

Rapid Communication**Discovery of Japanese gengorobuna *Carassius cuvieri* Temminck & Schlegel, 1846 in Ethiopia: implications for fisheries governance**

Million Tesfaye^{1,2,†}, Pradeep Kumkar^{3,†}, Mathewos Hailu^{4,5}, Chandani R. Verma³, Gashaw Tesfaye⁶, Miloslav Petrýl³, Abebe Getahun⁴, Marek Šmejkal¹ and Lukáš Kalous³

¹Institute of Hydrobiology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czechia

²Faculty of Fisheries and Protection of Waters, South Bohemian Research Centre for Aquaculture and Biodiversity of Hydrocenoses, University of South Bohemia in České Budějovice, Zátěží 728/II, 389 25 Vodňany, Czechia

³Department of Zoology and Fisheries, Faculty of Agrobiological Sciences, Czech University of Life Sciences Prague, Prague, Czechia

⁴Department of Zoological Sciences, Addis Ababa University, Addis Ababa, Ethiopia

⁵Batu Fish and Other Aquatic Life Research Center, Ziway (Batu), Ethiopia

⁶EIAR, National Fishery and Aquatic Life Research Center, Sebeta, Ethiopia

[†]Joint first authors

Corresponding author: Marek Šmejkal (marek.smejkal@hbu.cas.cz)

Citation: Tesfaye M, Kumkar P, Hailu M, Verma CR, Tesfaye G, Petrýl M, Getahun A, Šmejkal M, Kalous L (2025) Discovery of Japanese gengorobuna *Carassius cuvieri* Temminck & Schlegel, 1846 in Ethiopia: implications for fisheries governance. *BioInvasions Records* 14(1): 155–167, <https://doi.org/10.3391/bir.2025.14.1.13>

Received: 22 July 2024

Accepted: 10 December 2024

Published: 17 February 2025

Handling editor: Enrique Gonzalez Ortegon

Thematic editor: Karolina Bączela-Spychalska

Copyright: © Tesfaye et al.

This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International - CC BY 4.0).

OPEN ACCESS**Abstract**

Inland fisheries play a critical role in sustaining livelihoods and ensuring food security worldwide. Accurate fish species identification is vital for effective fish stock management and offers insights into ecosystem functioning. A study was conducted in January 2022 to validate the species of fish previously identified in the literature as *Carassius carassius*, purportedly present in Lake Ziway, Ethiopia. Ten individuals of the genus *Carassius* were collected from local fishermen, and morphological and genetic analyses, including CT scanning and mitochondrial gene sequencing, were performed to identify the established *Carassius* species in the lake. Our findings confirm the presence of *Carassius cuvieri*, a species endemic to Lake Biwa, Japan, within Lake Ziway, Ethiopia. Further investigations are needed to confirm the possible presence of other *Carassius* species previously reported in the region, enhancing fisheries management strategies. These fish species significantly contribute to inland fisheries in Ethiopia, emphasising the importance of their accurate identification and management.

Key words: Crucian carp, filter-feeding, inland fisheries, Lake Ziway, species identification

Introduction

Inland fisheries are crucial in ensuring food security and sustaining livelihoods, particularly in regions with limited alternative income sources (De Graaf and Garibaldi 2014; Funge-Smith and Bennett 2019). In Africa, inland fisheries contribute significantly, accounting for around 2.75 million tonnes of annual production and supporting the livelihoods of approximately 5 million people as their primary income source (Welcomme et al. 2010; Funge-Smith and Bennett 2019). Moreover, fishing activities also form an integral part of the livelihood strategies for many individuals with restricted resources (Béné 2006).

The introduction of non-native fish species into African waters has been a longstanding and intricate practice dating back to the early 1900s (Ogutu-Ohwayo 1989; March and Failler 2022). The motivations behind such introductions have often been driven by the anticipation of enhanced fisheries, the promotion of aquaculture, or strategies aimed at pest control (Miller 1989; Gozlan et al. 2010). It is of the utmost importance to identify species in order to manage fish stocks accurately and effectively. Identifying non-native species allows for assessing potential ecological impacts through comprehensive risk evaluations (Lee et al. 2008; Fisher 2014; Austen et al. 2018).

Ethiopia, a landlocked country in the Horn of Africa, has a diverse geography comprising highlands, plateaus, mountains, and lowlands, and its aquatic ecosystems host remarkable biodiversity. These ecosystems are home to over 180 freshwater fish species spanning 12 orders, 29 families, and 70 genera, with 41 species being endemic and 11 classified as introduced (Tesfaye and Wolff 2014; Getahun 2017; Froese and Pauly 2023). The Great Rift Valley, a prominent geological feature traversing Ethiopia, gives rise to a series of lakes that serve as vital fish sources (Golubtsov and Mina 2003). This Rift Valley system encompasses more than eight natural lakes and two large reservoirs holding significant socio-economic and ecological value (Breuil 1995).

With the rising demand for fish and the expansion of fisheries, non-native fish species have been introduced and successfully established in numerous lakes and reservoirs across Ethiopia (Getahun and Stiasny 1998), with the central Rift Valley region harbouring the highest number of introduced species (Golubtsov and Mina 2003; Tigabu 2010). While these introductions have led to increased fish production, their impacts on native fish populations remain inadequately studied (FAO 1997; Getahun and Stiasny 1998; Dadebo and Tugie 2009).

The limited understanding of fish introductions in Ethiopia can be attributed, in part, to the absence of comprehensive records. Some introductions have occurred without proper documentation, resulting in an incomplete grasp of the extent and taxonomy of non-native species present (Getahun and Stiasny 1998; Golubtsov et al. 2002; Golubtsov and Mina 2003). Identifying introduced fish species may pose challenges, especially in morphologically similar species, which may lead to misidentifications (Rylková et al. 2014; Belle et al. 2021). This study investigates discrepancies in the identification of *Carassius* fish species in Lake Ziway. This lake is the second-most productive waterbody in Ethiopia's Rift Valley, contributing 3180 tonnes (20%) of the nation's annual fish production (Tesfaye and Wolff 2014). The most frequently reported species is the crucian carp, often referred to as *C. carassius* (Linnaeus, 1758) (Dadebo and Tugie 2009; Tigabu 2018; Ayele et al. 2022; Hailu et al. 2022, 2023). However, Getahun and Stiasny (1998) reported the wild goldfish *Carassius auratus* (Linnaeus,

1758) from Lake Ziway, suggesting an East Asian origin. Furthermore, Golubtsov et al. (2002) captured two individuals of the *Carassius* sp. from the Bulbula River in the vicinity of its outlet from Lake Ziway and they tentatively identified these as *Carassius grandoculis* Temminck and Schlegel, 1846, based on the extremely high number of gill rakers on the first gill arch. We conducted morphological and molecular analyses of fish specimens collected from Lake Ziway to elucidate the issue. Our investigation aims to determine the species of *Carassius* present in the lake and contribute to the existing literature on fish introductions in Ethiopia.

Materials and methods

Location description

Lake Ziway is a shallow lake located in the Rift Valley (7°99'N, 38°84'E) at an altitude of 1636 m.a.s.l. with a surface area of 434 km². The lake has a maximum depth of 8.9 m and an average depth of 2.5 m (Dadebo and Tugie 2009; Abera, 2016). Two main rivers flow into the lake: the Meki River, which originates from the Gurage Mountains in the northwest, and the Katar River, which flows from the Arsi Mountains in the east. The lake has one outflow in the south through the Bulbula River, which drains into Lake Abijata.

Lake Ziway harbours six native fish species: *Labeobarbus ethiopicus* (Zolezzi, 1939), *Enteromius paludinosus* (Peters, 1852), *Labeobarbus intermedius* (Rüppell, 1835), *Garra makiensis* (Boulenger, 1904), *Garra dembecha* Getahun & Stiassny, 2007 and *Oreochromis niloticus* (Linnaeus, 1758) (Getahun and Stiassny 1998; Golubtsov et al. 2002). The species *Labeobarbus ethiopicus* and *G. makiensis* were reported as endemic to the lake. Additionally, non-native fish species, such as *Coptodon zillii* (Gervais, 1848), *Cyprinus carpio* Linnaeus, 1758, and *Carassius* sp., reported as *C. carassius*, have been introduced to increase fish production. The species *Clarias gariepinus* Burchell, 1822 was also found in Lake Ziway, having been accidentally introduced from a nearby fish processing plant (Tigabu 2010, 2018).

Fish collection

On 28th January 2022, a field visit was conducted at a fishing site located on Lake Ziway (7.919°N, 38.728°E) (Figure 1), where several individuals of *Carassius* sp. were observed caught by local fishermen using gill nets. Ten individuals were randomly selected and examined for general morphological traits, followed by photographic documentation. Subsequently, four of them were collected and fin-clipped for genetic analysis. Additionally, one individual was designated as a voucher specimen and transported to the laboratory for gill arch extraction, followed by CT scanning. This voucher specimen is currently preserved at the Addis Ababa University, Department of Zoological Sciences, Zoological Natural History Museum under the collection number AAUC170.

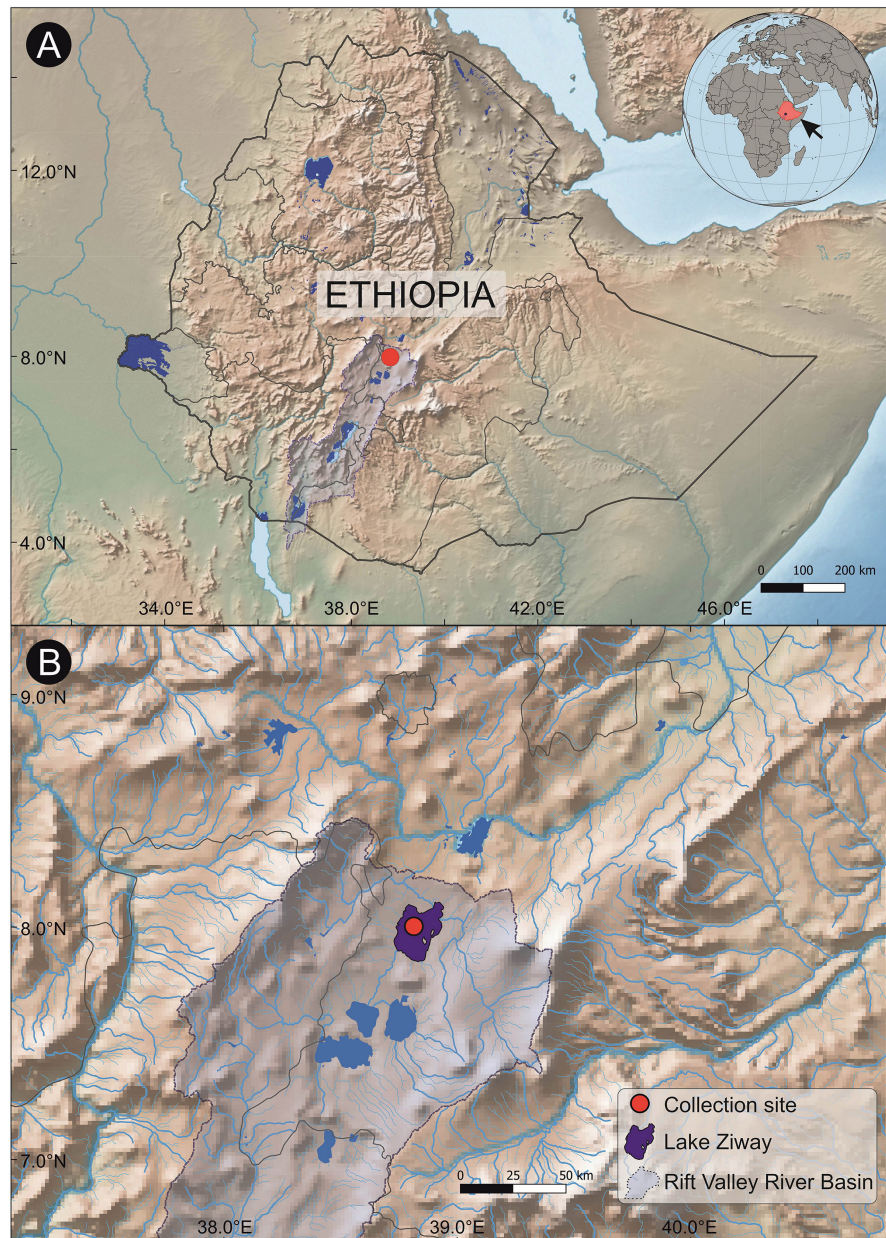


Figure 1. Map of the study area, Ethiopia with lakes and reservoirs: dark blue (A), Central Rift Valley River basin and study lake (dark blue) (B). Maps were drawn using the QGIS (QGIS Development Team 2018).

Morphological analysis and CT scanning

Measurements and counts were conducted following the methodology outlined by Kottelat and Freyhof (2007) and Asano and Kubo (1972), utilising digital callipers. All measurements were accurately recorded to the nearest 0.1 mm. Computerised tomography (CT) scanning was conducted utilising high-resolution X-ray microcomputed tomography (μ CT) with the XT H 225 industrial system (Nikon Metrology). The scanning parameters were set as follows: isotropic voxel size of 24 μ m, energy at 110 kV, current at 120 μ A, power at 13.2 W, exposure at two frames per second (fps), and a 360° rotation scan with 720 projections, averaging four frames per projection (fpp). Subsequently, the scanned images were reconstructed using Nikon CT

Pro 3D software (Nikon Metrology NV). Post-processing and final visualisation of the CT images were accomplished using VG Studio MAX 3.3 software (Volume Graphics, Heidelberg, Germany). The number of fin rays, vertebrae, and ribs were determined from digital high-resolution radiographs.

Genetic analyses

DNA was isolated from the fin clips (preserved in 98% ethanol) from the four individuals using the QIAamp® DNA Mini Kit (Qiagen, Germany, Cat. No. 51304), following protocols outlined by the manufacturer (Ali et al. 2013). The cytochrome *b* gene was amplified following the procedures outlined in Rylková et al. (2010), employing the forward primer Kai_F (5'-GAAGAACCACCGTTGTTATTC-3') and the reverse primer Kai_R (5'-ACCTCCRAYCTYCGGATTACA-3') as detailed by Šlechtová et al. (2006). We selected cytochrome *b* (Cyt *b*) because it is widely used in studies of *Carassius* to differentiate species and lineages (e.g., Takada et al. 2010; Yamamoto et al. 2010; Rylková et al. 2013; Gu et al. 2022). The extensive data available for Cyt *b* in this genus enabled a more effective comparison in our analysis. The polymerase chain reaction (PCR) was performed with a reaction mixture consisting of 4 µl template DNA, 1.5 µl of each primer, 10 µl VWR® Taq Plus 2X master mix (VWR International), and ddH₂O, bringing the final volume to 25 µl. The PCR profile, conducted on an MJ Mini™ thermocycler (Bio-Rad), began with an initial denaturation at 95 °C for 2 minutes, followed by 32 cycles of 95 °C for 1 minute (denaturation), 52 °C for 30 seconds (annealing), and 72 °C for 30 seconds (elongation). A final elongation step at 72 °C for 15 minutes. PCR amplification was verified on a 1% agarose gel, and positive samples were subsequently purified and sequenced by Macrogen Inc. in Seoul, Korea. Chromatograms were scrutinised using FinchTV 1.4.0 (Geospiza, Inc.; Seattle, WA, USA; <http://www.geospiza.com>) to assess the quality of base calls within the DNA sequences. No stop codons were found in the translated amino acid sequences, confirming the absence of nuclear mitochondrial sequences (NUMTs) (Zhang and Hewitt 1996). Corresponding GenBank accession numbers are provided for the sequences produced within this present study and supplementary sequence data concerning other *Carassius* species and *Cyprinus carpio* (Figure 2). The alignment of sequences was carried out separately utilising MUSCLE 3.8.31 (Edgar 2004). The best-fit model was selected using ModelFinder (Kalyaanamoorthy et al. 2017) and maximum likelihood (ML) analysis was performed using MEGA 11 (Tamura et al. 2021) with 1000 bootstrap replicates.

Results

Morphological description/ identification

The ten individuals collected displayed a uniform morphological phenotype, indicating phenotypic consistency within the sampled population. The standard length of the vouchered specimen was 180.6 mm, head medium,

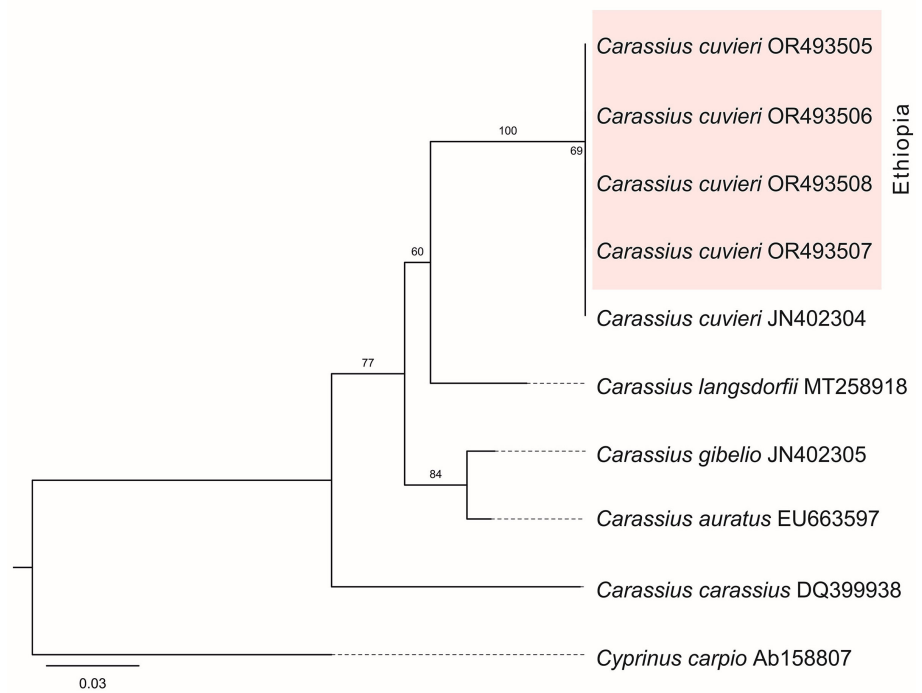


Figure 2. Maximum likelihood phylogram based on cytb gene sequences illustrating the position of *Carassius cuvieri* collected from Ethiopia. *Cyprinus carpio* is used as an outgroup. The red box represents sequences generated during the current study.

and no barbels were present. The body was compressed, the belly rounded, and the body depth high (Figure 3). The standard meristic features on the left side of the body were the following: dorsal fin rays: II 15; anal fin rays: III 5; 31 scales in the lateral line, 6–6 scales in the transverse row, and 2–3 scales in the circumpeduncular row, 88 gill rakers were counted on the first-gill arch and 4+4 pharyngeal teeth (Figure 3A, C, D). Total number of vertebrae is 32, and 13 ribs on each side (Figure 3B). The voucher specimen (AAUC170) collected from Lake Ziway in Ethiopia exhibits a high degree of morphological similarity to the description and illustration of *C. cuvieri* provided in the Fauna Japonica (Temminck and Schlegel 1846).

Genetic analyses

The calculated pairwise genetic distances in the dataset of sequences of fishes of the genus *Carassius* ranged from 1.61% to 10.63%. Interestingly, when comparing *Carassius* sp. individuals gathered from Lake Ziway, Ethiopia, with *Carassius cuvieri* Temminck and Schlegel, 1846 from their native range in Lake Biwa, Japan, the genetic distance was recorded as 0% (Table 1). The phylogenetic analysis results strongly indicated no genetic difference between *Carassius* sp. fish taken from Lake Ziway in Ethiopia and those from their native range. This formed a single clade. However, noticeable differences were observed for all other species, forming three separate clades. The species *Carassius gibelio* (Bloch, 1782) and *C. auratus* formed a distinct clade, and *Carassius langsdorfii* Temminck and Schlegel, 1846 and *C. carassius* formed two distinct clades (Figure 2).

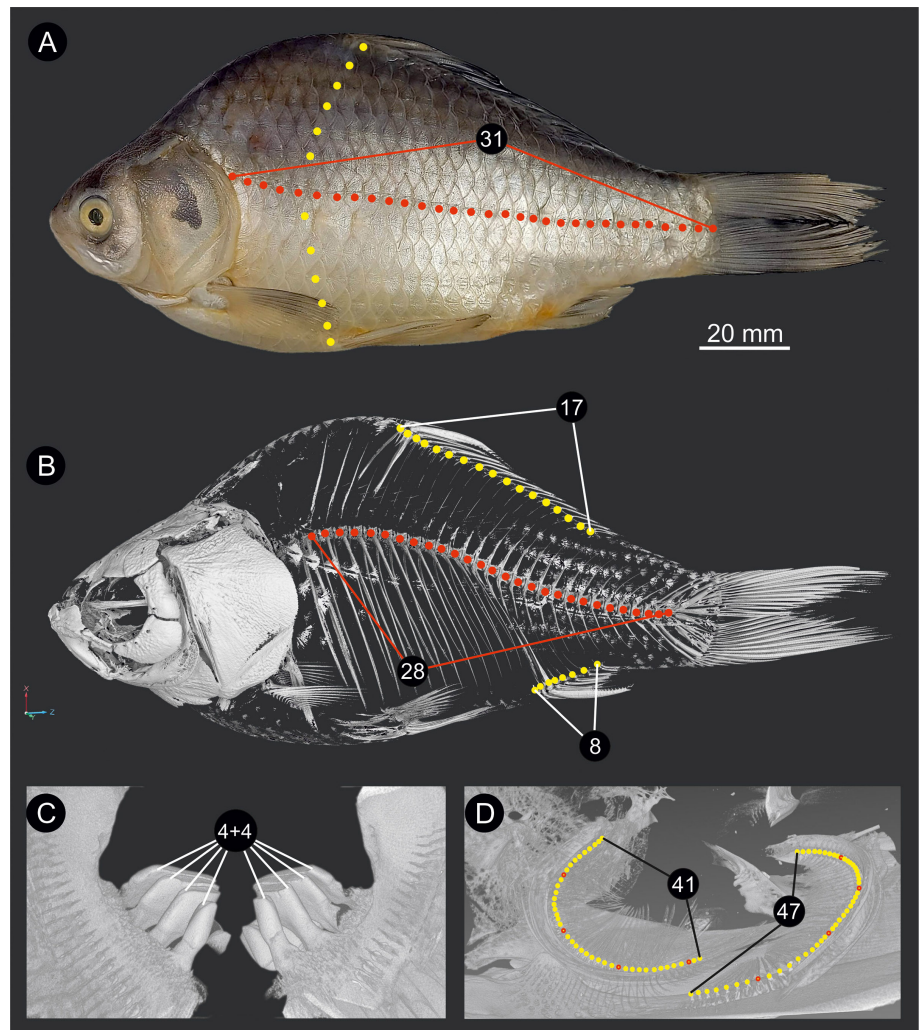


Figure 3. (A) Preserved specimen of *Carassius cuvieri* (AAUC170) from Lake Ziway, Ethiopia, displaying scale rows used for counting lateral and transverse scale rows, (B) CT scan image of the skeleton, indicating counts of vertebrae (excluding the Weberian apparatus) and dorsal and anal fin ray counts, (C) Pharyngeal teeth, (D) The first gill arch, with marks indicating the number of gill rakers (Note: The gill arch was damaged during collection and handling of the specimen). Photo credit: Prof. Lukáš Kalous

Table 1. Percentage raw genetic distances in cytochrome b gene. Values in brackets indicate within-population variation.

	(1)	(2)	(3)	(4)	(5)
<i>Carassius cuvieri</i> Ethiopia (1)	[0-0]				
<i>Carassius cuvieri</i> Japan (2)	0.00				
<i>Carassius langsdorfii</i> (3)	7.05	7.09			
<i>Carassius gibelio</i> (4)	7.54	7.53	6.29		
<i>Carassius auratus</i> (5)	7.15	7.16	6.29	1.64	
<i>Carassius carassius</i>	10.84	11.43	9.34	10.70	10.29

Discussion

It has been noted by Knytl et al. (2018) and Rylková et al. (2014) that identifying species within the genus *Carassius* using morphological analysis can be challenging. As presented in Table 2, our analysis indicates overlapping morphological parameters among different taxa. Only a few papers have combined morphological and genetic analysis to verify the reported meristic

Table 2. Morphological data of the specimen of *C. cuvieri* (AAUC170) found in the Lake Ziway, Ethiopia. The diagnostic characters of *C. langsdorfii* and *C. cuvieri* according to Nakabo (2002) and Kawanabe and Mizuno (1989). Diagnostic characteristics of *C. gibelio*, *C. carassius* and *C. auratus* according to Lusk and Baruš (1978), Szczerbowski, in Bănărescu and Paepke, 2002 and Kottelat (2017). (SL – standard length).

	AAUC170	<i>C. cuvieri</i>	<i>C. langsdorfii</i>	<i>C. gibelio</i>	<i>C. auratus</i>	<i>C. carassius</i>	<i>C. praecipuus</i>
Black dot at the base of caudal peduncle	No	No	No	No	No	Yes	No
Upper edge of the dorsal fin	Concave	Concave	Concave	Concave	Concave	Convex	Slightly Convex
Dorsal margin of head	Slightly concave	Slightly concave	Slightly convex	Slightly concave	Slightly convex	Convex	straight
Dorsal fin rays	II 15	IV 15–18	IV 15–18	II–IV 16–19	III–IV 14–19	III–IV 14–25	IV 9–11
Anal fin rays	III 5	III 4–5	III 5	III 6	II–IV 5–6	II–II 5–8	III 5
Scales in lateral line	30	29–33	28–31	28–32	21–36	21–38	26–28
Scales above lateral line	6	6–7	6–7	5–6	5–7	6–8	5
Scales below lateral line	6	4–6	5–6	5–6	5–8	5–7	6–7
Number of gill rakers	88	92–128	41–57	49–54	37–47	23–33	20–21
Pharyngeal teeth	4–4	4–4	4–4	4–4	4–4	4–4	–
Body depth (In % SL)	46.6	27–35	33–48	34–49	35–46	25–56	32.5–35.9

characters to a specific mtDNA lineage sensu (Rylková et al. 2013; Takada et al. 2010; Gao et al. 2012; Cheng et al. 2020; Gu et al. 2022), see e.g. Kalous et al. (2007). However, due to morphological overlap among fishes in the *Carassius auratus sensu lato* (Hensel 1971), the only indicative character seems to be the number of gill rakers, in which *C. cuvieri* reaches values of 92–128 (Yamamoto 2010; Taniguchi and Ishiwatari 1972). The observed count of gill rakers, notably reaching 88 (Figure 3D), stands out as a distinguishing feature from all other recognised species within the genus *Carassius*, where typical counts range between 20 and 57. Prior investigations have documented a range of 92 to 128 gill rakers for *C. cuvieri*; however, our study extends this range to 88 to 128 for this species (Vetešník et al. 2007; Papoušek et al. 2008). The lower number could be attributed to the high phenotypic plasticity of *C. cuvieri* in the new ecosystem as observed in other invasive taxa (Jarić et al. 2015; Hudson et al. 2020; Grabowska et al. 2021), or this number lower than 92 was not recorded before in *C. cuvieri* since only a few studies exist.

Interestingly, the finding of Golubtsov et al. (2002) refers most likely to *Carassius cuvieri*, but it should be noted that the authors misinterpreted the taxon as *C. grandoculis*, which is now considered a synonym of *C. auratus* according to the Eschmeyer's Catalog of Fishes (Fricke et al. 2024). However, it is worth mentioning that Yamamoto et al. (2010) suggest that the so-called nigoro-buna *C. grandoculis* is a morphotype of various Japanese genetic lineages of the genus *Carassius*.

Given the complexity of the morphology, the alternative approach of species identification gave clear results. The genetic data unequivocally demonstrate the presence of *C. cuvieri*. All four analysed individuals were sorted into the phylogenetic lineage of *C. cuvieri* based on Cyt *b* gene sequences. To our knowledge, this is the first study demonstrating the occurrence of *C. cuvieri* in Ethiopia.

The origin of *C. cuvieri* (gengoro-buna in Japanese) is Lake Biwa, the ancient lake in Japan that hosts 13 endemic species. The species *Carassius*

cuvieri has been registered in the Red List of Threatened Species by the Japanese Environment Ministry since 2007 because of significant decreases in their populations (Kunimune et al. 2011; Kanao et al. 2017).

However, *C. cuvieri* has been introduced to the Korean Peninsula, Taiwan, and mainland China (Walker and Yang 1999; Jang et al. 2002). In Korea, where it was introduced from Japan in the 1970s, *C. cuvieri* is one of the most abundant non-native fish in the river systems (Jang et al. 2002). It outperforms other fish species in fecundity and adaptation to environmental changes, subsequently threatening the native fish species (Song et al. 2007). This is an example of the conservation paradox (Marková et al. 2020; Baquero et al. 2023), where an organism under threat in its original range thrives in its new environment.

The adult *C. cuvieri* can filter fine particles from the water column, allowing it to consume phytoplankton as a food source. This adaptation is supported by its higher number of gill rakers (Miura 1966; Ohara et al. 2000). This can also be seen as an adaptation for lentic lake environments. Compared to *C. gibelio*, *C. cuvieri* has more gill rakers, highlighting its highly herbivorous nature. Studies have shown that invasive species like *C. gibelio* and *C. auratus* cause significant ecological impacts by competing for limited habitat and food resources, which ultimately caused declines in native fish populations (Tapkir et al. 2023; Šmejkal et al. 2024). Given these observations in related species, it is reasonable to infer that *C. cuvieri* may have similar ecological impacts.

The dominant fish species in the study area primarily feed on macrophytes and phytoplankton. Among these, *O. niloticus*: a key species in Lake Ziway and has experienced a decline in commercial catch in recent years due to various factors (Tesfaye et al., 2021). According to Fetahi et al. (2018), *O. niloticus* in Lake Ziway mainly consumes macrophytes and phytoplankton, suggesting a potential dietary overlap with *C. cuvieri*, but further studies are needed.

The introduction and transfer of fish into natural and artificial water bodies in Ethiopia began in the late 1930s and early 1940s, first at the initiative of Italian experts and subsequently by local scientists (Bazzi 1955). Tedla and Hailemeskel (1981) stated that the first attempt to introduce non-native fish species into the country was made in 1938 with the introduction of Northern pike (*Esox lucius* Linnaeus, 1758) and Eastern mosquitofish (*Gambusia holbrooki* Girard, 1859) into Lake Tana. Between 1973 and 1974, Rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792) was introduced into Ethiopian rivers and some lakes for recreational fishing (FAO 2015). In the late 1970's, the Ministry of Agriculture of Ethiopia introduced phytophagous fishes into the Ethiopian lakes, intending to increase fish production since it was believed that the niche was not occupied by any of the indigenous fish (FAO 1997; Tigabu 2018). Since its introduction, the fish has commonly been referred to as *C. carassius* in

statistics as well as in scientific literature (Getahun and Stiasny 1998; Dadebo and Tugie 2009; Spliethoff et al. 2009; Merga et al. 2020; Hailu et al. 2022, 2023). The introduction to Lake Ziway occurred in the 1970s (Tedla and Hailemeskel 1981; Tigabu 2018).

Conclusions

It is possible that there are multiple species and species complexes of the genus *Carassius* in Ethiopian waters. The species *C. cuvieri* occurs in Lake Ziway, but what other representatives of the genus *Carassius* occur in other waters remains to be investigated. Accurate identification of non-indigenous species is essential in designing effective management strategies. It is strongly recommended that investigations be carried out to distinguish which specific species and complexes of the genus *Carassius* fall under the general term “*Carassius carassius*” in Ethiopia, as these fish contribute substantial catches to inland fisheries.

Authors' contribution

Million Tesfaye: conceptualization, writing – original draft preparation, reviewing and editing; Pradeep Kumkar: conceptualization, writing – original draft preparation, analysis and illustrations; Mateos Hailu: writing – review and editing; Chandani R. Verma: methodology, writing – review and editing; Gashaw Tesfaye: writing – review and editing; Abebe Getahun: writing – review and editing; Miloslav Petrůl; methodology, illustrations, writing – review and editing; Marek Šmejkal: conceptualization, writing – review and editing, funding acquisition; Lukáš Kalous: conceptualization, original draft preparation, reviewing and editing, funding acquisition.

Acknowledgements

The authors acknowledge the fishermen of Lake Ziwaye for their assistance during sample collection. The suggestions provided by the editor and two anonymous reviewers greatly improved the manuscript.

Funding declaration

The authors thank the Research Programme Strategy AV21 Water for Life for valuable support. PK, CRV and LK were supported by the institutional grant SGS conducted at the Czech University of Life Sciences Prague under No. SV23-11-21260.

Ethical approval

The field sampling methods and experimental protocols used in this study were performed according to the guidelines and permission from Ethiopian Biodiversity Institute No. 482/2006 and other relevant Ethiopian laws.

References

- Abera L (2016). Current status and trends of fishes and fishery of a shallow rift valley lake, Lake Ziway, Ethiopia. Doctoral dissertation. Addis Ababa University, Department of Zoological Sciences, Addis Ababa, Ethiopia
- Asano H, Kubo Y (1972) Variations of spinal curvature and vertebral number in goldfish. *Japanese Journal of Applied Ichthyology* 19: 223–231
- Austen GE, Bindemann M, Griffiths RA, Roberts DL (2018) Species identification by conservation practitioners using online images: accuracy and agreement between experts. *PeerJ* 6: e4157, <https://doi.org/10.7717/peerj.4157>
- Ayele S, Mamo Y, Deribe E, Eklo OM (2022) Levels of organochlorine pesticides in five species of fish from Lake Ziway, Ethiopia. *Scientific African* 16: e01252, <https://doi.org/10.1016/j.sciaf.2022.e01252>

- Bănărescu PM, Paepke HJ (eds) (2002) The freshwater fishes of Europe. Cyprinidae 2 Part III: *Carassius* to *Cyprinus*. Aula Wiesbaden, 305 pp
- Baquero RA, Oficialdegui FJ, Ayllón D, Nicola GG (2023) The challenge of managing threatened invasive species at a continental scale. *Conservation Biology* 5: e14165, <https://doi.org/10.1111/cobi.14165>
- Bazzi F (1955) Fisheries of Ethiopia. Ministry of Agriculture, Addis Ababa, 25 pp
- Belle C, Stoeckle B, Cerwenka A, Kuehn R, Pander J, Geist J (2021) Taxonomic requirements for better documenting and understanding biological invasions – the example of genetic weatherfish *Misgurnus/Paramisgurnus* sp. identification. *BioInvasions Records* 10: 506–520, <https://doi.org/10.3391/bir.2021.10.3.01>
- Béné C (2006) Small-scale fisheries: assessing their contribution to rural livelihoods in developing countries. FAO Fisheries Circular 890, Rome, 58 pp
- Breuil C (1995) Review of fisheries and aquaculture sector: Ethiopia. FAO Fisheries Circular 890, Rome, 29 pp
- Cheng L, Lu C, Wang L, Li C, Yu X (2020) Coexistence of three divergent mtDNA lineages in northeast Asia provides new insights into phylogeography of goldfish (*Carassius auratus*). *Animals* 10: 1785, <https://doi.org/10.3390/ani10101785>
- Dadebo E, Tugie D (2009) Some aspects of reproductive biology of the crucian carp *Carassius carassius* (L. 1758) (Pisces: Cyprinidae) in Lake Ziway, Ethiopia. *The Biological Society of Ethiopia* 8: 109–121
- De Graaf G, Garibaldi L (2015) The value of African fisheries. FAO Fisheries and Aquaculture Circular No. C1093. Rome, 76 pp
- Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797, <https://doi.org/10.1093/nar/gkh340>
- FAO (1997) Aquaculture production statistics 1986–1996. FAO Fisheries Circular No. 815. Food and Agriculture Organization of the United Nations, Rome, 195 pp
- Fetahi T, Rothhaupt KO, Peeters F (2018) Dietary map of Nile tilapia using stable isotopes in three tropical lakes, Ethiopia. *Ecology of Freshwater Fish* 27: 460–470, <https://doi.org/10.1111/eff.12361>
- Fischer J (2014) Fish Identification Tools for Biodiversity and Fisheries Assessments: Review and Guidance for Decision-Makers. FAO Fisheries and Aquaculture Technical Paper. FAO, Rome, 108 pp
- Funge-Smith S, Bennett A (2019) A fresh look at inland fisheries and their role in food security and livelihoods. *Fish and Fisheries* 20: 1176–1195, <https://doi.org/10.1111/faf.12403>
- Gao Y, Wang SY, Luo J, Murphy RW, Du R, Wu SF, Zhu CL, Li Y, Poyarkov AD, Nguyen SN, Luan PT (2012) Quaternary palaeoenvironmental oscillations drove the evolution of the Eurasian *Carassius auratus* complex (Cypriniformes Cyprinidae). *Journal of Biogeography* 39: 2264–2278, <https://doi.org/10.1111/j.1365-2699.2012.02755.x>
- Getahun A (2017) The freshwater fishes of Ethiopia: diversity and utilization. View Graphics and Printing, Addis Ababa, Ethiopia, 349 pp
- Getahun A, Stiassny ML (1998) The freshwater biodiversity crisis: the case of the Ethiopian fish fauna. *SINET: Ethiopian Journal of Science* 21: 207–230, <https://doi.org/10.4314/sinet.v21i2.18121>
- Golubtsov AS, Mina MV (2003) Fish species diversity in the main drainage systems of Ethiopia: Current state of knowledge and research perspectives. *Ethiopian Journal of Natural Resources* 5: 281–318
- Golubtsov AS, Dgebuadze YY, Mina MV (2002) Fishes of the Ethiopian Rift Valley. *Ethiopian Rift Valley Lakes* 167: 258
- Gozlan RE, Britton JR, Cowx I, Copp GH (2010) Current knowledge on non-native freshwater fish introductions. *Journal of Fish Biology* 76: 751–786, <https://doi.org/10.1111/j.1095-8649.2010.02566.x>
- Grabowska J, Tarkan AS, Błońska D, Karakuş NT, Janic B, Przybylski M (2021) Prolific pioneers and reserved settlers. Changes in the life-history of the western tubenose goby (*Proterorhinus semilunaris*) at different invasion stages. *Science of the Total Environment* 750: 142316, <https://doi.org/10.1016/j.scitotenv.2020.142316>
- Gu Q, Wang S, Zhong H, Yuan H, Yang J, Yang C, Huang X, Xu X, Wang Y, Wei Z, Wang J (2022) Phylogeographic relationships and the evolutionary history of the *Carassius auratus* complex with a newly born homodiploid raw fish (2nNCRC). *BMC Genomics* 23: 242, <https://doi.org/10.1186/s12864-022-08468-x>
- Hailu M, Mengistou S, Fetahi T (2022) Ecosystem structure drivers and simulation scenarios of a shallow Lake Ziway, Ethiopia. *African Journal of Ecology* 60: 1043–1056, <https://doi.org/10.1111/aje.13073>
- Hailu M, Lemma B, Adugna M, Hailu Y (2023) Parasites of commercially important fish species caught for food in Lake Ziway, Ethiopia. *East African Journal of Science* 17: 33–42
- Hensel K (1971) Some notes on the systematic status of *Carassius auratus gibelio* (Bloch 1782) with further record of this fish from the Danube River in Czechoslovakia. *Věstník Československé Společnosti Zoologické* 3: 186–198
- Hudson CM, Vidal-García M, Murray TG, Shine R (2020) The accelerating anuran: evolution of locomotor performance in cane toads (*Rhinella marina*, Bufonidae) at an invasion front. *Proceedings of the Royal Society B* 287: 20201964, <https://doi.org/10.1098/rspb.2020.1964>
- Jang MH, Kim JG, Park SB, Jeong KS, Cho GI, Joo GJ (2002) The current status of the distribution of introduced fish in large river systems of South Korea. *International Review of Hydrobiology* 87: 319–328, [https://doi.org/10.1002/1522-2632\(200205\)87:2/3<319::AID-IROH319>3.0.CO;2-N](https://doi.org/10.1002/1522-2632(200205)87:2/3<319::AID-IROH319>3.0.CO;2-N)
- Jarić I, Jaćimović M, Cvijanović G, Knežević-Jarić J, Lenhardt M (2015) Demographic flexibility influences colonization success: profiling invasive fish species in the Danube River by the use of population models. *Biological Invasions* 17: 219–229, <https://doi.org/10.1007/s10530-014-0721-2>

- Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermin LS (2017) ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods* 14: 587–589, <https://doi.org/10.1038/nmeth.4285>
- Kawanabe H, Mizuno N (1989) Fishes in rivers and lakes part I. Hoikusha, Osaka, 200 pp [in Japanese]
- Kalous L, Šlechtová V, Bohlen J, Petrtyl M, Švátora M (2007) First European record of *Carassius langsdorfi* from the Elbe basin. *Journal of Fish Biology* 70: 132–138, <https://doi.org/10.1111/j.1095-8649.2006.01290.x>
- Knytl M, Kalous L, Rylková K, Choleva L, Merilä J, Ráb P (2018) Morphologically indistinguishable hybrid *Carassius* female with 156 chromosomes: A threat for the threatened crucian carp, *C. carassius*, L. *PLoS ONE* 13: e0190924, <https://doi.org/10.1371/journal.pone.0190924>
- Kottelat M (2017) *Carassius praecipuus*, a dwarf new species of goldfish from the Mekong drainage in central Laos (Teleostei: Cyprinidae). *Revue suisse de Zoologie* 124: 323–329, <https://doi.org/10.5281/zenodo.893541>
- Kottelat M, Freyhof J (2007) Handbook of European freshwaterfishes. Kottelat, Cornol & Freyhof, Berlin, XIV + 646 pp
- Kunimune Y, Mitsunaga Y, Komeyama K, Matsuda M, Kobayashi T, Takagi T, Yamane T (2011) Seasonal distribution of adult crucian carp nigorobuna *Carassius auratus grandoculis* and gengoroubuna *Carassius cuvieri* in Lake Biwa, Japan. *Fisheries Science* 77: 521–532, <https://doi.org/10.1007/s12562-011-0354-7>
- Lusk S, Baruš V (1978) Morphometric features of *Carassius auratus* from the drainage area of the Morava River. *Folia Zoologica* 27: 177–190
- Lee II HE, Reusser DA, Olden JD, Smith SS, Graham J, Burkett V, Dukes JS, Piorkowski RJ, McPhedran J (2008) Integrated monitoring and information systems for managing aquatic invasive species in a changing climate. *Conservation Biology* 22: 575–584, <https://doi.org/10.1111/j.1523-1739.2008.00955.x>
- March A, Failler P (2022) Small-scale fisheries development in Africa: Lessons learned and best practices for enhancing food security and livelihoods. *Marine Policy* 136: 104925, <https://doi.org/10.1016/j.marpol.2021.104925>
- Marková J, Jerikho R, Wardiatno Y, Kamal MM, Magalhães AL, Bohatá L, Kalous L, Patoka J (2020) Conservation paradox of giant arapaima *Arapaima gigas* (Schinz, 1822) (Pisces: Arapaimidae): endangered in its native range in Brazil and invasive in Indonesia. *Knowledge and Management of Aquatic Ecosystems* 421: 47, <https://doi.org/10.1051/kmae/2020039>
- Merga LB, Mengistie AA, Faber JH, Van den Brink PJ (2020) Trends in chemical pollution and ecological status of Lake Ziway, Ethiopia: a review focussing on nutrients, metals and pesticides. *African Journal of Aquatic Science* 45: 386–400, <https://doi.org/10.2989/16085914.2020.1735987>
- Miller DJ (1989) Introductions and extinction of fish in the African great lakes. *Trends in Ecology & Evolution* 4: 56–59, [https://doi.org/10.1016/0169-5347\(89\)90145-6](https://doi.org/10.1016/0169-5347(89)90145-6)
- Miura T (1966) Ecological notes of the fishes and the interspecific relations among them in Lake Biwa. *Japanese Journal of Limnology (Rikusuigaku Zasshi)* 27: 49–72, <https://doi.org/10.3739/rikusui.27.49>
- Nakabō T (ed) (2002) Fishes of Japan: with pictorial keys to the species. Tokai University Press, 1749 pp
- Ogutu-Ohwayo R (1989) The purpose, costs and benefits of fish introductions: with specific reference to the great lakes of Africa. Uganda Freshwater Fisheries Research Organization, 32 pp
- Ohara K, Ariyoshi T, Sumida E, Sitizyo K, Taniguchi N (2000) Natural hybridization between diploid crucian carp species and genetic independence of triploid crucian carp elucidated by DNA markers. *Zoological Science* 17: 357–364, <https://doi.org/10.2108/jzs.17.357>
- Papoušek I, Vetešník L, Halačka K, Lusková V, Humpl M, Mendel J (2008) Identification of natural hybrids of gibel carp *Carassius auratus gibelio* (Bloch) and crucian carp *Carassius carassius* (L.) from lower Dyje River floodplain (Czech Republic). *Journal of Fish Biology* 72: 1230–1235, <https://doi.org/10.1111/j.1095-8649.2007.01783.x>
- Rylková K, Kalous L, Šlechtová V, Bohlen J (2010) Many branches, one root: first evidence for a monophyly of the morphologically highly diverse goldfish (*Carassius auratus*). *Aquaculture* 302: 36–41, <https://doi.org/10.1016/j.aquaculture.2010.02.003>
- Rylková K, Kalous L, Bohlen J, Lamatsch DK, Petrtyl M (2013) Phylogeny and biogeographic history of the cyprinid fish genus *Carassius* (Teleostei: Cyprinidae) with focus on natural and anthropogenic arrivals in Europe. *Aquaculture* 380: 13–20, <https://doi.org/10.1016/j.aquaculture.2012.11.027>
- Rylková K, Kalous L, Petrtyl M (2014) Morphologic traits fail in species determination in genus *Carassius*. In: Kubík Š, Barták M (eds), 6th Workshop on Biodiversity. Jevany, Česká zemědělská univerzita v Praze, Czech Republic, pp 170–174, <https://doi.org/10.13140/2.1.2094.3685>
- Tedla S, Hailemeskel F (1981) Introduction and transplantation of freshwater fish species in Ethiopia. *SINET: Ethiopian Journal of Science* 4(2): 69–72
- Temminck CJ, Schlegel H (1846) Fishes. In: von Siebold PF (ed), Fauna Japonica: Description of the animals observed during a journey in Japan undertaken in the years 1823–1830. Leyden: A. Arnz., 658 pp
- Šlechtová V, Bohlen J, Freyhof J, Ráb P (2006) Molecular phylogeny of the Southeast Asian freshwater fish family Botiidae (Teleostei: Cobitoidea) and the origin of polyploidy in their evolution. *Molecular Phylogenetics and Evolution* 39: 529–541, <https://doi.org/10.1016/j.ympev.2005.09.018>

- Šmejkal M, Thomas K, Šmejkalová Z, Stepanyshyna Y, Bartoň D, Tapkir S, Meador T, Vašek M (2024) Isotopic niches reveal the impact of topmouth gudgeon and gibel carp on native crucian carp. *NeoBiota* 93: 203–224, <https://doi.org/10.3897/NEOBOTA.93.119274>
- Song KH, Jung JW, Koo HY, Kim W (2007) Development of species-specific molecular marker as a tool for discrimination between crucian carp gengorobuna (*Carassius cuvieri*) introduced from Japan and Korean native one (*C. auratus*). *Korean Journal of Ecology and Environment* 40: 143–148
- Spliethoff PC, Wudneh T, Tariku E, Senbeta G (2009) Past, current and potential production of fish in Lake Ziway-Central Rift Valley in Ethiopia. Centre for Development Innovation, 31 pp
- Takada M, Tachihara K, Kon T, Yamamoto G, Iguchi KI, Miya M, Nishida M (2010) Biogeography and evolution of the *Carassius auratus*-complex in East Asia. *BMC Evolutionary Biology* 10: 1–8, <https://doi.org/10.1186/1471-2148-10-7>
- Tamura K, Stecher G, Kumar S (2021) MEGA11: molecular evolutionary genetics analysis version 11. *Molecular Biology and Evolution* 38: 3022–3027, <https://doi.org/10.1093/molbev/msab120>
- Taniguchi N, Ishiwatari T (1972) Inter and intraspecific variations of muscle proteins in the Japanese Crucian Carp I. Cellulose-acetate Electrophoretic Pattern. *Japanese Journal of Ichthyology* 19: 217–222
- Tapkir S, Thomas K, Kalous L, Vašek M, Meador TB, Šmejkal M (2023) Invasive gibel carp use vacant space and occupy lower trophic niche compared to endangered native crucian carp. *Biological Invasions* 25: 2917–2928, <https://doi.org/10.1007/s10530-023-03081-9>
- Tesfaye A, Getahun A, Fetahi T (2021) Diet overlap of non-native common carp and native Nile tilapia: A potential cause for population reduction of Nile tilapia stock in Lake Ziway, Ethiopia. *African Journal of Ecology* 59: 159–167, <https://doi.org/10.1111/aje.12795>
- Tesfaye G, Wolff M (2014) The state of inland fisheries in Ethiopia: a synopsis with updated estimates of potential yield. *Ecohydrology & Hydrobiology* 14: 200–219, <https://doi.org/10.1016/j.ecohyd.2014.05.001>
- Tigabu Y (2010) Stocking based fishery enhancement programmes in Ethiopia. *Ecohydrology & Hydrobiology* 10: 241–246, <https://doi.org/10.2478/v10104-011-0012-9>
- Tigabu Y (2018) Assessment of the impact of introduction of culture based fisheries on fish production in water bodies of Ethiopia. *Ethiopian Journal of Environmental Studies & Management* 11: 825–836
- Vetešník L, Papoušek I, Halačka K, Lusková V, Mendel J (2007) Morphometric and genetic analysis of *Carassius auratus* complex from an artificial wetland in Morava River floodplain, Czech Republic. *Fisheries Science* 73: 817–822, <https://doi.org/10.1111/j.1444-2906.2007.01401.x>
- Walker KF, Yang HZ (1999) Fish and fisheries in western China. *Fish and Fisheries at Higher Altitudes: Asia* 385: 304
- Welcomme RL, Cowx IG, Coates D, Béné C, Funge-Smith S, Halls A, Lorenzen K (2010) Inland capture fisheries. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 2881–2896, <https://doi.org/10.1098/rstb.2010.0168>
- Yamamoto G, Takada M, Iguchi KI, Nishida M (2010) Genetic constitution and phylogenetic relationships of Japanese crucian carps (*Carassius*). *Ichthyological Research* 57: 215–222, <https://doi.org/10.1007/s10228-010-0152-8>
- Zhang D-X, Hewitt GM (1996) Nuclear integrations: Challenges for mitochondrial DNA markers. *Trends in Ecology & Evolution* 11: 247–251, [https://doi.org/10.1016/0169-5347\(96\)10031-8](https://doi.org/10.1016/0169-5347(96)10031-8)

Web sites, online databases and software

- FAO (2015) Fishery and Aquaculture Country Profiles: Ethiopia. <https://www.fao.org/figis/pdf/fishery/facp/ETH/en> (accessed 3 October 2023)
- Fricke R, Eschmeyer WN, Van der Laan R (eds) (2024) Eschmeyer’s catalog of fishes: Genera, species, references. <http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp> (accessed 7 April 2024)
- Froese R, Pauly D (2023) FishBase. <http://www.fishbase.org>, (accessed 4 February 2023)
- Kanao S, Hasegawa K, Mukai T (2017) *Carassius cuvieri* (Japanese White Crucian Carp). IUCN Red List Threat. Species 2019, <https://www.iucnredlist.org/species/166137/210023750> (accessed 9 August 2023)