



Revision of the cichlid fish genus *Gnathochromis* (Teleostei: Cichlidae) from Lake Tanganyika with the description of a new genus *Jabarichromis* gen. nov.

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Abstract

The cichlid species flock from Lake Tanganyika is a well-studied system for evolutionary biology research because its species assemblage shows a high degree of endemism and is a product of adaptive radiation. While our understanding of the evolutionary history of Lake Tanganyika cichlids has advanced tremendously over the past decades, their taxonomy received considerably less attention, despite numerous taxonomic misplacements (e.g., polyphyletic genera and species) that have been revealed by phylogenetic studies. One prominent example of a polyphyletic genus is *Gnathochromis*, which includes two distantly related species, belonging to two different tribes. To resolve this issue, here we present a taxonomic revision based on an extensive morphological dataset obtained from a comprehensive taxon sampling including 587 specimens from 63 taxa. We introduce a new monotypic genus, *Jabarichromis* gen. nov. for '*Gnathochromis*' *pfefferi*, a member of the tribe Tropheini, thereby separating it from the type species of *Gnathochromis*, *G. permaxillaris*. As a result, the genus *Gnathochromis*, which belongs to the tribe Limnochromini, is rendered monophyletic. Further, we provide an additional character to distinguish the recently described genus *Shuja*, which also belongs to the Tropheini, from its former mostly riverine congeners.

Key words: X-ray imaging, landmarks, morphology, cichlid taxonomy

Introduction

Lake Tanganyika—the largest of the East African Rift Lakes by water volume—harbours an outstanding diversity of cichlid fishes, not only in terms of species numbers but also in terms of their phenotypic diversity (Fryer & Iles 1972; Ronco *et al.* 2021; Salzburger *et al.* 2014). The number of cichlid species was recently estimated to be at least 241, of which 208 are nominally described and all but two are endemic to the lake and immediately proximate rivers (Ronco *et al.* 2020). This striking diversity is the product of a massive adaptive radiation, making the cichlid assemblage of Lake Tanganyika a prominent system for various aspects of evolutionary biology and speciation research (Berner & Salzburger 2015; Koblmüller *et al.* 2017; Salzburger *et al.* 2014; Santos *et al.* 2023; Van Steenberge *et al.* 2015; Winkelmann *et al.* 2014). Over the past two decades, numerous phylogenetic and phylogenomic studies have continuously improved our understanding of the evolutionary history of the cichlid adaptive radiation in Lake Tanganyika (Duftner *et al.* 2005; Irisarri *et al.* 2018; Muschick *et al.* 2012; Nishida 1997; Ronco *et al.* 2021; Salzburger *et al.* 2002; Schedel *et al.* 2019; Sturmbauer *et al.* 2003). However, despite a robust phylogenetic placement of almost all taxa, the taxonomic status of several species and genera remains unresolved (Ronco *et al.* 2020). For example, many species are still awaiting formal description, and there are also a handful of known instances of generic misplacement.

A well-documented case of such a generic misplacement is the focal species of this study, '*Gnathochromis*' *pfefferi* (Boulenger 1898). Since the introduction of the genus *Gnathochromis* Poll (1981), it included only its type species *Gnathochromis permaxillaris* (David 1936) and '*Gnathochromis*' *pfefferi*. However, while '*Gnathochromis*' *pfefferi* belongs to the endemic tribe Tropheini which is phylogenetically nested within the Haplochromini (Ronco *et al.* 2020; Salzburger *et al.* 2005), *G. permaxillaris* has repeatedly been demonstrated to be a member of the Limnochromini, a tribe that is morphologically (Takahashi 2003) and genetically clearly distinct from the Tropheini (Nishida 1997; Ronco *et al.* 2021; Salzburger *et al.* 2002; see Figure 1).

'*Gnathochromis*' *pfefferi* was first described as *Paratilapia pfefferi* Boulenger, 1898 and was reallocated to *Limnochromis* (Regan 1920) by Regan (1920) in his endeavour to improve the generic definitions of the cichlid fauna from Lake Tanganyika. He based his taxonomic revision and description of the genus *Limnochromis* on osteological traits, reporting mainly the characteristics of several bony structures from the neurocranium, alongside some features related to scales and teeth. He also introduced a classification of cichlids with respect to the structure of their apophysis at the base of the skull that supports the upper pharyngeal jaw bones, and divided the African cichlids into two groups, *Tilapia*-type and *Haplochromis*-type species. *Limnochromis* was allocated to the *Tilapia*-type. The type names supposedly stem from the genera which acted as a reference for this grouping. Later, Poll (1974) moved '*G.*' *pfefferi* to *Haplochromis* (Hilgendorf 1888) based on its dentition not corresponding with that of *Limnochromis*. About a decade later, however, when erecting the genus *Gnathochromis*, Poll (1981) stated—without any further explanation—that '*G.*' *pfefferi* could not be included into *Haplochromis*. Most probably, he referred to Greenwood (1978), who extended Regan's original classification of cichlids with respect to their pharyngeal apophysis structure. While Greenwood (1978) did not undertake any taxonomic revisions, he came to the same conclusion as Regan (1920) that '*G.*' *pfefferi* did not correspond with the *Haplochromis*-type apophysis. Poll (1974) did not consider the pharyngeal apophysis structure of '*G.*' *pfefferi* when moving it to *Haplochromis*, but apparently accepted Greenwood's view and erected the new genus *Gnathochromis* based on body proportions, dentition, coloration, and their commonality of the protractile mouth, which is more pronounced in *G. permaxillaris* than in '*G.*' *pfefferi*. When Poll (1986) subsequently introduced 12 tribes for all cichlid species known at that time from Lake Tanganyika, he grouped all species formally assigned to the genus *Limnochromis*, including '*G.*' *pfefferi* and *G. permaxillaris*, into the tribe Limnochromini.

Already from the first molecular phylogenetic hypothesis based on the mitochondrial ND2 gene that included '*G.*' *pfefferi* it was evident that '*G.*' *pfefferi* is nested within Tropheini and not related to the Limnochromini (Kocher *et al.* 1995). This was further supported by an analysis of squamation characters, in which '*G.*' *pfefferi* clustered with other Tropheini representatives instead of the Limnochromini (Lippitsch 1998). Lippitsch (1998) stated that '*G.*' *pfefferi* does not show any of the lepidological synapomorphies that characterize the Limnochromini/Ectodini assemblage. However, since '*G.*' *pfefferi* could not be assigned to any of the then established genera of Tropheini, Lippitsch (1998) did not undertake any taxonomic revisions. Additional phylogenetic studies based on mitochondrial DNA (mtDNA) consistently placed '*G.*' *pfefferi* alongside with other Tropheini species while firmly placing *G. permaxillaris* into Limnochromini (Duftner *et al.* 2005; Muschick *et al.* 2012; Nishida 1997; Salzburger *et al.* 2002; Schedel *et al.* 2019; Sturmbauer *et al.* 2003). More recent phylogenetic hypotheses based on nuclear markers (Irisarri *et al.* 2018; Muschick *et al.* 2012) as well as the most recent extensive phylogeny based on whole-genome sequence data (Ronco *et al.* 2021) corroborated these findings. Hence, there is overwhelming and undisputed molecular evidence that '*G.*' *pfefferi* is a member of the Tropheini, and *G. permaxillaris* belongs to the Limnochromini, two cichlid tribes that diverged more than 7 million years ago (Ronco *et al.* 2021).

The tribal misplacement of '*G.*' *pfefferi* was recognized by Takahashi (2003) and he therefore reallocated it to the Tropheini based on the previously conducted mtDNA studies (Nishida 1997; Salzburger *et al.* 2002; Sturmbauer *et al.* 2003) as well as his own cladistic analysis. Alongside '*G.*' *pfefferi*, also its sister species *Shuja horei* (Genner *et al.* 2022) was reallocated from the Haplochromini to the Tropheini by (Takahashi 2003). Note that *Shuja horei* underwent a generic revision only recently and that the genus to which it was previously allocated to (*Ctenochromis*) used to be polyphyletic with several species from different drainages and phylogenetic lineages associated to it (including the Lake Tanganyika Cyphotilapiini; Genner *et al.* 2022).

In this study, we introduce the new genus, *Jabarichromis* **gen. nov.** for '*G.*' *pfefferi* based on the examination of all Tropheini and Limnochromini species described to date. By also including specimens from the Cyphotilapiini in our analyses, alongside species that are (or have long been) associated with the genus *Ctenochromis*, we could identify an additional diagnostic trait—the total number of gill rakers (TGR)—to differentiate *Shuja* from *Ctenochromis* and the species allocated to it prior to the recent revision of this genus.

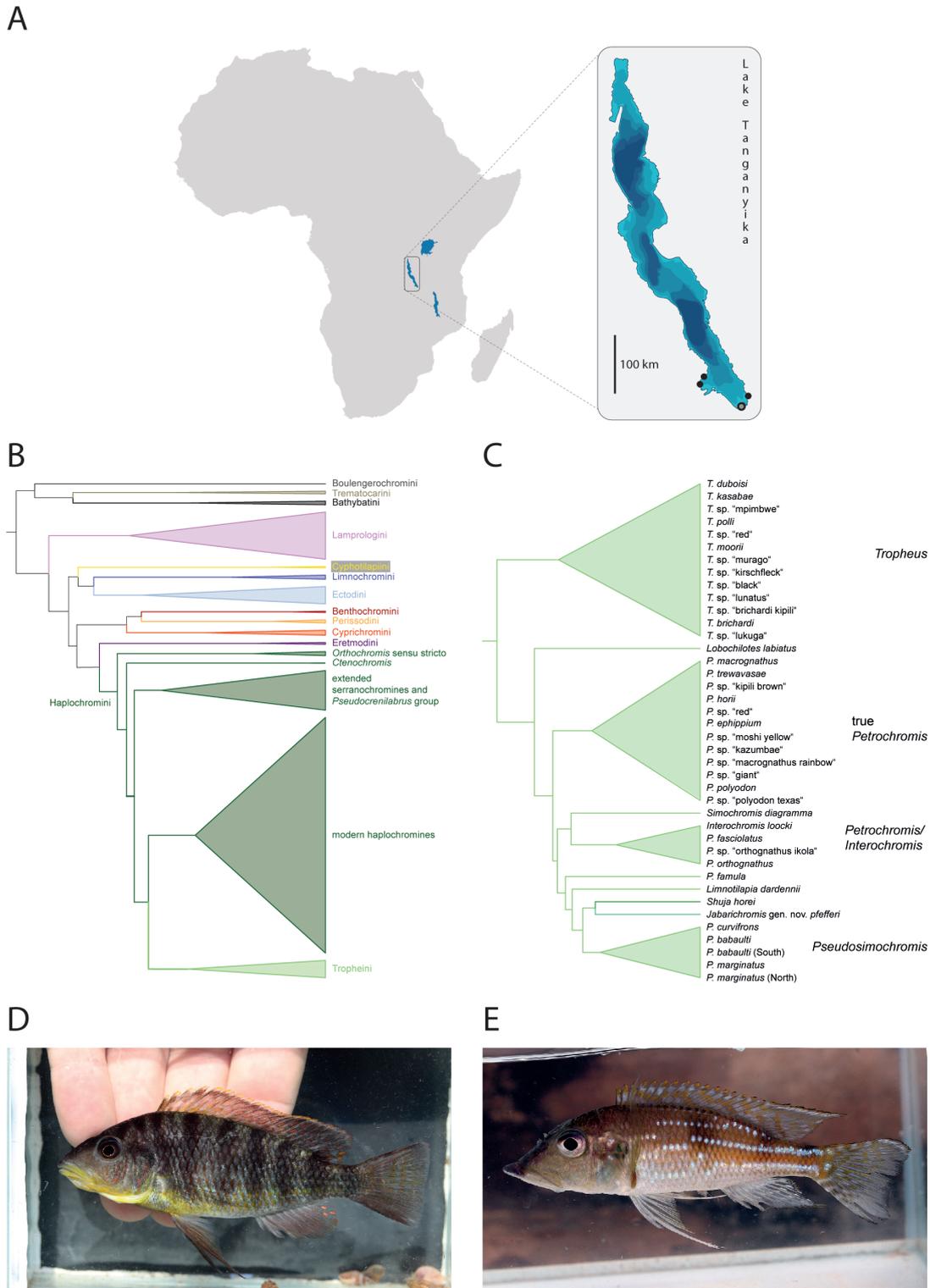
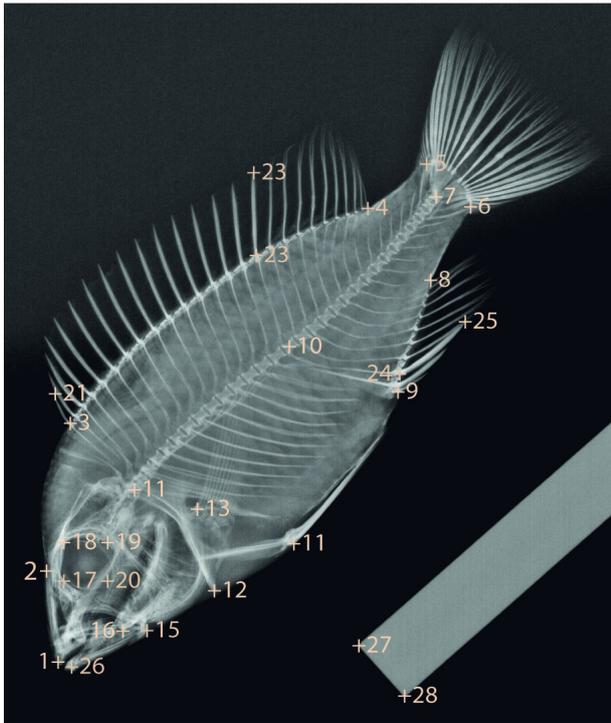


FIGURE 1. Study system. **A** Map of Africa and Lake Tanganyika (Ronco *et al.* 2021) with sampling sites of *Jabarichromis* **gen. nov.** *pfefferi* specimens examined in this study indicated with a black dot. The grey dot with a black lining displays the type locality of the species. **B** Phylogenetic relationships of the cichlid tribes in Lake Tanganyika plus the Haplochromini (topology based on Ronco *et al.* 2021 and Schedel 2020). **C** Species-tree of the Tropheini (based on Ronco *et al.* 2021). Four clades of species have been identified and given a provisional name (indicated on the right). The genus *Petrochromis* is split into three groups, the true *Petrochromis* comprising the genus type species *Petrochromis polyodon*, the other *Petrochromis* species together with *Interochromis* except for *Petrochromis famula*, which stands for its own. **D** Representative specimen of *Jabarichromis* **gen. nov.** *pfefferi* from Kigoma, Tanzania. Picture taken by AI. **E** Representative specimen of *Gnathochromis permaxillaris*, picture taken by Dr. Zuzana Musilová.



- AFL anal fin length
- DFL dorsal fin length
- FDS first dorsal spine length
- LDS last dorsal spine length
- LAS last anal spine length
- AVL abdominal spine length
- CVL caudal spine length
- PDD pre-dorsal distance
- HL head length
- PPeCD pre-dorsal distance
- PAD pre-anal distance
- PPeID pre-pelvic distance
- LJL lower jaw length
- CPL caudal peduncle length

- PMA premaxilla length
- PMH premaxilla height
- SnL snout length
- PML premaxilla length
- ED eye diameter
- BD body depth
- CPD caudal peduncle length
- SL standard length

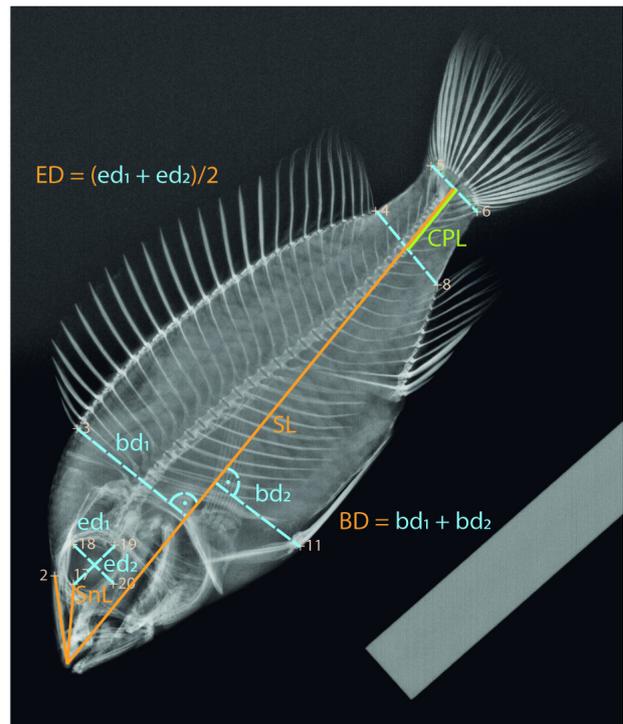
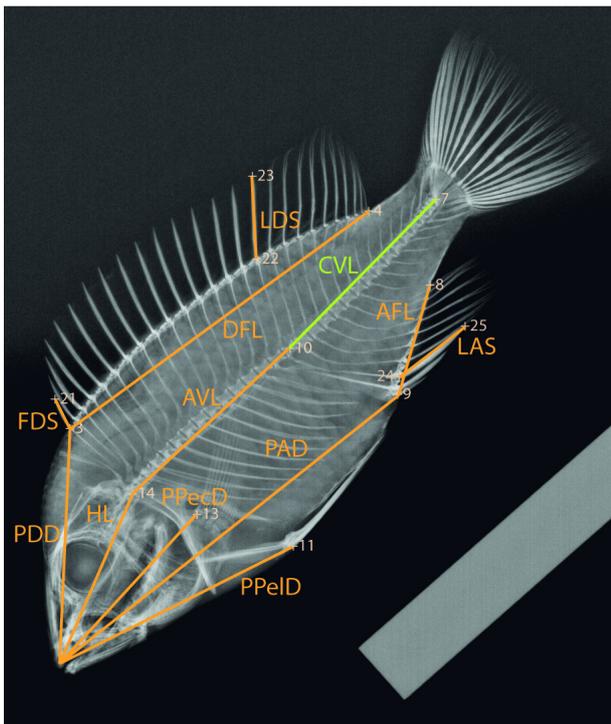


FIGURE 2: X-ray image of a *Jabarichromis* gen. nov. *pfefferi* specimen with the 28 landmarks and their derived measurements used in this study.

TABLE 1. Ranges of diagnostically relevant traits for *Jabarichromis* gen. nov. (see Table 2 for abbreviations) for all taxa belonging to the Tropheini, *G. permaxillaris*, all species included from the Haplochromini and *T. benthicola*. The far-right column indicates the number of individuals inspected per species.

Species	TGR	SHL	SULL	SLDF	SLDFSULL	PercR	HL	PMH in % of HL	LJL in % of SL	PMH in % of SL	PML in % of HL	SL in cm	n
<i>Jabarichromis</i> gen. nov. <i>pfefferi</i>	15 - 18	29 - 31	20 - 23	5 - 6	3	13 - 15	46.37 - 50.6	13.15 - 15.48	56.03 - 61.86	30.17 - 36.08	7.41 - 11.75	10	
<i>Gnathochromis permaxillaris</i>	24 - 27	33 - 34	25 - 30	4 - 5	2 - 3	15 - 16	58.29 - 63.29	15.6 - 17.29	51.09 - 54.84	41.36 - 47.79	10.86 - 13.02	10	
<i>Shuja horei</i>	17 - 19	27 - 30	20 - 23	5 - 7	2	14 - 15	30.5 - 37.21	11.78 - 15.78	50.7 - 57.47	23.06 - 36.05	5.49 - 10.37	10	
<i>Interochromis loocki</i>	13 - 16	29 - 30	23 - 25	5 - 6	2 - 3	15 - 16	20.61 - 25.62	7.08 - 9.81	56.85 - 61.37	22.91 - 32.28	6.38 - 9.79	10	
<i>Limnotilapia dardennii</i>	16 - 17	32 - 34	25 - 27	5 - 7	2 - 3	15 - 16	26.34 - 29.26	7.5 - 8.9	57.06 - 59.46	21.25 - 27.06	6.97 - 18.22	9	
<i>Lobochilotes labiatus</i>	22 - 27	30 - 33	22 - 25	7 - 9	3	16 - 17	36.89 - 49.31	9.4 - 13.37	54.29 - 59.51	23.1 - 33.18	7 - 13.76	9	
<i>Petrochromis ephippium</i>	13 - 16	31 - 33	24 - 25	7	3	15 - 16	22.8 - 24.64	5.28 - 6.92	59.53 - 62.51	28.68 - 35.18	7.27 - 12.49	9	
<i>Petrochromis famula</i>	14 - 19	29 - 33	22 - 24	4 - 7	3	14 - 16	16.06 - 24.07	6.26 - 8.97	59.39 - 63.55	32.4 - 37.41	6.65 - 13.19	10	
<i>Petrochromis fasciolatus</i>	16 - 18	30 - 32	23 - 25	5 - 6	3	15 - 16	16.84 - 20.32	8.11 - 10.1	59.67 - 63.46	30.68 - 38.27	6.85 - 13.99	10	
<i>Petrochromis horii</i>	14 - 17	30 - 34	23 - 25	7 - 9	3 - 4	15 - 16	17.11 - 19.6	6.14 - 7.7	59.53 - 63.03	27.28 - 35.45	7.24 - 9.1	10	
<i>Petrochromis macrognathus</i>	15 - 17	31 - 34	23 - 26	5 - 8	3 - 4	16 - 17	23.85 - 28.05	5.94 - 7.21	57.98 - 61.04	30.32 - 36.19	10.16 - 16.23	10	
<i>Petrochromis orthognathus</i>	16 - 20	29 - 31	22 - 23	5 - 7	2 - 3	14 - 16	19.65 - 25.43	6.28 - 8.17	60.97 - 63.35	26.05 - 32.46	7.24 - 10.17	10	
<i>Petrochromis polyodon</i>	14 - 18	28 - 32	22 - 24	5 - 7	2 - 3	15 - 17	22.21 - 26.2	5.75 - 7.97	55.79 - 59.26	31.22 - 40.68	6.55 - 13.78	9	
<i>Petrochromis</i> sp. "giant"	16 - 18	33 - 35	24	7 - 8	3 - 4	16 - 17	23.48 - 24.16	5.66 - 6.55	60.32 - 61.77	34.23 - 36.16	15.95 - 20.32	3	
<i>Petrochromis</i> sp. "kazumbae"	13 - 17	31 - 33	21 - 25	5 - 8	3	15 - 16	20.76 - 24.24	5.27 - 7.58	58.82 - 60.57	28.48 - 38.93	8.16 - 15.19	10	
<i>Petrochromis</i> sp. "kipili brown"	14 - 17	31 - 35	24 - 27	7 - 11	3 - 4	15 - 16	18.16 - 20.83	5.73 - 6.9	61.48 - 65.04	30.89 - 34.74	9.81 - 18.12	10	
<i>Petrochromis</i> sp. "macrognathus rainbow"	13 - 19	32 - 35	23 - 26	6 - 8	3	15 - 16	21.42 - 26.16	5.78 - 8.25	59.35 - 62.08	30.27 - 36.64	13.29 - 17.5	10	
<i>Petrochromis</i> sp. "moshi yellow"	12 - 16	31 - 34	21 - 25	6 - 8	3	14 - 16	20.59 - 23.9	5.93 - 6.92	58.89 - 62.9	34.69 - 38.3	11.49 - 15.39	10	
<i>Petrochromis</i> sp. "orthognathus ikola"	17 - 20	29 - 31	21 - 24	5 - 7	2 - 3	15 - 16	20.01 - 25.28	6.31 - 7.67	59.59 - 63.43	23.99 - 31.75	8.93 - 13.35	10	
<i>Petrochromis</i> sp. "polyodon texas"	15 - 17	31 - 34	20 - 27	5 - 8	3	15 - 17	21.39 - 26.43	5.4 - 6.4	58.87 - 61.61	34.47 - 38.27	12.87 - 21.8	10	
<i>Petrochromis</i> sp. "red"	12 - 16	30 - 34	23 - 25	6 - 7	2 - 3	15 - 16	12.99 - 19.7	6.29 - 8.33	59.43 - 63.75	35.96 - 40.14	10.33 - 16.83	10	
<i>Petrochromis trewavasae</i>	13 - 18	31 - 32	23 - 25	6 - 9	3	15 - 16	18.66 - 23.6	5.68 - 9.95	60.44 - 63.52	34.3 - 40.04	9.21 - 14.06	10	
<i>Pseudosimochromis babaulti</i>	9 - 13	27 - 30	21 - 24	4 - 5	2	15 - 16	22.82 - 26.03	7.05 - 8.63	58.53 - 61.68	18.79 - 22.74	4.95 - 6.45	10	
<i>Pseudosimochromis babaulti</i> (South)	9 - 14	29 - 30	21 - 24	4 - 6	2	16	22.58 - 28.43	6.22 - 7.7	57.58 - 62.87	20.88 - 26.85	5.55 - 7.94	10	
<i>Pseudosimochromis curvifrons</i>	14 - 17	29 - 31	21 - 25	4 - 6	2 - 3	14 - 17	33.34 - 36.33	5.86 - 7.53	63.56 - 68.77	15.31 - 18	7.12 - 9.45	10	

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TABLE 1. (Continued)

Species	TGR	SHL	SULL	SLDF	SLDSULL	PercR	PMH in % of HL	LJL in % of SL	PMH in % of SL	PML in % of HL	SL in cm	n
<i>Pseudosimochromis marginatus</i>	12-15	28-30	22-24	4-5	2	16-17	21.34 - 24.97	6.35 - 8.99	57.53 - 61.2	18.7 - 25.67	5.24 - 7.68	10
<i>Pseudosimochromis marginatus</i> (North)	11-15	28-30	21-23	4-5	2	16	22.04 - 25.39	6.77 - 9.12	58.01 - 64.68	19.07 - 22.17	5.44 - 8.55	10
<i>Simochromis diagramma</i>	13-18	29-32	22-25	5-6	2-3	16-17	25.08 - 29.61	7.02 - 8.51	59.15 - 64.25	18.32 - 28.13	6.42 - 11.93	10
<i>Tropheus brichardi</i>	14-17	28-30	22-23	5-6	1-2	16	25.95 - 31.78	6.41 - 7.2	64.45 - 68.47	13.46 - 19.14	4.62 - 6.82	10
<i>Tropheus duboisi</i>	11-16	30-33	22-23	4-6	1	15	30.08 - 34.05	7.29 - 8.6	64.06 - 67.79	15.51 - 21.12	6.27 - 9.66	10
<i>Tropheus kasabae</i>	14-17	29-31	22-25	4-6	1-2	15-16	20.16 - 37.68	4.75 - 10.05	63.78 - 66.53	16.63 - 27.84	5.73 - 8.06	11
<i>Tropheus moorii</i>	14-18	30-31	21-23	4-6	2	14-16	26.09 - 29.96	5.28 - 7.11	65.1 - 67.79	16.64 - 22.13	6.55 - 8.39	10
<i>Tropheus polli</i>	14-16	30-32	23-24	5-7	2-3	15-16	28.08 - 31.76	5.89 - 7.61	66.6 - 70.28	14.39 - 20.29	6.8 - 9.09	10
<i>Tropheus</i> sp. "black"	15-17	29-30	21-25	4-6	1-2	16-17	25.39 - 28.58	5.56 - 7.16	62.82 - 67.01	15.47 - 20.16	4.16 - 7.67	10
<i>Tropheus</i> sp. "brichardi kipili"	14-17	29-30	22-23	4-7	1-2	14-16	27.9 - 31.84	5.74 - 6.92	64.53 - 68.85	10.76 - 16.01	6.21 - 9.54	10
<i>Tropheus</i> sp. "kirschfleck"	14-17	29-30	23-25	5-6	1-2	16-17	26.16 - 29.88	5.32 - 7.48	65.31 - 68.85	14.82 - 20.01	6.64 - 8.87	10
<i>Tropheus</i> sp. "lukuga"	14-16	29-30	22-24	4-6	2	16	25.29 - 31.44	6.78 - 8.09	64.82 - 67.69	15.36 - 18.39	6.89 - 9.41	10
<i>Tropheus</i> sp. "lunatus"	14-16	20-30	22-24	5-7	2-3	16-17	27.75 - 30.64	5.54 - 8.25	65.36 - 68.49	16.35 - 18.43	6.59 - 8.84	10
<i>Tropheus</i> sp. "mpimbwe"	14-16	30-31	22-24	5-7	2	15	27.19 - 33.1	4.55 - 7.43	64.5 - 67.76	15.95 - 19.55	8.11 - 10.76	10
<i>Tropheus</i> sp. "murago"	14-16	29-32	23-24	5-6	2	14-16	27.54 - 31.79	5.64 - 10.1	64.91 - 69.57	14.93 - 19.19	7.69 - 10.69	10
<i>Tropheus</i> sp. "red"	14-17	29-31	22-23	3-5	2	15-16	27.09 - 30	5.91 - 9.52	65.79 - 70.38	12.34 - 18.54	7.45 - 8.67	10
<i>Ctenochromis pectoralis</i>	10-13	24-29	18-21	3-7	1-2	13-14	26.05 - 30.96	10.33 - 13.07	50.07 - 53.44	24.38 - 35.38	4.43 - 6.72	7
<i>Haplochromis cf. bakongo</i>	11-14	24-29	19-21	3-5	1-2	14	30.24 - 36.18	10.43 - 14.83	50.67 - 55.09	25.52 - 38.15	4.2 - 5.39	4
<i>Haplochromis demeusii</i>	10-13	24-25	16-19	3-5	1-2	14-16	29.92 - 37.77	11.03 - 14.34	51.79 - 59.63	25.04 - 34.57	3.85 - 7.31	11
<i>Haplochromis cf. demeusii</i>	12	24-26	18-19	4	2	14-15	33.95 - 35.82	12.61 - 12.85	56.38 - 56.95	30.21 - 35.26	6.71 - 7.14	2
<i>Haplochromis fasciatus</i>	11-14	24-28	16-21	4-5	1-2	13-14	29.31 - 37.88	8.02 - 13.62	53.14 - 59.7	25.5 - 33.04	3.51 - 9.46	8
<i>Haplochromis lutuae</i>	11-16	25-26	18-20	4-5	1-2	14-16	27.73 - 34.52	10.53 - 12.29	51.48 - 54.78	18.11 - 29.62	2.95 - 6.29	9
<i>Haplochromis oligacanthus</i>	11-14	24-26	18-20	4-5	1-2	14-15	28.4 - 36.92	13.49 - 14.89	52.29 - 54.56	25.44 - 32.05	3.85 - 5.71	7
<i>Haplochromis polli</i>	12-16	26-27	19-20	4-5	2	15-17	30.93 - 37.79	10.74 - 11.75	54.18 - 60.18	28.6 - 40.38	4.45 - 7.76	6
<i>Haplochromis cf. polli</i>	11-16	25-28	19-22	3-5	1-2	12-17	31.27 - 38.36	10.42 - 11.76	55.79 - 60.53	26.23 - 35.54	4.68 - 8.03	8
<i>Trematochromis benthicola</i>	16-17	30-33	22-27	7-8	2-3	14-15	44.49 - 50.32	15.27 - 18.18	54.01 - 57.8	33.94 - 48.7	10.28 - 12.97	13

Specimens and methods

Comparative material. To provide a thorough diagnosis for the new genus *Jabarichromis* **gen. nov.**, we compared it to all other members of the tribe Tropheini as well as to its former congener and all other members of the tribe Limnochromini. In total we examined 587 specimens belonging to 63 taxa that include all currently recognised species as well as undescribed taxa representing potential species from these two tribes (Ronco *et al.* 2020).

To evaluate possible diagnostic characters to distinguish *Shuja* from *Ctenochromis*, we further inspected specimens from all species that are associated with *Ctenochromis* (i.e., *Ctenochromis pectoralis* Pfeffer 1893), or were formerly associated with *Ctenochromis* before the recent revision by Genner *et al.* (2022): *Haplochromis bakongo* (Thys van den Audenaerde 1964), *Haplochromis demeusii* (Boulenger 1899), *Haplochromis fasciatus* (Perugia 1892), *Haplochromis luluae* (Fowler 1930), *Haplochromis oligacanthus* Regan 1922, *Haplochromis polli* Thys van den Audenaerde 1964. In addition to these riverine Haplochromines, we also inspected specimens of the species *Trematichromis benthicola* (Matthes 1962), formally '*Ctenochromis*' *benthicola*, which is endemic to Lake Tanganyika and is a member of the Cyphotilapiini (Muschick *et al.* 2012). We further included all taxa of the Cyphotilapiini to cover the morphological diversity of this tribe.

All examined specimens from Lake Tanganyika (i.e., all Tropheini, Limnochromini and Cyphotilapiini) are deposited in the Ichthyological collection of the Zoological Institute of the University of Basel, Switzerland (UNIBAS-IC). The specimens belonging to the Haplochromini are either deposited in the Royal Museum for Central Africa (RMCA) Tervuren, Belgium or in the Bavarian State Collection of Zoology (SNSB ZSM), Munich, Germany. It should be mentioned that we were unable to include the holotype of *Jabarichromis* **gen. nov.** *pfefferi*. Instead, we examined 10 specimens of this species available in the Ichthyological collection in Basel. All specimens investigated in this study are listed in the comparative material table in the supplement.

Morphological data collection and principal component analysis. In total, 33 meristic traits were scored (see Table 2; following Schedel & Schliewen 2017 and Schedel *et al.* 2020), of which 16 were obtained from digital X-ray images. X-rays of the specimens from Munich were newly acquired using a Faxitron Ultrafocus LLC X-ray unit, while X-rays from the specimens from Basel were taken from Ronco *et al.* (2021). The other 17 meristic traits were investigated on the specimens themselves using Leica microscopes.

In addition, we collected 23 morphometric measurements (Figure 2, Table 2) based on the X-rays by placing 26 landmarks on defined anatomical sites (modified from Ronco *et al.* 2021) in Fiji (v.2.3.0/1.53t, Schindelin *et al.* 2012). Two additional landmarks were used as a scale reference. With a total of 28 landmarks, we could obtain landmark coordinates scaled in cm and, thus, to measure the distance between individual landmarks as well as the premaxilla angle. The morphometric traits were size corrected by either the standard length or the head length (see Table 2). We performed a Procrustes alignment to screen for landmark outliers. All calculations were performed in R v.4.1.3 (R Development Core Team 2018) using the package geomorph (v.4.0.3, Adams & Otárola-Castillo 2013). We then performed a Principal Component Analysis (PCA) across all 45 meristic and morphometric traits and 518 individuals belonging to the Tropheini, Limnochromini and Haplochromini 26 specimens had to be excluded for the PCA because we were not able to collect data on all traits All plots were generated in R (v.4.1.1).

Results

The PCA, which included 518 individuals, 26 meristic and 19 morphometric characters showed a clear morphological clustering of the tribes and the major phylogenetic lineages within the Tropheini (Figure 3). PC1 explained 30%, PC2 16.9% and PC3 12.9% of the total variance. Although the Limnochromini comprise fewer taxa, their morphospace (PC1 and PC2) has a similar extent compared to the Tropheini. The morphospace occupied by the (riverine) Haplochromini representatives is relatively large compared to the other two tribes, especially considering that our dataset comprises only seven species of Haplochromini (excluding the Tropheini). These species are, however, phylogenetically distant from each other (see Figure 1).

PC1 clearly separated the genus *Tropheus*, the remaining Tropheini and the Limnochromini. The highest loading score for PC1 was dorsal fin length (DFL, Figure 3). Further traits which were associated with the dorsal fin are the number of dorsal spines (DFS) and the count value of the vertebra associated with the last dorsal spine (VDPS). The two latter featured the fourth- and fifth-highest loading scores for PC1. PC2 separated the (riverine) Haplochromini

from the other two tribes. The highest loading scores for PC2 were the number of total vertebrae (TV), the number of scales on the horizontal line (SHL), and the number of abdominal vertebrae (AV).

Jabarichromis **gen. nov.** *pfefferi* clustered with other Tropheini but is closer to Limnochromini than most other Tropheini representatives. Specimens of *Jabarichromis* **gen. nov.** *pfefferi* overlap in morphospace with its sister species, *S. horei*, but are clearly separated from its former congener *G. permaxillaris* along PC1. Our results based on the combination of morphometric measurements and meristic counts indicate a separation of the Tropheini from the Limnochromini including *Jabarichromis* **gen. nov.** from its former congener *G. permaxillaris*. Consequently, we used the quantified traits as basis for the diagnosis of a new genus, *Jabarichromis* **gen. nov.** (see Figure 4A, 4B, and Table 1).

Furthermore, *S. horei* slightly overlaps in morphospace with the (riverine) Haplochromini (Figure 3) but can clearly be separated by a larger number of gill rakers (TGR) in *S. horei* (Figure 5A). In addition, *S. horei* can be distinguished from its former congener within the Cyphotilapiini (*T. benthicola* formerly '*C.*' *benthicola*) by a higher premaxilla (PMH) in *T. benthicola* (Figure 5B).

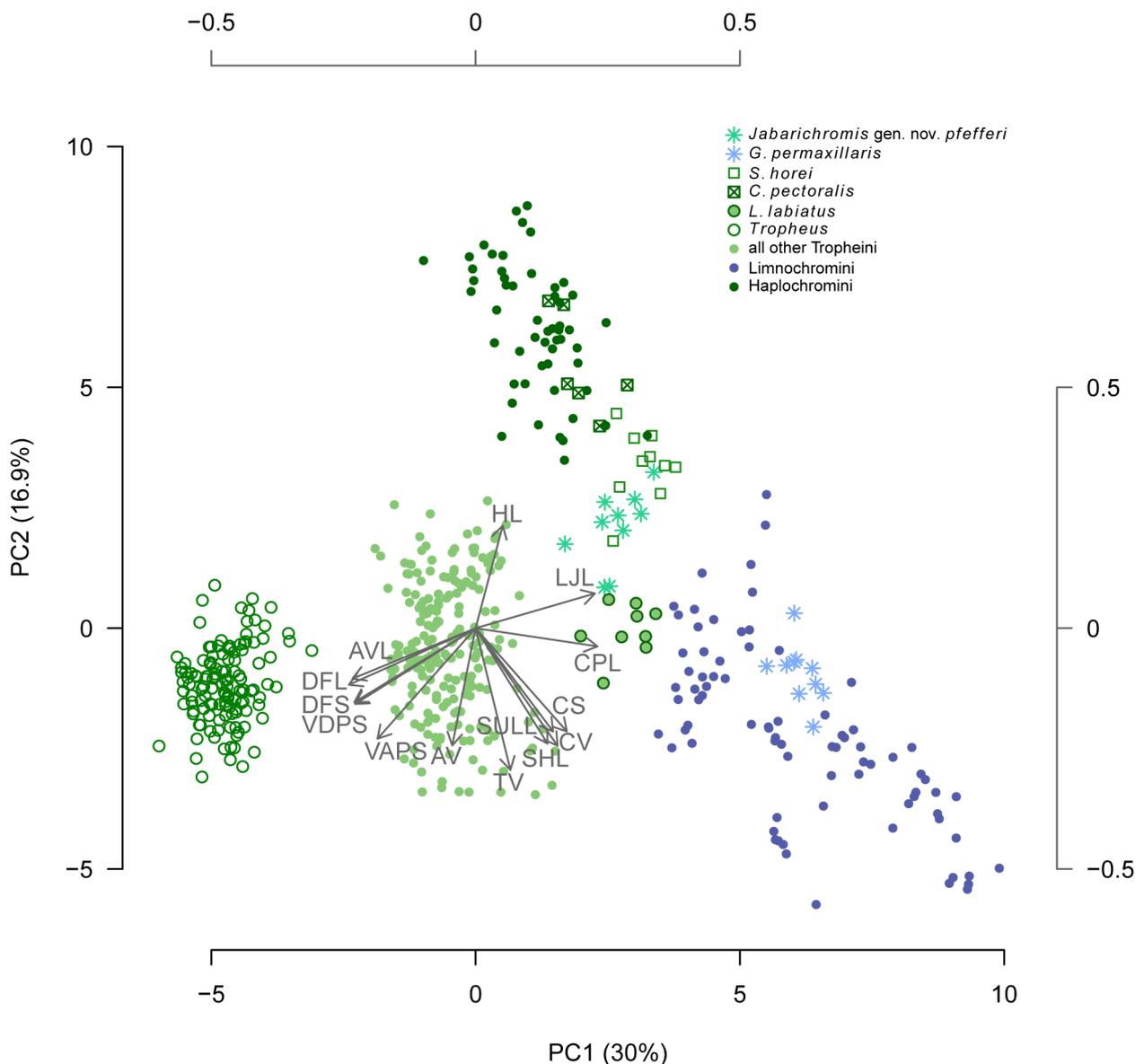


FIGURE 3. PCA plot of PC1 and PC2 based on 518 individuals, 26 meristic and 19 morphometric characters. The 6 highest loading scores for PC1 and the 8 highest loading scores for PC2 are indicated as vectors (top and right axes of the plot).

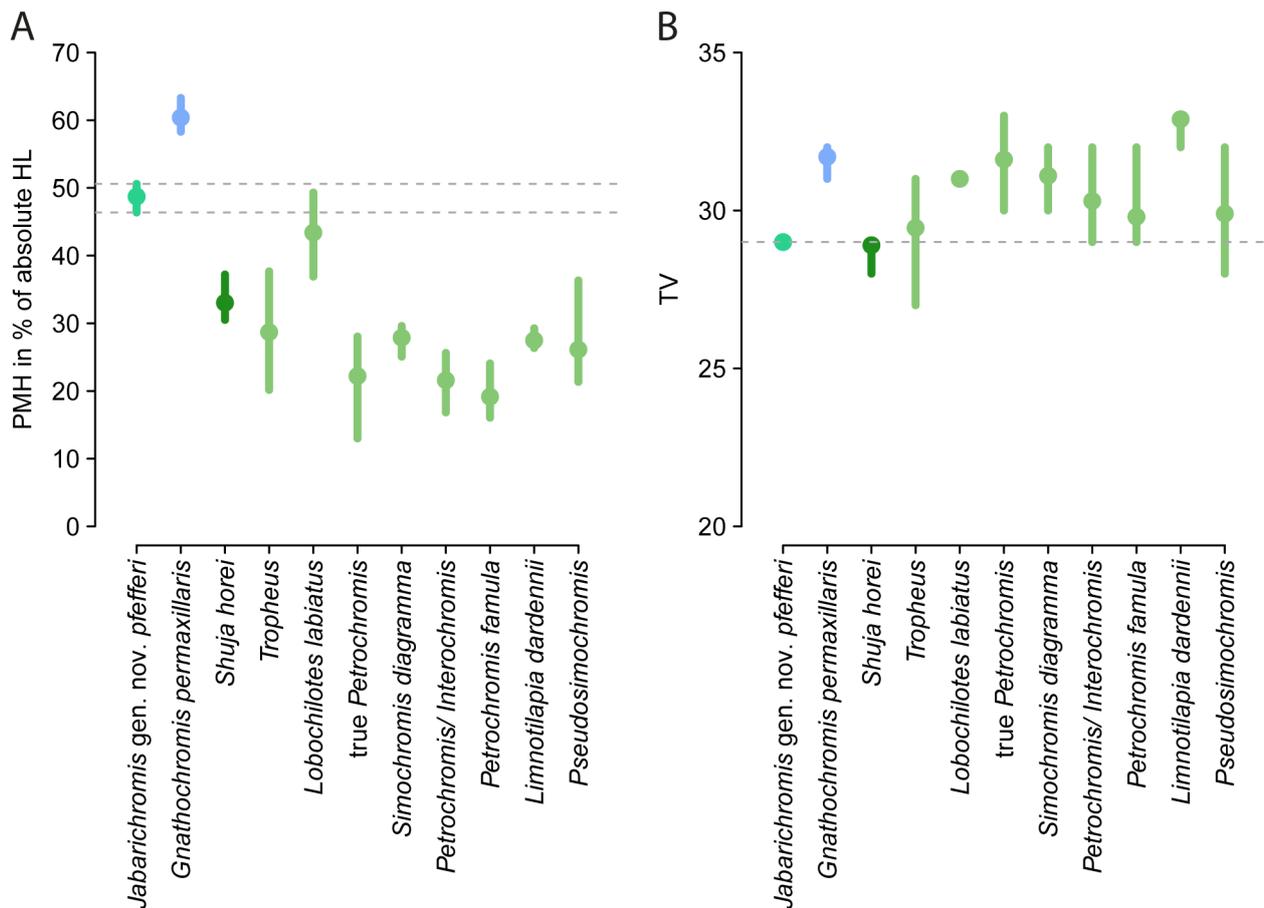


FIGURE 4. Range plot for (A) the premaxilla height (PMH) and (B) the total number of vertebra (TV). Data points are mean counts of the group and error bars show the range of the observed values (minimum and maximum). Horizontal lines indicate the range of observed values of *Jabarichromis gen. nov. pfefferi*, highlighting that (A) the observed range of PMH is clearly outside the distributions of the other Tropheini (except *Lobochilotes labiatus*) and *Gnathochromis permaxillaris* and (B) the observed range is clearly outside the distributions of *Gnathochromis permaxillaris* and *Lobochilotes labiatus*. See Figure 1 for group specification along the x-axis.

TABLE 2. Abbreviations for all measurements and counts used in this study. Traits that were quantified from X-ray images are marked with an (X) all other traits were obtained directly from the specimen. For each morphometric trait it is further indicated if they were size corrected to standard length (% SL) or absolute head length (% HL). Loading scores of PC1, PC2 and PC3 based on 518 individuals. Highest scores are indicated in bold font.

Abbreviation	Measurement/ count	PC1	PC2	PC3
AV	number of abdominal vertebrae (X)	-0.0441	-0.2435	-0.2363
CV	number of caudal vertebrae (X)	0.1468	-0.2146	0.0487
TV	total number of vertebrae (X)	0.0658	-0.2941	-0.1205
AFS	number of anal-fin spines (X)	-0.1959	-0.0866	0.1919
AFR	number of anal-fin rays (X)	0.1651	-0.0839	-0.1596
DFS	number of dorsal-fin spines (X)	-0.2295	-0.1537	-0.0044
DFR	number of dorsal-fin rays (X)	0.2106	0.0409	-0.1358
nPt12	number of pterygiophores between 1. and 2. neural spine (X)	0.0197	0.0671	-0.0056
nPt23	number of pterygiophores between 2. and 3. neural spine (X)	-0.0217	-0.0770	-0.0004

..... Continued on the next page

TABLE 2. (Continued)

Abbreviation	Measurement/ count	PC1	PC2	PC3
VDPS	vertebra number associated with last dorsal-fin spine pterygiophore (X)	-0.2279	-0.1573	-0.0059
VAPS	vertebra number associated with last anal-fin spine pterygiophore (X)	-0.1856	-0.2295	-0.0185
GRL	number of gill rakers on the ventral gill arch	0.0872	-0.2051	-0.0233
GRM	number of gill rakers in the center of the gill arch	-0.0042	0.0094	-0.0477
GRU	number of upper gill rakers on the dorsal arch	0.2107	-0.0785	0.0956
TGR	total number of gill rakers	0.1562	-0.1755	0.0248
SC	number of cheek scales	-0.0882	-0.0463	-0.1396
SO	number of operculum scales	-0.0452	0.0502	-0.0401
SHL	number of scales on horizontal line	0.1551	-0.2442	-0.0101
SULL	number of scales on upper lateral line	0.1361	-0.2396	0.0051
SLLL	number of scales on lower lateral line	0.1833	-0.1921	-0.0076
CS	number of scales around caudal peduncle	0.1727	-0.2144	-0.0379
ScRLL	number of scale rows between lateral lines	0.1138	-0.0991	0.0209
SLDF	number of scales between lateral line and dorsal-fin origin	0.0167	-0.1576	-0.2504
SLDSULL	number of scales between lateral line and last dorsal-fin spine	0.1400	-0.1957	-0.1808
ISTUJ	number of inner series of teeth upper jaw	-0.1307	-0.0886	-0.2968
ISTLJ	number of inner series of teeth lower jaw	-0.1002	-0.0844	-0.3260
PercR	number of pectoral rays	-0.0629	-0.1761	-0.0277
PMH	premaxilla height (% HL; X)	0.1277	0.0040	0.1853
LJL	lower jaw length (% SL; X)	0.2259	0.0722	0.1176
PDD	predorsal distance (% SL; X)	-0.0984	0.1321	0.0148
HL	head length (% SL; X)	0.0513	0.2129	-0.0977
PPecD	prepectoral distance (% SL; X)	0.1683	0.1577	-0.1897
PAD	preanal distance (% SL; X)	-0.0001	0.1692	-0.3132
PPelD	prepelvic distance (% SL; X)	0.0354	0.1835	-0.3069
DFL	dorsal-fin length (% SL; X)	-0.2399	-0.1175	0.0361
AVL	abdominal spine length (% SL; X)	-0.2331	-0.1049	-0.0260
CVL	caudal spine length (% SL; X)	0.0829	-0.1376	0.2725
AFL	anal-fin length (% SL; X)	-0.1812	-0.1430	0.1889
CPL	caudal peduncle length (% SL; X)	0.2305	-0.0378	0.0655
ED	eye diameter (% HL; X)	0.0902	0.0320	0.2161
SnL	snout length (% HL; X)	-0.1870	-0.1366	-0.0102
PML	premaxilla length (% HL; X)	0.2049	-0.0243	-0.1853
BD	body depth (% SL; X)	-0.2147	-0.0096	-0.1390
CPD	caudal peduncle depth (% SL; X)	-0.0294	0.1910	-0.0851
PMA	premaxilla angle (X)	-0.1420	0.0102	0.0987
	Eigenvalue	3.6773	2.7545	2.4101
	% variance	30.05	16.86	12.91

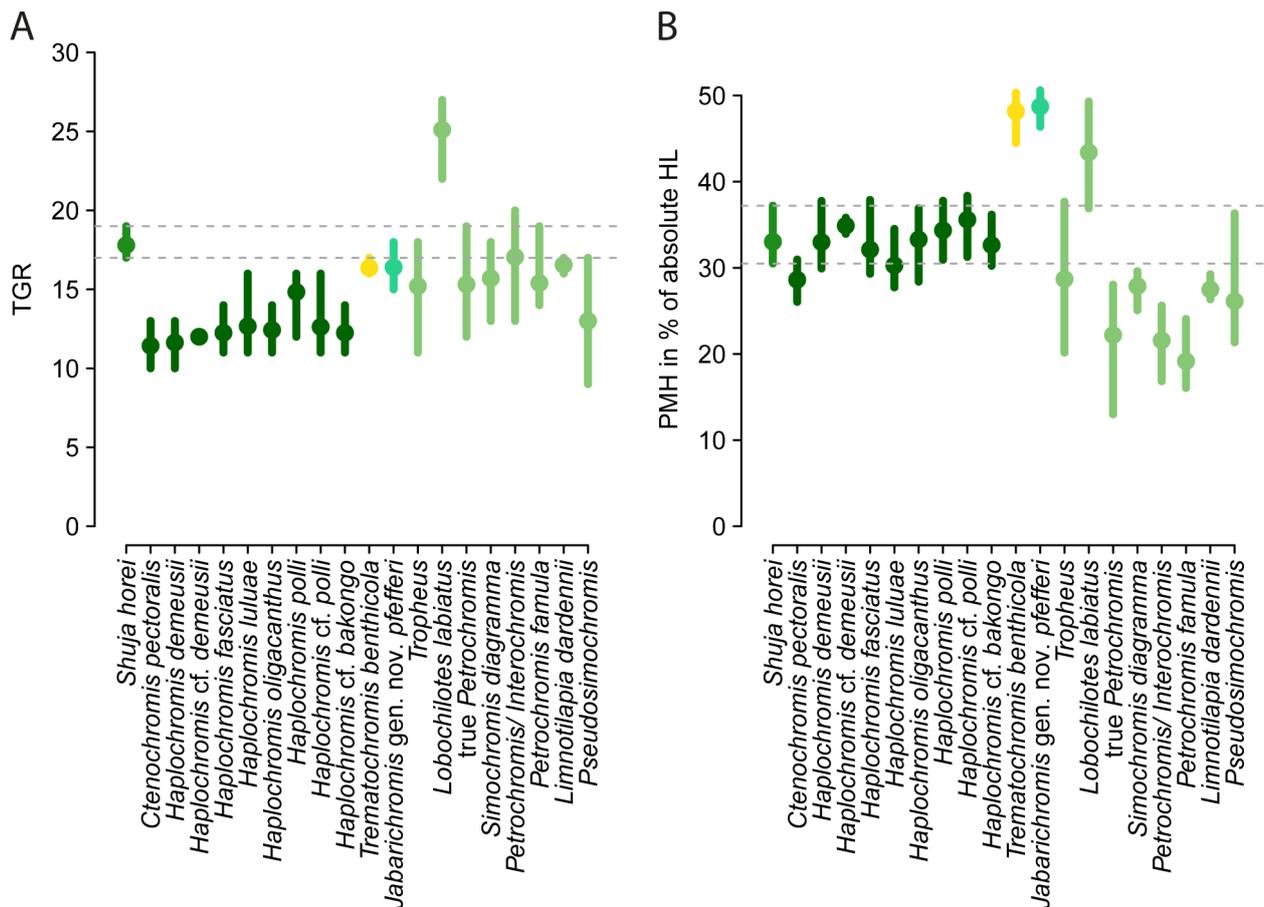


FIGURE 5. Range plot for (A) the total number of gill rakers (TGR) and (B) the premaxilla height (PMH). Data points are mean counts of the group and error bars show the range of the observed values (minimum and maximum). Horizontal lines indicate the range of observed values of *Shuja horei*, highlighting that (A) the observed range of TGR is clearly outside the distributions of the other species (formerly) associated with *Ctenochromis* (except *Trematochromis benthicola*), and (B) the observed range of PMH is clearly outside the distributions of *Trematochromis benthicola* and *Jabarichromis gen. nov. pfefferi*. See Figure 1 for group specification along the x-axis.

Taxonomy

Phylum Chordata Haeckel, 1874

Class Actinopterygii sensu Goodrich, 1930

Order Cichliformes Betancur-R *et al.* 2013

Family Cichlidae Bonaparte, 1840

Subfamily Pseudocrenilabrinae Fowler, 1934

Tribe Tropheini Poll, 1986

Genus *Jabarichromis gen. nov.*

Type Species. *Paratilapia pfefferi* (Boulenger 1898)

Diagnosis. *Jabarichromis* **gen. nov.** can be identified as a member of the Tropheini, which are nested within the Haplochromini (Ronco *et al.* 2021; Salzburger *et al.* 2005), by the definition from Takahashi (2003): “extensively granulated cycloid scales at midbody (granulations comprising irregularly arranged, variously shaped protrusions over almost entire exposed surface)”. A revision or specification of this definition is needed because all our specimens show additional scales with small ctenii along the midbody, increasing in numbers towards the ventral and posterior side. This state for *Jabarichromis* **gen. nov. pfefferi** was also reported by Genner *et al.* (2022). Further, ctenoid scales along the midbody for species belonging to the Tropheini were reported by Viertler *et al.* (2021).

Jabarichromis **gen. nov.** can be distinguished from the other genera within the Tropheini by their longer premaxilla height (except *Lobochilotes* Boulenger 1915) as well as their longer lower jaw length (except *Lobochilotes* and *Shuja*). It is distinguishable from *Lobochilotes* by the total number of vertebrae (29 in *Lobochilotes* and 30 in *Jabarichromis* **gen. nov.**), the total number of gill rakers (22–27 in *Lobochilotes* and 15–18 in *Jabarichromis* **gen. nov.**), the number of scales between the upper lateral line and the dorsal fin origin (7–9 in *Lobochilotes* and 5–6 in *Jabarichromis* **gen. nov.**), and the number of pectoral rays (16–17 in *Lobochilotes* and 13–15 in *Jabarichromis* **gen. nov.**). Further, it is distinguishable from *Shuja* by the number of scales between the upper lateral line and the last dorsal fin spine (2 in *Shuja* and 3 in *Jabarichromis* **gen. nov.**).

Finally, *Jabarichromis* **gen. nov.** is distinguishable from *Gnathochromis* and its only remaining member *G. permaxillaris* by the premaxilla height (58%–63% in head length in *G. permaxillaris* and 46%–51% of head length in *Jabarichromis* **gen. nov. pfefferi**), dorsal fin length (DFL) (51%–55% in standard length in *G. permaxillaris* and 56%–61% of standard length in *Jabarichromis* **gen. nov. pfefferi**), premaxilla length (41%–48% in head length in *G. permaxillaris* and 30%–36% of head length in *Jabarichromis* **gen. nov. pfefferi**), the number of total vertebrae (31–31 in *G. permaxillaris* and 29 in *Jabarichromis* **gen. nov. pfefferi**), the number of total gill rakers (24–27 in *G. permaxillaris* and 15–18 in *Jabarichromis* **gen. nov. pfefferi**), the number of scales on horizontal line (33–34 in *G. permaxillaris* and 29–31 in *Jabarichromis* **gen. nov. pfefferi**), and number of scales on upper lateral line (25–30 in *G. permaxillaris* and 20–23 in *Jabarichromis* **gen. nov. pfefferi**).

Description. *Jabarichromis* **gen. nov.** currently comprises one species, *Jabarichromis* **gen. nov. pfefferi**, which is endemic to Lake Tanganyika. The premaxilla height reaches 46%–51%, the lower jaw length 13%–15% and the premaxilla length ranges from 30%–36% of head length; the dorsal fin length ranges from 56%–62% of the standard length. The number of vertebrae is 29 (14–15 abdominal, 14–15 caudal); the total number of gill rakers ranges from 15–18; the number of scales between the upper lateral line and the dorsal fin origin ranges from 5–6; the number of scales between the upper lateral line and last dorsal fin spine is 3. The number of scales on the horizontal line ranges from 29–31 and the number of scales on the upper lateral line reaches from 20–23. The number of pectoral rays is 13–15. Like all members of the Tropheini *Jabarichromis* **gen. nov.** are mouthbrooders (Konings 2019; Takahashi 2003). The total length can reach up to 14 cm (Konings 2019).

Etymology. The genus name is derived from the Swahili word “Jabari” which is translated into English as “brave one” or “emperor”, “ruler”. It is referring to *Jabarichromis* **gen. nov. pfefferi**’s hunting behaviour as well as their large hunting territories which can reach up to 500m² (Konings 2019). “Chromis” is an Ancient Greek word for fish and refers to a widely used suffix for cichlid genera. The gender of *Jabarichromis* **gen. nov.** is masculine.

Included species. *Jabarichromis pfefferi* (Boulenger 1898)

Paratilapia pfefferi Boulenger, 1898

Limnochromis pfefferi (Boulenger), Regan, 1920

Haplochromis pfefferi (Boulenger), Poll, 1974

Gnathochromis pfefferi (Boulenger), Poll, 1981

Additional diagnostic characters for *Shuja horei*

Genner *et al.* (2022) erected the genus *Shuja* for *S. horei* to separate it from *Ctenochromis* and the other Tropheini. They pointed out the uniqueness of a prognathous lower jaw in *S. horei* compared to the other Tropheini with either a retrognathous or isognathous lower jaw. We can extend this diagnosis as we found that *S. horei* differs from its prior congeners in *Ctenochromis* also in their number of gill rakers (TGR) (Figure 5A), which is higher in *S. horei*. Further, it differs in their relative premaxilla height (PMH) from its sister species *Jabarichromis* **gen. nov. pfefferi** as well as from *Trematochromis benthicola*, which also used to be associated with *Ctenochromis* (Figure 5B).

Discussion

In this study, we erected a new genus *Jabarichromis* **gen. nov.** for '*Gnathochromis* *pfefferi*'. This ensures that the taxonomic status represents the evolutionary history of *Jabarichromis* **gen. nov.** *pfefferi*, which was consistently resolved as member of the Tropheini instead of the Limnochromini in phylogenetic studies (Duftner *et al.* 2005; Irisarri *et al.* 2018; Kocher *et al.* 1995; Lippitsch 1998; Muschick *et al.* 2012; Nishida 1997; Ronco *et al.* 2021; Salzburger *et al.* 2002; Schedel *et al.* 2019; Sturmbauer *et al.* 2003; Takahashi 2003). *Jabarichromis* **gen. nov.** *pfefferi* hereby constitutes not only the type species for *Jabarichromis* **gen. nov.** but also the only species contained within the genus for the moment. The same consequently applies to *G. permaxillaris*, the former only congener of *Jabarichromis* **gen. nov.** *pfefferi*, rendering the genus *Gnathochromis* monotypic. Further, we provide an additional character to delineate the recently re-allocated *Shuja horei* from its former congeners belonging to *Ctenochromis*. Although these two cases of (former) taxonomic misplacement have been known at least since 2003 (Takahashi), it took about two decades for both species to undergo generic revision.

Jabarichromis **gen. nov.** *pfefferi* has experienced several re-allocations to non-closely related genera since its first description. This is a symbolic example for various difficulties, which cichlid taxonomy faces to this day (reviewed in Ronco *et al.* 2020). Many of the taxonomic challenges regarding Lake Tanganyika cichlids can be attributed to the fact that the species flock is the product of an adaptive radiation (Salzburger 2018). The sheer number of species and their intrinsically close relatedness complicates the task to identify unambiguous traits that can be used as a reliable base for species and genera identification, especially within rapidly diversifying sub-lineages. Further, the adaptive radiation of cichlids in Lake Tanganyika was characterized by the explosive accumulation of morphological disparity in several trait complexes, which also resulted in high levels of morphological convergence among the lineages (Muschick *et al.* 2012; Ronco *et al.* 2021; Tada *et al.* 2017). This likely explains why *Jabarichromis* **gen. nov.** *pfefferi* was previously (morphologically) assigned to genera belonging to different tribes, which was however later undisputedly resolved with molecular data (Duftner *et al.* 2005; Irisarri *et al.* 2018; Kocher *et al.* 1995; Lippitsch 1998; Muschick *et al.* 2012; Nishida 1997; Ronco *et al.* 2021; Salzburger *et al.* 2002; Schedel *et al.* 2019; Sturmbauer *et al.* 2003). However, if we consider the latest genus to which *Jabarichromis* **gen. nov.** *pfefferi* was assigned, namely *Gnathochromis*, then apart from the similarity in mouth morphology and the protrudable upper jaw, it seems difficult to argue for similarities and thus convergent evolution in other traits. Even their mouth morphologies, or its function to be precise, differ from each other, with *G. permaxillaris* having a more pronounced maxilla; *G. permaxillaris* searches for food on the ground and protrudes its elongated jaws downwards, whereas *Jabarichromis* **gen. nov.** *pfefferi* pecks its prey from the water column (Konings 2019). Hence, based on isolated morphological traits, it is perhaps understandable that previous studies placed *Jabarichromis* **gen. nov.** *pfefferi* in a genus alongside distantly related species. However, this case once more highlights the need to base the taxonomy of cichlids on carefully selected character sets, and to support their classification with molecular data whenever possible.

Besides the generic misplacement of *Jabarichromis* **gen. nov.** *pfefferi* that grouped two species from different tribes with more than 7 million years of divergence time into a single genus, several taxonomic issues still remain within Lake Tanganyika cichlid tribes (Ronco *et al.* 2020). For example, within the Tropheini alone several taxonomic discrepancies on genus and species level are known. One of them is the genus *Petrochromis*, which was found to be polyphyletic (Koblmüller *et al.* 2010) consisting of three clades (Ronco *et al.* 2021; Singh *et al.* 2022) and containing several undescribed taxa (Konings 2019; Ronco *et al.* 2020; Van Steenberge & Snoeks 2014). The genus-type species of *Petrochromis*, *P. polyodon* Boulenger 1898, occurs lake-wide and displays substantial variation in coloration of males, which raises the question of their true species status (Konings 2019).

Another tribe that shows inconsistencies between taxonomic assignments and phylogenetic placement are the Lamprologini, which is the most species-rich tribe in the lake. Several genera have been shown to be para- and polyphyletic (Colombo *et al.* 2016; Day *et al.* 2007; Ronco *et al.* 2021; Schelly *et al.* 2006; Sturmbauer *et al.* 2010). Overall, with the increasing availability of molecular phylogenies, many cases of taxonomic misplacements among Lake Tanganyika cichlids have been revealed. However, much of this was a by-product of cichlids being extensively studied as a model system for evolutionary biology. In contrast, their taxonomy receives considerably less attention. Yet, the proper classification on higher taxonomic levels and descriptions of species would not only be in the interest of taxonomy but also every other field of cichlid research in order to reduce errors and ease scientific discussions.

Author Contributions

All authors contributed to study design. A.H. and F.D.B.S. acquired additional x-rays for this study. A.H. obtained the meristic data. A.H. and F.R. obtained the morphometrical data. Data analysis was performed by A.H. and F.R. The first draft of the manuscript was written by A.H. and the final version of the manuscript was written by all the authors.

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