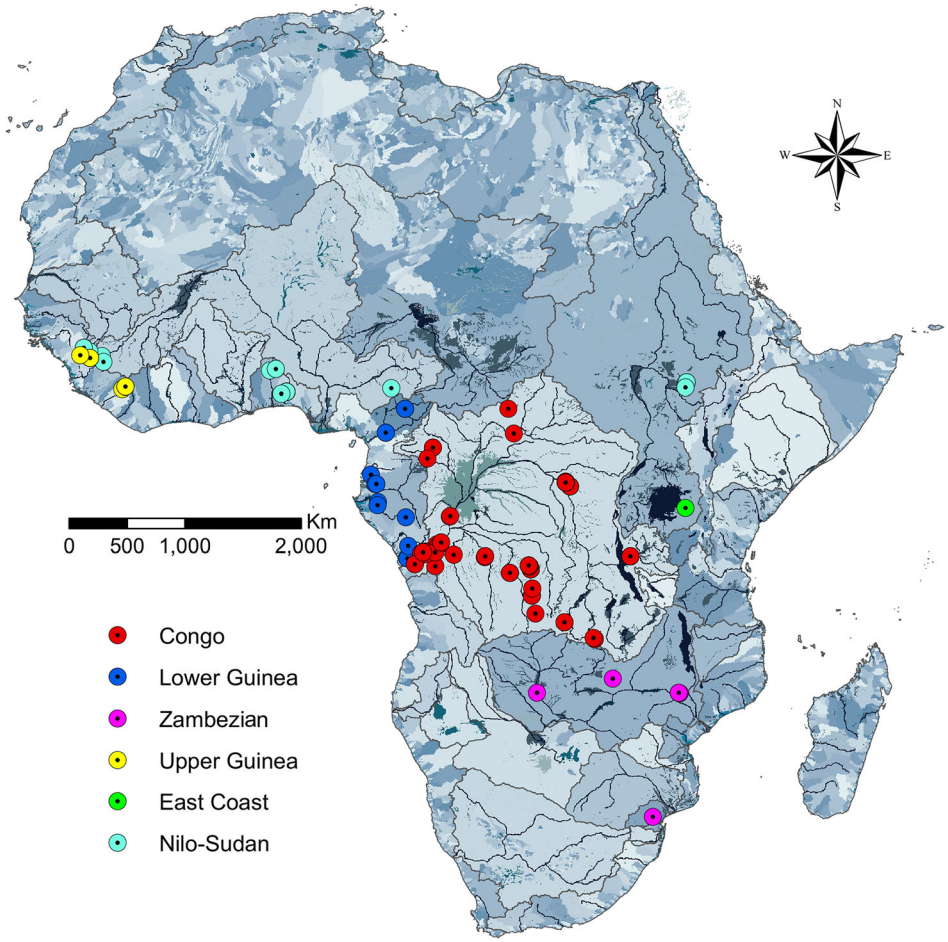


FIGURE 2 Map showing the distribution of different specimens of *L. forskalii*-group species included in both phylogenetic and morphological analyses. Colours represent ichthyofaunal provinces. The background map was obtained from https://www.hydrosheds.org

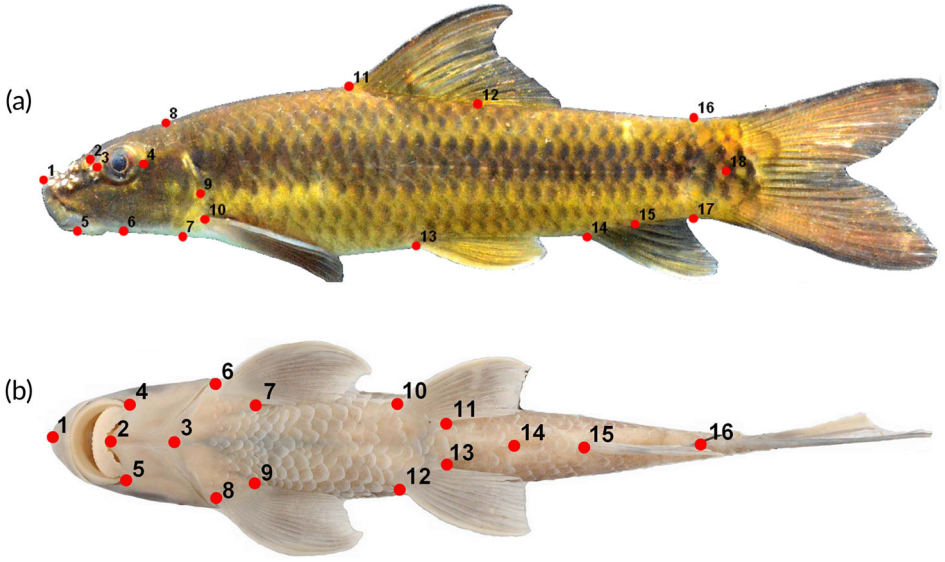


FIGURE 3 Different landmarks used in geometric morphometrics after Armbruster (2012). (a) In lateral view and (b) in ventral view

In this study we aim to highlight that morphological convergence is rampant among the *L. forskalii* group species of the Congo basin and may be contributing to considerable taxonomic confusion. To do this we applied a phylogenetic comparative approach to test a hypothesis of rampant phenotypic convergence in overall body shape among species of the *L. forskalii* group that are *L. parvus*-like in appearance and frequently misidentified in the literature and in museum collections. We used genetic and morphological data to compare *L. parvus ss* (Congo basin) and *L. ogunensis ss* (Ogun River) to other *L. parvus*-like species of the *L. forskalii* group from western (Niger, Senegal, Little Scarcies, Konkouré, Moa, Oueme and St Paul Basins) and central (Congo and Lower Guinean provinces) Africa. We included in our analyses other *L. forskalii*-group

species from different provinces (*e.g.*, East Coast and Zambezian) to better resolve the phylogenetic relationships among the focal species. The primary objective of this study was to investigate convergence in body shape between these lineages, use these results to establish the distribution of *L. parvus ss* and distinguish *L. oguensis ss* from its west African congeners.

2 | MATERIALS AND METHODS

This study was conducted entirely on catalogued museum specimens and tissue vouchers, and ethical information requirements are not applicable.

2.1 | Species identification

Museum specimens were reviewed following the most recent taxonomic revisional works available for each region. In west Africa, species were identified primarily following Reid (1985), while in the Congo basin and Lower Guinea (for *L. annectens* and *L. lukulae*), we primarily used Tshibwabwa (1997). Several other publications, including Tshibwabwa & Teugels (1995), and Tshibwabwa *et al*. (2006), and original descriptions were used as complements to these documents. In addition to morphological identification, we also used COI sequences to evaluate each identification.

2.2 | Morphological data collection and analyses

2.2.1 | Geometric morphometrics

Materials examined in geometric morphometric (GM) analyses include 110 specimens identified in museum collections as *L. parvus*, *L. ogunensis*, *L. obscurus*, *L.* cf. *obscurus* and *Labeo* spp. from Auburn University Museum (AUM), Cornell University Museum of Vertebrates (CUMV or CU), Oregon State University (OSU) and American Museum of Natural History (AMNH) collections. Thirty-five of these specimens, including four topotypes (Ubangi) of *L. parvus ss*, are from Central Africa (Congo basin) whereas 75, including eight topotypes of *L. ogunensis ss* and two of *L. obscurus ss*, are from west Africa (Niger, Ogun, St Paul, Little Scarcies, Konkouré and Senegal rivers) (Figure 2). Additionally, we included several individuals of other *L. forskalii*-group species morphologically close to *L. parvus* that have frequently been misidentified as *L. parvus* in museum collections. Among these are nine individuals catalogued in collections as *Labeo* sp. 'UCR' from Kisangani (Upper Congo River), 28 individuals of *Labeo* sp. 'mbimbii' from the Lulua River (Kasai basin), 10 individuals of *L. lukulae* from the Lukula and Louvila rivers (Chiloango basin), 14 individuals of *L. luluae* Fowler 1930 from the Lulua River (Kasai basin), 33 individuals of *L. simpsoni* from the lower and upper Congo River, 11 individuals of *L. annectens* from the Ogowe and Komo rivers, 10 individuals of *L. polli* from the Kafubu River, four individuals of *L. dhonti* from the Malagarasi River and three individuals of *L. quadribarbis* from Kisangani in the upper Congo. This resulting in a total of 232 individuals distributed among 17 currently recognized species.

Each specimen was photographed in ventral and lateral (left side) views using a lightbox and mounted Canon EOS 600D digital camera. Juvenile and adult individuals of both sexes in good condition were included in the analyses. Additional photographs of two *L. parvus* syntypes were obtained from the Natural History Museum, London data portal (http://data.nhm.ac.uk/dataset/collection-specimens). All photographs were used to create digital images for use with GM landmarks (Figure 3) following Armbruster (2012) using TpsDIG2 (Rohlf, 2015) to describe individual body shape. The *x*–*y* coordinates of landmarks generated by TpsDig2 were saved in a tps file with TpsUtil 1.70 (Rohlf, 2015). A generalized Procrustes analysis (GPA) was performed using MorphoJ 1.06d (Klingenberg, 2011) to scale landmarks of each specimen to a common body size, rotate each individual to a common alignment and generate a consensus shape by calculating the average shape of all specimens included in the analysis. After checking for outliers (improperly landmarked or distorted individuals were removed from the analyses), a covariate matrix was constructed to prepare data for a principal component analysis (PCA), which was conducted in MorphoJ. To assess variation across groups, a canonical variates analysis (CVA) incorporating a permutation test for pairwise differences with 10,000 iterations was conducted in MorphoJ.

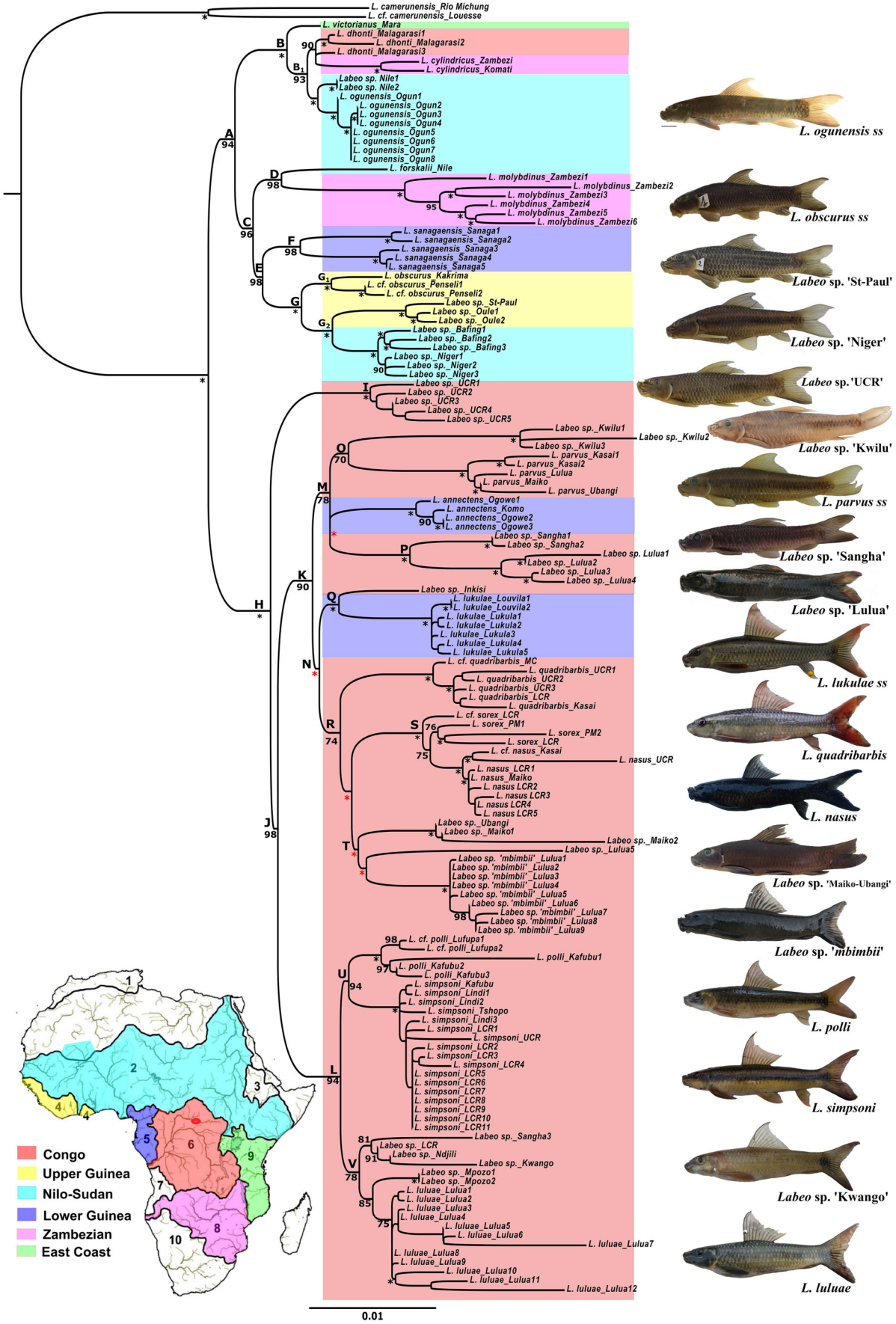
2.2.2 | Meristics

Additionally, traditional meristic data, following Tshibwabwa *et al.* (2006) and Reid (1985), were collected from a subset of 160 individuals (Supporting Information Tables S1 and S2). X-ray images were used to count the total number of vertebrae (precaudal + caudal), number of pleural ribs, number of procurrent and simple dorsal-fin rays, number of procurrent and simple anal-fin rays, and number of principal and procurrent caudal-fin rays. In contrast to Tshibwabwa *et al.* (2006) we counted all vertebrae possessing a hemal spine as caudal vertebrae whereas those bearing ribs or with hemal arches but lacking a hemal spine were counted as precaudal vertebrae (Aguirre *et al*., 2014). Vertebrae comprising the Weberian apparatus and the urostyle were not included in the counts. All meristic characters counted are given in Supporting Information Tables S1 and S2. Scale rows around the caudal penducle were counted following Reid (1985). The entire meristics dataset, excluding invariant characters (principal caudal-fin rays, simple dorsal-fin rays, simple pelvic-fin rays, branched pelvic-fin rays, procurrent anal-fin rays, simple anal-fin rays and branched anal-fin rays), was analysed using PCA as implemented in the R (R Core Team, 2013) package FactoMineR (Lê *et al*., 2008).

2.3 | Molecular data collection and analyses

2.3.1 | DNA extraction

Genomic DNA was extracted from 99 individuals representing 28 valid, putative and undescribed *Labeo* species of the *L. forskalii*-group, and



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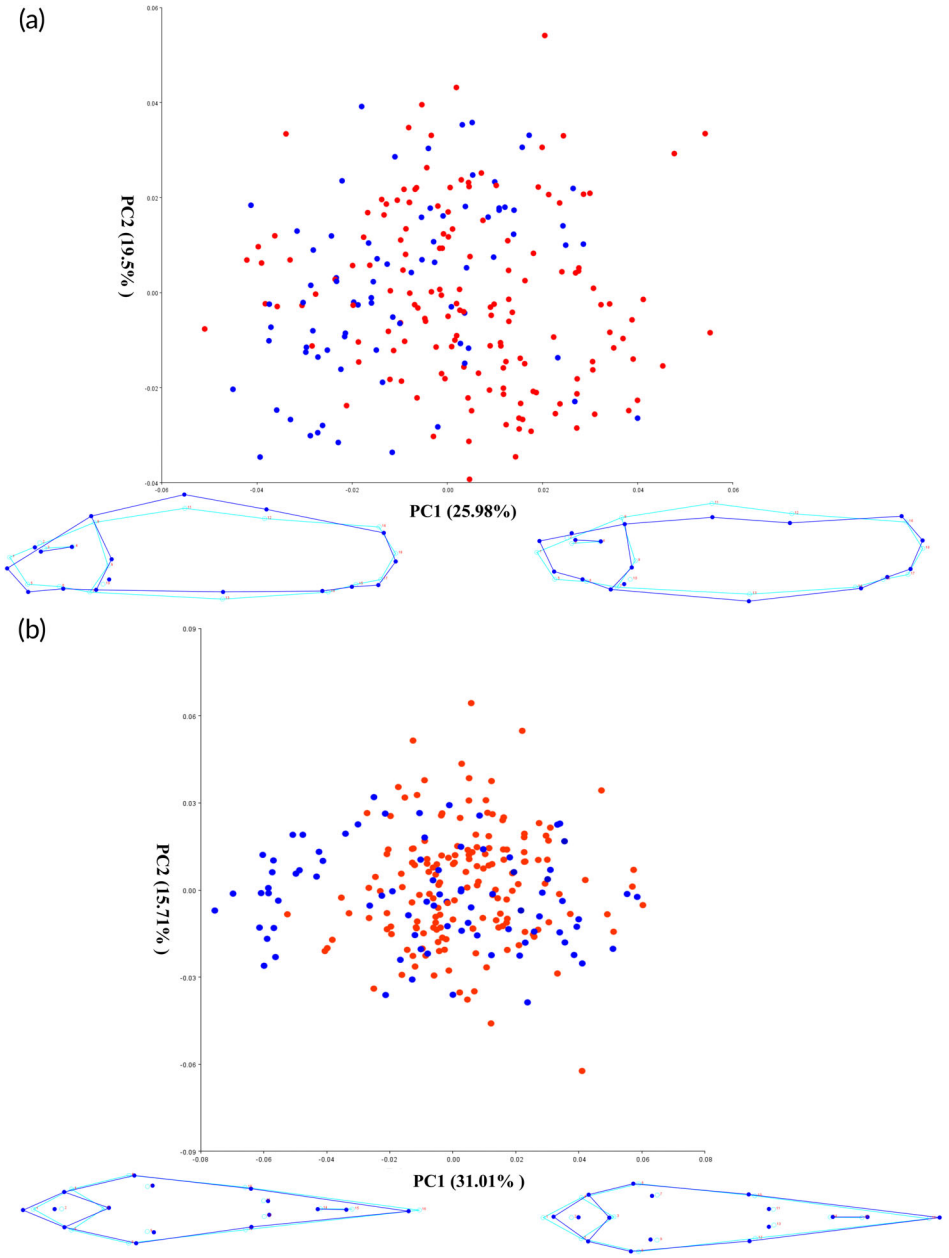

FIGURE 5 Principal component analysis of 232 individuals of 17 species of the *L. forskalii* group in Central Africa (red dots) and in West Africa (blue dots). (a) Lateral view and (b) ventral view. West Africa (clade A), Central Africa (clade H)

two individuals of *L. camerunensis* used as an outgroup. Extractions were conducted using the Omega BioTek E.Z.N.A. or Qiagen DNeasy Tissue kit following manufacturers' protocols.

2.3.2 | Gene amplification and sequencing

Polymerase chain reaction (Mullis *et al*., 1986; Saiki *et al*., 1988) was used to amplify part (c. 652 bp) of the mitochondrial cytochrome oxidase subunit 1 (COI) and the entire (c. 1500 bp) nuclear Recombination-Activation Gene 1 (RAG1). The COI gene region was amplified following Ivanova *et al*. (2007) while RAG1 was amplified following López *et al*. (2004) and Lowenstein *et al*. (2011) using the following primers: RAG1R1 (5′-CTGAGTCCTTGTGAGCTTCCATRAAYTT-3′), RAG1_JHL_Fi (5′-ATGCACGCTCTGCGACTCAA-3′), RAG1_JHL_Ri (5′-TTCATCGTGGCTGCGT- GTGA-3′), and RAG1F1 (5′-CTGAGCTG-CAGTCAGTACCATAAGATGT-3′). Fifty two percent of the obtained amplicons were submitted to Genewiz (https://www.genewiz.com) for

FIGURE 4 Phylogram inferred from maximum-likelihood analysis of the concatenated sequence dataset (COI and RAG1) of the African *Labeo* species of the *L. forskalii* group [bootstrap values are reported on/under branches with support above 69%, black asterisks (⁎) represent bootstrap values >98% whereas red asterisks (⁎) represent boostrap values <50%] and major ichthyofaunal provinces of continental Africa, from Snoeks *et al*. (2011). (1) Maghreb, (2) Nilo-Sudan, (3) Abyssinian Highlands, (4) Upper Guinea, (5) Lower Guinea, (6) Congo (Zaire), (7) Quanza (Kwanza), (8) Zambezian, (9) East Coast, (10) Southern (including Cape of Good Hope)

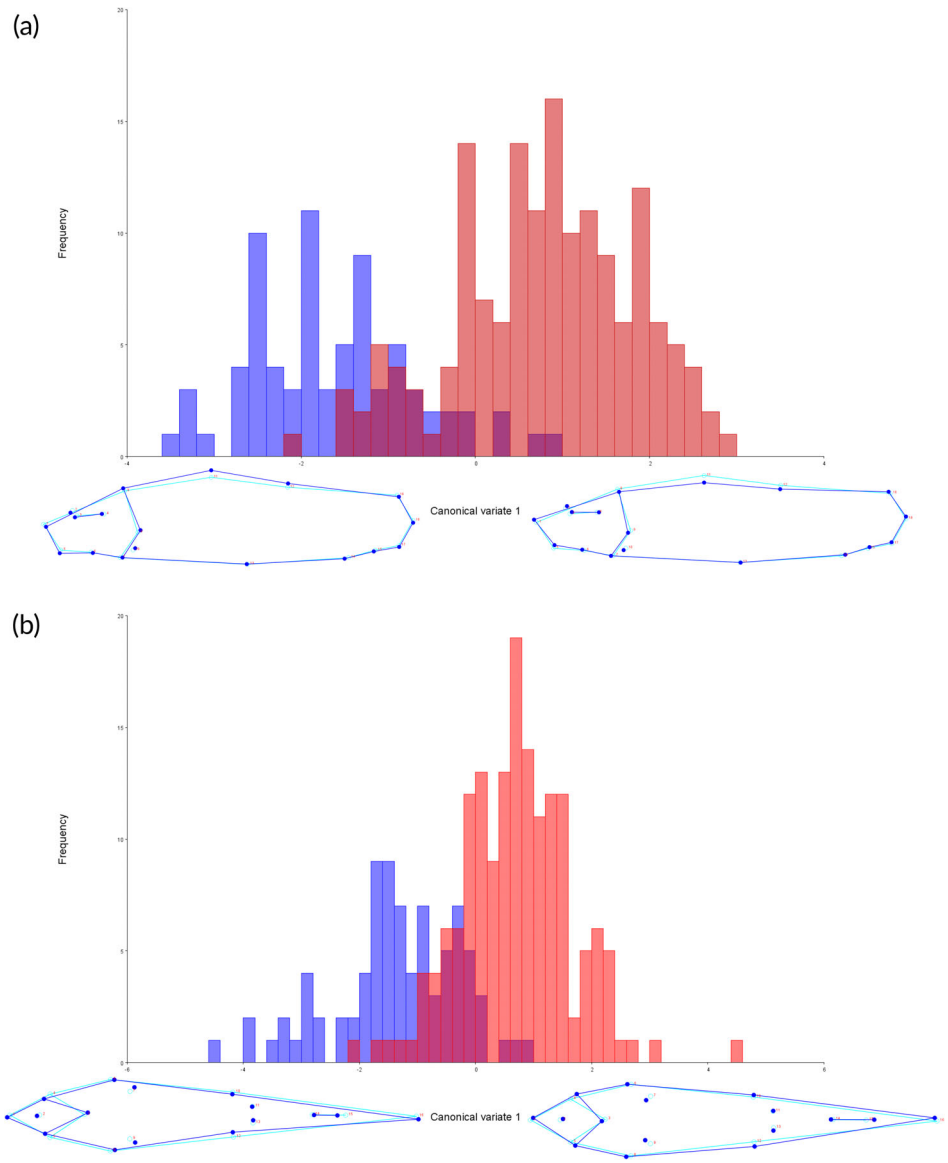

FIGURE 6 Morphospace plot visualizing body shape variation between clade A (West African species) and clade H (Central African species). (a) Lateral view and (b) ventral view

Sanger sequencing. The remaining amplicons (48%) were sequenced at the Sackler Institute for Comparative Genomics (SICG) of the AMNH following the protocol of Lowenstein *et al.* (2011). Additionally 45 COI and 45 RAG1 sequences (Supporting Information Table S3) were imported from GenBank (www.ncbi.nlm.nih.gov/genbank) and the Barcode of Life Data System (http://boldsystems.org/index.php). All sequences imported from the Barcode of Life Data System were linked to vouchers at the AMNH and their species identifications were verified. The three sequences from GenBank were not linked to vouchers and their identifications could not be formally verified.

2.3.3 | Phylogenetic analyses

A total of 144 assembled, aligned and trimmed contigs of COI (630 bp after trimming) and RAG1 (1393 bp after trimming) were concatenated (2023 bp) using Geneious Prime February 3, 2019 (https://www.geneious.com/resources/). Optimal models and partitioning schemes, by gene and codon position, for the Bayesian analysis were determined using Partionfider2 (v. 2.1.1.) (Lanfear *et al.*, 2017). General time-reversible with gamma distribution and invariant sites (GTR + I + G) models were used for the six subsets of the concatenated dataset. Bayesian inference (BI) analysis was conducted on the concatenated dataset using MrBayes 3.2.2 implemented on the CIPRES Science Gateway V.3.3 (http://www.phylo.org). Using MrBayes, Markov chain Monte Carlo (MCMC) analyses were run for 80 million generations, with trees sampled every 3000 generations. Maximum-likelihood (ML) analysis was conducted using IQ-TREE (Nguyen *et al.*, 2015) with K2P + R4 and TNe + R3 as best models for the COI and RAG1 partition schemes, respectively. One thousand (1000) bootstrap replicates were used to evaluate branch support in IQ-TREE, and the resultant phylogenetic trees were visualized and annotated with FigTree v1.4.3 (Rambaut, 2016).

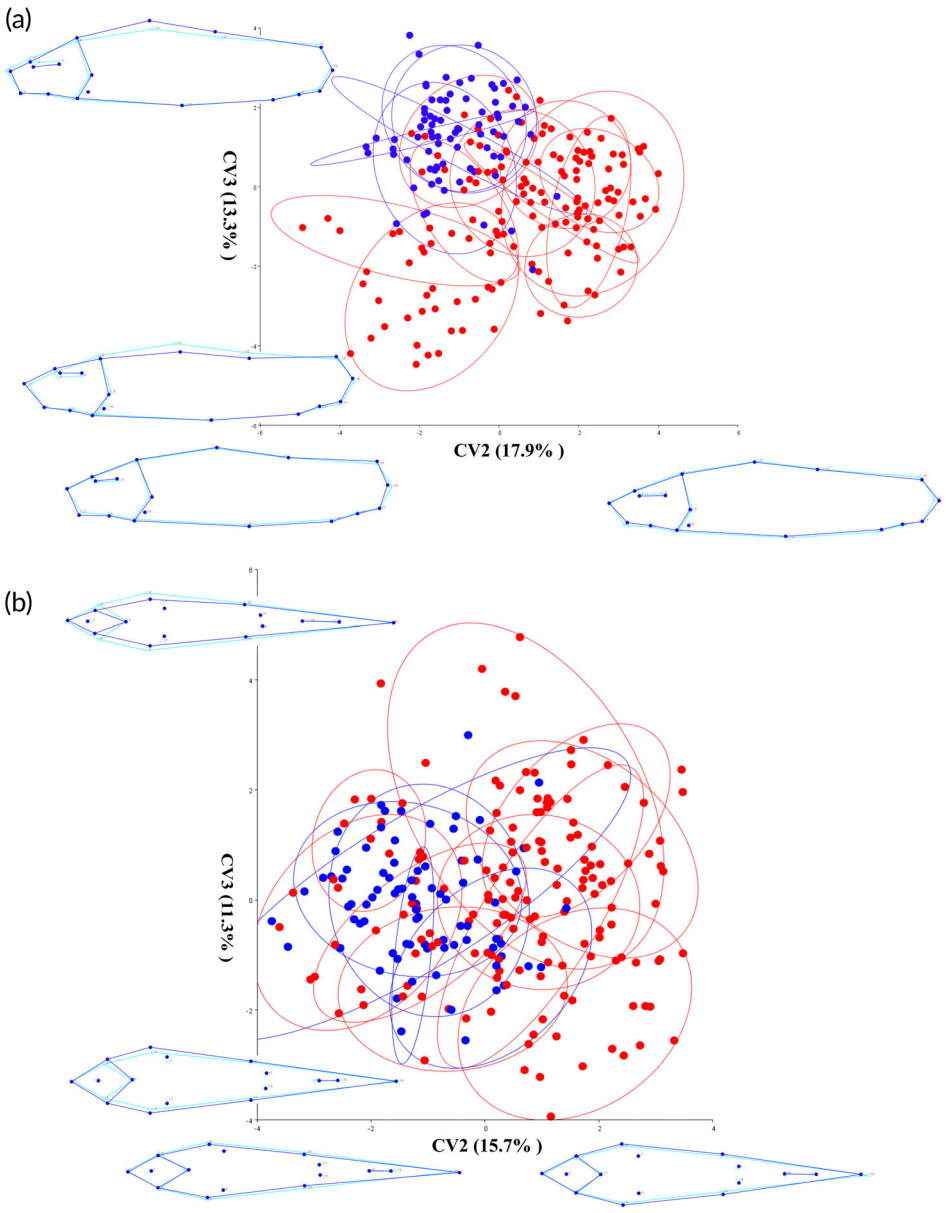

FIGURE 7 Morphospace plot visualizing body shape variation between the 17 species of the *L. forskalii* group in Central Africa (red dots) and in West Africa (blue dots) with 90% confidence ellipses by species. (a) Lateral view and (b) ventral view

2.3.4 | Phylogenetic signal test

The ML phylogenetic tree was pruned using the phytools (Revell, 2012) package in R3.4.1. (R Core Team, 2013) to match the operational taxonomic units (OTUs) in the phylogeny with those in the morphospace datasets, which focused on the *L. parvus*-like species. The pruned tree was imported into MorphoJ and mapped onto morphospaces (PCA and CVA) to generate phylomorphospace plots (Sidlauskas, 2008). The permutation test for phylogenetic signal, with 10,000 iterations and weighted by branch length, was applied to the resulting phylomorphospace plots to assess the direction of body shape change along evolutionary axes. Our data were also tested for phylogenetic signal using the physignal function in the R package geomorph (Adams & Otárola-Castillo, 2013). For that, we used the K_{mult} method (Adams, 2014) with 1000 random permutations.

2.3.5 | Testing for convergence

To test for morphological convergence we used the function *search.conv* of the R package RRphylo (Castiglione *et al*., 2019), which implements a phylogenetic ridge regression-based method to assess morphological convergence in clades or species grouped under different evolutionary states. The method tests if the angle θ (calculated as the inverse cosine of the ratio between the product of phenotypic vectors, in multivariate data, of given pairs of species and the product of their sizes) between species is less than expected by their phylogenetic distance under a Brownian motion model. For that, we time-calibrated our phylogeny using the RealTime-ML function of MEGA X (Kumar *et al*., 2018) with the oldest (c.17 Ma) known *Labeo*-like fossil in Africa (Stewart, 2001; Van Couvering, 1977) and the isolation of the Congo and Nilo-Sudanic watershed, estimated to be between 6.8

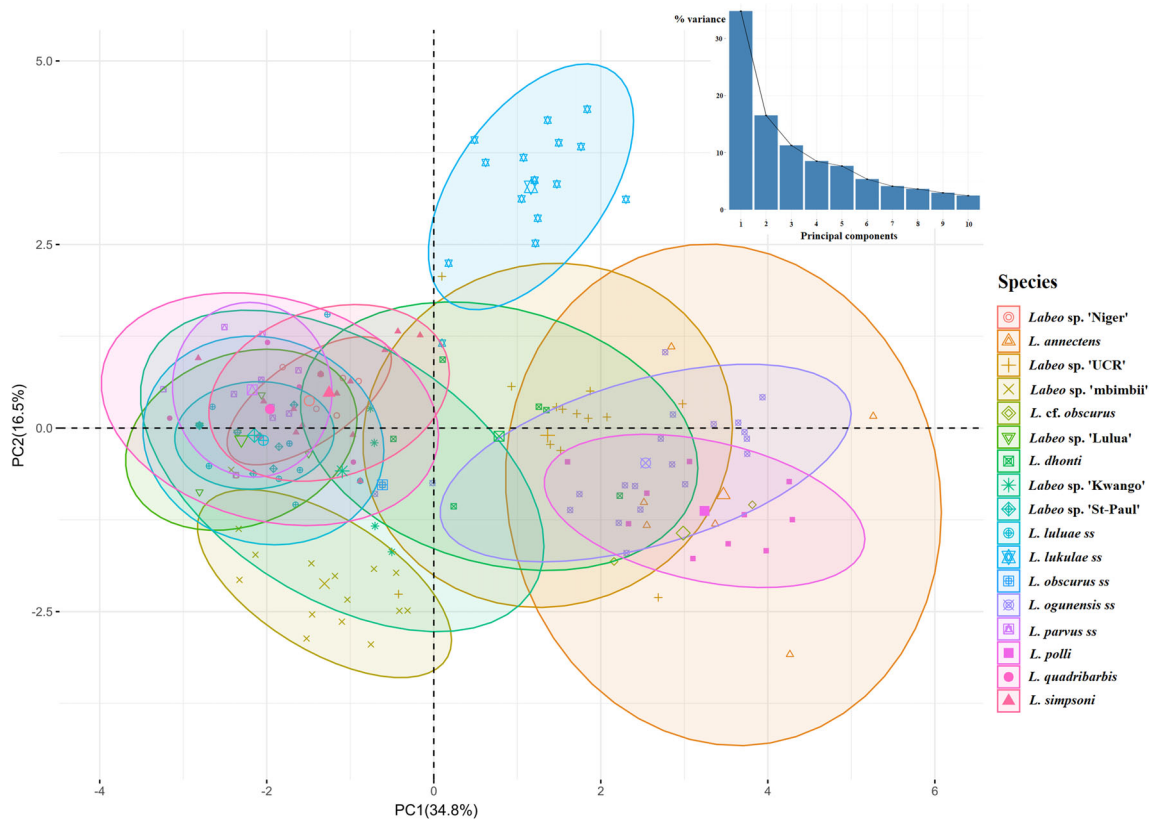

FIGURE 8 PC1 *vs*. PC2 scatterplot of the PCA on 13 meristic characters, collected on 160 specimens of 17 *L. forskalii*-group species visualizing higher similarities in meristics between *L. parvus*-like species

and 18.6 Ma (Goodier *et al*., 2011; Pinton *et al*., 2013), as constraints. The time-calibrated phylogeny was then pruned to contain the same species present in the morphospace used for testing the phylogentic signal as above. We used both PCA and CVA results in both views (ventral and lateral) and tested only for convergence between clades.

3 | RESULTS

3.1 | Phylogenetic relationships

In the following section, as both ML and BI phylogenetic analyses resulted in similar tree topologies, we use the ML tree (Figure 4) as a basis for discussion of results. The BI tree from the concatenated dataset and ML trees from individual loci are provided in Supporting Information Figures S1, S2 and S3. Although based on just two genetic markers, our study provides strong nodal support for a scheme of relationships among the many *L. parvus*-like species and other members of the *L. forskalii* group found across the continent, thereby providing a framework for investigating phenotypic diversification within and across these main lineages. Further study to address the formal taxonomic description of the numerous potentially undescribed lineages recognized in the present study, and for which sufficient material is available for detailed anatomical study, are currently underway (Liyandja in prep.).

As indicated in Figure 4, members of the *L. forskalii* group, excluding *L. alluaudi*, form two large, well-supported sister clades (A and H). Clade A is composed of species from the Upper Guinean, Nilo-Sudanian, Zambezian, East Coast, northern Lower Guinean, and Lake Tanganyika ecoregions. While the larger Clade H includes two species (*L. annectens* and *L. lukulae*) from rivers of southern Lower Guinea, it is otherwise composed exclusively of species from the Congo basin.

Within Clade A, the west African *L. ogunensis* is nested within subclade B with *L. victorianus* from the Mara River in the Lake Victoria system, *L. dhonti* from the Malagarazi River, members of the *L. cylindricus* complex from the Zambezi and Komati rivers, and two specimens from the Nile River identified as *L. parvus* by submitters to GenBank (*Labeo* sp. 'Nile'; Figure 4). By contrast, *L. obscurus* and other species often misidentified as *L. parvus* in west Africa are nested within three subclades (D, F and G). Clade D includes *L. forskalii* from the Nile River and members of the *L. molybdinus* complex from the Zambezi River. Clade F is composed of members of the *L. sanaganensis* complex from the Sanaga River, while Clade G includes *L. obscurus* from the Kakrima River (Konkoure system), *L.* cf. *obscurus* from the Penselli River (Little-Scarcies system) and the two additional undescribed lineages: *Labeo* sp. 'Niger' from the Bafing River (Senegal system) and Niger River, and *Labeo* sp. 'St Paul' from the St Paul system (Oule and other rivers).

The large central African clade (Clade H) is resolved into two main sister-clades (I and J). Clade I is represented by a single species, *Labeo*

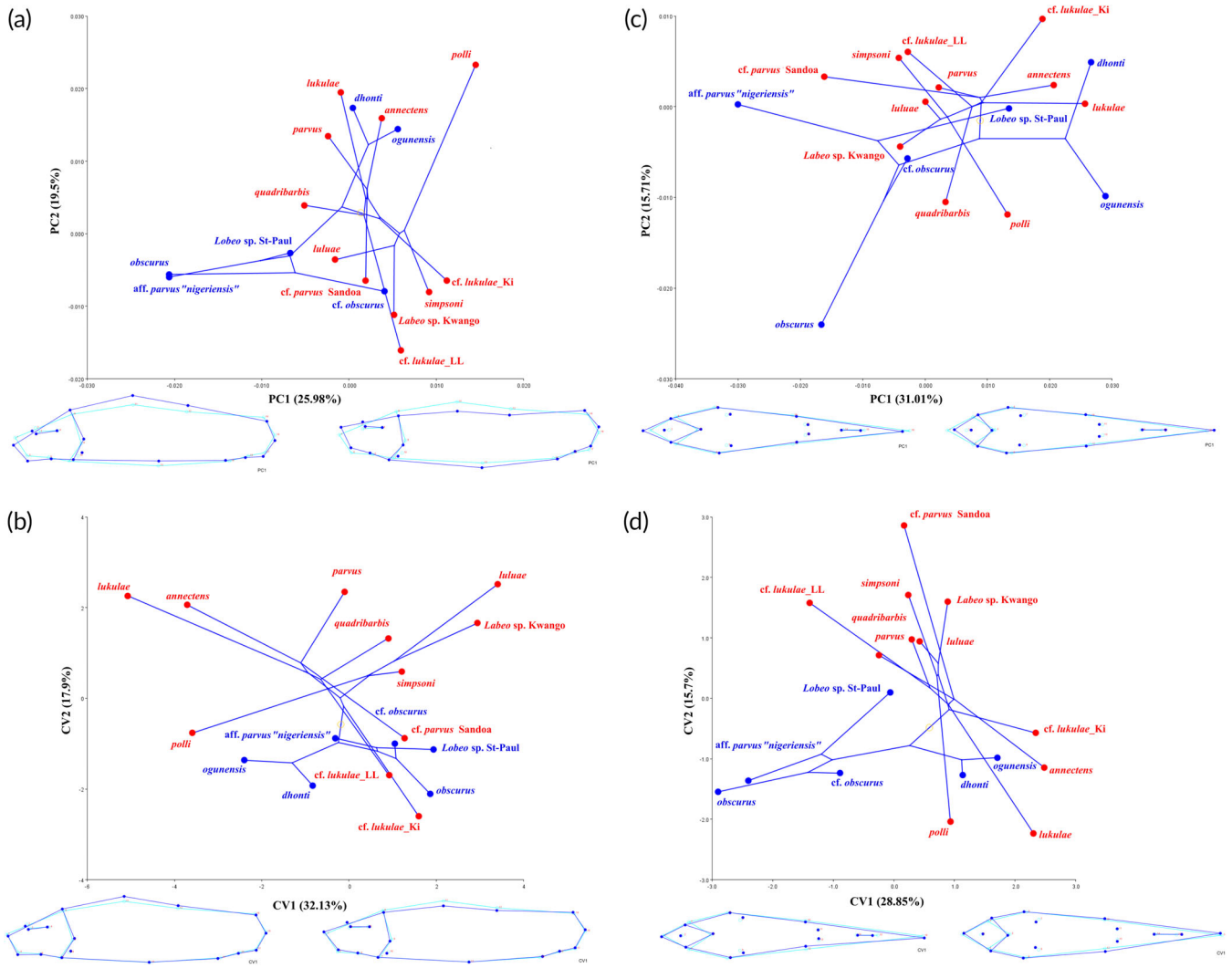

FIGURE 9 Phylomorphospace plots of body shape of 17 *L. forskalii*-group species from Central Africa and West Africa. (a) PC1 *vs*. PC2, (b) CV1 *vs*. CV2 in lateral view, (c) PC1 *vs*. PC2 and (d) CV1 *vs*. CV2 in ventral view

sp. 'UCR' from the Kisangani region in the upper Congo River, a taxon previously confused with *L. lukulae ss* which is suggested here to be endemic to the type locality (Chiloango basin) in southern Lower Guinea (Boulenger, 1912, 1916). Clade J is divided into two main subclades (K and L). Clade K includes two subclades, with Clade M composed of *L. parvus ss* and its close relatives. These include *L. annectens* from southern Lower Guinea and three previously unrecognized Congo basin lineages (*Labeo* sp. 'Kwilu', *Labeo* sp. 'Sangha' and *Labeo* sp. 'Lulua'), and based on the current analysis the sister species to *L. parvus ss* is resolved as *Labeo* sp. 'Kwilu' (Kasai basin). Clade N includes *L. lukulae ss*, *L. quadribarbis*, *L. sorex*, *L. nasus* and representatives of some previously unrecognized lineages. Among these *Labeo* sp. 'mbimbii' appears to be a well-defined taxon from the Lulua River in the Kasai basin, while the others are represented by few specimens and clearly additional sampling will be necessary before their taxonomic composition and status can be established. Clade L includes members of the *L. polli* complex (*L. polli* and *L.* cf. *polli*), *L. simpsoni*, *L. luluae* and a number of potentially unrecognized lineages for which further sampling is necessary before formal taxonomic changes can be proposed.

3.2 | Geometric morphometric analysis

Body shape PCAs (lateral and ventral views) show marked overlap between representatives of *L. parvus*-like species from west (Clade A) and central (Clade H) Africa (Figure 5). In PCAs of averaged Procrustes coordinates for each group many Clade A species fall closer in morphospace to Clade H species than they do to their immediate relatives (Supporting Information Figure S4). Separation of Clade A species (including *L. ogunenis* and *L. obscurus*) from those of Clade H (including *L. parvus ss*) becomes clearer in canonical variate analysis (CVA), which maximizes the difference between groups (Webster & Sheets, 2010) with input groups determined *a priori* based on phylogenetic structure, but nonetheless considerable overlap is still evident (Figure 6). Permutation tests (CVA) for Procrustes distances (PD) and Mahalanobis

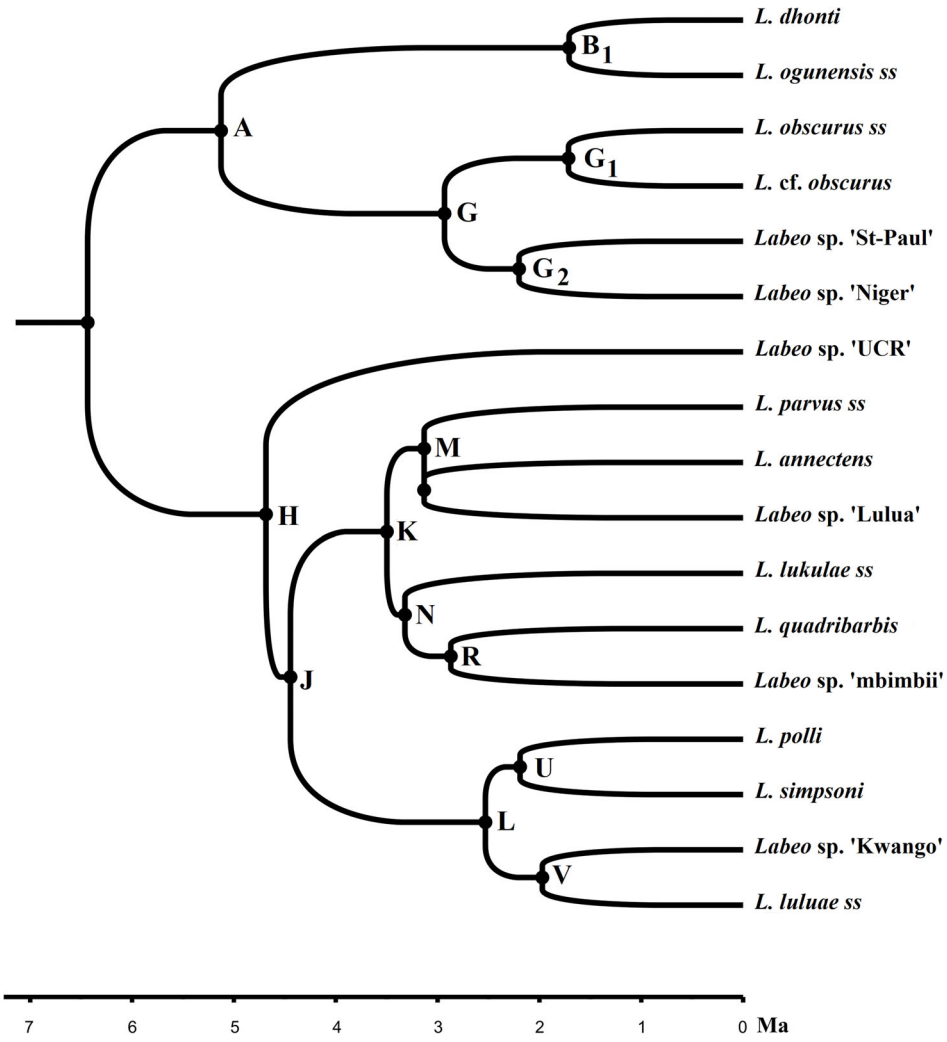

FIGURE 10 Pruned time-calibrated tree used to test for phylogenetic signal and convergence. The tree has been pruned to include only *Labeo* species also included in the morphospaces. Nodes correspond to node identifications in Figure 4

distances (MD) revealed significant differences in lateral and ventral body shapes between the two main clades ($P < 0.0001$, PD = 0.0164 and MD = 2.4173 in lateral view and PD = 0.0175 and MD = 2.0614 in ventral view). Lateral and ventral body shape differences between clade A and clade H individuals were mostly described by PC1 (25.98% lateral, 31.88% ventral) and CV1 (32.13% lateral, 28.85% ventral). Individuals from central Africa tended to have shallower and thicker bodies whereas west African individuals tend to be somewhat more laterally compressed with relatively deeper and narrower bodies. Additionally, west African individuals exhibit a shorter vent to anal-fin distance than do most central African individuals (Figure 6).

Further comparisons to assess shape differences among lineages delimited in our molecular phylogeny were conducted using CVA. In these, most species are significantly different both in ventral and lateral view as shown in the scatterplots of CV2 versus CV3 (Figure 7, and Supporting Information Tables S4 and S5). However, nonsignificant differences between distantly related taxa indicate marked similarities in body shape. For instance, no significant differences were detected, in either view, between specimens of *L. parvus ss*, *L. obscurus*, *L.* cf. *obscurus*, *L. quadribarbis* and *Labeo* sp. 'Lulua', and the marked phenotypic similarity observed among these individuals agrees with the PCA results in supporting a hypothesis of repeated convergent evolution among geographically and phylogenetically disparate lineages.

3.3 | Meristics analysis

Meristic counts are summarized in Supporting Information Tables S1 and S2. After removal of invariant counts, a PCA performed on 13 meristic features (Figure 8) revealed greater similarity between the geographically and phylogenetically heterogeneous grouping of *L. parvus ss*, *Labeo* sp. 'Niger', *L. quadribarbis*, *Labeo* sp. 'St Paul', *L. obscurus*, *L. simpsoni*, *Labeo* sp. 'Lulua' and *L. luluae* (lefthand side) than with *L. ogunensis*, *L. polli*, *L. annectens*, *L. dhonti*, *Labeo* sp. 'UCR' and *L.* cf. *obscurus* (right-hand side), with the first group generally exhibiting somewhat lower meristic counts, but with considerable overlap and no evidence of taxonomically discriminatory meristic features.

3.4 | Phylogenetic signal test

Permutation tests for phylogenetic signal were nonsignificant for both PCA ($P < 0.1428$ lateral view and $P = 0.2108$ ventral view) and CVA

TABLE 1 Converging clades (nodes) detected by *search.conv* applied to the body shape of 17 *L. forskalii*-group species by estimating ancestral phenotypes in RRphylo

Converging node pairs		ang.bydist.tip	ang.conv	ang.ace	ang.tip	nod.dist	time.dist	p.ang.bydist	p.ang.conv
A. In lateral view									
With CVA data									
G1	V	9.679978	19.82228	93.16827	88.92133	7	9.18611	0.051	0.012
B. In ventral view									
With PCA data									
B1	N	9.496237	18.89254	73.69509	74.47883	6	7.842984	0.127	0.036
With CVA data									
U	B1	10.47513	21.66779	100.4356	93.99701	6	8.97335	0.094	0.035
V	B1	11.05399	22.22949	102.7257	101.6088	6	9.192046	0.153	0.044

Note: *ang.bydist.tip*, the mean theta angle between clades divided by the time distance; *ang.conv*, the mean theta angle between clades plus the angle between aces, divided by the time distance; *ang.ace*, the angle between ancestors; *ang.tip*, the mean theta angle between clades; *nod.dist*, the distance intervening between clades in terms of number of nodes; *time.dist*, the time distance intervening between the clades; *p.ang.bydist*, the *P value* computed for *ang.bydist.tip*; *p.ang.conv*, the *P value* computed for ang.conv.

($P < 0.0626$ lateral view and $P = 0.1356$ ventral view) in MorphoJ as well as in Geomorph (PCA lateral view $P = 0.3167$ and $K = 0.6608$, ventral view $P = 0.5884$ and $K = 0.5487$; CVA lateral $P = 0.4096$ and $K = 0.6142$, ventral view $P = 0.5195$ and $K = 0.5717$). These results reject a finding that phylogenetic relatedness is responsible for overall body shape similarity. Additionally, low values of K (phylogenetic signal) strongly support a hypothesis of convergence in body shape among species. In corroboration, Figure 9 shows the phylomorphospaces on which the tests were conducted and Figure 10 illustrates the pruned tree on which analyses were performed.

3.5 | Convergence

Our study of body shape among clades of *L. forskalii*-group species found several instances of morphological convergence between subclades of west and central Africa. In lateral view, of seven node pairs tested with PCA scores, no convergence was found whereas with CVA scores two instances of convergence were detected. The first instance occurred between nodes V (*L. luluae* and *L.* sp. 'Kwango') and G_1 (*L. obscurus* and *L.* cf. *obscurus*) and the second between nodes G_2 (*Labeo* sp. 'Niger' and *Labeo* sp. 'St Paul') and V (Table 1). In ventral view, only one instance of morphological convergence, between nodes N (*L. lukulae*, *L. quadribarbis* and *L.* sp. 'mbimbii') and B_1 (*L. ogunensis* and *L. dhonti*), was detected with PCA scores and another single instance of convergence was also detected between nodes U (*L. polli* and *L. simpsoni*) and B_1 (Table 1) with CVA scores data.

4 | DISCUSSION

Our phylogenetic analyses strongly suggest that species of *Labeo* closely related to *L. parvus ss* are either Congo basin or southern Lower Guinean endemics. None of the Congolese species sharing phenotypic similarity with *L. parvus*, except for *L. dhonti*, are closely related to any members of the west African *L. ogunensis* and *L. obscurus* clades. Consequently, the occurrence of *L. parvus* in west Africa or in any African province other than the Congo or southern Lower Guinea (Guégan *et al*., 1988; Jegu & Lévêque, 1984; Lalèyè *et al*., 2004; Lévêque *et al*., 1990; Nwani *et al*., 2011) is, as originally suggested by Reid (1985), unsupported.

The results presented here reveal *L. parvus sl* to be deeply polyphyletic and that the numerous putative species from west Africa previously identified as *L. parvus* are not at all closely related to *L. parvus ss* yet the morphological similarities among and between them are striking. It is known that body shape in many aquatic animals, and fishes in particular, is highly responsive to environmental/hydrodynamic pressures (Bryant, 1977; Knouft, 2003), and that species that occupy similar niches and/or exhibiting similar behaviours (whether sympatric or allopatric) tend to produce similar body shapes in adaptation to the functional requirements imposed (Armbruster *et al*., 2016; Knouft, 2003).

Our phylogenetic signal results indicate that there is indeed low signal in overall body shape among these taxa. This suggests that there is lower than expected resemblance between closely related species in both clades (A and H) and higher than expected resemblance between distantly related species. Low phylogenetic signal is associated with convergent evolution and a rapid rate of character change (Ackerly, 2009). Here we suggest that such rampant convergence may be a response to the functional requirements imposed by occupation-specific habitats. In this case occupation of regions of rapid water flow and an ecological association with rocky, hard surface substrates, which are precisely the habitats where most *parvus*-like species included in this study are almost exclusively collected (pers. obs. and pers. commun. from local fishers). Recent studies (Alter *et al*., 2015; Stiassny & Alter, 2021) have demonstrated that regions of extreme rapids over rocky habitats of the lower Congo River harbour similar instances of phenotypic convergence in distantly related spiny eels, and in several other groups of fishes (*e.g*., mormyrids, cichlids, catfishes and cyprinids). However, also pertinent here is the observation that convergence has been extensively reported as a common feature of rapidly

radiating groups in both aquatic and terrestrial habitats (Blackledge & Gillespie, 2004; Gillespie *et al*., 2018; Kratochwil *et al*., 2018; Mahler *et al*., 2013; Ruber & Adams, 2001). Based on the high number of species in the *forskalii* group (several not included in the current study) and our preliminary estimation of the timing of their spread across the continent (see Figure 10) it appears likely that rapid colonization of new habitats may contribute, at least in part, to the elevated levels of phenotypic similarity observed. We can discount the alternative interpretation of a repeated retention of plesiomorphic morphology based on our recovered tree topology.

Interestingly, the similarity between many of the *L. parvus*-like species of the *L. forskalii* group is not limited to body shape but also includes a pigmentation patterning dominated by the presence of a conspicuous broad, lateral band running from the posterior border of the opercle to the base of the caudal peduncle (Figure 4), and even in taxa where adult banding is muted it is invariably present in juveniles and smaller specimens. Similar strongly marked horizontal stripes are present in many African Great Lake cichlids (Seehausen *et al*., 1999; Henning *et al*., 2014) and this dominant patterning has been shown to have evolved repeatedly numerous times in phylogenetically disparate lineages (Henning *et al*., 2014). Seehausen *et al*. (1999) suggested that the evolution of horizontal stripes in cichlids is associated with feeding (piscivory) and/or shoaling behaviour, and that shoaling behaviour can be associated with predation avoidance or predator intimidation. In a later study Kratochwil *et al*. (2018) found that the convergent evolution of horizontal stripes in cichlids is controlled by cis-regulation of the teleost-specific agouti-related protein 2 gene (*agrp2*).

Unfortunately, little is currently known of the trophic or behavioural ecology of *Labeo* in Africa, however the phylogenetic framework and evidence of rampant phenotypic convergence presented here provides an opportunity to begin to explore such questions. Additionally, our results provide a framework for further investigations into the drivers of morphological trait evolution among these species. Whether the evolution of a dominant, lateral stripe pigmentation patterning or a similar body shape among *L. parvus*-like species is driven by the same behavioural, ecological and genomic controls as those in cichlid fishes remains to be determined. Future studies (Liyandja *et al*., in prep.) are trying to address some of these questions using larger samples and comparative approaches using genome-wide data.

4.1 | Conservation implications

Based on the assumption that *L. parvus* is widely distributed throughout the African continent with no major widespread threats, the species is currently listed as of least concern in the most recent IUCN Red List of Threatened Species (Lalèyè *et al*., 2020). Our results have demonstrated that this is not the case and suggest instead that *Labeo parvus ss* is restricted to the Congo basin. However, the presence of within-basin associated genetic structure within *L. parvus ss* (Figure 4) suggests that additional study will be necessary to fully delimit the species' range beyond the type locality in the Ubangi system. Additionally, many of the species previously recognized as *L. parvus sl* are endemic to specific regions and river basins, and numerous previously unrecognized lineages have been identified here. Clearly, the conservation status of each of these is likely to be of much higher concern than is currently recognized. The importance of this finding is underscored by the fact that commercial and artisanal fishing pressures are rapidly increasing throughout the continent due to demographic growth, poverty and food insecurity (Chan *et al*., 2021; Mbimbi *et al*., 2021; Obiero *et al*., 2019). In east Africa, for example, populations of *L. parvus sl* have been assessed as endangered (Hanssens, 2010). In much of west Africa *L. parvus sl* are considered highly desirable food fish and are intensively harvested by artisanal fishers (Montchowui *et al*., 2009, 2011), and clearly regional reevaluation of the conservation status of each lineage previously included in *L. parvus sl* is necessary to determine what measures or conservation actions will be needed to ensure the long-term sustainable harvest of each of these species.

5 | CONCLUSION

Due to marked phenotypic similarity numerous specimens in the field and in museum collections have been misidentified, and many described species have erroneously been synonymized with *L. parvus*. Our results confirm that *L. parvus ss* is endemic to the Congo basin, and that *L. ogunensis* and *L. obscurus* from the Nilo-Sudan and Upper Guinean ecoregions, respectively, are valid species. *L. forskalii*-group taxa are partitioned into two main clades with both containing morphologically *L. parvus*-like described and cryptic species, with strikingly similar body shapes and pigmentation patterning resulting from convergent evolution. The two groups also show extensive overlap in the meristic features commonly used in traditional species descriptions. Hence, these characters alone are insufficient to differentiate *L. parvus*-like species across ecoregions, thus explaining why so many phylogenetically distinct and unrelated species have previously been confused with *L. parvus ss*.

Importantly, our study provides the necessary phylogenetic framework for ongoing work to provide a morphology-based taxonomic revision, with description of numerous previously unrecognized members of the *L. forskalii* lineage; a crucial step towards the development of sound strategies for fisheries resource management of these important food fishes across the continent.

AUTHOR CONTRIBUTIONS

T.L.D.L., M.L.J.S. and J.W.A. conceived and designed the experiments. T.L.D.L. collected and analysed the data. M.O.P. collected additional data for *L. ogunensis sensu stricto*. T.L.D.L. wrote the paper with input from all authors.

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CONFLICT OF INTEREST

We declare that this study was conducted in the absence of any commercial or financial relationships that could be considered as a potential conflict of interest.

SIGNIFICANCE STATEMENT

Species delimitation and taxonomy of *Labeo* in Africa have proven highly problematical due to rampant morphological homoplasy. To disentangle the taxonomic problems within this highly diverse genus integrative taxonomic methods are needed. This paper uses a phylogenetic comparative approach to assess phenotypic convergence among species of the *L. forskalii* group, investigate the taxonomic status of *L. parvus sensu lato* in west Africa and re-evaluate the composition and distribution of *L. parvus sensu stricto*. Our results provide no support for a sister relationship between *L. parvus ss* and any of the west African *Labeo parvus*-like species, and indicate that *L. parvus ss* is a Congo basin endemic that is replaced in west Africa by *L. ogunensis*, *L. obscurus* and other undescribed or previously synonymized species. Additionally, our results highlight the role of overall body shape similarity in contributing to the taxonomic confusion among these phenetically similar yet distantly related species. Based on the results of this work, the redescription of *L. parvus* and the description of several new *Labeo* species are in preparation.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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