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# *Paracapoeta*, a new genus of the Cyprinidae from Mesopotamia, Cilicia and Levant (Teleostei, Cypriniformes)

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<https://zoobank.org/BB7F843A-CAEC-46CC-A3EE-4EA1169FB4AB>

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## Abstract

The molecular and morphological studies carried out within the scope of this study revealed that the scrapers, known as the Mesopotamian group, belong to a different genus. The *Paracapoeta* **gen. nov.**, from the Mesopotamia and Levant, is distinguished from *Capoeta* and *Luciobarbus* species by the presence of a strong ligament between the base of the last simple and the first branched rays of the dorsal-fin (vs. no or a very weak ligament). The *Paracapoeta* further differs from *Capoeta* by the last simple dorsal-fin ray strongly ossified in adult specimens (more than 75%, vs. less than 75%). The *Paracapoeta* further differs from *Luciobarbus* by the lower lip with horny layer (vs. fleshy lips). The molecular phylogeny based on the combined dataset (COI + Cytb, 1312 bp.) showed that the genus *Paracapoeta* was recovered from the other groups in the subfamily Barbinae with high bootstrap and posterior probability values (BP: 94%, PP: 0.96). Also, *Paracapoeta* and *Capoeta* are well differentiated by an average genetic distance of 8.02±0.78%. The morphological and molecular findings have largely overlapped each other. Besides, *Capoeta turani* is treated as a synonym of *Capoeta erhani*.

## Key Words

*Capoeta*, Mesopotamia, molecular phylogeny, scrapers, taxonomy

## 1. Introduction

Cyprinid genus *Capoeta* Valenciennes, 1842 has a wide distribution in the Mediterranean, Middle East, Caucasus and South-West Asia. Even though the members of the genus occur in lakes and spring waters, they generally prefer fast-flowing streams (Kaya 2019). The genus has attracted the attention of various fish taxonomists and they have described a number of new species over the last fifteen years (Turan et al. 2006a, 2006b; Özuluğ and Freyhof 2008; Alwan 2010; Zareian et al. 2016; Turan et al. 2017; Elp et al. 2018). In parallel with this, many genetic studies have been performed (Turan 2008; Zareian et al. 2016; Bektaş et al. 2017; Bektaş et al. 2019). The Mesopotamian *Capoeta* group, which is proposed as a new genus in this study, appears to be in a different branch from the *Capoeta* genus in many genetic studies (Levin et al. 2012; Berrebi

et al. 2014; Ghanavi et al. 2016; Jouladeh-Roudbar et al. 2017; Zareian et al. 2018; Bektaş et al. 2017, 2019).

Molecular phylogenies based on nuclear and mitochondrial molecular markers unambiguously demonstrated that *Capoeta* is clustered together with the Western Palaearctic barbels of the genera *Barbus* Daudin, 1805 and *Luciobarbus* Heckel, 1843 (Durand et al. 2002; Gante 2011; Levin et al. 2012; Buonerba et al. 2015; Yang et al. 2015). However, hybridization-based polyploidy has likely played a major role in the evolution of the hexaploid genus *Capoeta* (Yang et al. 2015; Levin et al. 2019), which emerged through intergeneric hybridization of *Luciobarbus* (2n = 100) and *Cyprinion* Heckel, 1843 (2n = 50) (Yang et al. 2015). In fact, the genus *Capoeta* (6n; Turan 2008), a monophyletic unit and well-defined genus, probably evolved from the ancestors of a tetraploid *Luciobarbus* as it is closely related to *Luciobarbus mursa* (Güldenstädt,

1773) and *L. subquincunciatus* (Günther, 1868) (Levin et al. 2012; Berrebi et al. 2014; Yang et al. 2015).

The mtDNA sequences of the protein-coding, cytochrome oxidase subunit I (COI) and cytochrome b (Cytb) genes, are powerful markers for deducing evolutionary relationships at the species, genera, family, and higher levels (Johns and Avise 1998; Miya et al. 2003; Hebert et al. 2004; Kartavtsev and Lee 2006; Kartavtsev 2009, 2011; Kartavtsev et al. 2017). According to these mitochondrial datasets, it was reported that *Capoeta* is nested within *Luciobarbus* (Durand et al. 2002; Tsigenopoulos et al. 2003; Gante 2011; Levin et al. 2012; Yang et al. 2015), and probably the Mesopotamian *Capoeta* group [*Capoeta trutta* (Heckel, 1843), *C. erhani* Turan, Kottelat & Ekmeççi, 2008, *C. turani* Özüluğ & Freyhof, 2008, *C. barroisi* Lortet 1894, *C. anamisensis* Zareian, Esmacili & Freyhof, 2016, and *C. mandica* Bianco & Bănărescu, 1982] was initially diverged from other *Capoeta* groups (Berrebi et al. 2014; Ghanavi et al. 2016; Bektaş et al. 2017, 2019; Jouladeh-Roudbar et al. 2017; Zareian et al. 2018).

In recent years, various ideas have been put forward among researchers about the validity of Mesopotamian group species. Erk'akan and Özdemir (2011) compared *C. turani* (Seyhan) and *C. erhani* (Ceyhan) morphologically, based on data provided from literature and claimed that both are the synonyms of the *C. barroisi*. Later, Özdemir (2013) developed this claim further and stated that *C. turani* (Seyhan), *C. erhani* (Ceyhan), *C. barroisi* (Orontes) and *C. trutta* (Persian Gulf basin) are conspecific and all belong to *C. trutta*. Recent studies supported the close relationship between *C. turani* and *C. erhani*; however, *C. erhani*, *C. barroisi* and *C. trutta* are molecularly well distinguished (Bektaş et al. 2017, 2019). Detailed morphological comparisons among these species confirmed these genetic results (Kaya 2019).

Here (i) we discussed the validity of the *Capoeta turani* and (ii) proposed a new generic name, *Paracapoeta*, for the scrapers, formerly known as the Mesopotamian *Capoeta* group based on morphological and molecular analysis.

## 2. Materials and methods

### 2.1. Sample collection

See the list of materials examined in Turan et al. (2008), Elp et al. (2018), Kaya (2019), Kaya et al. (2020), Bayçelebi (2020).

### 2.2. Morphological analyses

The care of experimental animals was consistent with the Republic of Turkey's animal welfare laws, guidelines and policies approved by Recep Tayyip Erdogan University Local Ethics Committee for Animal Experiments (permit reference number 2014/77).

Samples were collected by electro-shocker. After anaesthesia, fish were fixed in 4% formaldehyde. Methods for counting followed Kottelat and Freyhof (2007). The later-

al line scales were counted from the first scale touching the shoulder girdle to the posterior-most scale at the end of the hypural complex. The last two branched rays articulating on a single pterygiophore in the dorsal and anal fins were counted as "1½." The simple dorsal- and anal-fin rays were not counted because the anteriormost rays are deeply embedded.

For osteological preparation (last simple dorsal-fin ray), one specimen of each selected species of *Paracapoeta* and *Capoeta* (*Paracapoeta trutta* [200 mm SL], *P. erhani* [190 mm SL], *P. barroisi* [190 mm SL], *Capoeta damascina* (Valenciennes, 1842) [205 mm SL], *C. tinca* (Heckel, 1843) [190 mm SL] and *C. pestai* (Pietschmann, 1933) [195 mm SL]) were cleared and stained with alizarin red S, according to the protocol of Taylor and Van Dyke (1985). The specimens were examined using a stereo microscope (Nikon SMZ1500), and photos were taken using a digital machine with a glycerol bath.

### 2.3. Molecular data analyses

The COI (577 bp.) and Cytb (735 bp.) fragments of the seventy-one samples for *Capoeta*, (Cytb: Hashemzadeh Segherloo et al. unpublished; Alwan et al. 2016; Zareian et al. 2016, 2018; Zareian and Esmacili 2017; Bektaş et al. 2017, 2019; COI: Levin et al. 2012; Ghanavi et al. 2016; Zareian et al. 2016, 2018; Zareian and Esmacili 2017), *Luciobarbus* (Cytb: Geiger et al. 2014; Yang et al. 2015; Khaefi et al. 2017, 2018; Hashemzadeh Segherloo et al. unpublished, COI: Zardoya and Doadrio 1998; Tsigenopoulos and Berrebi 2000; Doadrio et al. 2002, 2016; Tsigenopoulos et al. 2003; Mesquita et al. 2007; Levin et al. 2012; Buonerba et al. 2013; Yang et al. 2015; Brahimi et al. 2016, 2017; Touil et al. 2019; Benovics et al. 2020), *Barbus* (Cytb: Khaefi et al. 2017; Turan et al. 2018; Güçlü et al. 2020, COI: Keskin unpublished; Zardoya and Doadrio 1999; Meraner et al. 2013; Levin et al. 2019; Özpiçak and Polat 2019), *Cyprinion* (Cytb: Rahman et al. unpublished; Agha et al. unpublished, COI: Durand et al. 2002; Yang et al. 2015), *Scaphiodonichthys* (Cytb: Yang et al. 2013; Miya unpublished, COI: Yang et al. 2015) and *Aulopyge* species (Cytb: Geiger et al. 2014, COI: Ludoški et al. 2020), which are included in the subfamily Barbinae (GenBank accession number, Suppl. material 1: Table S1) were combined with the Clustal W method (Thompson et al. 1994) in the Bioedit 7.2.5 (Hall 1999) as a dataset with a total length of 1312 bp.

For genera *Capoeta*, *Luciobarbus*, *Barbus*, *Cyprinion*, *Scaphiodonichthys* Vinciguerra, 1890, *Aulopyge* Heckel, 1841 and *Paracapoeta* gen. nov., the average intra- and intergeneric distances were computed by the General Reversible Time (GTR) model with gamma distributed invariant sites (G+I) in MEGA X (Kumar et al. 2018). The program jModeltest 0.1.1 (Posada 2008) was used to obtain the best evolutionary model (GTR + I + G for AIC and TrN + I + G for BIC) for combined dataset (Cytb+COI). Bayesian inferences (BI) was conducted using MrBayes v3.2.1 program (Ronquist et al. 2012). Maximum likelihood (ML) algorithm was carried out with GARLI 2.0 (Zwickl 2006) program. For ML, Bootstrap analyses

were conducted with 300 pseudo-bootstrap replicates. Bayesian posterior probability support for each node was calculated with MrBayes v3.2.1 using  $4 \times 10^6$  Markov Chain Monte Carlo (MCMC) steps and the first 2500 trees (10000 generation) were discarded as burn in.

## 2.4. Abbreviations used

<b>FFR</b>	Recep Tayyip Erdogan University Zoology Museum of the Faculty of Fisheries, Rize;
<b>SL</b>	standard length; BI, Bayesian inference;
<b>ML</b>	maximum likelihood;
<b>mtDNA</b>	mitochondrial deoxyribonucleic acid;
<b>Cytb</b>	cytochrome b;
<b>COI</b>	cytochrome c oxidase subunit 1;
<b>AIC</b>	Akaike Information Criteria;
<b>BIC</b>	Bayesian Information Criteria;
<b>bp</b>	base pair;
<b>BP</b>	Bootstrap Percentage;
<b>PP</b>	Bayesian Posterior Probability.

## 3. Results

### 3.1. *Capoeta turani* Özuluğ & Freyhof, 2008, a synonym of *C. erhani*

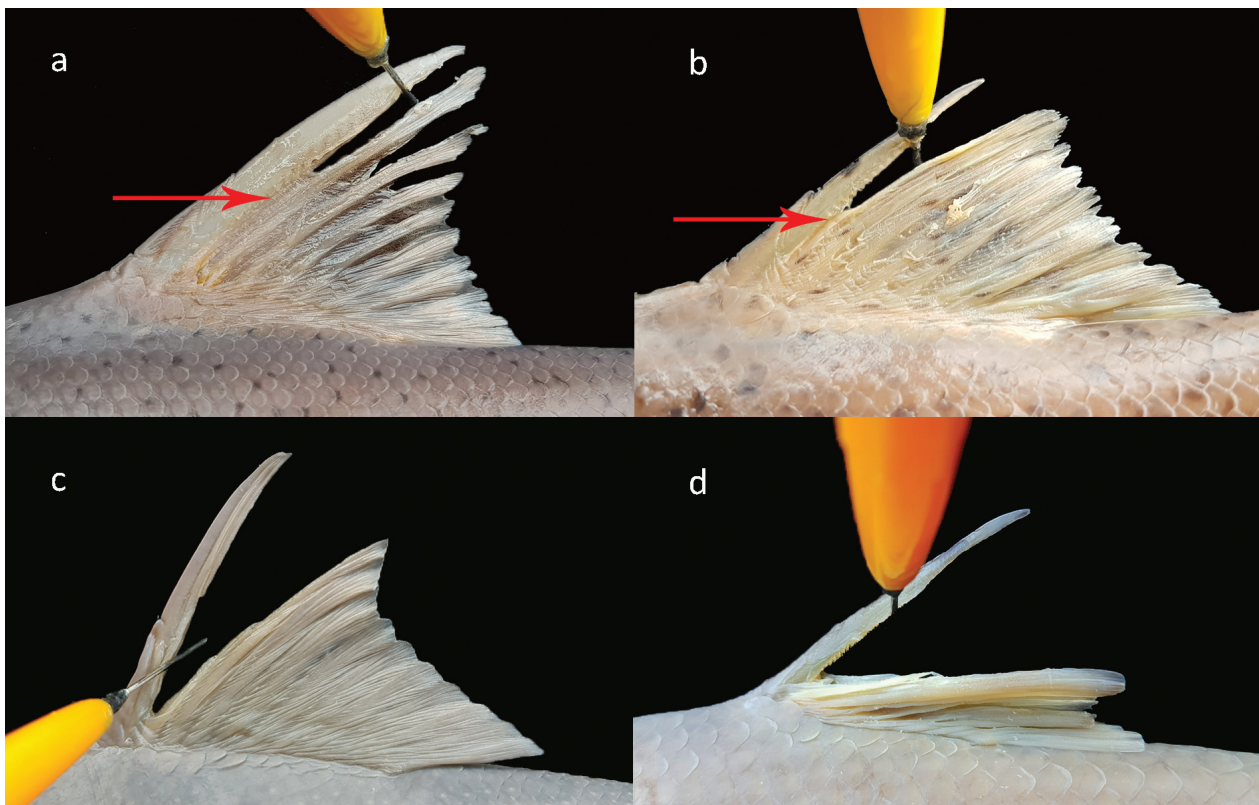
In the original description, *C. erhani* (Ceyhan River) is distinguished from *C. turani* (Seyhan River) by having

numerous spots (vs. few) and a brown back, lateral head and body (vs. silvery). Besides, the spots in *C. erhani* are large and often fused into blotches giving the fish a mottled appearance in individuals smaller than 120 mm SL (vs. spots are always small and never fused into blotches in *C. turani*). Also, caudal peduncle and operculum of *C. erhani* are always densely spotted (vs. few isolated spots or no spots).

Indeed, the silvery body color and the shape, form and number of the spots used in the original description were useful to distinguish both species. However, the fact is that Çakıt (type locality) is a constantly turbid stream (confirmed by Jörg Freyhof, pers. comm., 2019) which has possibly caused these differences in body color and pattern. These changes have also been observed in other species (*Capoeta damascina*, *Oxyzomacheilus sarus*, *Garra turcica*, *Squalius adanaensis*, *Chondrostoma ceyhanensis*, *Salariopsis* sp.) co-occurring with *Capoeta turani*.

Besides, in the original description, *C. turani* is distinguished from *C. erhani* by having more lateral line scales (64–70, vs. 69–78). However, our examination of lateral line scales of both species completely overlaps (63–70 in stream Aksu, Ceyhan; 63–76 in stream Çakıt, Seyhan; 71–79 in stream Üçürge, Seyhan).

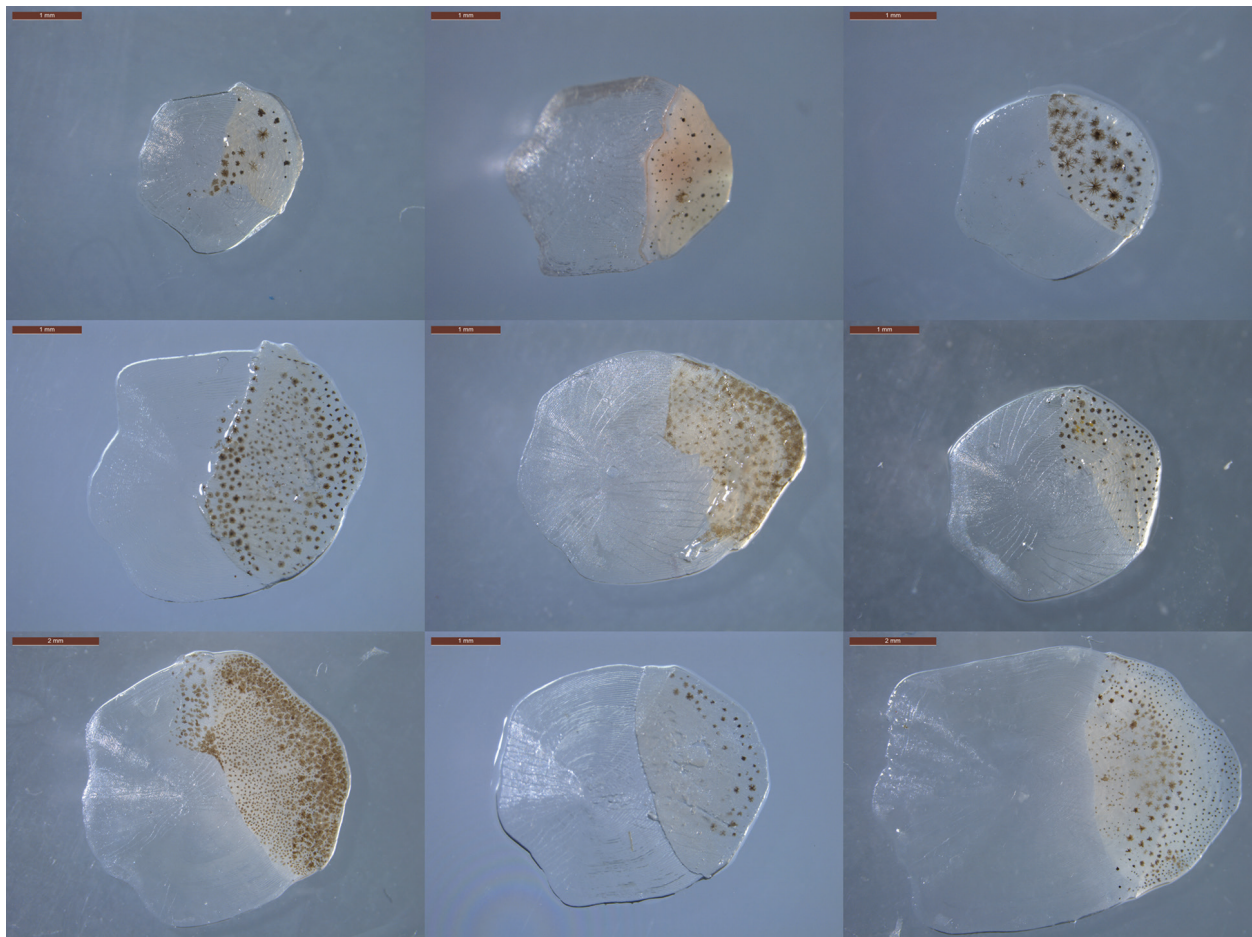
On the other hand, recent molecular studies have stated that there is no difference (0.35%) between these two species at species level (Bektaş et al. 2017, 2019). In the light of this information, we treated *C. turani* as a synonym of *C. erhani*.



**Figure 1.** Presence (a, b) and absence (c, d) of strong ligament between the base of the last simple and the first branched rays of the dorsal-fin; a. *Paracapoeta trutta*, 227 mm SL, Euphrates River; b. *P. erhani*, 265 mm SL, Ceyhan River; *Capoeta damascina*, 250 mm SL, Euphrates River; *Luciobarbus pectoralis*, 227 mm SL, Orontes River.

Key to *Paracapoeta* gen. nov., *Capoeta* and *Luciobarbus* genera

- 1 Lower lip with horny layer; no fleshy lips..... 2  
 – Lower lip without horny layer on; fleshy lips..... *Luciobarbus*  
 2 The presence of a strong ligament between the base of the last simple and the first branched rays of the dorsal-fin..... *Paracapoeta* gen. nov.  
 – No, or very weak ligament between the base of the last simple and the first branched rays of the dorsal-fin..... *Capoeta*



**Figure 2.** Melanophores on the free part of the flank scales: upper row from left, *P. trutta* 146 mm SL; *P. erhani*, 201 mm SL; *P. barroisi*, 155 mm SL; middle row from left, *C. capoeta*; 198 mm SL; *C. banarescui*; 181 mm SL; *C. damascina*, 181 mm SL; lower row from left, *Luciobarbus lydianus*, 192 mm SL; *L. barbulus*, 155 mm SL; *L. capito*, 220 mm SL.

3.2. Rediagnosis of *Capoeta****Capoeta* Valenciennes, 1842**

**Rediagnosis.** The body fusiform and slightly compressed laterally. In adult individuals, the general body color is brownish, and without dark brown or blackish spots (except *C. pestai*). The head plain brownish, and no black spots on head and cheek. The mouth inferior, mouth transversely slit or horseshoe-shaped. Lips not developed and lower lip with keratinize edge. One or two pairs of barbel around the mouth. The last simple dorsal-fin slightly or moderately ossified (less than %75) and its posterior edge serrated (except *C. antalyensis*). No or very weak ligament between the base of the last simple and the first branched rays of the dorsal-fin. There are melanophore

rows on the posterior edge of the flank scales. There is no keel in predorsal area, in front of dorsal-fin.

**Type species.** *Cyprinus capoeta* Gldenstdt, 1773 [actual status of the type species is *Capoeta capoeta* (Gldenstdt, 1773)].

**Included species.** *Capoeta aculeata*, *C. antalyensis*, *C. aydinensis*, *C. banarescui*, *C. bergamae*, *C. buhsei*, *C. caelestis*, *C. capoeta*, *C. coadi*, *C. damascina*, *C. ekmekciae*, *C. ferdowsii*, *C. fusca*, *C. gracilis*, *C. heratensis*, *C. kaput*, *C. macrolepis*, *C. oguzelii*, *C. pestai*, *C. pyragvi*, *C. razii*, *C. saadii*, *C. sevangi*, *C. shajariani*, *C. sieboldii*, *C. tinca*, *C. umbla*.

**Distribution.** Afghanistan, Armenia, Azerbaijan, Georgia, Iran, Iraq, Jordan, Syria, Pakistan, Kazakhstan, Palestine, Tajikistan, Turkey, Turkmenistan and Uzbekistan:

The genus *Capoeta* has a wide distribution in the Mediterranean, Middle East, Caucasus and South-West Asia.

### 3.3. *Paracapoeta*, new genus

#### *Paracapoeta* gen. nov.

<https://zoobank.org/C6B60697-9A20-4AA7-BD64-207A139D01DE>

**Type species.** *Scaphiodon trutta* Heckel 1843 [actual status of the type species is *Paracapoeta trutta* (Heckel, 1843)].

**Diagnosis.** The new genus *Paracapoeta* is distinguished from other genus of *Capoeta* and *Luciobarbus* by having a strong ligament between the base of the last simple and the first branched rays of the dorsal-fin (Fig. 1a, b) (vs. no or a very weak ligament in *Capoeta* and *Luciobarbus* (Fig. 1c, d)). The new genus is further distinguished from

*Capoeta* and *Luciobarbus* by the distribution of melanophores on the flank scales (Fig. 2). In *Paracapoeta*, the posterior part of the scales is covered by more or less melanophores that are irregularly scattered. In *Luciobarbus* and *Capoeta*, there are melanophore rows on the posterior edge of the flank scales, and there are no or numerous irregularly scattered melanophores pigments behind the melanophore rows (Fig. 2). It further differs from the genus *Capoeta* by the last simple dorsal-fin ray strongly ossified in adult specimens (more than % 75, vs. less than % 75) (Fig. 3), a well-developed naked keel in front of dorsal-fin (except *P. anamisensis*, vs. absent in *Capoeta*) and the body with numerous irregular-shaped small black spots on the back and flank (except *P. anamisensis*, vs. absent in *Capoeta*, except *C. pestai*) (Figs 4, 5). It further differs from *Luciobarbus* by having the lower lip with horny layer (vs. with fleshy lips) and lips without papillae (vs. lips with papillae).



**Figure 3.** The last simple dorsal fin rays of some *Paracapoeta* and *Capoeta* species: from left, *P. trutta*, 200 mm SL; *P. barroisi*, 190 mm SL; *P. erhani*, 190 mm SL; *C. damascina*, 205 mm SL; *C. tinca*, 190 mm SL; *C. pestai*, 195 mm SL.

**Table 1.** Nucleotide positions for some genera within the subfamily Barbinae. Diagnostic and distinctive nucleotide positions are represented in bold font and gray background, respectively.

Genera	Diagnostic nucleotide positions																																	
	1	1	2	2	3	3	3	4	4	4	6	6	7	7	8	8	8	8	9	9	9	9	0	0	0	1	1	1	1	1	1	1	1	
	6	8	0	8	0	9	4	7	8	1	7	9	1	4	1	8	4	5	5	8	9	4	9	7	9	3	4	4	5	0	1	4	8	9
	0	0	6	4	5	5	6	0	5	8	8	3	4	9	5	4	1	3	9	3	2	1	4	0	7	6	3	6	3	4	4	0	5	7
<i>Paracapoeta</i>	<b>C</b>	<b>A</b>	<b>T</b>	<b>C</b>	<b>C</b>	<b>T</b>	<b>G</b>	<b>A</b>	<b>T</b>	<b>T</b>	<b>T</b>	<b>T</b>	<b>T</b>	<b>T</b>	<b>C</b>	<b>C</b>	<b>G</b>	<b>G</b>	<b>C</b>	<b>C</b>	<b>T</b>	<b>T</b>	<b>G</b>	<b>C</b>	<b>T</b>	<b>T</b>	<b>T</b>	<b>C</b>	<b>G</b>	<b>T</b>	<b>C</b>	<b>T</b>	<b>T</b>	
<i>Capoeta</i>	T	G	C	T	A/G	C	A	G	C	C	C	C	<b>C</b>	<b>C</b>	<b>C</b>	<b>T</b>	<b>T</b>	<b>T</b>	<b>T</b>	<b>T</b>	<b>C</b>	G/A	A	T	C	<b>C</b>	<b>C</b>	<b>T</b>	A	C	A/G	C	C	
<i>Luciobarbus</i>	T	G	A/C/T	T	A/G	C	A	G	T/C	T/C	C	C	T	C	C	C	C	A	T	C	C	C	G/A	G/A	T	C/T	C	C/T	C	A	C/A	A/G	C/T	C/T
<i>Barbus</i>	T	G	C/T	T	A/G	C	G	G	T/C	T/C	T	T	T	C	C	C	C	A/G	T	C	C	C	G/A	A	T	T	C	C	C	A	C	A/G	C	C/T



**Figure 4.** Lateral view of *Paracapoeta erhani*; **a.** Not preserved, about 155 mm SL, stream Aksu at Kuyumcular, Ceyhan drainage; **b.** FFR 1952, 201 mm SL, stream Aksu at Pazarcık, Ceyhan drainage; **c.** Not preserved, about 200 mm SL, stream Üçürge at Karaisali, Seyhan drainage; **d.** FFR 1955, 130 mm SL, stream Çakıt at Salbaş (type locality of *C. turani*), Seyhan drainage.



**Figure 5.** Lateral view of some *Paracapoeta* species: From top, *P. trutta*, FFR 1873, 225 mm SL; *P. barroisi*, FFR 1725, 174 mm SL; *P. erhani*, FFR 1878, 150 mm SL.

Additionally, based on the combined dataset, twenty-three diagnostic and eleven distinctive nucleotide positions for genera *Paracapoeta* and *Capoeta* are shown in bold font and on gray backgrounds respectively in Table 1.

**Included species.** *Paracapoeta anamisensis*, *P. barroisi*, *P. erhani*, *P. mandica*, *P. trutta*.

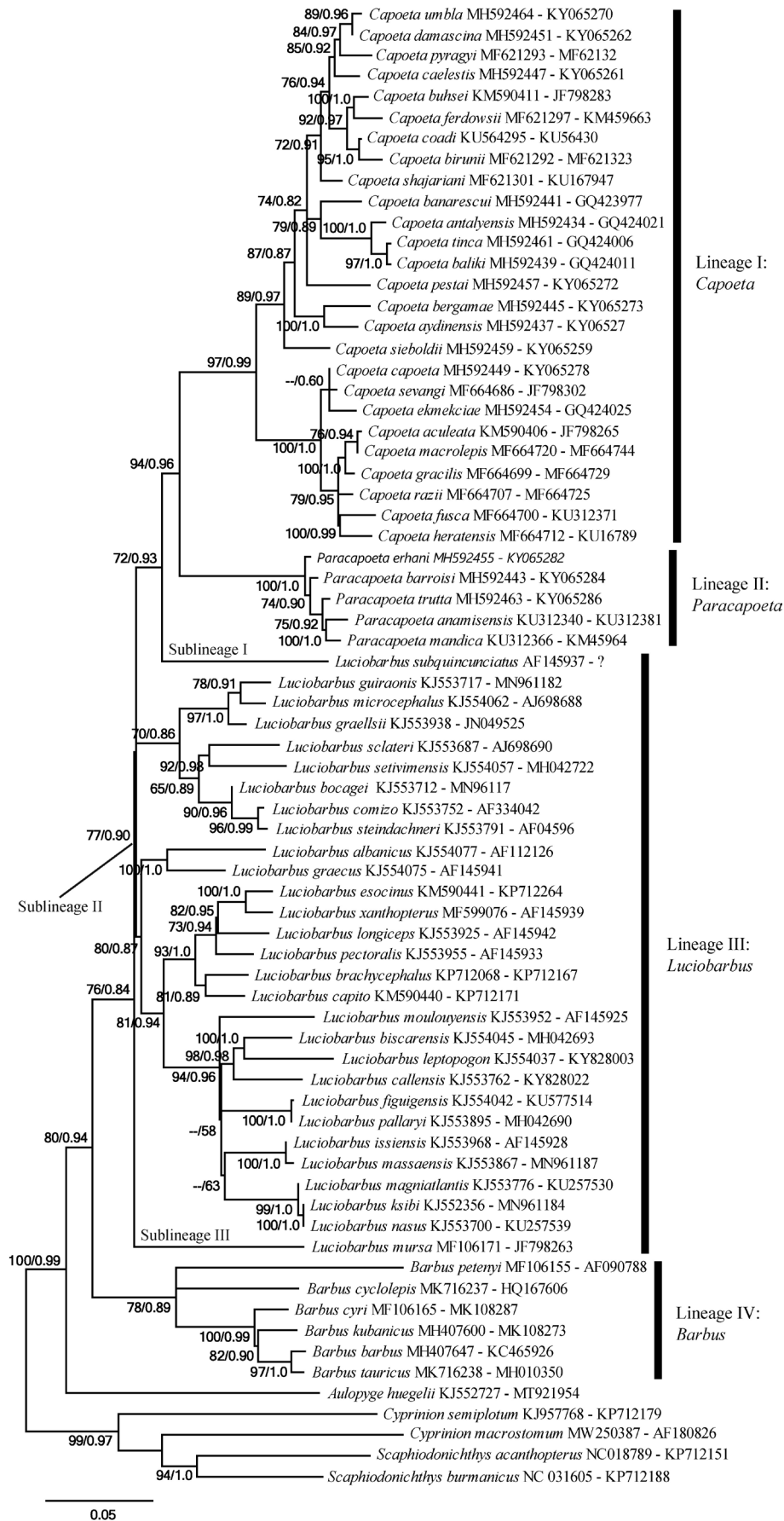
**Distribution.** Turkey, Iran, Iraq and Syria: Seyhan, Ceyhan and Orontes rivers, Levant drainages; Tigris, Euphrates, Mond and Minab River, Persian Gulf drainages.

**Etymology.** The name of the new genus is formed by combining the words “Para” and “*Capoeta*”. “Para” means “beside” or “near”, and “*Capoeta*” is the available name of the closest genus of *Paracapoeta*, deriving from the local vernacular name “kapwaeti” used in Georgia and Azerbaijan.

### 3.4. Results of molecular data analyses

Phylogenetic analyses using BI and ML methods provided similar topologies for the western Palearctic Barbinae genera, with high posterior probability (PP = 0.80–1.00) and high bootstrap (BP = 94–98%) values (Fig. 6). *Barbus* lineage is a sister lineage to *Capoeta*, *Paracapoeta*, and *Luciobarbus* lineages within the subfamily Barbinae (BP = 80%, PP = 0.94). *Luciobarbus* lineage is strongly supported as paraphyletic (BP = 76%, PP = 0.84) with three sublineages (sublineage I: *L. subquincunciatus*, sublineage II: *L. mursa* and sublineage III: other species). The presence of two lineages; “*Capoeta*”, and “Mesopotamian” as the previous different species group (BP = 94%, PP = 0.96) and its sister relationships to lineage III and





**Figure 6.** Phylogenetic tree generated based on the mitochondrial combined dataset. ML and BI methods recovered similar topologies, and therefore only the ML tree is presented here. The bootstrap percentage values (BP)  $\geq 50\%$  from ML analysis and Bayesian posterior probabilities (PP)  $\geq 0.90$  are shown on the nodes (BP/PP)

IV (*Luciobarbus* + *Barbus*) were revealed by the present study (Fig. 6).

The K2P-based distance analyses found a maximum intrageneric distance was 7.1%, in *Luciobarbus* (Lineage III) while the minimum intrageneric distance was 1.1% in *Paracapoeta* gen. nov. (Lineage II) (Table 2). The average intergroup genetic distance ranged from 8.02% (*Paracapoeta* lineage – *Capoeta* lineage) to 10.92% (*Capoeta* lineage – *Barbus* lineage). The second lowest intergeneric genetic distance was 8.77% (between *Paracapoeta* – *Luciobarbus*). The genetic distances between *Paracapoeta* and other groups varied from 8.02% to 10.66% (Table 2).

**Table 2.** The mean genetic distances (in percentages) within and among Barbini lineages.

Groups	1	2	3	4
1 <i>Capoeta</i>	4.5±0.3			
2 <i>Paracapoeta</i>	8.02±0.78	1.1±0.2		
3 <i>Luciobarbus</i>	8.70±0.65	8.77±0.60	7.1±0.5	
4 <i>Barbus</i>	10.92±0.92	10.66±0.77	10.71±0.74	5.4±0.5

**Note:** Values on the diagonal indicate the mean genetic distances within clades.

## 4. Discussion

In an effort to re-evaluate the generic structure of the scrapers, *Paracapoeta* gen. nov., formerly known as the Mesopotamian *Capoeta* group, was assessed based on morphological and molecular data.

In agreement with previous mitochondrial and nuclear markers-based phylogenies (Durand et al. 2002; Tsigonopoulos et al. 2003; Gante 2011; Levin et al. 2012; Yang et al. 2015), *Capoeta* and *Paracapoeta* lineages were recovered as a monophyletic group with its sister lineage, *Luciobarbus* (Fig. 6). Both Bayesian and likelihood inferences indicating the presence of the lineage II referred to as “*Paracapoeta*” (*Paracapoeta trutta*, *P. erhani*, *P. barroisi*, *P. anamisensis* and *P. mandica*) in Fig. 6, agree with the results of previous studies (Berrebi et al. 2014; Ghanavi et al. 2016; Jouladeh-Roudbar et al. 2017; Bektaş et al. 2017, 2019; Zareian et al. 2018) based on multilocus genetic datasets. Furthermore, the *Paracapoeta* gen. nov. (Lineage II) was recovered as a sister lineage to *Capoeta* (Lineage I) and a monophyletic group with high nodal support (BP = 89%, PP = 0.97) (Fig. 6). According to studies using morphological characters, there are numerous apomorphic/morphological features, which could easily differentiate the Mesopotamian group (the new genus *Paracapoeta*) from the *Capoeta* genus (Fig. 6; Table 2).

For a combined dataset of Cytb (735 bp) and COI (577 bp), the intergeneric genetic distances for *Paracapoeta* and *Capoeta* lineages (mean 8.02±0.78%) represent the lowest limit of the predicted intergeneric genetic distances estimated for especially the western Palearctic Barbinae genera, while it corresponds to the lower limits of intergeneric distance (8–10%; Ward et al. 2005; Hubert

et al. 2008; Nguyen et al. 2008; Lara et al. 2010; Perea et al. 2010; Schönhuth et al. 2012) for some closely related Cyprinid genera. On the other hand, *Luciobarbus* lineage exhibited the highest levels of intrageneric genetic diversity (7.1%, Table 2) for the combined dataset because of the presence of two distinct subclades. Since the newly uncovered lineage of *Paracapoeta* gen. nov. from genus *Capoeta* exhibited significant genetic distance in comparison with *Capoeta* species, the classification of the Mesopotamian *Capoeta* group as a subgroup of *Capoeta* is unjustifiable; therefore reclassification as a genus is suggested in the present study.

Consistent with previous studies (Levin et al. 2012; Doadrio et al. 2016; Šimková et al. 2017), our phylogenetic trees revealed some inconsistencies in the current taxonomy of the tribe Barbini, such as the paraphyletic status of the genus *Luciobarbus* and *L. subquincunciatus* having a more recent common ancestor with *Capoeta* and *Paracapoeta* than the other *Luciobarbus*.

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## Supplementary material 1

### Table S1

Authors: Davut Turan, Cüneyt Kaya, İsmail Aksu, Yusuf Bektaş

Data type: excel file

Explanation note: List of Genbank accession numbers of sequences used in molecular analyzes in this study.

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