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Review of Cyprinodontiform Fishes in the Upper Congo Drainage with Descriptions of Four New Species of Seasonal *Nothobranchius* (Nothobranchiidae) and a New Species of '*Lacustricola*' Lampeye (Procatopodidae) in South-Eastern DR Congo

Béla Nagy *

Independent Researcher, 15, voie de la Liberté, 77870 Vulaines-sur-Seine, France

* Corresponding author. E-mail: bela.nagy@neuf.fr (B.N.)

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ABSTRACT: The cyprinodontiform fish fauna of the Bangweulu–Mweru and Upper Lualaba freshwater ecoregions, situated in the uppermost Congo River drainage, has been reviewed. This study introduces four newly described species of seasonal *Nothobranchius* killifish and a novel species of lampeye belonging to the genus '*Lacustricola*'. *Nothobranchius iridescens*, new species, from the Kafila system in the Lufira drainage, is characterized in male colouration by anal fin with irregular red-brown spots and stripes, creating two irregular submedial and medial bands and with broad yellow subdistal band; and a caudal fin with a slender light blue subdistal band, densely marked with irregular red spots, and narrow dark brown distinct distal margin. *Nothobranchius katemomandai*, new species, from the Kay system in the upper Lualaba drainage, is characterized in male colouration by an anal fin with narrow brown submedial band, followed by a slender yellow band, a slender red-brown band and a slender dark brown distal band; and a caudal fin with brown spots proximally and medially, and with slender white to light blue subdistal band and a narrow dark grey distal band. *Nothobranchius marmoreus*, new species, from the Lufukwe system in the Lake Mweru basin, is characterized in male colouration by a body with irregular red-brown patches and stripes, forming a marble-like mottled pattern; and anal and caudal fins with slender yellow to amber subdistal band and broad dark brown distal band. *Nothobranchius dubieensis*, new species, from the Lubule system in the Luvua drainage, is characterized in male colouration by an anal fin with narrow dark brown submedial band, narrow yellow and orange medial bands, narrow white subdistal band, and slender dark brown distal band; and a caudal fin with irregular red-brown spots and stripes proximally and medially, followed by an irregular narrow red-brown subdistal band and slender white distal band, and with interrupted red-brown fin tips. '*Lacustricola*' *gemma*, new species, from the Kay system in the upper Lualaba drainage, is characterized by a pattern of iridescent, diamond-shaped, light blue spots in scale centres below mid-longitudinal series on posteroventral portion of flank; median fins yellow to hyaline, with dark grey stripes perpendicular to fin rays; dorsal fin with light blue distinct margin; anal fin with dark grey margin. Analysis of mitochondrial COI gene sequences revealed that the five new species represent phylogenetically distinct lineages. These findings not only underscore their genetic uniqueness but also confirm their placement within the *Nothobranchius brieni* species group and the genus '*Lacustricola*'. Species of the genus *Nothobranchius* complete their seasonal life cycle in ephemeral natural habitats within freshwater wetlands, while '*Lacustricola*' species migrate to breed in flooded areas of shallow, typically seasonal wetland habitats at the onset of the rainy season. These wetlands are highly vulnerable to a variety of human-induced stressors and threats, including agricultural cultivation, water extraction, urban expansion resulting in land-use pressure, and increased pollution, particularly from industrial activities such as mining. Therefore, it is essential to protect the integrity of these unique aquatic habitats throughout all the seasons of the year to maintain healthy wetland ecosystems and safeguard the distinctive seasonal freshwater biodiversity they support.

Keywords: Bangweulu–Mweru freshwater ecoregion; Barcoding; Conservation; Killifish; Upper Lualaba freshwater ecoregion

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1. Introduction

The study focuses on the southeasternmost part of the vast Congo River basin, specifically the uppermost section of the drainage system located in south-eastern Democratic Republic of the Congo and north-western Zambia. This region encompasses the Bangweulu–Mweru freshwater ecoregion (n°544 in [1].) and the Upper Lualaba freshwater ecoregion (n°545). The ichthyofauna includes representatives of two cyprinodontiform fish families: Nothobranchiidae and Procatopodidae.

1.1. Nothobranchiidae

Within the family, species of the seasonal killifish genus *Nothobranchius* [2], are found in the uppermost part of the Congo drainage (Table 1).

Table 1. Members of the *Nothobranchius brieni* species group, and their distribution according to drainage systems and freshwater ecoregions. Numbering of freshwater ecoregions according to [1].

***Nothobranchius* Species**	**River**			**Freshwater Ecoregion**	**Region of Occurrence**
	System	**Subdrainage**	**Drainage**		
N. capriviensis [3]	upper Zambezi		Zambezi	Upper Zambezi floodplains (556)	north-eastern Namibia
N. kafuensis [4]	upper and middle Zambezi			Upper Zambezi floodplains (556); Kafue (557)	south-eastern and southern Zambia
N. boklundi [5]	Luangwa			Middle Zambezi–Luangwa (558)	eastern Zambia
N. symoensi [6]	upper Luapula	Luapula	upper Congo	Bangweulu–Mweru (544)	northern Zambia
N. rosenstocki [7]					
N. cooperi [8]	middle Luapula				
N. sainthousei [9]					
N. chochamandai [10]					south-eastern DR Congo
N. spec. from upper Lubi, putative species, description in review [11]	lower Luapula				
N. malaissei [6]					
N. marmoreus, new species	Lake Mweru				
N. ditte [12]					
N. milvertzi [13]					northern Zambia
N. oestergaardi [14]	Lake Mweru Wantipa				
N. dubieensis, new species	Lubule	Luvua			south-eastern DR Congo
N. hassoni [15]	middle Lufira	Lufira		Upper Lualaba (545)	
N. iridescens, new species					
N. polli [6]	upper Lufira				
N. flagrans [16]	lower Lufira				
N. brieni [17]	upper Lualaba	Lualaba			
N. katemomandai, new species					

The genus overall currently comprises 97 valid species, occurring mainly in ephemeral wetlands of river drainages situated in the north-eastern, eastern, and south-eastern parts of Africa [18]. They are recognised as seasonal fishes, with all known species having an ‘annual’ life cycle [19,20], a key adaptation to live in the seasonally arid savannah biome characterised by periodic drying out of their natural habitats [21–24]. The life-cycle periodicity is determined by the rainfall pattern of the wetlands in which they occur. As such, each year, before these wetlands dry out, spawning takes place, and the eggs survive the dry season buried in the substrate mud. When the ensuing rainy season arrives, the rivers overflow their banks, inundate the floodplains again, and the buried eggs hatch [18,23–25].

Nothobranchius species are highly sexually dichromatic. The typically colourful and robust males are in contrast to the uniformly-coloured and slightly smaller females (e.g., [26–28]). The distinctive colour pattern of the males provides important diagnostic characters (e.g., [12,26–30]). They are small fishes, with most species reaching 30–70 mm in standard length (SL) with only a few species reaching 100 mm SL or more [28]. The genus has gained particular interest as it includes *N. furzeri* [31], the vertebrate species with the shortest lifespan recorded in captivity (less than 12 weeks), and which has emerged as a model organism for biological and molecular studies of ageing (e.g., [32]). Another member of the genus, *N. rachovii* [33], possesses a low diploid number ($2n = 16$) of rather large chromosomes, leading to its emergence as an excellent vertebrate model organism for laboratory chromosome studies (e.g., [34,35]).

Within the genus *Nothobranchius*, seven subgenera are recognised [36]. *Zononothobranchius* [37] is the largest subgenus with 46 valid species, occurring in wetland habitats on the inland plateaus of north-eastern, eastern, and south-eastern Africa. Its constituting species are organised into five well-identified species groups, namely: the subject group of the present paper, the *N. brieni* species group ($n = 16$ valid species) (*sensu* [12]), as well as the *N. neumanni* group ($n = 5$) (*sensu* [38]); the *N. rubroreticulatus* group ($n = 4$) (*sensu* [36]); the *N. taeniopygus* group ($n = 7$) (*sensu* [29]); and the *N. ugandensis* group ($n = 12$) (*sensu* [30]).

All currently known *Nothobranchius* species from the upper Congo drainage belong to the *N. brieni* species group [12]. Thirteen species of the species group have been known to occur in the upper Congo drainage, namely nine in the Bangweulu–Mweru freshwater ecoregion and four in the upper Lualaba freshwater ecoregion (see Table 1). The additional three members of the species group are known in the adjacent Zambezi drainage, from the upper Zambezi floodplains (n°556), Kafue (n°557), and middle Zambezi–Luangwa (n°558) freshwater ecoregions. The species of the *N. brieni* species group are the only representatives of the genus in the above-listed freshwater ecoregions in south-central Africa and represent the south-western limit of the range of the genus [3,18,23,39]

1.2. Procatopodidae

Species within the family Procatopodidae are endemic to Africa, primarily inhabiting continental freshwater environments, with a few species found in coastal brackish waters [40,41]. These fishes, commonly known as lampeyes, are named for the reflective pigments in their eyes that create a striking iridescent spot above the iris. Lampeyes are widely distributed from the western Sahel to southern Africa [27,42]. This family represents an ecologically diverse group, with species occupying various habitats such as small streams, swamps, ponds, lakes, and brackish water estuaries [42–44]. Currently, the family is divided into 14 genera encompassing approximately 80 valid species [41]. Procatopodidae species exhibit significant morphological diversity, with most being small fish that rarely exceed 30-40 mm in standard length (SL), although some have extremely reduced body sizes, and one species is known to exceed 100 mm SL [45].

Phylogenetic analysis performed by Bragança & Costa (2019) [41], aimed at assessing the internal relationships among the little known African lampeye genera, revealed polyphyly or paraphyly of some of its genera. Their findings suggest that the current taxonomic classifications may not accurately reflect the evolutionary history of these species. Specifically, a group of species constitutes a southern African clade of lampeyes, commonly referred to as the genus ‘*Lacustricola*’. This is an undescribed genus with the highest diversity in southern Africa, from coastal river systems in north-eastern South Africa to the northern tributaries of the Congo. There are three main species groups within the southern clade, namely the ‘*L.*’ *hutereaui* [46] group, the ‘*L.*’ *johnstoni* [47] group, and the ‘*L.*’ *katangae* [48] group. These groups have broadly similar distribution patterns, with some species occurring sympatrically [49–51].

Within the uppermost Congo drainage, eight valid species were known (Table 2). One species of the genus *Lacustricola* [52], is present in the upper Lualaba freshwater ecoregion, namely *Lacustricola lualabaensis* [17]. Six species belong to the southern African clade ‘*Lacustricola*’. Further, a species showing affinities to ‘*Hypsopanchax*’ *jubbi* [53], is also present in the target study area.

Procatopodid species in the target region of arid savannah are typically found forming schools near the surface of large bodies of water, such as rivers and lakes. However, with the onset of the rainy season, they move for breeding into flooded areas of shallow water, typically seasonal wetland habitats. They have a non-seasonal mode of reproduction, and eggs are deposited among floating or hanging vegetation. Parents and many of the juveniles are often found trapped in the progressively drying seasonal water bodies.

Table 2. Species of Procatopodidae found in the upper Congo drainage. Numbering of freshwater ecoregions according to [1].

Procatopodid Species	River System	Subdrainages in DR Congo	Freshwater Ecoregion in Congo Drainage	Region of Occurrence (Includes:)
'*Hypsopanchax*' *jubbi* [53]	upper Lualaba	Lualaba	Upper Lualaba (545)	SE DR Congo; Zambia
'*Lacustricola' gemma*, new species	Kay	Lualaba	Upper Lualaba (545)	SE DR Congo
'Lacustricola' hutereaui [46]	several systems	widespread overall	Bangweulu–Mweru (544); Upper Lualaba (545)	SE DR Congo; Zambia
'*Lacustricola*' *johnstoni* [47]	several systems	widespread overall	Bangweulu–Mweru (544); Upper Lualaba (545)	SE DR Congo; Zambia
'*Lacustricola*' *katangae* [48]	several systems	widespread overall	Bangweulu–Mweru (544); Upper Lualaba (545)	SE DR Congo; Zambia
Lacustricola lualabaensis [17]	several smaller systems	Lualaba	Upper Lualaba (545)	SE DR Congo
'*Lacustricola' moeruensis* [54]	several systems	Luapula, Lualaba	Bangweulu–Mweru (544); Upper Lualaba (545)	SE DR Congo; Zambia
'*Lacustricola' nitidus* [55]	Lufupa	Lualaba	Upper Lualaba (545)	SE DR Congo
'*Lacustricola*' *petnehazyi* [56]	Lake Tschangalele	Lufira	Upper Lualaba (545)	SE DR Congo

SE stands for south-eastern.

1.3. Objective of the Study

During recent field surveys aimed at documenting the cyprinodontiform species diversity in the upper Congo drainage, several new populations, considered potential new species, were collected by the author and colleagues from the University of Lubumbashi between April 2016 and April 2023. Examination of these specimens, along with analyses of combined morphometric and molecular data, revealed that some represent new species to science. Four new species belonging to the seasonal cyprinodont genus *Nothobranchius* in the family Nothobranchiidae, and one new species of lampeye genus '*Lacustricola*' in the family Procatopodidae are identified and described herein.

Furthermore, *Nothobranchius* species typically inhabit small, ephemeral wetland habitats, while lampeyes often migrate to these biotopes for breeding during the rainy season. This ecological adaptation makes them highly vulnerable, as the ephemeral wetland habitats frequently face degradation due to various human-induced stressors and threats. The significance of these discoveries from a conservation perspective is underscored by the numerous and increasing anthropogenic impacts documented in the region. These findings highlight the urgent need for active protection and conservation of the freshwater wetland habitats where these species occur.

2. Materials and Methods

The type series and comparative specimens are deposited in the following collections: RMCA, Royal Museum for Central Africa, Tervuren, Belgium (also referred to as MRAC in the past); MSNG, Museo Civico di Storia Naturale Giacomo Doria, Genova, Italy; and SAIAB, South African Institute for Aquatic Biodiversity, Grahamstown, South Africa. All locality data have been translated into English.

2.1. Morphological Analysis

Measurements and counts were taken as described in Nagy (2014a, 2018) [12,13]. Terminology of the cephalic sensory system and descriptions of colour markings follow Nagy (2018) [12]. Species of the genus *Nothobranchius* exhibit pronounced sexual dichromatism and dimorphism, therefore, descriptions of comparative colour pattern elements are based on mature males.

In order to compare measurements between species, multivariate biostatistical analyses of morphometric and meristic variables were performed using Minitab 16.2.1 [57]. Due to sexual dimorphism, statistical analyses are performed on male specimens that typically show interspecific variation, and not involving the generally uniform females. Proportions of measurements in the form of percentages were calculated in order to remove size effects from variation in body shape. Scatterplot graphs of morphometric variables against standard length or head length were accomplished to examine allometric growth effects individually. Meristic data were square-root transformed, whereas morphometric data were log-transformed with base 10 log before the statistical tests were carried out in order to meet standards for statistical and hypothesis testing and to ensure homogeneity of variables for subsequent multivariate analyses [58–62]

The best subset regression method was employed to identify the smallest subset of the most distinctive predictors of morphometric variables for each species among the specimens of the most closely related comparative species. R-squared values have been compared for models of the same size, whereas the adjusted R-squared coefficient was used to compare models with different numbers of predictors [63].

Following Baur and Leuenberger (2011) [64], shape principal component analysis (PCA) was applied using ratios from the best subsets of morphometric variables. This multivariate technique, supported by the ratio spectrum, highlights shape differences in morphometric characters between species. PCA is used as a distribution-free ordination method to graphically display uncorrelated linear combinations of the original variables in a multivariate dataset [62,65]. The correlation matrix was selected to standardise variables to a zero mean [65,66].

The multivariate technique of principal component analysis (PCA) was employed on the correlation matrix of the best subsets of morphometric variables in order to visualise differences in morphometric characters between species. The principal component analysis is used as a distribution-free ordination method to graphically display uncorrelated linear combinations of the original variables in a multivariate dataset [62,65]. The correlation matrix was selected to standardise variables to a zero mean and ignore differences between different scales and units [65,66].

2.2. Molecular COI Barcoding Analyses

Total genomic DNA of 21 specimens were isolated from ethanol-fixed tissue samples using a NucleoSpin Tissue Kit (Macherey-Nagel, Düren, Germany) by GenoScreen, Lille, France. 10 ng of each sample was subsequently amplified with universal LCO/HCO barcoding COI primers [67] under the following conditions: $MgCl_2$ 1.5 mM, dNTPs 0.24 mM, FastStart Taq DNA polymerase (Roche, Basel, Switzerland) 1 U in a final volume of 25 µL—PCR program 95 °C 5min, 45 cycles of 95 °C 30 s, 45 °C 30 s, 72 °C 1 min, final elongation 72 °C 7 min. After QIAxcel (Qiagen, Hilden, Germany) migration to check efficiency and specificity, all validated PCR products were purified and sequenced in both directions on ABI 3730XL. Sequences were deposited in the GenBank database with accession numbers PV794613 to PV794633 (Tables 3 and 4).

Phylogenetic trees were constructed for the purpose of molecular data interpretation for the *N. brieni* species group and for the procatopodid species of the upper Congo drainage. The phylogenetic hypotheses were based on the analysis of the mitochondrial gene Cytochrome oxidase subunit I (COI), known for being strongly discriminative in species resolution [36,49,68,69]. The new *Nothobranchius* populations were compared with all other known congeners from the *N. brieni* species group, which group also includes all the known *Nothobranchius* species in the studied ecoregions. The new procatopodid populations were compared to the species known in the studied ecoregions, as well as ‘*Lacustricola*’ *chobensis* [70] and ‘*Hypsopanchax*’ *jubbi* from the neighbouring Zambezi drainage, to understand better the relationships of the species in the upper Congo drainage. Further, *Lacustricola pumilus* [71], the type species of the genus *Lacustricola sensu stricto* from the Lake Tanganyika basin, was added to investigate the relationship between the clades of *Lacustricola* and ‘*Lacustricola*’.

Sequences of previously analysed taxa were taken from GenBank, as published in [8,29] and [36] for the genus *Nothobranchius* (Table 3), whereas in [41] and [49] for the procatopodid genera (Table 4). Sequences were cleaned and trimmed to equal lengths of 698 bp and 680 bp, respectively, using BioEdit [72]. Sequence alignment was performed with Clustal Omega [73]. *Nothobranchius neumanni* [74] and *Aliteranodon stuhlmanni* [75] were selected as outgroups, being representative of sister clades to the *N. brieni* species group, and to the Procatopodidae, respectively [36,41].

Phylogenetic analyses of the datasets were performed using Bayesian inference (BI) in MrBayes 3.2.7 [76] and maximum likelihood (ML) analyses in IQ-TREE 2.3.6 [77]. The BI analyses were set to Markov chain Monte Carlo simulation (mcmc) with default heating conditions. The evolutionary model for the GTR substitution model was set with gamma-distributed rate variation across sites and a proportion of invariable sites (GTR + I + Ґ), searching the tree space for 1 million generations starting with random trees and a sampling frequency of each 1000 generations. Tree files were imported into Figtree 1.4.4. [78] for final tree drawings. For comparison of tree topologies and representing alternative visual displays, additional phylogenetic analyses were performed using maximum likelihood (ML) analyses. The most likely trees were generated, and the phylogenetic analyses were rooted on the outgroup taxa *Nothobranchius neumanni* or *Aliteranodon stuhlmanni*.

Table 3. List of *Nothobranchius* species for which relevant mitochondrial DNA (COI) analytical data were used to examine the phylogenetic structure of the *N. brieni* species group, with population field code (if known), general locality, drainage system, and GenBank accession number.

Species	Field Code	Location	System and Drainage	GenBank No.
N. boklundi	ZAM 09-2	Kapani, Zambia	Luangwa, Zambezi	MN099866
N. brieni 1	CD 13-4	Bukama, DR Congo	Lualaba	MF069550
N. brieni 2	-	Mabwe, DR Congo	Katenga, Lualaba	PV794613
N. capriviensis	NA 07-1	Salambama, Namibia	Chobe, Zambezi	MN099867
N. chochamandai 1	CD 13-11	Kasomeno, DR Congo	Kinikabwimba, Luapula	MF069553
N. chochamandai 2	CD 13-11	Kasomeno, DR Congo	Kinikabwimba, Luapula	MF069554
N. cooperi 1	ZAM 07-8	Mansa, Zambia	Mansa, Luapula	MN099868
N. cooperi 2	ZAM 07-8	Mansa, Zambia	Mansa, Luapula	MF069524
N. cooperi 3	ZAM 07-8	Mansa, Zambia	Mansa, Luapula	MF069565
N. ditte 1	CD 16-13	Kilwa, DR Congo	Katate, Lake Mweru	MT991138
N. ditte 2	CD 16-13	Kilwa, DR Congo	Katate, Lake Mweru	MT991139
N. ditte 3	CD 23-6	Kilangela, DR Congo	Kabera, Lake Mweru	PV794614
N. dubieensis 1	CD 23-29	Dubie, DR Congo	Lubule, Luvua	PV794615
N. dubieensis 2	CD 23-29	Dubie, DR Congo	Lubule, Luvua	PV794616
N. flagrans 1	CD 13-7	Pande, DR Congo	Mufufya, Lufira	MF069552
N. flagrans 2	CD 13-7	Pande, DR Congo	Mufufya, Lufira	PV794617
N. hassoni 1	DRCH 2008-09	Bunkeya, DR Congo	Bunkeya, Lufira	MN105989
N. hassoni 2	CD 13-8	Bunkeya, DR Congo	Bunkeya, Lufira	MF069551
N. iridescens 1	CD 23-21	Lutandula, DR Congo	Kafila, Lufira	PV794618
N. iridescens 2	CD 23-30	Lutandula, DR Congo	Kafila, Lufira	PV794619
N. kafuensis 1	ZAM 07-1	Kayuni, Zambia	Kafue, Zambezi	MN099871
N. kafuensis 2	-	Kayuni, Zambia	Kafue, Zambezi	MK784244
N. katemomandai 1	CD 23-26	Lubule, DR Congo	Kay, Lualaba	PV794620
N. katemomandai 2	-	Kay, DR Congo	Kay, Lualaba	PV794621
N. malaissei 1	CD 16-18	Kabiasha, DR Congo	Luizi, Luapula	MT991161
N. malaissei 2	CD 16-18	Kabiasha, DR Congo	Luizi, Luapula	MT991159
N. malaissei 3	CD 23-12	Kabiasha, DR Congo	Luizi, Luapula	PQ784103
N. marmoreus 1	CD 16-12	Mukobe, DR Congo	Lufukwe, Lake Mweru	MT991167
N. marmoreus 2	CD 16-12	Mukobe, DR Congo	Lufukwe, Lake Mweru	MT991137
N. marmoreus 3	CD 23-9	Mukobe, DR Congo	Lufukwe, Lake Mweru	PV794622
N. milvertzi 1	ZM 12-20	Chienge, Zambia	Lushiba, Lake Mweru	MF069556
N. milvertzi 2	ZM 12-20	Chienge, Zambia	Lushiba, Lake Mweru	MF069555
N. neumanni	TNT 2014-02	Kintinku, Tanzania	Bahi Swamp	MN099877
N. oestergaardi	ZAM 10-4	Kalaba, Zambia	Lake Mweru Wantipa	PV794623
N. polli 1	CD 16-10	Kyembe, DR Congo	Tshipokokolo, Lufira	MF069547
N. polli 2	CD 13-9	Kyembe, DR Congo	Tshipokokolo, Lufira	PV794624
N. rosenstocki 1	ZAM 07-3	Chongola, Zambia	upper Luapula	MF069563
N. rosenstocki 2	ZAM 07-7	Kasanka, Zambia	upper Luapula	MF069564
N. sainthousei 1	ZM 12-19	Mweshi, Zambia	Chimbembe, Luapula	MF069559
N. sainthousei 2	ZM 12-19	Mweshi, Zambia	Chimbembe, Luapula	MF069558
N. symoensi	ZAM 07-4	Kapalala, Zambia	upper Luapula	MF069569
N. spec.	CD 23-23	Brakia, DR Congo	upper Lubi, Luapula	PQ784104
N. spec.	CD 23-25	Brakia, DR Congo	upper Lubi, Luapula	PQ784105
N. spec.	DRCP 2013-6	Brakia, DR Congo	upper Lubi, Luapula	MF069557

Table 4. List of Procatopodid species for which relevant mitochondrial DNA (COI) analytical data were used to examine the phylogenetic structure of the family in the upper Congo drainage, with population field code (if known), country, drainage system and general locality, and GenBank accession number.

Species	Field Code	Country	Drainage	GenBank No.
Aliteranodon stuhlmanni	KEN 10-10	Kenya	Kipungani Creek	MF497414
'Hypsopanchax' jubbi 1	-	Zambia	Zambezi	ZAFW071-12
'Hypsopanchax' jubbi 2	-	Zambia	Zambezi	ZAFW150-13
'Hypsopanchax' jubbi 3	-	DR Congo	Lualaba	MG869984
'Lacustricola' chobensis 1	-	Namibia	Okavango	MT075881
'Lacustricola' chobensis 2	-	Malawi	Shire	AY356594
'Lacustricola' chobensis 3	-	Namibia	Zambezi	MT075878
'Lacustricola' gemma 1	CD 23-26	DR Congo	Lualaba	PV794625
'Lacustricola' gemma 2	CD 23-26	DR Congo	Lualaba	PV794626
'Lacustricola' gemma 3	-	DR Congo	Lualaba	PV794627
'Lacustricola' hutereaui		Zambia	Luapula	MG869977
'Lacustricola' johnstoni 1	-	Mozambique	Zambezi	MT075901
'Lacustricola' johnstoni 2	-	Zambia	Luapula	MG869983
'Lacustricola' johnstoni 3	-	Malawi	Shire	MT075900
'Lacustricola' katangae 1	-	DR Congo	Lualaba	MG869978
'Lacustricola' katangae 2	-	Zambia	Zambezi	MT075889
'Lacustricola' moeruensis 1	CD 16-14	DR Congo	Lake Mweru	MG869981
'Lacustricola' moeruensis 2	CD 16-14	DR Congo	Lake Mweru	PV794628
'Lacustricola' moeruensis 3	CD 23-25	DR Congo	Lake Mweru	PV794629
'Lacustricola' nitida	CD 16-2	DR Congo	Lualaba	PV794630
'Lacustricola' petnehazyi 1	CD 23-16	DR Congo	Lufira	PV794631
'Lacustricola' petnehazyi 2	CD 23-16	DR Congo	Lufira	PV794632
'Lacustricola' petnehazyi 3	CD 23-14	DR Congo	Lufira	PV794633
Lacustricola lualabaensis	-	DR Congo	Lualaba	MG869967
Lacustricola pumilus	-	DR Congo	Lake Tanganyika	MG869967

2.3. Species Concept

Following Watters et al. (2019) [29] and Nagy et al. (2020) [30], lineages within cyprinodotiform fish families are recognized herein as distinct species under the Evolutionary Species Concept (ESC) of Wiley (1978) [79], operationalized by the Phylogenetic Species Concept (PSC) and additionally the Recognition Species Concept (RSC), following Mayden (1999, 2002) [80,81]. This consilient approach evaluates complementary datasets and integrates multiple independent lines of evidence.

3. Results

Within the cyprinodotiform fish families in the Bangweulu–Mweru and the upper Lualaba freshwater ecoregions in the upper Congo drainage, 20 species and one putative species of the family Nothobranchiidae are recovered, all belonging to the *Nothobranchius brieni* species group within the genus *Nothobranchius* (Table 1). All species can be identified based on the colour pattern of males, morphometrics, and molecular analysis.

There are nine species of the family Procatopodidae known in the uppermost Congo drainage, one belonging to the genus *Lacustricola* and eight species belonging to the undescribed genus '*Lacustricola*', including one species currently referred to as '*Hypsopanchax*' (Table 2). These species can be identified based on the colour pattern of males, meristics, morphometrics, and molecular analysis

3.1. Morphological Analysis

3.1.1. Nothobranchiidae

Divergence of morphological characters between males of species belonging to the *N. brieni* species group was found. Populations of the new species show diagnostic, non-overlapping morphometric characters from the most closely related species.

In order to highlight the biometric differences, the PCA technique was employed on the correlation matrices of the most distinctive morphometric characters, in order to corroborate the hypotheses of species delimitation. The best subsets regression resulted in distinctive subsets of the most significant predictors that are shown in Tables 5–8. The first two principal components were retained for each analysis, supported by the eigenvalue-one criterion and proportion of the components in total variance. The proportion of variance explained by the retained principal components and factor loadings of each variable is also shown in Tables 5–8. The series of analyses showed that the new members of the *N. brieni* species group cluster separately from other most similar and closely related species in the space of the first and second principal components (Figure 1a–d).

Nothobranchius iridescens was discriminated from *N. hassoni* and *N. polli* on the axis of the second principal component [PC2] (Figure 1a), shown by differences mainly associated with caudal peduncle length and anal-fin base length (Table 5).

Nothobranchius katemomandai was distinguished from *N. brieni* on PC1 (Figure 1b), reflecting differences mainly in postorbital length and dorsal-fin base length (Table 6).

Nothobranchius marmoreus was differentiated from *N. ditte*, *N. malaissei,* and *N. milvertzi* on PC2 (Figure 1c); associated with differences mainly in head width; whereas also on PC1 from *N. ditte* and *N. malaissei*, associated with caudal peduncle length, predorsal length in % of preanal length, and head length (Table 7).

Nothobranchius dubieensis was discriminated from *N. oestergaardi* on PC1 (Figure 1d), representing mainly morphometric differences in snout length and caudal peduncle length in % of its depth (Table 8).

The non-overlapping clusters of specimens recovered by the PCA support the hypothesis that the new species of the *N. brieni* species group can also be separated by morphological characters.

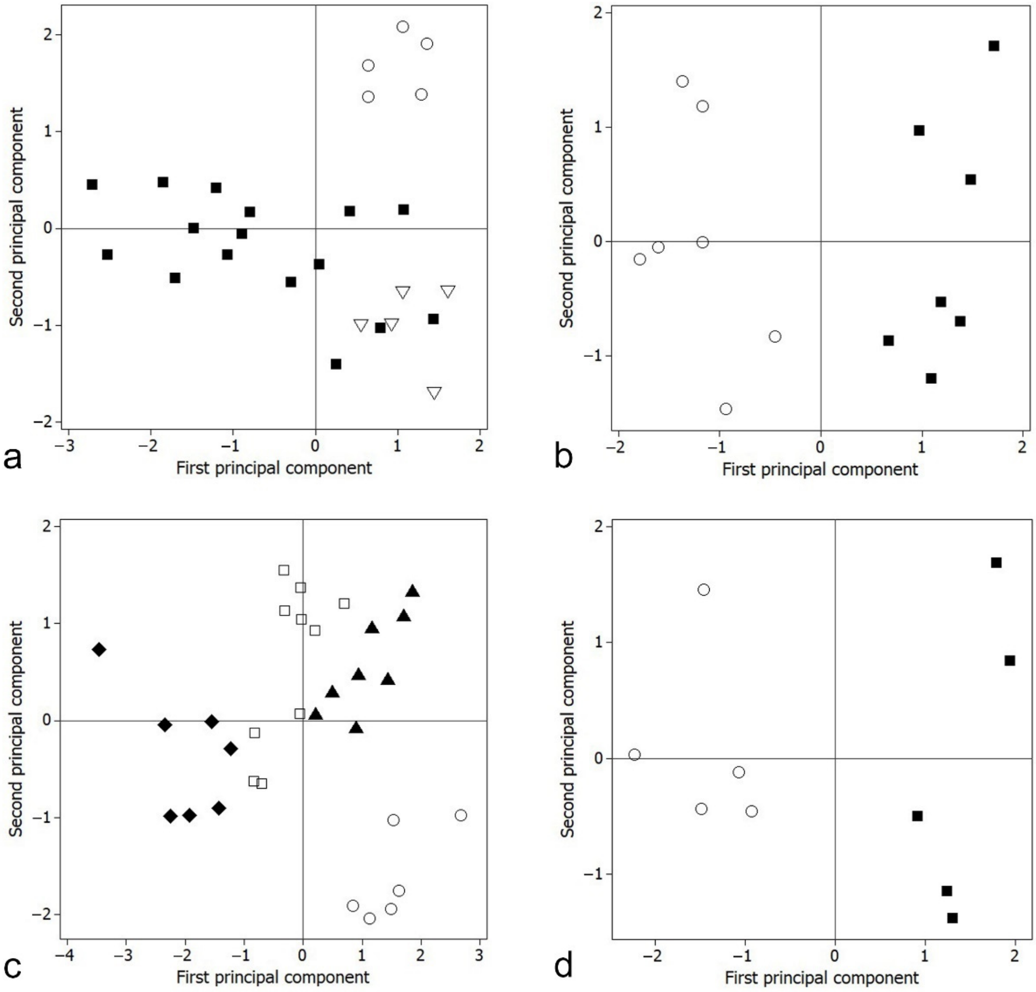

Figure 1. Comparative morphometry in males of the *Nothobranchius brieni* species group. Score plots of principal component analysis on best subsets of distinctive morphometric characters, first component *vs.* second component: (**a**). *N. iridescens* (○) *vs. N. hassoni* (■) and *N. polli* (▽); (**b**). *N. katemomandai* (○) *vs. N. brieni* (■); (**c**). *N. marmoreus* (○) vs *N. ditte* (□), *N. malaissei* (♦) and *N. milvertzi* (▲); and (**d**). *N. dubiensis* (○) *vs. N. oestergaardi* (■).

Table 5. Factor loadings and proportions of variance explained by the selected first two principal components (PC1 and PC2) of a principal component analysis (PCA) carried out on the log-transformed data of most distinctive combination of four measurement characters, identified by best subset regression for *Nothobranchius iridescens* and the comparative material. The most important loading values are in bold.

Variables and Eigenanalysis	**PC1**	**PC2**
Morphometric characters		
Caudal peduncle length in % of its depth	0.187	**0.881**
Caudal-fin length	**0.683**	0.023
Postorbital length	**−0.522**	−0.078
Anal-fin base length	0.475	−0.466
Eigenanalysis of the correlation matrix		
Eigenvalue	1.7158	1.0259
Explained variance (% of total variance)	42.9	25.6
Cumulative variance (%)		68.5

Table 6. Factor loadings and proportions of variance explained by the selected first two principal components (PC1 and PC2) of a principal component analysis (PCA) carried out on the log-transformed data of most distinctive combination of three measurement characters, identified by best subset regression for *Nothobranchius katemomandai* and the comparative material. The most important loading values are in bold.

Variables and Eigenanalysis	PC1	PC2
Morphometric characters		
Caudal peduncle depth	0.088	**0.974**
Postorbital length	**0.711**	0.084
Dorsal-fin base length	**−0.698**	0.208
Eigenanalysis of the correlation matrix		
Eigenvalue	1.7309	1.0282
Explained variance (% of total variance)	57.7	34.3
Cumulative variance (%)		92.0

Table 7. Factor loadings and proportions of variance explained by the selected first two principal components (PC1 and PC2) of a principal component analysis (PCA) carried out on the log-transformed data of most distinctive combination of four measurement characters, identified by best subset regression for *Nothobranchius marmoreus* and the comparative material. The most important loading values are in bold.

Variables and Eigenanalysis	PC1	PC2
Morphometric characters		
Head width	0.141	**0.915**
Caudal peduncle length in % of its depth	**0.589**	−0.235
Predorsal length in % of preanal length	**0.570**	−0.221
Head length	**−0.555**	−0.244
Eigenanalysis of the correlation matrix		
Eigenvalue	2.0847	1.0663
Explained variance (% of total variance)	52.1	26.7
Cumulative variance (%)		78.8

Table 8. Factor loadings and proportions of variance explained by the selected first two principal components (PC1 and PC2) of a principal component analysis (PCA) carried out on the log-transformed data of the most distinctive combination of four measurement characters, identified by best subset regression for *Nothobranchius dubieensis* and the comparative material. The most important loading values are in bold.

Variables and Eigenanalysis	PC1	PC2
Morphometric characters		
Preanal length	−0.348	**−0.779**
Snout length	**0.606**	0.173
Caudal peduncle length in % of its depth	**0.560**	−0.228
Body depth at pelvic-fin origin	−0.445	**0.558**
Eigenanalysis of the correlation matrix		
Eigenvalue	2.4876	1.0613
Explained variance (% of total variance)	62.2	26.5
Cumulative variance (%)		88.7

3.1.2. Procatopodidae

Divergence of morphological characters between populations of the new species and the most similar and closely related species have been found, showing diagnostic, non-overlapping morphometric characters.

The PCA reveals that the new population, here identified as a new species and named '*Lacustricola*' *gemma*, groups separately on score plots for PC1 *vs.* PC2 (Figure 2a,b) from '*L.*' *chobensis* and '*L.*' *hutereaui*. For meristic characters (Figure 2a), the first principal component is mostly associated with the scales in the circumpeduncular series, whereas the second component accounts for the scales in the transverse series and dorsal-fin rays (Table 9). For the morphometric characters (Figure 2b), the first principal component explains much of the variation among specimens in Head width in % of its depth and caudal fin length, whereas the second principal component is associated mainly with head width and body depth (Table 10).

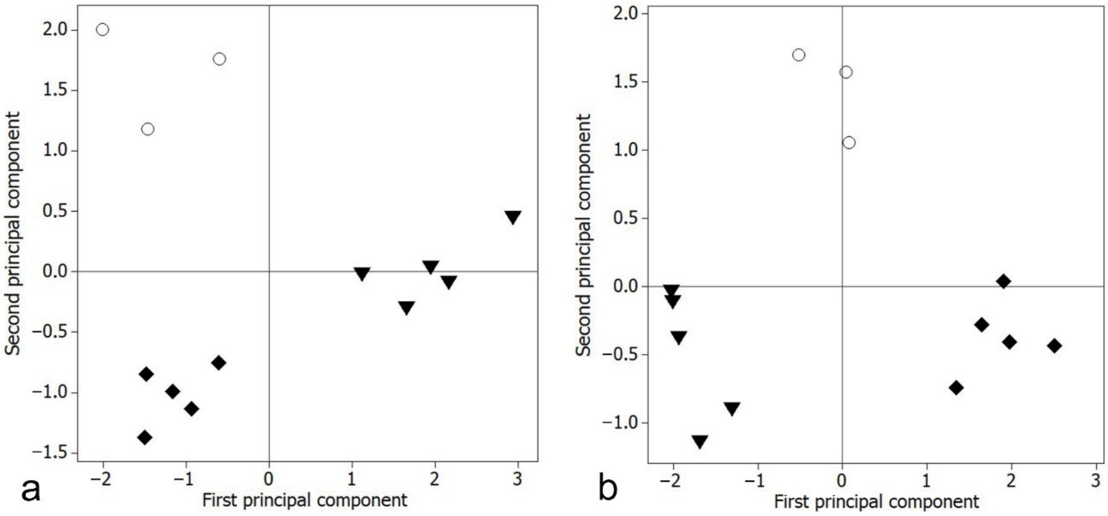

Figure 2. Comparative meristics and morphometry in males of '*Lacustricola*' *gemma* (○), '*L.*' *chobensis* (♦) and '*L.*' *hutereaui* (▼). Score plot of principal component analysis on first component *vs.* second component: (**a**). six meristic characters; (**b**). best subset of four distinctive morphometric characters.

Table 9. Factor loadings and proportions of variance explained by the selected first two principal components (PC1 and PC2) of a principal component analysis (PCA) carried out on the square-root transformed data of meristic characters for '*Lacustricola*' *gemma* and the comparative material. The most important loading values are in bold.

Variables and Eigenanalysis	PC1	PC2
Meristic characters		
Scales transverse	0.268	**−0.792**
Dorsal-fin rays	−0.140	**0.657**
Scales circumpeduncular	**0.558**	0.021
Anal-fin rays	0.460	**0.527**
Scales mid-longitudinal series	0.472	−0.250
Dorsal fin to anal fin relative position	0.428	0.178
Eigenanalysis of the correlation matrix		
Eigenvalue	2.4876	1.0613
Explained variance (% of total variance)	62.2	26.5
Cumulative variance (%)		88.7

Table 10. Factor loadings and proportions of variance explained by the selected first two principal components (PC1 and PC2) of a principal component analysis (PCA) carried out on the log-transformed data of the most distinctive combination of four measurement characters, identified by best subset regression for '*Lacustricola*' *gemma* and the comparative material. The most important loading values are in bold.

Variables and Eigenanalysis	PC1	PC2
Morphometric characters		
Head width in % of its depth	0.377	**0.822**
Caudal peduncle length in % of its depth	**0.565**	−0.148
Body depth at pelvic-fin origin	**−0.562**	−0.058
Caudal-fin length	−0.473	**0.547**
Eigenanalysis of the correlation matrix		
Eigenvalue	2.9202	1.0050
Explained variance (% of total variance)	73.0	20.1
Cumulative variance (%)		93.1

3.2. Molecular Analysis

DNA sequence data from the mitochondrial COI genes were generated and utilized for all taxa, complementing the sequences available from previous analyses. The BI and ML analyses recovered similar topologies. For Nothobranchiids, a full BI phylogeny including all analysed taxa is presented in Figure 3, while a simplified ML phylogeny, with one terminal per species and accompanying specimen images to illustrate species diversity, is shown in Figure 4. For Procatopodids, the corresponding BI and simplified ML phylogenies are presented in Figures 5 and 6, respectively.

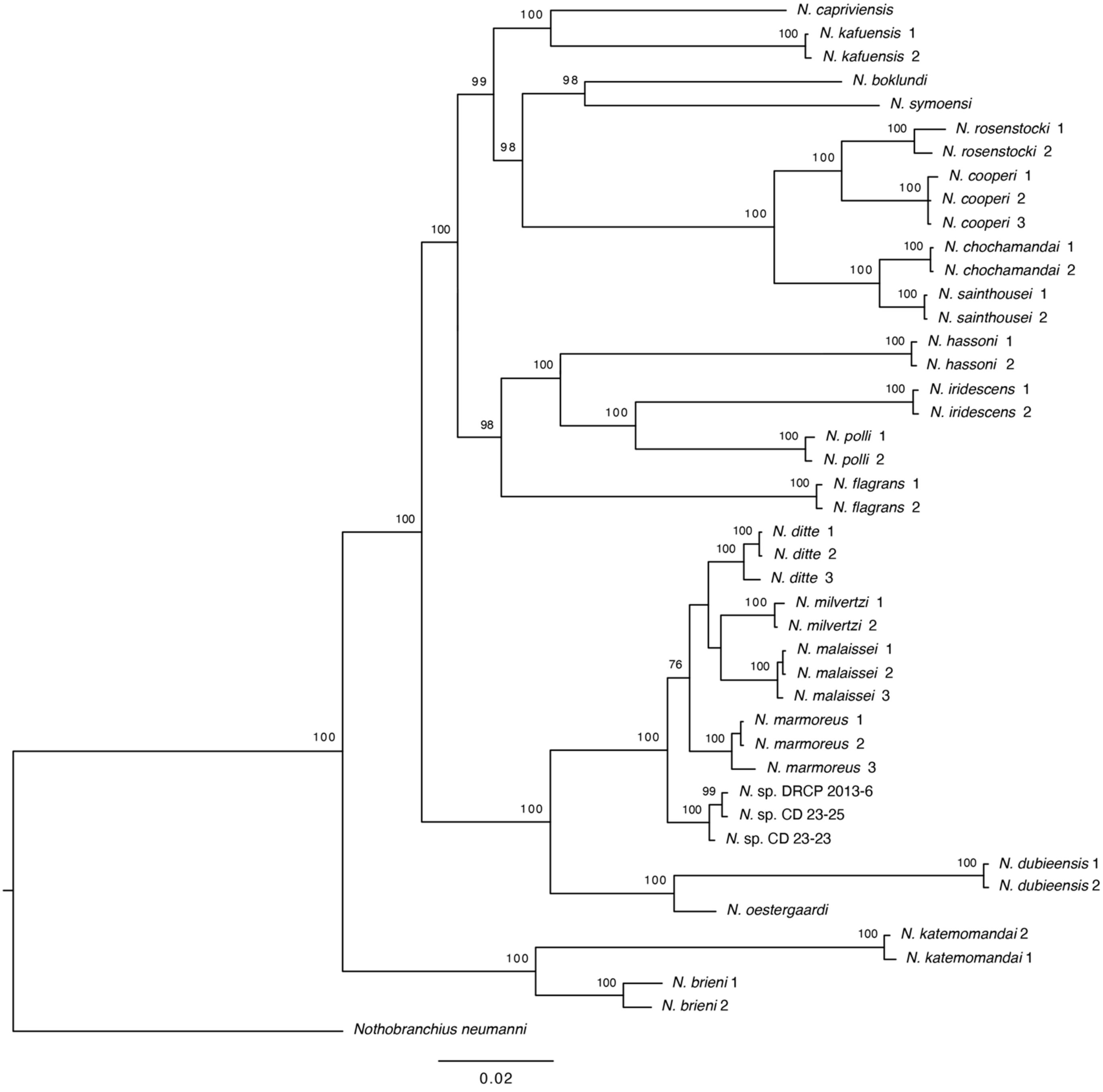

Figure 3. Phylogenetic tree of the *Nothobranchius brieni* species group, based on analysis of the mitochondrial molecular marker Cytochrome oxidase subunit I (COI), using Bayesian inference. Support values at nodes represent Bayesian posterior probability. Relevant data regarding specimens analysed for this tree are presented in Table 3.

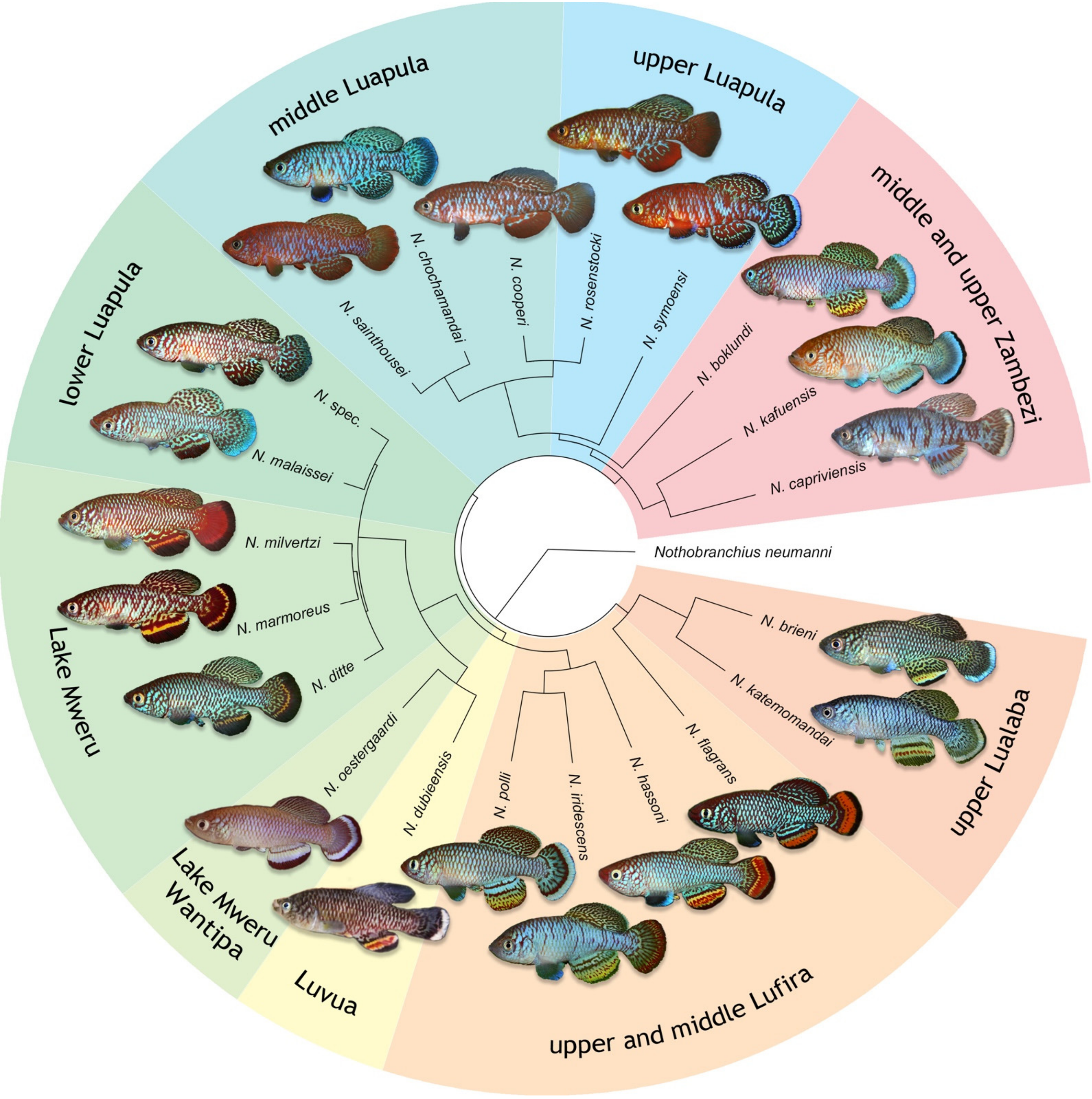

Figure 4. Colour images of representative male specimens of all members of the *Nothobranchius brieni* species group, plotted on a phylogenetic tree based on maximum likelihood analysis of the mitochondrial molecular marker Cytochrome Oxidase Subunit I (COI), and associated drainage system distribution information. Photographs by B. Nagy, except *N. kafuensis* by Cs. Nagy, *N. oestergaardi* by S. Valdesalici and *N. dubieensis* by A. Kalumba.

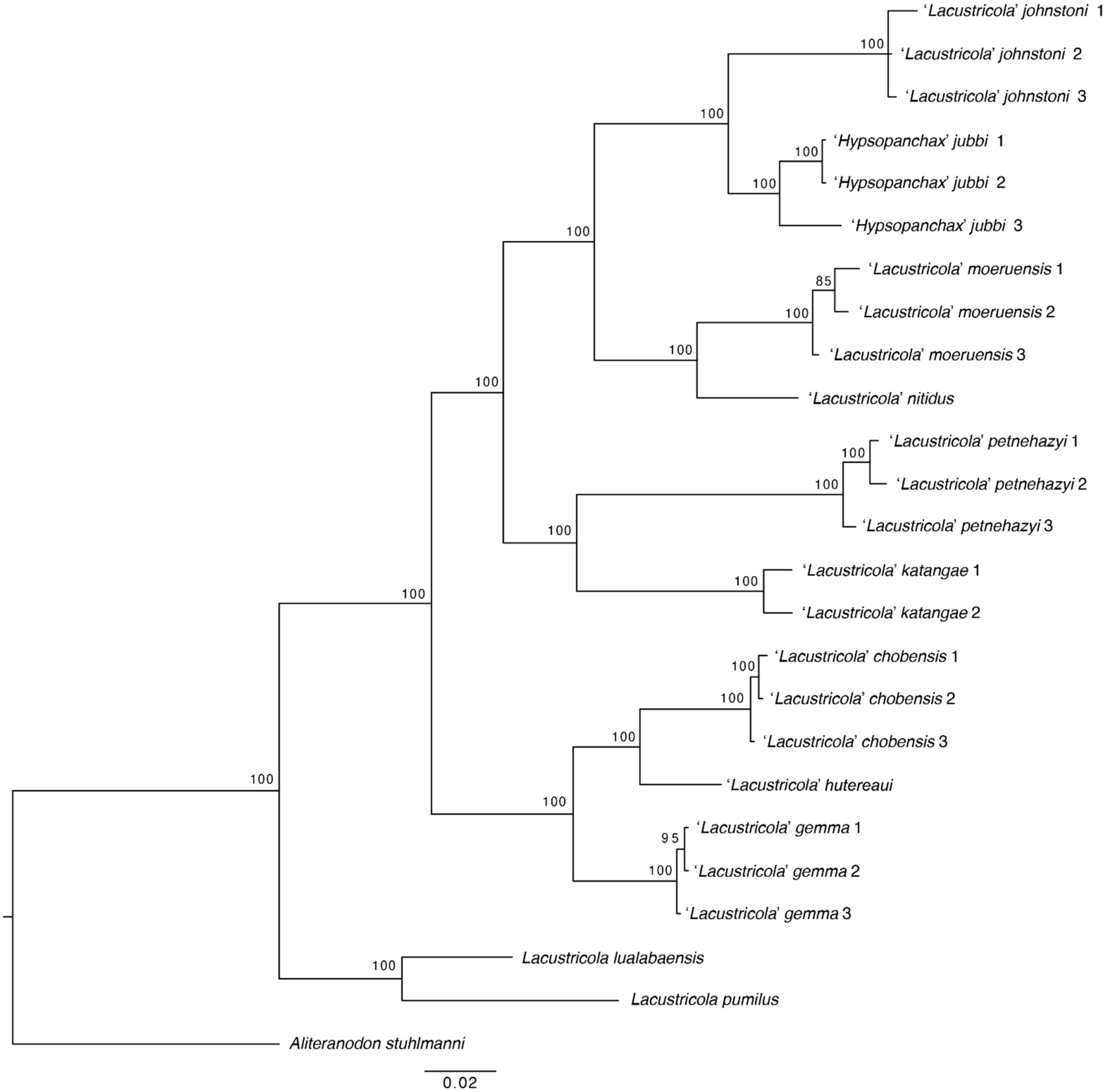

Figure 5. Phylogenetic tree of the Procatopodid species to examine the phylogenetic structure of the family in the upper Congo drainage, based on analysis of the mitochondrial molecular marker Cytochrome oxidase subunit I (COI), using Bayesian inference. Support values at nodes represent Bayesian posterior probability. Relevant data regarding specimens analysed for this tree are presented in Table 4.

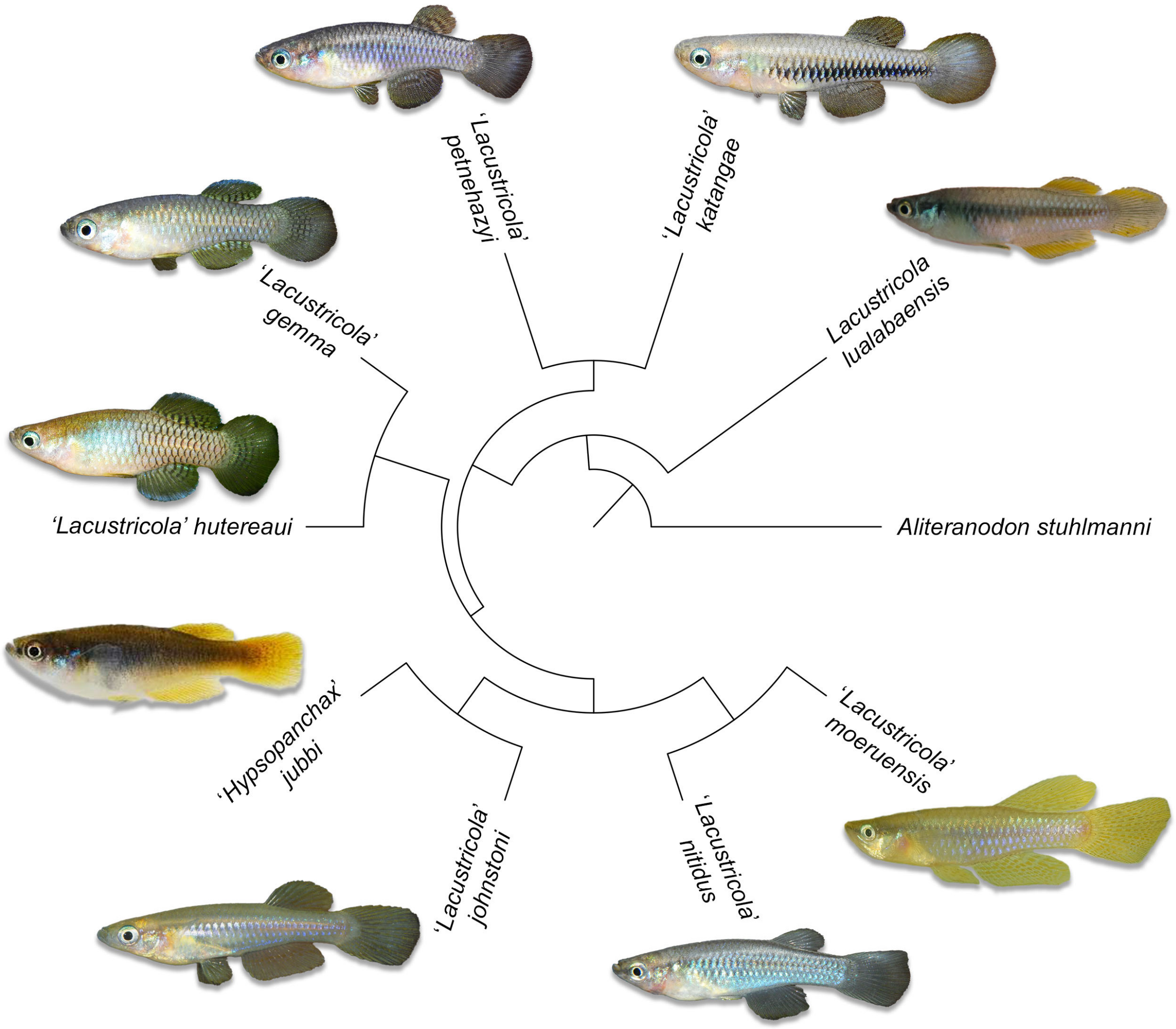

Figure 6. Colour images of representative male specimens of the Procatopodid species in the upper Congo drainage, plotted on phylogenetic tree based on maximum likelihood analysis of the mitochondrial molecular marker Cytochrome Oxidase Subunit I (COI). Photographs by B. Nagy, except '*H.*' *jubbi* by SAIAB, *L. lualabaensis* by B. Katemo Manda, and '*L.*' *johnstoni* by B. Watters.

3.2.1. Nothobranchiidae

The BI phylogeny (Figure 3) retrieved the *N. brieni* species group in four, geographically segregated clades: *Nothobranchius brieni* and *N. katemomandai* from the upper Lualaba drainage in a basal position; the species from lower Luapula drainage and Lake Mweru basin (referred to as Lake Mweru complex in [36]) as well as containing *N. oestergaardi* from Lake Mweru Wantipa and *N. dubieensis* from nearby Luvua system in a clade; the species from the upper and middle Lufira drainage in a clade; and the species from the middle and upper Luapula drainage and the Zambezi drainage were retrieved in a clade.

The ML phylogeny retrieved a similar topology, except that *N. brieni* and *N. katemomandai* were in a sister position to *N. flagrans*. The phylogeny based on ML reveals strong geographic segregation, with clades organized by the host river drainages. The ML phylogeny, including one terminal per species, and illustrated with colour pictures of each taxon, is represented in Figure 4.

In both analyses, the four new species of the *N. brieni* species group are retrieved as phylogenetically distinct lineages. The results of molecular analyses of COI gene sequences support the genetic distinction of the four new species and confirm their position, together with all known members in the *N. brieni* species group.

3.2.2. Procatopodidae

The BI phylogeny (Figure 5) retrieved the family in the upper Congo drainage in the following clades: *Lacustricola lualabaensis* from the upper Congo forms a clade with *L. pumilus* from the Lake Tanganyika basin; followed by clades likely belonging to the undescribed genus '*Lacustricola*', generally recognized as the '*L.*' *johnstoni* group, the '*L.*' *katangae* group, and the '*L.*' *hutereaui* group. The new populations were found to belong to the latter group.

The ML phylogeny retrieved a similar topology. The phylogeny based on ML, including one terminal per species from the target study area, and illustrated with colour pictures of each taxon, is represented in Figure 6.

The new populations are retrieved as a phylogenetically distinct lineage, and the analyses confirm the position within the '*Lacustricola*' genus.

3.3. Taxonomy

3.3.1. *Nothobranchius iridescens*, New Species

http://zoobank.org/urn:lsid:zoobank.org:act: 2CDB599E-DAFC-4FF6-BDEA-D9D4760E9049

Nothobranchius spec. 'Lutandula': Nagy 2024b: 73 [82].

Holotype. BE_RMCA_VERT.2025.008.P.0003, male, 41.8 mm SL; DR Congo: Kafila system: Lufira drainage: shallow remnant pools in seasonal floodplain, 8 km northwest of Lutandula village, 10°49′44″ S, 27°48′09″ E, 1062 m alt.; B. Nagy, A. Chocha Manda & A. Kalumba, 19 April 2023 (field code: CD 23-21).

Paratypes. BE_RMCA_VERT.2025.008.P.0004, male, 43.0 mm SL; collected with the holotype. — BE_RMCA_VERT.2025.008.P.0005–0010, 3 males, 29.2–36.2 mm SL & 3 females, 27.0–29.9 mm SL; DR Congo: Kafila system: Lufira drainage: shallow remnant pools in seasonal floodplain, 11 km northwest of Lutandula village, 10°48′36″ S, 27°47′19″ E; A. Kalumba, 28 May 2023 (field code: CD 23-30).

Diagnosis. *Nothobranchius iridescens* is distinguished from all other species of the genus by the unique combination in male colouration of having anal fin with irregular red-brown spots and stripes, creating two irregular submedial and medial bands and with broad yellow subdistal band; and caudal fin with a slender light blue subdistal band, densely marked with irregular red spots, and narrow dark brown distinct distal margin.

Further, *N. iridescens* is distinguished from the most closely related *N. polli* by greater caudal peduncle length (153–161 in % of its depth *vs.* 133–139); and greater eye diameter (31–34% HL *vs.* 23–26); and from *N. hassoni* by smaller predorsal length (52.4–55.6% SL *vs.* 55.7–59.5); and greater caudal peduncle length (153–161 in % of its depth *vs.* 133–143).

Description. General body features are illustrated in Figure 7. Morphometric and meristic characters of the holotype and paratypes are summarised in Table 11. A medium sized *Nothobranchius* species (maximum observed size: 43.0 mm SL in males and 29.9 mm SL in females).

Males: General body shape is robust, laterally compressed, and deep. Greatest body depth at vertical in front of pelvic-fin origin. Greatest body width at pectoral-fin base, with body progressively narrowing towards caudal-fin base. Dorsal profile straight from tip of snout to nape and convex to base of last dorsal-fin ray, straight to slightly concave on caudal peduncle. Ventral profile convex from lower jaw to base of last anal-fin ray, straight to slightly concave on caudal peduncle. Caudal peduncle shallow, length 1.5–1.6 times of its depth. Anus situated directly in front of anal-fin origin.

Head short, laterally compressed, deeper than wide. Snout slightly pointed, smaller than eye diameter. Mouth supraterminal, slightly oblique in profile. Jaws subequal, lower jaw longer than upper, posterior end of rictus at same level or slightly ventral to centre of eye. Premaxilla and dentary with many irregularly distributed conical, slightly curved teeth in the outer row of lower and upper jaws. Orbit large, in the anterior half of the head, in the dorsal portion of the head side. The branchiostegal membrane projects posteriorly from the operculum.

Dorsal-fin origin anterior to anal-fin origin, with both fins originating posterior to mid-length of the body. Overall distal part of dorsal and anal fins rounded, with small contact organs in form of papillae on fin rays and distal margin with short filamentous rays. Posterior tip/margin of dorsal fin reaching caudal-fin base. Pectoral fin subtriangular, insertion at about vertical or slightly posterior to margin of opercular opening, base slightly oblique, with 17–18 rays, upper fin rays placed slightly anteriorly to lower fin rays, tip reaching or slightly overlapping base of pelvic fin. Pelvic fin subabdominal, origin at about mid-length of body, short, bases medially separated, tip reaching urogenital papilla. Caudal fin rounded, with 17–18 branched rays, plus 2 to 3 unbranched, smaller rays at dorsal and ventral origins.

Scales cycloid. Body and head entirely scaled, except for the ventral surface of the head.

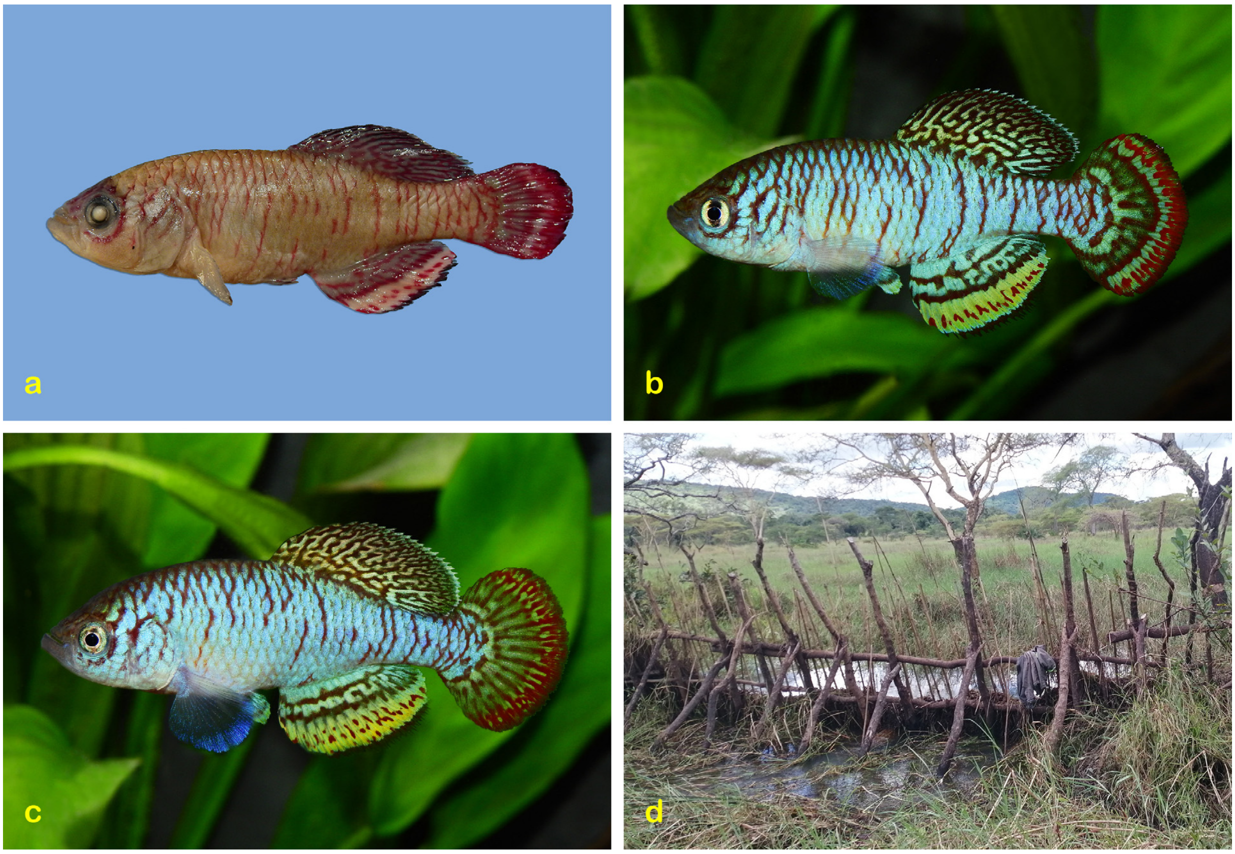

Figure 7. *Nothobranchius iridescens*: (**a**). BE_RMCA_VERT.2025.008.P.0003, holotype, preserved male, 41.8 mm SL; (**b**). holotype live; (**c**). BE_RMCA_VERT.2025.008.P.0004, paratype, live male, 43.0 mm SL; (**d**). type locality; DR Congo: Kafila system: Lufira drainage: shallow remnant pools in seasonal floodplain, 8 km northwest of Lutandula village, 10°49′44″ S, 27°48′09″ E, 1062 m alt.; B. Nagy, A. Chocha Manda & A. Kalumba, 19 April 2023 (field code: CD 23-21). Photographed by B. Nagy (**a**–**c**) and A. Kalumba (**d**).

Cephalic squamation pattern variable. Anterior nostril at the anterior tip of the snout, tubular opening lateral to the upper lip. Posterior nostril in front of the orbit, with oblique oval aperture. Frontal neuromasts are in a shallow groove. Cephalic sensory system at supraorbital level in a continuous, curved shallow groove, with two exposed neuromasts in the anterior part and four exposed neuromasts in the posterior part, whereas at supratemporal level in a curved groove, with four exposed neuromasts (Figure 8a). Preorbital canal in shallow groove with two exposed neuromasts; postorbital canal in shallow groove with one exposed neuromast; infraorbital series with about eight neuromasts at ventral margin of eye. Mandibular canal is in a shallow groove with a series of small neuromasts, curved to the lateral midline in front. One neuromast is on each scale along the trunk mid-longitudinal series.

Females: Smaller than males. Body generally similar but less laterally compressed and slightly more slender than in males (body depth at pelvic fin origin 27.4–28.1% SL *vs.* 29.1–32.3; head width in % of its depth greater than in males 77–82 *vs.* 64–72). Anal fin subtriangular, tip rounded, central rays longer and more rigid (*vs.* anal fin rounded in males). Anal, dorsal and pelvic fins positioned more posteriorly than in males (61.5–63.5% SL *vs.* 56.1–59.6; 57.5–58.0% SL *vs.* 52.4–55.6; 49.5–50.7% SL *vs.* 44.5–47.8, respectively). Anal-fin and dorsal-fin base lengths are smaller than in males (23.1–25.9% SL *vs.* 26.1–29.0; 17.7–18.1% SL *vs.* 22.3–23.5, respectively). Caudal peduncle is more slender than in males (161–164 in % of its depth *vs.* 153–161). Branchiostegal membrane not projecting distally (*vs.* projecting distally in males). No papillae or epidermal tissue present on dorsal and anal fins (*vs.* both present in males).

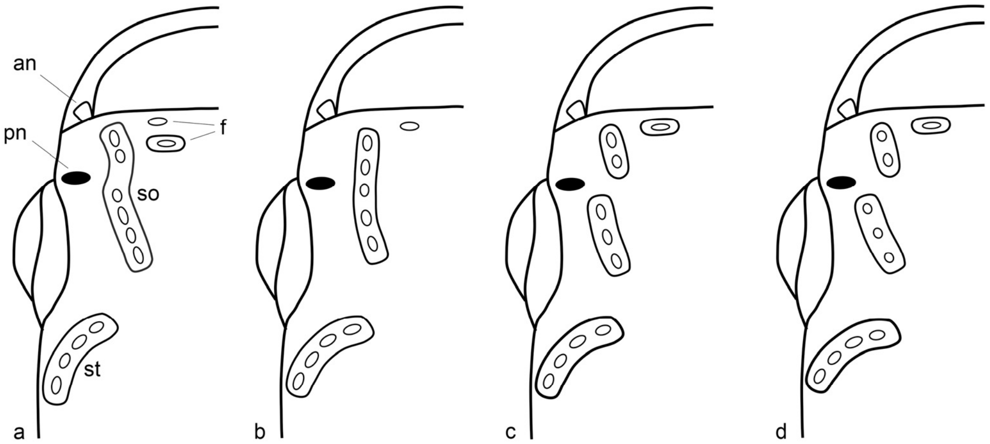

Figure 8. Diagrammatic representation of cephalic structure, dorsal view of head in: (**a**). *Nothobranchius iridescens*; (**b**). *N. katemomandai*; (**c**). *N. marmoreus*; and (**d**). *N. dubieensis*. Key to label abbreviations: an, anterior nostril; pn, posterior nostril; f, frontal neuromast; so, supraorbital canal; st, supratemporal canal.

Colouration. Live colouration of males (Figure 7b,c): scales on head and trunk light blue to green-blue with irregular red-brown posterior margin, forming irregular vertical, chevron-formed striped pattern on body. Snout, frontal and dorsal portion of head red-brown, throat light blue. Posterior scale margins on post-orbital portion of the operculum create three to four red-brown, anteriorly lowering, oblique bars. Exposed part of the branchiostegal membrane is light blue. Iris light yellow, with dark grey-black spots, especially on upper and lower-most parts, creating a dark vertical bar through the centre of the eye. Dorsal fin yellow to light blue with irregular red-brown stripes, perpendicular to fin rays proximally, parallel to fin rays medially and distally, fin tips light blue. Anal fin light blue, with irregular red-brown spots and stripes, creating two irregular submedial and medial bands, with broad yellow subdistal band, with irregular red-brown spots and narrow dark brown distal margin. Caudal fin yellow to light blue, with irregular red-brown spots and stripes parallel to fin rays proximally and medially, followed by an irregular narrow red-brown band and a slender light blue subdistal band, with irregular red spots, depending on the density, creating a red-brown band, and a narrow dark brown distinct distal margin. Pelvic fin light blue, with narrow red-brown medial band and yellow distal band. Pectoral fin hyaline with blue posterior distal margin.

Live colouration of females: scales on trunk and head light brown with narrow dark brown posterior margin, forming a slightly visible reticulated pattern on body. Overall light brown colour of scales, darker on dorsum and lighter to silvery on venter. Blue iridescence on the opercular region and anterior midlateral half of the trunk. Iris yellow. All fins are hyaline.

Table 11. Morphometric and meristic data of holotype and paratypes of *Nothobranchius iridescens*. Holotype values included in ranges, mean and standard deviation of males. H, holotype; SD, standard deviation.

Morphometric and Meristic Characters		**Males (*n* = 5)**			**Females (*n* = 3)**		
	H	**Range**	**Mean**	**SD**	**Range**	**Mean**	**SD**
Standard length	41.8	29.2–43.0			27.0–29.9		
Percent of standard length							
Total length	123.0	123.0–125.7	124.7	1.1	125.4–127.8	126.4	1.2
Body depth at pelvic-fin origin	32.3	29.1–32.3	30.8	1.3	27.4–28.1	27.8	0.4
Head length	30.6	27.6–31.9	29.8	1.7	31.4–33.3	32.3	1.0
Preanal length	59.6	56.1–59.6	57.1	1.4	61.5–63.5	62.2	1.2
Predorsal length	54.8	52.4–55.6	54.1	1.3	57.5–58.0	57.8	0.2
Prepelvic length	47.8	44.5–47.8	46.4	1.4	49.5–50.7	50.1	0.6
Prepectoral length	30.9	28.8–31.9	30.4	1.4	31.8–33.7	32.7	1.0
Caudal peduncle length	21.5	19.8–22.1	21.0	0.9	20.0–20.8	20.4	0.4
Caudal peduncle depth	13.4	12.8–14.1	13.4	0.5	12.2–12.7	12.6	0.3
Dorsal-fin base length	26.1	26.1–29.0	27.5	1.2	23.1–25.9	24.2	1.5
Anal-fin base length	23.0	22.3–23.5	22.8	0.5	17.7–18.1	18.0	0.3
Caudal-fin length	23.0	23.0–25.7	24.7	1.1	25.4–29.3	26.9	2.0
Percent of head length							
Head width	50	53–59	56.8	2.5	55–59	56.3	1.9
Head depth	87	82–87	84.7	2.6	69–72	70.9	1.5
Interorbital width	39	36–40	38.3	1.9	36–39	37.1	1.5
Postorbital length	50	50–55	51.7	2.0	48–52	50.2	2.2
Suborbital depth	24	19–24	21.0	2.0	17–21	18.5	2.4
Eye diameter	31	31–34	31.7	1.2	34–37	35.3	1.8
Snout to eye end length	50	45–50	48.3	2.0	48–52	49.8	2.2
Snout length	20	17–20	18.6	1.7	17–19	17.8	1.2
Other morphometric ratios							
Head width in % of its depth	68	64–72	67.1	3.1	77–82	79.5	2.6
Caudal peduncle length in % of its depth	161	153–161	156.4	2.7	161–164	162.7	1.9
Predorsal length in % of preanal length	92	92–98	94.8	2.8	91–94	92.9	2.1
Meristics		range	mode		range	mode	
Dorsal-fin rays	16	16–17	16		16–17	16	
Anal-fin rays	17	17–18	17		17–18	17	
Scales mid-longitudinal series	29	28–30	29		28–29	29	
Scales transverse	10	10	10		10	10	
Scales circumpeduncular	12	12	12		12	12	

Distribution. *Nothobranchius iridescens* is endemic to seasonal freshwater habitats of the upper Congo drainage in south-eastern DR Congo. It is currently known from ephemeral pools and marshes on floodplains associated with the Kafila river in the Lufira system (Figure 9). The Kafila is a major right bank affluent entering the middle Lufira just below the Mwadingusha Falls, which isolates the middle from the upper Lufira.

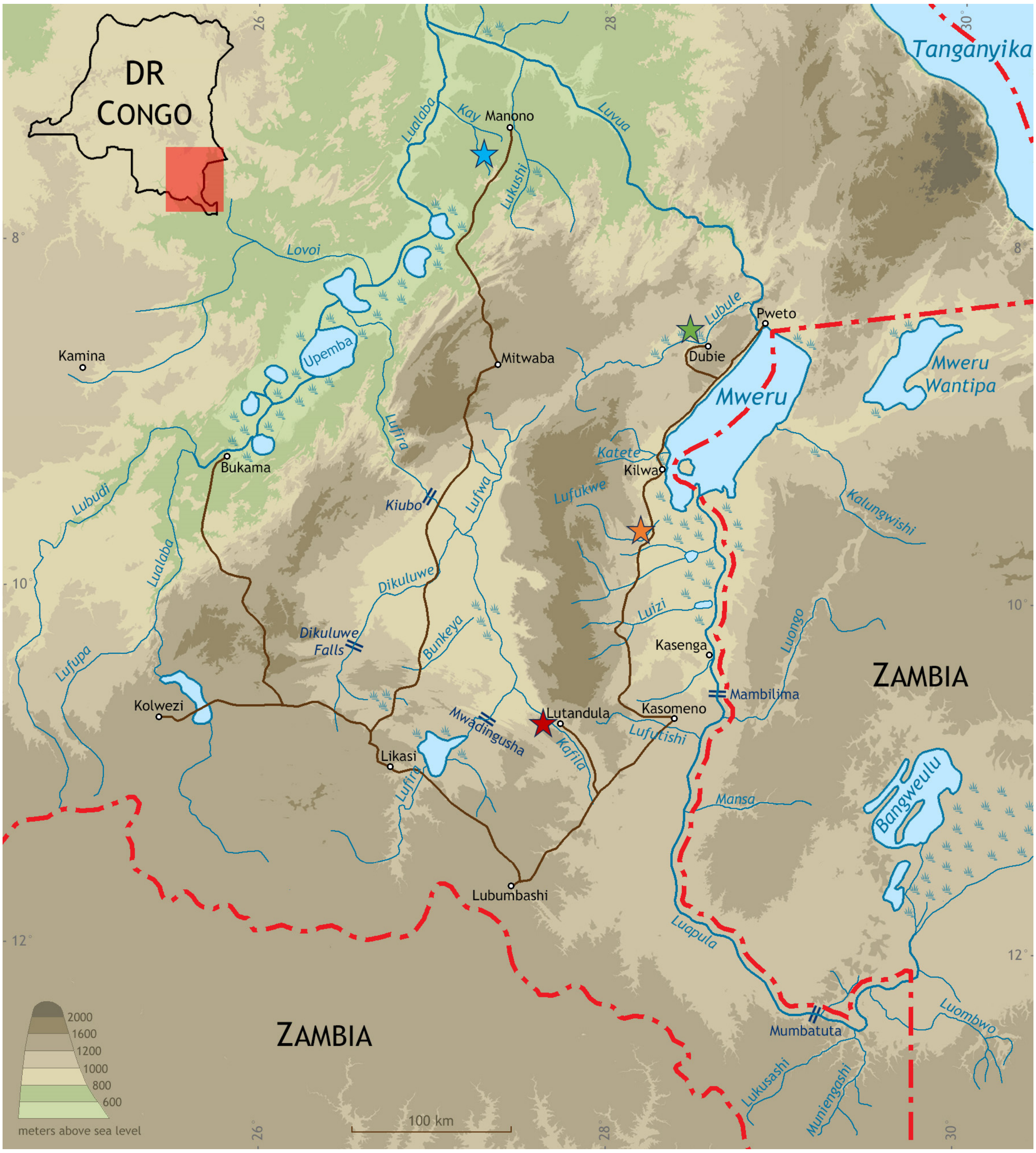

Figure 9. Localities of new species described in present paper: *Nothobranchius iridescens* (red star), *N. katemomandai* and '*Lacustricola*' *gemma* (blue star), *N. marmoreus* (orange star), and *N. dubieensis* (green star). Individual symbols may represent more than one locality or population. Map prepared by B. Nagy.

Ecology and biology. The climate of the ecoregion is tropical and moist, with a mean annual rainfall of around 1000 mm [83]. The rivers in the Lufira system flood seasonally in response to the rains. The waters are the highest during the rainy season and, from February to April and driest between September and January [83,84].

At the type locality, *Nothobranchius iridescens* was the only species of the genus observed. The accompanying fish fauna consisted of non-annual species belonging to the families Cichlidae and Cyprinidae. The type locality on 19 April 2023 was an ephemeral pool formed in the floodplain of the Kafila River (Figure 7d). The pool was about 50 cm deep at its deepest point, the water was turbid, and it covered an area that was partly overgrown with grass. The habitat principally belongs to category 1.2 as defined by Watters (2015a) [85], representing a pool and a flooded grassy area on a floodplain. However, the anthropogenic impact is evident, as the local population altered the natural habitat by placing fences and fish traps into the biotope.

Aquarium maintenance of selected specimens was undertaken in the facilities of the University of Lubumbashi for observation of breeding behaviour and biology. *Nothobranchius iridescens* has a mode of reproduction that is common for all known annual congeners under aquarium conditions.

Conservation status. *Nothobranchius iridescens* is recommended to be assessed as Endangered. The species is currently known only from the area of the type locality, two sites situated in a limited section of the Kafila system of the Lufira drainage. It might exist at some other sites within the drainage system of the Kafila, but its distribution will remain restricted, and any potential additional subpopulations are expected to be fragmented and not in contact or having limited contact with each other. The species is expected to be restricted to ephemeral wetlands within the Kafila drainage system. The section of the drainage in the Kafila system where the species is currently known is 67 km^2, whereas the estimated maximum extent of occurrence (EOO) would be less than 1000 km^2, the area of occupancy (AOO) with a maximum estimate of less than 100 km^2 and expected maximum of five threat-based locations. Currently known sites, including the type locality, are close to human populations. Phases in the seasonal life cycle of this species underscore the vulnerabilities of the ecological processes in the ephemeral habitats, as the survival of the species is dependent on suitable conditions during both dry and wet seasons. The author observed the expansion of agriculture in the area and, consequently, increasing anthropogenic pressures on the land and water use. The resultant habitat changes are likely to modify the habitats in ways that render them unsuitable and thus degraded when considering their support of the seasonal life cycle of the species, and thus represent an important extinction risk. Additionally, the natural habitat at the type locality has been altered by the local population through the installation of fences and the placement of fish traps within the biotope. Using IUCN (2012) principles [86], *N. iridescens* meets the criteria B1ab(iii)+2ab(iii) for Endangered, considering upper estimates of the EOO, AOO, and number of locations, as well as the risk of continuous decline of the known wetland habitats in which it is known to live.

Nevertheless, at present, no conservation/protection measures are in place for this species. Further, not a single protected area covers at least part of its presently known distribution. As such, there is a need for habitat protection at the type locality and a second close-by site, currently the only sites from which the species has been recorded to date. Further field surveys targeting additional suitable habitats should be conducted in the floodplains of the drainage system, in order better to document the full geographic distribution of this species and thus better envision how to elaborate on appropriate conservation measures.

Etymology. The specific epithet *iridescens* is a Latin participial adjective deriving from the ancient Greek word iris (ἶρις), rainbow, referring to the colourful appearance of the males, containing different colours of the rainbow, such as yellow and red in the fins, reflective blue on the body slightly shifting hue depending on the angle of light.

3.3.2. *Nothobranchius katemomandai*, New Species

http://zoobank.org/urn:lsid:zoobank.org:act: 22C69DA3-5C13-4C51-BEAF-F10BC311AB27

Nothobranchius spec. CD 23-26: Nagy 2024a: 2 [87].

Nothobranchius spec. 'Manono': Nagy 2024b: 72 [82]; Watters & Nagy 2025: 426 [88].

Holotype. BE_RMCA_VERT.2025.008.P.0011, male, 31.1 mm SL; DR Congo: Kay system: upper Lualaba drainage: shallow remnant pool in small seasonal riverbed, 0.5 km west of Lubule village, 07°31′47″ S, 27°13′24″ E, 634 m alt.; B. Katemo Manda, 17 April 2023 [field code: CD 23-26].

Paratypes. BE_RMCA_VERT.2025.008.P.0012–0020, 6 males, 30.3–43.2 mm SL & 3 females, 27.0–28.8 mm SL; collected with the holotype.

Diagnosis. *Nothobranchius katemomandai* is distinguished from all other species of the genus by the unique combination in male colouration of having anal fin with narrow brown submedial band, followed by a slender yellow band, a slender red-brown band and a slender dark brown distal band; and caudal fin with brown spots proximally and medially, and with slender white to light blue subdistal band and a narrow dark grey distal band.

Further, *N. katemomandai* is distinguished from most closely related *N. brieni* by greater dorsal-fin base length (25.7–28.0% SL *vs.* 24.1–25.4); smaller postorbital length (49–51% HL *vs.* 53–58); and smaller head width (68–74 in % of its depth *vs.* 76–83).

Description. General body features are illustrated in Figure 10. Morphometric and meristic characters of holotype and paratypes are summarised in Table 12. A medium sized *Nothobranchius* species (maximum observed size: 43.2 mm SL in males and 28.8 mm SL in females).

Males: General body shape is robust, laterally compressed, and deep. Greatest body depth at vertical in front of pelvic-fin origin. Greatest body width at pectoral-fin base, with body progressively narrowing towards caudal-fin base. Dorsal profile slightly concave to straight from tip of snout to nape and convex to base of last dorsal-fin ray, straight to slightly concave on caudal peduncle. Ventral profile convex from lower jaw to base of last anal-fin ray, straight to slightly concave on caudal peduncle. Caudal peduncle moderately shallow, length 1.3–1.4 times of its depth. Anus situated directly in front of anal-fin origin.

Head short, laterally compressed, deeper than wide. Snout slightly pointed, smaller than eye diameter. Mouth supraterminal, slightly oblique in profile. Jaws subequal, lower jaw longer than upper, posterior end of rictus at same level or slightly ventral to centre of eye. Premaxilla and dentary with many irregularly distributed conical, slightly curved teeth at the outer row of lower and upper jaws. Orbit large, almost entirely in the anterior half of the head, in the dorsal portion of the head side. Branchiostegal membrane projects posteriorly from the operculum.

Dorsal-fin origin anterior to anal-fin origin, with both fins originating posterior to mid-length of the body. Overall distal part of dorsal and anal fins rounded, with small contact organs in form of papillae on fin rays and distal margin with short filamentous rays. Posterior tip/margin of dorsal fin reaching caudal-fin base. Pectoral fin subtriangular, insertion at about vertical or slightly posterior to margin of opercular opening, base slightly oblique, with 15–16 rays, upper fin rays placed slightly anteriorly to lower fin rays, tip reaching or slightly overlapping base of pelvic fin. Pelvic fin subabdominal, origin at about mid-length of body, short, bases medially separated, tip reaching urogenital papilla. Caudal fin rounded, with 16–17 branched rays, plus 3 to 4 unbranched, smaller rays at dorsal and ventral origins.

Scales cycloid. Body and head entirely scaled, except for the ventral surface of the head.

Cephalic squamation pattern variable. Anterior nostril at the anterior tip of the snout, tubular opening lateral to the upper lip. Posterior nostril in front of the orbit, with oblique oval aperture. Frontal neuromast in shallow groove. Cephalic sensory system at supraorbital level in a continuous, slightly curved shallow groove, with five exposed neuromasts, whereas at supratemporal level in a curved groove, with four exposed neuromasts (Figure 8b). Preorbital canal in shallow groove with two exposed neuromasts; postorbital canal in shallow groove with one exposed neuromast; infraorbital series with about twelve small buttons at ventral margin of eye. Mandibular canal is in a shallow groove with a series of small neuromasts, curved to the lateral midline in front. One neuromast is on each scale along the trunk mid-longitudinal series.

Females: Smaller than males. Body generally similar but less laterally compressed and slightly more slender than in males (body depth at pelvic fin origin 27.1–28.6% SL *vs.* 29.0–35.6; head depth 77–82% of its depth *vs.* 68–74). Anal fin subtriangular, tip rounded, central rays longer and more rigid (*vs.* anal fin rounded in males). Anal fin positioned more posteriorly than in males (62.3–65.6% SL *vs.* 57.9–60.5). Dorsal-fin base length smaller than in males (22.2–23.8% SL *vs.* 25.7–28.0). Branchiostegal membrane not projecting distally (*vs.* projecting distally in males). No papillae or epidermal tissue present on dorsal and anal fins (*vs.* both present in males).

Table 12. Morphometric and meristic data of holotype and paratypes of *Nothobranchius katemomandai*. Holotype values included in ranges, mean and standard deviation of males. H, holotype; SD, standard deviation.

Morphometric and Meristic Characters		**Males (*n* = 7)**			**Females (*n* = 3)**		
	H	**Range**	**Mean**	**SD**	**Range**	**Mean**	**SD**
Standard length	31.1	30.3–43.2			27–28.8		
Percent of standard length							
Total length	125.7	121.5–125.7	124.5	1.4	122.6–127.1	124.7	2.3
Body depth at pelvic-fin origin	31.5	29.0–35.6	31.1	2.2	27.1–28.6	27.7	0.8
Head length	32.2	28.9–32.2	30.6	1.3	29.6–32.2	30.6	1.4
Preanal length	59.5	57.9–60.5	59.7	0.9	62.3–65.6	63.9	1.6
Predorsal length	57.6	56.2–59.0	57.6	1.0	58.9–59.7	59.2	0.5
Prepelvic length	47.9	43.5–48.8	46.5	1.8	50.4–51.0	50.7	0.3
Prepectoral length	33.1	29.2–33.1	31.5	1.3	29.6–32.6	31.4	1.6
Caudal peduncle length	20.3	18.3–20.6	19.5	0.8	17.4–20.1	18.7	1.4
Caudal peduncle depth	15.1	13.4–15.1	14.3	0.6	12.6–14.2	13.5	0.8
Dorsal-fin base length	28.0	25.7–28.0	27	0.8	22.2–23.8	23.2	0.9
Anal-fin base length	21.9	21.0–22.9	21.8	0.6	17.7–21.5	19.4	1.9
Caudal-fin length	25.7	21.5–25.7	24.5	1.4	22.6–27.1	24.7	2.3
Percent of head length							
Head width	58	58–63	59.6	1.5	58–61	59.5	1.6
Head depth	84	80–88	84.7	2.6	75–76	75.6	0.6
Interorbital width	43	40–46	42.8	1.9	40–44	41.4	2.1
Postorbital length	51	49–51	50.0	1.0	49–52	50.7	1.8
Suborbital depth	22	17–22	18.9	1.9	14–16	15.0	1.3
Eye diameter	31	31–40	35.2	2.7	35–36	35.8	0.5
Snout to eye end length	49	49–52	50.0	1.0	48–51	49.3	1.8
Snout length	19	15–19	18.0	1.8	17–21	18.6	2.3
Other morphometric ratios							
Head width in % of its depth	69	68–74	70.4	2.5	77–82	78.7	2.6
Caudal peduncle length in % of its depth	134	131–139	136.3	2.7	138–142	139.2	2.0
Predorsal length in % of preanal length	97	96–98	96.5	0.8	90–95	92.7	2.5
Meristics		range	mode		range	mode	
Dorsal-fin rays	16	15–17	16		16–18	16	
Anal-fin rays	17	15–17	17		16–18	18	
Scales mid-longitudinal series	27	26–29	27		27–28	27	
Scales transverse	10	10	10		10	10	
Scales circumpeduncular	12	12	12		12	12	

Figure 10. *Nothobranchius katemomandai*: (**a**). BE_RMCA_VERT.2025.008.P.0011, holotype, preserved male, 31.1 mm SL; (**b**). live wild-caught male; (**c**). live wild-caught female; (**d**). type locality; DR Congo: Kay system: upper Lualaba drainage: shallow remnant pool in small seasonal riverbed, 0.5 km west of Lubule village, 07°31′47″ S, 27°13′24″ E, 634 m alt.; B. Katemo Manda, 17 April 2023 (field code: CD 23-26). Photographed by B. Nagy (**a**–**c**) and B. Katemo Manda (**d**).

Colouration. Live colouration of males (Figure 10b–c): scales on head and trunk light blue with irregular red-brown posterior margin, forming irregular reticulation and oblique barred pattern on body. Snout, frontal and dorsal portion of head light grey, throat light blue to silver. Posterior scale margins on post-orbital portion of operculum forming two to three red-brown, anteriorly lowering, oblique bars. Exposed part of branchiostegal membrane white. Iris light yellow, with dark grey-black spots, creating a dark ring around the centre of the eye. Dorsal fin yellow to light blue with brown spots, forming in part irregular stipes perpendicular to fin rays, fin tips dark grey. Anal fin base light blue to yellow-blue, occasionally with irregular brown spots proximally, with narrow brown submedial band, followed by a slender yellow band, a slender red-brown band and a slender dark brown distal band. Caudal fin light blue, densely marked with brown spots proximally and medially, with slender white to light blue subdistal band and a narrow dark grey distal band. Pelvic fin transparent brown with yellow and light blue bands medially and distally, and with red-brown dots. Pectoral fin hyaline with blue posterior distal margin.

Live colouration of females: scales on trunk and head light brown with narrow dark brown posterior margin, forming reticulated pattern on body. Overall light brown colour of scales, darker on dorsum and lighter to silvery on venter. Blue iridescence on the opercular region and anterior midlateral half of the trunk. Iris yellow. All fins are hyaline.

Distribution. *Nothobranchius katemomandai* is endemic to seasonal freshwater habitats of the upper Congo drainage in south-eastern DR Congo. It is currently known from remnant pools in small ephemeral riverbeds associated with the Kay system in the upper Lualaba drainage (Figure 9). The Kay is a major right bank affluent entering the upper Lualaba below Lake Upemba.

Ecology and biology. The area of the upper Lualaba experiences a mean annual rainfall of around 1000 mm, with December the wettest month. In the Upemba System, the waters of the Lualaba are high from February-April and low from August to October [83]. The dry season lasts for around 160 days.

At the type locality, *N. katemomandai* was the only *Nothobranchius* species observed. The accompanying fish fauna consisted of the non-annual '*Lacustricola*'. The type locality on 17 April 2023 was a remnant pool formed in the riverbed of the seasonal Lubule River (Figure 10d). The habitat was 10–15 m in diameter, about 1 m deep at its deepest point, and connected to the 1–2 m large shallow seasonal riverbed. The edges of both the pool and the ephemeral riverbed were overgrown by grass. The water was turbid. The water temperature around noon was 27.3 °C, the pH was 7.2, and it contained 120 ppm of total dissolved solids. The habitat belongs to category 1.4.1 as defined by Watters (2015a), representing a remnant pool in a seasonal stream system on a floodplain.

Water parameters, measured by B. Katemo Manda at five different sites in the Kay system, where the existence of *N. katemomandai* has been proven, showed average values of: temperature of 28 °C; pH of 6.4; total dissolved solids of 36 ppm.

Aquarium maintenance of selected specimens was undertaken for observation of breeding behaviour and biology. *Nothobranchius katemomandai* has an annual mode of reproduction, the same as all of its known congeners. Under captive conditions, peat moss was used successfully as an artificial spawning substrate. A plastic container with the substrate was placed in the aquarium and removed after a period of two weeks, and dried to a slightly moist state. An embryonic development period of four to five months was observed at about 22–24 °C. Eggs are slightly oval, measuring 1.21 mm long and 1.13 mm wide on average (n = 10), with short adhesive filaments of up to 40 µm on the chorion, slightly attaching the eggs to the substrate.

Conservation status. *Nothobranchius katemomandai* is recommended to be assessed as Vulnerable. The species is currently known only from the area of the type locality, several sites in the Kay system of the Lualaba drainage. It might exist at some other sites within the drainage system of the upper Lualaba River, but its distribution will remain restricted, and any potential additional subpopulations are expected to be fragmented and not necessarily in contact with each other. The entire drainage area of the Kay system has an extent of 1142 km^2, and the species is expected to be found from a maximum of ten threat-based locations. Some of the known sites at present, including the type locality, are directly adjacent to human populations. There is an expansion of agriculture in seasonal wetland habitats of the known distribution area and, consequently, an increase in anthropogenic pressures on land and water use. Using IUCN (2012) principles [86], *N. katemomandai* meets the criteria B1ab(iii) for Vulnerable, considering the drainage area as maximum EOO and the number of estimated maximum threat-based locations, as well as the risk of continuous decline of the known wetland habitats in which it is known to live.

There are currently no conservation or protection measures in place for this species. Additionally, it is unknown whether any protected areas would partially encompass its known distribution. Therefore, habitat protection is needed at the type locality and other sites within the Kay system where the species has been recorded. Further field surveys should target additional suitable habitats within the drainage area to document the full geographic range of the species more accurately. This would help in developing appropriate conservation strategies.

Etymology. The specific epithet is given in honour of friend Bauchet Katemo Manda, professor at the University of Lubumbashi, the discoverer of this species, for his dedication to the research of the ichthyofauna of the Democratic Republic of Congo. The exciting adventures and numerous challenges faced during joint research expeditions will always remain vivid memories.

3.3.3. *Nothobranchius marmoreus*, New Species

http://zoobank.org/urn:lsid:zoobank.org:act: AE267C54-9106-4BCA-A793-3D205C5ECF42

Nothobranchius spec. 'Mokobe': van der Merwe et al. 2021: 10 [36].

Nothobranchius spec. 'Mukobe': Nagy 2024b: 75 [82].

Holotype. BE_RMCA_VERT.2025.008.P.0021, male, 36.3 mm SL; DR Congo: Lake Mweru basin: Lufukwe system: ephemeral pool in the floodplain of the seasonal river, 1.5 km west of Mukobe village, 09°41′32.9″ S, 28°12′42.5″ E, 962 m alt.; B. Nagy, A. Chocha Manda & A. Kalumba, 12 April 2023 [field code: CD 23-9].

Paratypes. BE_RMCA_VERT.2025.008.P.0022–0027, 3 males, 34.2–41.2 mm SL & 3 females, 31.4–33.9 mm SL; collected with the holotype. — BE_RMCA_VERT.2025.008.P.0028–0030, 2 males, 35.1–36.7 mm SL & 1 female, 31.7 mm SL; same locality; B. Nagy, A. Chocha Manda & G. Petneházy, 10 April 2016 [field code: CD 16-12].

Diagnosis. *Nothobranchius marmoreus* is distinguished from all other species of the genus by the unique combination in male colouration of having a body with irregular red-brown patches and stripes, forming a marble-like mottled pattern; and anal and caudal fins with slender yellow to amber subdistal band and broad dark brown distal band.

Further, *N. marmoreus* is distinguished from most closely related *N. ditte* by smaller head depth (80–84% HL *vs.* 87–94); and greater caudal peduncle length (152–159 in % of its depth *vs.* 130–140); from *N. malaissei* by smaller head length (25.5–30.9% SL *vs.* 32.7–35.4); and greater caudal peduncle length (152–159 in % of its depth *vs.* 124–131); and from *N. milvertzi* by smaller prepelvic length (45.5–46.7% SL *vs.* 46.9–50.8); and smaller head width (65.5–72.9 in % of its depth *vs.* 73.5–82.6).

Description. General body features are illustrated in Figure 11. Morphometric and meristic characters of holotype and paratypes are summarised in Table 13. A medium sized *Nothobranchius* species (maximum observed size: 41.2 mm SL in males and 33.9 mm SL in females).

Males: General body shape is robust, laterally compressed, and deep. Greatest body depth at vertical in front of pelvic-fin origin. Greatest body width at pectoral-fin base, with body progressively narrowing towards caudal-fin base. Dorsal profile slightly concave to straight from tip of snout to nape and convex to base of last dorsal-fin ray, straight to slightly concave on caudal peduncle. Ventral profile convex from lower jaw to base of last anal-fin ray, straight to slightly concave on caudal peduncle. Caudal peduncle shallow, length 1.5–1.6 times its depth. Anus situated directly in front of anal-fin origin.

Figure 11. *Nothobranchius marmoreus*: (**a**). BE_RMCA_VERT.2025.008.P.0021, holotype, preserved male, 36.3 mm SL; (**b**). live wild-caught male; (**c**). live wild-caught female; (**d**). type locality; DR Congo: Lake Mweru basin: Lufukwe system: ephemeral pool in the floodplain of the seasonal river, 1.5 km west of Mukobe village, 09°41′32.9″ S, 28°12′42.5″ E, 962 m alt.; B. Nagy, A. Chocha Manda & A. Kalumba, 12 April 2023 [field code: CD 23-9]. Photographed by B. Nagy.

Table 13. Morphometric and meristic data of holotype and paratypes of *Nothobranchius marmoreus*. Holotype values included in ranges, mean and standard deviation of males. H, holotype; SD, standard deviation.

Morphometric and Meristic Characters		**Males (*n* = 6)**			**Females (*n* = 4)**		
	H	**Range**	**Mean**	**SD**	**Range**	**Mean**	**SD**
Standard length	36.3	32.6–41.2			31.4–33.9		
Percent of standard length							
Total length	125.6	120.2–125.6	123.2	1.8	119.2–124.5	122.4	2.4
Body depth at pelvic–fin origin	30.0	26.7–32.0	28.3	2.2	24.5–27.4	25.5	1.3
Head length	30.9	25.5–30.9	29.4	2.0	28.7–32.5	31.0	1.6
Preanal length	56.5	56.1–59.1	57.3	1.0	59.6–64.4	62.1	2.0
Predorsal length	55.9	54.2–58.2	56.2	1.4	56.7–61.9	59.0	2.2
Prepelvic length	45.5	45.5–46.7	46.1	0.5	44.2–50.2	47.3	2.7
Prepectoral length	31.1	25.7–31.1	29.7	2.1	28.7–33.7	31.8	2.2
Caudal peduncle length	19.3	19.3–20.9	20.0	0.6	19.8–22.3	20.7	1.2
Caudal peduncle depth	12.1	12.1–13.6	12.8	0.5	10.3–11.8	11.0	0.6
Dorsal–fin base length	26.4	23.9–29.9	26.5	2.5	21.7–23.9	23.1	1.0
Anal–fin base length	22.9	21.6–24.0	22.7	1.0	18.5–19.5	19.0	0.4
Caudal–fin length	25.6	20.2–25.6	23.2	1.8	19.2–24.5	22.4	2.4
Percent of head length							
Head width	56	55–59	56.4	1.5	53–58	54.7	2.2
Head depth	83	80–84	82.2	1.3	68–72	70.2	1.8
Interorbital width	42	41–45	43.4	1.9	40–47	42.5	2.9
Postorbital length	49	49–56	51.5	2.7	51–56	53.5	2.7
Suborbital depth	14	14–17	15.8	1.3	12–17	14.4	2.2
Eye diameter	38	33–38	35.0	2.0	31–33	32.2	0.6
Snout to eye end length	51	44–51	48.5	2.7	44–49	46.5	2.7
Snout length	17	15–20	17.4	1.9	13–19	16.3	2.6
Other morphometric ratios							
Head width in % of its depth	68	66–73	68.7	2.7	76–81	78.0	2.7
Caudal peduncle length in % of its depth	159	152–159	155.5	2.8	185–191	188.7	2.5
Predorsal length in % of preanal length	99	97–100	98.1	1.3	94–96	95.0	0.9
Meristics		range	mode		range	mode	
Dorsal–fin rays	17	15–17	17		16–17	17	
Anal–fin rays	17	16–19	17		17–19	17	
Scales mid–longitudinal series	29	28–30	29		28–29	28	
Scales transverse	11	10–11	11		10–11	10	
Scales circumpeduncular	12	12–14	12		10	10	

Head short, laterally compressed, deeper than wide. Snout slightly pointed, smaller than eye diameter. Mouth supraterminal, slightly oblique in profile. Jaws subequal, lower jaw longer than upper, posterior end of rictus at same level or slightly ventral to centre of eye. Premaxilla and dentary with many irregularly distributed conical, slightly curved teeth in the outer row of lower and upper jaws. Orbit large, almost entirely in the anterior half of the head, in the dorsal portion of the head side. Branchiostegal membrane projects posteriorly from the operculum.

Dorsal-fin origin anterior to anal-fin origin, with both fins originating posterior to mid-length of body. Overall distal part of dorsal and anal fins rounded, with small contact organs in form of papillae on fin rays and distal margin with short filamentous rays. Posterior tip/margin of dorsal fin reaching caudal-fin base. Pectoral fin subtriangular, insertion at about vertical or slightly posterior to margin of opercular opening, base slightly oblique, with 18–19 rays, upper fin rays placed slightly anteriorly to lower fin rays, tip reaching or slightly overlapping base of pelvic fin. Pelvic fin subabdominal, origin at about mid-length of body, short, bases medially separated, tip reaching urogenital papilla. Caudal fin rounded, with 17–18 branched rays, plus 3 to 4 unbranched smaller rays at dorsal and ventral origins.

Scales cycloid. Body and head entirely scaled, except for the ventral surface of the head.

Cephalic squamation pattern variable. Anterior nostril at the anterior tip of the snout, tubular opening lateral to the upper lip. Posterior nostril in front of the orbit, with oblique oval aperture. Frontal neuromast in shallow groove. Cephalic sensory system at supraorbital level in a shallow groove fragmented into two portions, with two and three exposed neuromasts, respectively, whereas at the supratemporal level, it is in a curved groove, with four exposed neuromasts (Figure 8c). Preorbital canal in shallow groove with three to four exposed neuromasts; postorbital canal in shallow groove with one exposed neuromast; infraorbital series with about twelve small buttons at ventral margin of eye. Mandibular canal is in a shallow groove with a series of small neuromasts, curved to the lateral midline in front. One neuromast is located on each scale along the mid-longitudinal series of the trunk.

Females: Smaller than males. Body generally similar but somewhat less laterally compressed and slightly more slender than in males: head width greater (76–81% of its depth *vs.* 66–73), caudal peduncle more slender 185–191% of its depth *vs.* 152–159. Anal fin subtriangular, tip rounded, central rays longer and more rigid (*vs.* anal fin rounded in males). Dorsal-fin and anal-fin base lengths are smaller than in males (21.7–23.9% SL *vs.* 24.0–29.9, 18.5–19.5% SL *vs.* 21.6–24.0, respectively). Branchiostegal membrane not projecting distally (*vs.* projecting distally in males). No papillae or epidermal tissue present on dorsal and anal fins (*vs.* both present in males).

Colouration. Live colouration of males (Figure 11b): scales on head and trunk light green-blue to silver with irregular red-brown posterior margin, forming irregular marble-like patches and striped pattern on body. Snout, frontal and dorsal portion of head red-brown, throat light green-blue to silver. Posterior scale margins on post-orbital portion of operculum creating three red-brown, oblique, and vertical bars. Exposed part of branchiostegal membrane silver. Iris light yellow, with dark grey-black spots, especially on upper and lower-most parts, creating a dark vertical bar through the centre of the eye. Dorsal fin yellow to light green-blue with irregular red-brown stripes, perpendicular to fin rays proximally, parallel to fin rays medially and distally, fin tips with narrow dark brown distal band. Anal fin yellow to light green-blue, with irregular red-brown spots proximally, followed by a slender red-brown submedial band, a yellow to amber medial band and a broad dark brown distal band. Caudal fin base yellow to light green-blue, with irregular red-brown spots proximally, merging into a broad red-brown band medially, followed by an irregular narrow yellow to amber subdistal band and a broad dark brown distal band. Pelvic fin yellow to light green-blue, with red-brown proximal band and dark brown distal band. Pectoral fin hyaline with blue posterior distal margin.

Live colouration of females (Figure 11c): scales on trunk and head light brown with narrow dark grey posterior margin, forming a slightly visible reticulated pattern on body. Overall light brown colour of scales darker on dorsum and lighter to silvery on venter. Blue iridescence on the opercular region and on the trunk. Iris yellow. All fins are hyaline.

Distribution. *Nothobranchius marmoreus* is endemic to seasonal freshwater habitats of the upper Congo drainage in south-eastern DR Congo. It is currently known only from the type locality, a remnant pool associated with the Lufukwe system in the Lake Mweru basin (Figure 9). The Lufukwe is an affluent entering the lake from a south-western direction.

Ecology and biology. The area of the southern Lake Mweru basin experiences a mean annual rainfall of 1020–1120 mm [83]. The waters are the highest during the rainy season and, from March to May and driest between September and January [83,84].

At the type locality, *N. marmoreus* was the only *Nothobranchius* species observed. The type locality on 12 April 2023 was a large ephemeral pool formed in the floodplain of the seasonal Lufukwe River (Figure 11d). The habitat was 25–30 m in diameter, about 1.5 m deep at its deepest point. Shallower parts and edges of the pool were overgrown by grass. The water was turbid. The water temperature late morning was 24.0 °C, the pH was 7.4, and it contained 35 ppm of total dissolved solids. Water parameters, measured at the same location during the previous visit of 10 April 2016, showed the following values of: temperature of 27.8 °C in mid-afternoon; pH of 7.36; total dissolved solids of 42 ppm. The habitat primarily belongs to category 1.2 as defined by Watters (2015a) [85], representing a pool and flooded grassy area on a floodplain. However, the habitat also shows the influence of human activity: the pool lies where the road crosses the seasonal floodplain, and the natural pool has been excavated to make it larger and prevent flooding on the road. Therefore, the habitat falls into the secondary category of 2.1, modified by human activities related to road construction.

Aquarium maintenance of selected specimens was undertaken for observation of breeding behaviour and biology. *Nothobranchius marmoreus* has an annual mode of reproduction, the same as all of its known congeners. Under captive conditions, peat moss has been successfully used as an artificial spawning substrate. A plastic container with the substrate was placed in the aquarium and removed after a period of two weeks. It was then dried to a slightly moist state. An embryonic development period of three to four months was observed at about 22–24 °C. Eggs are slightly oval, measuring 1.26 mm long and 1.21 mm wide on average (n = 10), with short adhesive filaments of 40–90 µm on chorion, slightly attaching the eggs to the substrate.

Conservation status. *Nothobranchius marmoreus* is recommended to be assessed as Endangered. The species is currently known only from the type locality, a site situated in the Lufukwe system in the Lake Mweru basin. It might exist at some other sites within the drainage system of the Lufukwe, but its distribution will remain restricted, and any potential additional subpopulations are expected to be fragmented and have little or no contact with each other. The species is expected to be confined to ephemeral wetlands within the Lufukwe system, which has a drainage area of 559 km^2, representing the maximum estimated extent of occurrence. Its area of occupancy is estimated to be less than 100 km^2, with a likely maximum of five threat-based locations. The type locality, currently the only known site for the species, is located in close proximity to a human population. Phases in the seasonal life cycle of this species underscore the vulnerabilities of the ecological processes in the ephemeral habitats, as the survival of the species is dependent on suitable conditions during both dry and wet seasons. The author observed the expansion of agriculture in the general area and, consequently, increasing anthropogenic pressures on the land and water use. The resultant habitat changes are likely to modify the habitats in ways that render them unsuitable and thus degraded when considering their support of the seasonal life cycle of the species, and thus represent an important extinction risk. Further, the natural habitat at the type locality has been altered by the local human population through excavation to retain water for longer periods. This modification affects the natural rhythm and duration of the dry and wet seasons in the biotope. Additionally, specimens collected from the type locality during a first visit in 2016 have exhibited clinical signs, such as lesions suggestive of infection with *Aphanomyces* spp, and the fish were in a generally weak condition, with mortality within a few hours after capture. Using IUCN (2012) principles [86], *N. marmoreus* meets the criteria B1ab(iii)+2ab(iii) for Endangered, considering upper estimates of the EOO, AOO, and number of locations, as well as the risk of continuous decline of the known wetland habitats in which it is known to live.

There is currently no conservation or protection measure in place for this species. Additionally, its only known locality is not part of any protected area. Therefore, habitat protection is needed at the type locality. Further field surveys should target additional suitable habitats within the drainage area to document the full geographic range of the species more accurately. This would help in developing appropriate conservation strategies.

Etymology. The specific epithet *marmoreus* is a Latin adjective deriving from the ancient Greek word marmaros (μάρμαρος) in the meaning of resembling marble, marblelike, and in reference to the irregularly mottled marbled colour pattern on the body of the males.

3.3.4. *Nothobranchius dubieensis*, New Species

http://zoobank.org/urn:lsid:zoobank.org:act: DF33ED09-C5E6-499B-A478-7BEFC2732115

Holotype. BE_RMCA_VERT.2025.008.P.0031, male, 40.6 mm SL; DR Congo: Tambe stream: Lubule system: Luvua drainage: shallow remnant pool in small seasonal riverbed, 5.5 km west of Dubie village, 08°35′31″ S, 28°28′51″ E, 987 m alt.; A. Kalumba, 20 May 2023 (field code: CD 23-29).

Paratypes. BE_RMCA_VERT.2025.008.P.0032–0038, 4 males, 35.2–41.4 mm SL & 3 females, 29.5–37.2 mm SL; collected with the holotype.

Diagnosis. *Nothobranchius dubieensis* is distinguished from all other species of the genus by the unique combination in male colouration of having anal fin with narrow dark brown submedial band, narrow yellow and orange medial bands, narrow white subdistal band, and slender dark brown distal band; and caudal fin with irregular red-brown spots and stripes proximally and medially, followed by irregular narrow red-brown subdistal band and slender white distal band, with interrupted red-brown fin tips.

Further, *N. dubieensis* is distinguished from the most closely related *N. oestergaardi* by greater body depth (31.9–35.5% SL *vs.* 28.0–31.5); smaller snout length (14–16% HL 21–31); and smaller caudal peduncle length (119–125 in % of its depth *vs.* 125–140).

Description. General body features are illustrated in Figure 12. Morphometric and meristic characters of holotype and paratypes are summarised in Table 14. A medium sized *Nothobranchius* species (maximum observed size: 41.4 mm SL in males and 37.2 mm SL in females).

Figure 12. *Nothobranchius dubieensis*: (**a**). BE_RMCA_VERT.2025.008.P.0031, holotype, preserved male, 36.3 mm SL; (**b**,**c**). wild male photographed after capture; (**d**). type locality; DR Congo: Tambe stream: Lubule system: Luvua drainage: shallow remnant pool in small seasonal riverbed, 5.5 km west of Dubie village, 08°35′31″ S, 28°28′51″ E, 987 m alt.; A. Kalumba, 20 May 2023 (field code: CD 23-29). Photographed by B. Nagy (**a**) and A. Kalumba (**b**–**d**).

Males: General body shape is robust, laterally compressed, and deep. Greatest body depth at vertical in front of pelvic-fin origin. Greatest body width at pectoral-fin base, with body progressively narrowing towards caudal-fin base. Dorsal profile slightly concave to straight from tip of snout to nape and convex to base of last dorsal-fin ray, straight to slightly concave on caudal peduncle. Ventral profile convex from lower jaw to base of last anal-fin ray, straight to slightly concave on caudal peduncle. Caudal peduncle shallow, length 1.2–1.3 times its depth. Anus situated directly in front of anal-fin origin.

Head short, laterally compressed, deeper than wide. Snout slightly pointed, smaller than eye diameter. Mouth supraterminal, slightly oblique in profile. Jaws subequal, lower jaw longer than upper, posterior end of rictus at same level or slightly ventral to centre of eye. Premaxilla and dentary with many irregularly distributed conical, slightly curved teeth in the outer row of lower and upper jaws. Orbit large, in the anterior half of the head, in the dorsal portion of the head side. Branchiostegal membrane projects posteriorly from operculum.

Table 14. Morphometric and meristic data of holotype and paratypes of *Nothobranchius dubieensis*. Holotype values included in ranges, mean and standard deviation of males. H, holotype; SD, standard deviation.

Morphometric and Meristic Characters	**H**	**Males (*n* = 5)**			**Females (*n* = 3)**		
		Range	**Mean**	**SD**	**Range**	**Mean**	**SD**
Standard length	40.6	35.2–41.4			29.5–37.2		
Percent of standard length							
Total length	123.2	120.5–125.4	123.4	1.9	122.8–128.5	125.3	2.9
Body depth at pelvic-fin origin	32.5	31.9–35.5	33.5	1.7	27.9–29.8	28.6	1.0
Head length	31.8	30.9–32.4	31.7	0.7	29.2–30.4	29.8	0.6
Preanal length	65.0	59.7–65.6	63.4	2.3	65.3–67.8	66.6	1.2
Predorsal length	61.1	58.5–64.5	61.3	2.2	62.1–65.8	64.3	2.0
Prepelvic length	48.3	47.0–51.0	49.1	1.5	50.8–53.0	51.9	1.1
Prepectoral length	34.2	31.9–34.2	32.9	1.0	29.8–31.5	30.5	0.8
Caudal peduncle length	18.2	17.1–19.1	18.2	0.7	17.3–19.1	18.3	0.9
Caudal peduncle depth	15.3	13.7–16.1	15.0	0.9	11.9–12.6	12.3	0.4
Dorsal-fin base length	23.6	23.6–28.4	25.9	2.0	18.4–23.7	21.6	2.8
Anal-fin base length	17.5	17.5–23.7	19.8	2.4	15.0–16.4	15.8	0.7
Caudal-fin length	23.2	20.5–25.4	23.4	1.9	22.8–28.5	25.3	2.9
Percent of head length							
Head width	62	62–66	63.3	1.5	57–63	60.5	2.9
Head depth	95	90–96	92.6	2.4	76–78	77.2	1.1
Interorbital width	43	43–48	46.2	1.8	44–48	45.8	1.7
Postorbital length	58	56–59	57.3	1.1	56–60	57.3	2.5
Suborbital depth	16	13–18	15.8	1.9	11–15	12.9	2.1
Eye diameter	28	28–34	30.2	2.2	30–35	31.9	3.0
Snout to eye end length	42	42–44	42.7	1.1	40–44	42.7	2.5
Snout length	16	14–16	14.8	0.6	11–15	12.6	2.1
Other morphometric ratios							
Head width in % of its depth	66	66–71	68.3	1.9	75–81	78.4	3.0
Caudal peduncle length in % of its depth	119	119–125	121.6	3.0	146–151	147.8	2.9
Predorsal length in % of preanal length	94	94–98	96.8	1.8	95–98	96.7	1.5
Meristics		range	mode		range	mode	
Dorsal-fin rays	15	15–16	15		15–16	16	
Anal-fin rays	16	16–17	16		16–17	16	
Scales mid-longitudinal series	30	28–30	29		28–29	29	
Scales transverse	10	10–11	11		11	11	
Scales circumpeduncular	10	10–12	12		12	12	

Dorsal-fin origin anterior to anal-fin origin, with both fins originating posterior to mid-length of the body. Overall distal part of dorsal and anal fins rounded, with small contact organs in form of papillae on fin rays and distal margin with short filamentous rays. Posterior tip/margin of dorsal fin reaching caudal-fin base. Pectoral fin subtriangular, insertion at about vertical or slightly posterior to margin of opercular opening, base slightly oblique, with 18–19 rays, upper fin rays placed slightly anteriorly to lower fin rays, tip reaching or slightly overlapping base of pelvic fin.

Pelvic fin subabdominal, origin at about mid-length of body, short, bases medially separated, tip reaching urogenital papilla. Caudal fin rounded, with 17–18 branched rays, plus 3 to 4 unbranched smaller rays at dorsal and ventral origins.

Scales cycloid. Body and head entirely scaled, except for the ventral surface of the head.

Cephalic squamation pattern variable. Anterior nostril at the anterior tip of the snout, tubular opening lateral to the upper lip. Posterior nostril in front of the orbit, with oblique oval aperture. Frontal neuromast in shallow groove. Cephalic sensory system at supraorbital level in a shallow groove fragmented into two portions, with two and three exposed neuromasts, respectively, whereas at supratemporal level in a curved groove, with four exposed neuromasts (Figure 8d). Preorbital canal in shallow groove with two to three exposed neuromasts; postorbital canal in shallow groove with one exposed neuromast; infraorbital series not visible on most specimens. Mandibular canal in a shallow groove with a series of about a dozen small buttons, curved to the lateral midline in front. One neuromast is on each scale along the trunk mid-longitudinal series.

Females: Smaller than males. Body generally similar but less laterally compressed and slightly more slender than in males (body depth at pelvic fin origin 27.9–29.8% SL *vs.* 31.9–35.5 in males; head width 75–81% of its depth *vs.* 66–71; caudal peduncle length 146–151% of its depth *vs.* 119–125). Head length is smaller than in males, with 29.2–30.4% SL *vs.* 30.9–32.4. Anal fin subtriangular, tip rounded, central rays longer and more rigid (*vs.* anal fin rounded in males). Anal-fin base length smaller than in males (15.0–16.4% SL *vs.* 17.5–23.7). Branchiostegal membrane not projecting distally (*vs.* projecting distally in males). No papillae or epidermal tissue present on dorsal and anal fins (*vs.* both present in males).

Colouration. Live colouration of males (Figure 12c): scales on head and trunk light blue with red-brown posterior margin, forming irregular vertical, curved line pattern on body. Snout, frontal and dorsal portion of head red-brown to grey, throat light grey. Posterior scale margins on post-orbital portion of operculum create three red-brown, anteriorly lowering, oblique bars. Exposed part of branchiostegal membrane light blue. Iris light yellow, with dark grey-black spots, especially on upper and lower-most parts, creating a dark vertical bar through centre of eye. Dorsal fin light blue to light yellow with irregular red-brown stripes, perpendicular to fin rays proximally, parallel to fin rays medially and distally. Anal fin light blue, with irregular red-brown spots proximally, followed by narrow dark brown submedial band, narrow yellow and narrow orange medial bands, narrow white subdistal band, and slender dark brown distal band. Caudal fin light blue to yellow, with irregular red-brown spots and stripes proximally and medially, followed by irregular narrow red-brown subdistal band and slender white distal band, with interrupted red-brown fin tips. Pelvic fin with yellow and orange bands. Pectoral fin hyaline with blue posterior distal margin.

Females: scales on trunk and head light brown with narrow dark brown posterior margin, forming a slightly visible reticulated pattern on the body. Overall light brown colour of scales, darker on dorsum and lighter to silvery on venter. Blue iridescence on the opercular region and anterior midlateral half of the trunk. Iris yellow. All fins are hyaline.

Distribution. *Nothobranchius dubieensis* is endemic to seasonal freshwater habitats of the upper Congo drainage in south-eastern DR Congo. It is currently known from ephemeral marshes and ponds associated with the Lubule system in the Luvua drainage (Figure 9). The Lubule is a left affluent entering the Luvua from the southern direction.

Ecology. The area around the Lake Mweru basin experiences a mean annual rainfall of 1020–1120 mm [83]. The waters are the highest during the rainy season and this from March to May, and driest between September and January [83,84].

At the type locality, *N. dubieensis* was the only *Nothobranchius* species observed. The accompanying fish fauna consisted of non-annual '*Lacustricola*' species. The type locality on 20 May 2023 was a remnant, culvert-like pool, connecting to an ephemeral riverbed and a large swampy area, as part of the Tambe stream in the seasonal Lubule system (Figure 12d). The habitat was about 10 m long and 1 m wide, and about 50 cm deep at its deepest point. The edges of the biotope were overgrown by grass. The water was turbid, but the bottom was visible in shallower, undisturbed parts. The habitat principally belongs to category 1.2 as defined by Watters (2015a) [85], representing a pool and flooded grassy area on a floodplain. The habitat is close to human population, and the anthropogenic impact is evident, as there are fish trap constructions in the biotope and trash left behind in the biotope.

Conservation status. *Nothobranchius dubieensis* is recommended to be assessed as Vulnerable. The species is currently known only from the area of the type locality, several sites in the Lubule system of the Luvua drainage. It might exist at some other sites within the drainage system of the Luvua, but its distribution will remain restricted, and any potential additional subpopulations are expected to be fragmented and not necessarily in contact with each other. The area of the Lubule system where the species is found measures about 3600 km^2, which is expected to be the maximum extent of occurrence. It is expected to inhabit a maximum of ten threat-based locations. Presently known sites, including the type locality, are directly adjacent to human populations. There is an expansion of agricultural seasonal wetland habitats in the known distribution area, and consequently, an increase in anthropogenic pressures on land and water use. Using IUCN (2012) principles [86], *N. dubieensis* meets the criteria B1ab(iii) for Vulnerable, considering upper estimates of the EOO and number of threat-based locations, as well as the risk of continuous decline of the known wetland habitats in which it is known to live.

There are currently no conservation or protection measures in place for this species. Additionally, it is not known if any protected areas would partly encompass its known distribution. Therefore, habitat protection is needed at the type locality and other sites within the Lubule system where the species has been recorded. Further field surveys should target additional suitable habitats within the drainage area to document the full geographic range of the species more accurately. This would help in developing appropriate conservation strategies.

Etymology. The specific name is given in reference to Dubie township in south-eastern DR Congo, near which place this species is found, and the type locality is situated. An adjective derived from the geographical name.

3.3.5. *'Lacustricola' gemma*, New Species

http://zoobank.org/urn:lsid:zoobank.org:act: 5C225ABD-CE65-4450-B8F8-041415B5A95E

Holotype. BE_RMCA_VERT.2025.008.P.0039, male, 22.5 mm SL; DR Congo: Kay system: upper Lualaba drainage: shallow remnant pool in small seasonal riverbed, 0.5 km west of Lubule village, 07°31′47″ S, 27°13′24″ E; B. Katemo Manda, 17 April 2023 (field code: CD 23-26).

Paratypes. BE_RMCA_VERT.2025.008.P.0040–0043, male, 23.0 mm SL & 3 females, 20.7–22.4 mm SL; collected with the holotype. — BE_RMCA_VERT.2025.008.P.0044, male, 16.8 mm SL; DR Congo: Kay system: upper Lualaba drainage: Lake Bowe, 07°40′53″ S, 27°08′46″ E; B. Katemo Manda, 17 December 2022.

Diagnosis. *'Lacustricola' gemma* is distinguished from all other species of the genus by the unique combination in live colouration: in males, a pattern of iridescent, diamond-shaped, light blue spots in scale centres, especially evident below mid-longitudinal series on posteroventral portion of flank, and larger iridescent blue blotches on dorsum, creating an irregular reflective pattern on body; median fins yellow to hyaline, dorsal and anal fins with six to eight dark grey stripes perpendicular to fin rays basally and posteriorly, with light blue iridescence basally; dorsal with light blue distinct margin; anal with dark grey margin; caudal fin with four to five dark grey stripes perpendicular to fin rays; as well as in females, dorsal and anal fins hyaline with irregular brown stripes, fin tips with narrow light blue margin, caudal hyaline without markings.

Further, *'Lacustricola' gemma* is distinguished from both '*L.*' *hutereaui* and '*L.*' *chobensis* by the following morphometric characters in males: body depth at pelvic-fin origin 25.6–27.4 (*vs.* 21.1–24.1 and 30.0–32.3, respectively); anal-fin base length 18.7–19.6 (*vs.* 14.2–17.1 and 20.7–25.2); smaller head depth 79–83 (*vs.* 86–91 and 86–90); greater head width in % of its depth 83–87 (*vs.* 76–83 and 70–74); and caudal peduncle length in % of its depth 111–114 (*vs.* 150–156 and 98–105).

Description. General body features are illustrated in Figure 13. Morphometric and meristic characters of holotype and paratypes are summarised in Table 15.

Males: general body shape laterally compressed and moderately deep. Small species, maximum observed size 23.0 mm SL. Greatest vertical body depth in front of pelvic-fin origin and shallowest at mid-portion of caudal peduncle. Greatest body width at pectoral-fin base, with body progressively narrowing towards caudal-fin base. Dorsal profile slightly convex from snout to base of dorsal fin and straight to slightly concave from base of dorsal fin to caudal fin. Ventral profile convex from lower jaw to base of last anal-fin ray, straight to slightly concave on ventral midline of caudal peduncle. Caudal peduncle relatively deep, length 111–114 in % of its depth. Anus directly in front of anal-fin origin.

Head short, laterally compressed, deeper than wide (head width 83–87 in % of its depth). Snout rounded, smaller than eye diameter. Mouth superior, oblique in profile. Jaws not equal, lower jaw longer than upper, posterior end of corner of mouth at the same level as the centre of eye. Premaxilla and dentary with many irregularly distributed conical teeth. Orbit large (38–41% HL).

Dorsal fin set rearwards, origin posterior to anal-fin origin, both fins originating posterior to mid-length of body. Dorsal and anal fins rounded. Dorsal fin, 9; anal fin, 13–14. Pectoral fin subtriangular, insertion relatively high and posterior to margin of opercular opening; base oblique, upper fin rays placed anteriorly to lower fin rays, 10–11 rays. Pelvic fin sub-abdominal; its origin slightly posterior to mid-length between insertions of pectoral and anal fins, almost reaching origin of anal fin. Caudal fin large and truncate, with 14–15 branched rays, plus five or six dorsal and ventral procurrent rays.

Scales cycloid, body and head entirely scaled, except for the ventral surface of the head. Scales in mid-longitudinal series, 20–23, plus two or three small scales on caudal-fin base. Transverse rows of scales in front of dorsal-fin origin, 6; scale rows around caudal peduncle, 10.

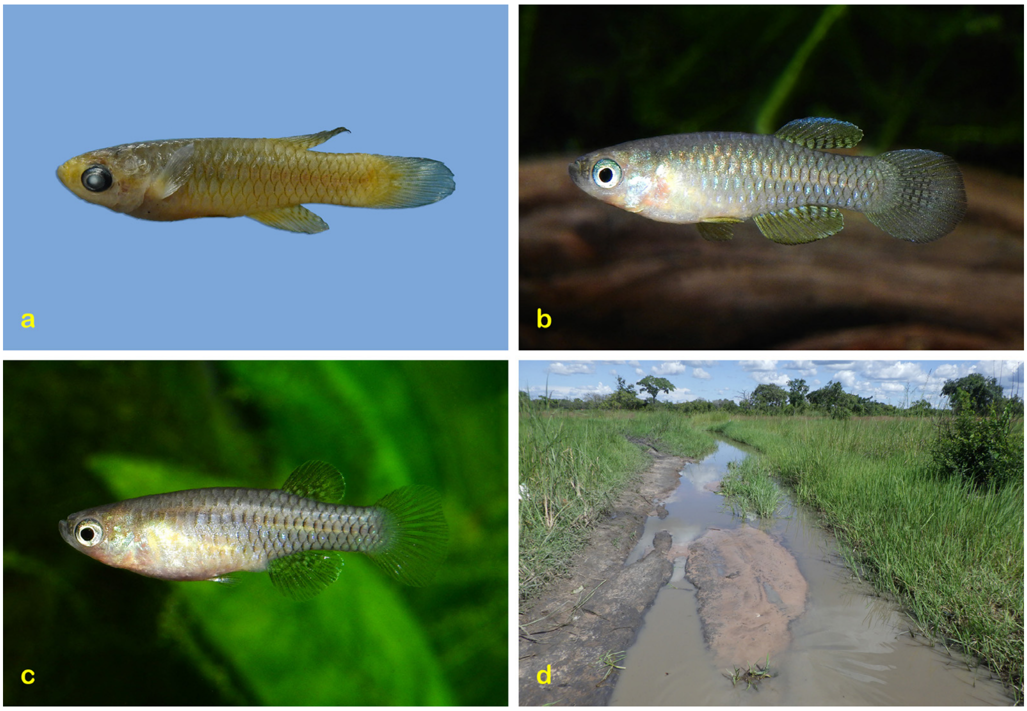

Figure 13. ‘*Lacustricola*’ *gemma*: (**a**). BE_RMCA_VERT.2025.008.P.0039, holotype, preserved male, 22.5 mm SL; (**b**). holotype live male; (**c**). live wild-caught female; (**d**). type locality; DR Congo: Kay system: upper Lualaba drainage: shallow remnant pool in small seasonal riverbed, 0.5 km west of Lubule village, 07°31′47″ S, 27°13′24″ E, 634 m alt.; B. Katemo Manda, 17 April 2023 (field code: CD 23-26). Photographed by B. Nagy (**a**–**c**) and B. Katemo Manda (**d**).

Two frontal neuromasts in a shallow groove. Cephalic sensory system at preorbital level in two discontinuous shallow grooves, with one and two neuromasts, respectively; infraorbital series with about a dozen small buttons; postorbital canal tubular with two pores; preopercular sensory systems tubular with seven pores (Figure 14a). Cephalic sensory system at supraorbital level in a short groove, with two neuromasts; whereas at supratemporal level, two to three exposed neuromasts (Figure 14b). Mandibular level with three to four exposed neuromasts parallel to the outer margin of lower jaw (Figure 14c).

Females: Body depth smaller than in males (27.6–29.5% SL *vs.* 25.6–27.4; head less laterally compressed than in males (head width 87–91% of its depth *vs.* 83–87); preanal, predorsal and prepelvic lengths greater than in male (63.8–64.7% SL *vs.* 59.1–62.2; 70.0–71.5% SL *vs.* 66.1–69.3; and 44.7–48.8% SL *vs.* 41.7–44.0); anal-fin base length smaller than in male (15.5–16.6% SL *vs.* 18.7–19.6); and caudal peduncle shallower than in males (caudal peduncle depth 15.2–16.4% SL *vs.* 16.7–17.4; caudal peduncle length 120–124% of its depth *vs.* 111–114).

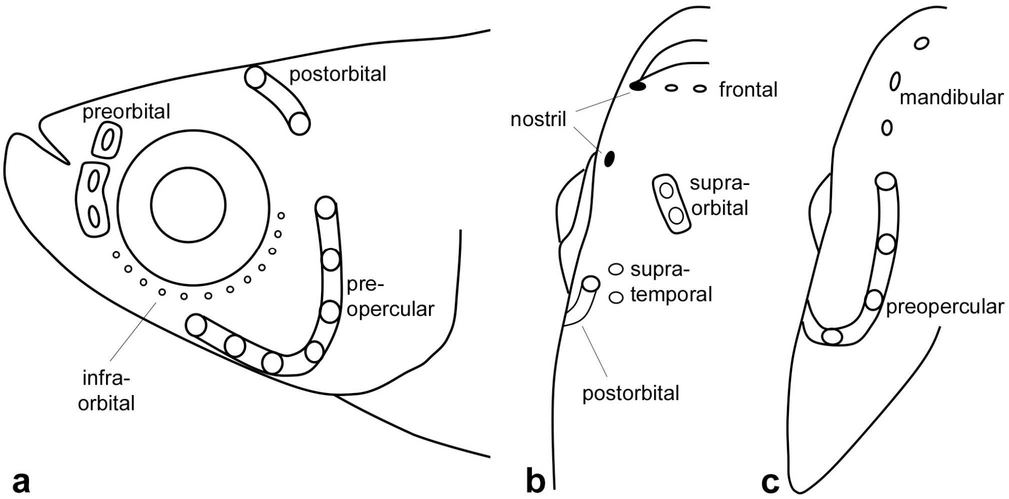

Figure 14. Diagrammatic representation of the cephalic sensory system in ‘*Lacustricola*’ *gemma*; BE_RMCA_VERT.2025.008.P.0039, holotype, male, 22.5 mm SL; (**a**). lateral view of head; (**b**). dorsal view of head; (**c**). ventral view of head.

Table 15. Morphometric and meristic data of holotype and paratypes of '*Lacustricola*' *gemma*. Holotype values included in ranges, mean and standard deviation of males. H, holotype; SD, standard deviation.

Morphometric and Meristic Characters		**Males (*n* = 3)**			**Females (*n* = 3)**		
	H	**Range**	**Mean**	**SD**	**Range**	**Mean**	**SD**
Standard length	22.5	16.8–23.0			20.7–22.4		
Percent of standard length							
Total length	133.3	129.6–133.3	130.9	2.1	130.4–133.8	132.4	1.8
Body depth at pelvic-fin origin	26.7	25.6–27.4	26.6	0.9	27.6–29.5	28.3	1.0
Head length	28.0	24.3–28.0	25.8	1.9	25.3–29.0	26.7	2.0
Preanal length	62.2	59.1–62.2	60.7	1.5	63.8–64.7	64.2	0.5
Predorsal length	69.3	66.1–69.3	67.5	1.7	70.0–71.5	70.7	0.7
Prepelvic length	44.0	41.7–44.0	42.9	1.2	44.7–48.8	46.6	2.1
Prepectoral length	30.7	26.1–30.7	27.8	2.5	26.7–30.0	27.8	1.8
Caudal peduncle length	18.7	18.7–19.6	19.1	0.5	18.8–19.8	19.3	0.5
Caudal peduncle depth	16.9	16.7–17.4	17.0	0.4	15.2–16.4	15.9	0.7
Dorsal-fin base length	14.2	14.2–16.7	15.7	1.3	12.9–14.5	13.9	0.9
Anal-fin base length	18.7	18.7–19.6	19.1	0.5	15.5–16.6	16.2	0.6
Caudal-fin length	33.3	29.6–33.3	30.9	2.1	30.4–33.8	32.4	1.8
Percent of head length							
Head width	67	67–71	69.0	2.4	70–73	71.7	1.5
Head depth	79	79–83	81.6	2.0	78–84	80.4	2.8
Interorbital width	52	52–57	55.0	2.4	56–59	57.2	1.2
Postorbital length	41	41–43	41.7	1.0	44–48	45.6	2.4
Suborbital depth	17	14–18	15.3	1.8	15–19	16.7	2.2
Eye diameter	38	38–41	38.7	1.6	38–42	40.5	1.9
Snout to eye end length	59	57–59	58.3	1.0	52–56	54.4	2.4
Snout length	22	19–22	20.3	1.7	17–18	17.4	0.8
Other morphometric ratios							
Head width in % of its depth	84	83–87	84.6	2.1	87–91	89.2	2.2
Caudal peduncle length in % of its depth	111	111–114	112.4	1.9	120–124	121.4	1.9
Predorsal length in % of preanal length	111	109–113	111.2	2.2	109–112	110.1	1.7
Meristics		range	mode		range	mode	
Dorsal-fin rays	9	9	9		9	9	
Anal-fin rays	13	13–14	13		13	13	
Dorsal fin to anal fin relative position	6	5–6	6		6	6	
Scales mid-longitudinal series	21	21–23	23		20–22	20	
Scales transverse	6	6	6		6	6	
Scales circumpeduncular	10	10	10		10	10	

Coloration. Live males and females (Figure 13): Scales on trunk with a pattern of discrete iridescent, diamond-shaped, light blue spots, especially evident below mid-longitudinal series on posteroventral portion of flank, creating an irregular reflective pattern on body. Scales on dorsum grey-brown, with light blue iridescent blotches in males. Scales on the abdomen from opercle to pelvic fin are white to silver. Head yellow to light brown-grey, snout and dorsal portion of head grey-brown, throat silver. Exposed branchiostegal membrane white. Iris silver, light blue iridescent in the upper portion. Iridescent silver to blue blotches on postorbital opercular region. Iridescent silver to blue humeral blotch on post-opercular region in males. Median fins yellow to hyaline, dorsal and anal fins with six to eight dark grey stripes perpendicular to fin rays basally and posteriorly, with light blue iridescence basally; dorsal with light blue distinct margin; anal with dark grey margin; caudal fin with four to five dark grey stripes perpendicular to fin rays. Dorsal and anal fin in female hyaline with irregular brown stripes, with fin tips with narrow light blue margin, caudal hyaline without markings. Pelvic fin yellow in males, hyaline in females.

Distribution. '*Lacustricola*' *gemma* is endemic to freshwater habitats of the upper Congo drainage in south-eastern DR Congo. It is currently known from waters associated with the Kay system in the upper Lualaba drainage (Figure 9). The Kay is a major right bank affluent entering the upper Lualaba below Lake Upemba.

Ecology and biology. The area of the upper Lualaba experiences a mean annual rainfall of around 1000 mm, with December the wettest month. In the Upemba System, the waters of the Lualaba are high from February–April and low from August–October [83]. The dry season lasts for around 160 days.

At the type locality, '*Lacustricola*' *gemma* was the only procatopodid species observed. The accompanying fish fauna consisted of the seasonal *Nothobranchius katemomandai*. The type locality on 17 April 2023 was a remnant pool formed in the riverbed of the seasonal Lubule River (Figure 13d). The habitat was a drying ephemeral riverbed about 1–2 m wide, the edges of which were overgrown by grass. The water was turbid. The water temperature around noon was 27.3 °C, the pH was 7.2, and it contained 120 ppm of total dissolved solids. The habitat belongs to category 1.4.1 as defined by Watters (2015a) [85], representing a remnant pool in a seasonal stream system on a floodplain.

Water parameters, measured by B. Katemo Manda at another confirmed site in Lake Bowe, showed a temperature of 28.4 °C; pH of 7.2; total dissolved solids of 30 ppm.

Aquarium maintenance of selected specimens was undertaken for observation of breeding behaviour and biology. '*Lacustricola*' *gemma* has a non-annual mode of reproduction, the same as all of its known congeners. Under captive conditions, a spawning mop prepared from acrylic yarn was used successfully as an artificial spawning medium, simulating submerged vegetation. Eggs were picked from the mop and stored in plastic containers with shallow water for development. An embryonic development period of about two to three weeks was observed at about 22–24 °C. Eggs are relatively large, round, measuring 1.6 mm in diameter on average ($n = 10$).

Conservation status. '*Lacustricola*' *gemma* is recommended to be assessed as Vulnerable. The species is currently known only from the area of the type locality, sites in the Kay system of the Lualaba drainage. It might exist at some other sites within the drainage system of the upper Lualaba River, but its distribution will remain restricted. The entire drainage area of the Kay system has an extent of 1142 km^2 and the species is expected to be found from a maximum of ten threat-based locations. Some of the known sites at present, including the type locality, are directly adjacent to human populations. There is an expansion of agriculture in seasonal wetland habitats of the known distribution area and, consequently, an increase in anthropogenic pressures on the land and water use. Using IUCN (2012) principles [86], '*L.*' *gemma* meets the criteria B1ab(iii) for Vulnerable, considering the drainage area as maximum EOO and the number of estimated maximum threat-based locations, as well as the risk of continuous decline of the known wetland habitats in which it is known to live.

There are currently no conservation or protection measures in place for this species. Additionally, it is unknown whether any protected areas would partially encompass its known distribution. Therefore, habitat protection is needed at the type locality and other sites within the Kay system where the species has been recorded. Further field surveys should target additional suitable habitats within the drainage area to document the full geographic range of the species more accurately. This would help in developing appropriate conservation strategies.

Etymology. The specific epithet *gemma* is derived from the ancient Greek word γέμω, originally meaning "precious stone" or "gem". It refers to the pattern of the body scales, which are adorned with numerous iridescent, diamond-shaped markings, evoking the appearance of tiny gems. The name also alludes to the relatively small adult size of the species. It is treated as a noun in the nominative singular, standing in apposition to the generic name.

4. Discussion

4.1. Nothobranchiidae

4.1.1. History of *Nothobranchius brieni* Species Group

The first documented species of *Nothobranchius* from the south-eastern upper Congo drainage was *N. brieni*, described from the Lualaba River by Poll (1938) [17]. This was followed by Wildekamp's (1978) redescription of *N. brieni* and the description of three additional species [6]. Since then, the recognised species richness within the group has grown to sixteen, followed by the identification of four more species in the present study (see Table 1). This expanding body of research reflects the remarkable complexity and diversity of the *N. brieni* species group and underscores the importance of continued exploration to better understand its evolutionary relationships and ecological significance better.

4.1.2. Phylogenetic Analysis of *Nothobranchius brieni* Species Group

Molecular phylogenetic reconstructions in different studies confirmed that species of the *N. brieni* species group form a well-supported monophyletic group (e.g., [3,8,9,36,55,68,89]), that is resolved as part of the geographically-structured Inland clade (*sensu* [68]). All *Nothobranchius* species found in the Katanga Province of the Congo, Zambia, and the Zambezi Region of Namibia have been found to comprise a distinct clade, referred to as the Kalahari Clade in [36]. These species constitute the *N. brieni* species group.

In this study, a phylogenetic analysis based on the COI gene sequence was conducted, demonstrating sufficient discriminative power for species resolution. The analysis included an expanded dataset of the *N. brieni* species group, with the primary aim of evaluating the internal structure of the group and identifying new species as phylogenetically distinct lineages. The author acknowledges the limitations of single-gene analyses but presents this study to offer insights in comparison to previous research. It serves as an additional element among multiple corroborating lines of evidence in species delimitation. The phylogeny retrieved in this study is largely congruent with previous analyses.

Within the Lake Mweru complex, in addition to the described members of the genus, a putative species from the upper Lubi system is represented by three terminals: *N.* spec. DRCP 2013-06 (also known as *N.* spec. Kasenga), and *N.* spec. CD 23-23 and *N.* spec. CD 23-25. The description of that putative species from the upper Lubi drainage is in review, and it is represented here for clarity [11].

4.1.3. Biogeography of *Nothobranchius brieni* Species Group

Species in the *N. brieni* group show allopatric distributions, each restricted to separate drainage systems or isolated parts of the same system, often divided by physical barriers such as mountains or waterfalls (e.g., [10,13,16,18]; Table 1). Their limited dispersal ability and strong habitat fidelity have led to speciation patterns closely aligned with historical drainage reorganisations across the south-central African plateau [90].

Phylogenetic patterns and landscape history suggest that ancient hydrological connections facilitated early diversification, later disrupted by river capture and drainage shifts [36,91]. Given these mechanisms, further exploration of remote floodplains in south-eastern DR Congo and northern Zambia is likely to uncover further, as yet undescribed species.

4.1.4. Conservation Aspects

All *Nothobranchius* fishes in the upper Congo drainage are subject to a high level of threat and belong to one of the threatened Red List categories [18]. The importance of the discoveries from conservation aspects is illustrated by the numerous increasing anthropogenic impacts, and requires the need for active protection of the freshwater wetland habitats in which these species occur. The impact of human activities was evident in three out of four types of localities, whereas the fourth type of locality in the Kay system is adjacent to human population.

Molecular analyses revealed evidence of fish-pathogenic oomycetes *Aphanomyces invadans* and *A. laevis* on samples collected in 2023, which represent a first-time record for the host of the fish genus *Nothobranchius* [87]. Observations involve at least two of the new species in this study. Specimens of *N. marmoreus* were observed by the present author in 2016 with lesions suggestive of infection with *Aphanomyces* spp, whereas molecular analysis revealed *Aphanomyces laevis* on *N. katemomandai* collected in 2023. Evidence of infection with oomycete pathogens documented in Nagy (2024a) [87] represents an important additional threat to the unique seasonal aquatic biodiversity of the region.

Conservation efforts for *Nothobranchius* species must focus on preserving their unique ephemeral wetland habitats and addressing the multiple human-induced threats they face. Their conservation is not only crucial for maintaining biodiversity but also for preserving valuable scientific research opportunities for aging studies.

4.2. Procatopodidae

4.2.1. History of Procatopodid Species in Upper Congo

Different forms of lampeyes in the upper Congo region have been long associated with three early-described species and typically lumped into them: *Haplochilus johnstoni* [47]; *Haplochilus katangae* [48]; and *Haplochilus hutereaui* [46]. These species were largely characterized by basic external features, such as elongated body and unmarked fins *vs.* a zigzag black stripe along the flank *vs.* barred median fins, respectively. Based on this simple characterization, many populations across the southern part of Africa were associated with each of these species, creating species groups. The status of an additional, long-described species, *Haplochilus moeruensis* [54], was not clear and was often associated with different species around the Lake Mweru drainage, until Seegers (1996) [92] selected a lectotype and published a photograph of it.

In parallel, the alpha taxonomy of lampeye cyprinodontiform fishes of Africa has been mostly neglected for a long time. Their phylogenetic relationships were poorly researched, and different hypotheses yielded inconsistent results among various authors [40,93–96].

Aforementioned species were assigned to several genera during several decades, namely to *Aplocheilichthys* (e.g., [22,45]), to *Micropanchax* (e.g., [40,56,97]) or to *Lacustricola* (e.g., [96,98]), whereas currently they are regarded as belonging to an undescribed genus ‘*Lacustricola*’ [41].

4.2.2. Phylogenetic Analysis of Procatopodid Species in Upper Congo

Phylogenetic analysis performed by Bragança & Costa (2019) [41] revealed evidence that the genus *Lacustricola* is polyphyletic, with included species occurring in two separate, geographically disjunct clades. The eastern African *Lacustricola* clade comprises species that are largely confined to coastal rivers and lakes in East Africa, including the type species of the genus *L. pumilus,* from the Lake Tanganyika basin. Another clade, comprising species predominantly distributed in southern Africa, represents an undescribed genus. The species of this clade are referred to in this paper as ‘*Lacustricola*’. The species from the upper Congo drainage mentioned above belong to this group (Figure 5). Additionally, three other members of Procatopodidae found in the upper Congo drainage also belong to this genus, such as ‘*L.*’ *petnehazyi* [56], ‘*L.*’ *nitidus* [55], as well as a form referred to herein as ‘*L.*’ cf. jubbi, initially described in the genus *Hypsopanchax* by Poll & Lambert (1965) [53] from the upper Zambezi (Figure 5).

However, one species described from the upper Congo basin was found to belong to the genus *Lacustricola* (*sensu stricto*) as *L. lualabaensis* was revealed to be part of the same phylogenetic clade as *L. pumilus*.

4.2.3. Geographical Distribution and Biogeography

The complex geological history of the Congo drainage and the diverse and changing aquatic environments it supports, likely provided numerous ecological niches for Procatopodids to adapt to and speciate. Periods of isolation due to forest fragmentation and changing water levels may have promoted allopatric and peripatric speciation in Procatopodid species [49,50].

The complex network of tributaries and rivers in the Congo drainage probably facilitated the dispersal and diversification of Procatopodid species. It is likely that many undiscovered or unidentified new species exist within the drainage system. To fully understand the evolution of Procatopodid species in the Upper Congo drainage, further research focusing specifically on these fish in the region is necessary.

4.2.4. Conservation Aspects

The conservation of southern African procatopodid species faces significant challenges due to the vulnerability of their habitats. During the rainy season, lampeyes typically migrate to shallow, flooded areas for breeding, highlighting the critical importance of these ephemeral aquatic environments. This seasonal behavioural pattern dependence makes them especially susceptible to habitat alterations and degradation. The conservation of these species is further complicated by the multitude of threats facing wetland ecosystems in southern Africa. Human activities such as agricultural expansion, water extraction, urban development, and industrial pollution, particularly from mining operations, pose severe risks to these delicate habitats. Recent taxonomic studies indicate that the Procatopodidae family is much more diverse than previously thought. In addition to some widely distributed species, it also includes narrowly distributed endemics [51]. As the majority of wetlands in southern Africa are unprotected, this underscores the urgent need for comprehensive conservation strategies. Preserving the integrity of these wetlands throughout all seasons is crucial for maintaining the ecological balance and safeguarding the distinctive seasonal freshwater biodiversity they support, including the vulnerable procatopodid species.

4.3. Comparative Material

‘L*acustricola*’ *chobensis*: SAIAB 30007, holotype, male, 24.7 mm SL; SAIAB 30008, 4 paratypes, males, 11.6–16.4 mm SL; Botswana: Chobe River: Kasane, 17°49′ S, 25°08′ E.

‘*Lacustricola*’ *hutereaui*: RMCA P-1822-3, syntypes, 2 males, 22.1–25.1 mm SL; DR Congo: Uele River: Dungu, 03°41′ N, 29°08′ E. — RMCA 73-23-P-10550-865, 3 males, 27.1–31.7 mm SL; DR Congo: Uele River: Buta, 02°47′ N, 24°46′ E.

Nothobranchius brieni: RMCA 50016, lectotype, male, 46.3 mm SL; RMCA 50018-27, paralectotypes, 4 males, 44.4–46.5 mm SL; DR Congo: Lualaba drainage: Bukama, 09°12′ S, 25°51′ E. — RMCA B4-019-P-0013-4, 2 males, 30.3–30.4 mm SL; DR Congo: Lualaba drainage: Bukama, 09°11′ S, 25°51′ E.

N. ditte: RMCA 2016-027-P-0001, holotype, male, 33.0 mm SL; RMCA 2016-027-P-0002, paratype, male, 38.9 mm SL; RMCA 2016- 027-P-0029, paratype, male, 42.4 mm SL; RMCA 2016-027-P-0004-10, 7, paratypes, males, 31.1–38.9 mm SL; DR Congo: Lake Mweru basin: Kilwa, 09°12′ S, 28°17′ E.

N. hassoni: MSNG 51837, holotype, male, 41.1 mm SL; MSNG 51838-9, paratypes, 2 males, 34.9–37.2 mm SL; MSNG 51840, paratype, male, 33.9 mm SL; RMCA A3-028- P-0003, paratype, male, 41.0 mm SL; DR Congo: middle Lufira drainage: Lufwa system: Kanvungwe, 09°29′ S, 27°17′ E. — RMCA A3-028-P-0004, paratype, male, 32.0 mm SL; DR Congo: middle Lufira drainage: Lwipa system, 09°08′ S, 27°20′ E. — RMCA B3-028-P- 0001-4, 4 males, 27.9–35.2 mm SL; RMCA B4-019-P-0012, male, 38.5 mm SL; DR Congo: middle Lufira drainage: Bunkeya, 10°25′ S, 26°58′ E. — RMCA B0-013-P-0001-0014, 5 males, 40.1–43.7 mm SL; DR Congo: middle Lufira drainage: Mwashya, 10°42′ S, 27°21′ E.

N. malaissei: RMCA 73-24-P-952, holotype, male, 33.0 mm SL; RMCA 73-24-P-914-919, RMCA 73-24-P-947-951, 6 males, 36.4–43.2 mm SL; DR Congo: Luapula drainage: Kabiasha, 10°17′ S, 28°09′ E.

N. milvertzi: RMCA B2-027-P-0001, holotype, male, 36.9 mm SL; RMCA B2-027-P-0002, 1, male, 36.0 mm SL; RMCA B2-027-P-0003-16, 14, 6 males, 30.5–35.9 mm SL; Zambia: Lake Mweru basin, Lushiba Marsh: Chienge, 08°36′ S, 29°07′ E.

N. oestergaardi: BMNH 2010.12.6.1, holotype, male, 31.8 mm SL; RMCA 2010-33-P-4, paratype, male, 30.4.0 mm SL; MSNG 56047A-B-C, paratype, male, 42.7 mm SL; paratype, male, 29.0 mm SL; SAIAB 98224, paratype, male, 26.4 mm SL; Zambia, Lake Mweru Wantipa basin: Kalaba, 8°25′ S, 29°50′ E.

N. polli: RMCA 192399, holotype, male, 28.9 mm SL; DR Congo: Katanga province: upper Lufira drainage: Dilungu swamp, 10°45′ S, 27°15′ E. — RMCA B4-019-P-0015, male, 34.1 mm SL; DR Congo: Katanga province: upper Lufira drainage, 11°02′ S, 27°18′ E. — RMCA B4-019-P-0016-8, 3 males, 26.1–35.1 mm SL; DR Congo: Katanga province: upper Lufira drainage: Kyembe, 11°02′ S, 27°18′ E.

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Ethics Statement

The study was conducted in accordance with the ethical standards and Congolese legislation, according to the guidelines of the Declaration of Helsinki, authorized by the University of Lubumbashi and approved on 20 March 2025 by the Ministry of Environment and Sustainable Development, Kinshasa, DR Congo (n°13 SG/EDD/BTB/ANCCB-RDC/03/2025).

Informed Consent Statement

Not applicable.

Data Availability Statement

Specimens of the type series and examined comparative material are deposited in ichthyology collections, whereas genetic sequences are deposited in GenBank. Additional data to support the findings of this study are available from the author upon reasonable request.

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The author declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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