Hydrobiologia (2018) 806:363–409
https://doi.org/10.1007/s10750-017-3375-0

PRIMARY RESEARCH PAPER

Diversity, mitochondrial phylogeny, and ichthyogeography of the *Capoeta capoeta* complex (Teleostei: Cyprinidae)

Halimeh Zareian · Hamid Reza Esmaeili · Ali Gholamhosseini · Bella Japoshvili · Müfit Özuluğ · Richard L. Mayden

Received: 4 June 2017 / Revised: 19 August 2017 / Accepted: 12 September 2017 / Published online: 3 October 2017

Abstract Fish species of the genus *Capoeta* are known for their special mouth morphology (inferior mouth with the horny edge to the lower jaw), short dorsal fin with seven to nine branched rays, and their tumultuous taxonomic history. The genus *Capoeta* has had a complex evolutionary history with high diversification in the Middle East and is closely related with genus *Luciobarbus*. Earlier attempts to clarify the complex taxonomy of the group established four species groups, namely *C. capoeta*, *C. damascina*, *C. tinca*, and *C. trutta* species group. Based on this study, the *C. capoeta* group currently includes nine taxa (seven previous + two newly included members) and all reviewed in this paper based on morphological characters and mitochondrial genes. *Capoeta macrolepis*, revalidated as a distinct species, and *Capoeta fusca* are additional members of the *C. capoeta* group. Molecular time tree shows that the separation of *Capoeta* from its relative *Luciobarbus* was about 12.43–16.99 MYA. Based on the time tree presented herein, the high diversity of *Capoeta* in the Tigris–Euphrates system, the nesting of *Capoeta* within the tetraploid *Luciobarbus* in the mitochondrial trees and the high diversity of *Luciobarbus* in the Tigris–Euphrates system, it is proposed that the origination and diversification of *Capoeta* occurred in the palaeodrainages of the Tigris–Euphrates system. From here, dispersion of *Capoeta* to the other nearby basins could have been possible through freshwater corridors during the Pliocene or Pleistocene.

Keywords *Capoeta* · Molecular analyses · Systematics · Biogeography · Distribution

---

Handling editor: Christian Sturmbauer

H. Zareian · H. R. Esmaeili (✉) · A. Gholamhosseini
Ichthyology and Molecular Systematics Research
Laboratory, Zoology Section, Department of Biology,
College of Sciences, Shiraz University, Shiraz, Iran
e-mail: hresmaeili@shirazu.ac.ir;
hresmaeili22@gmail.com

B. Japoshvili
Hydrobiology and Ichthyology Laboratory, Institute of
Zoology, Ilia State University, Tbilisi, Georgia

M. Özuluğ
Department of Biology, Faculty of Science, Istanbul
University, Istanbul 34134, Turkey

R. L. Mayden
Department of Biology, Saint Louis University, St. Louis,
MO 63103, USA

H. R. Esmaeili
Department of Earth and Environmental Sciences,
Palaeontology & Geobiology, Ludwig-Maximilians-
University Munich, Richard-Wagner-Str. 10,
80333 Munich, Germany

Introduction

The genus *Capoeta* Valenciennes, 1842, with about 30 species, is distributed across southwestern Asia in the Middle East, including the Levant, Mesopotamia, Turkey, and Iran (Fig. 1) (Alwan, 2010; Alwan et al., 2016a, b; Esmaeili et al., 2016; Zareian et al., 2016a, b). The genus is a member of the order Cypriniformes, a clade of fishes that today is recognized as the world's most diverse group of freshwater fishes with 13 families, about 489 genera and 4205 species (Nelson et al., 2016). Species of *Capoeta* are algae scrapers and are medium-sized to large cyprinids characterized by having an elongated, cylindrical body and a short dorsal fin. Scales are usually small; the mouth is in a ventral position (inferior), and the lower lip is covered with a horny sheath. Members of the genus have one pair of barbels (rarely two) and the pharyngeal teeth are arranged in three rows. This combination of characters distinguishes *Capoeta* from all other cyprinids (Krupp, 1985; Krupp & Schneider, 1989). According to Levin et al. (2012), the origin of *Capoeta* was found around the Langhian–Serravallian boundary and diversification within the genus occurred along Middle Miocene-Late Pliocene period. However, both the taxonomic position and number of valid species of *Capoeta* have been the center of debate over the past few decades, owing to high variation in morphological characters and phenotypic plasticity and may be because of unavailability of fresh specimens for some species (see Karaman, 1969; Saadati, 1977; Bănărescu, 1999; Turan et al., 2008; Levin et al., 2012; Alwan et al., 2016b). Karaman (1969) recognized seven species in the genus *Capoeta* and 11 subspecies within *C. capoeta*. Most of *C. capoeta* subspecies have been considered distinct species by subsequent authors (Krupp & Schneider, 1989; Coad & Krupp, 1994; Bănărescu, 1999; Bogutskaya & Naseka, 2004; Turan et al., 2006; Özulug & Freyhof, 2008; Zareian et al., 2016a) and now there are about 30 valid species in this genus (Eschmeyer et al., 2017).

There are three species groups in *Capoeta* in addition to *C. tinca* (Turan et al., 2006) including *C.*

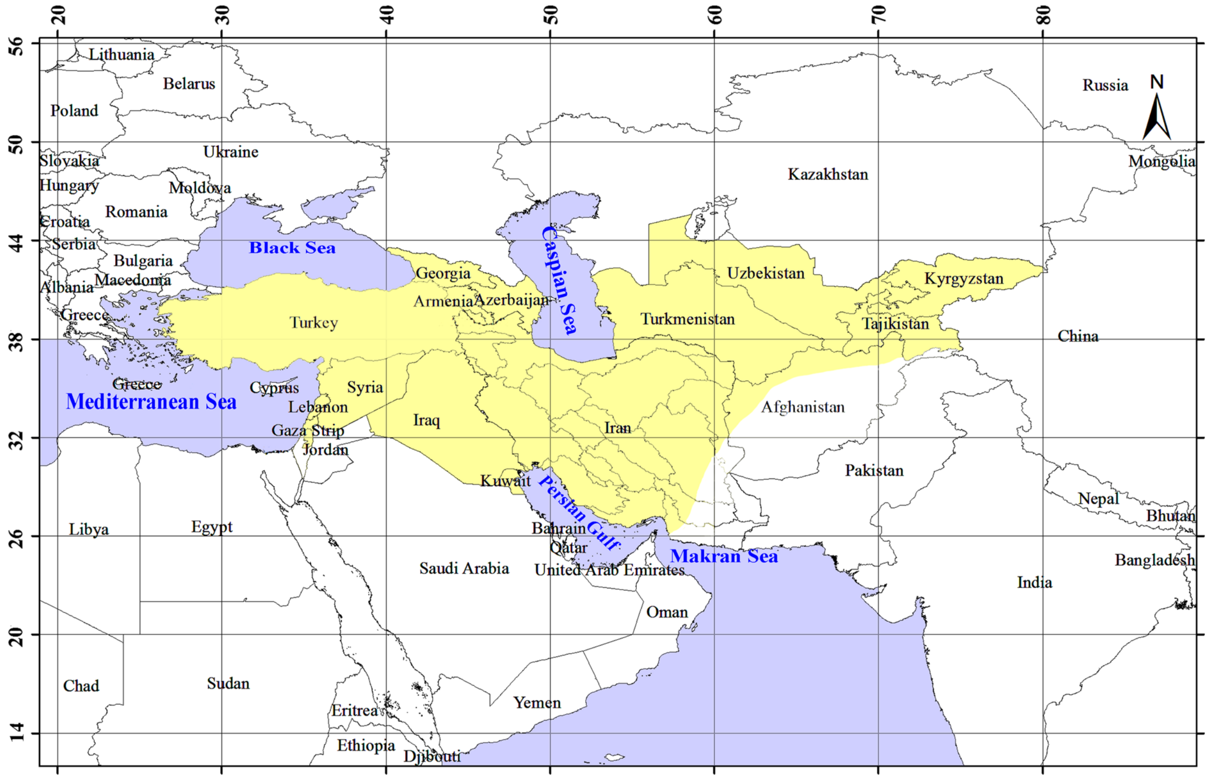


Fig. 1 Schematic map of the distribution of all species of the genus *Capoeta*

capoeta species group (Bănărescu, 1999), *C. trutta* group (Turan et al., 2008), and *C. damascina* group (Alwan et al., 2016b). *C. tinca* species group described only based on geographical distribution and do not supported by morphological and molecular data. Bănărescu (1999) recognized four valid species within the "*C. capoeta* group" including *C. capoeta*, *C. aculeata*, *C. macrolepis*, and *C. umbla* and three subspecies of *C. capoeta* (*C. capoeta, C. sevangi*, *C. gracilis*) as *Capoeta capoeta senso lato*. He reported them only from the Caspian Sea basin in the Sevan Lake, Kura and Aras Rivers, and their tributaries but did not mention Lake Urmia in the distribution range of these subspecies. Now large-scaled *Capoeta* or the *Capoeta capoeta* group includes very closely related taxa characterized by large scales and plain body coloration (absence of irregular black spots on the dorsal half of the body in adults) and include *C. aculeata, C. capoeta, C. gracilis, C. ekmekciae, C. heratensis,* and *C. sevangi*. These taxa are distributed in Aralo-Caspian water bodies (e.g., Kura and Aras River drainages, Lake Sevan drainages, Lake Aral, and many rivers from Sefidrud to Atrak) in the Caspian Sea basin, and Kor, Esfahan, Tigris, Namak, Lut, Hari River, and Kavir basins (Zareian et al., 2016a). This group was referred to as Aralo-Caspian by Levin et al. (2012). Recently, Ghanavi et al. (2016) suggested that *C. capoeta*, *C. ekmekciae*, and *C. sevangi* be considered members of the *C. capoeta* complex, whereas Bănărescu (1999) considered *C. capoeta*, *C. aculeata*, *C. macrolepis*, and *C. umbla* to be members of *C. capoeta* group. Ghanavi et al. (2016) also suggested the presence of a few additional species of *Capoeta* in Iran based on *cytb* sequences, of those, two new suggested species belong to large-scaled *Capoeta* species group, and recently, Jouladeh-Roudbar et al. (2016, 2017) described them as *C. alborzensis* and *C. razii*.

As noted above, the taxonomic status and phylogenetic relationships of the large-scaled species of *Capoeta* remain unresolved and controversial. In the current study, we (i) examine the taxonomic status of the *Capoeta capoeta* species group, (ii) redescribe nine species, (iii) reconstruct mitochondrial phylogenetic relationships within the genus *Capoeta*, and (iv) investigate some aspects of the biogeographic history of the group.

Materials and methods

Taxon sampling

Fish samples were collected from different endorheic (Caspian, Urmia, Namak, Kor, Kavir, Zayandehrud: Esfahan) and exorheic (Persis: Mond, Tigris, following into the Persian Gulf) basins (Fig. 2). After anesthesia, specimens were fixed in 10% formaldehyde and later stored in 70% ethanol for the morphological study. The right pectoral fin or tissue from below the dorsal fin on right side of each specimen was removed using sterile techniques and utensils and preserved in 96% ethanol and numbered separately at the sampling sites for the molecular analyses. To avoid contamination all dissection tools used for sampling tissues were thoroughly cleaned using 96% EtOH between sampling of tissue from individual specimens. No chemicals other than EtOH were used in tissue preservation that would alter the quality of tissues. All specimens were deposited in the Zoological Museum of Shiraz University, Collection of Biology Department, Shiraz, Iran (ZM-CBSU). Each tissue refers to the specific specimens and the tissue number is same of voucher specimen museum number. Measurements were made with a dial caliper and recorded to 0.1 mm. All measurements are made point-to-point, never by projections. Methods for counts and measurements follow Kottelat & Freyhof (2007). Standard length (SL) is measured from the tip of the snout to the end of the hypural complex. The length of the caudal peduncle is measured from behind the base of the last anal-fin ray to the end of the hypural complex, at mid-height of the caudal-fin base. Total lateral line scales are counted from the anterior-most (the first one to touch the shoulder girdle) to the last one at the end of lateral line. The last two branched rays articulating on the same pterygiophore in the dorsal and anal fins are counted as "1½." The holotype is included in the calculation of means and SD. Abbreviations: SL, standard length; TL, total length, HL, lateral head length; K2P, Kimura 2-parameter. IUSHM, Istanbul University Science Faculty Hydrobiology Museum, İstanbul; NMW, Naturhistorisches Museum Wien, Vienna, Austria; IZA, the collection of the Department of Biology and Zoological Museum of the Naples University, Italy; ZM-CBSU, Zoological Museum of Shiraz University,

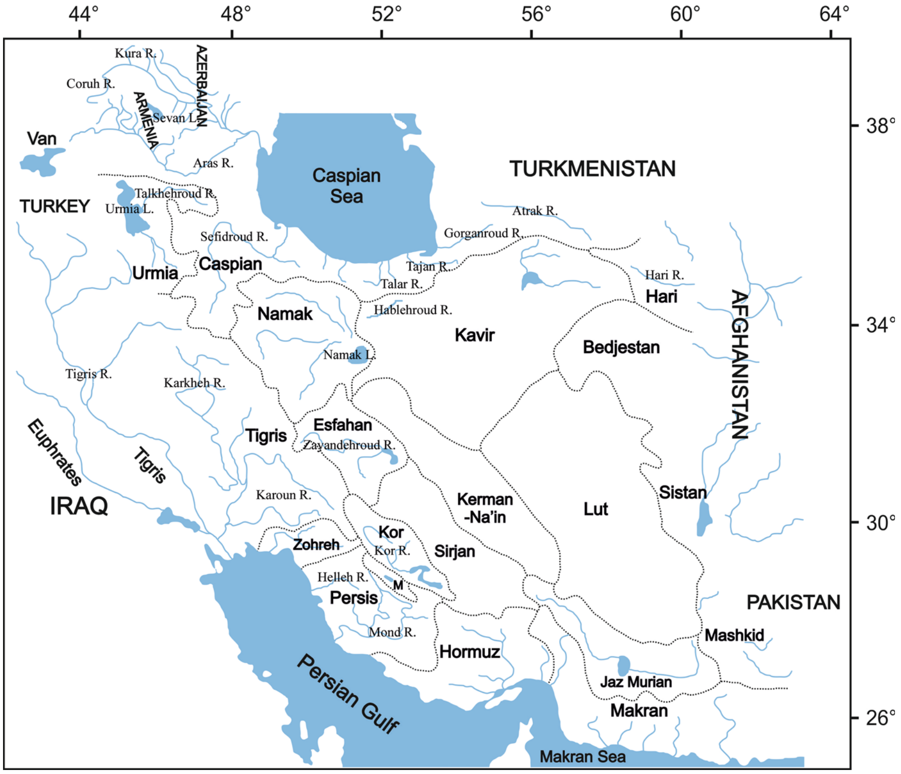


Fig. 2 Drainage basins of Iran and some major rivers and lakes. M: Lake Maharlu basin; L: Lake; R: River (Modified from Esmaeili et al., 2015; Coad, 2016)

Collection of Biology Department, Shiraz, Iran; ZISP, the Zoological Institute, St. Petersburg, Russia.

DNA extraction and amplification protocol

Total genomic DNA was extracted from the preserved tissues (fin and muscle) using standard salt extraction method (Bruford et al., 1992). The fragments of two mitochondrial genes, cytochrome b (*cytb*) and cytochrome subunit one (COI), were amplified using polymerase chain reaction procedure with universal primers L14724 (5′-GTGACTTGAAAAACCACCGTTG-3′) and H15915 (5′-CAACGATCTCCGGTTTAGAAGAC-3′) (Schmidt & Gold, 1993; Perdices et al., 2001) or GluF- (5′AACCACCGTTGTATTCAACTACAA3′) and H-15560 (5′TAGGCRAATAGGAARTATCA3′) (Palumbi, 1996) for *cytb* and FishF1-(5′TCAACCAACCACAAAGACATTGGCAC3′) and FishR1-(5′TAGACTTCTGGGTGGCCAAAGAATCA3′) (Ward et al., 2005) for CO1. Amplified products were evaluated by electrophoresis on a 1% agarose gel. Sequencing was carried out using the above-mentioned forward primers by Macrogen Service Centre (Seoul, South Korea). The obtained sequences were deposited in NCBI Genbank (www.ncbi.nlm.nih.gov) under specific accession numbers (Tables 1, 2, 3). The achieved sequences from this study were combined with additional sequences of *Capoeta* obtained from NCBI GenBank.

Sequence alignment and molecular analyses

Phylogenetic analyses were performed by examining the COI dataset and *cytb* dataset separately and as a combined dataset (COI + *cytb*). The final aligned dataset included 833 bp for *cytb* and 654 bp for COI for each specimen. The sequences were edited and aligned using BioEdit version 7.0.0 (Hall, 1999) and checked by eye for the presence of unexpected stop codons using Mega 6 software (Tamura et al., 2013). Genetic distances were calculated using the Kimura two-parameter implemented in Mega version 6.0 (Tamura et al., 2013). The Bayesian inference (BI) was done using MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003) with six million generations with four Markov Chains Monte Carlo and with a sampling frequency of 100 under the most generalizing model (GTR+G+I) (Huelsenbeck & Ranala, 2004); 10% of

Table 1 List of species used for molecular combined tree. Astricted value indicated accession number of COI gene and others are for *cytb* gene

Species	Basin	Museum no.	Accession no.	References
C. aculeata	Kavir	ZM-CBSU 865	MF664688*	This study
			MF664737	This study
C. aculeata	Namak	ZM-CBSU 1294	MF664690*	This study
			MF664739	This study
C. aculeata	Namak	ZM-CBSU 1450	MF664693*	This study
			MF664741	This study
C. aculeata	Namak	ZM-CBSU 1451	MF664694*	This study
			MF664742	This study
C. fusca	Lut	ZM-CBSU 795	KU312347*	This study
			KU312371	Zareian et al. (2016b)
C. fusca	Lut	ZM-CBSU 796	KU312348*	This study
			KU312372	Zareian et al. (2016b)
C. macrolepis	Kor	ZM-CBSU 1384	MF664720*	This study
			MF664744	This study
C. macrolepis	Kor	ZM-CBSU 1436	KU312345*	Zareian et al. (2016b)
			KU312377	Zareian et al. (2016b)
C. macrolepis	Kor	ZM-CBSU 1437	KU312346*	Zareian et al. (2016b)
			KU312378	Zareian et al. (2016b)
C. gracilis	Zayandehrud	ZM-CBSU 1414	MF664696*	This study
			MF664727	This study
C. gracilis	Zayandehrud	ZM-CBSU 1415	MF664698*	This study
			MF664728	This study
C. gracilis	Zayandehrud	ZM-CBSU 852	MF664699*	This study
			MF664729	This study
C. razii	Kavir	ZM-CBSU 631	MF664702*	This study
			MF664721	This study
C. razii	Caspian Sea	ZM-CBSU 643	MF664705*	This study
			MF664722	This study
C. razii	Caspian Sea	ZM-CBSU 1301	MF664701*	This study
			MF664725	This study
C. razii	Caspian Sea	ZM-CBSU 1302	MF664703*	This study
			MF664726	This study
C. heratensis	Hari	ZM-CBSU 814	KU564289*	Alwan et al. (2016a)
			MF664735	This study
C. heratensis	Hari	ZM-CBSU 819	MF664712*	This study
			MF664736	This study
C. sevangi	Urmia	ZM-CBSU 668	MF664684*	This study
			MF664730	This study
C. sevangi	Urmia	ZM-CBSU 669	MF664685*	This study
			MF664731	This study
C. sevangi	Urmia	ZM-CBSU 670	MF664686*	This study
			MF664732	This study
C. capoeta	Kura	ZM-CBSU 1726	MF664708*	This study
			MF664747	This study

Table 1 continued

Species	Basin	Museum no.	Accession no.	References
C. capoeta	Kura	ZM-CBSU 1728	MF664710*	This study
			MF664748	This study
C. capoeta	Kura	ZM-CBSU 1729	MF664711*	This study
			MF664749	This study
C. buhsei	Namak	ZM-CBSU 1289	KU564292*	Alwan et al. (2016b)
			MF621312	This study
C. buhsei	Namak	ZM-CBSU 1290	KU564293*	Alwan et al. (2016b)
			MF621311	This study
C. buhsei	Namak	ZM-CBSU 1292	MF621275*	This study
			MF621310	This study
C. buhsei	Namak	ZM-CBSU 1299	KU312349*	Zareian et al. (2016b)
			KU312369	Zareian et al. (2016b)
C. buhsei	Namak	ZM-CBSU 1300	KU312350*	Zareian et al. (2016b)
			KU312370	Zareian et al. (2016b)
C. coadi	Tigris	ZM-CBSU 1447	KU564297*	Alwan et al. (2016a)
			KU564303	Alwan et al. (2016a)
C. coadi	Tigris	ZM-CBSU 1448	KU564298*	Alwan et al. (2016a)
			KU564304	Alwan et al. (2016a)
C. coadi	Tigris	ZM-CBSU 1458	KU564294*	Alwan et al. (2016a)
			KU564305	Alwan et al. (2016a)
C. coadi	Tigris	ZM-CBSU 1459	KU564295*	Alwan et al. (2016a)
			KU564306	Alwan et al. (2016a)
C. saadii	Persis	ZM-CBSU 822	KU312362*	Zareian et al. (2016b)
			KU312374	Zareian et al. (2016b)
C. saadii	Persis	ZM-CBSU 824	KU312357*	Zareian et al. (2016b)
			MF621302	This study
C. saadii	Persis	ZM-CBSU 825	KU312361*	Zareian et al. (2016b)
			KU312373	Zareian et al. (2016b)
C. saadii	Persis	ZM-CBSU 1421	MF621266*	This study
			KU564309	Alwan et al. (2016a)
C. saadii	Persis	ZM-CBSU 1422	MF621267*	This study
			KU564310	Alwan et al. (2016a)
C. saadii	Persis	ZM-CBSU 1423	MF621268*	This study
			MF621318	This study
C. saadii	Kor	ZM-CBSU 1426	KU564299*	Alwan et al. (2016a)
			KU564312	Alwan et al. (2016a)
C. saadii	Kor	ZM-CBSU 1427	KU564300*	Alwan et al. (2016a)
			KU564313	Alwan et al. (2016a)
C. mandica	Persis	ZM-CBSU 1433	KU564301*	Alwan et al. (2016a)
			KU564307	Alwan et al. (2016a)
C. mandica	Persis	ZM-CBSU 1434	KU564302*	Alwan et al. (2016a)
			KU564308	Alwan et al. (2016a)
C. anamisensis	Minab	ZM-CBSU 1416	KU312342*	Zareian et al. (2016b)
			KU312379	Zareian et al. (2016b)

Table 1 continued

Species	Basin	Museum no.	Accession no.	References
C. anamisensis	Minab	ZM-CBSU 1417	KU312343*	Zareian et al. (2016b)
			KU312380	Zareian et al. (2016b)
C. anamisensis	Hasan Langi	ZM-CBSU 1475	KU312341*	Zareian et al. (2016b)
			KU312381	Zareian et al. (2016b)
Cyprinus carpio			KU050703	

Table 2 List of species used for molecular analysis for *cytb* with GenBank accession number

Species	Accession no.	Country, Basin	References
C. aculeata	MF664740	Iran, Namak	This study
C. aculeata	MF664741	Iran, Namak	This study
C. aculeata	MF664742	Iran, Namak	This study
C. aculeata	MF664737	Iran, Kavir	This study
C. sevangi	MF664734	Iran, Urmia	This study
C. macrolepis	MF664743	Iran, Tigris	This study
C. macrolepis	MF664745	Iran, Kor	This study
C. macrolepis	MF664744	Iran, Kor	This study
C. gracilis	MF664727	Iran, Zayandehrud	This study
C. gracilis	MF664728	Iran, Zayandehrud	This study
C. gracilis	MF664729	Iran, Zayandehrud	This study
C. razii	MF664721	Iran, Caspian Sea	This study
C. razii	MF664722	Iran, Caspian Sea	This study
C. razii	MF664723	Iran, Caspian Sea	This study
C. razii	MF664724	Iran, Caspian Sea	This study
C. razii	MF664725	Iran, Caspian Sea	This study
C. razii	MF664726	Iran, Caspian Sea	This study
C. sevangi	MF664730	Iran, Urmia	This study
C. sevangi	MF664731	Iran, Urmia	This study
C. sevangi	MF664732	Iran, Urmia	This study
C. sevangi	MF664733	Iran, Urmia	This study
C. capoeta	MF664747	Georgia, Kura	This study
C. capoeta	MF664748	Georgia, Kura	This study
C. capoeta	MF664749	Georgia, Kura	This study

the trees were discarded as burnin. Maximum Likelihood (ML) (Felsenstein, 1985) gene trees were inferred with RAxML 7.2.5 (Stamatakis, 2006) to examine the robustness the Bayesian results. The most appropriate sequence evolution model for the given data (GTR+G) was determined using the Mega software (Tamura et al., 2013). Parsimony haplotype networks were generated to infer relationships among 129 *cytb* and 182 COI sequences of *Capoeta* species using HaploView software (Barrett et al., 2005).

Molecular clocks and divergence time

Divergence times among the clades from *cytb* data were estimated using a relaxed clock model in BEAST v1.7.2 (Drummond & Rambaut, 2007). Because fossil evidence for Barbinii is well known time, calibration of the molecular clock was done following Levin et al. (2012). Branch rates were drawn following an uncorrelated lognormal distribution and a Yule speciation prior (Drummond et al., 2006). The analysis was run

Table 3 List of species used for molecular analysis for COI with GenBank accession number

Species	Accession no.	Country, Basin	References
C. aculeata	MF664689	Iran, Namak	This study
C. aculeata	MF664691	Iran, Namak	This study
C. gracilis	MF664697	Iran, Zayandehrud	This study
C. gracilis	MF664698	Iran, Zayandehrud	This study
C. macrolepis	MF664719	Iran, Kor	This study
C. macrolepis	MF664714	Iran, Kor	This study
C. macrolepis	MF664716	Iran, Kor	This study
C. macrolepis	MF664713	Iran, Kor	This study
C. macrolepis	MF664715	Iran, Kor	This study
C. macrolepis	MF664718	Iran, Kor	This study
C. sevangi	MF664682	Iran, Aras	This study
C. sevangi	MF664683	Iran, Aras	This study
C. xazari	MF664706	Iran, Kavir	This study
C. aculeata	MF664692	Iran, Namak	This study
C. aculeata	MF664687	Iran, Namak	This study

for 100 million generations under the GTR model with parameters sampled every 1000 steps. Tracer v1.4 (Drummond & Rambaut, 2007) was used to visualize the results following a preburnin of 10%. Finally, the resulting trees were summarized with the TreeAnnotator v1.7.4 and the time tree was visualized in FigTree v.1.3.1.

A total of 169 COI and 117 *cytb* sequences from individuals of *Capoeta* were used for phylogenetic analyses. A total of 134 sequences (67 COI and 67 *cytb*) were used for combined dataset analyses and 47 *cytb* sequences were used for the molecular time tree. The combined data set analyses were conducted only using sequences extracted from the same specimens. Molecular time tree was conducted for nearly a sequence per species per basin.

In phylogenetic analyses of COI, *cytb* and combined data set sequences, trees were rooted using the *Cyprinus carpio*. Molecular time tree was rooted using the *Cyprinus carpio, Cyprinion macrostomus*, and *Aulopyge huegelii* as implemented by Levin et al. (2012).

Ethics statement

This study was carried out in strict accordance with applicable national and international guidelines. The research work in Iran was funded by Shiraz University and was approved by the Ethics Committee of Biology Department (SU-909789). The field study did not involve endangered or protected species.

Results

This study examined COI and *cytb* sequences in phylogenetic analyses that were analyzed separately and in combination, and the most comprehensive morphological detailed framework of the *Capoeta capoeta* complex species group in Iran to date.

COI-based phylogenetic relationships

Tables 4 and 5 list the pairwise genetic distances and diagnostic nucleotide substitutions in the large-scaled *Capoeta* species group for COI nucleotide sequences. The nucleotide composition of the COI sequences was G-deficient (16.9%), whereas similar frequencies were observed for the other three nucleotides (A: 27.0%, C: 29.3%, T: 26.8%). The range of genetic distance among large-scaled *Capoeta* species varied from 0.38 (between *Capoeta sevangi* and *C. capoeta*) to 2.94 (between *C. capoeta* and *C. fusca*).

The two different phylogenetic analyses (ML and BI) based on COI sequences for *Capoeta* species produced similar topologies which confirm existence of three groups in the genus *Capoeta* including Anatolian-Iranian, Aralo-Caspian and Mesopotamian. Two main subclades were recognized in the *C.*

Table 4 Mean genetic distance for COI gene between species of the large-scaled *Capoeta* species group

Species	1	2	3	4	5	6	7
C. aculeata (1)							
C. capoeta (2)	2.58						
C. gracilis (3)	0.48	2.07					
C. heratensis (4)	2.58	2.37	2.06				
C. fusca (5)	1.09	2.94	0.80	2.92			
C. macrolepis (6)	0.78	2.60	0.49	2.59	1.11		
C. sevangi (7)	2.58	0.38	2.07	2.37	2.94	2.60	
C. razii (8)	0.84	1.84	0.55	1.83	1.17	0.85	1.84

Table 5 Diagnostic nucleotide substitutions found in COI of large-scaled *Capoeta* species group

	5588	5594	5597	5612	5651	5669	5684	5690	5732	5733	5765	5774	5795
C. aculeata	C	T	T	T	A	C	T	C	A	C	T	T	A
C. capoeta	T	T	T	C	A	T	C	C	A	C	C	T	A
C. gracilis	C	T	T	T	A	C	T	C	A	C	T	T	A
C. fusca	C	T	T	T	A	C	T	C	A	T	T	T	G
C. heratensis	C	C	A	T	G	T	T	T	A	C	C	C	A
C. macrolepis	C	T	T	T	A	C	T	C	G	C	T	T	A
C. sevangi	C	T	T	C	A	C	C	C	A	T	T	T	G
C. razii	C	T	T	T	A	T	T	C	A	C	T	T	A

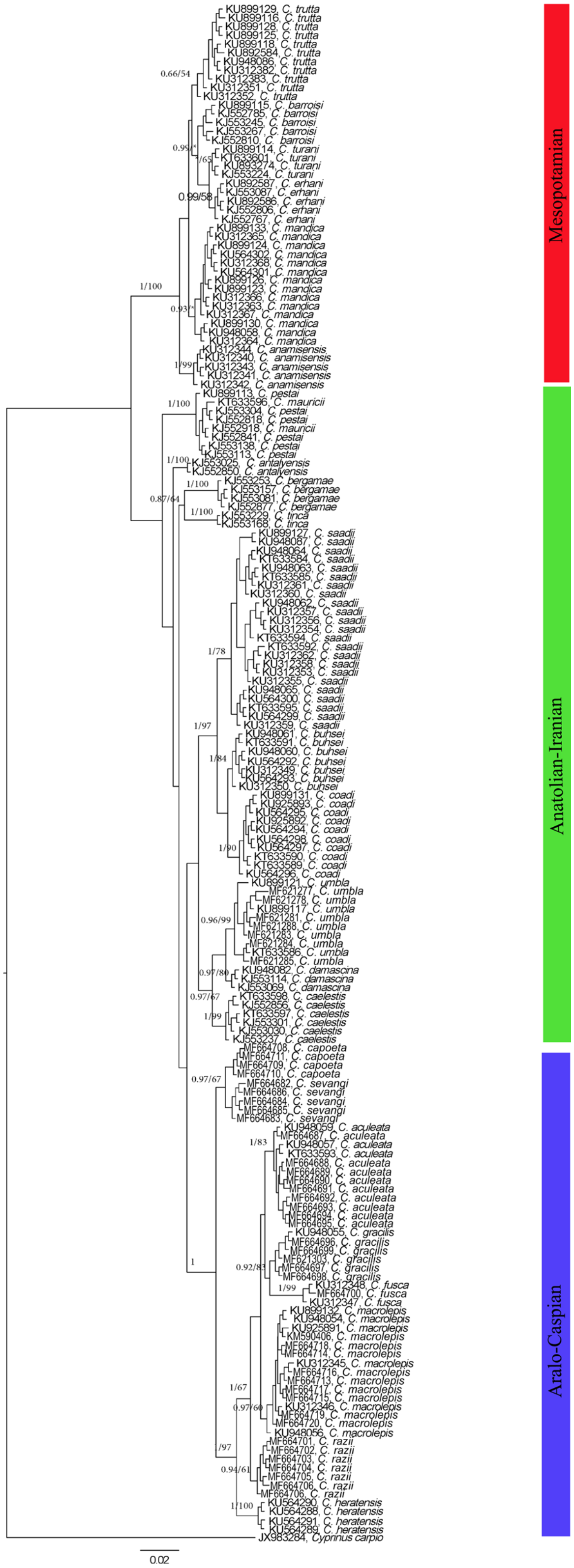
	5813	5816	5834	5852	5873	5876	5945	5951	5966	6029	6035	6077	6095	6116
C. aculeata	A	C	T	G	C	T	A	C	G	G	T	A	G	T
C. capoeta	G	T	C	G	C	C	G	C	A	A	C	A	G	C
C. gracilis	A/G	T	T	G	C	T	A	C	A	G	T	A	A	T
C. fusca	A	T	T	G	C	T	A	C	A	G	T	G	G	T
C. heratensis	G	T	T	G	T	C	A	C	A	G	C	A	G	T
C. macrolepis	A	T	T	G	C	T	A	T	A	G	T	A	G	T
C. sevangi	G	T	C	A	C	T	A	C	A	A	C	A	G	C
C. razii	A	T	T	G	C	T	A	C	A	G	C	A	G	T

Nucleotide position relative to *Luciobarbus capito* complete mitochondrial genome

capoeta or Aralo-Caspian group (Fig. 3). The first included specimens of *C. capoeta* from Kura River (type locality of *C. capoeta*) and those of *C. sevangi* from Aras River and Urmia basin. The second subclade consists of all other large-scaled species of *Capoeta*. In this subclade, individuals of *C. heratensis* formed a monophyletic group sister to other species. The validated *C. macrolepis*, *Capoeta aculeata, C. gracilis* and also *C. razii* formed distinct clades.

Analysis of this gene also indicated that only *C. buhsei*, *C. caelestis*, *C. coadi*, *C. damascina, C. saadii*, and *C. umbla* were nested in the *C. damascina* group as was also mentioned by Alwan et al. (2016b) (COI sequences were available for *C. kosswigi*), but with moderately supporting values (posterior probability of 0.87 and bootstrap of 64) which might be as a consequence of the reduce number of characters of this gene. Hereafter, we refer these species to the *Capoeta damascina* complex group (belong to Anatolian-Iranian *Capoeta* group) to differentiate them from the *C. capoeta* group (Aralo-Caspian *Capoeta* group) and the *C. trutta* group (Mesopotamian *Capoeta* group).

Fig. 3 Bayesian tree inferred from COI sequences. Numbers left of the slash indicate posterior probabilities; numbers right of the slash are the bootstrap support values for 10,000 replicates in Maximum Likelihood, using RaxML. Asterisks (*) indicate less than 50% Maximum Likelihood support for the node



A total of 54 haplotypes were recovered based on COI sequences of 182 individuals of *Capoeta* (Fig. 4). Each species has its own haplotype, but in the *C. trutta* group, *C. erhani* share a haplotype with *C. turani*. In the Anatolian-Iranian *Capoeta*, *C. pestai* and *C. mauricii* share a common haplotype. No haplotypes were shared among populations of the other species of the large-scaled *Capoeta* or the Aralo-Caspian group. With four haplotypes, *Capoeta macrolepis* was the most diverse taxon in this network.

Cytb-based phylogenetic relationships

The nucleotide composition of *cytb* sequences was G-deficient (14.8%), whereas similar frequencies were observed for the other three nucleotides (A: 28.3%, C: 29.3%, T: 27.7%).

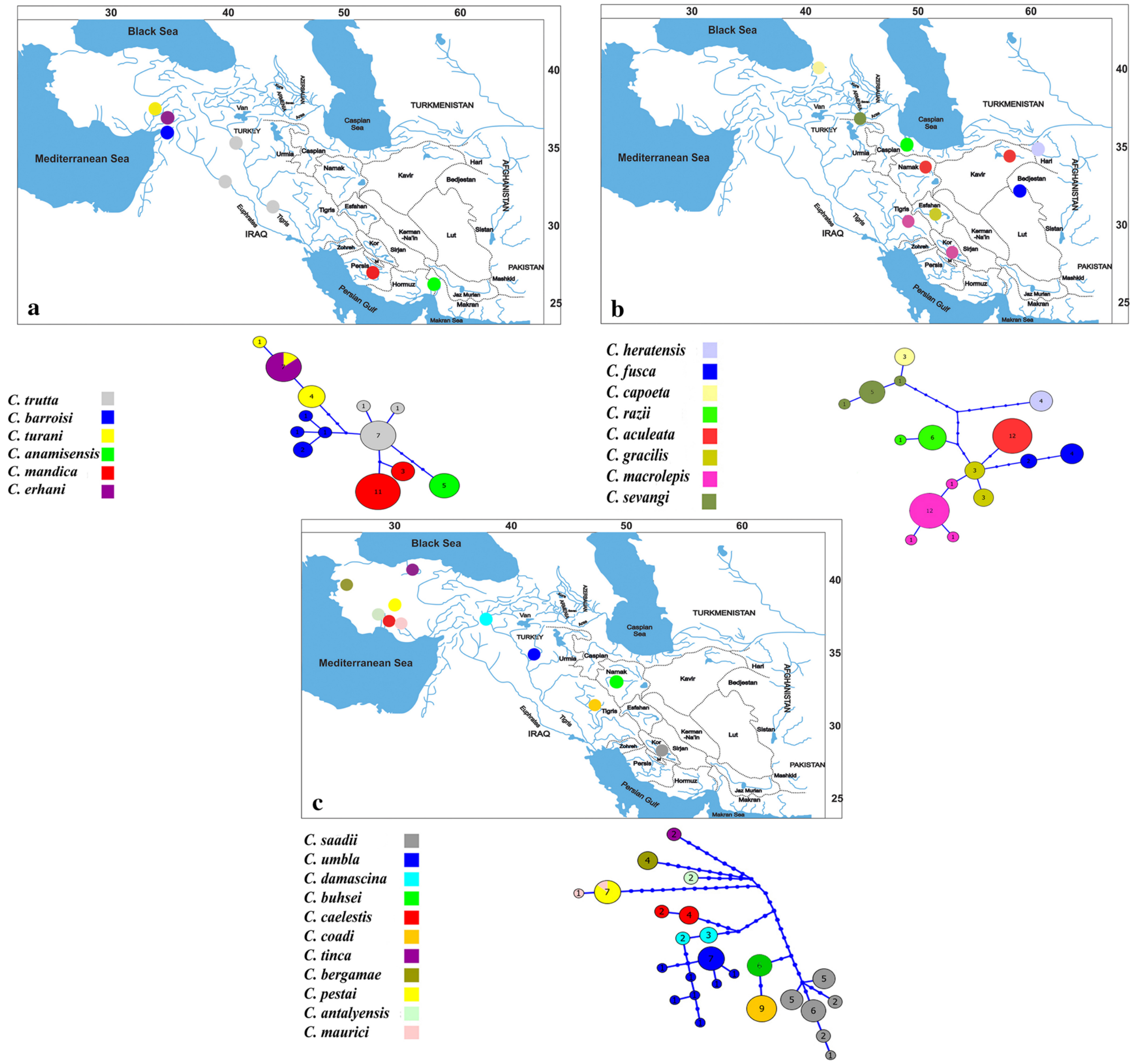


Fig. 4 Haplotype networks of *Capoeta* spp. based on COI. Each species is marked with a different color and eachcircle represents one haplotype. Circled area is proportional to the haplotype frequency. Blue dots on connecting lines indicate number of base substitutions. Distribution of haplotypes are presented on the study area map which included basin drainages. **A** *C. trutta* group; **B** Large-scaled *Capoeta*; **C** Small-scaled *Capoeta*

The two different phylogenetic analyses (ML and BI) produced similar topologies based on *cytb* gene for *Capoeta* species.

In this analysis, the *Capoeta capoeta* species clade corresponds to the traditionally large-scaled *Capoeta* group plus some other species with relatively large scales on the body; this clade included two main subclades (Fig. 5). These included, the first subclade, *C. capoeta* from Kura River (Tbilisi, type locality of *C. capoeta*) + *C. ekmekciae* from Çoruh River at Borçka, Turkey + *C. sevangi* from Urmia Lake, the Iranian Aras River drainage, and the Lake Sevan basin (type locality of *C. sevangi*). Phylogenetic relationships within this subclade were not completely resolved as the genetic distances between species were low (0.60 between *C. capoeta* and *C. sevangi*) in comparison to other *Capoeta capoeta* species group (Table 6). However, sequences of *C. capoeta*, *C. ekmekciae*, and *C. sevangi* were clustered together, and can be considered as a distinct evolutionary unit. The second subclade included all other species referred to large-scaled *Capoeta* group and sister to the first subclade.

The large-scaled *Capoeta* specimens from Zayanehrud (*C. gracilis*), Kavir and Namak Lake basins (*C. aculeata*), and Kor and Tigris basins (*C. macrolepis*) (Fig. 2) that were traditionally considered *C. aculeata* were nested in the second subclade. Populations from the south Caspian Sea (Sefidrud to Atrak River drainages) and the northern part of the Kavir basin were also nested in the same subclade identified as *C. razii*. Sequences of *C. alborzensis* which used in original description (KM459687, KM459688, KM459695, KM459696, KY365752, KY365753, and KY365754) grouped together with the sequences of the *C. aculeata* from the Lake Namak (type locality) and Kavir basins (Fig. 5).

The pairwise distances between species of the large-scaled *Capoeta* group for *cytb* are provided in Table 6. With respect to interspecific genetic divergences, distinct differences were found between *C. macrolepis* and *Capoeta gracilis* and other large-scaled *Capoeta* species (Table 6). The range of genetic distance among large-scaled *Capoeta* species varied from 0.60 (between *C. capoeta* and *C. sevangi*) to 3.53 (between *C. ekmekciae* and *C. fusca*). Table 7 lists the unique and diagnostic nucleotide substitutions found in the mtDNA *cytb* in large-scaled *Capoeta* group.

A total of 103 haplotypes were recovered from *cytb* sequences of 129 *Capoeta* individuals (Fig. 6). Each species possesses its own unique haplotype. A close relationship was found in this network among *C. damascina*, *C. kosswigi*, and *C. umbla*. No haplotypes were shared among populations of different species of the Aralo-Caspian group. With six haplotypes, *Capoeta razii* was the most diverse taxon.

COI + *cytb* phylogenetic relationships

In the combined data set tree, three major clades were recovered, including *C. capoeta* species group, *C. damascina* species group and *C. trutta* species group (Fig. 7). In the large-scaled clade, *C. capoeta* and *C. sevangi* grouped together and formed a sister clade to other species. All other large-scaled *Capoeta* species also formed distinct clades. *Capoeta aculeata*, *C. geacilis* and *C. macrolepis* which traditionally identified as *C. aculeata*, formed a distinct subclade.

Divergence time

Molecular timed tree is illustrated in Fig. 8. Divergence for *Capoeta* and *Luciobarbus* was estimated to have occurred 16.4 MYA (12.43–16.92). The first clade to diverge in *Capoeta* was the Mesopotamian group and its separation occurred 14.35 MYA (9.94–16.65); the separation of two clades (*Capoeta damascina* and *C. capoeta* groups) occurred in 9.4 MYA (6.37–12.3).

In the *C. trutta* group, the most divergent species was *C. mandica,* which separated from others of *C. trutta* species group about 2.24 MYA [1.13–3.71]. Following this divergence *C. anamisensis* separated in 1.83 MYA [0.92–3.05], *C. trutta* in 1.33 MYA [0.57–2.32] and *C. barroisi* from *C. turani* in 0.7 MYA [0.16–1.56].

Divergence in the Aralo-Caspian group began with the separation of two clades. The first species clade is from northwest Iran, Armenia, Azerbaijan, and Turkey and the second species clade includes the Iranian species of *Capoeta* at 3.3 MYA [1.99–5.01]. In the first clade, the northern-most species of *C. capoeta* were first separated in 1.78 MYA [0.86–3.19], followed by *C. ekmekciae* in 1.44 MYA [0.86–3.19], and *C. sevangi* in 0.72 MYA [0.62–2.53]. In the second species clade, Iranian species of *Capoeta*, the first separated species was *C. heratensis* which

Fig. 5 Bayesian tree inferred from *cytb* sequences. Numbers left of the slash indicate posterior probabilities; numbers right of the slash are bootstrap support values for 10,000 replicates in Maximum Likelihood, using RaxML. Asterisks (*) indicate less than 50% Maximum Likelihood support for the node

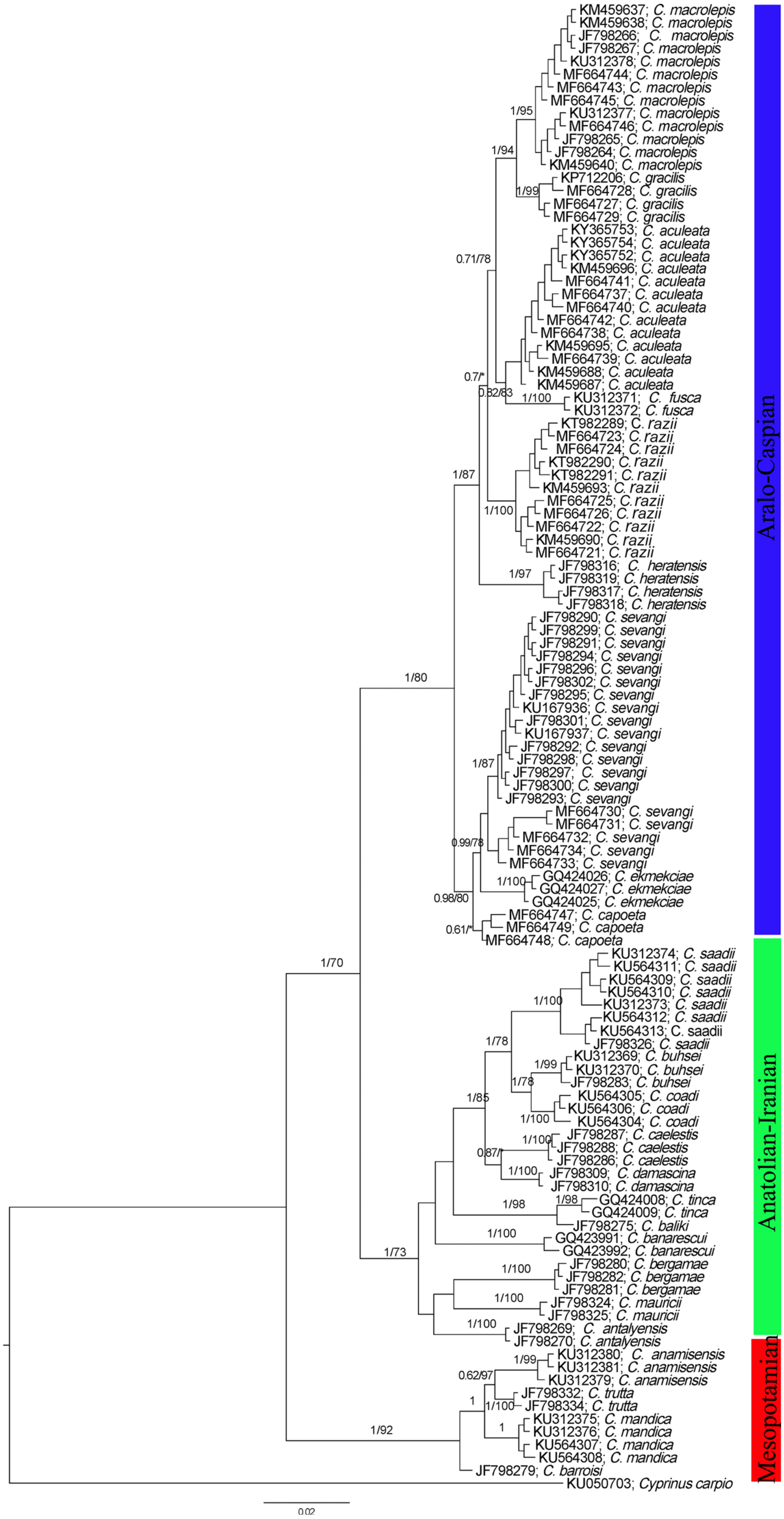


Table 6 Mean genetic distance for *cytb* gene between species of the large-scaled *Capoeta* species group

Species	1	2	3	4	5	6	7	8
C. aculeata (1)								
C. capoeta (2)	1.45							
C. gracilis (3)	1.30	1.78						
C. ekmekciae (4)	2.38	1.32	3.02					
C. heratensis (5)	1.53	1.68	1.90	3.00				
C. fusca (6)	1.78	2.42	2.41	3.53	2.39			
C. macrolepis (7)	1.33	1.84	1.17	3.04	1.98	2.43		
C. sevangi (8)	1.89	0.60	2.29	1.60	2.12	2.64	2.04	
C. razii (9)	1.21	1.70	1.54	2.94	1.82	2.33	1.62	2.21

diverged in 2.36 MYA [1.39–3.58]; and then two groups separated in 2.03 MYA [1.22–3.1]. The first divergence event was between *C. razii* and *C. gracilis* plus *C. macrolepis* in 1.78 MYA [0.96–2.75], and then *C. gracilis* and *C. macrolepis* were separated in 1.16 MYA [0.46–2.02]. *C. fusca* and *C. aculeata* separated in 1.52 MYA [0.7–2.5].

In the Iranian-Anatolian group, *Capoeta sieboldii* was the first species to diverge at 7.25 MYA [4.89–9.84]; other species separated into two clades that diverged at 6.31 MYA [4.27–8.52]. The first clade includes *C. bergamae*, *C. banarescui*, *C. antalyensis*, *C. baliki*, *C. mauricii*, and *C. tinca* and the second belongs to the *C. damascina* species group. The clade inclusive of *C. bergamae* and *C. mauricii* and the clade inclusive of *C. banarescui*, *C. antalyensis*, *C. baliki*, and *C. tinca* separated at 5.88 MYA [3.85–8.01], and *C. bergamae* and *C. mauricii* separated in 4.75 MYA [2.76–6.99]. *Capoeta banaresqui* was separated at 4.46 [2.7–6.4]; *C. antalyensis* separated at 1.69 MYA [0.77–2.9], and *C. baliki* and *C. tinca* separated in 0.63 MYA [0.17–1.32].

In the *C. damascina* species group, *C. buhsei*, *C. coadi*, and *C. saadii* separated from *C. caelestis*, *C. damascina*, and *C. umbla* at 4.24 MYA [2.7–6.04]. *Capoeta caelestis* diverged at 2.67 MYA [1.27–4.38] but separation of *C. damascina* and *C. umbla* was vague. In the second clade *C. saadii* separated at 1.54 MYA [0.76–2.53] and *C. buhsei* and *C. coadi* diverged in 2.69 MYA [1.35–4.17].

Morphology and taxonomic accounts

The molecular data and phylogenetic analyses examined above clearly indicate the occurrence of eight independent lineages valid as species within the *Capoeta capoeta* species group (*C. aculeata*, *C. capoeta*, *C. heratensis*, *C. gracilis*, *C. fusca*, *C. macrolepis*, *C. sevangi*, and *C. razii*). Below we provide identification key and taxonomic accounts of these species. Some morphometric data are shown in Tables 8 and 9.

Key to the Iranian large-scaled *Capoeta capoeta* group

Several large-scaled *Capoeta* species are distinguished by the number of the gill rakers on the first arch and by the size of scales on the body.

(1a) More than 58 lateral line scales ………… (*C. damascina* and *C. trutta* groups)
(1b) Lateral line scales equal to or less than 58 ………… (Large-scaled group) 2
(2a) Two pairs of barbels ………… *C. heratensis*
(2b) One pair of barbels …………3
(3a) Usually 7 soft dorsal fin rays; 11–15 total gill rakers ……………… *C. fusca*
(3b) Usually 8 soft dorsal fin rays; 16–30 total gill rakers …………… 4
(4a) Predorsal scales fewer than 18, scales along predorsal distance on the lateral line fewer than 19, scales along prepelvic distance on the lateral line fewer than 22 …………… 5
(4b) Predorsal scales equal to or more than 18, scales along predorsal distance on the lateral line equal to or more than 19, scales along prepelvic distance on the lateral line equal to or more than 22 …………… 7
(5a) Predorsal scales equal to or less than 15 …………… *C. aculeata* (Kavir and Namak)
(5b) Predorsal scales greater than 15 …………… 6

Table 7 Diagnostic nucleotide substitutions found in *cytb* for species in the of large scaled *Capoeta* species group. Nucleotide position relative to *Luciobarbus capito* complete mitochondrial genome

	14367	14421	14436	14460	14481	14565	14572	14625	14634	14643	14671	14697	14715	14721	14733
C. aculeata	T	A	A	G	C	T	A	A	C	T	G	A	G	G	A
C. capoeta	T	A	A	C	C	C	G/A	A	C	T	G	A	G	G	A
C. gracilis	C	A	A	G	C	C	A	A	C	T	G	A	G	G	G
C. ekmekciae	T	A	A	G	C	T	A	A	C	T	A	A	G	G	A
C. heratensis	–	A	A	G	C	C	G	A	C	T	G	G	G	G	A
C. fusca	T	A	G	G	C	C	G	A	C	T	A	A	A	C	A
C. macrolepis	T	G	A	G	C	C	A	A	T	T	G	A	G	G	A
C. sevangi	–	G	A	C	C	C	A	A	C	T	G	A	A	G	A
C. razii	T	A	A	G	T	C	A	G	C	C	G	A	G	G	A

	14736	14739	14745	14760	14766	14767	14771	14778	14790	14811	14820	14853	14872	14877	14884
C. aculeata	C	C	T	A	C	C	C	A	T	C	G	C	C	A	A
C. capoeta	C	C	T	A	C	T	C	A	T	C	G	C	C	A	A
C. gracilis	C	C	T	G	C	C	C	A	T	C	G	C	T	A	G
C. ekmekciae	C	T	T	A	T	T	T	A	T	T	G	T	C	A	A
C. fusca	A	C	T	A	C	C	C	A	T	C	A	C	C	A	A
C. heratensis	C	C	C	A	C	C	C	A	C	C	G	C	C	A	A
C. macrolepis	C	C	T	G	C	C	C	A	T	C	G	C	C	G	A
C. sevangi	C	C	T	A	C	T	C	A	T	C	G	C	C	A	A
C. razii	C	C	T	A	C	C	C	G	T	C	G	C	C	A	A

	14916	14921	14946	14949	14982	15006	15012	15024	15039	15067	15081	15090	15093	15114	15126
C. aculeata	T	A	T	A	T	G	A	A	A	T	A	C	C	G	A
C. capoeta	C	A	C	A	C	A	A	A	A	T	A	T	C	T	A
C. gracilis	T	A	C	A	C	G	A	A	A	T	A	C	G	G	A
C. ekmekciae	C	C	C	A	C	A	A	A	A	T	A	T	C	T	A
C. heratensis	T	A	C	A	C	G	G	A	G	T	A	C	C	G	G
C. fusca	T	A	T	G	C	G	A	G	A	T	G	C	C	G	A
C. macrolepis	T	A	C	A	C	G	A	A	A	C	A	C	G	G	A
C. sevangi	C	A	C	A	C	A	A	A	A	T	A	T	C	T	A
C. razii	T	A	C	A	C	G	A	A	A	T	A	C	C	G	A

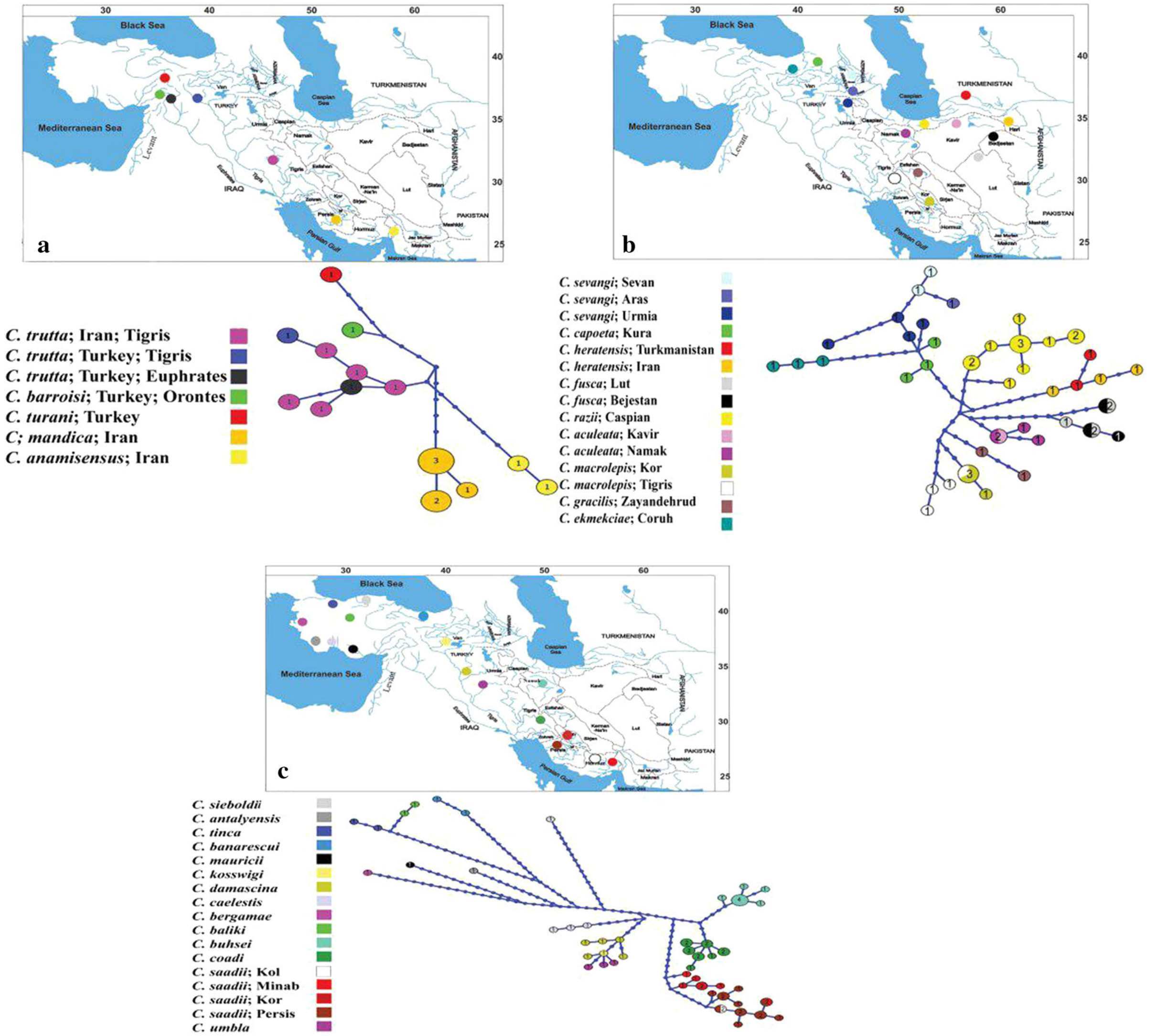


Fig. 6 Haplotype networks of *Capoeta* spp. based on *cytb* gene. Each species is marked with a different color and each circle represents one haplotype. Circle area is proportional the haplotype frequency. Blue dots on connecting lines indicate number of base substitutions. Distribution of haplotypes are presented on the study area amp which included basin drainages. **A** *C. trutta* group; **B** Large-scaled *Capoeta*; **C** Small scaled *Capoeta*

(6a) Sporadic pigments on lower operculum, 8–9 (usually 8) pelvic fin rays, 20–25, (usually 22–25) gill rakers on the first arch …………… *C. gracilis* (Zayandehrud)

(6b) No sporadic pigments on lower operculum; pigments only on lateral view of operculum, 7–10 (usually 9) pelvic fin rays, 17–22 (usually 18–22) gill rakers on the first arch ……………… *C. macrolepis* (Kor and Tigris)

(7a) Total vertebrae 44–47 ……………… *C. sevangi* (Aras and Urmia)

(7b) Total vertebrae fewer than 44 …………… *C. razii*

Capoeta Valenciennes, 1842

The genus *Capoeta* was established by Valenciennes [A.] in Cuvier and Valenciennes (1842): 278 for *Cyprinus capoeta* from the Kura River near Tiflis, Caspian Sea basin (but see Turan et al., 2006, pp. 151–152 for gender considerations). The genus

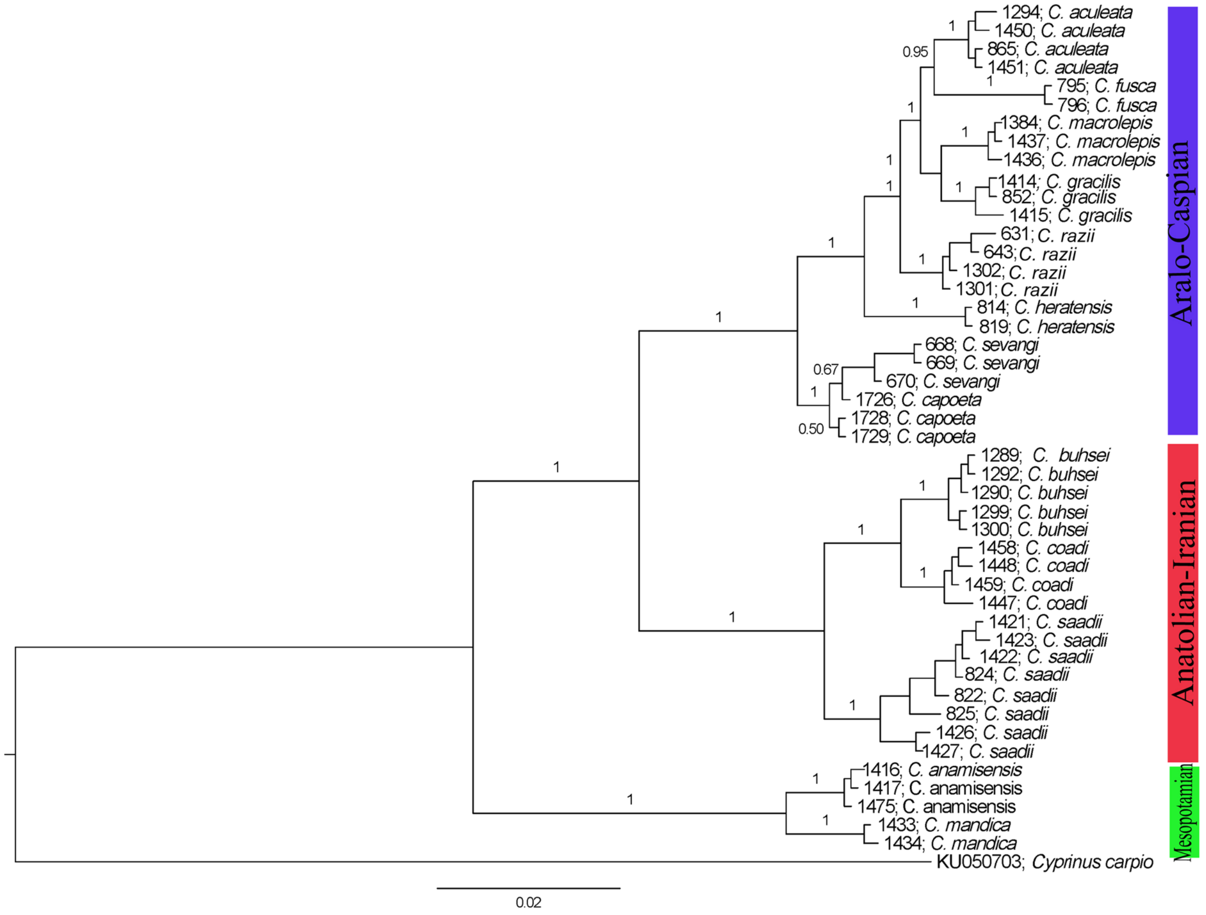


Fig. 7 The Bayesian tree based on the combination of COI and *Cytb* datasets. Numbers above branches are posterior probabilities

Capoeta include about 30 species distributed in such a wide area of southwest Asia. The name *Capoeta* is derived from the Armenian and Georgian name for female *Capoeta capoeta* packed with eggs, namely "Kapwaeti" (Coad, 2017).

Diagnosis The genus *Capoeta* is characterized by a compressed to rounded and moderately elongate body, small to moderately large scales (lateral line scale counts 37–99), scales at the anal-fin base and anus not usually enlarged (sometimes variably enlarged as is the case with certain cyprinids), an inferior and transverse mouth, lower jaw with a sharp, horny sheath, barbels absent or in 1 or 2 pairs, dorsal fin short (usually 7–9 branched rays) with the last unbranched ray thickened and bearing serrations (serrations sometimes reduced to absent), short anal fin (usually five branched rays), gill rakers short, moderate in number to numerous, pharyngeal teeth in three rows with spoon-shaped and truncate tips, gut very long and coiled (ca. 7–10 times body length) and mostly of uniform color, and a black peritoneum (Coad, 2014).

Distribution The genus *Capoeta* has a wide distribution across southwestern Asia in the Middle East, including the Levant, Mesopotamia, Turkey, and Iran (Fig. 1). A point distribution map of all nine species of the *Capoeta* species group examined herein is presented in Fig. 9.

Remarks The genus *Capoeta* was considered a synonym of *Varicorhinus* Rüppell, 1835 by Lévêque & Daget (1984). *Varicorhinus* is now considered a synonym of *Labeobarbus* Rüppell 1835 (see Vreven et al., 2016 for further details) and *Capoeta* considered as a monophyletic genus using complete cytochrome b mitochondrial gene sequences (Tsigenopoulos et al., 2010).

***Capoeta aculeata* (Valenciennes, 1844)**

(Figs. 10, 11)

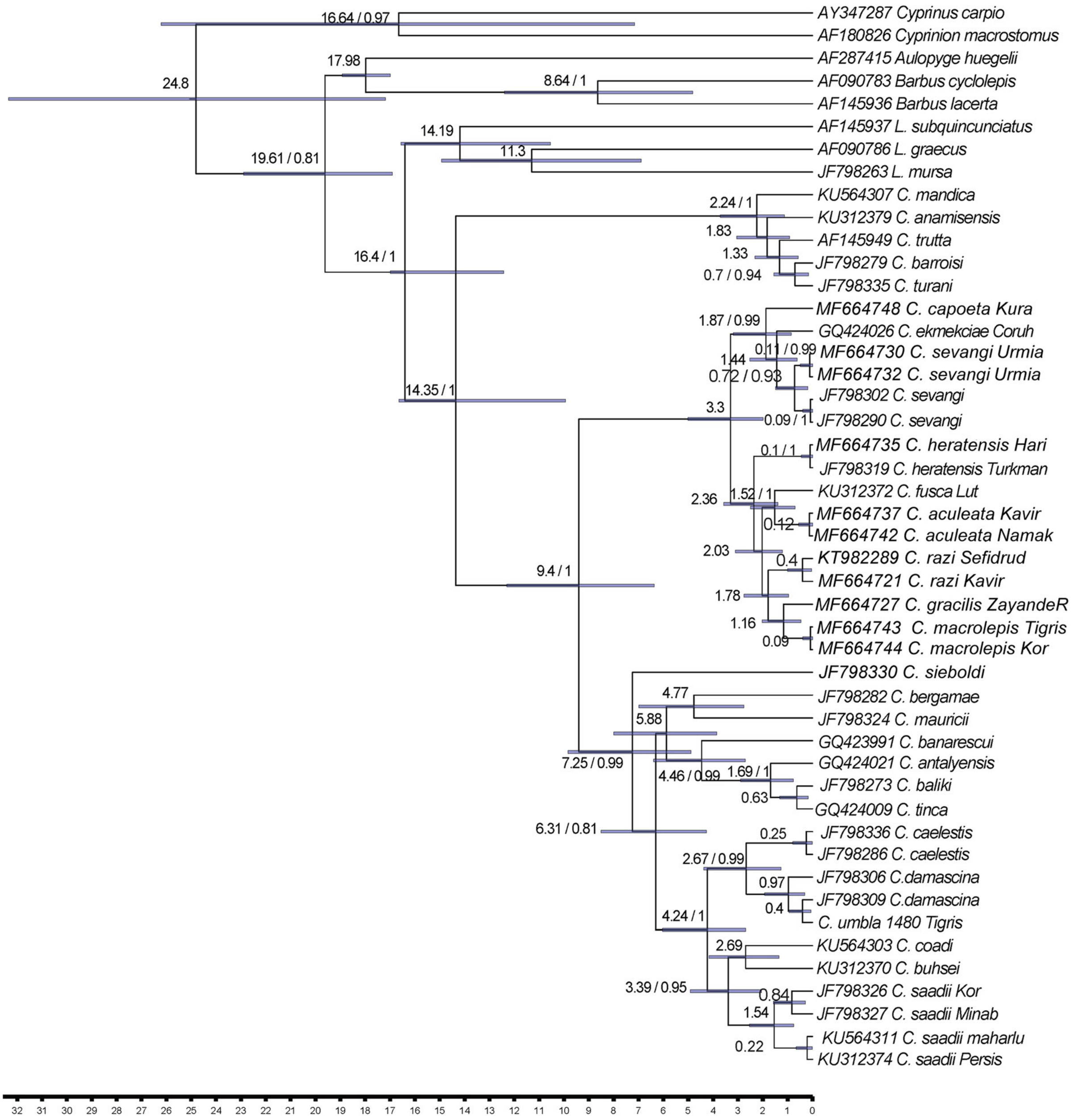


Fig. 8 Divergence time estimates of the major cladogenetic events for species of *Capoeta* based on *cytb* gene. Numbers before slash represent divergence age estimation. Numbers after slash are posterior probability values from Bayesian Inference. Node heights indicate mean ages and node bars indicate the 95% HPD

Chondrostoma aculeatum Valenciennes [A.] in Cuvier & Valenciennes 1844: 408 Iran.

Varicorhinus bergi Derjavin [A. N.] 1929:72, Fig. 1 Karaj River, 30 km from Teheran, Iran.

Varicorhinus aculeatus Berg 1949, p. 795, vicinity of Tehran.

Capoeta capoeta aculeatum Karaman 1969, p. 28, Iran. Umgebung von Tehran.

Capoeta capoeta aculeatus Coad 1979, p. 91 (sec. Karaman 1969).

Types Lectotype: MNHN 0000-2357. Paralectotypes: MNHN 1960-0611 [ex MNHN 0000-2357] (5). Type catalog: Bertin & Estève (1948). Lectotype

Table 8 Number of lateral line scales of species in the large-scaled *Capoeta* species group

	N	32	34	35	36	37	38	39	40	41	42	43	44	45
C. aculeata	18				1	1	2	3	7		2	1	1	
C. gracilis	28	1	1	2	1	3	4	2	4	3	4	1		1
C. heratensis	52													
C. fusca	30										2	5	3	3
C. macrolepis	33						1		1	4	2	13	12	8
C. sevangi	25													
C. razii	97							2		3	1	1	3	2

	46	47	48	49	50	51	52	53	54	55	56	57	58
C. aculeata													
C. gracilis	1												
C. heratensis			1	4	2	2	6	8	4	9	4	7	5
C. fusca	7	2	6		4								
C. macrolepis	5	2											
C. sevangi	1	1		1	5	4	2	4	2	1	1		
C. razii	7	5	14	13	12	8	10	9	3	1		1	5

Table 9 Number of gill rakers of species in the large-scaled *Capoeta* species group

	N	12	13	14	15	16	17	18	19	20	21	22	23	24	25
C. aculeata	22						1	7	7	2	4				
C. sevangi	24						4		4	6	3	6			
C. heratensis	47						2	2	9	11	11	12			
C. fusca	30	10	11	4	5										
C. macrolepis	33						1	5	9	9	4	5			
C. gracilis	22									1	2	3	7	6	2
C. razii	97				3	12	15	29	22	11	3	2			

selected by Coad & Krupp (1994). They indicated that the materials are in bad condition; most fin rays are damaged; fin membranes are missing and scales are partly or entirely missing. *Capoeta aculeata* was originally described as *Chondrostoma aculeatum* by Valenciennes (1844) from Persia (Iran; probably near Tehran) but no exact type locality data were given. Six syntypes (MNHN 2357) of *Chondrostoma aculeatum* in poor condition exist in the Muséum national d'Histoire naturelle, Paris (Bertin & Estève, 1948; Coad & Krupp, 1994). They measure 86–179 mm SL (Coad & Krupp, 1994) or 105–210 mm TL (Bertin & Estève, 1948). Coad & Krupp (1994) selected the largest syntype (179 mm SL) as the lectotype characterized by the possession of eight branched dorsal fin rays, 41 scales in the lateral line, 17 gill rakers on the lower limb of the first gill arch and 42 vertebrae.

Diagnosis Capoeta aculeata is distinguished from all other species of *Capoeta* by a combination of characters: presence of one pair of barbels; 17–21 total gill rakers on first arch (modally 18–19); smaller scales (36–44 scales in lateral line, modally 43) and 38–39 vertebrae. *Capoeta aculeata* is also distinguished from all other *Capoeta* in having one fixed, diagnostic nucleotide substitutions in the mtDNA *cytb* and two in COI.

Description General morphology of *C. aculeata* is shown in Figs. 10 and 11. Greatest body depth at level of dorsal-fin origin; pre-dorsal body profile straight to smoothly concave to dorsal-fin origin; post-dorsal profile straight, its depth decreasing towards caudal-fin base, profile of venter slightly arched or straight. Snout short and rounded. Mouth inferior, slightly arched or almost straight in ventral view, upper lip

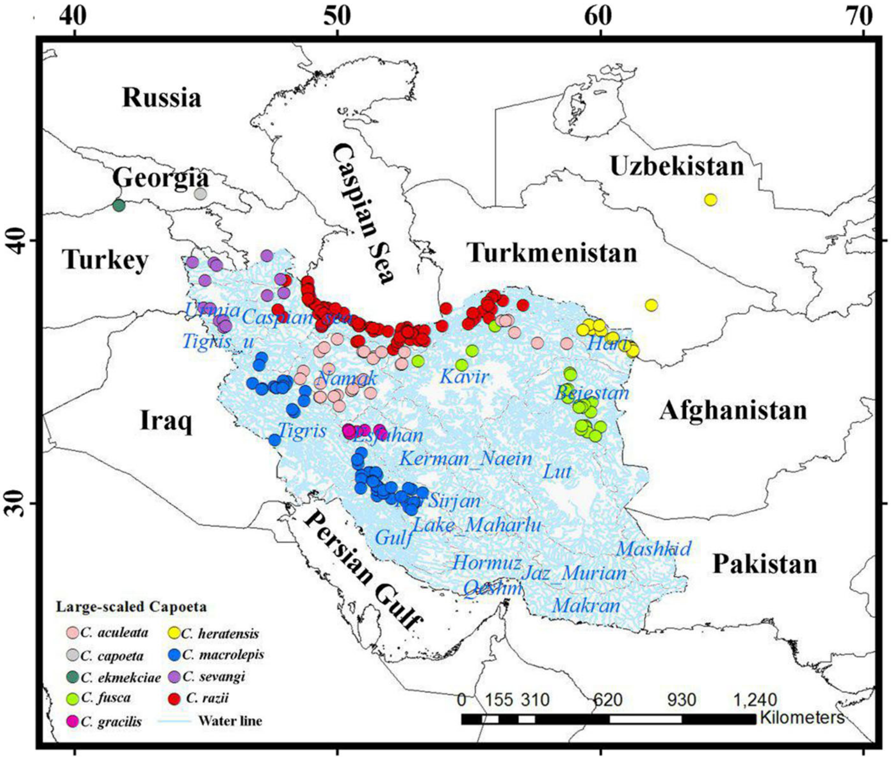


Fig. 9 Point distribution map of large-scaled *Capoeta* species in Iran and adjacent countries

very small, lower jaw usually covered by a well-developed horny sheath with a sharp edge. Only mandibular barbels present, reaching vertical of anterior margin of eye. Pectoral fins not reaching to dorsal-fin origin and pelvic-fin base, margins of pectoral fins slightly convex. Pelvic fins not extending to anal-fin base, outer margins straight or slightly rounded; pelvic axillary scale present. Anal fin almost exceeding 2/3 of caudal peduncle length or reaching to caudal-fin base, its outer margin slightly rounded. Caudal fin forked.

Dorsal fin with 3–4 unbranched (modally 4) and 7–10 (modally 8) branched rays. Anal fin with 3 unbranched and 5–6, modally 5, branched rays. Pectoral fin with 15–18 (modally 17) and pelvic fin with 7–9 (modally 8) branched rays. Caudal fin with 16–18, modally 17, branched rays. Lateral line scales 36–44. Caudal peduncle scales 6–10. Number of scale rows between dorsal-fin origin and lateral line 6–7 (modally 7), between anal-fin origin and lateral line 5–6 (modally 6) and between of pelvic-fin origin and lateral line 4–7 (modally 5–6). Gill rakers 17–21, modally 18–19. Total vertebrae 38–39.

Coloration The dorsum is light golden to dark olive; flanks light bright silver to golden yellowish; upper head surface light olive to golden yellowish. The belly and lower head surface are pearly-white to dirty cream. The iris is silvery, or golden in outer margin. The front of the dorsal fin and the margin of the caudal fin are orange; other areas of these fins are white or yellowish. The pectoral fin is orange to reddish; pelvic and anal fins are whitish, with yellow or orange color on the base or first unbranched ray. Vague dark olive stripes extending parallel to the lateral line on the flanks. Operculum with golden spot. Dorsal and ventral margins of caudal fin yellowish orange (Fig. 11).

Distribution *Capoeta aculeata* is found in the Namak Lake and Kavir basins (Figs. 2, 9).

Remarks The taxonomic status of this species varies by different authors (Heckel, 1849a, b; Günther, 1868; Berg, 1949; Kähsbauer, 1963; Karaman, 1969; Coad, 1979; Saadati, 1977; Coad, 1980; Bianco & Bănărescu, 1982; Howes, 1982). Coad & Krupp (1994) regarded *Capoeta aculeata* as a valid species. They redescribed it and plotted its distribution from the six syntypes and 551 freshly collected specimens. Coad &

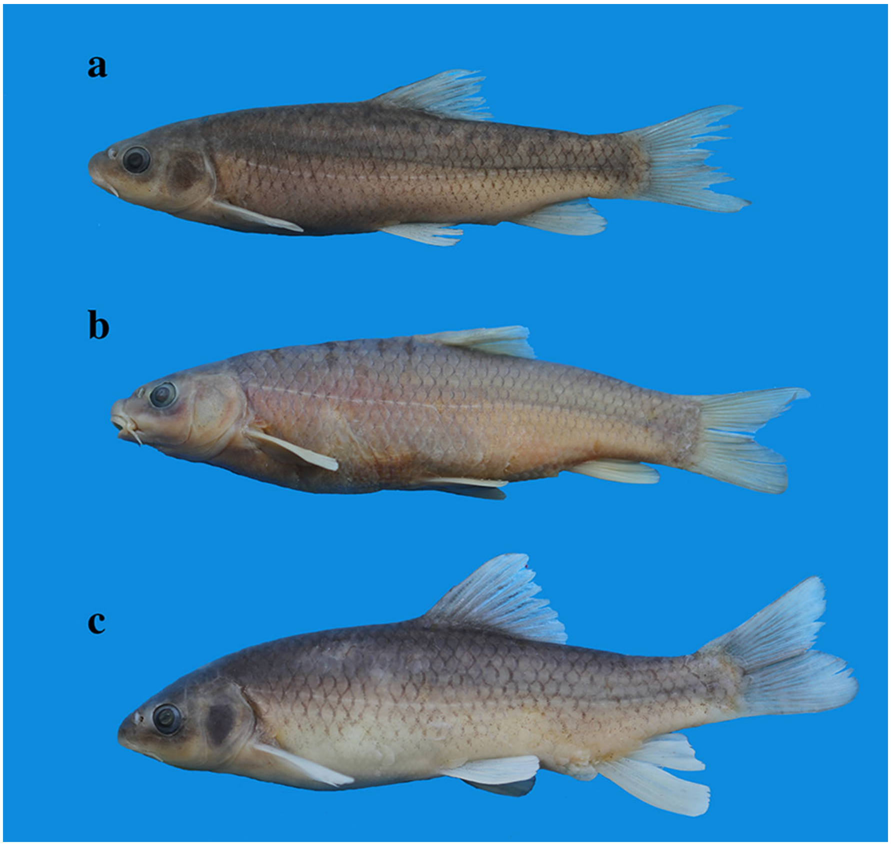


Fig. 10 *Capoeta aculeata*; *a* ZM-CBSU Z363; 84 mm SL; Arak Prov., Near Arak, Cheshmeh Nazi, Namak basin, 33°42′56.8″N, 50°04′21.9″E. *b* ZM-CBSU Z251; 90 mm SL; Semnan Prov., Garmsar, Hableh Rud, Kavir basin; 35°18′03.3″N, 52°24′58.7″E. *c* ZM-CBSU Z241; 92 mm SL; Qom Prov., Near Qom, Qom River, Namak basin 34°22′33.4″N, 50°36′04.8″E

Fig. 11 Live specimen of *C. aculeata* from Emamzadeh Abdollah River, Qom, Namak Basin

Krupp (1994) considered all the populations from Tigris, Namak Lake, Kavir, Kerman-Na'in or Yazd, Zayandehrud (Esfahan), and Kor River drainages (Fig. 2) as *C. aculeata* and treated *Scaphiodon macrolepis* Heckel, 1849 as a synonym of *C. aculeata*.

Ghanavi et al. (2016) assigned *C. aculeata* from Namak basin (include type locality) as sp. 6 and Jouladeh-Roudbar et al. (2016) described it as *C. alborzensis* and the populations from Tigris basin assigned as *C. aculeata*. However, we emphasize an important point that the type locality of *C. aculeata* is in the Namak Lake basin. This species confirmed by Ghanavi et al. (2016) using the two species-delimiting approaches; General Mixed Yule-Coalescent (GMYC) and Poisson Tree Process (PTP). Consideration to *C. alborzensis* population belongs to the

Namak Lake basin (Type locality of *C. aculeata*), the molecular results (Fig. 5) and existence of two names for a same population; now, we synonymize *C. alborzensis* with *C. aculeata*. Validity of the name *C. aculeata* is confirmed based on priority law of ICZN.

Material examined

All from Iran. ZM-CBSU Z240-249, 11, 70-117 mm SL; Qom Prov.: Near Qom, Qom River, Namak Lake basin 34°22′33.4″N, 50°36′04.8″E; Khaefi, R., Masoudi, M., Mehraban, H., 04 Jul. 2014. ZM-CBSU Z363-405, 43, 60–110 mm SL; Arak Prov.: Near Arak, Cheshmeh Nazi, Namak Lake basin, 33°42′56.8″N, 50°04′21.9″ E; Esmaeili, H.R., Zamaniannejad, R., Sayyadzadeh, G., Ghasemian, S., 17 Aug. 2011. ZM-CBSU Z250-257, 8, 77–92 mm SL; Semnan Prov.: Garmsar, Hableh Rud, Kavir basin; 35°18′03.3″N, 52°24′58.7″E; Esmaeili, H.R., Zamaniannejad, R., Sayyadzadeh, G., Ghasemian, S., 21 Aug. 2011.

Capoeta capoeta (Güldenstädt, 1773)

(Fig. 12)

Cyprinus capoeta Güldenstädt [J. A. von] 1773:508, Pl. 8 Tiflis, Caspian Sea.

Cyprinus fundulus Güldenstädt [J. A. von] 1787:222 Kura River at Tbilisi.

Capoeta fundulus Valenciennes [A.] in Cuvier & Valenciennes 1842:279 Cyrus (Kura) River, Asia.

Scaphiodon asmussii Keyserling [E. von] 1861:14 [17], Pl. 6 Near Herat, Afghanistan.

Capoeta gibbosa Nikolskii [A. M.] 1897:344, se Khorasan, Iran.

Capöeta guldenstädtii De Filippi [F.] 1865:313 Unneeded new name for *Cyprinus capoeta* Güldenstädt 1773 (see footnote 2, p. 312 in De Filippi 1865). Name originally as *Güldenstaedti*. Appeared in Tortonese 1940 as *Capoeta guldenstadtii* Filippi.

Varicorhinus capoeta Berg [L. s.] 1949: 220, Kura

Types. No types known. Tiflis, Caspian Sea.

Diagnosis Capoeta capoeta is distinguished from all species of *Capoeta* by the following combination of characters; lateral line scales 54–65 (usually 56–59) (Berg, 1949) and 50–66 (Bănărescui, 1999); total gill rakers 25–30 (Berg, 1949); dorsal fin emarginated above; dorsal fin spine strong with numerous denticles; predorsal area strongly compressed (Berg, 1948–1949; Abdurakhmanov, 1962).

Description General morphology of *C. capoeta* is shown in Fig. 12. Greatest body depth at dorsal-fin origin; pre-dorsal body profile straight to smoothly concave to origin of dorsal fin; post-dorsal profile straight, its depth decreasing towards base of caudal fin; ventral profile arched. Snout short and rounded. Mouth inferior; lower lip developed only in the corners of the mouth. One pair of mandibular barbels; Berg (1949) indicated barbels in small specimens, extending almost as far as the posterior margin of eye and in large specimens only to the anterior margin of eye. Dorsal-fin origin inserted anterior of pelvic fin insertion. Pectoral fins not reaching to dorsal-fin origin and pelvic-fin base. Pelvic fins not extending to base of anal fin; pelvic axillary scale present. Caudal fin forked.

Dorsal fin with 4 unbranched and 8–9 branched rays. Anal fin with 3 unbranched and 5 branched rays. Lateral line scales 54–65 (usually 56–59); 7–11 (modally 9) scale rows between dorsal-fin origin and lateral line; 6–8 (modally 7) scale rows between anal-fin origin and lateral line. Gill rakers 25–30 (Berg, 1949).

Coloration Sides brownish-gray; dorsum of head and area above of lateral line dark; iris golden; dorsal and caudal fins dark gray, pelvic, pectoral and anal fins

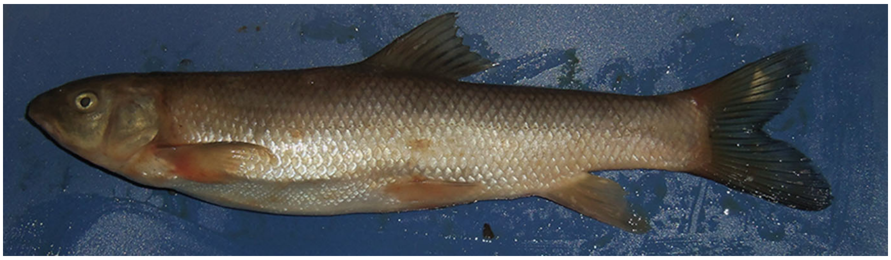


Fig. 12 *Capoeta capoeta*, Kura River, Tbilisi, Georgia

dirty orange, often with reddish tint. Venter white to silvery. Operculum and ventral surface of head dirty golden with reddish tint.

Distribution *Capoeta capoeta* exists in the Kura River and its tributaries in Georgia, North east of Turkey and Azerbaijan, and may be in the North Armenia (Figs. 2, 9).

Remarks *Capoeta capoeta* was originally described as *Cyprinus capoeta* by Gueldenstaedt (1773; spelt Güldenstädt, Güldenstadt or Guldenstedt on other papers or by other authors), based on a specimen captured in the Kura near Tbilisi (Fig. 2). Güldenstadt recorded that the species lives in the Caspian Sea and ascends the Kura [Cyrus] beyond Tiflis in the winter (Fig. 2).

According to Berg (1949), the Khramulya (*Capoeta capoeta*) is distributed in basins of the Caspian and Aral seas from eastern Transcaucasia to the south of Central Asia and is represented by four subspecies: the nominative subspecies *C. capoeta capoeta* (Güldenstädt, 1773), the Lake Sevan subspecies *C. capoeta sevangi* (Filippi, 1865), the Lenkoran subspecies *C. capoeta gracilis* (Keyserling, 1861), and the Transcaspian subspecies *C. capoeta heratensis* (Keyserling, 1861).

Abdurakhmanov (1962) compared *C. c. capoeta* from the Kura River basin with *C. c. gracilis* from the Lenkoranchai and Bilyashchai Rivers in Azerbaijan and found some morphological characters distinguishing specimens from the two systems without any taxonomic decision.

Bănărescu (1999) stated that *C. capoeta sevangi* de Filippi, 1865 is the subspecies in the Araxes River basin (Fig. 2), presumably including Iran, and distinguished from the type subspecies, *C. capoeta capoeta* of the Kura River basin, by having the dorsal fin margin straight or slightly convex as opposed to slightly to moderately notched.

Capoeta ekmekciae Turan, Kottelat, Kirankaya & Engin 2006

Types Holotype. ESFM-PISI/2004-076, 203, 203 mm SL; Paratypes. ESFM-PISI/2004-077, 4, 150–209 mm SL; CMK 18473, 3, 161–179 mm SL; FRR 703, 19, 91–280 mm SL; CMK 18554, 7, 123–180 mm SL; FRR 704, 6, 100–280 mm SL (Fig. 13).

We have only access to three specimens of *C. ekmekciae* preserved in 5% formaldehyde (Catalog number IUSHM 2016-1169). The description present herein is based on these materials.

Description General morphology of *C. ekmekciae* is shown in Fig. 13. Greatest body depth at dorsal-fin origin; pre-dorsal body profile straight to smoothly concave to origin of dorsal fin; post-dorsal profile straight, its depth decreasing towards base of caudal fin; ventral profile arched. Snout short and rounded. Mouth inferior; lower lip developed only in the corners of the mouth. One pair of mandibular barbels; Dorsal fin origin inserted anterior of pelvic fin insertion. Pectoral fins not reaching to dorsal-fin origin and pelvic-fin base. Pelvic fins not extending to base of anal fin; pelvic axillary scale present. Caudal fin forked.

Dorsal fin with four unbranched and eight branched rays. Anal fin with three unbranched and five branched rays. Lateral line scales 53, 61, 62; 9–10 scale rows between dorsal-fin origin and lateral line; 8–9 scale rows between anal-fin origin and lateral line.

Distribution *Capoeta ekmekciae* is known only from the lower Çoruh River near Borçka and Çavuslu.

Capoeta fusca Nikolskii, 1897

(Figs. 14, 15)

Capoeta nudiventris Nikolskii [A. M.] 1897:342 Saride, eastern Iran.

Varicorhrinus fuscus Saadadti [M. A.] 1977:68 Bedjestan, Iran.

Fig. 13 *Capoeta ekmekciae*, Çoruh River, Turkey

Fig. 14 *Capoeta fusca,* Syntype; Zoological Institute, St. Petersburg, Russia, ZIN 11112

Fig. 15 Live specimen of *Capoeta fusca* from Sharifabad Qanat, Birjand

Types Two syntypes of *C. fusca* are listed in Latin as from "Mondechi in Persia orientali" and are in the Zoological Institute, St. Petersburg (ZISP 11108), 121.9–172.9 mm SL. Berg (1949) gives the locality in Russian as "Mondekhi, northern periphery of the Bajistan Salt Desert in southeast Khorasan." This locality is possibly Mandehi or Miandehi at 34°53′N, 58°38′E (Khorasan Razavi Prov.) (Fig. 2). Nikolskii (1897) lists a series of specimens in Latin, presumably all of which he regarded as types, sic:- "11108. Mondechi in Persia orientali. 12.IV.96 (2). 11109. Persia orientalis. 1896. (6). 11110. Persia orientalis. 1896. (5). 11111. Persia orientalis. 1896. 11112 (Fig. 14). Kuss in Persia orientali. 6.IV.96.", the last two lacking museum number of specimens. Berg (1949) gives 20 specimens for 11109, 6 specimens for 11110, and 1 specimen for each of the last two. Catalogue dates in ZISP for all these are 26.IV.96 (presumably new style) while Berg (1949) gives new style dates 24.IV.1896 for the first and 18.IV.1896 for the last (and this last is 26.IV.1896 in the catalogue). Only the specimens of ZISP 11108 are regarded as syntypes by Berg (1949). Berg (1949) also points out the confusion over the date when Zarudnyi, the collector, was at "Kuss" (=Khusf at 32°46′N, 58°53′E) given by Nikolskii as 6.IV.96 old style but on this date Zarudnyi was at "Kiaz-khak" near Asadabad (35°38′N, 59°21′E) south of Mashhad and only reached Khusf on 8 (or 20 new style).VI.96. This is not particularly critical in this instance but serves to point out the difficulties of reconciling literature, field notes, catalogues, and jar labels.

Capoeta nudiventris Nikolskii, 1897 is a synonym of *Capoeta fusca* (Coad, 1981). According to Berg (1949), the syntypes are in the Zoological Institute, St. Petersburg (ZISP 11106) and include three specimens

(92.4–121.5 mm SL). Berg (1949) gives the type locality as "Zeride near Bajistan in southeast Khorasan, 30.IV.1896″ (the date in the jar is 26.IV.1896). Nikolskii (1897) lists three collections, all from "Saride in Persia orientali. 18.IV.96." with numbers 11105, 11105 (presumably an error for 11106), and 11107 and 6 (actually 7 in the jar and according to Berg (1949)), 3, and 5 specimens, respectively. Berg (1949) lists the five specimens under 11107 as from "Chakhak in the Al'kor region between Bajistan and Birjand. 9.V.1896,″ presumably at 33°17′N, 58°54′E. These 5 fish are 37.0–55.2 mm standard length, collected on 25.IV.1896 in the ZISP catalogue and not listed as types in the jar, nor in the catalogue, nor in Berg (1949). The 7 fish in ZISP 11105 measure 46.8–75.3 mm standard length, are from the same locality listed under ZISP 11106 in Berg (1949), and are listed as types in the ZISP catalogue, though not in Berg (1949). Judging from the labels and catalogue sheets, the types are probably from Sarideh at 34°22′N, 58°14′E and include 11105 and 11106.

Diagnosis Capoeta fusca is distinguished from all large-scaled *Capoeta* species by having fewer gill rakers (12–15, mode12). *C. fusca* is also distinguished from all other species of the *C. capoeta* species group by having six fixed, diagnostic nucleotide substitutions in the mtDNA *cytb* and two in COI regions.

Description General morphology of *C. fusca* is shown in Fig. 15. The greatest body depth anterior to origin of dorsal fin, pre-dorsal body profile straight; post-dorsal profile straight, its depth decreasing towards caudal-fin base and ventral profile slightly arched or straight. Snout very short and rounded. Mouth, inferior, usually arched or almost straight in ventral view, upper lip very small, lower jaw covered by a usually well-developed horny sheath with sharp edge. Only mandibular barbel present, reaching vertical of anterior margin of eye or may exceed vertical of midline of eye. Pectoral fins not reaching to dorsal-fin origin and pelvic-fin base, its outer margins usually slightly convex. Pelvic fins not extending to anal-fin base, outer margins usually rounded; pelvic axillary scale present. Anal fin reaching to near caudal-fin base, its outer margin slightly rounded. Caudal fin forked.

Dorsal fin with 3–4 (modally 3) unbranched and 7–8 (modally 7) branched rays. Anal fin with three unbranched and five branched rays, pectoral fin with 14–17 (modally 14–15) branched rays, and pelvic fin with 7–9 (modally 8) branched rays. Caudal fin with 15–18 (modally 17) branched rays. Lateral line scales 46–50 (modally 49). Caudal peduncle scales 7–10 (modally 10). Scale rows between dorsal-fin origin and lateral line 7–10 (modally 9); 6–8 (modally 7) scale rows between anal-fin origin and lateral line and 5–7 (modally 6) scale rows between pelvic-fin origin and lateral line. Scales regularly arranged over the whole body, enlarged around the anus and anal fin base. Scales oval in shape with a subcentral, markedly anterior focus, numerous radii on all fields and moderate numbers of circuli. Gill rakers 12–15 (modally 12). Mouth horseshoe-shaped. The pharyngeal teeth are very spatulate up to the tip but are thick. Gut very elongate with several anterior and posterior loops.

Coloration The dorsum and flanks dark; below lateral line body can be very light. The dorsal and caudal fin membranes dark. Young fish may have a mid-lateral stripe as wide as the eye ending in an indistinct dark blotch on the caudal-fin base. Peritoneum is dark brown to black.

Distribution Capoeta fusca is distributed in Kavir and Lut basins (Figs. 2, 9). It is found in eastern Iran in the Tedzhen River (including Kashaf River), Dasht-e Kavir, Bejestan, Dasht-e Lut and Sistan basins in rivers, springs and qanats (Fig. 16); some of the latter locations are not easily located on maps (Nikolskii, 1899; Berg, 1949). A record from the "Schalman Rud" presumably in the Caspian Sea basin is probably an error (Wossughi, 1978). Johari et al. (2009, 2010) recorded this species from the Ghoorghoori, Asafshad, Mardan Shah, Gazdmoo, and Afin rivers in Qae'nat province and in 44 qanats of Birjand County in eastern Iran. In the present study, we collected specimens from two Qanats (Sharif Abad and Abdolrahmati; Fig. 16) in South Khorasan Prov., Lut basin.

Remarks Rainboth (1981) places both *C. fusca* and *C. nudiventris* in the genus *Schizocypris* on the basis of the enlarged scales around the vent and anal-fin base, a condition also reported by Berg (1949) but not considered by this latter author to warrant inclusion of these fish in *Schizocypris*.

Coad (2017) gives meristics for the Iranian specimens as dorsal-fin branched rays 7(77); anal-fin branched rays 5(77); pectoral-fin branched rays 14(1), 15(1), 16(8), 17(23), 18(26), 19(13) or 20(5); pelvic-fin branched rays 7(8), 8(64) or 9(5); lateral line scales 46(4), 47(6), 48(8), 49(10), 50(10), 51(9), 52(9),

Fig. 16 Abdolrahamati Qanat, Birjand, habitat of *Capoeta fusca*

53(9), 54(9), 55(2) or 56(1); total gill rakers 13(1), 14(11), 15(25), 16(26), 17(11), 18(1), or 20(1); pharyngeal teeth 2,3,4-4,3,2(20); and total vertebrae 40(9), 41(42), 42(20), or 43(4).

Material examined

All from Iran. ZM-CBSU Z197-211, 15, 50–78 mm SL; South Khorasan Prov.: Birjand, Sharif Abad Qanat, Lut basin, 32°58′08.7″N, 59°17′03.4″E; Esmaeili, H.R., Zammaniannejad, R., Sayyadzadeh, G., Ghasemian, S., 28Aug. 2011. ZM-CBSU Z570-Z584, 15, 30–41 mm SL; South Khorasan Prov.: Birjand, Abdolrahmati qanat, Lut basin, 33°39′24.9″N, 59°11′28.7″E; Esmaeili, H.R., Zammaniannejad, R., Sayyadzadeh, G., Ghasemian, S., 28 Aug. 2011.

Capoeta gracilis (Keyserling, 1861)

Scaphiodon gracilis Keyserling [E. Von] 1861:9 [12], Pl. 4, Rivers near Esfahan, central Iran.

(Figs. 17, 18)

Types No types saved. Rivers near Esfahan, central Iran.

Diagnosis Capoeta gracilis is distinguished from other large-scaled *Capoeta* by the combination of the following characters: the species has more gill rakers on the first arch (20–25, modally 23) and larger scales (32–46 scales in lateral line, modally 42). *Capoeta gracilis* is also distinguished from all other species of the *C. capoeta* species group by having two fixed, diagnostic nucleotide substitutions in the mtDNA *cytb* and one in COI regions.

Description General morphology and appearance of *C. gracilis* is shown in Figs. 17 and 18. Morphometric data are given in Table 10. Dorsal head profile slightly convex. Predorsal profile slightly convex, ventral profile straight or slightly convex. No elevated keel anterior to the dorsal-fin origin. Greatest body depth anterior to origin of dorsal fin. Mouth inferior, small, transverse and almost straight. Lower jaw covered by a well-developed horny sheath, with a sharp edge. Rostral cap well developed, partly

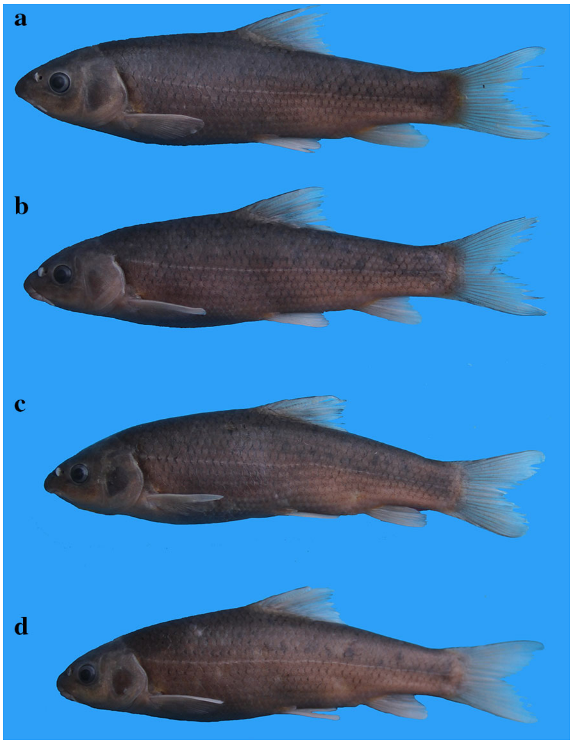


Fig. 17 *Capoeta gracilis*; *a* ZM-CBSU Z464; 98 mm SL; *b* ZM-CBSU Z465; 97 mm SL; *c* ZM-CBSU Z467; 93 mm SL; *d* ZM-CBSU Z469; 90 mm SL. Iran: Daran, Zayandeh-Rud River

overlapping upper lip. Only maxillary barbels present, reaching to anterior margin of eye or pass it.

Dorsal fin with 3–5 (modally 4) unbranched and 7–8½ (modally 8) branched rays, last unbranched ray of the dorsal fin thickened and serrated and denticles being long and narrowly spaced. Outer dorsal-fin margin almost concave or slightly straight. Dorsal-fin origin slightly in front of vertical through pelvic-fin insertion. Pectoral fin with 15–19 (modally 17) branched rays; fin with rounded tip and reaching to about 50–65% of distance between the pectoral and pelvic-fin insertions when depressed. Pelvic fin with 8–9 (modally 8) branched rays, rounded tip, and reaching to about 50-80% of distance between pelvic-fin tip and anal-fin origin when depressed. Pelvic axillary lobe present. Anal fin with 3 unbranched and 5½ branched rays, its posterior margin almost convex, not reaching to caudal-fin base. Caudal fin forked, its lobes pointed or rounded. Lateral line complete, with 32–46 (modally 42) scales. Caudal peduncle scales 6–9 (modally 9). Rows of scales between dorsal-fin origin and lateral line 6–8 (modally 7); scale rows between anal-fin origin and lateral line 5–6 (modally 6) and scale rows between lateral line and pelvic-fin origin 5–7 (modally 6). Gill rakers 20–25 (modally 23) on outer side of first gill arch. Vertebrae 39–40. Small horny tubercles may occur around the head region and on all fins.

Coloration The live specimen of *Capoeta gracilis* from Esfahan is illustrated in Fig. 18. The back is gray to blackish or green–brown, or golden olive-green in smaller individuals; upper flank darker than lower; belly and lower flank yellow up to the lateral line; median area of belly white. Some smaller fish with small black spots on the sides and fins. Flanks with some light and dark stripes along lateral line. Anterior base of scales on back and flanks are highly pigmented. Sides of head golden brown or golden gray. Fins often yellowish-brown or dirty green, although

Fig. 18 Live specimen of *Capoeta gracilis* from Geshnizjan, Zayandehrud, Zayandehrud basin

Table 10 Morphometric characters of *Capoeta gracilis* from Zayandehrud Basin. Holotype ZM-CBSU Z462, paratypes, ZM-CBSU Z463–478, (16)

	Range	Mean	SD
Standard length (mm)	77.45–101.92	87.94	7.55
In percent of standard length			
Head length	24.56–27.13	25.81	.77
Body depth at dorsal-fin origin	21.71–29.03	26.92	1.83
Predorsal length	53.10–57.37	55.02	1.02
Postdorsal length	58.33–64.95	61.51	2.02
Preanal length	75.70–82.22	79.85	1.66
Preventral length	55.80–59.32	57.85	.98
Distance between pectoral and pelvic-fin origins	31.54–34.31	33.12	.70
Distance between pelvic and anal-fin origins	20.98–34.76	26.97	5.09
Depth of caudal peduncle	11.03–12.84	11.82	.45
Length of caudal peduncle	18.12–20.47	19.34	.76
Dorsal-fin base length	13.69–18.99	15.80	1.21
Anal-fin base length	6.02–8.37	7.41	.64
Pectoral fin length	17.84–21.18	19.82	.89
Pelvic fin length	15.72–17.97	16.86	.63
In percent of head length			
Head depth at eye	51.37–58.78	54.33	2.37
Snout length	30.59–37.52	33.97	1.60
Postorbital length	50.05–56.05	52.38	1.64
Interorbital width	38.35–44.67	42.14	1.47
Eye diameter	16.69–20.83	19.3	1.08
Maximum head width	62.37–70.62	66.08	2.60

the dorsal and caudal fins are darker than others. Yellowish spot at base of pectoral and pelvic fins. Preserved fish have pigment on the rays and membranes of fins without any distinctive pattern. Dorsal and caudal fins darker than the anal, pelvic and pectoral fins. Iris golden to orange; upper part of iris darker than lower. Peritoneum black.

Distribution This species exists in Zayandehrud basin (Figs. 9, 19).

Remark Keyserling (1861) described *Scaphiodon gracilis* from rivers near Isphahan (Esfahan: Probably Zayandehrud) (Fig. 2). Bianco & Banaresqu (1982) restrict the distribution of this species to the southern slope of Caspian Sea, between Sefidroud and Atrak rivers, and not in the Kura-Aras drainage (Fig. 2). Berg (1949) regarded, based on the number of scales in the lateral line, specimens from Tehran as *V. aculeatus* while he referred specimens from near Esfahan to *V. macrolepis*. Coad & Krupp (1994) listed the specimens from Esfahan as *C. aculeata*. Nevertheless, Saadati (1977) considered all specimens from Lut, Yazd, Namak and Tigris as *V. macroleois* and *aculeata* as a subspecies. Based on our morphological and molecular results, the large-scaled specimens from the Zayandehrud basin are a distinct species and are diagnosable from all other species of *Capoeta*.

The name *Capoeta gracilis* (Keyserling, 1861) was already used by Temminck & Schlegel, (1846) for a species described from Japan (now known as *Squalidus gracilis* (Temminck & Schlegel, 1846)). The two names are secondary homonyms. The junior homonym (*gracilis* Keyerling) has never been replaced and the two taxa are no longer considered congeneric. In this case, the junior homonym (*gracilis* Keyerling) is valid and no replacement name is needed based on the Art. 59.2. (International Code of Zoological Nomenclature, 1999), and hence, the valid name of the species from Esfahan (Zayandehrud basin) is *Capoeta gracilis*.

Capoeta gracilis from Zayandehrud have more gill rakers on the first arch relative to other large-scaled *Capoeta*. This species is distinguished from *C. fusca*

Fig. 19 Zayandehrud, type locality of *Capoeta gracilis*

by number of gill rakers on the first arch (20–25 vs. 12–15 in *C. fusca*), from *C. heratensis* and *C. sevangi* by having larger scales (32–46 scales in lateral line vs. 48–58 in *C. heratensis* and 46–56 in *C. sevangi*) and from *C. heratensis* by having one pair of barbels (vs. two pairs). *Capoeta gracilis* is distinguished from *C. macrolepis* by more gill rakers on first arch (20–25, usually 22–25 vs. 17–22 in *C. macrolepis*), by the existence of number of single pigments on the lower margin of operculum (vs. absent in *C. macrolepis*) and by number of pectoral fin rays (8–9, usually 8 vs. 7–10, usually 9 in *C. macrolepis*). It is distinguished from *C. aculeata* and *C. razii* by number of predorsal scales (16–17 vs. equal or less than 15 in *C. aculeata*, more than 17 in *C. razii*).

Material examined

All from Iran. ZM-CBSU Z462-Z 478, 17, 82–111 mm SL; Iran: Esfahan Prov.: Daran River, Near Daran; Zayandehrud basin; 32°49′25.8″N, 50°25′47.4″ E; Esmaeili, H.R., Zammaniannejad, R., Sayyadzadeh, G., Ghasemian, S., 16. Aug. 2011. ZM-CBSU Z175-177, 3, 58–69 mm SL; ZM-CBSU Z183–186, 4, 46–50 mm SL; Esfahan Prov.: Komitak village, Zayandehrud River, Zayandehrud basin, 32°43′27.71″N, 50°28′11.8″E; Gholamhosseini, A., Masoudi, M., 01 Jun. 2014. ZM-CBSU Z180–182, 3, 87–95 mm SL; Esfahan Prov.: Eskandari village Zayandehrud River, Zayandehrud basin; 32°49′25.8″N, 50°25′47.4″E; Esmaeili, H.R., Zammaniannejad, R., Sayyadzadeh, G., Ghasemian, S., 16 Aug. 2011.

ZMCBSU Z486–489, 4, 89–149 mm SL; Isfahan Prov.: Geshnizjan, Zayandehrud River, Zayandehrud basin, 32°46′48.5″N, 50°27′04.3E; Gholamhosseini, A., Khaefi, R., Darvishnia, H., Sadeghi, R., Mehraban, H., Razbani, M., 20 Aug. 2015.

Capoeta heratensis (Keyserling, 1861)

(Fig. 20)

Scaphiodon heratensis Keyserling [E. von] 1861:11 [15], Pl. 6, Heri-rud at Herat, Afghanistan.

Varicorhinus capoeta heratensis Berg, 1949, Tedzhen River basin.

Types No types saved. Heri-rud at Herat, Afghanistan.

Diagnosis *Capoeta heratensis* is distinguished from all other species of large-scaled *Capoeta* by the presence of two pairs of barbels (mostly) and also by the following combination of characters: 17–22 gill rakers and 48–58 (modally 56–57) scales in lateral line, and by having six fixed, diagnostic nucleotide substitutions in the mtDNA *cytb* and five in COI.

Description General morphology of *C. heratensis* is shown in Fig. 20. Greatest body depth at dorsal-fin origin; pre-dorsal body profile straight to smoothly concave to dorsal-fin origin; post-dorsal profile

Fig. 20 Live specimen of *Capoeta heratensis* from Gilas Spring, Hari River basin

straight, its depth decreasing towards caudal-fin base, profile of venter slightly arched or straight. Snout short and rounded. Mouth inferior, slightly arched or almost straight in ventral view, upper lip very small, lower jaw covered by a usually well-developed horny sheath with a sharp edge. Two pairs of barbels present, maxillary barbels not reaching vertical of anterior margin of eye and mandibular barbels exceed vertical of midline of eye. Pectoral fins not reaching to dorsal-fin origin and pelvic-fin base, its outer margins usually straight. Pelvic fins not extending to anal-fin base, outer margins usually slightly rounded; pelvic axillary scale present. Anal fin almost reaching to near caudal-fin base, its outer margin slightly rounded. Caudal fin forked.

Dorsal fin with 3–4 (modally 3) unbranched and 7–9 (modally 8), branched rays. Anal fin with three unbranched and 5–6 (modally 5) branched rays, pectoral fin with 17–19 (modally 17) branched rays, and pelvic fin with 7–8 (modally 8) branched rays. Caudal fin with 17 branched rays. Lateral line scales 48–58 (modally 56–57). Caudal peduncle scales rows 9–11; scale rows between dorsal-fin origin and lateral line 9–10 (modally 10); scale rows between anal-fin origin and lateral line 7–8 (modally 7); scale rows between origin of pelvic fin and lateral line 7–9 (modally 9). Gill rakers 17–22.

Coloration Dorsum of head and above lateral line golden brown; ventral head surface and belly white to silvery. Iris white or golden yellowish. Operculum golden yellow. Pectoral fin and base of pelvic fin dark orange.

Distribution This species is found in the Hari River basin (Figs. 2, 9). The authors collected this species from localities mentioned under materials examined.

Remarks *Capoeta heratensis* displays major variation in body form, with specimens sometimes called *morpha elata,* with a deep body, and *morpha elongate,* with shallow and elongate body. These are not taxonomically significant but simply ecomorphs and all intermediates between the two extremes can be found. The deep-bodied form probably comprised part of the fishes identified as *asmussii* (Berg, 1964).

Berg (1949) gives the following characters for *Varicorhinus heratensis steindachneri*: Dorsal fin with 3–4 unbranched and 7–8 (9) branched rays. Anal fin with 3–4 unbranched and 5 branched rays. Lateral line scales 51–61 (usually 55–56), scales above lateral line 8–11 and scales below lateral line 7–10. Barbels 4 or 2 (sometimes 3). If two (or three), the anterior pair lacking. Out of 79 specimens from the Amu-Darya, 45 had two barbels, 31 had four barbels and 3 had three barbels (G. V. Nikolskii). In the Kafirnlgan, A. N. Svetovidov found two barbels in 7 specimens and four barbels in 6 specimens. Kessler (1872) reported two barbels for some specimens from the Zeravshan. The Samarkand Khramulya specimens with two barbels are very close to the type from the Kura. Besides the variation in the number of barbels, the *natio steindachneri* differs in having a more variable branched dorsal-fin ray count (often 7).

Berg (1949) gives the following characters for *Varicorhinus capoeta heratensis*: Dorsal fin with 3–4 unbranched and 8 branched rays. Anal fin with 3–4 unbranched and 5 branched rays. Lateral line scales 50–60 (mostly 57), 8–11 scales above and 7–10 below lateral line. Barbels 4, anterior barbels not reaching anterior margin of eye, posterior reaching middle of eye; young up to 25 mm long without barbels. Dorsal fin truncated, with eight branched rays; its spine

Fig. 21 *Capoeta macrolepis*, Syntypes; Naturhistorisches Museum Wien; NMW 55896:1–2; 100–175 mm SL

moderately thickened and denticulated usually up to 2/3 of its length (sometimes higher). Ventral side entirely covered with scales as far as the isthmus. Gill rakers thin, weak and about 25 on the first gill arch. Standard length up to 30 cm and over. Reshetnikov and Shakirova (1993) consider *C. heratensis* a distinct species.

Material examined

All from Iran. ZM-CBSU Z400-409, 10, 94–125 mm SL; Razavi Khorasan Prov.: Gilas Spring, Hari River basin; 36°36′55.6″N, 59°20′17.9″ E; Esmaeili, H.R., Zammaniannejad, R., Sayyadzadeh, G., Ghasemian, S., 25. Aug. 2011. ZM-CBSU Z500-Z535, 36, 25–60 mm SL; Razavi Khorasan Prov., Shourijeh Olia, Kashafrud, Hari River Basin, 36°01′09.5″N, 60°55′46.6″E; Esmaeili, H.R., Zammaniannejad, R., Sayyadzadeh, G., Ghasemian, S., 27 Aug. 2011. ZM-CBSU Z451-Z452; 2; 180–183 mm SL; Razavi Khorasan Prov., Dousti Reservoir, Hari River Basin, 35°49′12.0″N, 61°15′23.9″E; Esmaeili, H.R., Zammaniannejad, R., Sayyadzadeh, G., Ghasemian, S., 27 Aug. 2011. ZM-CBSU Z585-Z598, 14, 228–292 mm SL; Razavi Khorasan Prov.: Bezangan Lake, Hari River basin, 36°18′38.7″N, 60°29′03.3″E; Esmaeili, H.R., Zammaniannejad, R., Sayyadzadeh, G., Ghasemian, S., 26. Aug. 2011.

Capoeta macrolepis **(Heckel, 1847)**

(Figs. 21, 22, 23, 24)

Fig. 22 *Capoeta macrolepis*; *a* ZM-CBSU 7707; 94 mm SL; Fars Prov., Kamfirouz, Kor River, Kor River basin. *b* ZM-CBSU E255, 113 mm SL; Kermanshah Prov., Sahneh-Bistoun Road, Gamasiab River, Tigris basin. *c* ZM-CBSU D116; 123 mm SL; Hamadan Prov., Laklak village, Mir Soleiman Spring, Tigris basin; ca. 34°40′13.48″N, 47°56′28.29″E

Fig. 23 Live specimen of *Capoeta macrolepis* from Tange Tizab, Beshar River, Tigris Basin

Fig. 24 Live specimen of *Capoeta macrolepis* from Denjan Spring, Beiza, Kor River basin

Scaphiodon macrolepis, Heckel [J. J.] 1847:259 Confluents of Araxes River at Persepolis, Iran.

Types Syntypes: NMW 51653 (2), 55896 (2, 100–175 mm SL) (Fig. 21).

Diagnosis Capoeta macrolepis is distinguished from all other species of large-scaled *Capoeta* by the following combination of characters: presence of only mandibular barbels, 38–47 (modally 43) scales in lateral line and 17–22 (modally 19) gill rakers on the first arch. This species is further distinguished from all other species of the *C. capoeta* species group by having three fixed, diagnostic nucleotide substitutions in the mtDNA *cytb* and one in COI.

Description General morphology of *C. macrolepis* is shown in Figs. 21, 22, 23 and 24. Greatest body depth at dorsal-fin origin; pre-dorsal body profile straight to smoothly concave to dorsal-fin origin; post-dorsal profile straight, its depth decreasing towards caudal-fin base, ventral fish profile slightly arched or straight. Snout short and rounded. Mouth inferior, slightly arched or almost straight in ventral view, upper lip very small, lower jaw always covered by a well-developed horny sheath with very sharp edge. Only mandibular barbels present, reaching vertical of anterior margin of eye or exceeds it. Pectoral fins not reaching to dorsal-fin origin and pelvic-fin base, its outer margin usually slightly convex. Pelvic fins not extending to anal-fin base, outer margins straight or slightly rounded; pelvic axillary scale usually well developed. Anal fin almost not reaching to caudal-fin base, its outer margin slightly rounded. Caudal fin forked.

Dorsal fin with 3–5 unbranched (modally 4) and 7–9 branched rays (modally 8). Anal fin with three unbranched and 5–6 branched rays (modally 5), pectoral fin with 16–20 branched rays (modally 18), pelvic fin with 7–10 branched rays (modally 9) and caudal fin with 16–20 branched rays (modally 17). Lateral line scales 38–47 (modally 43), caudal peduncle scales 7–11 (modally 10). Scale rows between dorsal-fin origin and lateral line 6–9 (modally 8); scales rows between anal-fin origin and lateral line 5–8 (modally 6) and scale rows between pelvic-fin origin and lateral line 5–8 (modally 6). Gill rakers 17–22 (modally 19) on the first arch; vertebrae 39–40.

Coloration Dorsum gray to blackish or green–brown, or golden olive-green in smaller individuals; upper flank darker than lower; belly and lower flank yellow up to the lateral line, center of belly white. Some smaller individuals with small black spots on sides and fins. Flanks, up and down lateral line with some light and dark stripes Anterior base of scales on back and flanks heavily pigmented. Sides of head golden-brown or golden gray. Fins often yellowish-brown or dirty green, although the dorsal and caudal fins are darker than others. Yellowish spot on bases of the pectoral and pelvic fins. Dorsal and caudal fins darker than the lower fins. Iris golden to orange; upper part of iris darker than lower part (Figs. 23, 24). Preserved specimens with pigment on rays and membranes of fins but without any distinctive pattern. Peritoneum black.

Distribution This species is found in the Kor and Tigris river drainages (Figs. 25, 9).

Remarks Scaphiodon macrolepis was probably described from the Pulvar (=Sivand) River, Fars near Persepolis by Heckel (1847) (see Fig. 21 for syntypes). Subsequent authors considered different taxonomic status for this species (Günther, 1868; Berg, 1949; Karaman, 1969). Karaman (1969) studied a single specimen from the Tigris drainage (“Karasu-Gamasia-Siemareh”) that he referred to as *C. c.*

Fig. 25 Upstream of Kor River, natural habitat of *Capoeta macrolepis*

macrolepis. He did not, however, see any material of what he regarded as *C. c. aculeatum;* he thus referred to Berg (1949) for his description and data on distribution. Bianco & Bănărescu (1982) followed Karaman (l.c.). They stated that *C. c. macrolepis* has a modally higher number of scales in the lateral line series (41–47 vs. 37–45 in *C. c. aculeata*). However, Coad & Krupp (1994) synonymized this species with *C. aculeata*. Our molecular and morphological data provide validity for the independent lineage of this species and recognition of *Capoeta macrolepis*.

Material examined

All from Iran. ZM-CBSU 7701–7708; 8, 92–129 mm SL; ZM-CBSU 7495–7500, 6; 124–140 mm SL; Fars Prov., Kamfirouz, Kor River, Kor River basin; ca 30°25′2.11″N, 52°09′0.91″E, Esmaeili, H.R., 18. May. 2006. ZM-CBSU E251–265, 15, 59–139 mm SL; Kermanshah Prov., Sahneh-Bistoun Road, Gamasiab River, Tigris River drainage, ca 34°28′3.77″N, 47°36′49.63″E, Ebrahimi, M., Teimori, A., Gholamhosseini, A., Gholamifard, A. 28 Sep. 2007.

ZM-CBSU D106–116, 11; 126–172 mm SL; ZM-CBSU C730, 143 mm SL, ZM-CBSU C732, 150 mm SL; ZM-CBSU C734–735, 2; 126–148 mm SL; ZM-CBSU C737; 91 mm SL; ZM-CBSU C739; 124 mm SL; ZM-CBSU C742–743; 95–130 mm SL; Hamadan Prov., Laklak village, Mir Soleiman Spring, Tigris; ca. 34°40′13.48″N, 47°56′28.29″E; Ebrahimi, M., Teimori, A., Gholamhosseini, A., Gholamifard, A., 28 Sep. 2008.

Capoeta razii Jouladeh-Roudbar, Eagderi, Ghanavi & Doadrio, 2017
(Figs. 26, 27, 28)

Types Holotype: IMNRF-UT-1072-9, Ichtyological Museum of Natural Resources Faculty—University of Tehran; Iran.

Diagnosis *Capoeta razii* is distinguished from other species of the *C. capoeta* species group by a combination of characters: presence of one pair of barbels; 39–58 (modally 53) scales in lateral line, 44–47 vertebrae and 15–22 (modally 18) gill rakers. *Capoeta razii* is also distinguished from all other species of the *C. capoeta* species group by having four fixed, diagnostic nucleotide substitutions in the mtDNA *cytb* region.

Description General morphology of *C. razii* is shown in Figs. 26, 27, and 28. Morphometric data are given in Table 11. Dorsal head profile slightly convex or straight. Predorsal profile slightly convex or slightly straight, ventral profile straight or slightly convex. Greatest body depth in front of dorsal-fin origin. Mouth inferior, small, transverse and almost straight. Lower jaw covered by a well-developed horny sheath with a sharp edge. Rostral cap well developed, partly overlapping upper lip. Only maxillary barbels present,

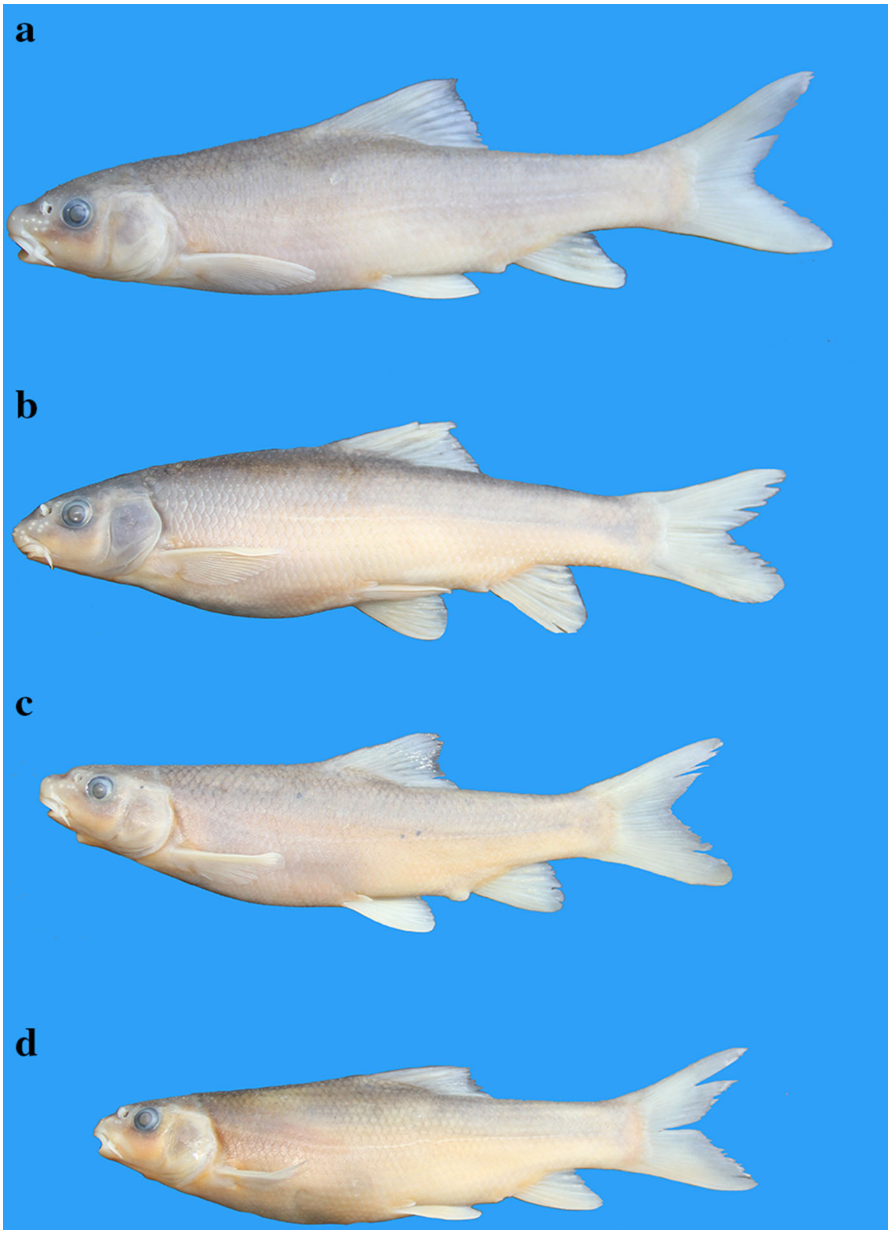


Fig. 26 *Capoeta razii*; *a* ZM-CBSU Z551; 112 mm SL; *b* ZM-CBSU Z552; 106 mm SL; *c* ZM-CBSU Z553; 94 mm SL; *d* ZM-CBSU Z554; 90 mm SL. Iran: Tajan River

barbels reaching almost to vertical of anterior margin of eye or past it.

Dorsal fin with 3–5 (modally 3) unbranched and 7–9½ (modally 8) branched rays, outer dorsal-fin margin almost concave or slightly straight. Dorsal-fin origin inserted anterior to vertical of pelvic-fin origin. Pectoral fin with 16–21 (modally 18) branched rays, its tip rounded, reaching to about 50–75% of distance between pectoral and pelvic-fin origins when folded back. Pelvic fin with 7–10 (modally 8) branched rays, its tip rounded, reaching to about 60–90% of distance between pelvic fin and anal-fin origin when folded down. Pelvic axillary lobe present. Anal fin with 2–4 (modally 3) unbranched and 5½ branched rays, its posterior margin almost convex, or slightly straight, not reaching to caudal-fin base. Caudal fin forked, its lobes pointed or rounded. Lateral line complete and with 39–58 (modally 53) scales. Caudal peduncle scales 7–11 (modally 11). Scale rows between dorsal-fin origin and lateral line 7–11 (modally 9), scale rows

Fig. 27 Live specimen of *Capoeta razii* from Laki Mahaleh, Tajan River, Caspian Sea basin

between anal-fin origin and lateral line 5–10 (modally 7), and scale rows between pelvic-fin origin and lateral line 5–9 (modally 7). Scales are regularly arranged over the body. Scales have a wavy anterior edge, few anterior and posterior radii and an almost central focus. Gill rakers 15–22 (modally 18) on outer side of first gill arch. Small horny tubercles may occur on the head region and on fin rays.

Coloration A live specimen of *C. razii* is illustrated in Figs. 27 and 28. The dorsum is light olive, or green to brownish, and the flanks light silver, silvery or silvery-gray, or yellowish. Dorsum of head dark olive to brownish. Belly and lower head surface pearly-white to dirty yellow. Iris silvery or golden in outer margin. Front of dorsal fin and margin of caudal fin black; remainder of these fins olive or yellowish. Black margin to caudal fin may be best developed on the upper and lower lobes as compared to the posterior margin. Pectoral, pelvic and anal fins whit, dark trace on the pectoral fin. Dark olive stripe extending along lateral line.

Distribution Capoeta razii is found in the central and southeastern Caspian Sea basin and North of Kavir basin, in Iran. The distribution of this species in Caspian Sea basin includes Garkanroud, Chalavand, Sefidrud, Tajan (Fig. 29), Gorganroud and Atrak river drainages. Furthermore, this species is found in some springs in the North Kavir basin (Figs. 2, 9).

Remarks Capoeta gracilis was described from near Esfahan (Zayandehrud basin) by Keyserling (1861). For a long time, *Capoeta* populations from Caspian Sea basin were considered *C. c. capoeta* or *C. c. gracilis* and specimens from Hari River basin were considered as *C. c. heratensis*. Bianco & Bănărescu (1982) limit *C. c. gracilis* to basins between the Sefidrud (Sefid River) and the Atrak River (Caspian Sea basin) while *C. c. capoeta* is found in the Kura-Aras basin. Holčík and Jedlička (1994) argued that the two subspecies *gracilis* and *heratensis* are not real and represent extremes in clinal variation of *C. capoeta*. Coad (2017) considered *C. gracilis* to occur across the Caspian Sea basin from the Astara to the Atrak and the Lake Urmia basin.

COI and *cytb* phylogenetic trees of the populations previously considered as subspecies of *C. capoeta*, revealed that *C. razii* was more distant from *C. capoeta* than from some other species of *Capoeta* (Figs. 4, 5, 6, 7, 8). Based on our data, *Capoeta gracilis* is restricted to the basin of its type locality. Different authors have debated the systematic position of *Capoeta gracilis.*

Recently, Jouladeh-Roudbar et al. (2017) described C. *razii* based on 16 collected specimens from the Caspian Sea basin and considered 46–54 scales in lateral line as diagnostic morphological character and a combination of other characters to distinguish *C. razii* from other Iranian *Capoeta* species. However,

Fig. 28 Live specimen of *Capoeta razii* from Bidvaz River, Kavir basin

Table 11 Morphometric characters of *Capoeta razii* ZM-CBSU Z550–568, (18)

	Range	Mean	SD
Standard length (mm)	67.04–117.25	91.04	
In percent of standard length			
Head length	23.69–26.89	25.58	.91
Body depth at dorsal-fin origin	24.37–29.67	27.21	1.63
Predorsal length	50.20–68.82	54.96	3.91
Postdoral length	6.45–64.53	58.84	13.55
Preanal length	76.97–86.27	79.83	2.23
Preventral length	54.30–78.94	58.62	5.54
Distance between pectoral and pelvic-fin origins	29.45–35.77	32.31	1.84
Distance between pelvic and anal-fin origins	19.26–24.97	23.25	1.46
Depth of caudal peduncle	10.20–12.86	11.75	.77
Length of caudal peduncle	17.64–23.11	20.38	1.52
Dorsal-fin base length	13.73–17.15	15.50	.99
Anal-fin base length	5.40–9.70	8.52	8.52
Pectoral fin length	19.39–23.21	21.44	.99
Pelvic fin length	16.39–19.30	17.67	.66
In percent of head length			
Head depth at eye	65.09–74.73	70.18	2.11
Snout length	31.57–41.86	37.18	2.76
Postorbital length	44.45–57.83	49.19	3.09
Interorbital width	36.67–43.92	40.19	1.64
Eye diameter	15.47–21.00	18.18	1.46
Maximum head width	60.55–68.00	64.23	2.4

based on examination of more collected materials through its distribution range, more characters are provided here. The presence of one pair of barbels in *C. razii* clearly sets this species apart from *C. heratensis* (two pairs of barbels). It is distinguished from *C. sevangi* in having more vertebrae (44–47 vs. <44) and from *C. fusca* by more gill rakers (15–22 vs. 12–15). This species is distinguished from *C. aculeata*, *C. gracilis*, and *C. macrolepis* by number of predorsal scales (more than 17 vs. <18 in others).

Material examined

All from Iran. ZM-CBSU Z568, 19, 72–127 mm SL; Iran: Mazandaran Prov.: Laki mahaleh, Tajan River, Caspian Sea basin, 36°12′13.8″N, 53°05′10.5″E; Khaefi, R., Masoudi, M., Mehraban, H., 10. Jul. 2014. ZM-CBSU Z149–162, 14, 86–120 mm SL; Mazandaran Prov.: Qaemshahr, Talar River, Caspian Sea basin, 36°28′42.8″N, 52°49′04.7″E; Khaefi, R., Masoudi, M., Mehraban, H., 13 Jul. 2014. ZM-CBSU Z10011–10040, 27, 113–200 mm SL; North Khorasan Prov.: Baba Aman, Atrak River, Caspian Sea basin, 37°29′37.1″N, 57°26′25.3″E; Esmaeili, H.R., Zammaniannejad, R., Sayyadzadeh, G., Ghasemian, S., 24 Aug. 2011. ZM-CBSU Z10071–10087, 17, 73–107 mm SL; Nroth Khorasan P.: Jajarm, Jalalodin Jajarmi Spring, Kavir basin, 36°58′24.1″N, 56°18′57.6″E; Esmaeili, H.R., Zammaniannejad, R., Sayyadzadeh, G., Ghasemian, S., 23 Aug. 2011. ZM-CBSU Z10041–10060, 20, 120–145 mm SL; Razavi Khorasan prov.: Quchan, lower part of Tabarak Dam, Atrak River, Caspian Sea basin, 37°08′08.5″N, 58°40′44.4″E; Esmaeili, H.R., Zammaniannejad, R., Sayyadzadeh, G., Ghasemian, S., 25 Aug. 2011. ZM-CBSU Z406-430, 25, 56–133 mm SL; Golestan Prov.: Aliabad-e-Katool, Zarrin Gol River, Caspian Sea basin, 36°50′39.0″N, 54°58′23.6″ E; Khaefi, R., Masoudi, M., Mehraban, H., 14 Jul. 2014. ZM-CBSU Z430–445, 14, 76–155 mm SL; Gilan Prov.: Havigh, Havigh River, Caspian Sea basin, 38°08′22.7″N, 48°51′31.7″E; Khaefi, R., Masoudi, M., Mehraban,

Fig. 29 Tajan River, natural habitat of *Capoeta razii*

H., 15 Jul. 2014. ZM-CBSU Z10096–10100, 5, 63–78 mm SL; Gilan Prov.: Emamzadeh Hashem, Sefidrud River, Caspian Sea basin, 37°01′08.8″N, 49°37′59.7″E; Esmaeili, H.R., Teimori, A., Mastafavi, H., Gholamifard, A., 29. Jun. 2009.

Capoeta sevangi de Filippi, 1865

(Figs. 30, 31)

Varicorhinus capoeta sevangi Abdurakhmanov, 1962 Araxes River basin.

Varicorhinus capoeta araxensis Dadikyan, 1986, Aras River basin, Armenia.

Types Holotype (unique): MZUT 695 (Istituto e Museo di Zoologia della R. Università di Torino: Institute and Museum of Zoology of the Royal University of Turin, Italy).

Diagnosis This diagnosis is based on materials from the Lake Urmia basin and Aras River in Iran (Fig. 2, 9). *Capoeta sevangi* is distinguished from all other species of large-scaled *Capoeta* by the following combination of characters: presence of one pair of barbels; 17–23 (modally 20) gill rakers on the first arch, 46–56 (modally 54) scales in the lateral line, 18 or more predorsal scales and 44–46 vertebrae. This species is also distinguished from all other species of the *C. capoeta* species group by having one fixed, diagnostic nucleotide substitutions in COI.

Description General morphology of *C. sevangi* is shown in Figs. 30 and 31. Greatest body depth at dorsal-fin origin; pre-dorsal body profile straight to smoothly concave to dorsal-fin origin; post-dorsal profile straight, its depth decreasing towards caudal-fin base, ventral fish profile slightly arched or straight. Snout short and rounded or slightly pointed in some specimens. Mouth inferior, slightly arched or almost straight in ventral view; upper lip very small, lower jaw covered by a usually well-developed horny sheath with sharp edge. Only mandibular barbels present, reaching vertical of anterior margin of eye. Pectoral fins not reaching to dorsal-fin origin and pelvic-fin base, outer margin of fin usually rounded. Pelvic fins not extending to anal-fin base, outer margin of fin straight or slightly rounded; small pelvic axillary scale present. Anal fin usually exceeding half the length of

Fig. 30 *Capoeta sevangi* from Lake Sevan

Fig. 31 Live specimen of *Capoeta sevangi* from Barandouz Chai River, Lake Urmia basin

caudal peduncle, its outer margin slightly rounded. Caudal fin forked.

Dorsal fin unbranched rays 3–5 (modally 4), branched rays 7–9 (modally 8), anal fin unbranched rays 3, branched rays 5, pectoral fin branched rays 16–23 (modally 19), and pelvic fin branched rays 8–10 (modally 9). Total lateral line scales 46–56 (modally 54). Gill rakers 17–23 (modally 20); caudal peduncle scales 8–11 (modally 11). Scale rows between dorsal-fin origin and lateral line 7–10 (modally 8); scale rows between anal-fin origin and lateral line 6–9 (modally 7); scale rows between pelvic-fin origin and lateral line 5–7 (modally 7).

Coloration Dorsum of head and above lateral line gray to dark brown; ventral surface of head and belly white to dirty cream. One or more parallel lines above lateral line, best developed anteriorly. Pores of lateral line scales distinctly dark or with bright color. Iris white or golden yellowish. Operculum dark or dirty orange with black dots. Pectoral, pelvic and anal fins yellow to dark orange with row of pigments on some first rays. Base of caudal fin dirty yellow or golden, dorsal and ventral margin of caudal fin dirty orange.

Distribution This species is distributed in the tributaries of the Aras and Lake Sevan (Caspian Sea basin) and Lake Urmia basin (Figs. 2, 9).

Remarks Capoeta sevangi was described by De Filippi in 1865 from Lake Goktscha (Sevan), Armenia. Berg (1949) described specimens from Lake Sevan with 50–62 scales in lateral line, 19–28 gill rakers on the first gill arch, four unbranched and 7–9 branched dorsal fin rays and 44–47 vertebrae, and referred them to *C. sevangi*. Berg (1964) regarded *Varicorhinus sevangi* a subspecies of *V. capoeta*. Banarescu (1999) also considered specimens with almost the same characters and same locality as *C. sevangi* (50–62 scales in lateral line, 7–9 branched dorsal fin rays and 18–32 gill rakers on the first gill arch). Based on *cytb* sequence analysis, *Capoeta c. sevangi* was also recognized as a species, *Capoeta sevangi,* by Zareian et al. (2016a) but these authors did not examine specimens of *C. capoeta* in Tbilisi as type locality of genus and species.

The above morphological data for *C. sevangi* (Lake Sevan, Aras River drainage) agree with our materials from Lake Urmia basin and Aras River drainage in northwestern Iran (49–58 scales in lateral line; 7–9 branched dorsal fin rays, 17–23 gill rakers on the first gill arch and 44–46 vertebrae), so presumably *C. sevangi* exists in both the Aras and Lake Urmia basins of Iran.

Specimens from Kura River in Tiblisi (type locality of *C. capoeta*), from Lake Sevan (type locality of *C.*

sevangi) and other specimens from Aras River and Lake Urmia basins have low genetic distances.

Material examined

All from Iran. ZM-CBSU Z110–117, 8, 71–89 mm SL; Iran: Ardabil Prov.: near Nir, Aras River, Caspian Sea basin, 38°00′52.9″N, 47°58′29.7″E, Esmaeili H.R., Vatandoust, S., Khaefi, R., Zamanian Najad, R., Babaei, S., 21. Jun. 2012.

ZM-CBSU-D636–650; 15; 80–170 mm SL; West Azerbaijan Prov., Nazluo Chai River, Lake Urmia basin, Ca. 37°42′42.88″N, 45°03′49.66″E; 1. Oct. 2007; Ebrahimi, M., Teimori, A., Gholamhosseini, A., Gholamifard, A.

ZM-CBSU E449–461; 13; 93–139 mm SL; Iran: West Azerbaijan Prov.: Aghchai; Aras River basin; ca 38°50′53.87″N, 44°49′46.53″E, 1. Oct. 2007; Ebrahimi, M., Teimori, A., Gholamhosseini, A., Gholamifard, A.

A note on *Capoeta capoeta intermedia* (Fig. 32)

Capoeta capoeta intermedia was first described by Bianco & Bănărescu (1982) from specimens of the Mand (Mond) River in Akbar (presumably Kavar) and some specimens from Borazjan (Helleh River drainage, Persian Gulf basin) (Fig. 2). The description was based on the following morphological characters: 62–70 scales in the lateral line (M: 66.2), 19–24 gill rakers (M: 21.3), transversal mouth (but smaller than in *C. c. umbla*), a rather light coloration, and 24–28 scales around caudal peduncle. The authors considered it a subspecies of *C. capoeta* and intermediate between *C. c. macrolepis* and *C. c. umbla* because of the number of lateral line scales (62–70 in *C. c. intermedia*, 81–89 in *C.c. umbla* and 41–47 in *C.c. macrolepis*). It was first considered as synonym of *Capoeta damascina* (Valenciennes, 1842) by Coad (1991, 1995) and Esmaeili et al., (2010) and recently as a synonym of *Capoeta saadii* (Heckel, 1847) (see Esmaeili et al., 2015; Jouladeh-Roudbar et al., 2015; Alwan et al., 2016a, b; Zareian et al., 2016a, b).

Fig. 32 Holotype of *Capoeta intermedia*, IZA 7892, (now = *C. saadii*)

Discussion

Phylogenetic relationships, polyploidy origin, mouth phenotype, and number of barbels

The present study provides a comprehensive morphological and molecular phylogenetic framework of all species of the *Capoeta capoeta* group in the Caspian Sea, Urmia Lake, Sevan Lake, Namak Lake, Kavir, Zayanehrud, Kor, Kura, and Persian Gulf basins and molecular phylogeny of the genus *Capoeta*. The genus *Capoeta* was found to be monophyletic, and closely related (sister) to the studied species of *Luciobarbus* (Fig. 8). The molecular phylogenetic relationship between *Capoeta* and *Luciobarbus* was first formulated for three species of *Capoeta* (Berrebi & Tsigenopoulos, 2003; Tsigenopoulos et al., 2010), later for 20 *Capoeta* species (Levin et al., 2012) considering *Luciobarbus* as paraphyletic.

Based on the molecular data provided by Levin et al. (2012) and here, the genus *Capoeta* probably originated in the Middle Miocene. The Middle Miocene (about 15.97 ± 0.05 to 11.608 ± 0.005 MYA) was characterized by geographic changes resulting from the final closure of the eastern Tethys seaway, and the end of water exchanges between the Indian Ocean and the proto-Mediterranean Basin (Ramsay et al., 1998). The subsequent uplift of mountains in the western Mediterranean region and a global fall in sea levels together resulted in a temporary drying of the Mediterranean Sea (known as the Messinian salinity crisis) near the end of the Miocene and the changing of water regimes in the basins.

It is assumed that the origination and diversification of *Capoeta* took place in the palaeo-drainage of the Tigris–Euphrates system or adjacent water bodies in light of the present restricted distribution of *L.*

subquincunciatus (the closest mitochondrial relative) (see Levin et al., 2012). The Tigris–Euphrates system might be considering one of the important centers of speciation for the inland fauna as well as a basin of exchange for the fish fauna during the Late Miocene (Por & Dimentman, 1989; Coad, 1996; Durand et al., 2002).

Following Por & Dimentman (1989), a Proto-Euphrates system collected water from the Levant and had contact with the Black and Caspian Sea drainages before the Pliocene orogeny. Headwaters of a number of the Tigris–Euphrates rivers interdigitate with the upper reaches of the Black-Caspian Seas basin, e.g., the Aras River of the Caspian Sea and the Kizilirmak of the Black Sea with the Euphrates near Erzurum and Silvas, respectively, the Qezel Owzan (a tributary of Sefidrud) of the Caspian Sea with the tributaries of the Tigris (Coad, 1996), Urmia lake to both the Caspian Sea and Tigris basins and the Kor River with the Tigris via the Paleo-Kor River (Esmaeili et al., 2014). The several geomorphological processes in the area would have facilitated fish dispersal through these basins. Since the main phylogenetic relationships in *Capoeta* agree with its geographic distribution, it seems likely that the tree topology is reflective of the general movement of lineages of *Capoeta*.

MtDNA-based studies indicate that *Capoeta* as a hexaploid genus (see Arai, 2011, p. 49) is phylogenetically nested within the tetraploid genus *Luciobarbus* (see Tsigenopoulos et al., 2003: Fig. 1; see also Tsigenopoulos et al., 2010: Fig. 1). It seems that all the studied species of *Capoeta* from Caucasian and western Asian are hexaploids ($2n = 150$) including the type species (*C. capoeta*), *C. trutta*, *C. umbla*, *C. antalyensis*, *C. baliki*, *C. sevangi*, *Capoeta* from Caspian Sea basin (now = *C. razii*), *Capoeta* from Karun River (now = *C. coadi*), *C. mandica* (Mond River drainage) and those fish identified as *C. damascina* from the Wadi Karak, Jordan (see Krysanov, 1999; Safar et al., 2000; Kiliç & Ünlü, 2001; Gorshkova et al., 2002; Pourali et al., 2006; Arai, 2011; Dorafshan & Roozdar, 2016). Based on these data, there is strong support for the hypothesis by Levin et al. (2012) that *Capoeta* originated as a result of a polyploidization event.

The genus *Capoeta* is a member of a distantly related mitochondrial lineage defined as the *Barbus s.s.* lineage by Berrebi et al. (2014) and Cyprininae (Tribe: Barbini) in Yang et al. (2015: Table 3). This lineage also includes *Luciobarbus* Heckel, from Europe, Middle East, and northwest Africa (see Tsigenopoulos et al., 2003), genus *Barbus s.s.* from Europe and West-Asia (see Kottelat & Freyhof, 2007), and the Bosnia-Herzegovinan and Croatian endemic (see Kottelat & Freyhof, 2007) and the monospecific genus *Aulopyge* Heckel, 1841. In contrast to *Capoeta*, all the latter genera have an ancestral tetraploid origin of $2n = 100$ including the type species, i.e., *Barbus barbus* (Linnaeus, 1758), *Luciobarbus esocinus* Heckel, 1843 (and also *L. barbulus*) and *Aulopyge huegelii* Heckel, 1843 (see Collares-Pereira & Madeira, 1990; Collares-Pereira & Moreira da Costa, 1999; Amirinia et al., 2005; Arai, 2011; Vreven et al., 2016). *Mesopotamichthys sharpeyi* (Günther, 1874) and *Arabibarbus grypus* (Heckel, 1843) are also tetraploid (Amirinia et al., 2005). *Labeobarbus marequensis* (A. Smith, 1841), *L. capensis* (A. Smith, 1841), and *L. polylepis* (Boulenger, 1907) are hexaploid (see Naran et al., 2007). It has been proposed that the hexaploid African *Labeobarbus* and allies and *Capoeta* from Western Asia are likely derived from two independent ancient hybridization events between their respective maternal tetraploid ancestors i.e., tetraploid Torini and *Luciobarbus*, members of the barbins, respectively, and paternal source i.e., *Cyprinion* with the widened straight mouth, horny edge of the lower jaw (Levin et al., 2012, 2013; Yang et al., 2015; Vreven et al., 2016). Thus, it is not unexpected that the hexaploid *Capoeta* is placed as closely related taxon (sister group) to the studied tetraploid *Luciobarbus* in the mitochondrial tree (Fig. 8). According to Levin et al. (2012), *Capoeta* forms a strongly supported monophyletic subclade nested within the *Luciobarbus* clade (using more species of the genus *Luciobarbus*) and thus the genus *Luciobarbus* has a paraphyletic entity.

Beside the karyotype characteristics, mouth shape also differs in these distantly related mitochondrial lineages. Whereas species of *Capoeta* invariably exhibit a typical chiselmouth phenotype, with a characteristic cutting edge covered by a horny sheet on the lower jaw (see Bănărescu, 1999), *Luciobarbus*, *Barbus* (see Kottelat & Freyhof, 2007: fig. 31), and *Aulopyge* instead have a rubbermouth-like or intermediate mouth phenotype. As such, and in contrast to the polymorphic African *Labeobarbus*, the mouth phenotype polymorphism in these other genera appears to covary with mitochondrial lineages

(Vreven et al., 2016) and consistent with the phylogenetic relationships of the genera *Capoeta*, *Luciobarbus*, and *Barbus*.

Based on the data presented here, the genus *Capoeta* is subtended of three highly divergent lineages viz. the *Capoeta trutta* group (Mesopotamian group), the *Capoeta capoeta* group (Aralo-Caspian group), and the Anatolian-Iranian group (includes *Capoeta damascina* group) previously reported by Levin et al. (2012) and Zareian et al. (2016a). The first clade to diverge in *Capoeta* was the Mesopotamian group; its separation occurred in the Middle Miocene about 14.35 MYA (9.94–16.65), and the separation of two other clades (Aralo-Caspian and the Anatolian-Iranian groups) occurred in 9.4 MYA (6.37–12.3). These divergences are mostly in agreement with Levin et al., (2012). In the Mesopotamian group, the most divergent species is *C. mandica* Bianco & Bănărescu, 1982. This species diverged from others of the *C. trutta* species group at 2.24 MYA (1.13–3.71). Following this *C. anamisensis* Zareian, Esmaeili & Freyhof, 2016 separated at 1.83 MYA (0.92–3.05), *C. trutta* (Heckel 1843) at 1.33 MYA (0.57–2.32), and *C. barroisi* Lortet, 1894 from *C. turani* Özuluğ & Freyhof, 2008 at 0.7 MYA (0.16–1.56). Species of the *C. trutta* group, the earliest diverged lineage of the genus (*C. mandica, C. barroisi*, *C. trutta*, *C. turani*), all have single pair of barbels without a horseshoe-shaped lower jaw (Karaman, 1969).

The Anatolian-Iranian clade includes species widespread throughout the Anatolian peninsula and river basins of western and central Iran. This well-supported clade was the most diverse among *Capoeta*, consisting of six subclades; support for these relationships included posterior probabilities ranging from 1 to 0.81 for *cytb* and 1 to 0.87 for COI genes (Figs. 3, 5). Members of this group have 2–4 barbels and a horseshoe-shaped lower jaw (Karaman, 1969) and some of them (e.g., *C. saadii* from Iran) display intra-populational variability in the number of barbels (two, three or four; Nikolskii, 1938; Levin et al., 2005, 2012; Alwan et al., 2016a).

The *Capoeta capoeta* complex group includes highly debated large-scale taxa *C. aculeata*, *C. capoeta*, *C. ekmekciae*, *C. fusca*, *C. gracilis*, *C. heratensis*, *C. macrolepis, C. sevangi*, and *C. razii* (Figs. 3, 5) with genetic distances ranging from 0.38 to 2.94% for COI and 0.60–3.53% for *cytb* genes (Tables 4, 5, 6), mostly having two and for some (e.g. *C. heratensis*, *C. steindachneri*) four barbels. It has already been proposed that species of *Capoeta* with four barbels are more basal than species with only two as all species of *Luciobarbus* have four barbels (Karaman, 1969; Levin et al., 2012). However, this hypothesis may not be supported based on the phylogenetic relationships of the three *Capoeta* species groups (Figs. 3, 5). Species of the *C. trutta* group, the earliest lineage to diverge in the genus, have two barbels. Members of the two other clades have 2–4 barbels. It therefore appears that the number of barbels may be retained in some taxa, whereas other species could rapidly lose them independently of their branch (see Levin et al., 2012) due to the specialization required to scrape algae from stones. It has been proposed that the number of barbels is an evolutionarily reversible character in *Capoeta* (Levin et al., 2012).

The number of vertebrae has also been proposed to be an important taxonomic character, at least in the *C. capoeta* complex group (see Levin et al., 2005). This complex is clearly subdivided into two groups: multivertebrate ("*capoeta*" and "*sevangi,*" *Vert* = 45-48) and oligovertebrate ("*gracilis* = here *razii*," "*heratensis*," and "*steidachneri,*" *Vert* = 41–45). According to Levin et al. (2005), morphometry and longevity also differ between these two groups and it was assumed that they belong to different phyletic lines, relationships corroborated here based on the mtDNA sequences of two genes (Figs. 3, 5).

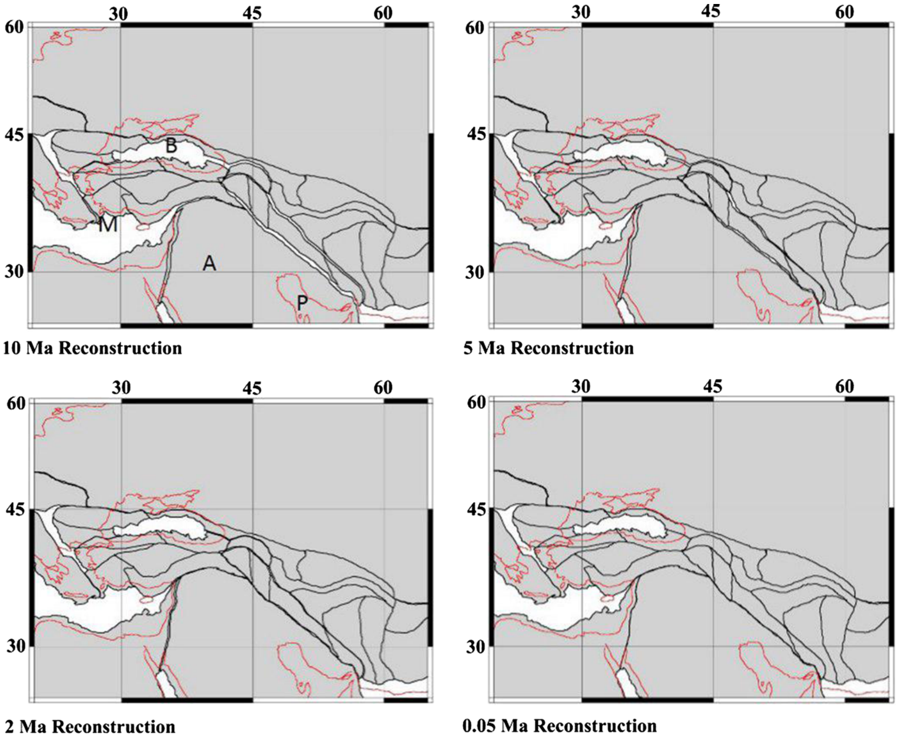
The clade of the *Capoeta capoeta* complex group is formed by two recently diverged subgroups approximately 3.3 MYA [1.99–5.01] in this study and 2.6 MYA in Levin et al. (2012). The main diversification events of the species belonging to these two groups occurred during the Pliocene. The first subgroup includes *C. sevangi*, *C. capoeta*, and *C. ekmekciae* that are widespread in the Kura and Aras Rivers and Lake Sevan drainages (western Caspian Sea basin); interrelationships of these species are not well resolved. The second subgroup comprised a well-supported subgroup of species (bootstrap values of 98% to 99%) distributed in central and eastern parts of the South Caspian Sea basin from the Sefidrud to Atrak Rivers and the northern part of Kavir basin (*C. razii*), in the Tedzhen or Hari River basin (*C. heratensis*) and also from isolated waterbodies in the Lut basin (*C. fusca*).

In our analyses, we revealed some low genetic distances (*cytb* and COI), shared or closely related haplotypes and also partly similar morphology among some species (e.g., *C. sevangi*, *C. capoeta*). This could be attributed to population differences within the same species (Ghanavi et al., 2016), to recent divergence events in this group, or retained ancestral conditions. Differences between forms of *C. capoeta* were noted in some characteristics of external morphology, number of barbels, and special biological traits (Levin et al., 2005). The number of vertebrae in fishes is an important systematic character useful in the diagnosis of taxa of the lower ranks and for the elucidation of the phylogenetic relationships (Kozhara et al., 1996; Naseka, 1996).

Although *C. gracilis* was previously thought to exist in Zayandehrud, Lake Urmia and Caspian Sea basins, further examination of specimens indicates that these three basins include different species, *C. gracilis*, *C. sevangi*, and *C. razii,* respectively. In the original description, *C. gracilis* refers to specimens with black and white parallel stripes extending along the flanks, but our molecular results placed both specimens with and without these parallel lines in the same clade.

Phylogeography

The genus *Capoeta* is distributed across southwestern Asia in the Middle East including Levant, Mesopotamia, Turkey, and Iran (Alwan, 2010; Alwan et al., 2016a, b; Esmaeili et al., 2016; Zareian et al., 2016a, b). It is assumed that the evolutionary history, dispersal, and distribution pattern of taxa in this area are closely related to the paleo-geohydrological events and past movement of Eurasia, Africa (including Arabia), and India, as well as to the geology and past history of Indian Ocean (Fig. 33). These events are also correlated with the presence of the Tethyan Ocean that existed in the present area of the Middle East in the Mesozoic and probably the Paleozoic or even earlier which has already been discussed in detail (see Takin, 1972; Horowitz, 1979). The tectonic events that started in the Middle East during the Upper Miocene played a major role in shaping its geomorphological features and had considerable influence on its fluvial catchment basins, and thus affecting the dispersal of *Capoeta* (Takin, 1972; Horowitz, 1979; Berberian & Yeats, 1999; fig. 1) in these ways: (I) Drainage of the major Levantine River systems (Orontes, Litani, and Jordan) to the Euphrates during the Miocene and for



10 Ma Reconstruction

5 Ma Reconstruction

2 Ma Reconstruction

0.05 Ma Reconstruction

Fig. 33 A simplified account of the geological history of the conglomeration of Iranian plate based on maps of the website of the Ocean Drilling Stratigraphic Network. *A* Arabian plate; *B* Black Sea; *M* Mediterranean Sea; *P* Persian Gulf; Red line: Present day shoreline; Black line: Border of tectonic plate much of the Pliocene (Vaumas, 1957; Wolfart, 1967; Kinzelbach, 1980). (II) Drainage of the confluence of the Litani and Jordan rivers into the Mediterranean during the Pliocene (Horowitz, 1979). (III) Connection of Euphrates and the Jordan-Litani system by Damascus and Palmyra basins (Wolfart, 1967; Krupp, 1987). (IV) Connections between the western affluent of the Euphrates River and upper courses of the Ceyhan Nehri during the Pliocene and probably continuing into the Pleistocene (Kinzelbach, 1987).

Based on the molecular time tree presented herein (Fig. 8), high diversity of the genus *Capoeta* in the Tigris–Euphrates system (e.g., *C. trutta*, *C. macrolepis*, *C. damascina*, *C. umbla*, *C. coadi*), the nesting of *Capoeta* within the tetraploid *Luciobarbus* in the mitochondrial tree (see Levin et al., 2012), and the high diversity of *Luciobarbus* in the Tigris–Euphrates system (e.g., *L. barbulus*, *L. esocinus*, *L. kersin*, *L. subquincunciatus*, *L. xanthopterus*), it can be proposed that the origin and diversification of basal *Capoeta* took place in the palaeo-drainages of the Tigris–Euphrates system (see also Levin et al., 2012; Alwan et al., 2016b; Ghanavi et al., 2016). From the Tigris–Euphrates system, movement of lineages of *Capoeta* to the other nearby basins could have been possible through freshwater corridors during the Pliocene or Pleistocene. Based on the mitochondrial trees, haplotype networks, and geohydrology of the Middle East, it can be proposed that, from its origin, *Capoeta* dispersed to (I) the Levantine River systems (northwestern route), through the headwater capture of the Levant Rivers and the river systems of Mesopotamia during the late Pliocene (3.6–2.58 Ma) (see Kosswig, 1965, 1973); (II) the Urmia and Caspian Sea River systems (north eastern route); and III) the endorheic river systems of Iran (eastern and southern route) (endorehic basins, e.g., Namak Lake, Esfahan, and Kor basins).

Our molecular time tree and existence of members of different species groups in the Tigris basin support divergence of *Capoeta* ancestor into three lineages now referred to as tribes in the Tigris–Euphrates River basin around 6.37–16.65 MYA. This result agrees with Levin et al. (2012) (around 6–12 MYA) rather than Ghanavi et al. (2016) (around 12–15 MYA).

In the most diverged group, *C. trutta* or the Mesopotamian group, different populations of ancestral species expanded from the Tigris basin through the Orontes, Ceyhan, and Seyhan basins to the west and the Persis and Hormuz basins to the east. The common ancestor of the other two groups formed two descendent populations (Anatolian-Iranian and *C. capoeta* species groups) in the Tigris basin (6.37–12.3 MYA). The *C. capoeta* species group was distributed and diverged in Caspian Sea, Lake Urmia, Namak, Kavir, Zayandehrud, and Tigris basins.

Capoeta capoeta and *C. ekmekciae* were distributed and diverged in Caspian Sea and Lake Urmia basins. Urmia Lake basin is considered to be isolated from the Kura drainage since only relatively recently, in the post-glacial epoch (Naseka, 2010). The low genetic distance and age of these species may be related to this fact. In the Anatolian-Iranian *Capoeta* group, a common ancestral population dispersed in two directions, at first to west into the Euphrates, Orontes, Ceyhan, and Seyhan. The second was through the Mediterranean and Black Sea shoreline and then south to Namak, Kor, Persis, and Hormuz basins (4.99–2.06 MYA).

Although it seems that this distribution pattern occurred almost simultaneously in different groups, these events may have happened as a result of the conglomeration between blocks and due to extensive indentation of the Arabian plate into the Iranian plate that started around 10 MYA (Dercourt et al., 1986). This resulted in new connections between basins and then disconnection by uplifting of the Zagros Mountains at the southern edge of the Iranian plate. Continued northeastern movement of the Arabian plate and a northerly movement of India resulted in additional mountain building 5 MYA along the northern edge of the Iranian plateau and different drainage basins (Fig. 33).

Other events that affected the connection and disconnection among basins and populations were the Quaternary glaciation cycles and repetition of the global fall in sea level and pluvial conditions (1.82 Ma–11 Ka BP). These events affected the gene flow of different populations present in this area, providing preliminary population isolation, promoting speciation and resulting in the high biodiversity in Iran.

Acknowledgements We are grateful to M. Masoudi, M. Razbani, H. Mehraban, R. Khaefi, H. Darvishnia and R. Sadeghi for their help during fieldwork and G. Sayyadzadeh for her help in photography. We express our thanks to Environment Departments of Iran for supporting field surveys in Iran. We would like to thank N. Bogutskaya and A. Naseka (Dolsko) for preparing the syntype photos of *C. macrolepis* and A. Palandacic and E. Mikschi, (NMW) for sending the photos and providing permission for their use. We would like to thank D. Turan and E. Bayçelebi for preparing and sending us type photo of *C. ekmekciae* and A. V. Balushkin and M. Tahami for preparing and sending us type photo of *C. fusca*. We would like to thank P.G. Bianco for preparing and sending the syntype photo of *C. c. intermedia*. This work was funded by the Shiraz University and was approved by the Ethics Committee of Biology Department (ECBD-SU-909789).

Author contributions Conceived and designed the experiments: HZ-HRE. Fish collection: HRE-HZ-AG-MO-BJ. Performed the experiments: HZ. Analyzed the data: HZ-AG-HRE. Contributed reagents/materials/analysis tools: HZ-HRE. Wrote the paper: HZ-HRE-RLM.

References

Abdurakhmanov, Yu A, 1962. Ryby Presnykh vod Azerbaidzhana [Freshwater Fishes of Azerbaidzhan]. Akademii Nauk Azerbaidzhanskoi SSR, Institut Zoologii, Baku: 407.

Alwan, N., 2010. Systematics, taxonomy, phylogeny and zoogeography of the *Capoeta damascina* species complex (Pisces: Teleostei: Cyprinidae) inferred from comparative morphology and molecular markers. Unpublished PhD Thesis Dissertation. Johann Wolfgang Goethe-Universität, Frankfurt am Main.

Alwan, N., H. R. Esmaeili & F. Krupp, 2016a. Molecular phylogeny and zoogeography of the *Capoeta damascina* species complex (Pisces: Teleostei: Cyprinidae). PLoS ONE 11: e0156434.

Alwan, N., H. Zareian & H. R. Esmaeili, 2016b. *Capoeta coadi*, a new species of cyprinid fish from the Karun River drainage, Iran based on morphological and molecular evidences (Teleostei, Cyprinidae). Zookeys 572: 155–180.

Amirinia, S., A., Bagherian & E., Jarfi, 2005. Karyotype of four *Barbus* species of Iran. Report submitted to the Ministry of Agriculture Jehad of Iran.

Arai, R., 2011. Fish Karyotypes. A Check List. Springer, Tokyo.

Bănărescu, P. M., 1999. The Freshwater Fishes of Europe. Cyprinidae 2. Part I: *Rhodeus* to *Capoeta*, Vol. 5. Wiebelsheim: AULA-Verlag.

Barrett, J. C., B. Fry, J. Maller & M. J. Daly, 2005. Haploview: analysis and visualization of LD and haplotype maps. Bioinformatics 21: 263.

Berberian, M. & R. S. Yeats, 1999. Patterns of historical earthquake rupture in the Iranian Plateau. Bulletin of the Seismological Society of America 89: 120–139.

Berg, L. S., 1949. Presnovodnye ryby Irana i sopredel'nykh stran [Freshwater fishes of Iran and adjacent countries]. Trudy Zoologicheskogo Instituta Akademii Nauk SSSR 8: 783–858.

Berg, L. S., 1964. Freshwater fishes of the U.S.S.R. and adjacent countries. 4th edition. Israel Program for Scientific Translations Ltd, Jerusalem, Israel.

Berrebi, P., & C. S. Tsigenopoulos, 2003. Phylogenetic organization of the genus *Barbus* sensu stricto: a review based on data using molecular markers. In Bănărescu, P & N. G. Bogutskaya (eds) The Freshwater Fishes of Europe, Vol. 5/II: Cyprinidae, Part II: *Barbus*. AULA-Verlag: 11–22.

Berrebi, P., A. Chenuil, P. Kotlík, A. Machordom & C. S. Tsigenopoulos, 2014. Disentangling the evolutionary history of the genus *Barbus* sensu lato, a twenty years adventure. In Alves, M. J., A. Cartaxana, A. M. Correia & L. F. Lopes (eds), Professor Carlos Almaça (1934–2010) – Estado da arte em áreas científicas do seu interesse. Museu Nacional de História Natural e da Ciência, Lisboa: 29–55.

Bertin, L. & R. Estève, 1948. Catalogue des types de Poissons du Muséum National d'Histoire Naturelle. 4è partie Ostariophysaires (Cypriniformes). Paris.

Bianco, P. G. & P. Bănărescu, 1982. A contribution to the knowledge of the Cyprinidae of Iran (Pisces, Cypriniformes). Cybium 6: 75–96.

Bogutskaya, N. G. & A. M. Naseka, 2004. Katalog beschelyustnykh i ryb presnykh i solonovatykh vod Rossii c nomenklaturnymi i taksonomicheskimi kommentariyami [Catalogue of Agnathans and Fishes of Fresh and Brackish Waters of Russia with comments on nomenclature and taxonomy]. Zoological Institute, Russian Academy of Sciences and KMK Scientific Press Ltd, Moscow.

Bruford, M. W., O. Hanotte, J. F. Y. Brokfield & T. Burke, 1992. Single-locus and multilocus DNA fingerprinting. In Hoelzel, A.R. (ed.) Molecular Genetic Analysis of Populations: A Practical Approach. Oxford University Press, New York: 225–269.

Coad, B. W., 1979. Poisonous and venomous freshwater fishes of Iran. Pahlavi Medical Journal 9: 388–407.

Coad, B. W., 1980. A provisional, annotated checklist of the freshwater fishes of Iran. Journal of the Bombay Natural History Society 76: 86–105.

Coad, B. W. 1981. Fishes of Afghanistan, an annotated checklist. National Museum of Canada Publications in Zoology No. 14: i-v+1-26.

Coad, B. W., 1991. Fishes of the Tigris-Euphrates Basin: a critical checklist. Syllogeus 68: 1–49.

Coad, B. W., 1995. Freshwater fishes of Iran. Acta scientiarum naturalium Academiae scientiarum Bohemicae – Brno 29: 1–64.

Coad, B. W., 1996. Fishes from the qanats of Iran. Publicaciones Especiales Instituto Español de Oceanografía 21: 63–79.

Coad, B. W., 2014. Fishes of Afghanistan. Pensoft Publisher, Sofia, Moscow.

Coad, B. W. 2017. Freshwater fishes of Iran. Retrieved from http://www.briancoad.com. Accessed: February 2017.

Coad, B. W. & F. Krupp, 1994. *Capoeta aculeata* (Valenciennes in Cuv. and Val. 1844), a valid species of cyprinid fish from Iran (Teleostei: Cyprinidae). Zoology in the Middle East 10: 63–72.

Collares-Pereira, M. J. & J. M. Madeira, 1990. Cytotaxonomic studies in Iberian cyprinids. III. Karyology of Portuguese populations of *Barbus* Cuvier, 1817, with some reconsiderations on the karyological evolution of Cyprinidae. Caryologia 43: 17–26.

Collares-Pereira, M. J. & L. Moreira Da Costa, 1999. Intraspecific and interspecific genome size variation in Iberian Cyprinidae and the problem of diploidy and polyploidy, with review of genomes sizes within the family. Folia Zoologica 48: 61–76.

Dadikyan, M. G., 1986. Ryby Armenii [Fishes of Armenia]. Izdatel'stvo Akademiya Nauk Armyanskoi SSR, Yerevan.

Dercourt, J. E. A., L. P. Zonenshain, L. E. Ricou, V. G. Kazmin, X. Le Pichon, A. L. Knipper & B. Biju-Duval, 1986. Geological evolution of the Tethys belt from the Atlantic to the Pamirs since the Lias. Tectonophysics 123: 241–315.

Dorafshan, S. & A. Roozdar, 2016. Karyological analysis of small-scaled Damascus barbel, *Capoeta damascina* (Valenciennes, 1842) from Tigris Basin. Iranian Journal of Fisheries Sciences 15: 542–551.

Drummond, A. J. & A. Rambaut, 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7: 214.

Drummond, A. J., S. Y. Ho, M. J. Phillips & A. Rambaut, 2006. Relaxed phylogenetics and dating with confidence. PLOS Biology 4: e88.

Durand, J. D., C. S. Tsigenopoulos, E. Unlu & P. Berrebi, 2002. Phylogeny and biogeography of the family Cyprinidae in the Middle East inferred from mitochondrial cytochrome b DNA evolutionary significance of the region. Molecular Phylogenetics and Evolution 22: 91–100.

Eschmeyer, F. & Van Der Laan 2017. Catalog of Fishes: Genera, Species, References.10/10/2016.

Esmaeili, H. R., B. W. Coad, A. Gholamifard, N. Nazari & A. Teimory, 2010. Annotated checklist of the freshwater fishes of Iran. Zoosystematica Rossica 19: 361–386.

Esmaeili, H. R., A. Teimori, G. Sayyadzadeh, M. Masoudi & B. Reichenbacher, 2014. Phylogenetic relationships of the tooth-carp *Aphanius* (Teleostei: Cyprinodontidae) in the river systems of southern and south-western Iran based on mtDNA sequences. Zoology in the Middle East 60: 29–38.

Esmaeili, H. R., S. Babai, A. Gholamifard, A. Pazira, A. Gholamhosseini & B. W. Coad, 2015. Fishes of the Persis region of Iran: an updated checklist and ichthyogeography. Iranian Journal of Ichthyology 2: 201–223.

Esmaeili, H. R., H. Zareian, S. Eagderi & N. Alwan, 2016. Review on the taxonomy of Tigris scraper, *Capoeta umbla* (Heckel, 1843) and its confirmation record from the Iranian part of Tigris River, Persian Gulf basin (Teleostei: Cyprinidae). FishTaxa 1: 35–44.

Felsenstein, J., 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39: 783–791.

Ghanavi, H. R., E. G. Gonzalez & I. Doadrio, 2016. Phylogenetic relationships of freshwater fishes of the genus *Capoeta* (Actinopterygii, Cyprinidae) in Iran. Ecology and Evolution 6: 8205–8222.

Gorshkova, G., S. Gorshkov & D. Golani, 2002. Karyotypes of *Barbus canis* and *Capoeta damascina* (Pisces, Cyprinidae) from the Middle East. Italian Journal of Zoology 69: 191–194.

Günther, A., 1868. Catalogue of the Physostomi in the Collection of the British Museum. London.

Hall, T. A., 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series 41: 95–98.

Heckel, J. J., 1843. Ichthyologie [von Syrien]. In von Russegger,J. Reisen in Europa, Asien und Africa, mit besonderer Rücksicht auf die naturwissenschaftlichen Verhältnisse der betreffenden Länder unternommen in den Jahren 1835 bis 1841, etc. E. Schweizerbart'sche Verlagshandlung, Vol. 1. Stuttgart: 990–1099.

Heckel, J. J., 1849. Die Fische Persiens gesammelt von Theodor Kotschy. In Russegger, J. (ed.), Reisen in Europa, Asien und Afrika, Vol. 2. Stuttgart: Schweizerbartsche Verlagsbuchhandlung, Stuttgart: 255–335.

Heckel, J. J., 1849. Naturhistorischer Anhang. In: J. Russegger (ed.) Reisen in Europa, Asien und Afrika, Vol. 2(3). Stuttgart: 209–357.

Holčík, J. & L. Jedlička, 1994. Geographical variation of some taxonomically important characters in fishes: the case of the bitterling *Rhodeus sericeus*. Environmental Biology of Fishes 41: 147–170.

Horowitz, A., 1979. The Quaternary of Israel. Academic Press, Inc., New York: 1–394.

Howes, G. J., 1982. Anatomy and evolution of the jaw in the semiplotine carps with a review of the genus *Cyprinion* Heckel, 1843 (Teleostei: Cyprinidae). Bulletin of the British Museum of Natural History 42: 299–335.

Huelsenbeck, J. P. & B. Ranala, 2004. Frequentist properties of Bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. Systematic Biology 53: 904–913.

Johari, S. A., B. W. Coad, S. Mazloomi, M. Kheyri & S. Asghari, 2009. Biological and morphometric characteristics of *Capoeta fusca*, a cyprinid fish living in the qanats of south Khorasan, Iran (Osteichthyes: Cyprinidae). Zoology in the Middle East 47: 63–70.

Johari, S. A., S. Mazloumi, A. Abdoli, H. Khajavi & S. Asghari, 2010. Identification and distribution of fish fauna in qanats and standing rivers of Qae'nat (South Khorasan Province, I. R. Iran). Journal of Fisheries 4: 115–120. **In Farsi**.

Jouladeh-Roudbar, A., S. Vatandoust, S. Eagderi, S. Jafari-Kenari & H. Mousavi-Sabet, 2015. Freshwater fishes of Iran; an updated checklist. AACL Bioflux 8: 855–909.

Jouladeh-Roudbar, A., S. Eagderi, H. R. Ghanavi & I. Doadrio, 2016. Taxonomic review of the genus *Capoeta* Valenciennes, 1842 (Actinopterygii, Cyprinidae) from central Iran with the description of a new species. FishTaxa 1: 166–175.

Jouladeh-Roudbar, A., S. Eagderi, H. R. Ghanavi & I. Doadrio, 2017. A new species of the genus *Capoeta* Valenciennes, 1842 from the Caspian Sea basin in Iran (Teleostei, Cyprinidae). ZooKeys 682: 137–155.

Kähsbauer, P., 1963. Zur Kenntnis der Ichthyofauna von Iran. Annalen des Naturhistorischen Museums Wien 66: 317–355.

Karaman, M. S., 1969. Süßwasserfische der Türkei. 7. Teil. Revision der kleinasiatischen und vorderasiatischen Arten des Genus *Capoeta* (*Varicorhinus*, Partim). Mitteilungen aus dem hamburgischen Zoologischen Museum und Institut 66: 17–54.

Keyserling, E., 1861. Neue Cypriniden aus Persien. Zeitschrift für die Gesammten. Naturwissenschaften Halle 17: 1–24.

Kiliç, D. N. & E. Ünlü, 2001. Karyotypes of cyprinid fish *Capoeta trutta* and *Capoeta capoeta umbla* (Cyprinidae) from the Tigris River. Turkish Journal of Zoology 25: 389–393.

Kinzelbach, R., 1980. Hydrobiologie am orontes. Natur und Museum 110(1): 9–18.

Kinzelbach, R., 1987. Faunal history of some freshwater invertebrates of the northern Levant. In Krupp, F., W. Schneider, & R. Kinzelbach, (eds), Proceedings of the

Symposium on the Fauna and Zoogeography of the Middle East, Mainz, 1985. Dr. Ludwig Reichert Verlag, Wiesbaden: 41–61.

Kosswig, C., 1965. Zur historischen Zoogeographie der Ichthyofauna im Süsswasser des südlichen Kleinasiens. Zoologische Jahrbücher für Systematik 92: 83–90.

Kosswig, C., 1973. Uber die Ausbreitungswege sogenannter perimediterraner Süsswasserfische. Bonner Zoologische Beiträge 24: 165–177.

Kottelat, M. & J. Freyhof, 2007. Handbook of European Freshwater Fishes. Published by the authors, Cornol.

Kozhara, A. V., Yu G Izyumov & A. N. Kas'yanov, 1996. General and geographic variation of the vertebral numbers in some freshwater fish. Journal of Ichthyology 36: 179–194.

Krupp, F., 1985. Systematik und Zoogeographie der Süßwasserfische des levantinischen Grabenbruchsystems und der Ostküste des Mittelmeeres. Dissertation zur Erlangung des Grades "Doktor der Naturwissenschaften" am Fachbereich Biologie der Johannes Gutenberg - Universität in Mainz, Mainz.

Krupp, F. 1987. Freshwater ichthyogeography of the Levant. In Krupp, F., W. Schneider, & R. Kinzelbach (eds), Proceedings of the Symposium on the Fauna and Zoogeography of the Middle East, Mainz, 1985. Beihefte zum Tübinger Atlas des Vorderen Orients, Reihe A (Naturwissenschaften), 28, Dr. Ludwig Reichert Verlag, Wiesbaden: 229–237.

Krupp, F. & W. Schneider, 1989. The fishes of the Jordan River drainage basin and Azraq Oasis. Fauna of Saudi Arabia 10: 347–416.

Krysanov, E. Y., 1999. Karyotypes of *Varicorhinus capoeta* and *Barbus goktschaicus* (Cypriniformes) from Lake Sevan, Armenia. Journal of Ichthyology 39: 187–189.

Lévêque, C. & J. Daget, 1984. Cyprinidae. In Daget, J., Gosse, J.-P. (ed.), Thys van den Audenaerde DFE. Check-list of the freshwater fishes of Africa, Vol. I. Paris: ORSTOM. MRAC, Tervuren: 217–342.

Levin, B. A., A. R. Rubenyan & V. B. Salnikov, 2005. Phenetic diversity of khramulya *Capoeta capoeta* (Ostariophysi, Cyprinidae). Journal of Ichthyology 45: 754–767.

Levin, B. A., J. Freyhof, Z. Lajbner, S. Perea, A. Abdoli, M. Gaffaroğlu, M. Özulug, H. R. Rubenyan, V. B. Salnikov & I. Doadrio, 2012. Phylogenetic relationships of the algae scraping cyprinid genus *Capoeta* (Teleostei: Cyprinidae). Molecular Phylogenetics and Evolution 62: 542–549.

Levin, B. A., A. S. Golubtsov, Y. Y. Dgebuadze & N. S. Mugue, 2013. New evidence of homoplasy within the African genus *Varicorhinus* (Cyprinidae): an independent origin of specialized scraping forms in the adjacent drainage systems of Ethiopia inferred from mtDNA analysis. African Zoology 48: 400–406.

Naran, D., P. H. Skelton & M. H. Villet, 2007. Karyology of three evolutionarily hexaploid southern African species of yellowfish, *Labeobarbus* Rüppell, 1836 (Cyprinidae). African Zoology 42: 254–260.

Naseka, A. M., 1996. Comparative study on vertebral column in the Gobioninae (Cyprinidae, Pisces) with special reference to its systematics. Publicaciones Especiales Instituto Español de Oceanografía 21: 149–167.

Naseka, A. M., 2010. Zoogeographical freshwater divisions of the Caucasus as a part of the West Asian Transitional Region. Proceedings of the Zoological Institute, Russian Academy of Sciences 314: 469–492.

Nelson, J. S., T. Grande & M. V. H. Wilson, 2016. Fishes of the World, 5th ed. Wiley, New Jersey.

Nikolskii, A. M., 1897. Reptiles, amphibians and fishes, collected by N. A. Zarudnyi in eastern Persia. Ezhegodnik Zoologicheskogo Muzeya Imperatorskoi Akademii Nauk. St. Petersburg 2: 306–348. **(in Russian)**.

Nikolskii, A. M., 1899. Reptiles, amphibians and fishes collected on the second expedition of N. A. Zarudnyi to Persia in 1898. Ezhegodnik Zoologicheskago Muzeya Imperatorskoi Akademii Nauk. St. Petersburg 4: 375–417. **(in Russian)**.

Nikolskii, G. V., 1938. Ryby Tadzhikistana [Fishes of Tadzhikistan]. Izdatel'stvo Akademii Nauk SSSR, Leningrad (in Russian).

Ocean Drilling Stratigraphic Network. http://www.odsn.de.

Özuluğ, M. & J. Freyhof, 2008. *Capoeta turani*, a new species of barbel from River Seyhan, Turkey (Teleostei: Cyprinidae). Ichthyological Exploration of Freshwaters 19: 289–296.

Palumbi, S. R., 1996. Nucleic acids II: The polymerase chain reaction. In Hillis, D. M., C. Moritz, & B. K. Mable (eds), Molecular Systematics, 2nd ed. Sinauer, Sunderland, MA.

Perdices, A., J. A. Carmona, C. Fernandez-Delgado & I. Doadrio, 2001. Nuclear and mitochondrial data reveal high genetic divergence among Atlantic and Mediterranean populations of the Iberian killifish *Aphanius iberus* (Teleostei, Cyprinodotidae). Heredity 87: 314–324.

Por, F. D. & C. Dimentman, 1989. The legacy of Tethys. An aquatic biogeography of the Levant. Monographiae Biologicae 63: 214.

Pourali, D. S., L. A. Bazyar & K. B. Hasanzadeh, 2006. A karyological study of *Barbus capito*, *Barbus mursa* and two populations of *Capoeta capoeta* from Northern Iran. Iranian Journal of Natural Resources 58: 831–842.

Rainboth, W. J., 1981. Systematics of the Asiatic Barbins (Pisces, Cyprinidae). Unpublished Ph.D. Dissertation. The University of Michigan, Ann Arbor.

Ramsay, A. T., C. W. Smart & J. C. Zachos, 1998. A model of early to middle Miocene deep ocean circulation for the Atlantic and Indian Oceans. Geological Society, London 131: 55–70.

Reshetnikov, Yu S & F. M. Shakirova, 1993. Zoogeograficheskii analiz ikhtiofauny srednei Asii po spiskam presnovodnykh ryb [Zoogeographical analysis of the ichthyofauna of Central Asia by lists of freshwater fish]. Voprosy Ikhtiologii 33: 37–45.

Ronquist, F. & J. P. Huelsenbeck, 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574.

Saadati, M., 1977. Taxonomy and distribution of the freshwater fishes of Iran. M. Sc. Thesis. Colorado State University, Fort Collins, Colorado.

Safar, P., K. Mahmood, K. Bahram & S. Masoud, 2000. Karyological study of two populations of *Capoeta capoeta* from North Iran. Cytologia 65: 231–234.

Schmidt, T. R. & J. R. Gold, 1993. Complete sequence of the mitochondrial cytochrome *b* gene in the cherry fin shiner, *Lythrurus roseipinnis* (teleostei, Cyprinidae). Copeia 3: 880–883.

Stamatakis, A., 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22: 2688–2690.

Takin, M., 1972. Iranian geology and continental drift in the Middle East. Nature 235: 147–150.

Tamura, K., G. Stecher, D. Peterson, A. Filipski & S. Kumar, 2013. MEGA6: molecular evolutionary genetics analysis version 6.0. Molecular Biology and Evolution 30: 2725–2729.

Tsigenopoulos, C. S., J. D. Durand, E. Ünlü & P. Berrebi, 2003. Rapid radiation of the Mediterranean Luciobarbus species (Cyprinidae) after the Messinian salinity crisis of the Mediterranean Sea, inferred from mitochondrial phylogenetic analysis. Biological Journal of the Linnean Society 80: 207–222.

Tsigenopoulos, C. S., P. Kasapidis & P. Berrebi, 2010. Phylogenetic relationships of hexaploid large-sized barbs (genus *Labeobarbus*, Cyprinidae) based on mtDNA data. Molecular Phylogenetics and Evolution 56: 851–856.

Turan, D., M. Kottelat, S. G. Kirankaya & S. Engin, 2006. *Capoeta ekmekciae*, a new species of cyprinid fish from northeastern Anatolia (Teleostei: Cyprinidae). Ichthyological Exploration of Freshwaters 17: 147–156.

Turan, D., M. Kottelat & F. G. Ekmekçi, 2008. *Capoeta erhani*, a new species of cyprinid fish from Ceyhan River, Turkey (Teleostei: Cyprinidae). Ichthyological Exploration of Freshwaters 19: 263–270.

Vaumas, E. De., 1957. Plateaux, plaines et dépressions de la Syrie intérieure septentrionale. Bull la Société géographie d'Égypte 30: 97–235.

Vreven, E. J., T. Musschoot, J. Snoeks & U. K. Schliewen, 2016. The African hexaploid Torini (Cypriniformes: Cyprinidae): review of a tumultuous history. Zoological Journal of the Linnean Society 177: 231–305.

Ward, R. D., T. S. Zemlak, B. H. Innes, P. R. Last & P. D. N. Hebert, 2005. DNA barcoding Australia's fish species. Philosophical Transactions of the Royal Society of London Series B, Biological Sciences 360: 1847–1857.

Wolfart, R., 1967. Geologie von Syrien und dem Libanon. Gebrüder Bornträger, Berlin.

Wossughi Gh., 1978. Beitrag zur Systematik und Zoogeographie der Cyprinidae (Pisces: Teleostei) des Mittleren Ostens, unter besonderer Berllcksichtigung des Irans. Ph.D. thesis, Fachbereich Biologie der Universitlit Hamburg

Yang, L., T. Sado, M. V. Hirt, E. Pasco-Viel, M. Arunachalam, J. Li, X. Wang, J. Freyhof, K. Saitoh, A. M. Simons, M. Miya, S. He & R. L. Mayden, 2015. Phylogeny and polyploidy: resolving the classification of cyprinine fishes (Teleostei: Cypriniformes). Molecular Phylogenetics and Evolution 85: 97–116.

Zareian, H., H. R. Esmaeili & J. Freyhof, 2016a. *Capoeta anamisensis*, a new species from the Minab and Hasan Langhi River drainages in Iran (Teleostei: Cyprinidae). Zootaxa 4083: 126–142.

Zareian, H., H. R. Esmaeili, A. Heidari, M. R. Khoshkholgh & H. Mousavi-Sabet, 2016b. Contribution to the molecular systematics of the genus *Capoeta* from the south Caspian Sea basin using mitochondrial cytochrome b sequences (Teleostei: Cyprinidae). Molecular Biology Research Communications 5: 65–75.