3D morphology of pharyngeal dentition in barbin fishes (Pisces: Teleostei: Cyprinidae): Implications for taxonomy, phylogeny and palaeobiogeography

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Acknowledgments

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Thesis

Zusammenfassung

Cyprinidae ist die zweitgrößte Fischfamilie der Welt und eine der am weitesten verbreiteten Fischgruppen im Süßwasser. Diese Fische zeigen einen hohen Endemismus für die Entwässerungssysteme in denen sie leben. Ihre geographische Verbreitung hängt von Süßwasseranschlüssen ab und spiegelt damit die Paläogeographie sowie die Geschichte der Wasserbecken dieses Gebietes wieder. Daher sind Süßwasserfische ein gut geeignetes Modell für paläo(bio)gegographische und evolutionäre Studien. Dies ist jedoch nur möglich, wenn fossile Cypriniden auf Artniveau bestimmt werden können. Allerdings sind das rezente Vergleichsmaterial und die verfügbaren Methoden zur Taxonomie isolierter Knochen und Zähne von Cypriniden beschränkt. Innerhalb dieser Studie habe ich erfolgreich eine Methodik zur Identifizierung von isolierten Schlundzähnen barbiner Cypriniden auf Artenebne unter Verwendung der 3D Morphologie etabliert. Die Anwendung dieser Methode auf isolierte Schlundzähne von Kratzbarben der Gattung *Capoeta* ergab folgenden Ergebnisse:

- Die Morphologie von Schlundzähnen beinhaltet ein phylogenetisches Signal und erlaubt Schlussfolgerungen zur Evolution der Gattung zu ziehen;

- Die Evolution von *Capoeta* erfolgte wahrscheinlich in einem Arten-Schwarm während des Pliozän in See-Ökosystemen des Armenischen Hochlandes;

- Diese entwickelte Methode hat großes Potenzial die Evolutionsgeschichte anderer Barbini zu entschlüsseln.

Summary

Cyprinidae is the largest fish family in the world and one of the most widespread in freshwater and shows high endemism to the drainage systems, which they inhabite. Their distribution in water basins depends on freshwater connections and, therewith, reflects the palaeogeographic development as well as the history of the drainage systems of this area. Thus, the freshwater fishes are considered as a proper model for palaeo(bio)geographic and evolutionary studies. These studies can be possible only if the fossil remains are identified at species level. However, the recent comparative material as well as the methods for species level taxonomy of isolated bones and teeth of cyprinid fishes are limited. Here, I successfully provide a tool/methodology for species level identification of isolated pharyngeal teeth of barbine fishes by applying the analysis of the 3D morphology.

By applying this methodology to isolated pharyngeal teeth of extant ten *Capoeta* species as well as to the fossil record of *Capoeta*, I recorded:

- phylogenetic significance of pharyngeal tooth morphology and its insight into evolutionary scenario of the genus;

- the evolution of *Capoeta* was possibly represented by a species-flock model in a huge unrecognized palaeolake system in the present-day Armenian Highland at 4Ma;

- This method has great potential to disentangle the evolutionary history for other Barbini groups.

Abstract

Capoeta is a monophyletic clade of Barbini, endemic to Western Asian and Ponto-Caspian drainage basins. It serves as a valuable model for studying the history of the hydrographic system of this region, as well as provide the evolutionary model of this genus. This can be provided only in case of species level identification of the fossil remains of *Capoeta*, which are mainly represented by well-preserved isolated pharyngeal teeth. Until now, the specie level identification of teeth of any cyprinid is not recorded.

For the first time within this study, the methodology based on the 3D approaches is established to study the detailed morphology of isolated pharyngeal teeth of ten extant *Capoeta* species, to understand its taxonomic and phylogenetic significance. For this purpose, two 3D stage characters (lateral outline and transverse cross section) are imported to describe and categorize the isolated pharyngeal teeth into 18 shape classes. Results show that the detailed morphology can provide species level identification and has phylogenetic significance. This methodology is applied to the fossil record of cyprinids from the early Pliocene locality Çevırme (Turkey), Miocene sites Jradzor (Armenia) and Kisatibi (Georgia), and latest Oligocene to middle Miocene Kargı 1, Kargı 2, Harami1, Hancılı, Keseköy (all from Turkey) localities.

The isolated fossil pharyngeal teeth from Çevırme are identified at species level and four *Capoeta* species (*C.* cf. *umbla, C.* cf. *baliki, C.* cf. *sieboldi* and *C.* cf. *capoeta/C.* cf. *sevangi*) are recorded. This high local diversity of closely related four species I suggest to represent a species-flock model of the genus *Capoeta* in the Tekman palaeo-lake at 4 Ma. I hypothesized that the genus *Capoeta* evolved in the huge late Miocene to Pliocene palaeo-lake system in the present-day Armenian Highland (in the Tekman palaeo-lake). Later in the Pliocene, this extensive palaeo-lake system was disrupted by tectonic activities and resulted the present biogeographic distribution of *Capoeta* in West Asian and Ponto-Caspian drainage systems.

To get the complete view of the evolution of this genus as well as the history of the drainage systems of the Western Asian and Ponto-Caspian regions further studies of fossil sites from these regions are necessary. Within this thesis, two more fossil late Miocene sites (Jradzor and Kisatibi) and latest Oligocene to middle Miocene localities (Kargı 1, Kargı 2, Harami1, Hancılı, Keseköy) are included. The preliminary analyses of the fossil remains from these localities show the presence of the genus diagnostic

shape class "C" and, therewith, indicate that the studied material belongs to the genus *Capoeta.*

The isolated fossil pharyngeal teeth from the Kargı 1, Kargı 2, Harami1, Hancılı, Keseköy localities (Turkey) are identified at generic level and belong to the genera *Barbus* and *Luciobarbus.* However, the species level identification was not possible due to the lack of the detailed morphological studies of this element in the extant barbin species.

The 3D methodology applied within this study (on the example of the genus *Capoeta)* aimed to show that the detailed morphology of pharyngeal teeth provides significant taxonomic and phylogenetic information. Based on this example the similar methodology can be established for the other groups of cyprinid/barbin fishes as *Barbus* and *Luciobarbus.*

1. Introduction

This section consists of two parts. First part includes a brief overview of present day geographic distribution of the cyprinid genus *Capoeta*, its fossil record and its importance to palaeobiogeographic analysis of the Western Asian and Ponto-Caspian regions. The second part is devoted to the 3D morphology of the pharyngeal teeth as a useful tool for taxonomic and phylogenetic studies, as well as its application to the fossil record.

Freshwater fishes, as well as their fossil remains, are very suitable for zoogeographic and palaeobiogeographic studies since their migration(s) from one to another water basin depends largely on connections of the drainage basins. Thus, only the species level identification of these fishes provides the possibility to study the history of the hydrographic system and palaeogeography of the studied area (1).

The family Cyprinidae is the most diverse freshwater fish family represented with around 3000 species (2). The family includes several large clades (subfamilies), i.e. Cyprininae, Leuciscinae (3). Among cyprinins the genus *Capoeta* is not widely distributed. It inhabits only the water basins of Western Asia. This genus shows an endemism to this region, which makes it a valuable and interesting model to study palaeobiogegogrpahy as well as the history of the drainage system evolution of this area.

Currently, more than 30 *Capoeta* species are described (4–6). The earlier taxonomical studies of the genus *Capoeta* are mainly based on morphometric and meristic characters (7, 8), whereas the recent studies mostly on genetic analyses (4, 9). The cyprinid genus *Capoeta,* as other cyprinids, is also characterised by the presence of pharyngeal jaw. The pharyngeal jaws carry pharyngeal teeth, which are arranged in three rows. The number of the pharyngeal tooth rows and tooth number in the each row are mentioned as one of the significant taxonomic characters for the genus *Capoeta* (7, 8, 10, 11). Several studies have shown that the pharyngeal dentition, is an essential character complex at least at genus level, to study the evolution of cyprinids (12–16). Despite of this, the detailed morphological study of pharyngeal teeth of any cyprinid at species level is missing.

For the first time Heckel (1843) described the pharyngeal teeth of cyprinid fishes based on single morphological character (shape of grinding surface) and distinguished four

main groups and 13 subgroups. According to him, the pharyngeal teeth of the genus *Capoeta* belong to the subgroup "shovel-shaped teeth" and are characterized by 4.3.2 (outer, middle and last tooth rows) formula (17). Later studies recorded the presence of four or five teeth in the main, two to four in the second and two in the third rows (7, 8, 11).

Recent studies of the pharyngeal teeth are mainly concentrated on the number of the tooth rows, the tooth number in these rows, some measurements of teeth and pharyngeal bone as well as tooth shapes (11, 12, 14, 16, 18). However, the detailed morphological study of pharyngeal teeth and its significance for the taxonomy and phylogeny of any cyprinid, as well as the genus *Capoeta,* is missing. Besides this, the fossil remains of cyprinids are mainly represented by isolated pharyngeal teeth (19) therefore, the fossil record of many cyprinids, including the genus *Capoeta*, is still largely unknown. This is mainly caused by the problems with lower level (generic/specific levels) taxonomy of isolated pharyngeal teeth.

This dissertation aims to: 1) establish a new methodology to identify isolated pharyngeal teeth at species level; 2) apply it to the suitable group of cyprinids; 3) give an evolutionary model of the genus *Capoeta*; and 4) study the history of drainage basins and palaeobiogeography of the Western Asian and Ponto-Caspian regions.

1.1. The genus *Capoeta* and its biogeographical distribution

The genus *Capoeta* Valenciennes in Cuvier & Valenciennes, 1842, distributed across western Asia from Anatolia to the Levant, Transcaucasia, the Tigris and Euphrates basins, most of Iran, Turkmenistan, Northern Afghanistan and the upper reaches of the Amu-Darya and Syr-Darya drainages (20) (Figs. 1, 2).

Figure 1. *Capoeta damascina* from the Homs (Qattinah) Lake, Orontes River drainage, Syria (SYR08/25, SMF). The scale bar equals to 1cm.

The molecular genetic data shows that the genus *Capoeta* is a monophyletic group, which is nested within the *Luciobarbus* lineage and a sister group of *Luciobarbus subquincunciatus* (Fig. 3) (4, 21, 22). According to the phylogenetic analyses three main groups/clades within the genus *Capoeta* are distinguished: Mesopotamian, Anatolian-
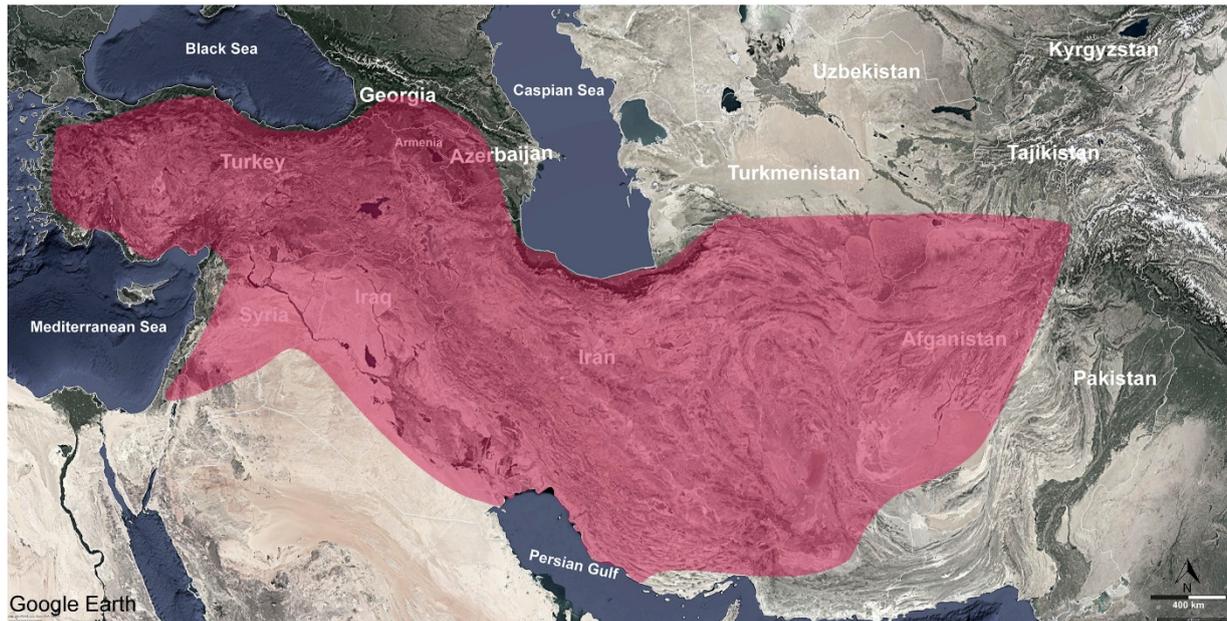
Figure 2. Map showing the present day distibution of the genus *Capoeta* (highlited in red). © Google Earth Pro.

Iranian and Aralo-Caspian clades. The Mesopotamian group contains species distributed in the Tigris-Euphrates drainage system and adjacent water basins: *Capoeta trutta* (Heckel, 1843), *Capoeta turani* Özulu & Freyhof, 2008 and *Capoeta barroisi* Lortet, 1894. The Anatolian-Iranian group includes species inhabiting the Black Sea Basin: *Capoeta sieboldi* Steindachner, 1864*, Capoeta baliki* Turan, Kottelat, Ekmekçi & Imamoglu, 2006*, Capoeta banarescui* Turan, Kottelat, Ekmekçi & Imamoglu, 2006. The Mediterranean drainage basins (Anatolian-Iranian clade) of southeastern Turkey, the Tigris–Euphrates river system, and small rivers, which drain into the gulfs of Persia and Oman, as well as inland water bodies in Iran contain the following species: *Capoeta buhsei* Kessler, 1877*, Capoeta saadii* (Heckel, 1847)*, Capoeta caelestis* Schöter, Özulu & Freyhof, 2009, *Capoeta damascina, Capoeta angorae* (Hankó, 1925) and *Capoeta kosswigi* Karaman, 1969. Finally, the Aralo-Caspian group includes the species distributed in the Kura and Araxes rivers, as well as Aral and Caspian Sea drainages: *Capoeta capoeta* Güldenstädt, 1773*, Capoeta sevangi* De Filippi, 1865*, Capoeta aculeata* (Valenciennes, 1844) (4, 6, 21)
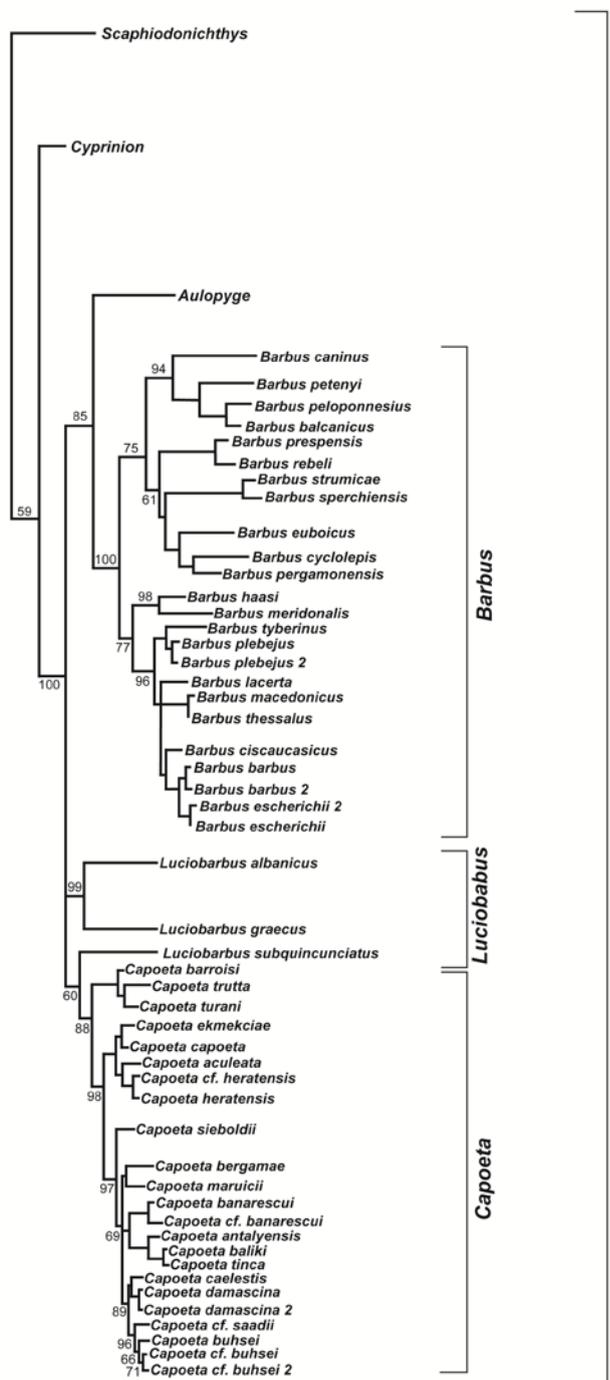
Figure 3. Cladogram showng the location of the genus *Capoeta* on the phylogenetic tree based on the molecular genetic analysis. The phylogenetic tree is taken from Yang et al. 2015. Clades of *Luciobarbus*, *Cyprinion* and *Scaphiodonichthys* are simplified.

The detailed distribution of the studied extant *Capoeta* species see Table 1 Ayvazyan et al., 2018 (21).

1.2.   Cyprinid pharyngeal dentition

Cyprinids are characterized by the toothless jaws (e.g. dentary, maxilla, premaxilla) and by presence of the pharyngeal bones. The pharyngeal jaws form as a result of ossification of the fifth left and right ceratobranchials. They are specialized for the food processing and are located in the posterior part of fish cranium (Fig. 4 A, B). The pharyngeal jaw carries pharyngeal teeth, which are arranged in up to three rows and can be represented by following formula: 4.3.2. - 2.3.4. – numbers indicate number of the teeth on the left and right jaws from the first to the third and the third to the first raw correspondingly (23, 24). As it is already mentioned, the numbers of the rows and the number of the teeth in these rows have a taxonomic significance for cyprinid fishes and they are considered as one of the

criteria mentioned in identification keys.
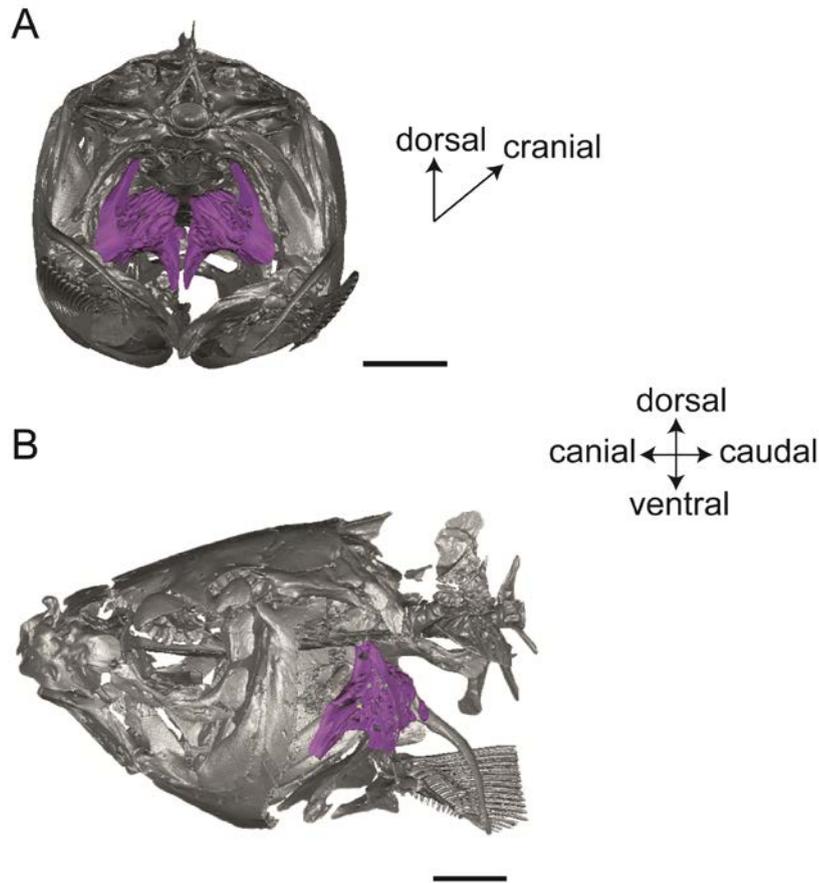
Figure 4. Anatomical location of the pharyngeal bones in *Capoeta sevangi*, Sevan Lake, (A) posterior and (B) lateral views. The scale bars equal to 1cm. Modified from Ayvazyan et al., 2018.

1.3.   The fossil record of *Capoeta*

According to the molecular data, the genus *Capoeta* originated around the Langhian–Serravallian boundary (13.9 Ma) and diversification within the genus occurred along the middle Miocene – late Pliocene (Levin et al., 2012).

The fossil record of *Capoeta* is scarce. So far, until my dissertation they are known only from four localities. Two of them from the late Miocene and other two from the Pleistocene localities. Miocene *Capoeta* fossils are known from Armenia and Georgia; both in the present-day Kura-Araxes drainage basin (Fig. 5).

The first fossil remains of *Capoeta* ('*Varhicorinius*' *nuntius*) have been described by Bogachev (1927) from the late Miocene (early Pliocene at that time) locality in the Kisatibi, Samtskhe-Javakheti region, Georgia (Fig. 5). The material was represented by three more or less complete and a few strongly destroyed skeletons as well as more than 70 bone fragments. Vasilyan & Carnevale (2013) have mentioned skeletons of *Capoeta* sp. from the Jradzor locality (latest Miocene) in Armenia (25).

The record of the genus *Capoeta* from the late Pliocene sediments of Ericek (Cameli Basin, SW Anatolia; Van den Hoek et al., 2015) is doubtful. The tooth morphologies (Fig. 4 a-d in Van den Hoek et al., 2015) are not found within pharyngeal teeth of the *Capoeta* species. Vasilyan et al. (2014) described two isolated pharyngeal teeth and two fragments of serrated dorsal fin rays referred to *Capoeta sp.* from the early

Pleistocene locality Paşinler (Erzurum Province, north-eastern Turkey). Fossil remains of *Capoeta damascina* Valenciennes, 1842 have been recorded during the study of the fish community of the palaeolake Hula (26). The site is situated in the northern part of the Dead Sea Rift, Israel and has been dated to the middle Pleistocene (0.78 Ma).
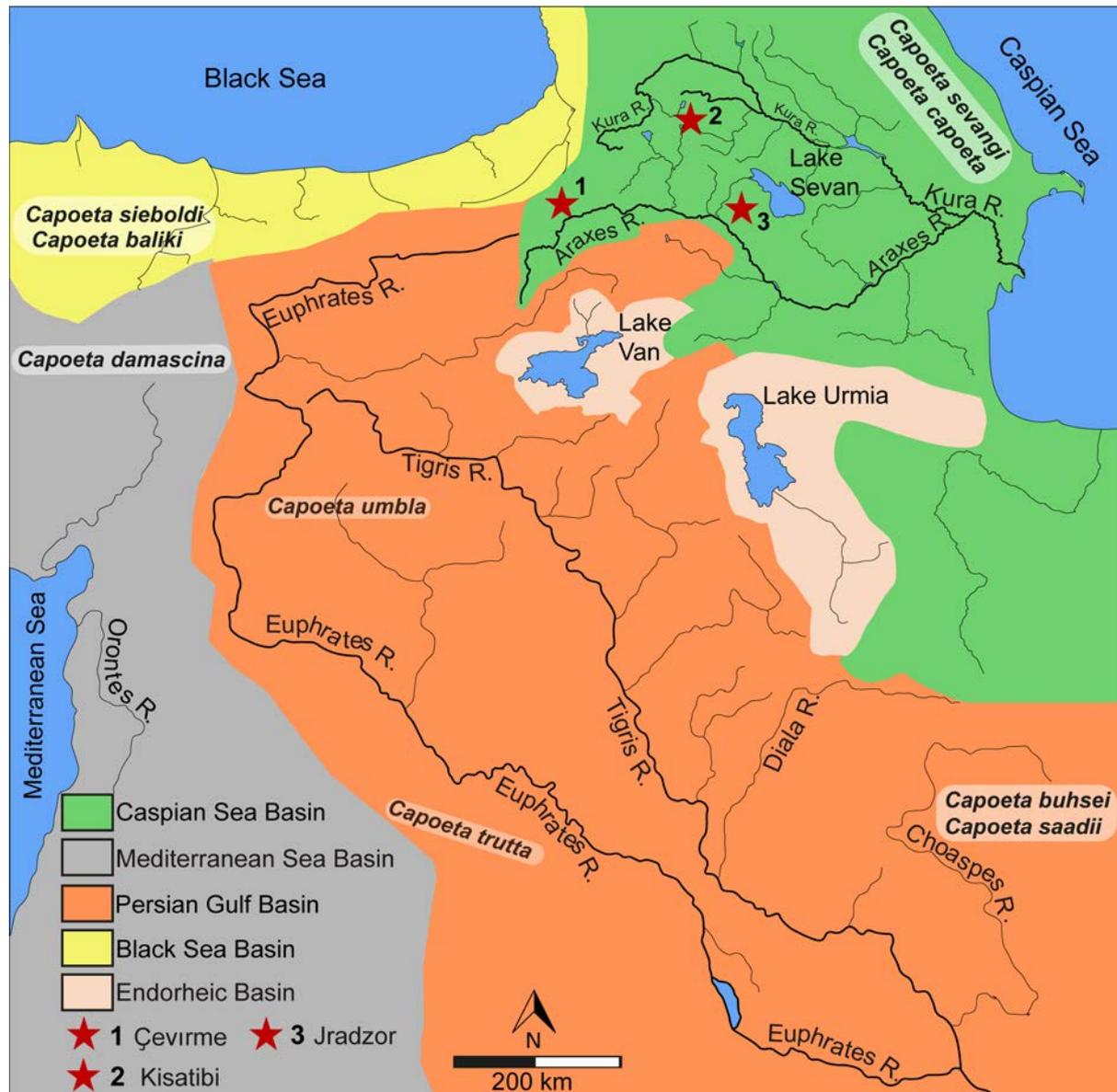
Figure 5. Geographical overview of the drainage systems of Western Asia and Ponto-Caspian regions (Euphrates-Tigris, Araxes-Kura). Red stars indicate the positions of the fossil localities of recorded fossil remains of the genus *Capoeta*.

1.4. What is "species flock"?

A species flock is a monophyletic group of closely related sympatric species inhabiting the same or geographically restricted area. Among both vertebrate and invertebrate animals examples of species flocks are recorded. This phenomena is connected to the rapid adaptive radiation, morphological divergence and speciation (27–30). The species flock concept is known within both living and fossil fishes (31–36) (details see Ayvazyan et al., 2019).

1.5. Ecology and trophic preferences of *Capoeta*

The monophyletic genus *Capoeta* includes herbivorous scrapers, feeding mainly on algae and periphyton, which they scrap from the substrate by the horny sheath on their lower lip. These species generally inhabiting the lakes and streams with fast and slow-flowing waters (7, 20, 37).

1.6. 3D morphology and its importance

3D morphology considered as a morphological study based on the 3D models of studied material. 3D models are created through (micro)computed tomography. Microcomputed tomography is an X-ray transmission technique. X-rays are emitted from generator and travel/penetrate through a sample. They are recorded by a detector on the other side to produce projection image of the sample. The final data of scanning consist of two-dimensional (2D) trans-axial projections, or slices of a scanned specimen, which should be reconstructed in 3D software to get the 3D models (38). These models are used for further examinations and measurements.

3D morphology is one of the modern methods widely applied to the different groups of organisms. The high demand of three-dimensional computed tomography has many reasons: 1) high-resolution images of the study objects are provided; 2) measurements of different morphological structures can be obtained; 3) the 3D image can be rotated easily by changing the rotational axis; 4) the inner structures can be observed by removing the outer surfaces; and 5) different effects or virtual experiments can be

applied (e.g. wearing process of teeth).

The role of the 3D morphology is priceless for the fossil record. Especially if the fossil remain is partly or completely in the sediment. By applying this technique, it is possible to get the complete view of the fossil, without losing any information/material, which could be in the sediment and invisible for us.

The disadvantage of this technique is that the possibility to scan the study material is limited and the costs are high. Besides this, the reconstruction and preparation of the material could be very time consuming.

Objectives and expected outcome of doctoral research

This research addresses to the questions regarding to the taxonomic and phylogenetic significance of the morphology of the isolated pharyngeal teeth of cyprinid fishes. I expected to establish a morphological methodology based on 3D methodology, which is applicable to identify the isolated pharyngeal teeth at species/generic level. For this purpose, the pharyngeal teeth of the monophyletic genus *Capoeta* are studied. This genus shows an endemism to the water basins of the Western Asia and Ponto-Caspian regions, therefore the low level taxonomic identification of the fossil remains (mainly represented by isolated pharyngeal teeth) can serve as a basis to track the evolution of this genus and to perform a palaeobiogeogrpahical analysis of the water drainages of these regions.

Thus, the goals of the present study are:

- to establish methodology by applying 3D approaches to species level identification of isolated pharyngeal teeth of 10 extant *Capoeta* species;

- to check the interspecific and topologic variations of pharyngeal tooth mophology;

- to test the possible phylogenetic signal embedded in the tooth morphology;

- to apply the resulting methodology to the fossil record of *Capoeta*;

- to determine species composition within the fossil sample;

- to evaluate the history and coverage of lake system in Western Asia and Ponto-Caspian regions;

- to discuss evolutionary models for the genus *Capoeta* in respect to its biogeography;

- to test the applicability of this methodology to other barbin fishes.

2. Results and Discussion

2.1. Results

The results of this study are divided into three parts. The first part is devoted to the 3D morphology of the pharyngeal teeth of ten extant *Capoeta* species and its significance to the taxonomy and phylogeny.

The second part concerns to the fossil record of the genus *Capoeta* and the studied main fossil sites where fossil remains of *Capoeta* are recorded.

The third part includes the results of the applicability of the established methodology (within the first part of this study) to the fossil record of cyprinids.

Supplementary material (figures, graphs and tables) is included in Appendix III.

2.1.1. General aspects of the pharyngeal apparatus morphology of the genus *Capoeta*
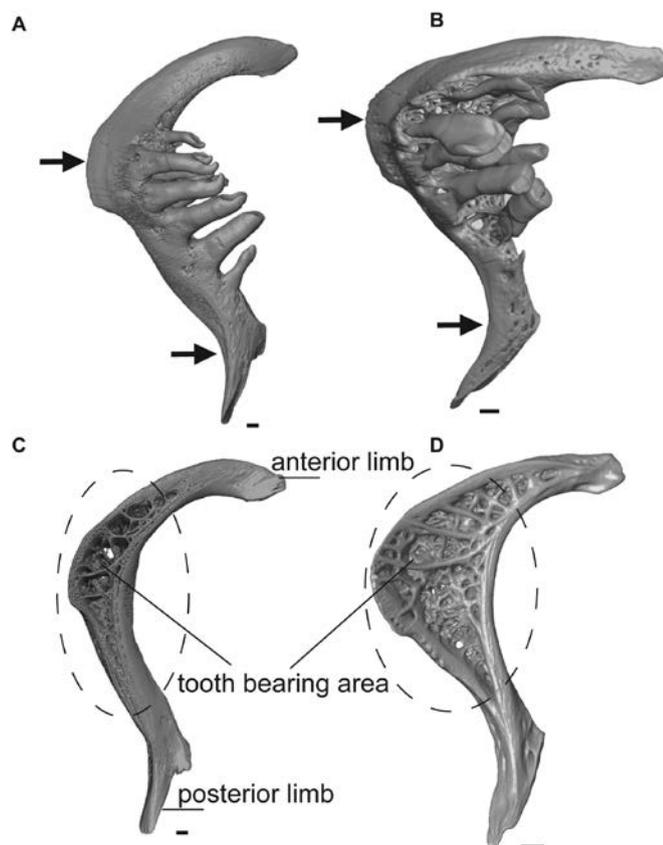
Figure 6. Morphological differences of pharyngeal bones in dorsal (A, B) and ventral (C, D) views: (A, C) *Barbus barbus*; (B, D), *Capoeta umbla*. Black arrows point the main morphological characters and the circles marked the tooth bearing areas. Scale bars equal to 1mm.

The pharyngeal bones of the genus *Capoeta* are relatively robust and wide compare to the pharyngeal bones of the genus *Barbus* (Fig. 6 A, B). They are characterized by relatively large tooth bearing area and well-expressed anterior and curved posterior limbs. A well-developed pharyngeal bone is an evidence of the strong muscles attached to the bone (Fig. 6 C, D).

Each pharyngeal jaw possesses nine to ten pharyngeal teeth, which are arranged at the pharyngeal bone in three rows (I, II, III). Each of them has different tooth number.

The first or main row possesses four or five teeth (a1, a2, a3, a4, a5), the second row three (b1, b2, b3) and the third row two (c1, c2) teeth (Fig. 7, A). Each tooth consistes of a tooth foot, a crown, a foot-crown border, a grinding surface and an edge of the grinding surface (Fig. 7 B).
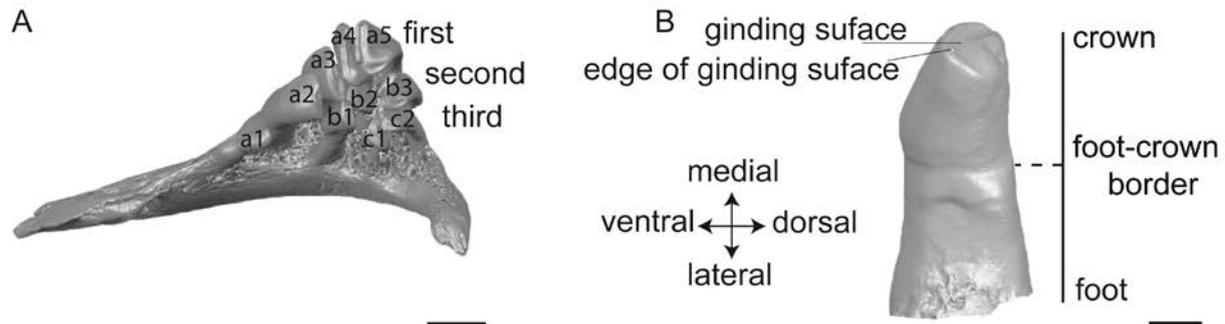
Figure 7. Pharyngeal bone of *C. damascina*: (A) the distribution of pharyngeal teeth into first (a1, a2, a3, a4 and a5), second (b1, b2 and b3) and third teeth (c1 and c2) rows; (B) *C. baliki*, tooth morphology. Scale bars equal to 1mm. Modified from Ayvazyan et al., 2018.

Within the studied ten extant *Capoeta* species from different water basins, two main formulas of the pharyngeal teeth distribution into tooth rows, are recorded: 1) 4.3.2-2.3.4 in *C. capoeta, C. sevangi, C. sieboldi, C. trutta* and *Capoeta sp*; or 2) 5.3.2-2.3.5 in *C. damascina, C. umbla, C. buhsei, C. saadii* and *C. baliki.* The species with the second formula have a1 tooth or the tooth base, which indicates the possible presence of the a1. *Capoeta* shows a heterodont dentition based on recorded high morphological diversity among the studied ten species.

The teeth of the main/first row are relatively larger (except a1) than those of the second and third rows. The first tooth of the main row (a1) is a small accessorial tooth and can be easily broken. It is absent (*C. capoeta, C. sevangi, C. sieboldi, C. trutta* and *Capoeta* sp.), strongly reduced (*C. umbla*) or less reduced (*C. damascina*). In case of *C. saadii, C. buhsei* and *C. baliki* it is broken and only the tooth basis is visible (Fig. 8). As a rule, the second tooth of the main row (a2) is usually easily distinguished from other teeth. It is robust, relatively large with a wide tooth base and grinding surface. The other teeth of the main row (a3, a4, a5), as well as the teeth of two other rows (b2, b3, c1, c2) are slender compared to the a2. They widen distally and bent laterally. These characters are more pronounced ventrodorsally along the main row and well expressed in the most dorsal tooth (a5). The first tooth of the second row (b2) is the second largest tooth after the a2. The other teeth of the second row are slender and bent laterally. Two teeth of

the third row (c1, c2) are usually the smallest. The grinding surfaces in all three rows narrow ventradorsally. Among two control groups *C. sevangi* (n=9) and *C. capoeta* (n=13) intraspecific variation, as well as left-right asymmetry are not recorded.
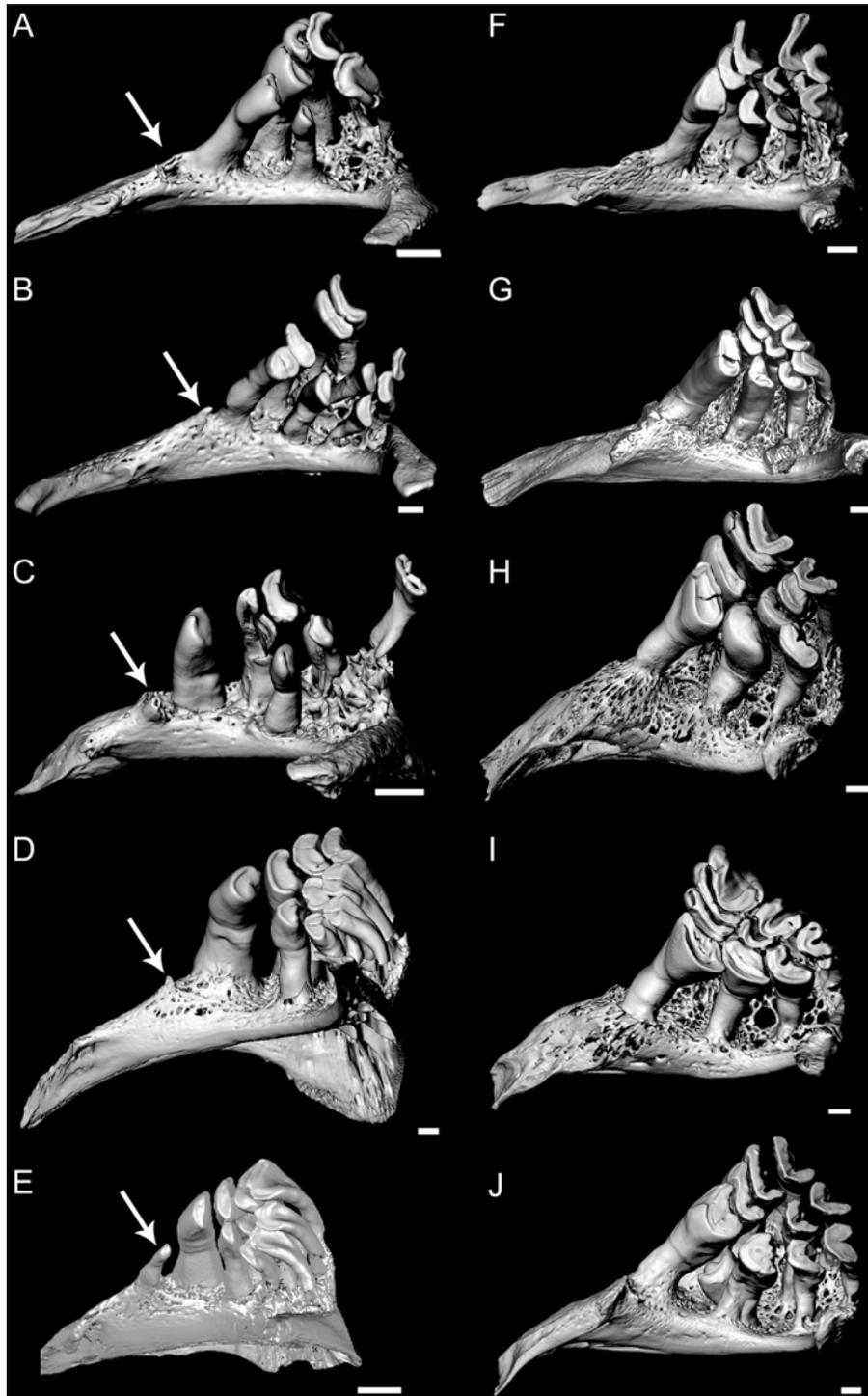
Figure 8. Images of 3D models of pharyngeal bones with teeth of the studied ten extant *Capoeta* species (A–J). (A) *Capoeta buhsei*; (B) *Capoeta umbla* (mirrored); (C) *Capoeta saadii*; (D) *Capoeta baliki*; (E) *Capoeta damascina* (mirrored); (F) *Capoeta capoeta*; (G) *Capoeta sevangi*; (H) *Capoeta sp.*; (I) *Capoeta trutta*; and (J) *Capoeta sieboldi*. The white arrows show a1 or presence of its bases. Scale bars equal to 1mm. From Ayvazyan et al., 2018.

2.1.2. 3D morphology of the pharyngeal tooth: recorded characters and characterization

The morphology of pharyngeal teeth is examined based on 3D models of isolated pharyngeal teeth (n=84) of studied ten extant species. Each pharyngeal tooth is virtually separated from the pharyngeal bone as an apart 3D model and the teeth set for each studied species is established to characterise and categorize these teeth into shape classes (morphotypes) (Fig. 9). Other set of teeth, including extant comparative material of the genus *Capoeta*, are incluided in Appendix, Figure S1.
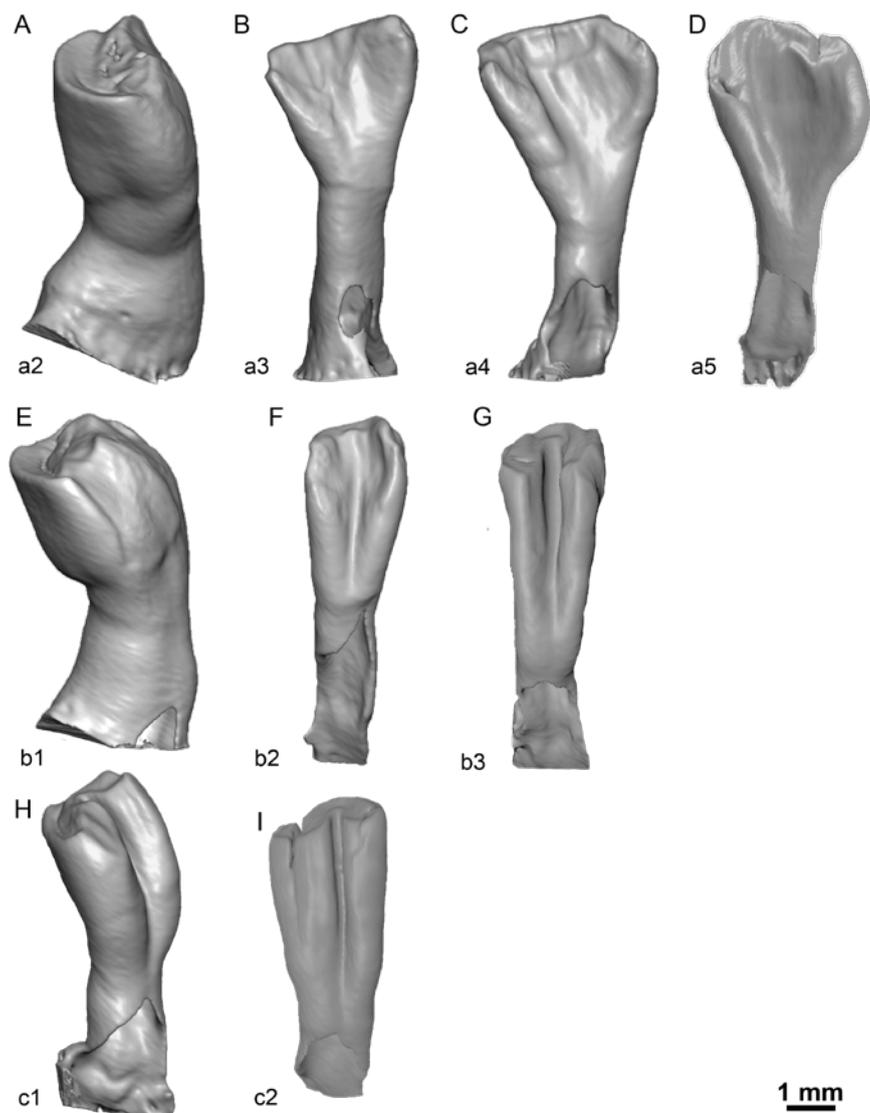
Figure 9. Set of the isolated pharyngeal teeth of *Capoeta trutta*. (A-D)Teeth of the first (a2, a3, a4 and a5), (E-G) second (b1, b2 and b3) and third (H, I) (c1 and c2) rows. Ayvazyan et al., 2018 (supplementary material).

The detailed examination of 3D models of isolated pharyngeal teeth is performed in the 3D software Avizo (8.0, 9.0), as well as under the light microscopes Leica DVM5000 digital- and M50 stereomicroscope (pharyngeal bones/teeth). To formulize better tooth morphology we introduced shape classes defined by character stages: lateral outline (α, the contour of the tooth body) and transverse cross-section (β, measured at the distal tooth crown) (Fig. 9 A, B). Within the studied pharyngeal teeth (n=84), we define 14 character stages of lateral outline (α1-α14) (Fig. 10A). The most frequently lateral outline has a spatulate form. It occurs mainly in the a3-a5, b2-b3 and c1-c2 tooth positions. According to the transverse cross-section, we record in total eleven characters stages (β1-β11) (Fig. 10B).
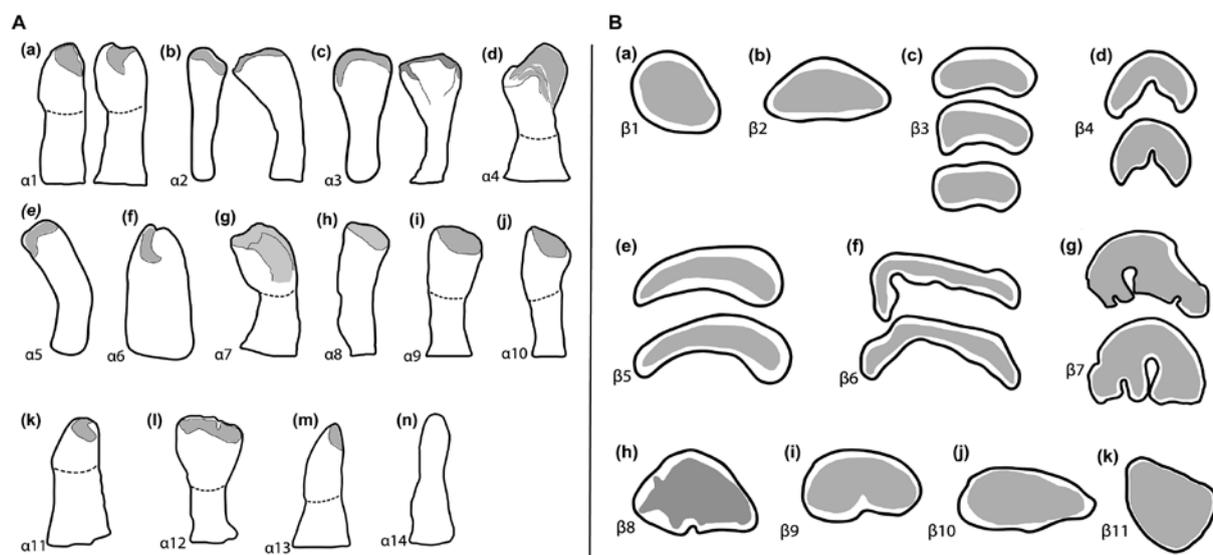
Figure 10. Illustration of character stages: (A) lateral outlines (α1–α14) and (B) transverse cross sections (β1–β11) of isolated pharyngeal tooth within the studied extant *Capoeta* species. Modified from Ayvazyan et al., 2018.

To check the robustness of the transverse cross-section the artificial (virtual) wear experiment is applied (for details see "Material and methods", Ayvazyan et al. 2018). In this experiment the different layers/slices from the top of the grinding surface were cutten to follow the variability, i.e. development of these characters during the wearing process. Thus, three different height sections from the top of the grinding surface (0.57mm, 0.87mm and 1.42mm) were processed. The results did not show any significant changes of transverse cross-section (β) and it stays stable during applied wearing process.

This virtual experiment allows to test also the stability of other characters e.g. foldity

and serrated posterior edge of the grinding surface, which were recorded but not applied to teeth description as these characters depend on degree of tooth wearing (S2 Fig. A1-A3).

Thus, two main groups of characters of the pharyngeal teeth can be identified: 1) applicable for the tooth description as the lateral outline (α) and transverse cross section (β); and 2) variable during the ontogeny as folded, serrated and sloped edge of the grinding surface. The first group of characters (α, β) can be applied to categorize the pharyngeal teeth of the studied ten *Capoeta* species into 18 shape classes. The detailed description of all the shape characters and classes can be found in the Appendix III (Fig. 11, Tables S1, S2).
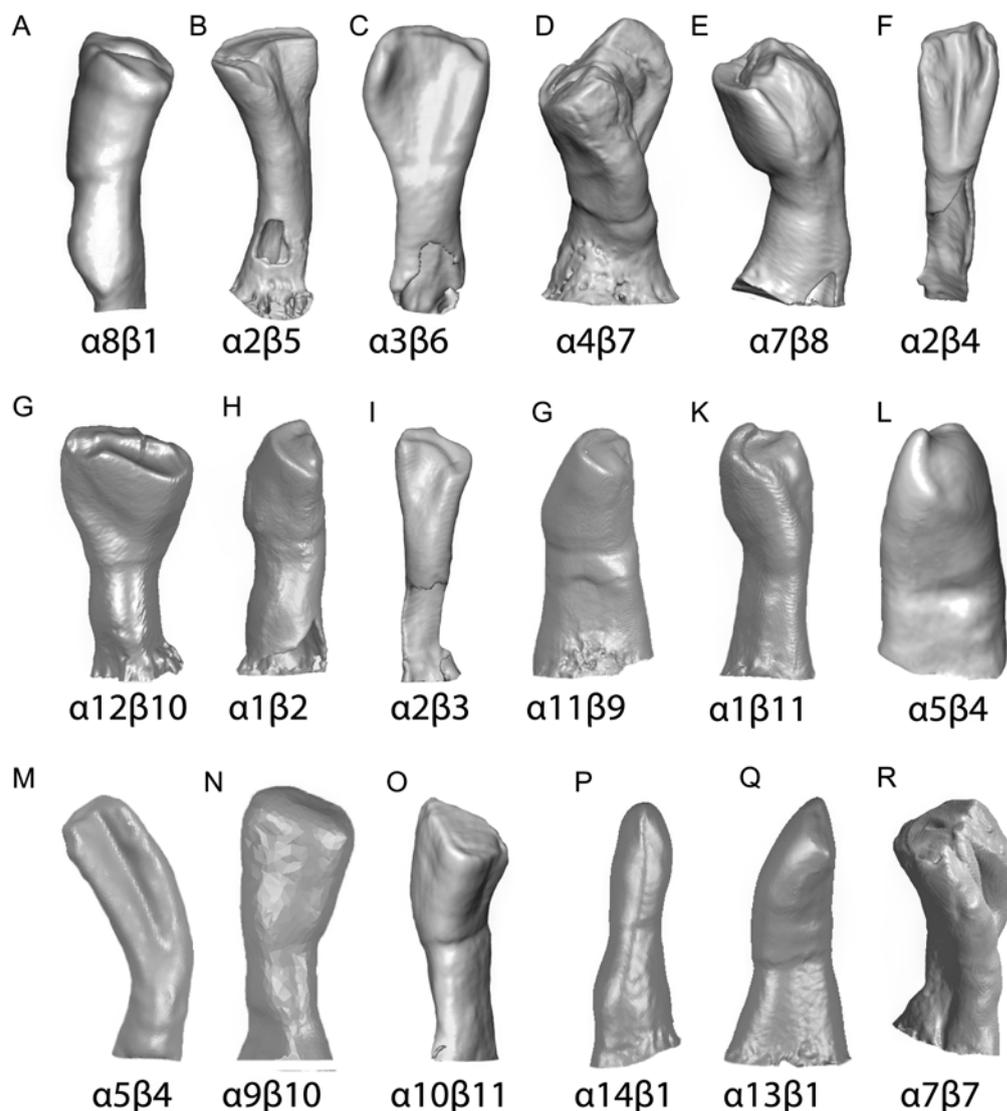
Figure 11. 3D images of the recorded shape classes of the pharyngeal tooth of the genus *Capoeta*. (A-R shape) classes proposed in the present work. The scales are not given in order to avoid scaling up of the figures (Ayvazyan et al., 2018).

2.1.3. Recorded shape classes and distribution within studied species

To test the potential taxonomic and phylogenetic signal of the pharyngeal tooth morphology a dendrogram is performed based on the distribution of recorded shape classes within studied ten extant *Capoeta* species. According to the dendrogram, the studied species are divided into four phenotypic clades: Clade I (*C. saadii, C. buhsei, C. damascina, C. umbla* and *C. baliki*), Clade II (*C. sieboldi*), Clade III (*C. capoeta* and *C. sevangi*) and Clade IV (*C. trutta* and *Capoeta* sp.) (Fig.12, Table S3).
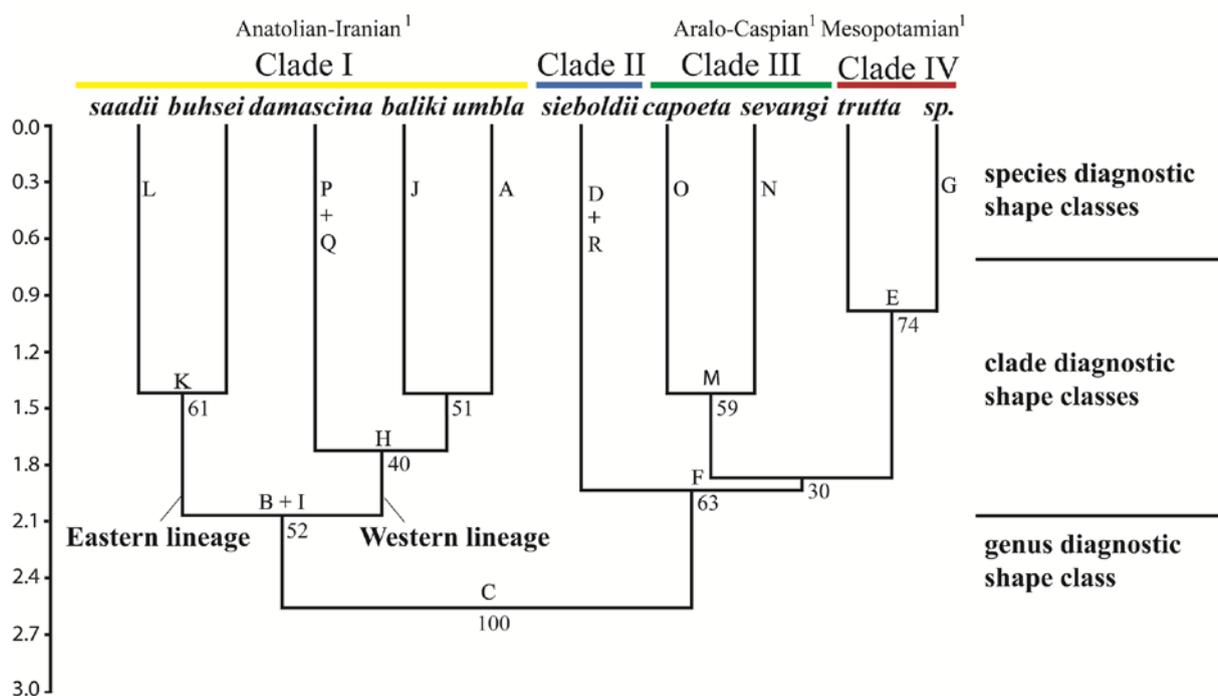
Figure 12. Phenotypic dendrogram generated based on the pharyngeal tooth shape classes of the *Capoeta* species. The letters (A-N) indicate the characteristic shape classes for nodes or branches. Numbers indicate the bootstrap support (branch support). [1]Distinguished clades of the genus *Capoeta* follows Levin et al. (2012). [2]Eastern (E lineage) and Western (W lineage) lineages within the *C. damascina* complex established by Alwan et al., 2016. Modified from Ayvazyan et al., 2018.

Based on the distribution of the recorded 18 shape classes within studied species (shown on the dendrogram) three main groups of the shape classes are distinguished: diagnostic for the **genus, clade** and **species**. The **genus diagnostic shape class** is the shape class "C", since it occurs in all studied species and is characteristic for the genus *Capoeta.* Thus, this shape class is the most frequent within all recoded shape classes (S3 Fig.). The **clade diagnostic shape classes** are characteristic for a group of species, which belong to the same clade, e.g. shape classes "B, E, F, H, I, K and M".

The other shape classes are **species diagnostic**: "D, G, J, L, N, O, P, Q and R" are characteristic for certain species and can be used at **species level identification** of isolated pharyngeal teeth. They occur mainly at the tooth position a2 (S4 Fig). Based on the presence of the different level of shape classes (genus/species/clade diagnostic) and their distribution within ten extant species an identification key is established (S5 Fig.). I found a correlation between tooth positions and shape classes, e.g. shape class "C" occurs in tooth positions a3-a5 in all studied species, whereas species diagnostic shape classes mainly characterise the teeth at the tooth position a2 (except b1 tooth of *C. sieboldi*) (S6 Fig.).

2.1.4. Geological overview

2.1.4.1. Euphrates-Tigris and Kura-Araxes: A brief overview

Four main rivers of the northeast part of Western Asia are the Euphrates, Tigris, Kura and Araxes, which all originate in the Armenian Highland (Fig. 4). The Euphrates and Tigris with their tributaries are life arteries of the entire Mesopotamian area. Both rivers originate from numerous streams in the Armenian Highland (Turkish High Plateau according to Illies & Rzóska, 1980) near the Erzurum Province at an altitude of over 2000 m above sea level (39).

The Euphrates is about 2600 km long. It flows through Syria and Iraq to join the Tigris, form Shatt al-Arab and ends in the Persian Gulf. The Tigris is nearly 2000 km long. The river has five tributaries which drain the mountains (Khabur, Greater and Lesser Zab, Adheym and the Diyala) and carry their erosion products into the plain, where they join the Tigris. The water of the rivers is mainly supplied from the snowmelt and rain (39, 40).

The Kura-Araxes (Araxes also known as Aras and Araks) River Basin is located in the Southern Caucasus. The Kura River is the longest river in the Caucasus (around 1,364 km). It encompasses Turkey, Iran, Armenia (does not pass Armenia but its tributaries), Georgia and Azerbaijan. It starts in the Armenian Highland at the Kizil-Giadik Mountain, and flows southeast through Georgia into Azerbaijan. The main tributary of the Kura is the Araxes River (USAID, 2002) (41, 42). The Araxes River originates in the Bingöl Dağ region, Erzurum Province, where it is separated from headwaters of Euphrates River

through low divide. The total length of the Araxes is 1072 km. It flows through Turkey, Armenia, Azerbaijan and Iran (Kura-Aras River Basin Transboundary Diagnostic Analysis; Campana et al, 2012) (43).

2.1.4.2. Late Neogene lacustrine sedimentation in the Armenian Highland

Present-day Armenian Highland (Eastern Anatolia, Armenia, Iranian Azerbaijan, Samtskhe-Javakheti region of Georgia) is composed of the high mountainous landscapes of the Eastern Taurides and Lesser Caucasus with elevations between 1.700 to over 5.000 meters above sea level. Because of the dominant arid climate during the later Holocene, lakes are rare in this region. Two endorheic saline lakes, Lake Van and Lake Urmia, as well as Lake Sevan are notable exceptions (Fig. 13).

Figure 13. Map of the Armenian Highland. Three main lakes of the region: two endorheic saline lakes Van and Urmia, freshwater Lake Sevan. Figure is redrawn from Vasilyan et al., 2014, background data from © OpenStreetMap contributors, CC BY-SA. Modified from Ayvazyan et al., 2019.

However, geologic mapping revealed, that during the pre-Quaternary lacustrine, sedimentation was widespread and long lasting in this region. According to Altınlı

(1966) during the Late Miocene and Pliocene (11.6-2.6 Ma) lacustrine sedimentation dominates Eastern Anatolia with regional thicknesses of over 1.000 m. These sediments contain a rich freshwater fauna (e.g. diatoms, gastropods, mussels, ostracods, fishes) and have been variously attributed to the Horasan Formation, Gelinkaya Formation, Işıklar Formation (all in the Erzurum Province), Zırnak Formation (Bitlis Province), Çaybaği Formation (Elazığ Province), or to the Parçikan Formation (Malatya Province) (44–49). Despite extensive syn-sedimentary volcanism, none of these formations is fully radiometrically dated. However, few available K-Ar data (50) and rare rodent fossils (51, 52) suggest that the main lacustrine phase in Eastern Anatolia centred between 6 and 3 Ma, probably coeval with the supposed uplift of this region.

Late Miocene to Pliocene lacustrine sediments in Armenia are described from the 500 m thick Voghjaberd Suite (53). Index ostracods of the Caspian Productive Series (dated to between ~5.3 and 2.7 Ma, (54) and small mammals (55) a point to Pliocene age of this formation, and recently discovered rodents from the *Capoeta* bearing site Jradzor have a latest Miocene age (25).

An older lacustrine period is documented in Iranian Azerbaijan, where fish bearing (Atherinidae, Cyprinodontidae, Leuciscinae, but no Barbinae) lake sediments from the Tabriz Basin ('lignite beds', 'fish beds') have been dated to between 12 and 7.5 Ma (56). These late Neogene lacustrine sediments have a tectonically fragmented exposure over a huge area in the Eastern Taurides stretching several hundreds of kilometres, notably including the upper reaches of present-day Euphrates, Tigris, Kura and Araxes rivers (Fig. 13).

2.1.4.3. Fossil locality Çevırme

The fossil site Çevırme (Erzurum Province, Tekman district) (Tekman palaeo-lake) is located 12 km west of the Haciömer village on the road from Haciömer to Tekman, 500 m after the bridge over the Araxes River (coordinates: N 39° 37´ 37˝; E 41° 38´; Figs. 5, 13 and 14).

Figure 14. High resolution map (from Google Earth Pro) showing the fossil locality Çevırme marked by red contoured circle. The whitish sediment north of the Araxes River represent the lacustrine Işıklar Formation. Modified from Ayvazyan et al., 2019.

The locality belongs to the Tekman Basin (East-Anatolian Taurides; Irrlitz, 1972), approximately 40 km south from the Pasinler Basin and 120 km north-northwest of Lake Van. Late Neogene sediments in the Tekman Basin laying discordantly over early Miocene marine limestones (57). The sedimentary facies of the basin infill change from fluvial-alluvial to lacustrine. The late Miocene sedimentary formation (Hacıömer Formation) is composed of an approximately 300 m thick reddish-brown sequence of conglomerates, sandstone and silts with minor intercalation of marls. In the south of the basin, the alteration with vulcanites appear. These terrestrial-fluvial fossils free layers intercalate in their upper parts with nearly 200 m thick lacustrine sediments of the Işıklar Formation, which mainly consist of light gray, as well as slightly reddish freshwater carbonates (see fig. 4 in Ayvzayan et al., 2019). Layers of marl, organic rich clay and tufa are also present. The section is covered by Pleistocene basalts from the Bingöl Dag area (57).

The fossil site Çevırme, discovered and first described by Sickenberg et al. (1975: 95), belongs to the lacustrine upper part of the Işıklar Formation (58). The 65 m thick stratigraphic section is subdivided based on lithological and sedimentological characters. The fossil remains of fishes, molluscs and mammals are found at 18 m of the section (see fig. 4 in Ayvzayan et al., 2018).

Earlier palynological studies at Çevırme section indicate an early Pliocene pollen

spectrum in accordance to the small mammal fauna (57, 58). A recent preliminary taxonomic update of the rodent association revealed among others the genera *Mimomys* and *Occitanomys.* This suggests correlation to MN15a mammal zone, roughly of about 4 Ma in the middle part of the Pliocene (51).

2.1.4.4. Fossil locality Jradzor, Armenia

The fossil locality Jradzor is located in the Yeranos mountainous range at the present-day elevation of the 1920 m asl (Central Armenia) (Figs. 5, 15). The fossil site is represented mainly by pure and porous diatomite rock with extremely low clay and sand content. It has thickness of about 8 m and lateral extension in the outcrop of ca. 150 m.

Figure 15. Fossil locality Jradzor, Central Armenia. The red arrow shows the diatomit sediment section from where the fossil remains of *Capoeta* were recoded.

The presence of two black sandstones in the lower part of the section, indicating erosion of the lake surrounding volcanic rocks and their fluvial transport. The upper 7m tick diatomite bed shows red to yellow colouring and fine lamination. Several 2-10 cm tick layers rich of clay occur, indicating phases with terrestrial input during the lake development. Grey-brown clayey diatomite and overlying grey-bluish sandstone are compose in the uppermost 60 cm of the section. The diatomite is covered by conglomerate, showing sharp erosive contact with underlying beds. Laterally the upper bed is eroded and conglomerates lie directly on upper part of the 7 m thick diatomite pocket. The following stratigraphic markers are recorder: pennatic diatoms *Cymbella elongata* and *Pinnularia meisteri* f. *armenica*.

The diatomite deposit of the fossil site Jradzor provides well preserved fossil diatom algae, remains of fishes (*Leuciscus* cf. *souffia*, *Leuciscus* sp., *Garra* sp., *Capoeta* sp.), an amphibian (*Pelophylax* cf. *ridibundus*), a reptile (Geoemydae indet.) and mammals (? *Hypolagus* sp.). Both complete and incomplete skeletons of fishes are found. The taphonomy of the fish remains allow to conclude about their resident lacustrine populations in the lake, at least in earlier staged of the lake sedimentation. The overlying river and palaeosol deposits contain small mammal species characteristic for latest Miocene assemblages (25).

2.1.4.5.   Fossil locality Kisatibi, Georgia

The fossil locality Kisatibi is a part of a large Goderdzskaya Formation (900-1100 m). Kisatibi is located in the Samtskhe-Javakheti region (southern Georgia), in the middle of the extended gorges of the Kura and Potskhovi rivers (Fig. 5) (59). Skhirtladze (1958) provides the sedimentary succession of the Goderdzskaya Formation at the fossil site Kisatibi (nearly 150 m) (59).

Palaeoflora of Kisatibi is represented by 22 species (59). The fossil remains of vertebrates are almost absent in Goderdzskaya Formation. Only the diatomite layers have relatively rich fossil fauna, which is mainly represented by fossil remains of freshwater fishes. The records of fossil mammals are rare.

Bogachev (1938) described all fish remains from Kisatibi as one genus *Varicorhinus* and as a new species Varicorhinus nuntius. Based on palaeontological and palaeobotanical data, he dated the fossil site Kisatibi to Pliocene (Late Miocene now days) (Gabelaja, 1976).

Later, Gabelaja (1976) studied the fossil remains of fishes from Kisatibi and record the presence of two genera *Barbus* and *Capoeta*. Wherein, the main part of the recorded fossil fish material belong to *Caepota nuntius* and relatively few specimens to *Barbus orientalis*.

2.1.4.6. Latest Oligocene to the middle Miocene localities from Tukey

Fossil locality Kargı is located in a coal quarry near the village of Dodurga. The sediments are represented by white limestones and dark green clays. The biostratigraphic correlations suggest that Kargi 2 lies at the Oligocene–Miocene transition (local zone A, MP 30–MN 1), and Kargi 3 is of Early Miocene age (local zone B, MN1). The fossil remains from Kargi are recovered from bioturbated, blackish, solid clay. Karg1 2 sediments, darkly coloured and bioturbated, indicate a typical lacustrine bottom. Karg1 3 sediments are grey clays, rich in diatomite (60, 61).

The Harami section constitutes the sedimentary overburden of the main coal level of the Harami mine near the town of Ilgin. It contains *Eumyarion* and *Spano/Democricetodon* dominated assemblages attributed to zone MN 1 or 2. Greenbrown laminated or homogeneous clays comprise the main part of the section. At several levels small coal layers (1- 10 cm) are present (62).

Hancılı locality is a former lake. Its sediments are finely laminated, coalbearing and mildy bioturbated. It considered as a MN 4 locality (61).

Keseköy locality is a coal quarry near the town of Kizilcahamam. The section predominantly consists of green-brown, partly laminated clays, intercalated with several coal layers. It contains an assemblage of small mammals that is attributed to the local zone D, being correlated to MN 3 (60, 61).

2.1.5. Application of the established methodology to the fossil record of cyprinids

The established methodology is applied to the fossil material represented by isolated fossil pharyngeal teeth as well as to the teeth founded within the skull or complete fish skeleton samples.

2.1.5.1.   Isolated fossil pharyngeal teeth from Çevirme

Isolated fossil pharyngeal teeth (n=247) (Depository numbers and other details see Table 1, Ayvazyan et al., 2019) collected from the Pliocene age locality Çevirme (Erzurum Province, Tekman district) (BGR Çevırme 1-247) are studied based on already established methodology within the first part of this research. Distinguished two characters stages lateral outline and transverse cross section (αβ), recorded shape

classes and identification key are applied correspondingly to describe, categorise and identify these fossil isolated pharyngeal teeth. Each fossil tooth is characterises by lateral outline (α) and transverse cross section (β) (details see 2.1.2) (Fig. 16).
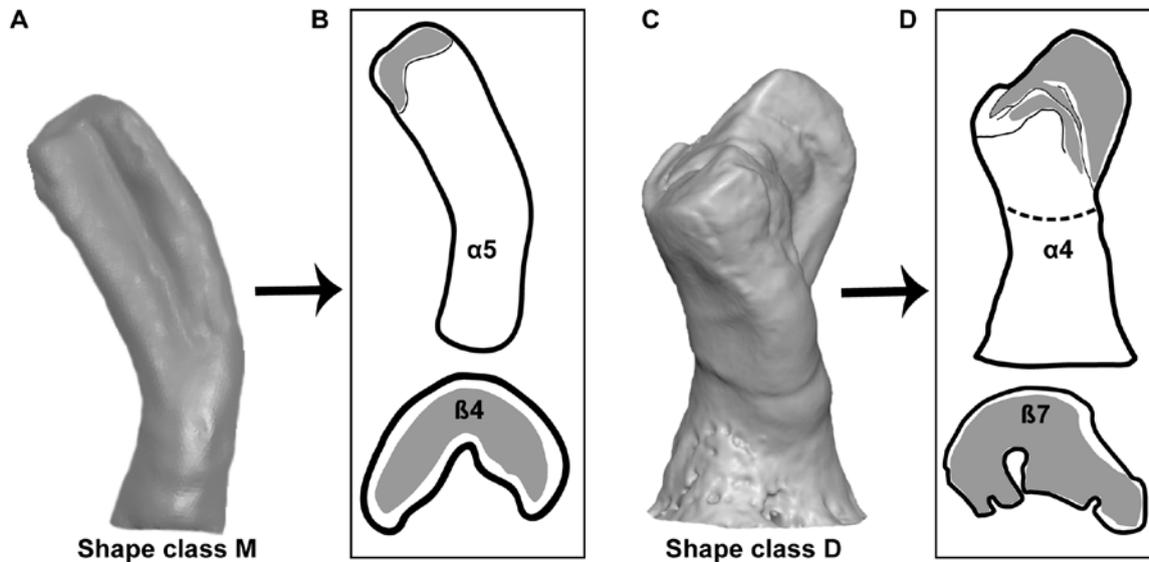
Figure 16. Methodology to describe the isolated pharyngeal teeth based on the character stages and shape classes. (A) shape class "M", b2 tooth of extant *C. capoeta*. (B) shape character α5 (lateral outline). (C) shape character β4 (transverse cross-section). Shape class "M" is characterised by shape characters α5 and β4. (D) shape class "D", a2 tooth of extant *C. sieboldi*. α4, shape character (lateral outline). β7, shape character (transverse cross-section). Shape class "D" is characterised by shape characters α4 and β7. The scales are not given to avoid scaling up of the figures. Avyazyan et al., 2019.

Within studied fossil material eight shape classes are recorded (Fig. 17). They represent **genus, species** and **clade** diagnostic shape classes, therefore, the studied fossil material is identified as pharyngeal teeth of the genus *Capoeta.* These three level of shape classes are illustrated on Figure 12. The most frequent shape class among fossil material is the genus diagnostic shape class "C" and relatively rare ones are the species diagnostic shape classes. Expectedly, the same pattern can be found through the study of the extant pharyngeal teeth (S3, S7 Figs.). In some cases due to the presence of three species diagnostic shape classes ("A", "J" and "R"), species level identification of isolated pharyngeal teeth was possible. Thus, three fossil *Capoeta* species are identified*: C. umbla, C. baliki* and *C. sieboldi.* The presence of the clade diagnostic shape class "M" indicates the presence of *C. capoeta*/*C. sevangi,* which compose the Ararlo-Caspian clade.
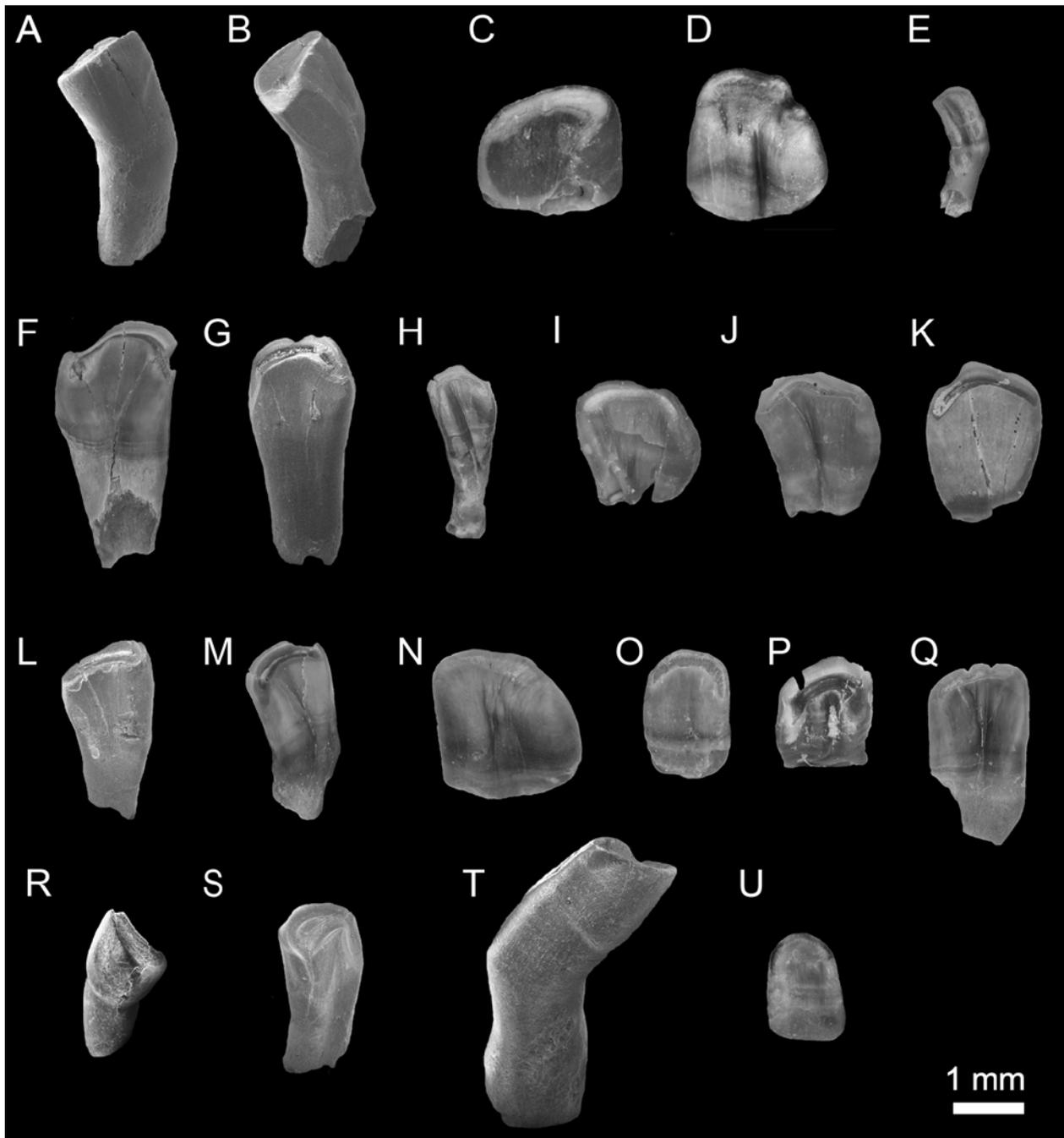
Figure 17. Isolated fossil pharyngeal teeth from the early Pliocene locality Çevırme (Erzurum Province, Tekman district)**.** (A-E) species/clade diagnostic shape classes: (A) shape class "A" characteristic of *C. umbla* (BGR Çevırme 1)**.** (B) shape class "R", characteristic of *C. sieboldi* (BGR Çevırme 3)**.** (C-D) shape class "J", characteristic of *C. baliki* (BGR Çevırme 4, 5)**.** (E), clade diagnostic shape class "M", characteristic of Aralo-Caspian clade of genus *Capoeta* (*C. sevangi* and *C. capoeta*) BGR Çevırme 23). (F-K) genus diagnostic shape class "C" (BGR Çevırme 24, 25, 26, 27, 28, 29). (L-S) common shape classes shared by different species. (L-N) shape class "B" (BGR Çevırme 155, 156, 157). (O-Q) shape class "F" (BGR Çevırme 195, 196, 197). (R-S) shape class "H" (BGR Çevırme 226, 227). (T) not identified, possibly tooth pathology (BGR Çevırme 237). (U) not identified (BGR Çevırme 238). Ayvazyan et al., 2019.

The clades recorded within the fossil material, based on the species/clade diagnostic

shape classes are plotted on the phylogenetic tree based on the molecular genetic

analyses, which shows that the recorded shape classes belong to one monophyletic clade (Fig. 18).
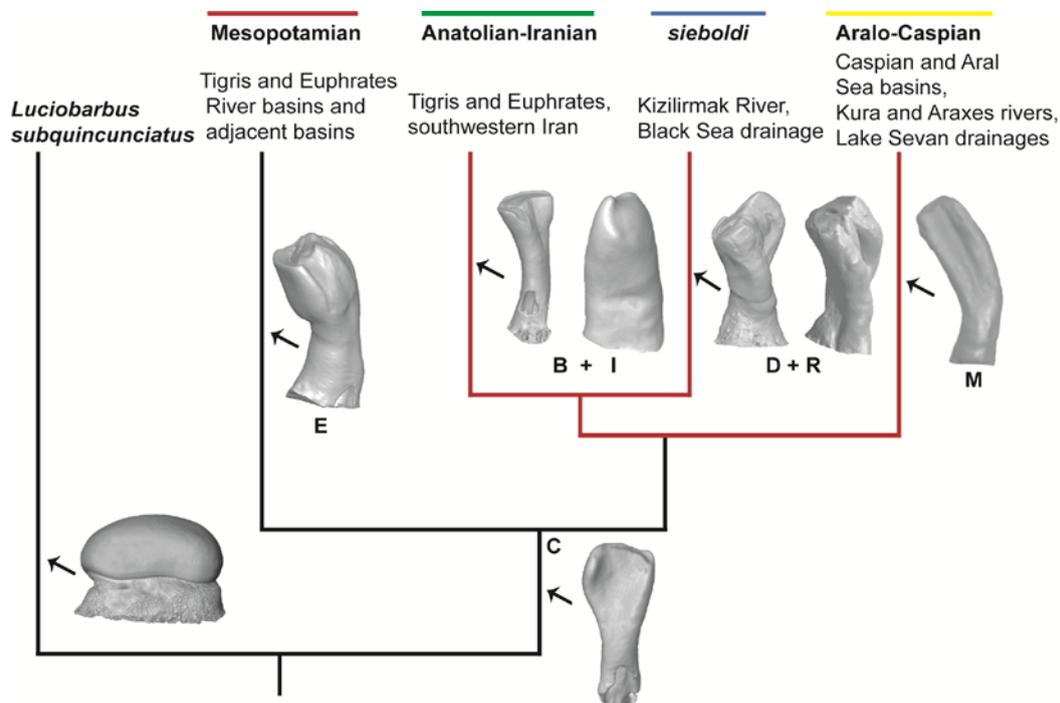
Figure 18. Phylogeny of the genus *Capoeta:* distinguished clades within the genus *Capoeta* (*Luciobarbus suquincunciatus* is the sister clade) (Levin et al., 2012). The clade diagnostic shape classes (capital letters) and respectively the 3Dimages of teeth of *Capoeta* as well as a2 tooth of *L. subquincunciatus* are mapped on the tree. The monophyletic Anatolia-Iranian/Aralo-*Caspian/sieboldi* clade, for which we propose a species flock model of evolution marked with red colour. Ayvazyan et al., 2019.

2.1.5.2.   Fossil remains of *Capoeta sp.* from Jradzor (Armenia)

The fossil material from Jradzor is stored at the Institute of Geological Sciences, NASRA (IGS). Four fossil samples (excavations are continuing) are scanned and reconstructed at the University of Fribourg and YXLON International GmbH, Heilbronn. The main steps of the application of the X-ray computed tomography (µCT) to the fossil material in the sediment is shown on the Figure 19. The material included in this work is represented by a complete fish skeleton and three skulls. The settings applied to scan the fossil material given in Table S4. The preliminary study of the 3D models of the isolated fossil pharyngeal teeth shows the presence of the shape class "C" (Fig. 19D), which is a species diagnostic for the genus *Capoeta* and indicates that the fossil specimens belong to the genus *Capoeta*. This material is not yet complete reconstructed, further studies are necessary for low-level taxonomic identification. Besides teeth, the skeletons of the fins and vertebra can give additional information

about these specimens and their taxonomy.
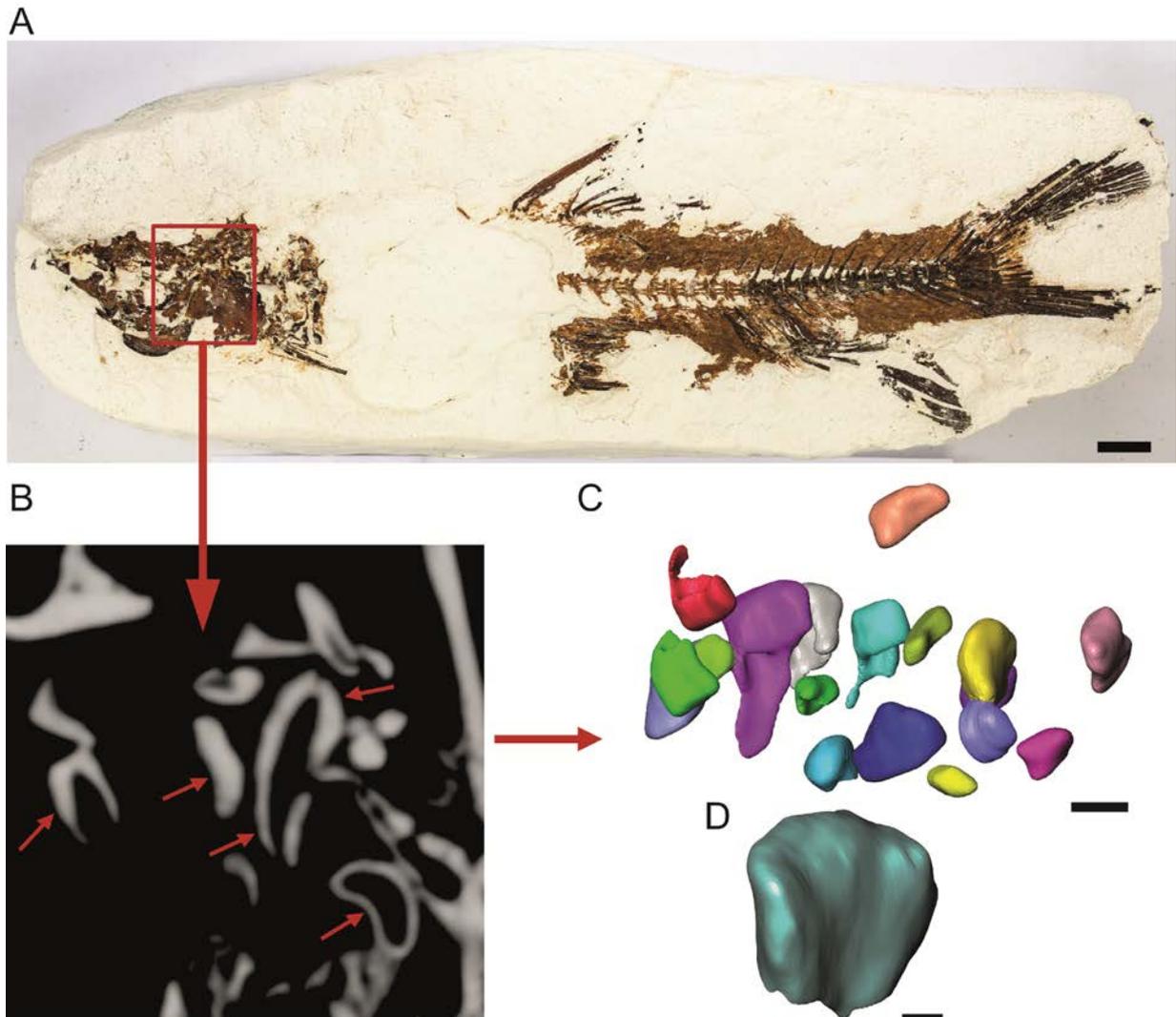
Figure 19. (A) *Capoeta sp.* (JRD-17/07); (B) a slice showing the teeth before reconstruction (teeth are marked by red arrows); (C) part of reconstructed isolated pharyngeal teeth; (D) recorded shape class "C".. The red quadrat shows the approximate locality of shown reconstruction in the sediment. Scale bar (A) = 1 cm, scale bar (C, D) = 1 mm.

2.1.5.3.   Fossil remains of *Capoeta* from Kisatibi (Georgia)

The fossil material from the late Miocene locality Ksatibi is stored at the Georgian National Museum (GNM). This material was described by Bogachev, 1927 as a species *Capoeta nuntius.* There are more than 30 specimens in the collection of GNM. Four specimens (for now) are borrowed to restudy these samples by applying X-ray computed tomography and the methodology established by Ayvazyan et al., 2018 (Table 1).

Figure 20. *Capoeta nuntius* (GNM 13-4) from the late Miocene localty Kisatbi, Georgia.

Four specimens are scanned and some of them are reconstructed (Fig.20). The preliminary results show the presence of a complete pharyngeal bone with the teeth (Fig. 21, GNM 10-1) as well as nearly 30 isolated teeth are reconstructed so far. The examination of the 3D models of the reconstructed fossil pharyngeal teeth the **shape class "C"** is recorded (Fig. 21C). Thus, the fossil material belongs to the genus *Capoeta*. Fortunately, one of the so far studied samples (GNM 8-2) contains a complete pharyngeal bone with the pharyngeal teeth on it (Fig. 21D). Interestingly, this **sample possess an a1 tooth** (Fig. 22), within studied extant *Capoeta* species only the species belong to Anatolia-Iranian or *damascina* clade have a1 tooth. The further research will allow to understand if the presence of a1 tooth is plesiomorphic character (reduction of a1) or homoplasy for the genus *Capoeta*. The settings applied to scan the fossil material given in Table S4.
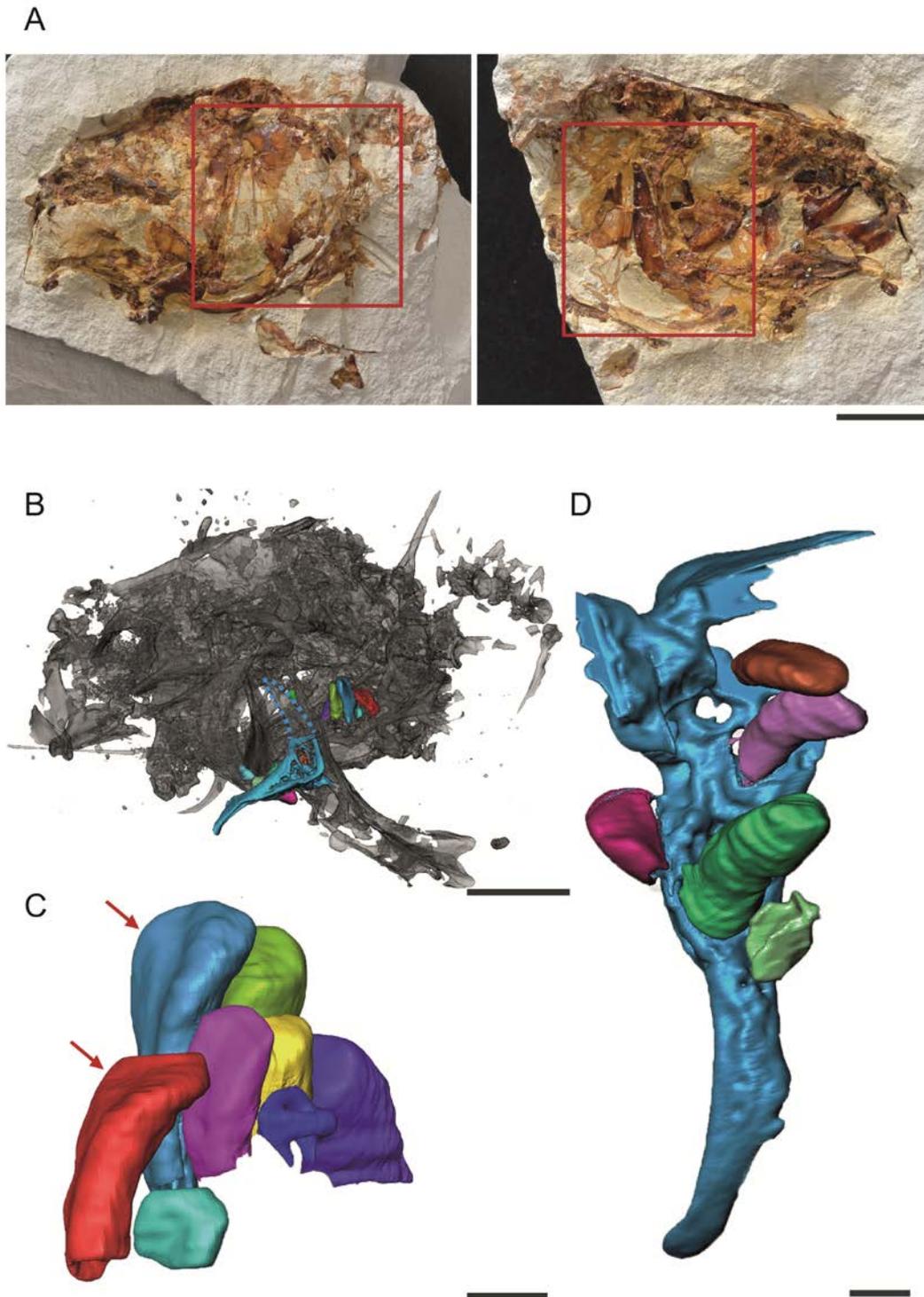
Figure 21. *Capoeta nuntius* (GNM 10-1): (A, B) reconstruction of the skull, (C) part of the reconstructed isolated pharyngeal teeth, (D) reconstructed pharyngeal bone with teeth. The red rectables shows the position of shown reconstruction in the sediment. The arrows show the teeth of shape class "C". Scale bar (A, B) = 1 cm, scale bars (C, D) = 1 mm.
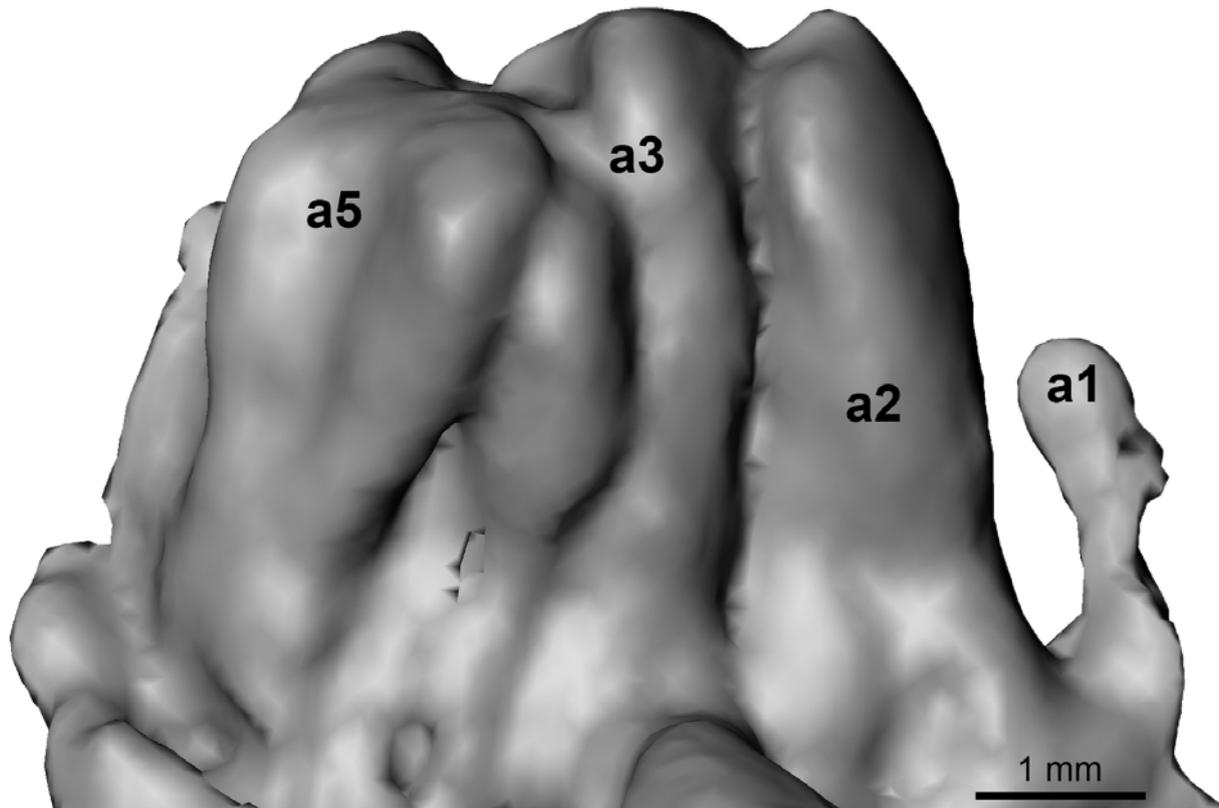
Figure 22. Surface view of the part of the pharyngeal bone with the teeth of *Capoeta nuntius* (GNM 8-1). a1, a2, a3 and a5 show respectively the teeth positions in the first tooth row.

2.1.5.4.   Isolated pharyngeal teeth from Turkey

The fossil pharyngeal teeth (isolated or attached to the bone) (n=279) from latest Oligocene to middle Miocene localities Kargı 1, Kargı 2, Harami1, Hancılı, Keseköy (Turkey) are studied. The material is stored in the palaeontological collection of the University Utrecht (UU). The fossil material is compared to the extant material stored at the osteological collection of National Museum of Natural Sciences of Madrid (MNCN) and at the Bavarian State Collection for Anthropology and Palaeoanatomy, Munich (SNSB) (Depository numbers and other details see Table 2, Ayvazyan et al., 2019). The pharyngeal bones of the extant comparison material (*Barbus and Luciobarbus* species) are scanned using the microtomography systems NIKON XT H 160 at the Scanning electron   microscopy   at   the   analytic   laboratory   of   MNCN   (Fig.   23).
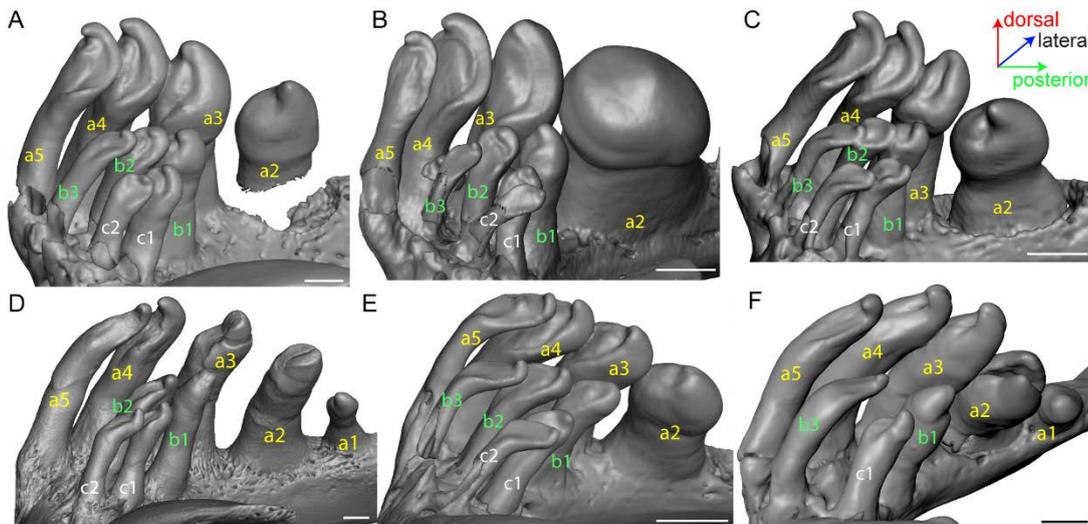
Figure 23. Images of the 3D models of the pharyngeal bones with teeth of the *Luciobarbus* and *Barbus* species. (A) *Luciobarbus comizo* (MNCN 69304), (B) *Luciobarbus longiceps* (MNCN E 54), (C) *Luciobarbus sclateri* (MNCN 69331), (D) *Barbus barbus* (SNSB SPAM-PI-00608), (E) *Barbus sacratus* (MNCN GUI 17), (F) *Barbus meridonalis* (MNCN 19933). The letters a, b, c correspond to the first (main), second and third row, the numbers (1-5) the tooth positions in those rows. The scale bars equal 1 mm.Vasilyan et al., unpublished.

The settings of the scanned pharyngeal bones are introduced in Table S6. The tomographic reconstruction was performed using Avizo 9.0 software at the Tübingen University.

Within the fossil material eight morphotypes of the pharyngeal teeth are distinguished (d1-d8). Morphological comparison with the 3D models of the extant *Barbus* and *Luciobarbus* species shows that seven from distinguished eight morphotypes (d1-d7) belongs to these two genera. This is additionally supported by the presence of the fossil remains of serrated rays of the dorsal fin (Fig. 24). The last d8 morphotype (Fig. 24 V, W) reminds the morphology of the pharyngeal teeth of the genus *Capoeta*, but this morphology is so far not recorded within the morphotypes of the extant *Capoeta* species distinguished by Ayvazyan et al., 2018.

Figure 24. Cyprinid remains from the studied localities. *Luciobarbus* sp., Morphotype d7 – from Hancılı, UU HAN 5315 (A); UU HAN 5316 (B); Morphotype d5 – UU HAN 5333 (C), UU HAR1 5300, loc. Hancılı (D); Morphotype d3 – UU HAN 5334, loc. Hancılı (E); UU HAN 5305, loc. Hancılı (F). *Barbus* sp., Morphotype d6 from the loc. Harami 1, UU HAR1 5301 (G), loc. Hancılı, UU HAN 5321 (H), UU HAN 5311 (I– J), UU HAN 5335 (K), Morphotype d4 - UU HAN 5308 (L), UU HAN 5309 (M). *Lucioarbus* vel *Barbus* sp., Morphotype d1 from loc. Hancıl ı, UU HAN 5300 (N – O), Morphotype d2, UU HAN 5303 (P), UU HAN 5306 (Q); Morphotype s1, UU HAN 5324 (R); Morphotype s2, UU HAN 5325 (S), UU HAN 5326 (T); Morphotype s3, UU HAN 5329 (U). aff. *Capoeta* sp. from the loc. Hancılı, UU HAN 5317 (V, W). Barbini indet. (Y – DD), UU KAR1 1304, loc. Kargi 1 (X), UU KAR1 1301, loc. Kargi 1 (Y), UU KAR2 1301, loc. Kargi 2 (AA), UU KAR2 1306, loc. Kargi 2 (DD), UU KAR2 1303, loc. Kargi 2 (EE), UU KE 5307, loc. Keseköy (BB), UU KE 5305, loc. Keseköy (CC). *Leuciscus* sp. from loc. Hancılı, UU HAN 5318 (FF). Vasilyan et al., in review.

The species level identification of the fossil material is not possible due to the absence of the detailed morphological report of the extant comparative material. The establishment of the identification key for these genera, which can be applied

for the identification of the isolated fossil pharyngeal teeth at low taxonomic level (species), is planned in my further research project.

2.2. Discussion

2.2.1.   Pharyngeal tooth morphology as a key for species level identification

The detailed morphological study, based on the 3D approaches of the isolated pharyngeal teeth of ten extant *Capoeta* species, shows that the tooth morphology can serve as a key character for the species level identification. However, the species level identification is possible only based on the tooth morphology in the tooth position a2. Besides, the pharyngeal tooth morphology provides also an identification at the generic level based on the presence of the genus diagnostic shape class "C" (as the preliminary studies of the fossil material from Jradzor and Kisatibi show). More details see Ayvazyan et al., 2018.

2.2.2.   Phylogenetic significance of pharyngeal tooth morphology

To test the possible phylogenetic signal embedded in the pharyngeal tooth morphology, the performed phenotypic dendrogram (based on the tooth morphology, respectively on the distribution of the recorded shape classes within studied species) is compared with three different phylogenetic trees based on the molecular genetic analyses of the genus *Capoeta*. This comparison shows a significant similarity of the results based on morphological and genetic data. The genetic data supports our results regarding to the recorded three main clades: Anatolian-Iranian or *Capoeta damascina* complex group, Aralo-Caspian or *Capoeta capoeta* complex group and Mesopotamian *Capoeta* or *Capoeta trutta* group (for details see Ayvazyan et al., 2018) (Fig. 25).
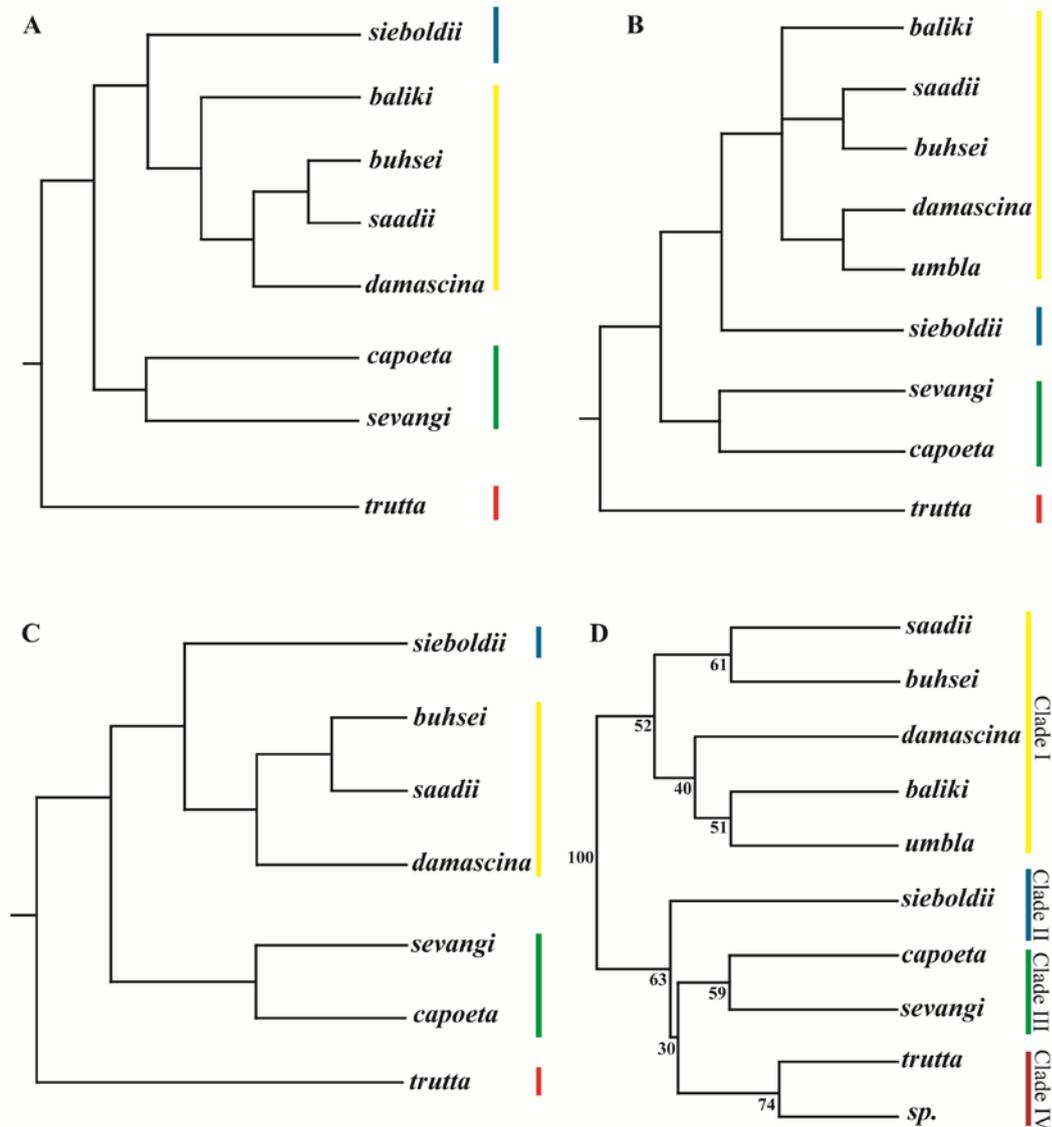
Figure 25. Simplified phylogenetic trees show the distribution of the studied *Capoeta* species within phylogenetic trees, based on genetic analyses of (A) Levin et al. 2012, (B) Bektas et al. 2017, (C) Zareian et al. 2016, (D) this study. Ayvazyan et al., 2018.

2.2.3.   Taxonomy of the isolated fossil pharyngeal teeth from Çevirme

Within the isolated fossil pharyngeal teeth from Çevirme (Erzurum Province, Tekman District) eight shape classes are recorded where the shape class "C" is dominat in the assemblage (53%) (S6 Fig.) This indicates that the fossil material belongs to the genus *Capoeta.* Besides this, the presence of three species (A, J, R) and a clade diagnostic (M) shape classes suggests the presence of four palaeo-species (*C.* cf. *umbla, C.* cf. *baliki, C.* cf. *sieboldi* and *C.* cf. *capoeta/C.* cf. *sevangi*). In our days, the extant relatives of these species are distributed in three different water basins (Black

and Caspian Seas and Persian Gulf basins) (Fig. 5). According to the genetic and morphological (our data) data, they belong to different clades (Fig. 25). Whereas, the recorded palaeo-species (*C.* cf. *umbla, C.* cf. *baliki, C.* cf. *sieboldi* and *C.* cf. *capoeta/C.* cf. *sevangi*) belong to one monophyletic clade as it is shown on the Figure 18. Thus, the main questions are: 1) does the fossil assemblage represent one species characterised by high heterodonty, which was the ancestor of the genus *Capoeta* or it represents closely related four species; 2) is this high morphological diversity conditioned by plasticity or allometry; and 3) how does the present-day distribution of these species within the different water basins formed.

The recent *Capoeta* species are characterized by different degree of heterodonty, which varies between three and six shape classes per species. As it has been already mentioned, within fossil assemblage, eight shape classes are documented and it is unprecedented among extant species. It is also highly unlikely that a fossil species shows this degree of heterodonty, given the ten tooth positions at pharyngeal bones. Therefore, we consider the 'single species' interpretation as unlikely.

Based on the recoded four species/clade diagnostic shape classes the Çevırme assemblage is constituted by four species, which belong to three different clades (Anatolian-Iranian, Aralo-Caspian, and *sieboldi* clades) of the genus *Capoeta*. According to all molecular studies (5, 21, 63), these three clades are monophyletic and sister to the Mesopotamian clade (see Fig.) (more details see Ayvazyan et al., 2019).

2.2.4.   Possible influence of plasticity and allometry on high diversity of recorded shape classes

The literature provides examples of the potential effects of plasticity on the dentary bone and tooth morphology mainly in cichlid fish cultures by applying contrasting diets (soft and hard) (64–66). These studies recorded some degree of phenotypic plasticity of dentary bone morphology and in some cases tooth size. The influence of these two diets on the development of the cyprinid pharyngeal dentition is also tested in the benthophagous cyprinid black carp. Dietary did not change the tooth morphology, but, instead, it has been found that broad diet may influence the frequency of tooth

replacement and size patterns (67). These studies are mainly based on aquarium experiments in benthophagous species where two extreme diets (commercial fish as a soft and snails as hard food) are tested. Under natural conditions, fishes are not forced to feed on only one type of food. Thus, it is data can be applied to, in the present paper studied algae-scrapping species *Capoeta*, which are recorded from single geological layer and are sympatric individuals in a uniform environment. Considering this, the effect of feeding on different food should not be considered biasing on the carp pharyngeal tooth morphology, and, thus, we exclude the effect of plasticity on the studied fossil material.

Allometric shifts in pharyngeal tooth morphology cannot explain the high diversity of recorded shape classes in the studied fossil samples. Morphological shape remodeling in cyprinids happens in very early stages of their ontogeny. Juveniles (standard size of a few mm) have different tooth morphology than the adult samples, but the significant morphological changes are finalized in this early stage. Thus, the adult dentition in cyprinid fishes is completed by at the later larvae or juvenile stages (68). Our fossil material is represented by adult individulas, as the studied fossil pharyngeal teeth sizes vary between 0.8 – 3 mm (it is a sampling artifact introduced by mesh size limitation washing collection technique). Therefore, our fossil samples is composed of isolated pharyngeal teeth of adult individuals.

2.2.5. Species flock scenario of evolution of the genus *Capoeta*: palaeogeographical interpretation of the fossil site Çevirme (palaeolake Tekman)

We interpret this high local diversity of closely related species from the fossil site

Çevirme, **as a species-flock** model. Five main criteria are recorded to distinguish the group of animals as a species flock: 1) monophyly, 2) high species diversity (speciosity), 3) high level of endemism, 4) morphological and ecological diversity and 5) habitat dominance in terms of biomass (30, 69). A later study (70) suggests to concentrate on the three robust, easier to determine criteria such as monophyly, endemism and speciosity. The studied fossil *Capoeta* samples correspond to all five criteria sensu Eastman and McCune (2000) and can be regarded as a species flock (69) (details see Ayvazyan et. al., 2018). Thus, the species flock of the genus *Capoeta,* represented by four near related species, inhabited Tekman Basin 4 Ma years ago. This study hypothesizes, that the Tekman palaeo-lake (part of Armenian Highland) was the "center" of the speciation of *Capoeta* species related to the three recent clades of the genus (Anatolian-Iranian, Aralo-Caspian and *sieboldi*). It is already known, that the lake system of Armenian Highland was formed during the late Miocene and represents the source of all major rivers in Western Asia to which *Capoeta* is endemic (58). Thus, it could represent the center of origin of *Capoeta*.

According to the recent geologic work the tectonic reorganization in the region, starting about the Miocene-Pliocene transition (ca. 5.5 Myr) along the East and North Anatolian faults (71, 72), resulted in substantial surface uplift and probably caused the gradual reshaping of the hydrological network in the area. This could contribute to dispersal and speciation of the members of the species flock into their nowadays distribution areas. The other possible explanation of my results could be the concept of secondary contact. This scenario (speciation of hybrids) is very similar to the above suggested species flock model, however, without any genetic information, we cannot be confident about this hypothesis. More studies and more fossil sites inside and outside of the distribution area of *Capoeta* are needed to test these hypotheses. However, according to the current available data, the fossil species flock interpretation is the most plausible.

2.2.6.   Taxonomy of the isolated fossil pharyngeal teeth from Jradzor, Kisatibi, Kargı 1, Kargı 2, Harami1, Hancılı and Keseköy

The studies on the fossil material from Jradzor and Kisatibi are still ongoing. The preliminary results show, however, that the both fossil material possibly belong to the

genus *Capoeta*, as the genus diagnostic shape class "C" is present. Species level identification is not completed, as the reconstruction of the scanned material is not yet finalized. The fossil remains of these both sites will be studied in more details in my further research project, including also the fossil remains of fin rays skeletons and vertebra. The fossil material from early Miocene (to middle Miocene) localities Kargı 1, Kargı 2, Harami1, Hancılı and Keseköy (Turkey) belongs to the family Cyprinidae. Above-mentioned localities provide fossil remains of barbin fishes, the remains of leuciscin are found only from Hancılı locality (Table S7). The studied oldest localities (Kargı 1, Kargı 2, Keseköy,latest Oligocene to early Miocene) can be assigned to a small-sized barbin.

The recorded tooth morphology from these localities cannot be referred to any fossil form known from Eurasia. Probably, they represent an ancient extinct barbin group. The fossil material from Harami 1 and Hancılı, based on the isolated fossil pharyngeal teeth, is identified as two widely distributed barbin genera *Luciobarbus* and *Barbus*. Besides the isolated pharyngeal teeth, the fossil remains of the three different morphotypes of serrated rays of the dorsal fin from Hancılı could indicate the presence of three barbin taxa in this locality. However, this cannot be stated with confidence due to the lack of comparative osteological studies of this element in the extant barbin species.

The record of the Harami 1 locality can be considered as the oldest known remains of *Barbus* and *Luciobarbus* genera (details see Vasilyan et al., in review). So far the oldest record of the genus *Luciobarbus* was known from the earliest late Miocene of Austria (loc. Mataschen, 73). Böhme & Ilg (74) mentioned oldest *Luciobarbus* from contemporaneous to Mataschen sites in Turkey, however, this material stays unfigured. We suggest that *Barbus* sp. Harami 1 and Hancılı should be considered as the oldest representatives of this genus, since earlier publications describing *Barbus* sp. do not represent the genus *Barbus* sensu Yang et al. (2015) (3). The results of this study would provide important information also for the calibration of the molecular trees, which estimates the divergence time and origination of different barbin clade.

3.   Conclusion

For the first time, the methodology is applied to identify isolated pharyngeal teeth at species level (on the example of the cyprinid genus *Capoeta* and is applicable to the fossil record.

The results of my study show that the detailed 3D morphology is very promising tool applicable to the low level taxonomic identification of the isolated pharyngeal teeth. This pattern is very important not only for the taxonomy, but also for the fossil record of cyprinids, as the fossil remains of these fishes are mainly represented by isolated fossil pharyngeal teeth. Despite this, until now, the species level identification of isolated teeth is not recorded due to the lack of the comprehensive studies and comparative material of the pharyngeal dentition of the recent cyprinids. Within the palaeontological studies, the isolated teeth are generally identified only at the generic level. This study aimed to fill this gap by applying modern methodology to get maximum information about the morphological structures of the pharyngeal teeth, which can be the base for species level identification.

The species level identification of the fish fauna will allow to trace back the evolution of cyprinids, to investigate the history of the drainage basins evolution and provide details for the palaeobiogeogrphical analyses of the studied regions.

Besides its significance for taxonomy and the fossil record, the results of this study show that the 3D detailed morphology of the pharyngeal dentitions provides also phylogenetic signal, which is in accordance with the molecular genetic data. This additionally supports the study of the cyprinids evolution.

However, the applied methodology is quite time consuming, but as I already show, on an example of the genus *Capoeta*, it is feasible and very informative. This methodology can serve as a basis to establish the identifications keys (based on the detailed morphology of the pharyngeal teeth) of the isolated pharyngeal teeth of the other groups of cyprinids.

Summing up the results of this study, I conclude that:
- the detailed morphology using the 3D microtomography of pharyngeal teeth is a useful tool for the species and generic level identification of the isolated pharyngeal teeth, as well as in certain cases the tooth positon in tooth rows etc.;

- the morphology of the pharyngeal teeth provides an obvious phylogenetic signal and highly supported by results derived from molecular genetic analyses;
- both these patterns are important for the taxonomy and can be also applied to the fossil record;
- the established methodology is applicable to the fossil record of the genus *Capoeta* and provides species level identification of the isolated fossil pharyngeal teeth;
- within fossil material from the Pliocene age locality Çevirme, eight shape classes are distinguished, four of them are species or clade diagnostic and indicate the presence of the four sympatric *Capoeta* species (*C.* cf. *sieboldi, C.* cf. *umbla, C.* cf. *baliki* and *C.* cf. *capoeta/sevangi*);
- this high local diversity of closely related four species is interpreted in terms of the species-flock model of *Capoeta* in the Tekman palaeo-lake at 4 Ma;
- I hypothesized that the genus *Capoeta* occurred in the huge late Miocene to Pliocene palaeo-lake system in the present-day Armenian Highland, more specifically in the Tekman palaeo-lake, which was a part of that huge palaeo-lake system;
- present-day distribution of the genus *Capoeta* in different water basins has been caused by Pliocene tectonic activities which disrupted this lake system and resulted in the very characteristic biogeographic distribution of *Capoeta* in Western Asian and Ponto-Caspian drainage systems;
- further studies of the fossil remains of the genus *Capoeta* from Jradzor (Armenia and Kisatibi (Georgia) can give a complete view of the evolution of this genus as well as trace back the history of the drainage systems of this region;
- so far the preliminary results show that the recorded fossil remains belong to the genus *Capoeta,* as the genus diagnostic shape class "C" is recorded within both samples (ongoing project);
- the isolated fossil pharyngeal teeth from latest Oligocene to early Miocene localities Kargı 1, Kargı 2, Harami1, Hancılı and Keseköy are identified at generic level and belong to barbin genera *Luciobarbus* and *Barbus;*
- the species level identification of isolated fossil pharyngeal teeth from above mentioned localities is not possible, due to the lack of the comparative osteological studies of this element in the extant barbin species. The established

-   methodology for the genus *Capoeta* can serve as a base for the similar study on the other barbin generas as *Barbus* and *Luciobarbus*.

4.   Outlook

3D detailed morphology is useful tool to study the pharyngeal teeth morphology. This methodology is time consuming regarding to the material collection, microcomputed tomography, reconstruction of 3D models and further analyses. However, it worths, and there is a necessarily to apply this methodology and establish identification key of other groups of cyprinid fishes.

Besides the isolated teeth, it will be also very interesting to apply this methodology to study the morphology of the pharyngeal bones. I am inclined to think, that the morphology of the pharyngeal bones also embed important information. These patterns are included in my further research projects and would be studied.

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6.   Appendix I: Published and Accepted Manuscripts

3D morphology of pharyngeal dentition of the genus *Capoeta* (Cyprinidae): Implications for taxonomy and phylogeny

ORIGINAL ARTICLE

WILEY JOURNAL OF ZOOLOGICAL SYSTEMATICS EVOLUTIONARY RESEARCH

3D morphology of pharyngeal dentition of the genus *Capoeta* (Cyprinidae): Implications for taxonomy and phylogeny

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Abstract

Capoeta is a herbivorous cyprinid fish genus, widely distributed in water bodies of Western Asia. Recent species show a distinct biogeographic pattern with endemic distribution in large fluvial drainage basins. As other cyprinids, the species of this genus are characterized by the presence of the pharyngeal bone with pharyngeal teeth. Despite this, the detailed morphology of the pharyngeal teeth, its interspecific and topologic variations, and the importance for taxonomy and phylogeny of the genus *Capoeta* are still not established. For the first time, a detailed comprehensive study of the pharyngeal dentition of 10 *Capoeta* species has been provided. The morphologic study of the pharyngeal dentition bases on the 3D microtomography and follows the purpose to evaluate the potential taxonomic and phylogenetic signals of these elements, as well as to study interspecific and topologic variations of the pharyngeal teeth. In this study, we propose a new methodology to categorize the studied pharyngeal teeth in 18 shape classes. The results of this study show that the detailed 3D morphology of the pharyngeal teeth is a useful tool for the identification of isolated teeth at the generic and/or specific level and that in certain cases, the tooth position in the teeth rows can be identified. Additionally, the preliminary analysis shows that the morphology of the pharyngeal teeth provides a potential phylogenetic signal. Both these patterns are very important for the taxonomy of cyprinid fishes and especially can be applied to fossil records.

KEYWORDS
3D microtomography, *Capoeta*, Cyprinidae, pharyngeal teeth

1 | INTRODUCTION

Extant cyprinid fishes are known with more than 2,000 species and represent the most diverse family of bony fishes in Eurasia and Africa (Nelson, 2006). In fresh water bodies, they build the main part of the biodiversity of the fish community. The family includes several large clades (subfamilies), that is, Cyprininae and Leuciscinae. In Western Asia among cyprinids, one of the widely distributed genera is the cyprinine *Capoeta*, which is considered as endemic to the region. The monophyletic genus *Capoeta* includes herbivorous species, feeding mainly on algae and periphyton, which they scrap from the substrate by the horny sheath on their lower lip (Banarescu, 1999; Karaman, 1969; Türkmen, Erdoğan, Yıldırım, & Akyurt, 2002).

Currently, more than 20 *Capoeta* species are described based on genetic studies and morphologic and meristic characters (Levin, Rubenyan, & Salnikov, 2005; Levin et al., 2012; Turan, Kottelat, & Ekmekçi, 2008). The earlier taxonomical studies of the genus *Capoeta* are based mainly on morphometrics and meristic characters (Karaman, 1969; Krupp & Schneider, 1989), whereas the recent studies mostly rely on genetic analyses (Alwan, Esmaeili, & Krupp, 2016; Levin et al., 2012; Turan, 2008).

Levin et al. (2012) studied the phylogenetic relationships of the genus *Capoeta* based on the complete mitochondrial gene for

cytochrome *b* sequences obtained from 20 species. According to the study (Levin et al., 2012), three main groups are recognized: the Mesopotamian, the Anatolian–Iranian, and the Aralo-Caspian. Later, Zarearn, Esmaeili, Heuidari, Khoshkholgh, and Mousavi-Sabet (2016) based on mitochondrial cytochrome *b* gene sequences distinguished three main groups: the *Capoeta trutta* group (the Mesopotamian *Capoeta* group), the *Capoeta damascina* complex group (the Anatolian–Iranian group), and the *Capoeta capoeta* complex group (the Aralo-Caspian group) (Zareian et al., 2016).

A diagnostic character of all cyprinid fishes is the presence of the pharyngeal bone with pharyngeal teeth located in up to three rows (Howes, 1991). It builds as a result of ossification of the right and left fifth ceratobranchials and forms tooth-bearing pharyngeal jaw, which is specialized for food processing. The morphology of the pharyngeal jaw and pharyngeal tooth shape and configuration also have taxonomic significance for cyprinids (Howes, 1991) and can be represented by a formula, for example, 4.3.2-2.3.4; these numbers indicate the amount of the teeth on the left and right jaws from the first to the third and the third to the first row correspondingly. The number of tooth rows and the amount of teeth in the each row are mentioned as one of the significant taxonomic characters for the genus *Capoeta* (Banarescu, 1999; Karaman, 1969; Krupp & Schneider, 1989). Besides this, several studies have shown that the pharyngeal dentition can also be considered as an essential character complex for the study of cyprinid evolution (Ahnelt, Herdina, & Metscher, 2015; Böhme, 2002; Pasco-Viel et al., 2010; Zardoya & Ignacio, 1999; Zeng & Liu, 2011). However, little is known about the morphology of pharyngeal bones and teeth of the genus *Capoeta*, as well as its significance for taxonomy and phylogeny.

Heckel (1843) described the pharyngeal teeth of cyprinid fishes for the first time. He classified them according to the grinding surfaces in four main groups and 13 subgroups. One of the subgroups described by him with "shovel-shaped teeth" includes the genus *Capoeta*. According to Heckel (1843), the teeth formula of the genus *Capoeta* is 2.3.4-4.3.2 (respectively from the third to the first and from the first to the third row). By examining different species of the genus, later studies (Banarescu, 1999; Karaman, 1969; Krupp & Schneider, 1989) found four or five teeth to be present in the main row, two to four in the second row, and two in the third row. Banarescu (1999) gave a rough morphologic description of the pharyngeal teeth and mentioned that the teeth in the main row are compressed and have irregular shape and those in the second and third rows are more or less cylindrical in shape (Banarescu, 1999). However, the detailed morphology, interspecific and topologic variations, and the importance of the tooth morphology for taxonomy and phylogeny of this genus are still not established.

Taking this into account, the main goals of this publication were (i) to provide a detailed morphologic description of pharyngeal teeth in 10 *Capoeta* species by applying 3D approaches; (ii) to check the interspecific and topologic variations of pharyngeal teeth; and (iii) to test the possible phylogenetic signal embedded in the tooth morphology.

2 | MATERIALS AND METHODS

2.1 | Sampling

Pharyngeal dentitions of 10 *Capoeta* species from different water basins of Anatolia, Iraq, Iran, Armenia, Georgia, and Syria are studied (Table 1). The comparative material of pharyngeal bones is stored at the Bavarian State Collection for Anthropology and Palaeoanatomy, Munich (SNSB); the National Museum of Natural Sciences of Madrid (MNCN); the Palaeontological Collection of Tübingen University (GPIT); and Senckenberg Naturmuseum Frankfurt (SMF). The sampled information about studied specimens and locations is listed in Table 1 and Figures 1 and 2. The osteologic and morphologic description of the pharyngeal bones and teeth follows the nomenclature introduced in Figure 3.

The left pharyngeal bones of adult individuals are used in the study (except for *Capoeta umbla* and *C. damascina*). Each pharyngeal bone possesses 9 to 10 teeth (pharyngeal teeth a3, a5, c1, and c2 in *Capoeta saadii* and b2, c1, and c2 in *Capoeta buhsei* are missing). So, in total, the morphologic characters of 84 teeth are examined and analyzed. The other samples of the same species were examined according to an established morphologic set of characters.

2.2 | Species identification

The studied species were collected and identified by different scholars. *C. saadii* and *C. buhsei* are collected by Ignacio Doadrio in 2015, *C. umbla* by Angela Van den Driesch, *C. trutta* and *Capoeta* sp. by Eva Maria Cornelssen in 1978, *Capoeta baliki* and *Capoeta sieboldii* by Madelaine Böhme in 2010, *C. capoeta* by Samvel Pipoyan in 2012, *Capoeta sevangi* by Anna Ayvazyan in 2014, and *C. damascina* by Nisreen Alwan in 2008. All species are identified by the collectors based on external morphology and meristic characters.

Capoeta sp. from the Dokan Reservoir, Iraq, was collected by Cornelssen and stored as dried skeleton in SNSB as *Barbus belayewi*. According to our results, this specimen is closely related but not identical to the species *C. trutta*, which is also supported by the detailed study and comparison of the morphology of the last unbranched ray of the dorsal fin (unpublished results).

2.3 | X-ray microtomography

The pharyngeal bones were prepared in small polystyrene boxes for scanning.

The pharyngeal bones of the extant *Capoeta* species were scanned using X-ray computed tomography (µCT). MicroCT images were taken using the microtomography system Phoenix v|tome|x s at the Tübingen University and Erlangen University, as well as NIKON XT H 160 at the Scanning electron microscopy and analytic laboratories of MNCN. The pharyngeal bones were scanned with the following settings: 0.025 mm resolution, 100 to 150 mA, and 83 to 150 kV depending on the size of the bones and teeth (the bigger the bone, the higher the voltage due to the increased thickness of

TABLE 1 *Capoeta* species included in the present study

Scientific name	Locality	Number of samples (*n*)	Depository
Capoeta sieboldii	Kizilirmak River, town of Avanos, Turkey	1	GPIT-OS-00858
Capoeta baliki	Kizilirmak River, Avanos, Turkey	1	GPIT-OS-00859
Capoeta trutta	Assad Sea, Syria	2	SAPM-PI-02908, SNSB SAPM-PI-02910, SNSB
Capoeta capoeta	Saghamo Lake, Georgia	13	GPIT-OS-00860[a]
Capoeta umbla	Khata River, Adiyaman, eastern Turkey	1	SAPM-PI-00718, SNSB
Capoeta sevangi	Sevan Lake, Armenia	9	GPIT-OS-00861[a]
Capoeta sp.	Dokan Reservoir, Iraq	2	SAPM-PI-00719, SNSB SAPM-PI-00721, SNSB
Capoeta buhsei	Soleghan River, Namak Lake, Tehran, Iran	1	AT241586, MNCN
Capoeta saadii	Shahpur River, Dalaki River, Bishapur, Iran	1	IR3, MNCN
Capoeta damascina	Homs or Qattinah Lake, Orontes River drainage, Syria	1	SYR08/25, SMF

SNSB, Bavarian State Collection for Anthropology and Palaeoanatomy, Munich; MNCN, National Museum of Natural Sciences of Madrid; GPIT, Palaeontological Collection of Tübingen University; SMF, Senckenberg Naturmuseum Frankfurt.
[a]Collection numbers of scanned samples.

the element the X-rays must traverse). The tomographic reconstruction was performed using the following software: Phoenix datos|x CT in Tübingen, VGStudio 3.0 in Erlangen, and Amira 8.0 in Madrid.

2.4 | Morphological analyses

The virtual sections and 3D volume renderings from the reconstructed volume images were evaluated in the Avizo package (version 8.0). The digitalization of the bones allows observing models from different sides and recording the microstructures of bones and teeth which are difficult to observe under a light microscope. The teeth were further edited in the Geomagic professional engineering (version 15.3.0) and Freeform Plus (2014.3.0. 172) software packages. Besides these, the pharyngeal bones were examined under the Leica DVM5000 digital microscope and Leica M50 stereomicroscope available at the University of Tübingen.

To study the morphology of each pharyngeal tooth, we reconstructed 3D models of pharyngeal bones and virtually separated each tooth as an isolated model (in Avizo and Geomagic). The isolated 3D tooth models allow for an examination of the tooth from different sides by rotating the models, as in the tooth rows the teeth are covered sidewise by others and it is difficult to observe all morphologic features of the teeth. Based on these 3D models, the set of teeth for each species is generated, which makes it easy to categorize teeth and record the intraspecific variation (Figure S1).

We established a set of shape characters: lateral outline (α) and transverse cross section (β). Based on them, the teeth were described and categorized into shape classes. To record the lateral outline of each tooth, we used the images of isolated 3D tooth models and marked the outlines using Adobe Illustrator. The lateral outlines were taken for each tooth in dorsal view, from the top of the tooth until its foot basis. The transverse cross section is performed using the tool "Slice" from the Avizo package. To record the cross sections, the tooth surfaces of every sample were virtually cut at the

same anatomical position where the surfaces of all teeth appear on the slice plate. To describe the shape characters, the coding used in phytolith (silicified plant particles) nomenclature is applied (Wautier, van der Heyden, & Huysseune, 2001). The same "Slice" tool is used to apply a virtual experiment to understand the robustness of the transverse cross section (β). For this experiment, the teeth surfaces of *C. sieboldii* were cut together in one slice and a4 of *C. buhsei* was cut separately from the other teeth to get the section at the uppermost part of the surface.

To describe and categorize the pharyngeal teeth of *Capoeta* species based on 3D models of 84 pharyngeal teeth, we used basic terminology (Wautier et al., 2001). In addition, to better formulize tooth morphology, we introduced shape classes defined by character stages α and β. To check the intraspecific variation of tooth morphology and left–right asymmetry among studied species, two control groups, *C. sevangi* (*n* = 13) and *C. capoeta* (*n* = 9), as well as all other species represented with two or more samples were examined.

To test the phylogenetic information of shape classes, the dendrogram has been performed using the morphologic characters by applying the Euclidean similarity index in the PAST (Paleontological Statistics, version 3) software.

3 | RESULTS

3.1 | General aspects of the pharyngeal tooth morphology of the genus *Capoeta*

Figure 3a and b shows the localization of the pharyngeal dentition in the fish body. The pharyngeal bones of the genus *Capoeta* can be distinguished by the well-developed dorsal and curved ventral limbs as well as the relatively large tooth-bearing area (Figure 3c and d). Each tooth consists of a tooth foot, a crown, a foot–crown border, a grinding surface, and an edge of the grinding surface (Figure 3e and f). The pharyngeal teeth of studied species are arranged at the
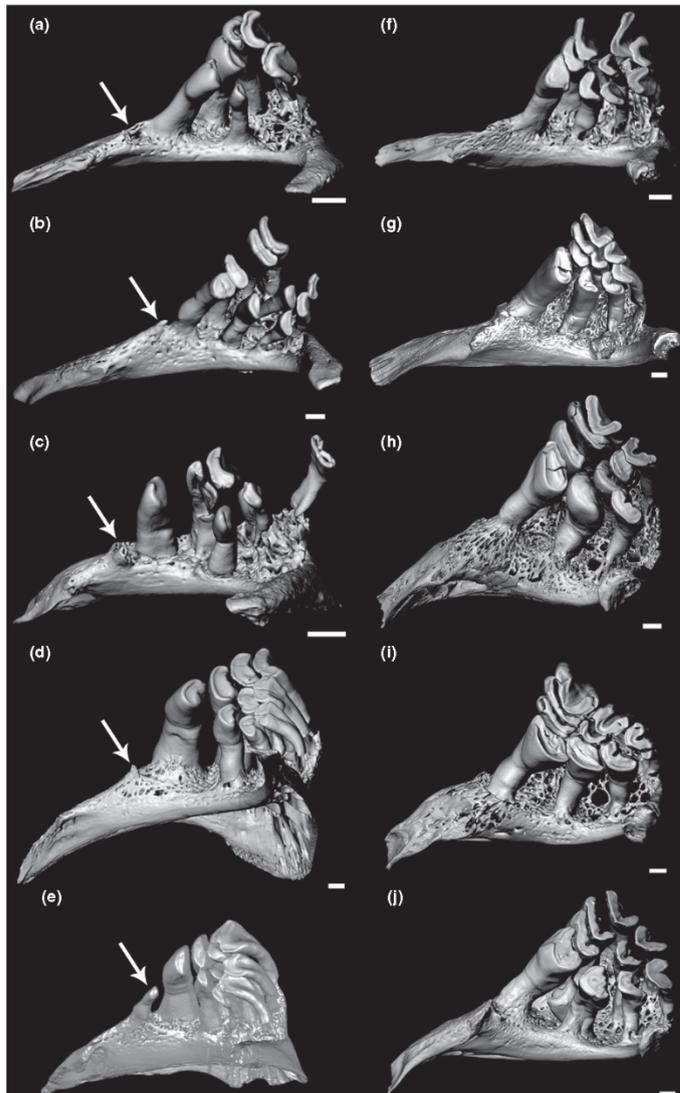
FIGURE 1 (a–j) Pharyngeal bones with teeth of the studied nine extant species of the genus *Capoeta*. (a) *Capoeta buhsei*; (b) *Capoeta umbla* (mirrored); (c) *Capoeta saadii*; (d) *Capoeta baliki*; (e) *Capoeta damascina* (mirrored); (f) *Capoeta capoeta*; (g) *Capoeta sevangi*; (h) *Capoeta* sp.; (i) *Capoeta trutta*; and (j) *Capoeta sieboldii*. The white arrows show a1 or presence of its bases. The scales are equal to 1 mm

pharyngeal bone in three rows. Each of them has different tooth count. The main row possesses five or four (a1, a2, a3, a4, a5), the second row three (b1, b2, b3), and the third row two (c1, c2) teeth (Figure 3c). The pharyngeal tooth formula is (i) 4.3.2-2.3.4 in *C. capoeta*, *C. sevangi*, *C. sieboldii*, *C. trutta*, and *Capoeta* sp; or (ii) 5.3.2-2.3.5 in *C. damascina*, *C. umbla*, *C. buhsei*, *C. saadii*, and *C. baliki*, which have a1 (*C. damascina*) or the tooth base at the a1 position.

The pharyngeal bone of *Capoeta* shows heterodont dentition. The teeth of the main row are larger than those of the second and third rows. The first tooth of the main row can be absent (*C. capoeta*, *C. sevangi*, *C. sieboldii*, *C. trutta*, and *Capoeta* sp.), strongly reduced (*C. umbla*), or less reduced as in *C. damascina*. A1 is a small accessorial tooth and can be easily broken. In the case of *C. saadii*, *C. buhsei*, and *C. baliki*, it is broken and only the tooth basis is visible.

As a rule, the second tooth of the main row (a2) within all studied species is robust and relatively large with a wide tooth base and grinding surface. The other teeth of the main row (a3, a4, a5) as well as the teeth of two other rows (b2, b3, c1, c2) compared to
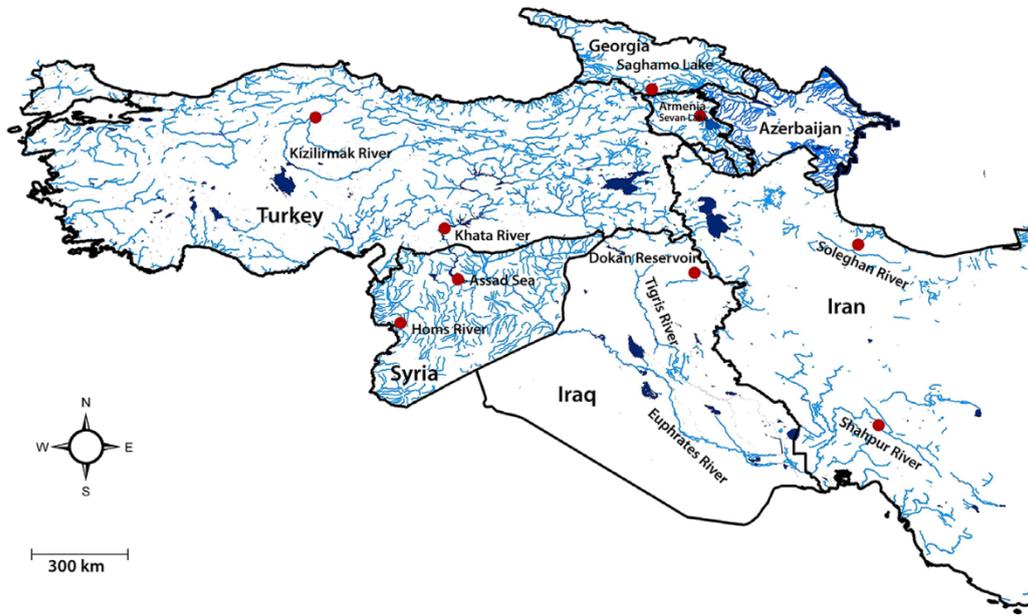
FIGURE 2 Drainage system of Western Asia (Turkey, Iraq, Iran, Armenia, Georgia, and Syria). The sampled (circles) localities of the studied *Capoeta* species
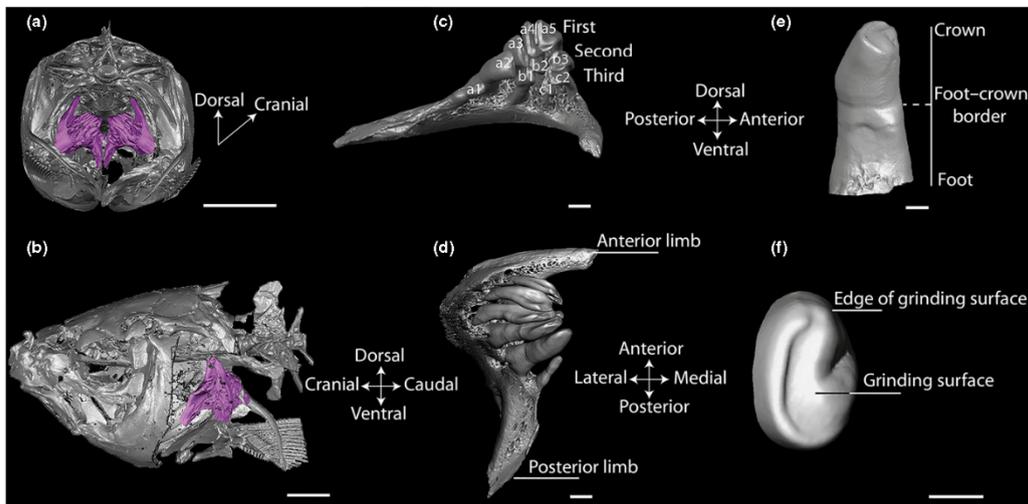
FIGURE 3 The terminology of the pharyngeal bones and teeth used in the present work: Skull of *Capoeta sevangi* in (a) posterior and (b) lateral views, showing the position of pharyngeal bones. Pharyngeal bone with teeth in (c) anterior and (d) medial views. The pharyngeal tooth (e) and grinding surface (f). The scale bars are equal to 1 cm (a, b) and 1 mm (c–f)

a2 are slender. They widen distally and are bent laterally. These characters are more pronounced ventrodorsally along the main row and well expressed in the most dorsal tooth (a5). The first tooth of the second row (b1) is usually similar to the a2 with its morphology, but it is more slender. The other teeth of the second row are slender and bent laterally. Two teeth of the third row (c1, c2) are

usually the smallest. The grinding surfaces in all three rows narrow ventrodorsally.

The intraspecific variation and left–right asymmetry among both studied control groups (*C. sevangi* and *C. capoeta*) were not recorded.

3.2 | Pharyngeal tooth characterization and classification

On the basis of the 3D models and images of pharyngeal teeth, we describe *Capoeta* tooth morphology using two sets of the shape characters: lateral outline (α) and transverse cross section (β, measured at the distal tooth crown). According to the lateral outline, we define 14 character stages (α1–α14; Figure 4; Table S1). Among the studied species, the most frequently occurring lateral outline has spatulate form. It occurs mainly in the a3–a5, b2–b3, and c1–c2 tooth positions. As a rule, nearly all a2 teeth are molariform with a few differences.

The outline of the transverse cross section is variable among the studied teeth, and overall, eleven character stages (β1–β11; Figure 5, Table S1) can be defined for them. The variability of the outline of the transverse cross section of the grinding surfaces is a result of the morphological diversity of the masticatory surface in the studied 10 species.

We applied the (virtual) artificial wear experiment (for details, see Materials and methods) to understand the robustness of the

transverse cross section (β). Different layers/slices from the top of the grinding surface were cut to follow the variability, that is, development of these characters during the wearing process. In this experiment, the pharyngeal teeth of *C. sieboldii* were examined as the folded edge of grinding surface is characteristic of them and the applied experiment allows to test the development of the crenated grinding surface during the wearing process. Therefore, three different height sections from the top of the grinding surface (0.57 mm, 0.87 mm, and 1.42 mm) were processed. The heights of the cut slices are the points after which the form of the examined characters (crenated edge of the grinding surface) was changed. As shown in Figure S2, there are no any significant changes of transverse cross section (β) and it stays stable during applied wearing process, while folds of the grinding surface can change during the wearing process: They deepen, enlarge, or disappear (Figure S2 A1–A3). Therefore, the number or deepening of these folds cannot be used to describe the tooth as they are not applicable for the comparison if the samples have different degree of tooth wearing. The other example is the serrated posterior edge of the grinding surface, which is well expressed in the a4 tooth of *C. buhsei* (Figure S2 B). Its presence can be considered as a character of an unworn or less worn tooth. The application of virtual wearing by applying four different height sections of grinding surface (0.42 mm, 0.78 mm, 1.31 mm, and 1.87 mm) allows to observe the development of the serration during the wearing process. As shown in Figure S2, the serration of the surface is disappearing after a few layers were cut which can be identified during the wearing process (Figure S2 C1–C4).

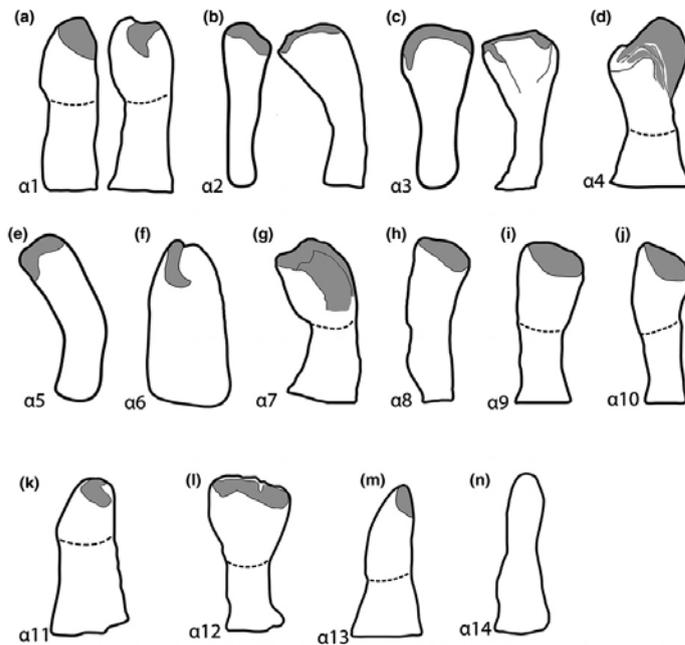**FIGURE 4** Lateral outlines of pharyngeal teeth in the studied *Capoeta* species. Illustrations (a–n) of the 14 character stages (α1–α14) for the tooth lateral outline. The presence of the groove on the grinding surface is indicated in gray color
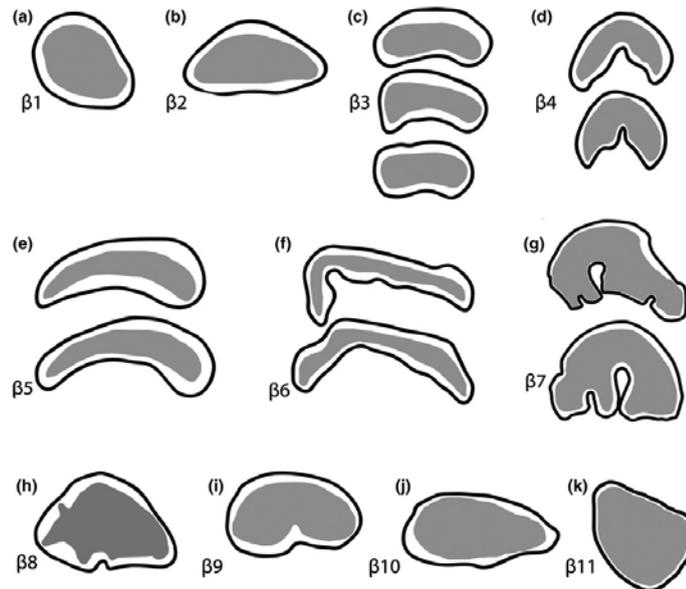
FIGURE 5 Eleven character stages (β1–β11) (a–f) of the transverse cross sections of pharyngeal teeth of the studied *Capoeta* species. The gray color indicates the presence of the groove on the grinding surface, and the white color corresponds to the tooth "enamel"

The grinding surface of some studied dorsal teeth has sloped edges. This character appears in teeth of different rows and possibly points out the tooth's movement direction during the grinding or which part of the grinding surface is actively participating in the grinding process (Figure S2 D, E).

So two main groups of characters of the pharyngeal teeth were distinguished: (i) applicable for the teeth description as the lateral outline (α) and transverse cross section (β); and (ii) variable during the ontogeny as folded, serrated, and sloped edge of the grinding surface.

The lateral outline (α) and the outline of the transverse cross section (β) were used to categorize the pharyngeal teeth of the studied 10 *Capoeta* species into 18 shape classes (Figure 6a–r; Table S2). Within the described shape classes, the most frequent one is shape class "C," which is common to all studied species (Figures S3 and S4).

The detailed description of all the shape classes can be found in the Supporting Information (Tables S1 and S2).

3.3 | Dendrogram based on the tooth shape classes

To test the potential taxonomic and phylogenetic signal of the pharyngeal tooth morphology, we performed a simple dendrogram based on the distribution (presence/absence) of the described shape classes within the studied species (Figure 7; Table S3). The dendrogram divided the studied species into four phenotypic clades: Clade I (*C. saadii*, *C. buhsei*, *C. damascina*, *C. umbla*, and *C. baliki*), Clade II (*C. sieboldii*), Clade III (*C. capoeta* and *C. sevangi*), and Clade IV (*C. trutta* and *Capoeta* sp.).

3.4 | Distribution of shape classes across species

The distribution of the studied species on the dendrogram is based on the morphological characters of these elements. The clustering of a few species inside one clade not only indicates that these species have similar (but not identical) tooth morphology, but also points out their close phylogenetic relationship.

According to the dendrogram, each clade is described with shape classes, and certain species on the dendrogram have own characteristic shape classes (Figure 7). Therefore, the described 18 shape classes are divided into three groups: diagnostic for the genus, clade, and species. The shape class "C" appears in all 10 studied *Capoeta* species, and it is the characteristic shape class of the genus *Capoeta*. The clade diagnostic shape classes are characteristic of a group of species which belong to the same clade, for example, shape classes "B, E, F, H, I, K, and M." The other shape classes, "D, G, J, L, N, O, P, Q, and R," are characteristic of certain species (Figure 7). Besides this, the described tooth shape classes are characteristic of certain tooth positions as well; for example, the shape class "C" is characteristic of teeth belonging to the main row (besides a1 and a2). To test the frequency of the occurrences of shape classes in different teeth positions, the graph was drawn (Figure S5). It shows that the teeth in a2 and b1 positions are the most heteromorph and the ones in position a5 are homomorph or less heteromorph. So the second tooth of the main row (a2) of each studied species (expect *C. buhsei*) has a distinct shape class found only in one species; thus, a2 can be used for the identification at species level. The identification key of the pharyngeal teeth within the studied species was established based on the shape classes (Figure S6).
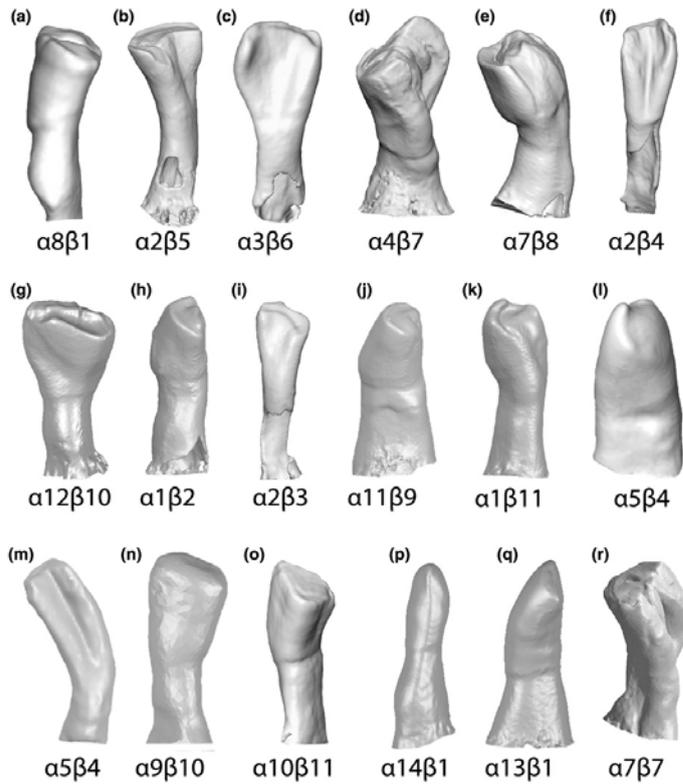
FIGURE 6 3D images of the recorded shape classes of the pharyngeal tooth of the genus *Capoeta*. (a–r) Shape classes proposed in the present work; for the descriptions, Tables S1 and S2. The scales are not given to avoid scaling up of the figures
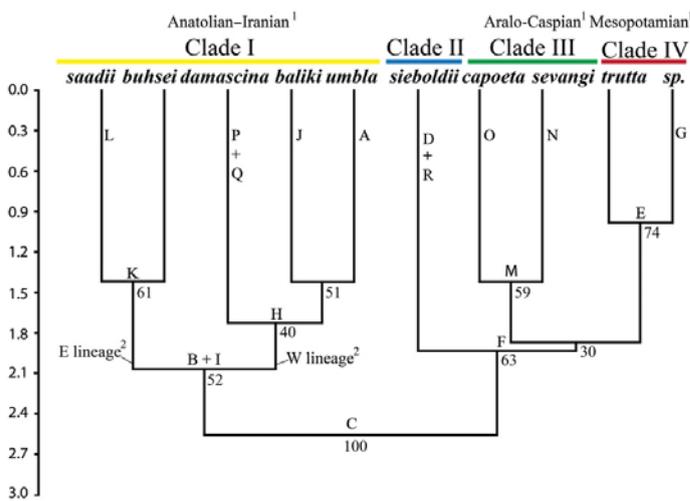
FIGURE 7 Phenotypic dendrogram generated based on the pharyngeal tooth shape classes of the *Capoeta* species. The letters (a–n) indicate the characteristic shape classes of nodes or branches. Numbers indicate the bootstrap support (branch support). [1]Distinguished clades of the genus *Capoeta* following Levin et al. (2012). [2]Eastern (E lineage) and Western (W lineage) lineages within the *Capoeta damascina* complex established by Alwan, Esmaeili, & Krupp, 2016; Alwan, Zareian, & Esmaeili, 2016

4 | DISCUSSION

4.1 | Presence of a1 as a diagnostic character for Clade I

The presence of the a1 within 10 studied *Capoeta* species is characteristic of five of them, which are all clustered in Clade I: *C. saadi*, *C. buhsei*, *C. umbla*, *C. damascina*, and *C. baliki*. The tooth is well developed in *C. damascina*, and in the other above-mentioned species, it is reduced, missing, or broken, but the tooth base is well visible (Figures 1 and 8).

4.2 | Potential phylogenetic signal of the pharyngeal tooth morphology

The performed dendrogram shows not only the morphologic similarity of the species, which belong to the same clade, but also the potential phylogenetic relationship of these species.

C. damascina is considered as a complex of nearly related species with two distinguished lineages: the eastern represented by *C. buhsei*, *Capoeta coadi*, and *C. saadii* and the western represented by *Capoeta caelestis*, *C. damascina*, and *C. umbla*. In this study, the members of both lineages are included: *C. buhsei*, *C. saadii*, *C. damascina*, and *C. umbla*. As the dendrogram shows, these species are clustered (based on their pharyngeal tooth morphology as well as the presence of the a1) in one group and form the *damascina* complex clade (Clade I, Anatolian–Iranian group), respectively with the western and eastern lineages as it has been shown based on genetic analyses (Alwan, Zareian, & Esmaeili, 2016; Alwan, Esmaeili, & Krupp, 2016).

To check the correspondence between morphological and genetic results, we simplify already existing phylogenetic trees based on genetic analyses to show how the studied species cluster within phylogenetic trees based on genetic and morphologic analyses (Figure 9). Therefore, phylogenetic trees from three recent studies were used (Bektas et al., 2017; Levin et al., 2012; Zareian et al., 2016). The comparison of dendrograms (Figure 9) shows that the species of Anatolian–Iranian or *C. damascina* complex group (*saadi*, *buhsei*, *damascina*, *umbla*, and *baliki*) cluster within one clade (indicated by yellow color). The Aralo-Caspian or *C. capoeta* complex group (*C. sevangi* and *C. capoeta*) cluster together in the same clade and are indicated in green. *C. trutta* in all three dendrograms as well as in our results clusters as the distinct clade Mesopotamian *Capoeta* or *C. trutta* group and is indicated in red.

According to the dendrogram (Figure 7), *C.* sp. from Dokan Reservoir clusters within the *trutta* clade, and we suppose it is one of the closely related species of the *trutta* complex.

The studies of Levin et al. (2012) and Zareian et al. (2016) have shown that *C. sieboldii* clusters as a sister lineage to the *damascina* complex. According to Bektas et al. (2017), *C. sieboldii* is easily distinguishable from all *Capoeta* species distributed in Anatolian rivers by its pleated lips and single-paired barbels (the other *Capoeta* species distributed in Anatolian rivers are characterized by double-paired barbels) and represented as a separate clade. This
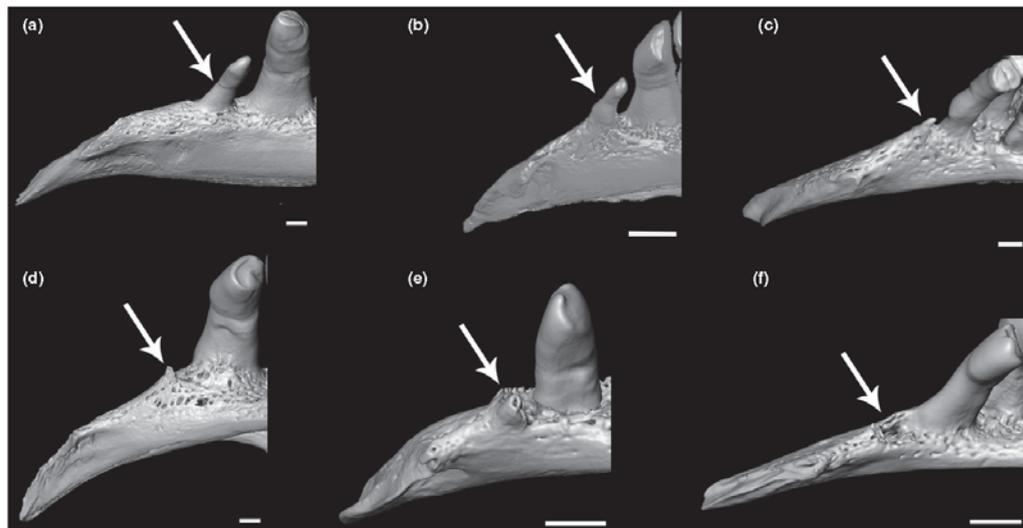
FIGURE 8 Reduction of the a1 tooth in the genus *Capoeta* in comparison with *Barbus barbus*. (a) *B. barbus*, (b) *Capoeta damascina*, (c) *Capoeta umbla* (strongly reduced), (d) *Capoeta baliki* (tooth broken), (e) *Capoeta saadii* (tooth broken), and (f) *Capoeta buhsei* (resorption pit visible). The white arrows show the a1 tooth or the position of its tooth basis. The scale bars are equal to 1 mm
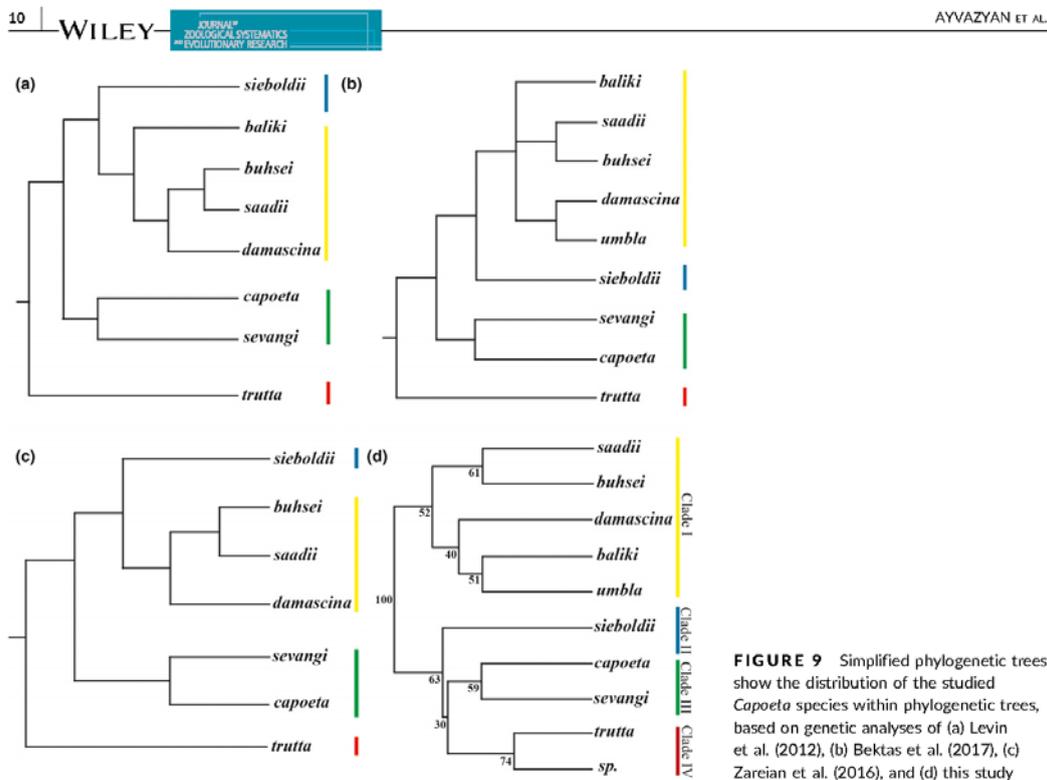
FIGURE 9 Simplified phylogenetic trees show the distribution of the studied *Capoeta* species within phylogenetic trees, based on genetic analyses of (a) Levin et al. (2012), (b) Bektas et al. (2017), (c) Zareian et al. (2016), and (d) this study

pattern is also supported by our results. According to our data, *C. sieboldii* is represented as a distinct clade (Figure 7, in blue color, Clade II). However, our analysis shows only one difference from genetic results (Bektas et al., 2017): *C. sieboldii* is placed as a sister clade to Aralo-Caspian (Clade III) and Mesopotamian (Clade IV) clades (Figure 7), whereas the genetic data cluster it as a sister clade to *C. damascina* (Clade I, small scale; Bektas et al., 2017).

4.3 | Is the reduction of a1 plesiomorphic or apomorphic for the genus *Capoeta*?

The phylogenetic tree based on molecular analyses of the genus *Capoeta* published by Levin et al. (2012) was simplified to show the presence of the a1 in different clades within this genus and its sister groups (Figure 10). The pharyngeal bones most of species of *Barbus* and *Luciobarbus* clades were available to us and the presence/absence of a1 was recorded first-hand, and the information about missing species was taken from the existing literature. This dendrogram shows that a1 tooth or its basis is present in representatives of clade *Barbus* and clade B (*Capoeta* clade), but absent in the other two sister groups (*Luciobarbus* and *L. subquincunciatus*). We assume that the absence of a1 is plesiomorphic for the genus *Capoeta*, which means it was lost among the species of clades A and C and reappeared or was regained in the species of
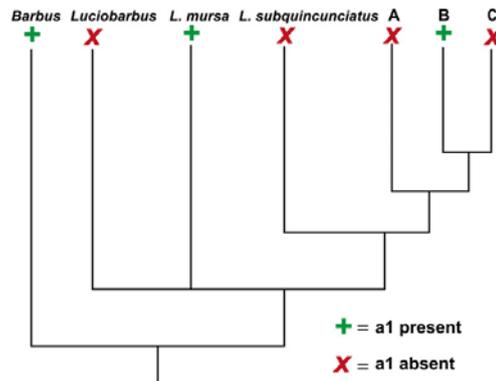
FIGURE 10 Presence/absence of a1 tooth shown on the phylogenetic tree based on mitochondrial gene for cytochrome b sequences (Levin et al., 2012). The clades are respectively corresponding to the clades mentioned in the work. A, B, and C the Mesopotamian group (A), the Anatolian–Iranian group (B), and the Aralo-Caspian group (C), are included in the clade *Capoeta*

clade B. The other possibility is that the presence of a1 tooth or its basis is a derived character that distinguishes the *damascina* clade.

4.4 | Potential ecological signal of the pharyngeal tooth

The preliminary interpretation of the possible ecological signal or the connection between feeding habits and pharyngeal tooth morphology of the studied species is provided based on literature data (Coad, 2010; Karaman, 1969; Krupp & Schneider, 1989).

The studies regarding the feeding habits of the genus *Capoeta* are unanimous and suggest that these species are herbivorous and feeding mainly on algae and periphyton, which they scrape from the substrate using the horny sheath on their lower lip (Banarescu, 1999; Karaman, 1969; Krupp & Schneider, 1989; Türkmen et al., 2002). The similar feeding habits should indicate that the tooth morphology is identical, in other words that the studied species should have homodont dentitions if the main driven factor is ecology, which has not been supported by our study. According to our results, the studied *Capoeta* species have heterodont dentitions and there is an interspecific variation of tooth morphology and tooth numbers within the studied species. Besides this, the dense packaging of the tooth arrangement in the tooth rows on the tooth-bearing area differs as well.

On the other hand, in case the a1 tooth is an apomorphic character of the *C. damascina* clade, a more omnivorous diet of the species of this complex could be suggested, as in *L. subquincunciatus* having a specialized dentition for feeding on algae or benthos. Thus, the a1 tooth could not be considered to provide selective advantage. This indicates the possible trophic segregation within these species.

The mouth and the lower lip covered by horny sheath are used mainly to scrap the algae; therefore, their morphology could also be an important trait to understand the trophic variation of the species and its reflection in tooth morphology.

Within the genus *Capoeta*, two types of mouth forms have been described: horseshoe-shaped and transverse (Karaman, 1969). The horseshoe-shaped is the basal form and can develop into the highly specialized transverse form. In the study by Karaman (1969), it has also been mentioned that all studied populations, during their development, first have the horseshoe mouth form without horny sheath. So we can assume that the horseshoe form of the mouth is a plesiomorphic and the transverse form is an apomorphic character. The mouth form has been described in different studies (Banarescu, 1999; Coad, 2010; Krupp & Schneider, 1989), but we could not find any significant difference between the given morphological descriptions.

So additional morphologic and ecologic studies are necessary to understand whether there is indeed trophic segregation between the *Capoeta* clades and whether there is a possible relation of the tooth morphology and feeding habits.

5 | CONCLUSION

5.1 | Pharyngeal tooth characterization and classification

For the first time, the detailed comprehensive study of pharyngeal dentition of 10 species of the genus *Capoeta* has been provided. The morphology of the pharyngeal dentition has been studied using the 3D microtomography to test its potential relevance for answering to taxonomic and phylogenetic questions. Special tools in the 3D software Avizo 8.0 allow to perform different effects (wearing process) and to test the stability of the morphological characters. These can be applied for the characterization and identification of pharyngeal teeth.

In this study, the set of morphological characters (αβ) were established to categorize the studied pharyngeal teeth into 18 shape classes. The results of different analyses based on the described shape classes show that based on the detailed morphology of these elements, the isolated pharyngeal teeth can be identified at the generic or specific level. Besides this, it is also possible to determine the relative or even the exact position of the isolated tooth in the tooth rows.

The identification key of the pharyngeal teeth of the studied species could be used for the identification of the isolated pharyngeal teeth, which is important not only for the taxonomy of recent species but also for the fossil record, as mainly the isolated pharyngeal teeth are found in the fossil record.

5.2 | Correspondence between morphological and molecular results

The comparison of the results of morphology and genetic analyses shows significant similarities of the generated trees. This supports our assumption that the pharyngeal tooth morphology of this genus has not only taxonomic but also phylogenetic relevance. The morphological results strongly support the presence of four clades: (i) *C. damascina* clade; (ii) *C. sieboldii* clade; (iii) *C. capoeta* clade; and (iv) *C. trutta* clade.

Summing up our results, we conclude that:

1. the detailed morphology using the 3D microtomography of pharyngeal teeth is a useful tool for the identification of the isolated pharyngeal teeth at the generic and specific levels, as well as in certain cases the tooth position in tooth rows;
2. the morphology of the pharyngeal teeth provides an obvious phylogenetic signal, supporting results derived from molecular genetic analyses;
3. both these patterns are important for the taxonomy of the genus and can be applied for the fossil records as well;
4. the a1 tooth is an apomorphic character for the *C. damascina* complex;
5. there is possible trophic segregation (the species of the *C. damascina* complex are more omnivorous/less dietary specialized); further studies are necessary to confirm this.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Possible species-flock scenario for the evolution of the cyprinid genus *Capoeta* (Cypriniformes: Cyprinidae) within late Neogene lake systems of the Armenian Highland

PLOS ONE

Possible species-flock scenario for the evolution of the cyprinid genus Capoeta (Cypriniformes: Cyprinidae) within late Neogene lake systems of the Armenian Highland
--Manuscript Draft--

Manuscript Number:	PONE-D-18-32717R2
Article Type:	Research Article
Full Title:	Possible species-flock scenario for the evolution of the cyprinid genus Capoeta (Cypriniformes: Cyprinidae) within late Neogene lake systems of the Armenian Highland
Short Title:	Possible species-flock scenario for the evolution of the cyprinid genus Capoeta
Corresponding Author:	Anna Ayvazyan Eberhard Karls Universitat Tubingen Tübingen, GERMANY
Keywords:	Erzurum, fishes, fossils, palaeobiogeography, pharyngeal teeth, Tekman, Çevirme
Abstract:	We studied 4 Ma old isolated pharyngeal teeth from lake sediments of Çevirme (Tekman Palaeolake, Erzurum Province) based on 3D morphology. As a result, we found that the Pliocene lake constitutes sympatric occurrence of four Capoeta species (C. cf. umbla, C. cf. baliki, C. cf. sieboldi and C. sp. sevangi/capoeta), whose modern relatives belong to a monophyletic clade inhabiting three different drainage systems of this region (Euphrates River, Kura River and Black Sea). We interpreted this high local diversity of closely related species in terms of the species-flock model. The Tekman palaeolake was a part of an unrecognized extended late Miocene to Pliocene palaeo-lake system in the present-day Armenian Highland, which has been disrupted by Pliocene tectonic activities. Surface uplift of the Armenian Highland contributed to the very characteristic biogeographic distribution and endemism of Capoeta in West Asian drainage systems. Thus, we proposed a species-flock scenario for the evolution and dispersal of the cyprinid genus Capoeta in a huge unrecognized palaeolake system in the present-day Armenian Highland.
Order of Authors:	Anna Ayvazyan
	Davit Vasilyan
	Madelaine Böhme
Opposed Reviewers:	
Response to Reviewers:	Rebuttal PONE-D-18-32717R1 Possible species-flock scenario for the evolution of the cyprinid genus Capoeta (Cypriniformes: Cyprinidae) within late Neogene lake systems of the Armenian Highland Comment #1: Using '3D shape characters' for inferring results as indicated in the abstract still is ambiguous, because you do not provide any corresponding analysis (as indicated by the reviewer). Just changing "3D morphology" into "3D shape characters" is not sufficient since 'lateral outline' and 'transverse cross sections' are 2D rather than 3D aspects! Therefore, using 3D referring to such characters is incorrect. To analyse 3D shape characters you have to use sophisticated analytical procedures such as geometric morphometrics, which, you, however argue to not be possible. I wonder if this really is true, because from my experience you are always able to find at least a few homologous points (even if there are only three to five). This, nevertheless, is still sufficient in most cases to produce results. Of course, you also have to use teeth from the same position for this, which has to be clarified before. Concluding: You have to change this if you are using 2D characters, or you have to make a detailed justification why these characters are 3-dimensionally in the method's section. Respond. We changed this part in abstract ''Based on shape characters defined for 3D

models of modern species…" as these characters are distinguished within our previous study (Ayvazyan et al. 2018) based on the 3D models of studied samples.

Comment #2: Please include Table 2 based on a modification of Table 1 of your previous publication and add the necessary size information.
Respond: Table 2 is added.

Comment #3: Change the captions of figures 1 and 2 into "… redrawn and modified from…"
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Comment #4: Please make sure that the newly included section (lines 380 ff) will be proof read by a native speaker. There are some typos, grammar and wording errors (e.g., line 389, third word: it should read 'provides'; line 393: it should read "… also tested in benthophagous"; line 396: delete punctuation before "These…"; line 402: it should read "… should not be considered…."; line 407: "teeth" should read "tooth"
Respond: Thank you, we took all the corrections in consideration and newly proof this section.

Comment #5: You answered in detail the questions concerning the patterns of tooth wear in your letter to the editor but you did not include any of this in the manuscript. Please include a summary of your answer in the method's section and also a short paragraph in the discussion's section that tooth wear patterns are not considered by you as taxonomic characters based on Ayvazyan et al. (2018).
Respond. We added a summary regarding to the patterns of tooth wear in Material and methods
We think this information does not fit into any section of Discussion.

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48 system include rather short and small but numerous drainage systems of the

49 Mediterranean Sea Basin (this territory includes southern Anatolia, Syria, Lebanon, Israel,

50 the Arabian Peninsula), Black Sea Basin (northern Anatolia and Western Georgia), the

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53 The four main rivers of Western Asia and the Ponto-Caspian region (Euphrates, Tigris,

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3

70   **Fig 1. The Armenian Highland.** (a), Fossil locality marked by red contoured circle in a relation to

71   the Euphrates-Tigris and Araxes-Kura water basins. (b), map showing the fossil locality marked

72   by red contoured circle. Map data: Figure 1 (a, b) is redrawn and modified from U. S. Geological

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74   **Species flock concept in ichthyology**

75   A species flock is a monophyletic group of closely related sympatric species inhabiting the

76   same area or geographically restricted area. The species flock is common for both

77   vertebrate and invertebrate animals, which show rapid adaptive radiation, morphological

78   divergence and speciation [10–13]. The examples of species flock are recorded in

79   different groups of animals: insects, fishes, lizards and birds, [14–19]. Especially

80   monophyletic groups of fishes represent a particular interest, as one of the criteria of the

81   species to be considered as a species flock is the monophyly of the described

82   groups/species [20, 21].

83   Two main well-known species flocks of cyprinids fishes are found in the Philippine Lake

84   Lanao and the Ethiopian Lake Tana [18, 22–24]. Besides the extant species flocks, some

85   potential fossil species flocks are also reported, e.g., from the Eocene site in Tanzania,

86   the upper Miocene Lukeino Formation in the Tugen Hills of the Central Rift Valley of Kenya

87   [17].

88

89   **Cyprinid pharyngeal dentition**

90   The oral jaws (e.g. dentary, maxilla, premaxilla) of cyprinids are toothless. Instead they

91   have pharyngeal teeth located on the pharyngeal bones [25]. Both left and right fifth

92   ceratobranchials are modified into pharyngeal jaws, which have the function of food

4

93   processing [25, 26]. The pharyngeal bones and teeth provide important taxonomic

94   characters for systematics of the cyprinid fishes. The number and arrangement of the

95   pharyngeal teeth in tooth rows are recognized and widely used diagnostic characters for

96   cyprinid classification [27].

97   The fossil remains of cyprinids are mainly represented by isolated pharyngeal teeth [28]

98   and it is hard to identify specimens based on sole isolated teeth. Therefore, the fossil

99   record of many cyprinids, included the genus *Capoeta*, is still largely unknown.

100

101   **The fossil record of the genus *Capoeta***

102   According to the molecular data, the genus *Capoeta* originates around the Langhian–

103   Serravallian boundary (13.9 Ma) and diversification within the genus occurs along the

104   Middle Miocene – Late Pliocene period [29] .

105   The scarce fossil record of *Capoeta* comes from four localities, two from the late Miocene

106   and two from the Pleistocene. Miocene *Capoeta* fossils are known from Armenia and

107   Georgia, both in the present-day Kura-Araxes drainage basin (Fig 2). The first fossil

108   remains of *Capoeta nuntius* are described by Bogachev (1927) at the late Miocene locality

109   in the Kisatibi, Samtskhe-Javakheti region, Georgia [30, 31]. The material is represented

110   by three more or less complete and a few strongly damaged skeletons as well as more

111   than 70 isolated bone fragments. Vasilyan & Carnevale (2013) describe skeletons of

112   *Capoeta* sp. from the Jradzor locality (latest Miocene) in Armenia [32]. The record of

113   *Capoeta* from late Pliocene sediments at Ericek (Cameli Basin, SW Anatolia) is doubtful

114   [33], since the tooth morphologies (Fig 4 a-d in [33]) are not found within pharyngeal teeth

5

115 of the *Capoeta* species. Instead of this, they resemble the morphology of the genus

116 *Luciobarbus*; as the reported cobitid and gobiid remains are snake jawbones. Vasilyan et

117 al. (2014) describe two isolated pharyngeal teeth and two fragments of serrated dorsal fin

118 rays referred to *Capoeta* sp. from the early Pleistocene locality Pasinler (Erzurum

119 Province, north-eastern Turkey). Fossil remains of *Capoeta damascina* Valenciennes,

120 1842 are also recorded from the Hula Palaeolake [34]. The site is situated in the northern

121 part of the Dead Sea Rift, Israel and dated to the Middle Pleistocene (0.78 Ma).

122 **Fig 2. Geographical overview of the drainage systems of Western Asia and the Ponto-**

123 **Caspian regions (Euphrates-Tigris, Araxes-Kura).** Red star (1) indicates the position of the

124 Çevırme locality. The red circle shows the possible extension of palaeolake system of the

125 Armenian Highland. The arrows show the late distribution of the recorded fossil *Capoeta* species

126 into the different water basins due to the tectonic disruption of the Lake system during the Pliocene

127 uplift period. The two already known late Miocene fossil sites Kisatibi (red star 2) and Jradzor (red

128 star 3) are included as well. Map data: Figure 2 is redrawn and modified from U. S. Geological

129 Survey CC BY 4.0.

130

131 **Biogeographical distribution of extant *Capoeta* species**

132 According to the molecular data, the monophyletic genus *Capoeta* is represented by three

133 main clades: Mesopotamian, Anatolian-Iranian and Aralo-Caspian clades and nested

134 within the genus *Luciobarbus* as a sister group of the species *Luciobarbus*

135 *subquincunciatus* [29, 35, 36] (Fig 3a and 3b). The Mesopotamian group contains species

136 distributed in the Tigris-Euphrates drainage system and adjacent water basins: *Capoeta*

137 *trutta* (Heckel, 1843), *Capoeta turani* Özulu & Freyhof, 2008 and *Capoeta barroisi* Lortet,

138 1894. The Anatolian-Iranian group includes species inhabiting the Black Sea Basin:

6

139   *Capoeta sieboldi* Steindachner, 1864, *Capoeta baliki* Turan, Kottelat, Ekmekçi &

140   Imamoglu, 2006, *Capoeta banarescui* Turan, Kottelat, Ekmekçi & Imamoglu, 2006. The

141   Mediterranean drainage basins (Anatolian-Iranian clade) of southeastern Turkey, the

142   Tigris–Euphrates river system, and small rivers, which drain into the gulfs of Persia and

143   Oman, as well as inland water bodies in Iran contain the following species: *Capoeta*

144   *buhsei* Kessler, 1877, *Capoeta saadii* (Heckel, 1847), *Capoeta caelestis* Schöter, Özulu

145   & Freyhof, 2009, *Capoeta damascina*, *Capoeta angorae* (Hankó, 1925) and *Capoeta*

146   *kosswigi* Karaman, 1969. Finally, the Aralo-Caspian group includes the species

147   distributed in the Kura and Araxes rivers, as well as Aral and Caspian Sea drainages:

148   *Capoeta capoeta* Güldenstädt, 1773, *Capoeta sevangi* De Filippi, 1865, *Capoeta aculeata*

149   (Valenciennes, 1844) (S1 Table) [29].

150   A recent phylogenetic analysis [9], using the morphologies of pharyngeal teeth of ten

151   *Capoeta* species, groups them in four main clades. Three of these clades show the same

152   tree topography that the molecular data provides, the remaining clade groups differently

153   [9].

154   **Fig 3. Phylogeny of the genus *Capoeta*.** (**a**), distinguished clades within the genus

155   *Capoeta* (*Luciobarbus suquincunciatus* is the sister clade) (Levin et al., 2012). The clade

156   diagnostic shape classes of recorded clades within the fossil material (see Fig.7,

157   Ayvazyan et al. 2018) are given in capital letters included 3D images of teeth of *Capoeta*

158   as well as the a2 tooth of *L. subquincunciatus*. The monophyletic Anatolia-Iranian/Aralo-

159   Caspian/*sieboldi* clade, for which we propose a species flock model of evolution, is

160   marked by red colour. (**b**), the location of *Capoeta* clade within phylogenetic tree based

161   on the molecular genetic analysis (Levin et al., 2012).

162

7

163   **Late Neogene lacustrine sedimentation in the Armenian Highland**

164   Present-day Armenian Highland (Eastern Anatolia, Armenia, Iranian Azerbaijan,

165   Samtskhe-Javakheti region of Georgia) is composed of the high mountainous landscapes

166   of the Eastern Taurides with elevations between 1.700 to over 5.000 meters above sea

167   level. Because of the dominant arid climate during the late Holocene, lakes are rare in this

168   region. Two endorheic saline lakes, Lake Van and Lake Urmia, as well as the freshwater

169   Lake Sevan are notable exceptions (Figs 1a and 2). However, geologic mapping revealed,

170   that during the pre-Quaternary lacustrine, sedimentation was widespread and long lasting

171   in this region. According to Altınlı (1966) during the Late Miocene and Pliocene (11.6-2.6

172   Ma) lacustrine sedimentation dominated Eastern Anatolia with regional thicknesses of

173   deposits over 1.000 m. These sediments contain a rich freshwater fauna (e.g. diatoms,

174   gastropods, bivalvs, ostracods, fishes); [37–42] and have been variously attributed to the

175   Horasan Formation, Gelinkaya Formation, Işıklar Formation (all in the Erzurum Province),

176   Zırnak Formation (Bitlis Province), Çaybaği Formation (Elazığ Province), or to the

177   Parçikan Formation (Malatya Province). Despite extensive syn-sedimentary volcanism,

178   none of these formations are radiometrically dated, but available K-Ar data [43] and rare

179   rodent fossils [44, 45] suggest that the main lacustrine phase in Eastern Anatolia centred

180   between 6 and 3 Ma, probably coeval with the supposed uplift of this region [46].

181   An older lacustrine period is documented in Iranian Azerbaijan, where fish bearing

182   (Atherinidae, Cyprinodontidae, Leuciscinae, but no Barbinae) lake sediments from the

183   Tabriz Basin ('lignite beds', 'fish beds') have been dated to between 12 and 7.5 Ma [47].

184   These late Neogene lacustrine sediments have tectonically fragmented exposure over a

185   huge area in the Eastern Taurides stretching several hundreds of kilometres, notably

8

186   including the upper reaches of present-day Euphrates, Tigris, Kura and Araxes rivers (Fig

187   2).

188

189   **Fossil locality Çevırme**

190   The fossil site Çevırme (Erzurum Province, Tekman district) is located 12 km west of the

191   Haciömer village on the road from Haciömer to Tekman, 500 m after the bridge over the

192   Araxes River (coordinates: N 39° 37′ 37″; E 41° 38′; Figs 1a, 1b and 2). The locality

193   belongs to the Tekman Basin (East-Anatolian Taurides), approximately 40 km south from

194   the Pasinler Basin and 120 km north-northwest of Lake Van. Late Neogene sediments in

195   the Tekman Basin laying discordant over early Miocene marine limestones [48]. The

196   sedimentary facies of the basin infill change from fluvial-alluvial to lacustrine. The late

197   Miocene sedimentary formation (Hacıömer Formation) is composed of an approximately

198   300 m thick reddish-brown sequence of conglomerates, sandstone and silts with minor

199   intercalation of marls. In the south of the basin, the alteration with vulcanites appear. These

200   terrestrial-fluvial fossil free layers intercalate in their upper parts with nearly 200 m thick

201   lacustrine sediments of the Işıklar Formation, which mainly consist of light grey, as well as

202   slightly reddish freshwater carbonates (Fig 1b). Layers of marl, organic rich clay and tufa

203   are also present. The section is covered by Pleistocene basalts from the Bingöl Dag area

204   [48].

205   The fossil site Çevırme, discovered and first described by Sickenberg (1975), belongs to

206   the lacustrine upper part of the Işıklar Formation. The 65 m thick stratigraphic section is

207   subdivided based on lithological and sedimentological characters. The fossil remains of

208   fishes, molluscs and mammals are found at 18 m depth of the section (Fig 4). Earlier

9

368   shape classes "A", "J" and "R" (a2 tooth position) comprise 10% of studied isolated fossil

369   pharyngeal teeth (S1 and S2 Figs).

370   Morphological observations of isolated fossil pharyngeal teeth revealed, besides the main

371   distinguished characters (lateral outline (α) and transverse cross-section (β)), further

372   charcters commonly occuring within both recent and fossil *Capoeta.* They are "ruptures"

373   of the grinding surface and the crenated edge of the grinding surface, which are variable

374   and depending on the degree of tooth wearing (Fig 7) (details see Ayvazyan et al., 2018).

375   These structures are not considered as a species characteristic.

376   **Fig 7. Additional morphological characters (besides the shape characters ($\alpha\beta$) in**

377   **fossil and extant pharyngeal teeth (not to scale)**. (**a**), *Capoeta* sp., b3 tooth (extant)

378   (SAPM-PI-00719, SNSB). (**b**), *C. trutta*, a5 tooth (extant) (SAPM-PI-02908, SNSB). (**c-d**),

379   isolated fossil pharyngeal teeth (identified as shape class "C" and "F" respectively) (BGR

380   6, 16). (**e**), isolated fossil pharyngeal tooth (BGR 5). (**f**), *C. capoeta*, b2 tooth (extant)

381   (GPIT-OS-00860[a]), both are identified as shape class "M". The ruptures of grinding

382   surface are marked by red arrows (a, b, c, d) and an example of very similar tooth

383   morphology in fossil (e) and extant (f) isolated pharyngeal teeth.

384

385   # Discussion

386   In our fossil samples, we record eight shape classes where the genus diagnostic shape

387   class "C" dominates the assemblage (53%). Identified shape classes as species or clade

388   diagnostic (A, J, R, M) compose 10% of the assemblage (S1 Fig).

18

389   **Possible influence of plasticity and allometry on high diversity of recorded shape**

390   **classes**

391   The literature provides examples of the potential effects of plasticity on the dentary bone

392   and tooth morphology mainly in cichlid fish cultures by applying contrasting diets (soft and

393   hard) [50–53]. These studies recorded some degree of phenotypic plasticity of dentary

394   bone morphology and in some cases tooth size. The influence of these two diets on the

395   development of the cyprinid pharyngeal dentition is also tested in the benthophagous

396   cyprinid black carp. Dietary did not change the tooth morphology, but, instead, it has been

397   found that broad diet may influence the frequency of tooth replacement and size patterns

398   [54]. These studies are mainly based on aquarium experiments in benthophagous species

399   where two extreme diets (commercial fish as a soft and snails as hard food) are tested.

400   Under natural conditions, fishes are not forced to feed on only one type of food. Thus, it

401   is data can be applied to, in the present paper studied algae-scrapping species *Capoeta*,

402   which are recorded from single geological layer and are sympatric individuals in a uniform

403   environment. Considering this, the effect of feeding on different food should not be

404   considered biasing on the carp pharyngeal tooth morphology, and, thus, we exclude the

405   effect of plasticity on the studied fossil material.

406   Allometric shifts in pharyngeal tooth morphology cannot explain the high diversity of

407   recorded shape classes in the studied fossil samples. Morphological shape remodeling in

408   cyprinids happens in very early stages of their ontogeny. Juveniles (standard size of a few

409   mm) have different tooth morphology than the adult samples, but the significant

410   morphological changes are finalized in this early stage. Thus, the adult dentition in cyprinid

411   fishes is completed by at the later larvae or juvenile stages [55]. Our fossil material is

19

412   represented by adult individulas, as the studied fossil pharyngeal teeth sizes vary between

413   0.8 – 3 mm (it is a sampling artifact introduced by mesh size limitation washing collection

414   technique). Therefore, our fossil samples is composed of isolated pharyngeal teeth of

415   adult individuals.

416

417   **Taxonomic assignment**

418   For species-level taxonomy we discuss two possible interpretations. The assemblage can

419   be interpreted to document either a single, very heterodont species or several *Capoeta*

420   species.

421   **1. The fossil assemblage documents one species.** The recent *Capoeta* species are

422   characterized by different degree of heterodonty, which varies between three and six

423   shape classes per species. For instance, *C. damascina*, the most heterodont extant

424   species, is characterized by six different shape classes [9]. The second most heterodont

425   species *C. umbla* (Heckel, 1843) is characterized by five different shape classes, four of

426   them are shared with *C. damascina*. Eight shape classes, as found in our fossil samples,

427   is unprecedented among extant species. It is also highly unlikely that a fossil species

428   shows this degree of heterodonty, given the ten tooth positions at pharyngeal bones are

429   present. Therefore, we consider the 'single species' interpretation as rather unlikely.

430   **2. The fossil assemblage represents more than one species.** The specific

431   identification of extant *Capoeta* species is possible only on the morphology of the teeth at

432   the tooth position a2 [9]. The Çevırme association contains four shape classes, which are

433   species-specific among recent taxa at the a2 position: the shape class "A" characterizes

20

434   *C. umbla*, the shape class "J" is typical for *C. baliki* (both species belong to the Anatolian-

435   Iranian clade) and the shape class "R" is found only in *C. sieboldi* (*sieboldi* clade). The

436   shape class "M" is shared at the a2 position by two closely related Aralo-Caspian species

437   *C. capoeta* and *C. sevangi*. Therefore, we assume that the Çevırme assemblage is

438   constituted of four species.

439   The four discussed extant species are also characterized by other shape classes, which

440   are not found within the studied fossil material. The shape class "I" is common in *C. umbla*

441   and *C. baliki*, it occurs at the topological positions b2, b3 and c2. These teeth are small

442   and may not be found due to taphonomic or sampling bias (tooth diameter is smaller than

443   0.8 mm). Two additional shape classes "N" and "O", which are missing in our sample,

444   characterize the two Aralo-Caspian *Capoeta* species *Capoeta sevangi* and *Capoeta*

445   *capoeta*, at the tooth position a2. We interpret the lack of these species characteristic

446   shape classes by younger divergence of these species (see below).

447   Our results indicate the presence of possible four species in the fossil assemblage, which

448   belong to three different clades (Anatolian-Iranian, Aralo-Caspian, and *sieboldi* clades) of

449   the genus *Capoeta*. According to all molecular studies [29, 56, 57], these three clades are

450   monophyletic and sister groups to the Mesopotamian clade (Fig 3a).

451   **The evolution of the genus *Capoeta* as a species flock scenario**

452   Greenwood (1984) suggests that, in order to identify a group of organisms as species

453   flock, the representatives should be monophyletic and endemic to an area they inhabiting

454   [21]. Later on, five main criteria are distinguished to detect the flock species [13, 58]: 1)

455   monophyly, 2) high species diversity (speciosity), 3) high level of endemism, 4)

456   morphological and ecological diversity; and 5) habitat dominance in terms of biomass. A

21

457   later study [59], suggests to concentrate on three robust, easier to determine criteria such

458   as monophyly, endemism and speciosity. This study suggests ranking the ecological

459   criterion as secondary. Our fossil *Capoeta* samples correspond to all five criteria sensu

460   Eastman and McCune (2000) and can thus be regarded as a species flock. The extant

461   *Capoeta* is a monophyletic phytophagous barbin genus, widely distributed in West Asian

462   and the Ponto-Caspian water basins and comprise 30 extant species [5, 29, 35, 56]. Our

463   four fossil species (*Capoeta* cf. *umbla*, *C.* cf. *baliki*, *C.* cf. *sieboldi*, *C.* sp. *capoeta/sevangi*)

464   belong to a monophyletic clade composed of *Capoeta sieboldi*, Anatolian-Iranian and

465   Aralo-Caspian species (Fig 3a) endemic to the drainage systems of the Black and Caspian

466   seas and Persian Gulf (Fig 2), thus, fulfilling the three main criteria for species flock

467   recognition [59]. Certainly, we cannot be fully definite that our fossil taxa are also

468   monophyletic. However, considering that the phylogenetic analysis using the morphology

469   of extant pharyngeal teeth [9] placed the species in the same topology as the molecular

470   phylogenetic analysis, we are confident that the fossil species attribution correspond to

471   extant taxa. Nevertheless, as in every biological study species identification retain certain

472   degree of uncertainty, which would potentially affect the probable monophyly of the fossil

473   taxa.

474   The endemic occurrence of the genus *Capoeta* in Western Asia and the Ponto-Caspian

475   region is supported by its exclusive extant and fossil record in the region [7, 30, 60–62].

476   The taxonomic studies of this genus show the morphological and meristic diversity of the

477   extant *Capoeta* species [9, 39, 63–65], but detailed ecologic studies are lacking so far.

478   The fifth criteria (habitat dominance in terms of biomass) is more difficult to access for the

479   fossil palaeocommunity. However, within the studied samples from the locality Çevırme

480   *Capoeta* dominates not only by the species richness over *Leuciscus* (one undetermined

22

481 medium-size species), but also in terms of numbers of specimens (247 *Capoeta* teeth

482 versus 41 *Leuciscus* teeth), suggesting habitat dominance of *Capoeta* in the Tekman

483 Palaeolake of the Işıklar Formation 4 Ma ago.

484 Our results are largely in agreement with estimated divergence times within *Capoeta* [57],

485 showing that at 4 Ma *C. sieboldi* is already diverged and the Aralo-Caspian clade species

486 *C. capoeta* and *C. sevangi* are not yet separated, which explains the lack of their species-

487 specific tooth shape classes "N" and "O". The fossil Aralo-Caspian clade taxon may,

488 therefore, represent a newundescribed species ancestral to the extant members of this

489 clade. However, published divergence times seem to be overestimated since the fossil

490 calibration points used for the molecular clock are too old, maybe by a factor of two *Barbus*

491 sp. set at 18 Ma citing Böhme & Ilg 2003 refer in fact to *Barbus* s. l., which is probably

492 closer related to *Cyprinion*; the oldest *Barbus* s. s. fossils are known from sediments of

493 age at least 8 Ma, Böhme unpublished data) [66]. Nevertheless, the oldest unequivocal

494 *Luciobarbus* with affinities to *L. subquincunciatus* (the sister clade of *Capoeta*, Fig. 3a and

495 3b) is *L. vindobonensis* from 9.8 Ma old deposits in Austria [67], suggesting that the

496 evolution of *Capoeta* is largely a late Miocene event.

497 The presence of a four-million-year old *Capoeta* species flock in the Tekman Basin with

498 members of three recent clades is very remarkable. We hypothesize, that the Tekman

499 Palaeolake, which was part of a large Armenian Highland lake system, was a place of the

500 speciation of *Capoeta* species related to the three recent clades of the genus (Anatolian-

501 Iranian, Aralo-Caspian and *sieboldi*). Moreover, the huge Armenian Highland lake system,

502 which formed during the late Miocene and represents the source of all major rivers in

23

503 Western Asia and the Ponto-Caspian region where *Capoeta* is widely distributed, could

504 represent the centre of origin of *Capoeta* including its Mesopotamian clade.

505 A recent study shows that tectonic reorganization in the region, starting about the

506 Miocene-Pliocene transition (ca. 5.5 Ma) along the East and North Anatolian faults [46,

507 68]. It resulted in substantial surface uplift and probably caused the gradual reshaping of

508 the hydrological network in the area. This could largely contribute to dispersal and further

509 speciation of the members of the species flock into their distribution areas nowadays.

510 The possible species flock scenario of the genus *Capoeta* as well as the reorganization

511 of the palaeolake system in Armenian Highland are hypothetically illustrated in Figure 8,

512 where three main stages of lake evolution.

513 **Fig 8. Hypothetical evolutionary stages of the palaeolake system of Armenian**

514 **Highland since latest Miocene.** Three main stages are suggested (marked by blueish

515 colours): formation, maximum of lake expansion, decay and fully development of present-

516 day drainage system. The monophyletic clade of recorded species within the fossil

517 material shows the presence of the species flock of *Capoeta* at 4 Ma ago in palaeolake

518 system of Armenian Highland.

519 The other possible explanation of our results could be the concept of secondary contact.

520 This scenario (speciation of hybrids) is very similar to the above suggested species flock

521 model, however, without any genetic information we cannot be precise about this

522 hypothesis. More studies and more fossil sites inside and outside distribution area of

523 *Capoeta* are needed to test our hypothesis, but according to the current available data,

524 the fossil species flock interpretation is the most plausible.

24

92

Conclusions

525

526	For the first time, a detailed study of the isolated fossil pharyngeal teeth of the genus

527	*Capoeta* (n=247) is provided. The description and identification of the fossil material

528	from Çevırme (Erzurum Province, Tekman district) is based on the methodology

529	introduced by Ayvazyan et al. 2018. We show that our methodology is applicable to

530	the fossil record of the genus *Capoeta* and allows identification of the isolated fossil

531	pharyngeal teeth at species level. Within the studied fossil material eight shape classes

532	are distinguished, four of them are species or clade diagnostic and indicate the

533	presence of the four sympatric *Capoeta* species (*C.* cf. *sieboldi*, *C.* cf. *umbla*, *C.* cf.

534	*baliki* and *C.* sp. *capoeta*/*sevangi*) in the Tekman Palaeolake at 4 Ma. These four

535	species belong to a monophyletic clade of the genus and today they are distributed in

536	different water basins (Euphrates/Kura/Black Sea) of Western and Ponto-Caspian

537	region. We interpret this high local diversity of closely related species in terms of the

538	species-flock model.

539	Literature review suggests that the Tekman Palaeolake was part of an unrecognized

540	huge late Miocene to Pliocene palaeolake system in the present-day Armenian

541	Highland and we hypothesized that the evolution of *Capoeta* occurred there during the

542	late Miocene. Pliocene tectonic activities disrupted this lake system and resulted in the

543	very characteristic biogeographic distribution of *Capoeta* in West Asian and Ponto-

544	Caspian drainage systems today.

545

Acknowledgments

546

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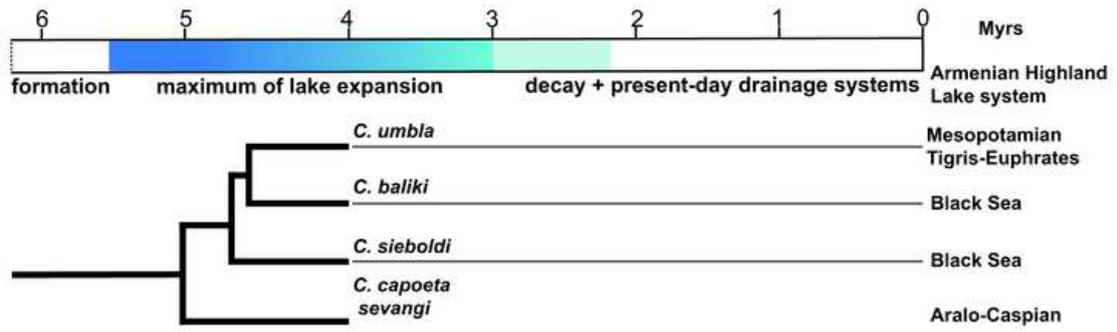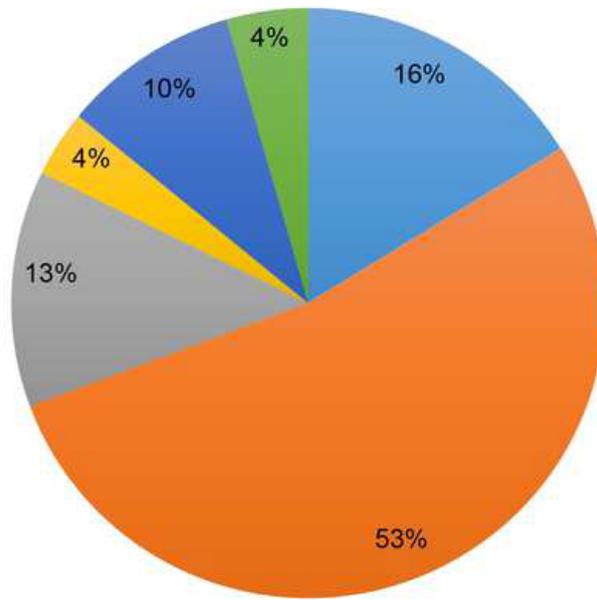
S2_Fig

7.   Appendix II: Submitted Manuscript

Fish, amphibian and reptilian faunas from the latest Oligocene o middle Miocene localities from Central Turkey

Palaeobiodiversity and Palaeoenvironments
Fish, amphibian and reptilian faunas from the latest Oligocene to middle Miocene localities from Central Turkey
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Abstract:	In this paper, we describe ectothermic vertebrate assemblages from the Kargı 1, Kargı 2, Kargı 3, Harami1, Harami 3, Hancılı, Keseköy, Çandır, Bağiçi localities in Turky. The ages of these localities range from the latest Oligocene to the middle Miocene. The preserved non-mammalian fauna of the studied localities includes fishes (Luciobarbus sp., Barbus sp., Luciobarbus vel Barbus sp., aff. Capoeta sp., Barbini indet., Leuciscus sp.), anurans (Bufonidae indet., Pelobatidae indet., Latonia sp., Palaeobatrachidae indet.), lizards (Pseudopus sp., Lacertidae indet. 1, Lacertidae indet. 2, Lacertidae indet. 3, Lacertidae indet. 4, Blanidae indet. (?Blanus sp.)), snakes (Albaneryx sp., Erycinae indet.) and crocodiles (Crocodylia indet.). Here we describe, for the first time, the fossil occurence of the genera Salamandra, Albaneryx and Pseudopus from Anatolia, as well as the first fossil representative of the clade of the Western Asian lizards (Lacertidae indet. 3). Our study provides the earliest known fossil occurece for of the genera Luciobarbus, Barbus, Pseudopus and Albaneryx. Palaeobiogeographic relationships of each studied group are discussed and compared with the European and Asiatic record. A tentative palaeoenvironmental reconstruction is provided for each locality.
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1   Fish, amphibian and reptilian faunas from the latest Oligocene to middle Miocene localities

2   from Central Turkey

3

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20   Keywords

21   Fishes, amphibians, reptiles, Turkey, latest Oligocene – middle Miocene,

22   palaeobiogeography.

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24   **Abstract**

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3   25   In this paper, we describe ectothermic vertebrate assemblages from the Kargı 1, Kargı 2,

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5   26   Kargı 3, Harami1, Harami 3, Hancılı, Keseköy, Çandır, Bağiçi localities in Turky. The ages of

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8   27   these localities range from the latest Oligocene to the middle Miocene. The preserved non-

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11 28   mammalian fauna of the studied localities includes fishes (*Luciobarbus* sp., *Barbus* sp.,

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13 29   *Luciobarbus* vel *Barbus* sp., aff. *Capoeta* sp., Barbini indet., *Leuciscus* sp.), anurans

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16 30   (Bufonidae indet., Pelobatidae indet., *Latonia* sp., Palaeobatrachidae indet.), lizards

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18 31   (*Pseudopus* sp., Lacertidae indet. 1, Lacertidae indet. 2, Lacertidae indet. 3, Lacertidae indet.

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21 32   4, Blanidae indet. (?*Blanus* sp.)), snakes (*Albaneryx* sp., Erycinae indet.) and crocodiles

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23 33   (Crocodylia indet.). Here we describe, for the first time, the fossil occurence of the genera

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25 34   *Salamandra*, *Albaneryx* and *Pseudopus* from Anatolia, as well as the first fossil representative

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28 35   of the clade of the Western Asian lizards (Lacertidae indet. 3). Our study provides the earliest

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30 36   known fossil occurece for of the genera *Luciobarbus*, *Barbus*, *Pseudopus* and *Albaneryx*.

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33 37   Palaeobiogeographic relationships of each studied group are discussed and compared with the

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35 38   European and Asiatic record. A tentative palaeoenvironmental reconstruction is provided for

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37 39   each locality.

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42 **Introduction**

43 Multiple publications dealing with assemblages of small and large mammals have

44 summarized the rich fossil record of this group in Anatolia (Marković et al. 2018; Wang et al.

45 2013). In contrast, fossil fishes, amphibians and reptiles from Anatolia have not been

46 thoroughly investigated. In order to understand migrations of vertebrates between Asia and

47 Europe in the late Paleogene and early Neogene (Bruijn et al. 2013; Rössner and Heissig

48 1999), it is essential to have an understanding the fossil record of Anatolia, which likely lay

49 on the migration route between Europe and Asia for many species.

50 A brief overview (Böhme et al. 2003), based on disarticulated fossil material, stood at the

51 basis for a review of the possible relationships between the Anatolian Neogene freshwater fish

52 fauna and those of Europe and Asia. Similarities of the Anatolian fauna were recognized: 1)

53 with that from the central Europe for the most part of the early Miocene; 2) with those from

54 Central Asia for the late early Miocene and early middle Miocene. Few early Miocene

55 localities, e.g., Ağaöz (Paicheler et al. 1978) and Alpagut-Dodurga (Rückert-Ülkümen 1998),

56 provided articulated skeletons of cyprinid fishes. However, this material does not allow

57 observation of the morphology of the pharyngeal teeth, or association to postcranial and other

58 cranial elements.

59 Hitherto published amphibians of Anatolia include Salamandridae indet., *Pelobates*,

60 *Pelophylax, Rana* (Paicheler et al. 1978), Palaeobatrachidae indet. and *Bufotes* (Claessens

61 1997). Claessens (1997) also suggested a migration route for the genus *Bufotes* from Asia to

62 Europe via Anatolia.

63 Recently, Vasilyan et al. (2017) analysed the European and Western Asian amphibian and

64 reptilian Neogene record, suggested that Anatolia played an important role in the dispersal of

65 some amphibians and reptilian linages, especially during the early Miocene. Around a dozen

66 publications have studied the non-mammalian vertebrate faunas from Anatolia (Table 1).

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67 Among them, the recent study by Čerňanský et al. (2017) suggested relations of the

68 *Ophisaurus* sp. from the Kargi 2 locality (Oligo-Miocene boundary) with *Ophisaurus* from

69 the Middle Miocene of Kazakhstan (Vasilyan et al. 2016).

70 Further ectothermic vertebrates, such as lizards *Pseudopus* and *Varanus*, have their earliest

71 appearances in Europe during the early Miocene, around 18-17 Ma, during the so-called

72 Proboscidean Datum Event. As it has been documented for mammals, they arrived to Europe

73 from Anatolia (Rössner and Heissig 1999). Similar migrations, however, have never been

74 documented for other vertebrate groups. Only the discovery of the genus *Bavariboa* in the

75 eastern Anatolia (Szyndlar and Hoşgör 2013) provided a strong evidence of biogeographic

76 connection of the European and southwestern Asian ophidian faunas at the

77 Oligocene/Miocene boundary.

78 Summarizing the known fossil record of Anatolia in the context of those from Europe and

79 Asia, holds significant potential for Cenozoic fish, amphibians and reptiles from Anatolia for

80 resolution of numerous palaeogeographic questions about the origin of European groups as

81 well as for shedding light on timing of migration events for fish, amphibians and reptiles

82 between Europe, Asia and Africa.

83 In the present study, we present: (1) our results focused on ectothermic vertebrates recovered

84 from localities previously studied for small mammals; (2) their interpretations in

85 palaeobiogeographic context; and (3) tentative palaeoenvironmental interpretations of the

86 localities.

4

87 **Materials and methods**

88 The fossil material described in this study originates from nine latest Oligocene to middle

89 Miocene localities (Kargı 1, Kargı 2, Kargı 3, Harami1, Harami 3, Keseköy, Çandır, Hancılı,

90 Bağıçi). Part of the material has been studied and discussed by one of the authors in his

91 unpublished Master's thesis (Claessens 1996). The depositional environments, small mammal

92 faunas, biochronologic correlations and absolute ages of the localities has been discussed and

93 summarized in Bruijn et al. (2013); Čerňanský et al. (2017); Claessens (1996); Kaymekci

94 (2000); Krijgsman et al. (1996); Krijgsman (2003) (Figure 1).

95 The studied fossil material has been collected from the fossiliferous horizons by screen

96 washing of the sediment samples and later picked from the sediment residue. The described

97 material is stored in the palaeontological collection of the University Utrecht (UU). The

98 material has been photographed by the digital microscope, Leica DVM5000 (Tübingen,

99 Germany), the electronic miscropscope FEI XL 30 Sirion, and a Canon EOS 50D camera.

100 The extant comparison material of fishes is stored at the osteological collection of National

101 Museum of Natural Sciences of Madrid (MNCN) and at the Bavarian State Collection for

102 Anthropology and Palaeoanatomy, Munich (SNSB). The pharyngeal bones of the extant

103 *Barbus and Luciobarbus* species are scanned using X-ray computed tomography (μCT).

104 MicroCT images were taken using the microtomography systems NIKON XT H 160 at the

105 Scanning electron microscopy, analytic laboratories of MNCN. The scan settings of the

106 pharyngeal bones are introduced in Supplementary Material 1. The tomographic

107 reconstruction was performed using Avizo 9.0 software in the Tübingen University.

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109 **Systematic palaeontology**

110 Class Actinopterygii Cope, 1887

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111   Clade Teleosteomorpha Arratia, 2000

112   Order Cypriniformes Bleeker, 1859

113   Family Cyprinidae Rafinesque, 1815

114   Subfamily Cyprininae (Rafinesque, 1815) (sensu Yang et al., 2015)

115   Tribe Barbini Bleeker, 1859 (sensu Yang et al., 2015)

116   Genus *Luciobarbus* Heckel, 1843

117   Fig. 2a-c

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119   Below we provide short notes on the pharyngeal dentition of the genus *Luciobarbus* and

120   illustrate the teeth, using the following species *Luciobarbus longiceps* (MNCN E 54),

121   *Luciobarbus comizo* (MNCN 69304) and *Luciobarbus sclateri* (MNCN 69331). The

122   pharyngeal teeth of the studied *Luciobarbus* species are arranged on the pharyngeal bone in

123   three rows. The first (a) row contains four teeth, the second (b) three and the third row (c) two

124   teeth.

125   The pharyngeal tooth of the first row (a2-a5) are larger than the others in other two rows [since

126   the a1 tooth in the studied species is reduced (absent), the first tooth in the first (main) row a is

127   the a2 tooth]. The tooth at the a2 position is molariform with a small "hook" (*L. longiceps and*

128   *L. sclateri*) or has flat surface (*L. comizo*). The a3 tooth is the second large tooth of the main

129   row after the a2. The tooth foot is longer than the crown, the foot-crown border is well-

130   distinguished. The crown is posteriorly convexed. The grinding surface has a C-shape with the

131   hook on the top of it (not well developed at a3 of *L. longiceps* (Fig. 2b) and *L. sclateri* (Fig.

132   2c)). The teeth at the tooth positions a4 and a5 are spoon-shaped and compressed

133   anteroposteriorly. A hook is present at the laterodorsal corner of tooth, which projects anteriorly

134   over the grinding surface.

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135   The pharyngeal teeth at the second (b1-b3) and third (c1-c2) rows are smaller in comparison to

136   those of the first row. Within the studied three extant *Luciobarbus* species, the teeth of the

137   second and third rows can be grouped in two tooth morphogroups: 1) b1, c1 and 2) b2-b3 and

138   c2. The teeth of the first morphogroup (b1 and c1 tooth positions) have posteriorly bent rounded

139   tooth body. The foot-crown border is well distinguished. In anterior view, the grinding surface

140   ruptures slightly and possesses one or two enhancements. The grinding surface has a well-

141   developed, antrodorsally oriented hook on its tip. The second tooth morpogoups (b2, b3 and c2

142   tooth positions) are slender among all teeth. The tooth body widens distally and is compressed

143   anteroposteriorly. The grinding surface ruptures anteriorly and have one or two enhancements.

144   These teeth are also characterized by the presence of the hook on the top of the grinding surface.

145   In comparision to the teeth of the first tooth morphogroup, the grinding surface of these teeth

146   (b2, b3, c2) are more expanded.

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148   *Luciobarbus* sp.

149   Fig. 3a-g

150

151   **Material:** loc. Hancılı: tooth morphotype d3 – eight pharyngeal teeth (UU HAN 5304, 5305,

152   5334); tooth morphotype d5 – four pharyngeal teeth (UU HAN 5332–5333) and one

153   pharyngeal tooth (HAR1 5300); tooth morphotype d7 – 21 pharyngeal teeth (UU HAN 5313–

154   5316).

155   **Description and remarks:**

156   *Tooth morphotype d3.* The teeth are elongate to robust, with either straight or medially

157   benting tooth crown (Fig. 3f-g). The tooth crown possesses a hook, located either at the tooth

158   axis or lateral from it. The hook is anteriorly pointed. The grinding surface is located at the

7

159   anterior surface of the bone. It bears moderately high longitudinal eminence ("crest"), which

160   length varies depending on tooth crown height. The lateral margins of the grinding surfaces

161   are elevated, dorsally the margins reduce in height at the basis of the hook, building

162   constrictions. A similar morphology can be observed at the b1 and c1 tooth positions of some

163   extant *Luciobarbus* spp (Fig. 2a-c).

164   *Tooth morphotype d5.* The tooth is elongate and slightly curved along its longitudinal axis and

165   bends medially (Fig. 3d-e). The anterior surface of the tooth crown is concave. The grinding

166   surface is narrow. It extends lateromedially on the tooth dorsal surface and extends ventrally,

167   parallel to the medial margin of the tooth. The posterior margin of the tooth is significantly

168   higher than the anterior margin. It possesses an anteriorly directed reduced, pointy and

169   medially oriented hook, which is located slightly lateral from the tooth center. This tooth

170   morphotype can be found at the b2, b3 and c2 tooth positions of the recent genus *Luciobarbus*

171   (Fig. 2a-c).

172   *Tooth morphotype d7.* The tooth crown is spoon-shaped, anteroposteriorly compressed. Its

173   anterior surface is concave (Fig. 3a-c). The grinding surface has a C-shape and is located on

174   the dorsal tip of the bone. The lateral corner of the tooth possesses an anteriorly oriented

175   hook, which shows different degree of development in different individuals. The medial

176   corner of the grinding surface, in teeth with more pronounced hook, extends slightly ventrally

177   to the tooth foot. The anterior margin of the tooth (anterior wall of the grinding surface) is

178   lower than the posterior one. It has either convex or concave surfaces, corresponding to less or

179   more degree of tooth wearing. This tooth morphotype is characteristic for the genus

180   *Luciobarbus* and can be found at the a4 to a5 tooth positions (Fig. 2b).

181

182   Genus *Barbus* Cuvier and Cloquet, 1816 (sensu Yang et al., 2015)

8

183   Fig. 2d-f

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185   The morphology of the pharyngeal dentition of the genus *Barbus* follows using *Barbus*

186   *barbus* (SNSB SPAM-PI-00608), *Barbus meridonalis* (MNCN 19933) and *Barbus sacratus*

187   (MNCN GUI 17).

188   The pharyngeal teeth of the genus *Barbus* within studied three extant species are located in

189   three rows. Five teeth are present at the first (a) row, three in the second (b) and two in the

190   third (c) row. The teeth in the first row are larger than those in other two rows, excepting the

191   a1 tooth. The a1 tooth is small. It has wide tooth base which narrows distally. The tooth body

192   is compressed at the foot-crown border. The tooth crown is slightly narrower than the tooth

193   base. The grinding surface bears a hook on the top of it. The second tooth of the first row (a2)

194   has molariform morphology, somewhat comparable to the a1 tooth. Howerver, the a2 tooth is

195   several times larger than the a1. The teeth from the a3 to a5 tooth positions shows gradual

196   transition from the tooth morphology with robust teeth with thick crowns; rather small

197   grinding surface (a3) to tooth morphology with slender teeth, narrow crown with expanded

198   grinding surface. In all these tooth positions the teeth are bent, possesses hooks and smooth

199   grinding surface, which is delimitated by a high (a3, a4) or low (a4, a5) ridge.

200   The tooth body of the b1 tooth narrows distally. The crown is robust. The tooth body bents

201   slightly posteriorly at the foot-crown border. The grinding surface ruptures anteriorly and

202   possesse hook on the top. In anterior view, few grooves are observable on the grinding

203   surface. The b2 tooth has a straight tooth body, whereas the tooth crown is bent posteriorly.

204   The grinding surface is spilled with the hook on the top. Anteriorly the grinding surface is

205   ruptured. The morphology of the b3 and c2 teeth are similar and nearly same as the one of b2,

206   but these teeth are slender and they bend extremely posteriorly. Besides this, the grinding

207   surfaces of those teeth are narrower than that grinding surface of the b1. The c1 tooth has a

9

208   straight body as the b1, but it is shorter and smaller than the b1. The grinding surface is with

209   the hook on the top and has ruptures from anterior side.

210

211   *Barbus* sp.

212   Fig. 3h-n

213

214   **Material:** Loc. Hancılı: tooth morphotype d4 – 23 pharyngeal teeth (UU HAN 5307, 5307-1,

215   5308, 5309); tooth morphotype d6 – 28 pharyngeal teeth (UU HAN 5310-5312, 5321, 5335).

216   Loc. Harami 1: tooth morphotype d6 – one pharyngeal tooth (UU HAR1 5301).

217   **Description and remarks:**

218   *Tooth morphotype d6.* The teeth are elongate, rather slender and bent medially. They are

219   twisted along their longitudinal axis (Fig. 3h-l). The grinding surface is well expressed,

220   oriented and exposed anteriorly. It has rough surface composed of longitudinally running

221   crests. The grinding surface is encircled by a moderately high, thin margin. The lateral margin

222   of the grinding surface can be slightly serrated. The ventral wall of this margin in some teeth

223   can reduced so that the grinding surface flows in the tooth foot. The tooth crown possesses a

224   pointy hook directed anteriorly and projects over the grinding surface. This morphotype of the

225   pharyngeal tooth can be observed at the tooth positions a3-a5, b1-b3 of the extant genus

226   *Barbus* (Fig. 2d-e).

227   *Tooth morphotype d4.* The teeth are elongate, slightly bent, rather thick and robust. The tooth

228   crown is shorter than the tooth foot (Fig. 3m-n). The grinding surface is less developed than in

229   the Morphotype d6. It is limited mostly to the most dorsal portion of the tooth crown. The

230   grinding surface is rather smooth but still can possess few uneven structures. The grinding

231   surface is encircled mostly by high and sharp lateral walls possessing irregular margins. The

232   ventral wall can be reduced or well-developed. Dorsally, a pointy hook is projecting over the

233   grinding surface. The hook can be reduced or moderately developed, but never reaches the

234   size of that in the Morphotype d6. Its orientation varies in the available teeth from dorsally

235   directed to anteriorly directed ones. A comparable morphology can be found at the b2 tooth

236   position of the genus *Barbus* (Fig. 2d, f).

237

238   *Luciobarbus* vel *Barbus* sp.

239   Fig. 3o-v

240

241   **Material:** Loc. Hancılı: tooth morphotype d1 – 15 pharyngeal teeth (UU HAN 5300, 5301,

242   5321), toth morphotype d2 – 27 pharyngeal teeth (UU HAN 5302, 5303, 5306). Dorsal fin

243   spine morphotype s1 – seven unbranched last spine of the dorsal fin (UU HAN 5322 – 5324);

244   dorsal fin spine morphotype s2 – five unbranched last spine of the dorsal fin (UU HAN 5325

245   – 5328); dorsal fin spine morphotype s3 – two unbranched last spine of the dorsal fin (UU

246   HAN 5329 – 5330).

247   **Description and remarks:**

248   *Tooth morphotype d1.* The teeth are large and robust. In cross section, the teeth are either

249   rounded or lateromedially compressed (Fig. 3o-p). The tooth foot is always longer than the

250   tooth crown. The grinding surface is reduced and it has irregular surface. The margins of the

251   grinding surface are distinct and possess uneven (serration-like) structures. The hook is

252   moderately pointly and shows anterodorsal orientation. This tooth morphology is

253   characteristic for the b1 tooth position of *Barbus* genera (Fig. 2d-e).

11

254   *Tooth morphotype d2.* The teeth are rounded, robust, small in size, lateromedially compressed

255   (Fig. 3q-r). Both tooth foot and crown are short, in some of teeth a constriction marks the foot

256   crown boarder. The tooth crown has a molariform shape. The grinding surface is either fully

257   absent or extremely reduced. In those teeth with grinding surface, its surface is exposed

258   dorsally or anteriorly. The griding surface is rough and laterally boardered by low walls. The

259   hook is small and dorsally oriented. The described tooth morphology is characteristic of the

260   first tooth of the main row (a2) of *Barbus* and *Luciobarbus* genera (Fig. 3a, f).

261   *Morphotype s1.* The preserved spine fragments shows no serration at their posterior margins

262   (Fig. 3s). Slightly above the base of the spine, small posteroventrally pointed serrae apprears,

263   dorsally they become longer. The dorsal serrae are sharp and possess poorly-pronounced

264   edges. In lateral and medial views, the spine body is narrow, although in larger individuals, it

265   can widen slightly.

266   *Morphotype s2.* The spine body is slender. It possesses directly at its base short posteriorly

267   directed serrae (Fig. 3t-u). Dorsally, the serrae become longer and cylindrical in shape,

268   sometimes they can have curved shape and point with their tip dorsally. The serrae surfaces

269   do not possess any structures.

270   *Morphotype s3.* In lateral and medial views, the bodies of the spines are broad (Fig. 3v). The

271   ventral margin of the preserved portions of the bones nearly lacks serration. Only on the

272   preserved upper part (most probably, corresponding to the middle portion of the spine)

273   possesses very small serrae.

274   The described forms of the unbranched last spine of the dorsal fin clearly can be distinguished

275   from each other, including that of the Barbini indet, from the locality Kargı 2 by: 1) the shape,

276   orientation and surface structure of the serrae; 2) the position, where the serration appears on

277   the spine; 3) the dimensions of the spine body.

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278   In the neoichthyological studies the unbranched last spine of the dorsal fin and its serration is

279   broadly used for taxonomic proposes within different genera or among species of the same

280   genus (Kottelat and Freyhof 2007). Doadrio (1990) made an attempt to use the morphology

281   and peculiarities of this spine for intergeneric taxonomy, but, unfortunately, did not include

282   all barbin genera.

283   Taking into account, the presence of three different morphotypes of the unbranched last spine

284   of the dorsal fin and eight tooth morphotypes in the locality Hancılı, we can state about the

285   presence of at least three different barbin taxa, which could belong to the genera *Barbus*

286   and/or *Luiobarbus*. More comprehensive studies on recent barbin genera are necessary, to be

287   able to identify certain tooth morphologies or dorsal spine morphotypes to certain species.

288

289   Genus *Capoeta* Valenciennes, 1842 in Cuvier and Valenciennes, 1842

290

291   aff. *Capoeta* sp.

292   Fig. 3w-x

293

294   **Material:** Loc. Hancılı: tooth morphotype d8 – one tooth (UU HAN 5317).

295   **Description and remarks:** a single tooth is rather anterodorsally compressed and spoon-

296   shaped. The grinding surface is reduced and it is represented in a form of a narrow strip. The

297   anterior margin of the tooth (anterior wall of the grinding surface) is lower than the posterior

298   one. This morphology remind the morphology of the pharyngeal teeth of the genus *Capoeta*

299   (Ayvazyan et al. 2018) corresponding to the character stage α2 of the lateral outline and β5 of

300   the transverse cross section, however, so far a comparable morphology have not been reported

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301   for *Capoeta* (Ayvazyan et al. 2018). This tooth can be characterized by character stage β5 of

302   the transverse cross section, but no corresponding character stage α of the lateral outline is

303   found within the given character stages by Ayvazyan et el. (2018). However, so far a

304   comparable morphology have not been reported for *Capoeta* (Ayvazyan et al. 2018). Taking

305   into account these observations, as well as that the tooth is only one so far found, we prefer to

306   assign tentatively the tooth to the genus *Capoeta*.

307

308   Barbini indet.

309   Fig. 3y-ee

310

311   **Material:** Loc. Kargı 1: 15 pharyngeal teeth isolated or attached to pharyngeal bone (UU

312   KAR1 1300 – 1305). Loc. Kargı 2: 19 pharyngeal teeth isolated or attached to pharyngeal

313   bone (UU KAR2 1301 – 1302, 1304-1306), one unbranched dorsal fin ray (UU KAR2 1303).

314   Loc. Kesekoy: 116 pharyngeal teeth isolated or attached to pharyngeal bone (UU KE 5305 –

315   5310).

316   **Description:** the pharyngeal teeth are mediolaterally compressed, small-sized and slender.

317   The grinding surface is located at the anterior side of the tooth crown (Fig. 3z, dd, aa, bb). It is

318   narrow and dorsoventrally elongated. In short teeth, the grinding surface is shifted dorsally,

319   whereas in long teeth it corresponds to the half of the entire tooth length. The grinding surface

320   is surrounded by a moderately high crest, which displays uneven structures (serration-shaped)

321   at its lateral wall. A well-developed hook projected over the grinding surface. The hook is

322   variously oriented – dorsoanteriorly (Fig. 3y) to anteriorly (Fig. 3z). At the posterior tooth

323   positions (a1 or a2; Fig. 3y, 3aa) the teeth are more robust, the grinding surface is reduced.

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324   The preserved fragment of the last unbranched spine of the dorsal fin possesses three rather

325   robust, short, pointy, ventroposteriorly directed serrae. Their surface is smooth (Fig. 3ee).

326   **Remarks:** The morphology of the pharyngeal teeth is so far (to the authors knowledge)

327   unknown both in the fossil record and among recent species. The shape of the teeth and the

328   grinding surface has similarities with e.g. *Barbus* sp. from Gračanica, Bosnia and

329   Herzogovina, middle Miocene (Vasilyan in review). Besides the tooth material, the presence

330   of a fragment of the serrated last unbranched spine of the dorsal fin suggests also the presence

331   of barbin (Kottelat and Freyhof 2007) fishes in the locality Kargı 1. Due to lack of the

332   comprehensive studied and comparative material of the pharyngeal dentition of the recent

333   barbins, we prefer to assign these remains to the tribe Barbini.

334

335   Subfamily Leuciscinae Bonaparte, 1835

336   Genus *Leuciscus* Cuvier, 1816-1817

337   *Leuciscus* sp.

338   Fig. 3ff

339

340   **Material:** Loc. Hancılı: three isolated pharyngeal teeth (UU HAN 5318–5320).

341   **Description and remarks:** The teeth are lateromedially compressed (Fig. 3ff-1, 3ff-3). The

342   grinding surface is elongate, narrow and located at the anterior side of the tooth. Its surface is

343   nearly smooth with some rugosities. Its lateral margin possesses up to five denticles with

344   rounded tips. Ventrally they become smaller. The dorsal tip of the tooth terminates with an

345   anteriorly oriented hook. This morphology resembles that of the genus *Leuciscus* (Rutte

346   1962).

15

347

348   Cyprinidae indet.

349

350   **Material:** Loc. Keseköy: 17 fragments of the pharyngeal bones (UU KE 5302 – 5304).

351   **Remarks:** fragments of the pharyngeal bone, showing the places (if different sizes) of the

352   attachment of the pharyngeal teeth are present. One or two rows are observable on pharyngeal

353   bones, where the teeth have been arranged. Pharyngeal bones with dentition are widely known

354   in cypriniform fishes, specially in the family Cyprinidae (Winfield and Nelson 1991). Taking

355   into account the fact that in this locality only cyprinid remains are known, we tentatively

356   assign this material to the family Cyprinidae.

357

358   Teleostei indet.

359

360   **Material:** Loc. Kargı 1: 14 vertebrae (UU KAR1 1303). Loc. Kargı 2: ten vertebrae (UU

361   KAR2 1300). Loc. Keseköy: 17 atlases (UU KE 5301) and 128 trunk/caudal vertebrae (UU

362   KE 5300). Loc. Hancılı: one vertebra (UU HAN 5331).

363   **Description and remarks:** numerous vertebrae, including those from trunk and caudal

364   positions, as well as the atlases, have been found. They show amphicoelous morphology, the

365   atlases are anteroposteriorly strongly flattened. Any further identification of the material is

366   impossible.

367

368   Class Amphibia Linnaeus, 1758

16

369   Order Caudata Scopoli, 1777

370   Family Salamandridae Goldfuss, 1820

371   Genus *Salamandra* Garsault et al., 1764

372

373   *Salamandra* sp.

374   Fig. 4a-l

375

376   **Material:** Loc. Harami 1: one caudal vertebra (UU HAR1 5055). Loc. Bağiçi: one trunk

377   vertebrae (UU BAG 1002) and two humeri (UU BAG 1003, UU BAG 1004).

378   **Description:** A relatively well preserved trunk vertebra (UU BAG 1002) is present from the

379   locality Bağiçi (Fig. 4a-e). It is remarkable with its large size; the centrum length measures 6

380   mm. In lateral view, the neural arch and centrum are dorsoventrally flattened, due to this they

381   are low and broad. The opisthocelous centrum is flexuous. The praezygapophysis is

382   connected with the parapophysis by a posteroventrally directed accessory allar process,

383   whereas the postzygapophysis is connected with the diapophysis by a horizontally directed

384   dorsal lamina. In anterior and posterior views, the neural canal is round and narrow. Several

385   foramina of different sizes are piecing the bases of the prezygapophysis. The neural spine is

386   missing, but the neural arch possesses traces of its base, suggesting that it reached nearly the

387   anterior tip of the neural arch.

388   The anterior portion of a caudal vertebra (UU HAR1 5055) is preserved (Fig. 4f-i). In ventral

389   view, the lateral edges of the vertebral centrum possess the bases of the haemapophysis. The

390   centrum possesses an anterior condyle, suggesting a probable opisthocelous morphology of

391   the vertebra. In anterior view, the neural arch is rounded, only its base is flat. Distinct

17

392 subprezygapophyseal formina are observable at the base of the praezygapophysis. In lateral

393 view, the neural spine is visible which arises behind the short zygosphene.

394 Distal portions of two humeri are present in the locality Bağiçi. The bones are lateromedially

395 flattened. The lateral surface of the distal tip of the humeri possesses a longitudinal and rather

396 shallow olecranon fossa. The shallow cubital ventral fossa of the humeri is observable on the

397 medial surface of the bones. It has semilunar outline. The capitum (radial condyle) is located

398 at its base (UU BAG 1004, fig. 4j) or is missing (UU BAG 1003, fig. 4k-l). The humeri, at

399 their mid-diaphyseal position possesses a small remnant of the humeral dorsal crista. The

400 longest preserved humerus fragments (representing the distal half of the bone) measures 6

401 mm, suggesting the humerus had the length of around 11-12 mm.

402 **Remarks:** The large size of the bones and the observed morphology, i.e. dorsoventrally

403 flattened, broad and robust trunk vertebrae; caudal vertebra with round neural canal and

404 neural spine; and the general morphology of the humeral fragments, agrees with the genus

405 *Salamandra* (Estes and Hoffstetter 1976; Rage 1984). Also the large bone sizes agrees with

406 that of the *Salamandra sansaniensis* (Estes and Hoffstetter 1976; Rage and Hossini 2000).

407 Nevertheless, the lack of the studies on vertebral morphology of all recent *Salamandra*

408 species, including that of the largest representative of the genus, i.e., *Salamandra*

409 *infraimmaculata,* makes the reliable identification of the fossil remains impossible.

410

411 Order Anura Fischer, 1813

412 Family Pelobatidae Bonaparte, 1850

413

414 Pelobatidae indet.

18

415   Figure 4m–v

416

417   **Material:** Loc. Harami 1: one fragmentary maxilla (UU HAR1 5051). Loc. Keseköy: one

418   fragmentary maxilla (UU KE 5006). Loc. Hancılı: three frontoparietals (UU HAN 5051–

419   5053). Loc. Bağiçi: one fragmentary maxilla (UU BAG 1001).

420   **Description:** All maxillae are fragmentary. The labial surface bears the pit-and-ridge

421   ornamentation. The specimen UU HAR1 5051 (Harami 1; Fig. 4m, n) represents the smallest

422   individual; it is rather weathered, due to which its surface structures are poorly pronounced. In

423   UU KE 5006 (Keseköy; Fig. 4q, r), the bone is provided with the dorsal, posterodorsally

424   inclined and rather pointed zygomaticomaxillar process, and with the posterior process. Its

425   end is most probably undamaged (judging by the intact zygomaticomaxillar process),

426   suggesting a broad contact with a short but robust quadratojugal. Between both processes, the

427   margin of the bone is concave. In lingual view, UU KE 5006 (loc. Keseköy) and UU BAG

428   1001 (loc. Bağiçi) possess a moderately developed pit behind the pterygoid process (Fig. 4p,

429   r). The pterygoid process is the well prominent posterior termination of the horizontal lamina

430   roofing the tooth row dorsally. The lamina horizontalis is represented by a rather sharp and

431   not high flange in UU HAR1 5051 (loc. Harami 1), or by a distinct, robust flange with a

432   rounded surface in UU KE 5006 (loc. Keseköy) and UU BAG 1001 (loc. Bağiçi). The latter

433   maxilla, however, differs from that from Keseköy in absence of the pterygoid process and in

434   subdivided zygomaticomaxillar process. Unless these two features are artifacts caused by

435   fossilization, they could represent significant taxonomic differences.

436   Two frontoparietals from Hançcılı roughly correspond to one another in their general shape

437   and size (Figs. 4s–v). They are paired, which means that they were in contact with their

438   counterparts from the opposite side in a slightly serrated median suture. Their orbital margin

439   is nearly straight or only slightly concave, and it is deflected ventrally. Consequently, the

19

440 tectum supraorbitale is poorly developed and does not extend into the orbit. The margo

441 orbitalis ends posteriorly in a lateral process, which is discernible only because the margin of

442 the frontoparietal breaks here and runs posteromedially. There, it terminates in a process

443 which represents the most posterior part of the frontoparietal. The margin then turns sharply

444 and runs anteromedially towards the posterior end of the median suture. This suggests that

445 posteromedial margins of both frontoparietals enclosed nearly rectangular, wedge-like space.

446 The frontoparietal incrassation on the ventral surface of the bone is typically pelobatid-like,

447 which means that it is undivided, broad posteriorly and narrower anteriorly. In a living

448 animal, it fitted in a large fenestra in the roof of the endocranial braincase. The dorsal surface

449 of the frontoparietal is covered by sculpture; that in UU HAN 5051 (Figs. 4s, t) is represented

450 by indistinct mounds, arranged radially from the center of the bone, that in UU HAN 5052

451 (Figs. 4u, v) is pustular in the middle, with indistinct radial mounds in the peripheral parts of

452 the bone.

453 **Remarks**: General morphology of the maxilla, together with morphology of the

454 frontoparietals that corresponds to a postmetamorphic but not-yet ultimate developmental

455 stage of the Pelobatidae, and the pit-and-ridge type of ornamentation, is a combination of

456 characters that indicate relations to the Pelobatidae (Roček 1981), but do not allow

457 identification at the generic level (see Discussion).

458

459 Family Bufonidae Gray, 1825

460

461 Bufonidae indet.

462 Figure 4w-y

463

20

464   **Material:** Loc. Keseköy: one ilium (UU KE 5001).

465   **Description:** The fragment of this ilium measures 4.2 mm at its highest portion,

466   corresponding to the highest point of the dorsal tubercle and lowest preserved point of the

467   pars descendens. The anterior portion of the acetabulum and posterior part of the iliac shaft

468   are preserved. The dorsal tubercle is pointy and well-pronounced, it is relatively high and

469   broad. It is composed of two or three lobes (Fig. 4w). The anterior border of the acetabular

470   rim is high. The pars descendens is moderately high. It narrows ventrally. A small

471   preacetabular fossa pierces the anterodorsal corner between acetabulum and pars descendens.

472   The iliac shaft has rounded outline and flat surface. It does not possess any structures. (Fig.

473   4w).

474   **Remarks:** The preserved ilium can be assigned to the family Bufonidae based on

475   combination of the following characters: pointy, bi-(tri-)lobed dorsal tubercle, flat medial

476   surface, the iliac shaft is smooth and does not possess a dorsal crest (Blain et al. 2010). The

477   family Bufonidae represents a group with numerous species distributed in both Old and New

478   Worlds (Frost 2014). The morphology of the ilium is broadly uniform in many forms (Sanchíz

479   1998; Tihen 1962) and other skeletal elements are necessary for closer identification. The

480   comparison with both recent and fossil Western Asian bufonids reveals strong similarities

481   with its morphology and size to the genus *Pseudepidalea* (Blain et al. 2010) and clearly can

482   be separated from the genus *Bufo*. Due to the incomplete preservation of the ilium and the

483   lack of further skeletal elements as well as poor knowledge of the osteology of the family, we

484   prefer to name the fossil bone from the locality Keseköy as Bufonidae ident. (?

485   *Pseudepidalea*).

486

487   Family Alytidae Fitzinger, 1843

21

488   Genus *Latonia* Meyer, 1843

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3   489
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5
6   490   *Latonia* sp.
7
8
9   491   Figure 5
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12 492
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16 493   **Material:** Loc. Kargı 1: four cranial bones (UU KAR1 1001 - 1005), seven maxillae (UU
17
18 494   KAR1 1006 -1011), one atlas (UU KAR1 1012), one vertebra (UU KAR1 1013), one costa
19
20 495   (UU KAR1 1014), two sacral vertebrae (UU KAR1 1015–1016), one ilium (UU KAR1 1054),
21
22
23 496   two urostyles (UU KAR1 1017–1018), one coracoid (UU KAR1 1019), one humerus (UU
24
25 497   KAR1 1020), two radioulnae (UU KAR1 1021–1022). Loc. Kargı 2: eight maxillae (UU
26
27
28 498   KAR2 1006–1012), three angulars (UU KAR2 1013–1015), one atlas (UU KAR2 1013), one
29
30 499   vertebra (UU KAR2 1014), two transverse processes (UU KAR2 1015, 1016), two costae
31
32
33 500   (UU KAR2 1017, 1018), 11 ilia (UU KAR2 1022 –1032), three urostyles (UU KAR2 1019 –
34
35 501   1021), two coracoids (UU KAR2 1033, 1034), six humeri (UU KAR2 1035 –1040). Loc.
36
37
38 502   Kargı 3: three maxillae (UU KAR3 1001 –1003), one ilium (UU KAR3 1207). Loc. Harami
39
40 503   1: nine maxillae (UU HAR1 5062, 5062-1, 5062-2, 5062-3). Loc. Harami 3: one maxilla (UU
41
42 504   HAR3 5052), one angular (UU KAR3 5012), two scapulae (UU HAR3 5051), one sacral
43
44
45 505   vertebra (UU HAR3 5013), one costa (UU HAR3 5014), one ilium (UU HAR3 5015), one
46
47 506   ischium (UU HAR3 5016). Loc. Keseköy: three anglars (UU KE 5012–5014), 71 maxillae
48
49
50 507   (UU KE 5012–5019, 5055–5057), two atlases (UU KE 5020–5021), six scapulae (UU KE
51
52 508   5022–5025, 5051), four costae (UU KE 5026–5029), six transverse processes (UU KE 5030 –
53
54
55 509   5035), 49 urostyles (UU KE 5052–5053). Loc. Hancılı: two frontoparietals (UU HAN 5054,
56
57 510   5055), four maxillary fragments (UU HAN 5056), one parasphenoid (UU HAN 5058), three
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62   22
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511   vertebrae (UU HAN 5057). Loc. Çandır: six maxillae (UU CD 5001), three cranial bones (UU

512   CD 5004), one atlas (UU CD 5002), three vertebral centra (UU CD 5003).

513   **Description and remarks**: The frontoparietal (UU HAN 5055) (Fig. 5a, b) preserved only its

514   anterolateral portion, which is, however, important for determination of the genus (Roček

515   1994). Its dorsal surface is horizontal, extending into the orbit by a thin supraorbital tectum.

516   The dorsal surface in that part is covered by antero-posteriorly oriented rounded ridges,

517   typical for *Latonia gigantea* (Roček 1994; fig. 7F). The frontoparietal incrassation in the

518   middle portion of the inner surface of the bone is depressed, but rimmed with a prominent

519   crista, which was part of the contacting surface with the braincase in living animal. The

520   scapula (UU HAR3 5051) (Fig. 5c, d) has incomplete anterior margin, so its shape cannot be

521   restored with certainty. It seems that it was rather short and squarish. The maxillae are

522   preserved as short fragments (Fig. 5g-l) but a typical morphology of its inner surface, with the

523   sulcus for the nasolacrimal duct, which is manifested also on the dorsal margin of the bone, is

524   a typical feature of *Latonia*. On the lateral surface of the ilium, at the level of the anterior

525   margin of the acetabulum, there is a typical triangular depression which in its most posterior

526   part is pierced by several foramina (filled with whitish sediment in Fig. 5m). This is also a

527   typical feature of the genus *Latonia*. Finally, opisthocoelous atlas, although with neural arches

528   broken off, seems to be another evidence of *Latonia*. However, it differs from the atlas of

529   *Latonia* from the middle Miocene of Sansan and La Grive St. Alban in that both cotyles are

530   interconnected (Fig. 5f). Morphology of the cranio-vertebral articulation is often considered

531   important in anuran taxonomy, but nothing is known about individual and developmental

532   variation of this anatomical character.

533   The material is too fragmentary for more precise taxonomic evaluations, but the mentioned

534   fragments of the frontoparietal (UU HAN 5055), maxilla (UU HAR1 5062-1) and ilium

535   represent doubtless evidence of *Latonia* in the sample (Roček 1994).

23

536

537   Family Palaeobatrachidae

538   Palaeobatrachidae indet.

539

540   Figures 6, 7

541   **Material:** Loc. Kargı 1: one angular (UU KAR1 1052), two neural arches (UU KAR1 1053).

542   Loc. Kargı 2: one angular (UU KAR2 1104), two scapulae (UU KAR2 1105), one humerus

543   (UU KAR2 1001). Loc. Harami 1: one maxilla (UU HAR1 5059), six sphenethmoids (UU

544   HAR1 5005 – 5007, 5060), eight angulars (UU HAR1 5001 – 5004, 5061), one scapula (UU

545   HAR1 5009), one coracoid (UU HAR1 5010), 25 humeri (UU HAR1 5011 – 5035), one

546   illium (UU HAR1 5008), two neural arches (UU HAR1 5054). Loc. Harami 3: one

547   sphenethmoid (UU HAR3 5003), eight humeri (UU HAR3 5004 – 5011), two angulars (UU

548   HAR3 5001 – 5001). Loc. Keseköy: five maxillae (UU KE 5054), one urostyle (UU KE

549   5011).

550   **Description:** The largest of the three sphenethmoids from Harami 1 is UU HAR1 5005 (Fig.

551   6a-c); its widest diameter is 5.65 mm, so it represents a medium-sized individual, probably

552   not exceeding SVL of 60 mm. Its lateral processes display spongy bone, but are symmetrical

553   and not too prominent beyond the lamina supraorbitalis; this suggests that they were

554   completed by cartilage in living animal and exposed spongy bone is not an artifact. Similarly,

555   the anterior median process (i.e., ossified part of the septum nasi) is not too much prominent

556   beyond the floor of the nasal capsules (i.e., ossified part of the solum nasi). The anterior

557   margin of the floor of the nasal capsules is almost straight, thick, and was undoubtedly

558   extended by cartilage, whereas the anterior margin of the roof of the nasal capsules (i.e.,

559   ossified part of the tectum nasi) is deeply concave (Fig. 6a), thin, and was not completed by

24

560   cartilage (Fig. 6c). The articular facet for the frontoparietal is slightly depressed due to

561   elevated margins, covered by a few irregular and indistinct grooves. The borderline between

562   the contact facets for the nasals and the frontoparietal indicates the shape of the anterior

563   margin of the frontoparietal, which extended in a median point. On the right side, the

564   posterior margin of the lateral braincase wall is covered by periost, which suggests its natural

565   antero-posterior extent. This, compared with the maximum width of the bone, suggests that

566   the sphenethmoid was not elongated, but approximately as long as broad. The bottom of the

567   braincase reached posteriorly at least the same level as the lateral walls or more, the roof is

568   only moderately incised anteriorly (incisura semielliptica *sensu* Hossini and Rage 2000). The

569   ventral surface of the bottom of the braincase is rimmed by a rounded ridge on either side; the

570   ridges are at the transition between the bottom and lateral walls of the braincase, and delimit

571   laterally the groove-like articular facet for the parasphenoid. The braincase is connected with

572   each nasal capsule by a canal for the olfactorius nerve (canalis olfactorius). The medial

573   section of the ossified part of the postnasal wall is pierced by a canal for the medial branch of

574   the ophthalmic nerve (ramus medialis nervi ophthalmici), which enters the nasal capsule

575   dorsolateral to the orifice of the canalis olfactorius (Fig. 6c). Although the orbitonasal canal is

576   ellipsoid in cross-section, the longest diameters of both canals are about the same.

577   In contrast to UU HAR1 5005 (Fig. 6a-c), UU HAR1 5006 (Fig. 6d-f) is small, with its widest

578   diameter about 3.6 mm; this should correspond to an individual with SVL of about 40 mm.

579   Although this sphenethmoid is rather worn out both anteriorly and posteriorly (hence shorter

580   than broad), the nasal facets and the groove for the parasphenoid are similar to UU HAR1

581   5005. Principal differences between both bones are the narrow contact facet for the

582   frontoparietal (Fig. 6d) and deeply V-incised incisura semielliptica, which reaches up to the

583   level of the partition between both olfactory canals. Also the canals entering the nasal

584   capsules are rather different (canalis olfactorius is much larger than that for the medial branch

585   of the ophthalmicus nerve). On the left side of the bone, both fuse with one another close to

25

126

586   their entrance into the nasal capsule, but this may be a matter of individual variation. The

587   most important is that both the floor and the roof of the nasal capsules were completed by

588   cartilage in life, which rather suggests that the differences between both sphenethmoids are

589   due to degree of development, rather than indication of two different species. Alternatively,

590   they might be a result of developmental heterochrony of two closely related species, which is

591   the case with recent *Bombina bombina* and *B. variegata*.

592   A relative complete maxilla is from Harami 1 (UU HAR1 5059; Fig. 6o, p). It is obvious that

593   the tooth row terminates below the posterior base of the frontal process, that the most

594   posterior tooth position is of the same size as the more anterior ones, and that the orbital

595   margin is a flat, horizontal plate extending labially in a distinct ledge (marked by arrow in

596   Fig. 6p). In addition, the frontal process is clearly inclined towards the anterior.

597   The angulars UU HAR1 5004 (Fig. 6g), UU HAR1 5002 (Fig. 6h), and UU HAR1 5001 (Fig.

598   6i, j) all have the dorsoventrally compressed coronoid process, which continues posteriorly by

599   a long, horizontal ridge extending to the dorsomedial margin of the bone where it meets with

600   the gradually lowering medial wall of Meckel's groove (marked by arrow in Fig. 6g) whereas

601   anteriorly, the coronoid process terminates rather abruptly. Besides, all these angulars have a

602   tubercle or protuberance on the dorsal edge of the medial wall of the Meckel's groove, and a

603   smooth, depressed area for the adductor mandibulae externus muscle. There is some variation

604   in shape of the coronoid process – it may be divided by a delicate ridge or crista into the

605   anterior and posterior flat or slightly depressed areas, or can be a single convexity. Right

606   angular UU HAR1 5003 (Fig. 6k, l), however, is different, especially in the position and

607   shape of the coronoid process. In medial view (Fig. 6l), the coronoid process has a markedly

608   oblique position, with its longitudinal axis slanting down posteriorly, so its posterior margin is

609   located almost at the level of the ventral surface of the bone. In the dorsal aspect, it is

610   markedly prominent medially. Besides, the medial wall of the Meckel's groove is not

611   extended dorsally. It rather recalls MNHN LAU 11 from the early Miocene of Laugnac

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612   (Hossini and Rage 2000, fig. 1-2). Two angulars from Harami 3 are less well preserved (Fig.

613   6m, n), but they fit into variation range of the angulars from Harami 1 (and of

614   *Palaeobatrachus* in general).

615   One fragmentary scapula (UU HAR1 5009) from Harami 1 is available (Fig. 7a–c). Both its

616   anterior and posterior margins are concave and its distal (suprascapular) portion is narrower

617   than the proximal part. As in other Palaeobatrachidae, the glenoidal and acromial parts with

618   their articular cavities are separated by a deep depression (Fig. 7c), but not by a complete

619   incisure into the outlines of the bone. The urostyle (UU KE 5011) from Keseköy is rather

620   worn out, such that both condyloid fossae lost their lateral margins and the intercondyloid

621   process seems to be remarkably prominent anteriorly (Fig. 7f), but this can be due to

622   preservation. On the other hand, two longitudinal, parallel ridges close to the midline on the

623   dorsal surface of the bone, typical for *Palaeobatrachus*, are well seen both in dorsal and

624   anterior aspects. The ilium (UU HAR1 5008) from Harami 1 markedly differs from the ilia of

625   other Palaeobatrachidae by reduced pars ascendens (even if it can be partly damaged in this

626   part), extremely large acetabulum (well seen in medial aspect; Fig. 7e), indistinct tuber

627   superius which is neither prominent dorsally nor laterally, and by a spike-like spina iliaca

628   (marked by arrow in Fig. 7e).

629   The humeri (Fig. 7h-u) are the most numerous among all skeletal elements, even if none of

630   them is complete. They vary in their size, proportions of the medial and lateral epicondyles,

631   and by relative size and position of the caput humeri. In great majority of them there is no

632   cubital fossa, so the caput humeri is continuous with the ventral surface of the humeral shaft,

633   but it seems that in large individuals there is a narrow, semilunar depression parallel with the

634   proximal surface of the caput humeri (Fig. 7h). This would suggest that relatively large

635   individuals bent the fore limb in the elbow joint, such that the capitulum of the radioulna

636   inserted into this depression, whereas in smaller (= younger) individuals the fore limbs were

637   stretched forwards, as is the case with swimming *Xenopus*. Besides this speculative

27

638   interpretation, no taxonomic conclusions can be inferred from morphological variation of the

639   humeri.

640   **Remarks:** The sphenethmoid is the ossified portion of the anterior part of the braincase with

641   adjacent parts of the septum nasi and postnasal walls, so the degree of its ossification may be

642   used in assessing relative ontogenetic stages. In fully developed adults, ossified parts of

643   postnasal walls, septum nasi, and braincase walls should be more extensive, compared with

644   their cartilaginous portions, than in juveniles of the same species. In *Palaeobatrachus*, this

645   may be combined with fusion of the sphenethmoid with some dermal bones, like the

646   frontoparietal and parasphenoid. The maxilla is remarkable by obviously reduced number of

647   tooth positions, which is characteristic for Pliocene and Pleistocene species of

648   *Palaeobatrachus*, such as *P. eurydices* and *P. langhae*, whereas Oligocene taxa have higher

649   number of small teeth. The scapula seems to be different from those in Oligocene species by

650   its markedly concave anterior margin and narrow suprascapular portion; for instance,

651   *Palaeobatrachus* from Enspel has the anterior margin straight, meeting with the suprascapular

652   margin in a right angle.

653

654   Anura indet.

655   Figures 4z-cc

656

657   **Material:** loc. Kargı 1: one maxilla fragment (UU KAR1 1051). Loc. Harami 1: three

658   radioulnae (UU HAR1 5052), one neural arch (UU HAR1 5053), three phalanges (UU HAR1

659   5056–5058). Loc. Bağiçi: one radioulna (UU BAG 1203).

660   **Description:** Two different morphotypes of phalanges are present in Harami 1. Those of the

661   morphotype A (one phalanx, UU HAR1 5056, Fig. 4bb) are robust and triangular, the bulb is

28

662   large and possesses well-developed rugosities on its surface. The phalanges of the

663   morphotype B (two phalanges, UU HAR1 5057, 5058, Figs. 4cc) are shorter but slender, the

664   bulb is rounded with less rugosities than in the morphotype A.

665   The fragment of a maxilla (UU KAR1 1051) with both teeth and tooth pedicles is preserved

666   from the locality Kargı 1 (Fig. 4z-aa). The teeth are bicuspid and inclined lingually at their

667   tips. The labial cusps are smaller than the lingual ones. Its labial surface is smooth with few

668   small nutrition foramina.

669   **Remarks:** The phalanges can be clearly assigned to the Anura based on their morphology

670   (Kamermans and Vences 2009), but any precise identification is impossible. The tooth

671   morphology of the maxilla from Kargı 1 resembles that of e.g. Ranidae, Alytidae,

672   Pelobatidae, Bombinatoridae, Hylidae (Greven and Laumeier 1987; Greven and Ritz

673   2008/2009). Other families, such as Palaeobatrachidae (with non-pedicellated and

674   monocuspid teeth, lack of knobs between teeth) (Wuttke et al. 2012), Bufonidae (no teeth on

675   maxilla) (Sanchíz 1998) can be excluded. Taking this into account, this maxilla can be

676   considered only as Anura indet.

677

678   Class Reptilia Laurenti, 1768

679   Order Squamata Oppel, 1811

680   Family Anguidae Gray, 1825

681   Genus *Pseudopus* Merrem, 1820

682   *Pseudopus* sp.

683   Figure 8a-b

684

29

685 **Material:** Loc. Kargı 1: one jaw fragment (UU KAR1 1205). Loc. Kargı 2: one tooth (UU

686 KAR2 1204).

687 **Description and remarks:** A jaw fragment with two teeth (UU KAR1 1205, Fig. 8a) and an

688 isolated tooth (UU KAR2 1204, Fig. 8b) are preserved. The teeth are robust, cylindrical to

689 conical, subpleurodont and stout. Lateromedially they are slightly compressed. There are

690 distinct striae observable on the crown. The lateral and medial surfaces of the crowns possess

691 striae directed vertically (to the tooth axis). The anterior and posterior edges possess

692 moderately (UU KAR1 1205) or weakly developed (UU KAR2 1204) cutting edges. The

693 observed morphology on the available tooth material allows its identification as *Pseudopus*

694 (Klembara et al. 2014). Also the rather molariform morphology of teeth suggest their origin

695 from the posterior part of the jaws (Klembara et al. 2014).

696

697 *Ophisaurus* sp.

698 **Material:** Loc. Kargı 2: five trunk vertebra (UU KAR2 1201).

699 **Description and remarks:** These remains represent additional bone remains to the earlier

700 published material of *Ophisaurus* sp. in Čerňanský et al.(2017). See description and

701 discussion therein.

702

703 Anguinae indet.

704 Figure 8c-e

705

30

131

706   **Material:** Loc. Kargı 2: one right dentary (UU KAR2 1203), two osteoderms (UU KAR2

707   1202). Loc. Kargı 3: two osteoderms (UU KAR3 1202). Loc. Çandır: 22 osteoderms (UU CD

708   5207, 5208), one vertebra (UU CD 5209). Loc. Bağiçi: three osteoderms (UU BAG 1200).

709   **Description and remarks:** An anterior portion of a dentary (UU KAR1 1203, Fig. 8c) is

710   available from the locality Kargı 2. The labial surface is smooth, possessing only three mental

711   foramina. In lingual view, five tooth positions are visible. The base of the preserved tooth

712   pedicles are pierced by small foramina. The subdental shelf (sensu Evans 2008; dental crest

713   sensu Klembara et al. 2014) is low and have rounded surface. The dental lamina is more than

714   twice as high as the subdental shelf. The Meckelian groove is narrow and exposed ventrally.

715   The symphysis projects linguoposteriorly. The preserved anterior portion of the dentary

716   without teeth, can be identified as Anguinae indet. based on the ventrally exposed Meckelian

717   groove and general shape of the bone (Klembara et al. 2014).

718   Besides the herein described jaw material, we list in the material a further vertebra and

719   osteoderms representing an additional material to the already published remains of anguins

720   from Turkish localites (Čerňanský et al. 2017).

721

722   Family Lacertidae

723   Lacertidae indet. 1

724   Figure 8f-h

725

726   **Material:** Loc. Kargı 1: one dentary (UU KAR1 1206).

727   **Description:** The dentary is partially preserved with 14 tooth positions. The bone is robust,

728   the subdental shelf is thick, massive, and widens anteriorly (Fig. 8h). The Meckelian groove

31

729 opens lingually. The teeth are pleurodont, bicuspid, short, robust. They are located close to

730 each other. Their apices are oriented posterolingually. The tooth crown possess a large main,

731 blunt casp and a small mesial (anterior) caps. The main caps shows at its lingual surface

732 vertical striae terimating apically at the caps tip. The dental lamina is relatively high, reaching

733 the bases of the tooth crown (Fig. 8f). The labial surface of the dentary, is pierced by five

734 small-sized mental foramina, which are arranged in a row and located in the lower half of the

735 bone.

736 **Remarks:** see Remarks of Lacertidae indet. 4

737

738 Lacertidae indet. 2

739 Figure 8i-o

740

741 **Material:** Loc. Keseköy: ten maxillae (UU KE 5200 – 5202), 15 dentaries (UU KE 5203 –

742 5206, 5213). Loc. Çandır: one dentary (UU CD 5200).

743 **Description:** The dentary is slender. The subdental shelf is flat posteriorly to rounded

744 anteriorly (Fig. 8j). It has nearly the same height along its length but at the 9-10th tooth

745 positions, it increases in height. The ventral margin of the bone and the subdental shelf run

746 close and subparallel to each other. The Meckelian groove is lingually exposed, but anteriorly

747 it changes its orientation rather ventrally (Fig. 8j, 8l). The symphyseal part of the bone is

748 reduced. The dentition is remarkably heterodont: four different tooth morphologies can be

749 observed.

750 The first morphotype resembles that of the skinks. Located at the first tooth positions (1-5th

751 positions in UU KE 5213, Fig. 8l, 8n; 1(?)-7th positions in UU KE 5206, Fig. 8j, 8k), the

32

133

752 teeth are slender, monocuspid and pointed. At the lingual surface, the tooth crown possesses

753 vertical striae, directed to the tooth tip. The crista lingualis and crista labialis are separated

754 (not connection with carina intercuspidalis) and run parallel to each other. The former one in

755 less pronounced than the former. The antrum intercristatum is broad. The crista labialis is

756 slightly projecting over the antrum intercristatum.

757 The second morphotypes is characterised by rather short, robust bicuspid teeth, with rounded

758 crowns. The lingual surface of the crown possess vertical striae fusing at the tip of the tooth.

759 The main casp is larger and higher than the lateral one. In the tooth row, the second

760 morphotype can be observed posteriorly from the teeth of the first morphotype (8th tooth

761 position, UU KE 5206, Fig. 8k) and on maxilla (UU KE 5200, Fig. 8i).

762 The third tooth morphotype resembles the typical lacertid morphology, widely found in

763 European Neogene and recent forms. The tooth is bicuspic, cylindrical, with sharp apex. The

764 tooth crown composes of a large main caps and small lateral (anterior) casp. The lingual

765 surface of the tooth crown is nearly flat or bears weakly-developed vertical striae. The third

766 morphotype can be observed in the middle or posterior half of the dentary (15th tooth

767 positions in UU KE 5200, Fig. 8j and UU KE 5213, Fig. 8l).

768 The fourth morphotype is represented by short and robust tricuspid teeth. The crown has

769 smooth surface. It is composed of the main (central) large cusp and two anterior and posterior

770 cusps. The anterior cusp is slightly larger than the posterior one (last tooth positions, UU KE

771 5219, fig. 8o).

772 The teeth are oriented in the first three tooth positions anteriorly. Posteriorly in the tooth row

773 the teeth change their orientation to posterior direction. In labial view, the dentary has smooth

774 surface and possess at least five mental foramina, which are arranged in a row. The first

775 foramen is located very close to the symphysis and opens anteriorly. Three first foramina are

33

776   located close to each other (at the 1st, 4th and 7th tooth positions correspondingly) whereas

777   the last two ones 11th and 16-15th tooth positions correspondingly (UU KE 5213, Fig. 8l-n)

778   **Remarks:** see Remarks of Lacertidae indet. 4

779

780   Lacertidae indet. 3

781   Figure 8p-r

782

783   **Material:** Loc. Keseköy: eight maxillae (UU KE 5207 – 5210), 16 dentaries (UU KE 5211 –

784   5212, 5214 – 5216, 5220). Loc. Hancılı: one maxilla (UU HAN 5200). Loc. Çandır: four jaw

785   bones (UU CD 5201, 5210).

786   **Description:** The dentaries are fragmentary preserved. The subdental shelf is flat. The

787   Meckelian groove exposes lingually. All teeth including the posterior ones are bicuspid,

788   cylindrical, with sharp apices. The main cusp is large and pointed, it possesses at its lingual

789   surface weakly-developed vertical striae. The small lateral (anterior) cusp is significantly

790   lower than the main one. All preserved teeth are oriented posteriorly. In labial view, the bone

791   possesses four rather large mental foramina (UU KE 5215, Fig. 8aa), which are located in the

792   preserved specimen at the first 12 tooth positions.

793   **Remarks:** see Remarks of Lacertidae indet. 4.

794

795   Lacertidae indet. 4

796   Figure 8s-u

797

34

798   **Material:** Loc. Çandır: one dentary (UU CD 5202).

799   **Description:** The preserved dentary is robust. The dental shelf is high with a flat surface. The

800   symphysis is reduced. The teeth are arranged close to each other. The dentition is heterodont.

801   At the sixth tooth position, the tooth crown is bicuspid, with large main cups and small

802   anterior cusp (Fig. 8u). At the seventh tooth position, the tooth is thick; the tooth crown is

803   bicuspid with clearly separated pointy cusps, which are nearly similar in height. The 9-10th

804   tooth positions, the tooth crowns are monoscuptid, with rounded, spoon-shaped cusp. All

805   teeth have smooth lingual surfaces. The Meckelian groove is narrow and opens

806   linugoventrally, anteriorly it turns more ventrally. The labial surface of the bone is pierced by

807   six, closely situated, rather large mental foramina. Among them, the first one is located

808   slightly ventrally from the main row (Fig. 8t).

809   **Remarks:** The described four forms of lacertid lizards can be clearly distinguished from each

810   other by several characters:

811   1) the mental foramina:

812   a. in Lacertidae indet. 1 they are small in size, arranged at the ventral half of the bone and not

813   very far from each other;

814   b. in Lacertidae indet. 2 the foramina are larger than in Lacertidae indet. 1, and the first three-

815   four foramina are closely located to each other, a further foramen is located significantly far

816   from the rest;

817   c. in Lacertidae indet. 3 the foramina are larger and they are arranged rather close to each

818   other in Lacertidae indet. 2;

819   d. the mental foramina are small and located very close to each other in Lacertidae indet. 4.

820   2) dentition:

35

821   a. Lacertidae indet. 2 and 4 have heterodont dentition with four and (at least) two

822   morphotypes correspondingly.

823   b. Lacertidae indet. 1 has the shortest and thickest teeth in comparison to other studied forms.

824   c. Lacertidae indet. 3 has a typical lacertid dentition, commonly found in all fossil and recent

825   species of the genus.

826   3) the subdental shelf:

827   a. it is robust, massive and (most) well-pronounced in Lacertidae indet. 1,

828   b. Lacertidae indet. 4 has slightly less robust subdental shelf than in Lacertidae indet. 1, but is

829   is still more pronounced than in Lacertidae indet. 2 and Lacertidae indet. 3;

830   c. Lacertidae indet. 2 and Lacertidae indet. 3 have slender subdental shelf, which is

831   significantly less developed than in Lacertidae indet. 1 and/or Lacertidae indet. 4.

832   **Taxonomic considerations:** Remarkable is the presence of two lizards Lacertidae indet. 2

833   and 4 with heterodont dentition. Heterodont dentition has been earlier reported in fossil

834   lizards, e.g. *Miolacerta* (Roček 1984), *Lacerta filholi* (Müller 1996), Scincidae gen. et sp.

835   indet. from Gratkorn (Böhme and Vasilyan 2014) (which should be considered to belong to

836   the family Lacertidae, pers. observations of DV). In many forms the heterodonty was

837   characterised by the presence of anterior monocuspid teeth, posteriorly they become bicuspid

838   or tricuspid, those forms with bicuspid teeth changes posteriorly to fully to tricuspid tooth

839   morphology. Until now in different works, these forms have been described by comparing

840   limited number of lacertid genera, without including e.g. Anatolian (*Anatololacerta*,

841   *Parvilacerta*) and Southern Caucasian (e.g. *Darevskia*, *Iranlacerta*) genera. Kosma (2004)

842   provides rather comprehensive study on dentition of this family, describing the dentition of

843   some species from non-European genera. According to him, among lacertids the heterodont

844   dentition, with up to three different tooth morphotypes (mono-, bi- and tricuspid), can be

36

845   observed in some species of the genera *Darevskia, Algyroides, Lacerta, Iberolacerta*. Among

846   these lizards, *Darevskia rudis* (Kosma, 2004: fig. 28) is characterised by three tooth

847   morphotypes (1-3), which we observe in Lacertidae indet. 2. Moreover, the tooth crown in *D.*

848   *rudis* is divided into a prominent cuspis labialis and a lower cuspis lingualis and bears

849   lingually fine striation. This characters have been also found in the Lacertidae indet. 2, both

850   from Keseköy and Çandır localties. *Darevskia chlorogaster* (Kosma 2004), do not show the

851   tricuspid teeth (only mono- and bicuspid) but has a similar structure of the tooth crown.

852   Nonetheless, to refer the Lacertidae indet. 2 to *Darevskia, Algyroides* or other genera, a large

853   comparative osteological study is necessary, in order to document the osteological differences

854   among the genera and species. However, the affiliation of the Lacertidae indet. 2 to the

855   Western Asian lacertids seems most plausible.

856   It is important to note, that our observations question also the validity of the genus *Miolacerta*

857   (Roček 1984) considering also the fact that the genus has been erected using only limited

858   lacertid genera for comparison.

859   Further identification or comparison of Lacertidae 1, 3 and 4 is difficult due to the presence of

860   generous characteris (bicuspic teeth) or the lack of available both osteological collections and

861   comprehensive osteological studied of lizards.

862

863   Lacertidae indet.

864   Figure 8v-w

865

866   **Material:** Loc. Keseköy: five dentaries (UU KE 5217). Loc. Çandır: one dentary (UU CD

867   5203). Loc. Bağiçi: one maxilla (UU BAG 1201).

37

868   **Description and Remarks:** The available dentaries are poorly preserved. They possess few

869   bicuspid teeth of different sizes, which are characteristic to the family Lacertidae (Kosma

870   2004). Due to the poor preservation, any further taxonomic identification is impossible.

871   The partially preserved maxilla possesses pleurodont, linguoposteriorly directed bicuspid

872   teeth (Fig. 8v-w). Parallel to the ventral margin of the maxilla a row of four rounded foramina

873   for mandibular division of the fifth cranial nerve are present. Above the foramina, the bone

874   possesses dermal ornamentation on the labial surface of the bone, composed of small pits

875   (Fig. 8v). The premaxillar process is mainly broken. In lingal view, a prominent arched ridge

876   is present, which builds the anteriodorsal wall for a rather deep cavity. Anteriorly from the

877   arched ridge the surface of the bone concave and builds rather deep depression. The

878   combination of characters as bicuspid pleurodont teeth, presence of the dermal ornamentation,

879   have been found in *Lacerta* cf. *viridis* (Venczel 2006), however, as recently have been

880   reported (Villa 2018) the dermal ornamentation can be found in different lacertid generae.

881   Thus, an open nomenclature at the familiar level is preferable for the maxilla from Çandır

882   (Lacertidae indet.)

883

884   Amphisbaenia Gray, 1844

885   Family Blanidae (Kearney, 2003)

886   Blanidae indet. (? *Blanus* sp.)

887   Figure 8x-y

888

889   **Material:** Loc. Çandır: one dentary (UU CD 5204).

38

890 **Description:** the posterior part of a dentary with the single most posterior tooth is preserved.

891 The tooth is short, conical and oriented anterodorsally. Its tip has a small, sharp, posteriorly

892 oriented tip. Basis of two further teeth are present anteriorly from the last teeth. Considering

893 the large diameter of the tooth traces, their larger sizes in comparison to the last tooth can be

894 concluded. Resorption pits are present and have circular outlines. In labial view, the bone

895 surface is smooth, it is pierced only by a rather small mental foramina (Fig. 8x). In lingual

896 view, the subdental shelf of dentary is high and has flat lingual surface. It has the same height

897 along its length, only at the last tooth position it narrows and projects dorsally terminating

898 behind the last tooth. The Meckelian canal is open, it widens posteriorly. The intermandibular

899 septum is preserved. It has a triangular shape and is located ventrally from the last tooth. The

900 posterior cavity is large. Posteriorly, the ventral margin of the dentary extends ventrally, and

901 builts a "cavity" corresponding, most probably, to the articulation surface with angular.

902 Ventrally from the intermandibular septum, a shallow distinct anteroposteriorly directed

903 deepening is visible, corresponding to the surface of attachement with the splenial. The

904 coronoid process is partially preserved. It shows thin coronoid facet, which is dorsally broken

905 off.

906 **Remarks:** The combination of the following features, characteristic for the family Blanidae

907 (Čerňanský et al. 2016), can be observed on the Çandır dentary: 1) Meckelian groove is open

908 and well developed; 2) pleurodont teeth; 3) presence of the splenial (can be assumed based on

909 the available attachment surface). Further characters observable in the Çandır dentary such as

910 4) intermandibular septum extending anteriorly and reaching/surpassing the level of the

911 posterior end of the tooth raw; 5) a strong splenial facet in the posteroventral region of the

912 dentary have been mentioned to be characteristic for Blanidae and Bipedidae (Folie et al.

913 2013). Nevertheless, Čerňanský et al. (2016) did not mention either splenial bone or splenial

914 facet to be characteristic for the family Bipedidae. Due to incomplete preservation of the

39

915   dentary, the number and size of the teeth and mental foramina, which are diagnostic for

916   familiar or generic attribution of the remains (Cernanski et al., 2016/2017 Herrlingen 11+9),

917   can not be counted. The presence of slightly posteriorly recurved teeth in the Çandır specimen

918   suggests it attribution of the European *Blanus* (Cernanski et al., 2016/2017 Herrlingen 11+9).

919   The comparison of the described specimen with the only known worm lizard from Turkey

920   (Blanus ssp., loc. Gebeceler Georgalis et al. 2018) does not reveal any differences. Thus, an

921   assignment of the Çandır dentary to the genus *Blanus* appears to be possible, but an

922   identification of the material at the family level is preferable.

923

924   Lacertilia indet.

925   Figure 8z

926

927   **Material:** Loc. Kargı 1: one ilium (UU KAR1 1208). Loc. Çandır: one autotomy septa (UU

928   CD 5209).

929   **Description and Remarks:** The ilium from Kargı 1 is a robust bone, the bone body is thick.

930   The preacetabular process is thick, pointy and oriented posteriorly (Fig. 8z). The acetabular

931   fossa has lunar shape. The morphology of the ilium is typical to lizards (Russell and Bauer

932   2008). The autotomy septum (UU CD 5209) is small in size and corresponds to the anterior

933   portion. The septum has a trapezoid form and possesses two small and short transverse

934   processes. The morphology of the septum corresponds to the "pattern (b)" or "type 3 of

935   Etheridge" sensu Hoffstetter and Gasc (1969), which is characteristic to e.g. Teiidae,

936   Lacertidae, Anguidae and some Scincidae. In the locality Çandır both Lacertidae and

937   Anguidae have been recorded and most probably, this septum could belong to one of these

938   groups.

40

939

940   Clade Serpentes Linnaeus, 1758

941   Family Boidae Gray, 1825

942   Subfamily Erycinae Bonaparte, 1831

943   Genus *Albaneryx* Hoffstetter and Rage, 1972

944   *Albaneryx* sp.

945   Figure 9a-e

946

947   **Material:** Loc. Kargı 3: one trunk vertebra (UU KAR3 1204).

948   **Description:** The vertebra UU KAR3 1204 is fragmentary preserved, the dia-, para-, pre- and

949   postzygapophyses and condyle are missing. The vertebra, judging by its preserved

950   dimensions, was longer than short (cl=2 mm (+ ~0.3 mm condyle), naw=2.33, cl/naw=0.86

951   (0.98 with condyle)). The lateral walls of the zygosphene are rounded. The lateral lobs project

952   slightly dorsally, the cranial margin is provided by a short central lobe (Fig. 9d). The neural

953   arch is low and is located at the posterior half of the neural arch. It arises dorsoposteriorly

954   directly behind the zygosphene and bends caudally after reaching its highest point. In dorsal

955   view, the neural spine is thickened and has a triangular shape. In anterior view, the

956   paracotylar foramina are absent (Fig. 9a). Deep depressions are present on both lateral sides

957   of the cotyle. The cotyle is round. In ventral view, the vertebra centrum possesses a distinct

958   and well-expressed haemal keel. Two small subcentral foramina are present at both sides of

959   the haemal keel. They are located in anteroposteriorly running subcentral grooves, which

960   extends cranially. The lateral foramina are small and located in the corner between weakly-

961   pronounced interzygapophyseal ridge and synapophysis (Fig. 9c).

41

962   **Remarks:** The small size of the vertebra (cl=2 mm), the absence of paracotylar foramina, the

963   presence of the pronounced haemal keel, low and expended neural spine allow to attritute the

964   vertabra to the family Erycinae (Ivanov et al. 2018; Rage 1984), excluding the genera

965   *Bransateryx* and *Gonglophis* which have larger sizes of vertebra (Szyndlar 1987; Szyndlar

966   and Schleich 1993). UU KAR3 1204 resemble the genus *Albaneryx* and distinguished from

967   the genera *Eryx* and *Gongylophys* by tickened neural spine, situated at the posterior half of the

968   neural arch directely behind the zygosphene (Ivanov et al. 2018; Szyndlar and Schleich 1993).

969   Additionally, the vertebra differs from *Eryx* by pronounced haemal keel of the vertebra

970   centrum (Blain 2016; Szyndlar 1991). Further vertebra comparison with species of the genus

971   *Albaneryx* is difficult due to the poor preservation of the bone.

972

973   Erycinae indet.

974   Figure 9f-n

975

976   **Material:** Loc. Harami 1: one trunk vertebra (UU HAR1 5200).

977   **Descriptions and Remarks:** the vertebra UU HAR1 5200 (Fig. 9f-i) is smaller than the UU

978   KAR3 1204 (*Albaneryx* sp.) (Fig. 9a-e), its centrum length (cl) equals 1.29 mm (+ ~0.2 mm

979   condyle). The vertebra is wide (naw=1,62 mm) than long, cl/naw=0.8 mm (0.92 with

980   condyle). In anterior view, the neural arch is high and has rounded outline. The cotyle is

981   incomplete. The paracotylar foramina are absent in the broad depressions on both sited of the

982   cotyle (Fig. 9f). In lateral view, the vertebrae centrum bents posteroventrally and possessses a

983   weakly-pronounced haemal keel. The preserved anterior portion of the neural spine is low and

984   rises slightly posteriorly (Fig. 9i). In dorsal view, the right lateral lobe of the zygosphene is

985   observable, as well as it is visible that the neural spine arises not directly behind the

42

986   zygoshene, but slightly posteriorly (Fig. 9h). In ventral view, two subcentral foramina are

987   present laterally on both sides of the haemal keel at the anterior half of the vertebra centrum

988   (Fig. 9g). The small vertebrae sizes, cl/naw > 1, absence of the paracotylar formina suggest

989   the assignment of the vertebra to the subfamily of Erycinae (Szyndlar 1991). UU HAR1 5200

990   can be distinguished from UU KAR3 1204 (*Albaneryx* sp.) by its smaller size, less developed

991   haemal keel and shorter neural spine. Herewith this vertebra can be considered to be belong to

992   different taxa than *Albaneryx* sp. However, the poor preservation of the vertebra does not

993   allow any further identification.

994   **Material:** Loc. Bağiçi: one caudal vertebra (UU BAG 1202).

995   **Descriptions and Remarks:** The preserved caudal vertebra is fragmentary preserved. Its

996   surface is eroded. The vertebra is small, with longer preserved vertebra centrum (cl=1.13 mm)

997   and shorter naw value equalling 0.96, cl/naw=1.19. Prezyg-, postzyg- and haem- and

998   pleurapophyses are broken.

999   In anterior view, the neural canal is small and rounded. The cotyle is anterodorsally flattened.

1000 The paracotylar depressions are deep and possess paracotylar foramina (Fig. 9j). The neural

1001 arch rises posteriorly. The neural spine is broken but, based on its preserved portion, it can be

1002 assumed that it was high (Fig. 9k). In dorsal view, it is visible that the neural spine is short

1003 and arises behind the zygosphene (Fig. 9n). The small size of vertebra and its dimensions

1004 suggests its assignment to subfamily Erycinae (Szyndlar 1991). Its further identification,

1005 however, is difficult, due to its poor preservation.

1006

1007 Serpentes indet.

1008 Figure 9o-t

1009

43

1010   **Material:** Loc. Kargı 1: one tooth (UU KAR1 1207). Loc. Kargı 3: two vertebra (UU KAR3

1011   1203, 1205, 1206). Loc. Keseköy: one tooth (UU KE 5218). Loc. Bağiçi: one axis (UU BAG

1012   1204).

1013   **Descriptions and Remarks:** the preserved teeth are conical and posteriorly oriented. UU

1014   KAR1 1207 has sharp tip without any canal (Fig. 9t).

1015   The preserved axis (UU BAG 1204) lacks the posterior (third) intercentrum (hypapophysis),

1016   transverse process and neural spine. The odontoid process is flattened anteriorly, with clear

1017   two articulation surfaces (Fig. 9o). Ventrally from the odontoid process, the anteroventrally

1018   exposed articulation surface of the second intercentrum is visible. The vertebra centrum

1019   between the second and third intercentra in concave. The neural arch is long. In posterior

1020   view, the roof of the neural arch shows a shape of dorsally flattened triangle. The

1021   postzygapophysis is nearly horizontally oriented (Fig. 9q). The posteroventral corners of the

1022   neural arch, located above the postzygapophyses, possess weakly pronounces posteriorly

1023   oriented processes. The articulation surface of the zyngatrum is oriented at about 45°. The

1024   observed morphology of the preserved axis resembles mostly that of the natricin snakes (the

1025   weakly pronounced posterior processes of the neural arch, long axis) (Szyndlar 1991).

1026   However, due to lack of the comparative material of other groups we prefer to assign the axis

1027   to snakes.

1028   Three further verterbrae (UU KAR3 1203, 1205, 1206) are very fragmentary preserved, which

1029   makes any identification impossible.

1030

1031   Crocodylia Gmelin, 1789

1032   Crocodylia indet.

1033   Figure 9u-w

1034

1

2

3 1035   **Material:** Loc. Kargı 1: 78 teeth (UU KAR1 1200 – 1202), four osteoderms (UU KAR1

4

5 1036   1203, 1204). Loc. Kargı 2: 97 teeth (UU KAR2 1200). Loc. Kargı 3: five teeth (UU KAR3
6

7

8 1037   1201). Loc. Harami 1: six teeth (UU UU HAR1 5202). Loc. Hancılı: 49 teeth (UU KE 5201).
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10 1038   Loc. Çandır: one tooth (UU CD 5205).
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13 1039   **Description and remarks:** All studied teeth belong to small-sized individuals. They are
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16 1040   lingolabially compressed and conical in shape. They are represented by different
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18 1041   morphologies from slender, high and narrow to rather blunt, short, broad. At their bases, they
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21 1042   show a crown-root construction. The both lingual and labial tooth surfaces possess weakly-
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23 1043   pronounced striae (Fig. 9u-v). The anterior and posterior tooth margins possess sharp cutting
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26 1044   edges. The fragments of osteoderms displays characteristic for crocodiles ornamentation
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28 1045   composed of deep rounded well-pronounced pits (Fig. 9w).
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33 1047   **Discussion**

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36 1048   Collectively, the fish, amphibian and reptilian faunal record of the Kargı 1, Kargı 2, Kargı 3,
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39 1049   Harami1, Harami 3, Hancılı, Keseköy, Çandır, and Bağiçi localities is diverse (Table 2), and
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41 1050   contains carps (*Luciobarbus* sp., *Barbus* sp., *Luciobarbus* vel *Barbus* sp., aff. *Capoeta* sp.,
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44 1051   Barbini indet., *Leuciscus* sp.), a salamander (*Salamandra* sp.), anurans (Bufonidae indet.,
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46 1052   Pelobatidae indet., *Latonia* sp., Palaeobatrachidae indet.), lizards (*Pseudopus* sp., Lacertidae
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49 1053   indet. 1, Lacertidae indet. 2, Lacertidae indet. 3, Lacertidae indet. 4, Blanidae indet. (?*Blanus*
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51 1054   sp.)), snakes (*Albaneryx* sp., Erycinae indet.) and crocodiles (Crocodylia indet.). However,
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54 1055   each individual locality yielded only a very limited number of taxa and, moreover, all studied
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56 1056   samples are represented by small, disarticulated bones and skeletal fragments. Fossil remains
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59 1057   of some groups, such as turtles and tortoises, are not included in the samples. In this light, the
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61 1058   assemblages reported here are unlikely to represent complete reconstructions of
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1059   paleoherpetological assemblages, due to both sampling (washing and subsequent screening

1060   which resulted in sampling bones of just certain size range) and taphonomic biases.

1061   Consequently, our palaeobiogeographic and palaeoecological inferences are tentative.

1062

1063   Cyprinids

1064   The identifiable fish material from the studied localities belongs to the family Cyprinidae.

1065   Only the locality the Hancılı provided leuciscin remains, the other localities contain abundant

1066   remains of barbin fishes (Table 2). The oldest fish remains from the studied localities (Kargı

1067   1, Kargı 2, Keseköy, latest Oligocene to early Miocene) can be assigned to a small-sized

1068   barbin. The observed tooth morphology cannot be referred to any fossil form known from

1069   Eurasia. Most probably, they could represent an ancient extinct barbin group. Both Harami 1

1070   and Hancılı localities provide remains of two widely distributed barbin genera *Luciobarbus*

1071   and *Barbus*. Indeed, the barbin record from the Hancılı, which is identified by isolated

1072   pharyngeal teeth as *Barbus* sp. and *Luciobarbus* sp., could include three barbin taxa, if

1073   considering only the three different morphotypes of the serrated rays of the dorsal fin.

1074   However, this cannot be stated with confidence due to the lack of comparative osteological

1075   studies of this element in the extant barbin species.

1076   The record of the Harami 1 locality can be considered as the oldest known remains of *Barbus*

1077   and *Luciobarbus* genera. So far the oldest record of the genus *Luciobarbus* was known from

1078   the earliest late Miocene of Austria (loc. Mataschen, Schultz 2004). Böhme and Ilg (2003)

1079   mentioned oldest *Luciobarbus* from contemporaneous to Mataschen sites in Turkey, however,

1080   this material stays unfigured. We suggest that *Barbus* sp. Harami 1 and Hancılı should be

1081   considered as the oldest representatives of this genus, since earlier publications describing

1082   *Barbus* sp. do not represent the genus *Barbus* sensu Yang et al. (2015). Our finds would

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1083   provide important information also for the calibration of the molecular trees, which estimates

1084   the divergence time and origination of different barbin clades.

1085   Amphibians

1086   The only caudate taxon from the studied Anatolian sites is *Salamandra* sp., recovered from

1087   the localities Harami 1 and Bağiçi. It is the first fossil record of the genus in this region. The

1088   genus is well known from the Neogene of Europe, but its out-of-Europe occurrence was

1089   hitherto unknown. Our records is the evidence of caudate amphibians in Anatolia as early as

1090   in the earliest Miocene and at least during middle Miocene. Because of absence of

1091   osteological data on the genus *Salamandra*, it is not possible to decide whether this fossil is

1092   related to the recent species *Salamandra infraimmaculata* distributed in Anatolia and Middle

1093   East. Until now, the fossil record of caudates in Anatolia was represented by imprints of

1094   Salamandridae indet. from the locality Ağaöz, early Miocene (Paicheler et al. 1978) which,

1095   however, can not be compared with our specimens.

1096   Hitherto, only few fossil anuran taxa have been reported from Anatolia, mainly from the early

1097   and middle Miocene (Table 1). They include brown frog (*Rana*), green frogs (*Pelophylax*,

1098   originally described as *Rana* sp. in Paicheler et al. (1978)), and spadefoot toad (*Pelobates* sp.).

1099   The evidence of *Pelobates* is based on premetamorphic tadpoles (Dubois et al. 2010;

1100   Paicheler et al. 1978) in which, however, it is difficult to decide whether they belong to

1101   *Pelobates* or *Eopelobates*. Similarly, Wassersug and Wake (1995) reported on two tadpoles

1102   from the middle Miocene of Gürcü (not included in Table 1) that they assigned to *Pelobates*

1103   sp.

1104   In the studied localities, the remains of the genus *Latonia*, found in nearly all of them (Table

1105   2), suggest presence of this genus in central Anatolia from the latest Oligocene to middle

1106   Miocene. The remains represent small to large individuals (e.g. Fig. 4). The oldest record of

1107   the genus is known from the earliest Oligocene of Europe (e.g., localities Grafenmühle 10,

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1108 Möhren 12 and 13; Böhme and Ilg 2003). Their appearance in Europe coincides with the

1109 Grande Coupure event, during which the vertebrate fauna of Europe has been replaced by new

1110 arrivals including large and small mammals (Hooker 2010; Legendre 1989), as well as

1111 amphibians and reptiles (Rage 2012; Vasilyan 2018). Whether *Latonia* invaded Europe (e.g.,

1112 via Anatolia) or evolved here from some other discoglossoids by means of heterochrony

1113 (which may be suggested by the fact that *Latonia* is sometimes accompanied by discoglossoid

1114 anurans of smaller size which, although being adult, correspond to early developmental stages

1115 of *Latonia*) can be only hypothesized. In order to illustrate this background, one can mention

1116 *Discoglossus troscheli* from the Oligocene and *Opisthocoelellus weigelti* and *O. hessi* from

1117 the Eocene and Oligocene of central Europe, or *Eodiscoglossus, Iberobatrachus,*

1118 *Bakonybatrachus* or *Paralatonia* from the Cretaceous of Spain, Hungary and Romania (see

1119 literature summerized in Roček 2013).

1120 Because of uniformity of species within the genus *Palaeobatrachus* and because majority of

1121 them was based on articulated skeletons, disarticulated bones of the Palaeobatrachidae usually

1122 provide only a limited information for taxonomic assignments. However, our material is an

1123 exception. Taking into account that the earliest palaeobatrachids were recorded from the

1124 Cretaceous of Iberian Penninsula from where they only in the Eocene and post-Eocene times

1125 spread to the central and eastern part of Europe (Wuttke et al. 2012), and that they occurred

1126 only in Europe (with a few exceptions, one of them being Anatolia), it can be taken granted

1127 that the palaeobatrachids from Anatolia must have their origin in pre-Miocene Europe and

1128 that they are not immigrants from Asia (Fig. 9). Their occurrences in the late Miocene of

1129 northern Caucasus (Syromyatnikova 2018; Tesakov et al. 2017) and in the Pliocene and

1130 Pleistocene of the east-European Plateau (Wuttke et al. 2012) seem to be relatively late for

1131 immigration of palaeobatrachids to Anatolia. An interesting problem associated with

1132 Anatolian Miocene occurrences of palaeobatrachids is the record of *Palaeobatrachus* from the

1133 locality Gaverdovsky in northern Caucasus (Syromyatnikova 2018; Tesakov et al. 2017),

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1134   whose contact with the main area of pre-Miocene distribution of palaeobatrachids in Europe

1135   was probably during a very short time (Fig. 10).

1136   The remains of Pelobatidae indet. from the Harami 1, Keseköy, Bağiçi provide new data on

1137   the early Miocene record of the family in Anatolia. Earlier, tadpoles assigned to *Pelobates* sp.

1138   were described from the early Miocene localities Ağaöz and Ahlath Dere (Dubois et al. 2010;

1139   Paicheler et al. 1978) and from the the early Miocene of Gürcü Valley (Beşkonak and Akoz

1140   (Agaöz) sites) (Wassersug and Wake 1995). The former two localities are situated in the

1141   Beşkonak sequence of lacustrine origin of the Dereköy piroclysts, at the base of the Güvem

1142   Formation (Paicheler 1978). The locality Keseköy is also in the Beşkonak sequence (Yavuz-

1143   Işık 2008). The age of the sequence has been dated using the radiometric analysis between

1144   19.7 Ma (underlaying Çukurviran dacite) and 17.9 Ma (overlaying Bakacak andesite) (Denk

1145   et al. 2017; Wilson et al. 1997; Yavuz-Işık 2008). Pelobatidae indet. from the locality Harami

1146   1 represents the oldest record (early early Miocene, 22.2 – 22.3 Ma) of the family in Anatolia,

1147   whereas the Bağiçi specimen is the so far known youngest (late middle Miocene) form of the

1148   family in Anatolia.

1149   At first sight, the frontoparietals from Hancılı, obviously belonging to adult individuals, differ

1150   in their overall appearance from those in recent pelobatids, which are coalesced. However,

1151   when the development of the frontoparietal in *Eopelobates* and *Pelobates* (both recent and

1152   fossil) is followed (Maus and Wuttke 2004; e.g. Roček 1981; fig. 43; Roček et al. 2014; fig.

1153   11-n; Roček and Wuttke 2010; fig. 8), then we see that the frontoparietal takes its origin from

1154   a pair of bones, which later come in contact along the midline. Besides, another, unpaired

1155   median ossification arises posteriorly and inserts into the wedge-like space between the

1156   posterior parts of both frontoparietals. It is only during metamorphosis when all three parts

1157   fuse into a single frontoparietal complex. It was discovered recently that the developmental

1158   scheme of the tripartite pelobatid frontoparietal may persist till adulthood in some taxa (e.g.,

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1159   *Eopelobates deani*; Roček et al. 2014; fig. 4c). Arrested development of the frontoparietal in

1160   some extinct pelobatids may be thus taken as a case of heterochrony. Our frontoparietals

1161   could have been parts of a larger complex, as seems to be supported by the fact that the

1162   frontoparietal incrassation on the inner surface of the bones reached their medial margin (i.e.,

1163   the incrassation extended onto the opposite frontoparietal), and the same holds for the

1164   posteromedial margin of the bone, which can be taken as an evidence that the incrassation

1165   extended onto the ventral surface of the posterior unpaired element. Pelobatidae were for the

1166   whole period of their existence restricted to Europe, even if their earliest representatives

1167   probably invaded Europe from North America in the early Eocene (Roček et al. 2014; Wang

1168   et al. 2017). One may speculate that heterochrony could have been a response to conditions in

1169   the marginal areas of distribution, such as today's Anatolia. Whereas isolated bones of adults

1170   and of the mentioned fossil tadpoles may be considered unequivocal evidence of the

1171   Pelobatidae, their generic assignment (either to the genus *Eopelobates* or *Pelobates*) is more

1172   difficult. It was already mentioned above (see Description) that the maxillae rather differ in

1173   shape of their zygomaticomaxillar process, which is almost pointed and inclined posteriorly in

1174   UU KE 5006 (Fig. 4q, r) and probably also in UU HAR1 5051 (Fig. 4m, n), whereas the

1175   maxilla in UU BAG 1001 (Fig. 4o, p) is different – it has its zygomaticomaxillar process

1176   divided in two parts (which means that its contact with the squamosum was longer than in

1177   *Pelobates*), the maxilla had its articulation with pterygoid by means of a deep but not

1178   prominent horizontal lamina instead of processus pterygoideus, sculpture on its labial surface

1179   is of the pit-and-ridge type. All these characters point to *Eopelobates*. This is also supported

1180   by the tripartite frontoparietal, only moderately extended laterally (Figs. 4s-v). Thus, it is

1181   possible that there occurred representatives of both genera in Anatolia, or at least some sort of

1182   transitional form between them, as it was, e.g., in Gritsev (Roček et al. 2014). However,

1183   occurrence of pelobatid tripartite frontoparietals from Anatolia (Figs. 4s-v) not necessarily

1184   mean that they represent pelobatids closely related to *E. deani*. Rather, they could support the

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1185   view that some characters, such as those associated with rate of development, could evolve

1186   independently in forms distant both geographicallly and chronologically.

1187   As regards the tadpoles, their generic assignment is also not easy. Tadpoles of

1188   *Eopelobates* have the posterior part of the parasphenoid covered with sculpture whereas it is

1189   smooth in *Pelobates*. Such details, however, are not discernible in our tadpoles, so their

1190   generic assignment remains open.

1191   The true toad record has very limited stratigraphic occurrence. It has been only found

1192   from the locality Keseköy (Table 2). In Claessens (1996, 1997) it has been referred to the

1193   genus *Bufotes*, which we after critical revision refer to as Bufonidae indet. Whether *Bufotes*

1194   has entered from Asia to Europe via Turkey (Claessens 1997; Vasilyan et al. 2017), we can

1195   not state here. Further finds from early Miocene localities, would allow to shed more light on

1196   this palaeobiogeographic question.

1197   Surprisingly, the samples from our studied localities do not contain any ranid remains

1198   which, however, can be a result of limited sampling or taphonomic bias.

1199

1200   Lizards

1201   *Pseudopus* sp. from the localities Kargı 1 and Kargı 2 represents the first and oldest known

1202   record of the genus from Anatolia and entire Eurasia. So far, *Pseudopus* was known

1203   exclusively from Europe since the earliest Miocene until the Late Pleistocene (Čerňanský et

1204   al. 2015; e.g. Klembara et al. 2010). The oldest European record of the genus (*Pseudopus* aff.

1205   *ahnikoviensis*) has been described from the locality Wiesbaden-Amöneburg, Germany of the

1206   late Aquitanian age (21-22 Ma) (Čerňanský et al. 2015). Thus, *Pseudopus* sp. from the two

1207   studied Turkish localities Kargı 1 and Kargı 2 of latest Oligocene and latest Oligocene-earliest

1208   Miocene (earliest Aquitanian) ages respectively, can be considered as the earliest documented

1209   remains of the genus from Eurasia. Taking into account the European and Anatolian records

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1210   of the genus, we hypothesis that the genus, being present in Anatolia during the latest

1211   Oligocene and earliest Miocene, could migrate into Europe during the early Miocene from

1212   Anatolia. Considering the present finds, the probable origin of the genus in Anatolia and its

1213   later dispersed by establishing landbridges can be suggested. However, when it could

1214   happened, stays unclear, since the European record is scarce and restricted to the Central

1215   Europe. Further finds from Eastern and Southern Europe will be necessary to trace the

1216   migration routes of this genus.

1217   The lacertid lizards are represented by at least four forms in the studied localities. Lacertidae

1218   indet. 1 is the oldest (latest Oligocene, loc. Kargı 1) form. Lacertidae indet. 2 and Lacertidae

1219   indet. 3 occur in late early Miocene and/to middle Miocene localities (Keseköy, Hancılı,

1220   Çandır), whereas Lacertidae indet. 4 is known only from the middle Miocene locality Çandır.

1221   Lacertidae indet. 1 and Lacertidae indet. 3 have tooth morphology well-known from

1222   numerous Neogene localities of Europe, but forms with morphology (shape of bone and teeth)

1223   comparable to Lacertidae indet. 1 can not be found. We suggest that Lacertidae indet. 3 from

1224   loc. Keseköy and Çandır represents a fossil form of recent Western Asian genera like

1225   *Darevskia, Algyroides,* indicating the presence of this group in the region already since the

1226   early Miocene.

1227   Until recently, worm lizards have been completely unknown from the Anatolian fossil record.

1228   A fossil form of the *Blanus strauchi* complex have been newly described from the middle

1229   Miocene (13.6 Ma) Gebeceler locality in Western Turkey (Georgalis et al. 2018). Here we

1230   report another worm lizard (Blanidae indet. ? [*Blanus* sp.]) record from Turkey coming from

1231   the Çandır locality, which has comparable or slightly older age than Gebeceler fossil. Our find

1232   suggest that this lizard group was distributed in the middle Miocene much northern and

1233   eastern from both their known fossil and recent distribution areas. This provides an excellent

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1234   example that the reptilian fossil record of Anatolia is understudied and numerous important

1235   fossil founds are still waiting to be uncovered.

1236

1237   Snakes

1238   Among the scarce snake finds the most interesting is the vertebra referable to the the genus

1239   *Albaneryx* (*Albaneryx* sp.) from the locality Kargı 3 (earliest Miocene). Until now, the

1240   stratigraphic record of this genus covered very short time period (several few million years)

1241   from the middle Miocene to the earliest late Miocene of Europe and Western Asia (Böhme

1242   and Ilg 2003; Ivanov et al. 2018). The oldest record of the genus is known from the middle

1243   Miocene age (13.5-13.7 Ma) locality Sansan (Augé and Rage 2000), whereas the youngest

1244   record is documented from the e.g. Grytsiv, Ukraine (11.1 Ma) (Zerova 1989). Considering

1245   the morphological similarities of *Albaneryx* with the North American genus *Lichanura*, it has

1246   been hypothesised (Augé and Rage 2000; e.g. Zerova 1989) that the genus arrived in Europe

1247   from Northern America via Asia. However, no evidences for this hypothesis have been

1248   provided and the appearance of the genus in Europe stays still enigmatic.

1249   Interestingly, the oldest record of *Albaneryx* coincides with the end of the Miocene Climatic

1250   Optimum (MCO) (loc. Sansan), when a significant temperature drop has been observed

1251   (Böhme 2003; Zachos et al. 2001). The new early Miocene find of the genus from Central

1252   Anatolia favours to the hypothesis of their arrival from Asia into Europe, which was, most

1253   probably, linked to peculiar climatic conditions necessary for their dispersal and live,

1254   prevailing in Europe after the MCO.

1255   Further finds of small-sized erycins from the localities Harami 1 and Bağiçi, suggests the

1256   (rather continuous) presence of this groups in the Neogene fossil record of the Central

<div align="center">53</div>

1257   Anatolia. More fragmentary preserved snake material (Table 2, Serpentes indet.) is available

1258   from the studied localities, but too poorly preserved for any consideration.

1259

1260   Crocodiles

1261   The crocodile remains are present in five studied localities suggesting their presence (with

1262   some gaps) in Central Anatolia from the latest Oligocene (Kargı 1) to middle Miocene

1263   (Çandır) (Fig. 1, table 2). So far, the fossil crocodiles (*Diplocynodon* sp.) from Turkey is

1264   known from the early early Miocene of eastern Turkey (loc.Tuz-6, Turabi Formation) (Sen et

1265   al. 2011) and mid Oligocene – mid Miocene of western Turkey (Küçükdoganaca Kökü)

1266   (Schleich 1994). However, since based on tooth material any identifications are not

1267   appropriate (Delfino 2002), this fossils should be considered as Crocodylia indet. As

1268   suggested by Böhme (2003), the presence of crocodiles indicate a warm climate with a mean

1269   annual temperature not lower than 15.7° C, minimal cold and warm month temperatures not

1270   lower than -1.7° C and 18.3° C respectively.

1271

1272   Palaeoenvironmental interpretations

1273   We reconstructed tentatively palaeoenvironments of the localities taking into account both

1274   depositional environments of the fossiliferous horizons and assemblage of the ectothermic

1275   vertebrates. The fossil faunas of Kargı 1 is found from organic reach black clays; Kargı 2 –

1276   most probably from comparable sediments as in Kargı 1; Kargı 3 – from greyish clays rich in

1277   diatomite; Harami 1 – from darkish clay/coal; Harami 3 – from a layer of fine laminated coal

1278   (Claessens 1996); Keseköy – from green-brown, partly laminated clays and marly clays

1279   (Krijgsman et al. 1996; Yavuz-Işık 2008); Hancılı – from fine laminated clays and coal

1280   (Kaymekci 2000). The depositional palaeoenvironment of the sites Kargı 1, Kargı 2, Harami

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1281   1, Harami 3 and Hancılı can be interpreted as swamp or marsh, whereas for Kargı 3 and

1282   Keseköy a lacustrine environment are characteristic, for Hancılı mix of lake and swampy

1283   environment can be suggested. The fossil fauna of Çandır is yielded from the reddish silts

1284   (Krijgsman 2003), that likely represent pedogenically modified package of the coastal lagoons

1285   or lake margin. The sedimentology of the Bağiçi locality is unknown but lacustrine

1286   environment has been suggested (Claessens 1996).

1287   Palaeoenvironmental reconstructions for the studied localities, considering the assemblages of

1288   ectothermic vertebrates, reflect a mosaic of different environments. In Kargı 1 and 2 an

1289   environment with transition from water (Barbini indet., *Palaeobatrachus* sp., Crocodylia

1290   indet.) to (wet) nearshore (semi-terrestrial *Latonia* sp.) and terrestrial open habitats

1291   (*Pseudopus* sp., *Ophisaurus* sp., Lacertidae indet. 1) can be suggested. The few fossil remains

1292   from Kargı 3 suggest the presence of water body (Crocodylia indet.) with surrounding it

1293   sandy (*Albaneryx* sp.) wet nearshore (*Latonia* sp.) areas, whereas in Harami 3 water body

1294   (*Palaeobatrachus* sp.) and wet nearshore areas (*Latonia* sp.). The Harami 1 represents among

1295   the studied localities the most diverse palaeoenvironments from aquatic habitats (*Luciobarbus*

1296   sp., *Barbus* sp., *Palaeobatrachus* sp., Crocodylia indet.), to nearshore areas (Latonia sp.) with

1297   sandy soils (Pelobatidae indet., Erycinae indet.) and forested areas (*Salamandra* sp.). The

1298   Keseköy assemblage of the ectotermic vertebrates suggests the presence of an aquatic

1299   environment (Barbini indet., *Palaeobatrachus* sp.), surrounding it nearshore habitats (*Latonia*

1300   sp.) with sandy soils (Pelobatidae indet.) and large areas with open stony areas (Bufonidae

1301   indet., *Ophisaurus* sp., Laceridae indet. 1 and 2). The Hancılı locality is dominated by aquatic

1302   groups (at least three barbins, *Leuciscus* sp., Crocodylia indet.), but groups inhabiting

1303   nearshore areas (*Latonia* sp.) with sandy soils (Pelobatidae indet.) and open habitats

1304   (Lacertidae indet. 3) were also present. The Çandır association is dominated by terrestrial

1305   heliophile groups such as *Ophisaurus* sp., Lacertidae indet. 1, Lacertidae indet. 2 and

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1306   Lacertidae indet. 3, but also aquatic (Crocodylia indet.), semiterrestrial (*Latonia* sp.) and

1307   woodland (Blanidae indet.) forms were also present. The herpetofaunistic assemblage of the

1308   Bağiçi locality suggest a terrestrial environment with sandy cover (Pelobatidae indet.,

1309   Erycindae indet.), forested area (*Salamandra* sp., *Anguis* sp.) and open habitats (*Ophisaurus*

1310   sp., Laceridae indet.).

1311

Conclusions

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1313   The results of the present study significantly enlarge the knowledge of the fish, amphibian and

1314   reptilian fossil record of Anatolia and shed more light on the palaeobiogeographic importance

1315   and significance of the Anatolia for the distribution of the these vertebrate groups.

1316   The earlier studies of the Anatolian fish record documented several species of the genera

1317   *Leuciscus*, *Barbus*, *Tinca* from early Miocene (to middle Miocene) (Table 1). However, the

1318   fossil material has been assigned to a given genus only using cranial and postcranial bone

1319   characteristics, and did not include the characters of the pharyngeal dentition. This makes

1320   impossible to compare them with fossil material from our study and vice versa. Since we can

1321   not securely assign the pharyngeal tooth material of our study to a recent genera, we are aware

1322   of comparing with the known fossil record. More studies and better material are necessary to

1323   provide data for linking the cyprinid taxa identified by the pharyngeal teeth and other skeletal

1324   elements.

1325   Previously among early to middle Miocene amphibians four different taxa have been

1326   documented in the Anatolia record (Table 1). Our present study found two comparable groups

1327   (*Salamandra* sp. and Pelobatidae indet.) and added three more taxa (*Latonia* sp.,

1328   *Palaeobatrachus* sp. and Bufonidae indet.). Earlier known both green (*Pelophylax* sp.) and

1329   brown (*Rana* sp.) have not been documented in our study.

1330   Until recently, no fossil lizards have been recorded from Anatolia. Čerňanský et al. (2017)

1331   and Georgalis et al. (2018) have reported first anguid and amphisbaenids from Turkey. The

1332   studied localities provided addition lizard material, such as the oldest *Pseudopus* record,

1333   diverse lacertids (Lacertidae sp. 1 – 4). Earlier known snake record from Turkey is limited to

1334   Colubroidea indet. and *Bavariboa* sp. (Table 1). As Szyndlar and Hoşgör (2013) has

1335   suggested, the find of *Bavariboa* sp. evidence about the link between terrestrial faunas of Asia

1336   and Europe. Our find of *Albaneryx* sp. provide additional support for this hypothesis.

1337   In summary, the latest Paleogene and middle Miocene fish, amphibian and reptilian fauna of

1338   Central Turkey (Anatolia) is represented by the following groups: Barbini, Leuciscinae,

1339   Salamandridae, Pelobatidae, Bufonidae, Alytidae, Palaeobatrachidae, Ranidae, Anguinae,

1340   Lacertidae, Amphisbaena, Erycinae, Boinae, Chelydridae, Crocodylia. All these groups are

1341   broadly known in the fossil record of the Europe and suggest strong link between European

1342   and Anatolian ectothermic faunas. The present study is an outstanding example, showing the

1343   important role of Anatolia in the dispersal of the other vertebrate groups than mammals, as

1344   well as how much informative can be poor samples. Further studies on the Anatolian fossil

1345   record of these groups will provide important clues of the understanding of the formation and

1346   shaping the European fossil record.

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201354   **Conflict of Interest:** The author declares that he has no conflict of interest.
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1628   **Figure captions**

1629   Figure 1. **a** an overview map of Turkey and **b** geographic locations of the studied localities on

1630   a topographic map. **c** stratigraphic chart with the studied fossil localities. The + and – in the

1631   brackets indicates correspondingly the normal or reverse polarity patterns of the fossiliferous

1632   layer according to Krijgsman et al. (1996) and Krijgsman (2003).

1633

1634   Figure 2. Images of the 3D models of the pharyngeal bones with teeth of the *Luciobarbus* and

1635   *Barbus* species. **a.** *Luciobarbus comizo* (MNCN 69304), **b.** *Luciobarbus longiceps* (MNCN E

1636   54), **c.** *Luciobarbus sclateri* (MNCN 69331), **d.** *Barbus barbus* (SNSB SPAM-PI-00608), **e.**

1637   *Barbus sacratus* (MNCN GUI 17), **f.** *Barbus meridonalis* (MNCN 19933). The letters a, b, c

1638   correspond to the first (main), second and third row, the numbers (1-5) the tooth positions in

1639   those rows. The scale bars equal 1 mm.

1640

1641   Figure 3. Cyprinids from the studied localities. *Luciobarbus* sp., Morphotype d7 – from

1642   Hancılı, UU HAN 5315 (**a** – **b**); UU HAN 5316 (**c**); Morphotype d5 – UU HAN 5333 (**d**), UU

1643   HAR1 5300, loc. Hancılı (**e**); Morphotype d3 – UU HAN 5334, loc. Hancılı (**f**); UU HAN

1644   5305, loc. Hancılı (**g**). *Barbus* sp., Morphotype d6 from the loc. Harami 1, UU HAR1 5301

1645   (**h**), loc. Hancılı, UU HAN 5321 (**i**), UU HAN 5311 (**j** – **k**), UU HAN 5335 (**l**), Morphotype

1646   d4 - UU HAN 5308 (**m**), UU HAN 5309 (**n**). *Lucioarbus* vel *Barbus* sp., Morphotype d1 from

1647   loc. Hancıl ı, UU HAN 5300 (**o** – **p**), Morphotype d2, UU HAN 5303 (**q**), UU HAN 5306 (**r**);

1648   Morphotype s1, UU HAN 5324 (**s**); Morphotype s2, UU HAN 5325 (**t**), UU HAN 5326 (**u**);

1649   Morphotype s3, UU HAN 5329 (**v**). aff. *Capoeta* sp. from the loc. Hancılı, UU HAN 5317 (**w**,

1650   **x**). Barbini indet. (**z** – **dd**), UU KAR1 1304, loc. Kargi 1 (**y**), UU KAR1 1301, loc. Kargi 1

1651   (**z**), UU KAR2 1301, loc. Kargi 2 (**aa**), UU KAR2 1306, loc. Kargi 2 (**dd**), UU KAR2 1303,

65

1652   loc. Kargi 2 (**ee**), UU KE 5307, loc. Keseköy (**bb**), UU KE 5305, loc. Keseköy (**cc**).

1653   *Leuciscus* sp. from loc. Hancılı, UU HAN 5318 (**ff**).

1654

1655   Figure 4. Salamander and some frogs from Turkish localities. **a** – **l** *Salamandra* sp., **a** – **e**

1656   trunk vertebra (UU BAG 1001) in anterior (**a**), posterior (**b**), right lateral (**c**), dorsal (**d**) and

1657   ventral (**e**) views; **f** – **i** caudal vertebra (UU HAR1 5055) from loc. Harami 1 in anterior (**f**),

1658   left lateral (**g**), dorsal (**h**) and ventral (**i**) views; **j** – **l** humeri (UU BAG 1004 [**j**] and 1003 [**k** –

1659   **l**]) from loc. Bağiçi in ventral (**j**, **k**) and dorsal (**l**) views. **m** – **v** Pelobatidae indet. from **m** – **n**

1660   loc. Harami 1, left maxilla (UU HAR1 5051) in outer (**m**) and inner (**n**) views; **o** – **p** loc.

1661   Bağiçi, right maxilla (UU BAG 1001) in outer (**o**) and inner (**p**) views; **q** – **r** loc. Keseköy,

1662   complete posterior half of right maxilla (UU KE 5006) in outer (**q**) and inner (r) views; **s** – **v**

1663   loc. Hancılı; right frontoparietal (UU HAN 5051) in ventral (**s**) and dorsal (**t**) views; left

1664   frontoparietal (UU HAN 5052) in dorsal (**u**) and ventral (**v**) views. **w** – **y** Bufonidae indet.

1665   from loc. Keseköy, right ilium (UU KE 5001) in lateral (**w**), ventrolateral (**x**) and medial (**y**)

1666   views. **z** – **aa** Anura indet., fragment of left maxilla (UU KAR1 1051) in inner view (**z**), with

1667   magnified teeth of the same specimen in ventral view (**aa**); **bb** phalanx, morphotype A (UU

1668   HAR1 5056) in dorsal (**bb-1**) and ventral (**bb-2**) views; **cc** phalanx, morphotype B (UU

1669   HAR1 5057) in dorsal (**bb-1**) and ventral (**bb-2**) views.

1670

1671   Figure 5. Remains of *Latonia* from the studied Turkish localities. **a** – **b** Left part of the

1672   frontoparietal (UU HAN 5055) in dorsal (**a**) and ventral (**b**) views. **c** – **d** Right scapula (UU

1673   HAR3 5051) in inner (**c**) and outer (**d**) views. **e** – **f** Atlas (UU CD 5002) in dorsal (**e**) and

1674   anterior (**f**) views. **g** – **h** Fragment of right maxilla (UU HAR1 5012-1) in lingual (**g**) and

1675   labial (**h**) views. The sulcus for the nasolacrimal duct, which runs posteroventrally on the

1676   inner surface of the bone, is marked by an arrow. **i** – **j** Left maxilla (UU HAR1 5012-2) in

66

1677   lingual (**i**) and labial (**j**) views. **k** – **e** Right maxilla (UU HAR1 5012-3) in labial (**k**) and

1678   lingual (**e**) views. **m** – **n** Right ilium (UU KAR3 1207) in lateral (**m**) and medial (**n**) aspects. **o**

1679   urostyle (UU UU KE 5053) in dorsal view.

1680

1681   Figure 6. Cranial elements of Palaeobatrachidae. **a** – **c** Sphenethmoid UU HAR1 5005 from

1682   loc. Harami 1 in dorsal (**a**), ventral (**b**), and anterior (**c**) views. The arrow in (**a**) marks the

1683   braincase cavity, the arrow in (**b**) marks the posterior orifice of the canal for the ramus

1684   medialis nervi ophthalmici. **d** – **f** Sphenethmoid UU HAR1 5006 from loc. Harami 1 in dorsal

1685   (**d**), ventral (**e**), and anterior (**f**) views. **g** Left angular UU HAR1 5004 in dorsal view. Note a

1686   distinct ridge on the dorsal surface of the coronoid process, separating anterior and posterior

1687   depression. The posterior margin of the coronoid process is nearly straight, reaching the

1688   medial margin of the bone at the level of the posterior end of the medial wall of the sulcus

1689   Meckeli (marked by arrow). **h** Right angular UU HAR1 5002 in dorsal view. **i** – **j** Right

1690   angular UU HAR1 5001 in dorsolateral (**i**) and lateral (**j**) views; the arrows mark tubercle

1691   protruding from the medial wall of the Meckelian groove, and a distinct concavity on the

1692   lateral surface. **k** – **l** Posterior part of right angular UU HAR1 5003 in dorsomedial (**k**) and

1693   medial (**l**) views; the longitudinal axis of the coronoid process is marked by a white broken

1694   line, the arrow marks the medial wall of the Meckelian groove. Note absence of a tubercle or

1695   protuberance on dorsal margin of the wall. **m** Left angular UU HAR3 5001 from loc. Harami

1696   3 in dorsomedial view; the arrow marks a tubercle protruding from the medial wall of the

1697   Meckelian groove, as in (**i**). **n** Left angular UU HAR3 5002 in dorsal view. **o** – **p** Right

1698   maxilla (UU HAR1 5059) in lingual (o) and labial (p) views. The white arrow in (o) points to

1699   a contact ridge with the pterygoid, that in (**p**) marks a horizontal ledge that extends labially.

1700

67

168

1701   Figure 7. Postcranial elements of Palaeobatrachidae. **a** – **c** Left scapula (UU HAR1 5009)

1702   from loc. Harami 1 in lateral (**a**), medial (**b**) and posteromedial (**c**) views. The arrows in (**b**)

1703   mark the anterior and posterior margins of the bone, the arrows in (**c**) mark the external and

1704   internal surfaces of the bone. **d** – **e** Left ilium (UU HAR1 5008) in lateral (**d**) and medial (**e**)

1705   views. Note prominent spina iliaca (marked by an arrow in **e**). **f** – **g** Urostyle (UU KE 5011)

1706   from loc. Keseköy in dorsal (**f**) and anterior (**g**) views. **h** Right humerus (UU KAR2 5000)

1707   from loc. Kargi 2. **i** – **m** Variation of humeri from loc. Harami 3. **i** Right humerus (UU HAR3

1708   5006). **j** Left humerus (UU HAR3 5005). **k** Left humerus (UU HAR3 5007). **l** Left humerus

1709   (UU HAR3 5004). **m** Left humerus (UU HAR3 5008). **n** – **u** Variation of right humeri from

1710   loc. Harami 1. **n** UU HAR1 5022, **o** UU HAR1 5023 (mirrored for comparison), **p** UU HAR1

1711   5011, **q** UU HAR1 5026, **r** UU HAR1 5024, **s** UU HAR1 5021, **t** UU HAR1 5015, **u** UU

1712   HAR1-5031.

1713

1714   Figure 8. Lizards remains from the studied Turkish localities. **a** – **b** *Pseudopus* sp. from loc.

1715   Kargı 1 (**a** – UU KAR1 1205) and loc. Kargı 2 (**b** – UU KAR2 1204), **c** – **e** Anguidae indet.

1716   from loc. Kargı 2 (UU KAR2 1203). **f-e** Lacertidae indet. 1 from Kargı 1 (UU KAR1 1206),

1717   in labial (**f**) and lingual (**g**), **e1** – magnified view on teeth. **i** – **o** Lacertiade indet. 2 from loc.

1718   Keseköy (**i** UU KE 5200, **j** – **k** UU KE 5206, **l** – **n** UU KE 5213, **o** UU KE 5219), maginified

1719   views on teeth of the specimens **k** UU KE 5206, and **n** UU KE 5213. **p** – **r**, **aa** Lacertidae

1720   indet. 3 from loc. Keseköy (**p** – **q** UU KE 5220) (**q** – magnified view on the teeth of the

1721   specimen UU KE 5220) (**aa** UU KE 5215), from loc. Çandır (**r** – UU CD 5210). **s** – **u**

1722   Lacertiade indet. 4 from loc. Çandır UU CD 5202, **u** magnified view on the teeth of the

1723   specimen UU CD 5202. **v** – **w** Lacertidae indet. from loc. Bağiçi (UU BAG 1201). **x** – **y**

1724   Amphisbaena indet. from loc. Çandır (UU CD 5204). All bones are figured from lingual view,

1725   except for **d**, **f**, **v**, **x** figured in labial view and **e** in ventral view.

68

169

1726

1727   Figure 9. Snake and crocodile remains from Turkish localities. **a** – **e** trunk vertebra of

1728   *Albaneryx* sp. from loc. Kargı 3 (UU KAR3 1204). **f** – **i** trunk vertebra of Erycinae indet. from

1729   loc. Harami 1 (UU HAR1 5200). **j** – **n** caudal vertebra of Erycinae indet. from the loc. Bağiçi

1730   (UU BAG 1202). **o** – **s** axis of Serpentes indet. from Bağiçi (UU BAG 1204), **t** – tooth of

1731   Serpentes indet. from loc. Kargı 1 (UU KAR1 1207). **u** – **w** Crocodylia indet. from loc. Kargı

1732   1, teeth **u** – UU KAR1 1202 and **v** – UU KAR1 1201, **w** – osteoderm UU KAR1 1204.

1733

1734   Figure 10. Paleogeographic relations of Anatolia (marked by red square) to Europe between

1735   late Oligocene and late Miocene. Noteworthy is permanent isolation of the area in northern

1736   Caucasus (marked by red arrow) where *Palaeobatrachus* was reported by Syromyatnikova

1737   (2018), which means that immigration from the main area of distribution had to occur

1738   relatively quick. Maps are from Rögl (1999).

69

Figure 3

Figure 4

can. for ramus medialis
nervi ophthalmici

tectum nasi

canalis olfactorius

septum nasi

solum nasi

ossified part of
postnasal wall

articular facet for nasal

lamina
supraorbitalis

articular facet for frontoparital

articular facet for parasphenoid

processus
cornoideus

sulcus for
cartilago
Meckeli

extremitas spatulata

processus frontalis

margo orbitalis

1 mm

a

margo
anterior   b   d   f

facies
externa   margo
posterior

c

facies
interna   e

g

i   l

h   k   m

j   n

o

2 mm

p   q   r   t

u

Figure 9   Click here to access/download;Figure;Fig_9.tif ⬇

Late Oligocene (Chattian)

Early Miocene (Aquitanian)

Early Miocene (latest Burdigalian)

Middle Miocene (Langhian)

Middle Miocene (Serravalian)

Late Miocene (Tortonian)
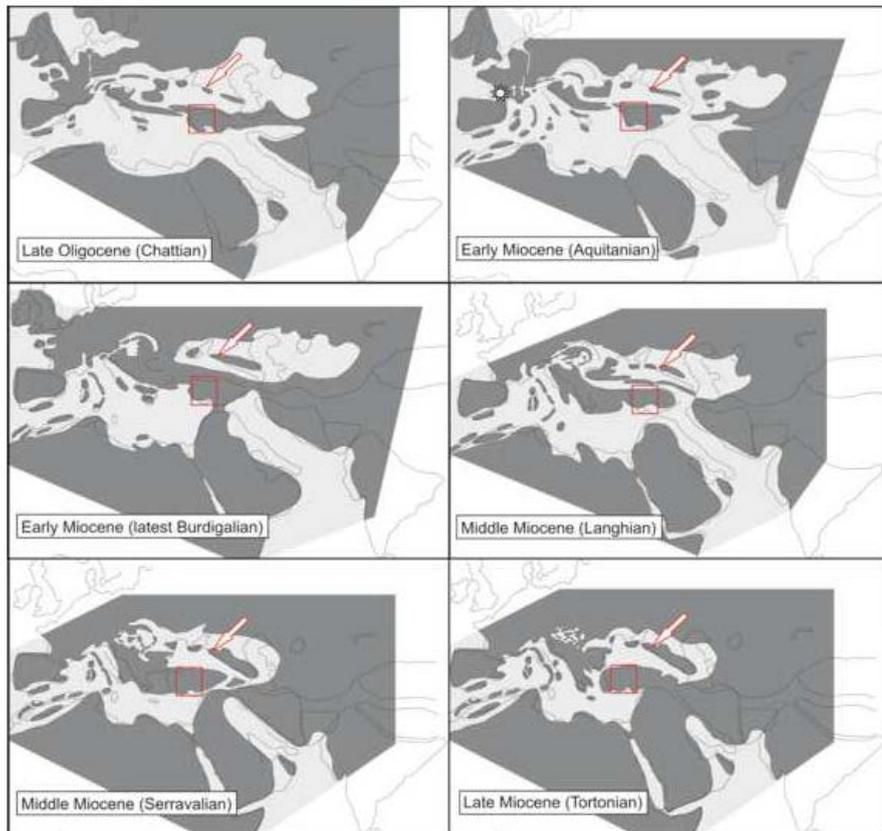
Table 1

Table 1. Review of litareture data on the fossil record of ectothermic vertebrates from the O

		Locality	Kocayarma & Kavakdare	Kargi 2
		Formation		
		Age	e. Oligocene	transition l. Oligocene - e. Miocene
		Reference	Čerňanský et al. 2017	Čerňanský et al. 2017
Taxon	Teleostei	Cyprinidae		
	Urodela	Salamandridae		
	Anura	Ranidae		
		Pelobatidae		
	Lacertilia	Blanidae		
		Anguidae	Anguidae indet.	Anguidae indet. *Ophisaurus* sp.
	Crocodylia			
	Serpentes			
		Boidae		
	Testudines	Emydidae		
		Chelydridae		

ligocene to middle Miocene of Turkey.

Kargi 1	Kurucan (54m-S10AT1) Medikdere	Kilçak 3b	Sabuncubeli
e. Miocene	l. Oligocene - e. Miocene	e. Miocene	e. Miocene
Čerňanský et al. 2017	Szyndlar and Hoşgör 2013	Čerňanský et al. 2017	Čerňanský et al. 2017
Anguidae indet.		Anguidae indet.	Anguidae indet.
	Bavarioboa sp.		

Tuz-6 Turabi	Ağaöz (Aköz) Güvem Formation	Ahlath Dere Güvem Formation	Keseköy
e. Miocene	e. Miocene	e. Miocene	e. Miocene
Sen et al. 2011	Paicheler et al., 1978; Dubois et al., 2010	Dubois et al., 2010	Čerňanský et al. 2017
	Leuciscus etilius *Barbus bispinosus*		
	Salamandridae indet.		
	Pelophylax sp. *Pelobates* sp.	*Pelobates* sp.	
			Anguidae indet. *Ophisaurus* sp.
Crocodylia indet.			
	Colubroidea indet.		
	Chelydropsis sp.		

Çandir & Çandir HW	Bağiçi	Alpagut-Dodurga
m. m. Miocene	l. m. Miocene	e. Miocene - m. Miocene
Čerňanský et al. 2017	Čerňanský et al. 2017	Rückert-Ülkümen 1998, 2003
		Barbus guendogani *Barbus schizakanthus* *Leuciscus dodurgaensis* *Leuciscus macrurus* *Tinca* cf. *furcatus*
		Rana (?*Pelophylax*) sp.
Anguidae indet. *Ophisaurus* sp.	Anguidae indet. *Ophisaurus* sp. *Anguis* sp.	

Gebeceler Gebeceler	Küçükdoganaca Kökü
(e.) m. Miocene	m. Oligocene - m. Miocene
Georgalis et al. 2018	Schleich 1994
Blanus cf. *strauchi*	
	Crocodylia indet.
	Emydidae indet. "*Palaeochelys*" *rueckerti* "*Palaeochelys*" *turcica* *Chelydropsis* sp. Testudines indet.

Table 2

Table 2. Fauna of ectothermic vertebrates from the studied localities. Orange cells - results of the present study, green cells - Čerňanský et al. 2017

	Taxa	locality								
		Kargı 1	Kargı 2	Kargı 3	Harami 1	Harami 3	Keseköy	Hançılı	Çandır	Bağıçi
	palaeoenvironment	swamp	swamp	lake	swamp	swamp	lake	swamp/lake	palacosol	lake ?
Teleostei	*Luciobarbus* sp.				■					
	Barbus sp.				■					
	Luciobarbus vel *Barbus* sp.							sp. 1 - 3		
	aff. *Capoeta* sp.									
	Barbini indet.	■	■				■			
	Leuciscus sp.						■			
	Cyprinidae indet.						■			
	Teleostei indet.	■	■				■			
Lissamphibia	*Salamandra* sp.				■			■		■
	Pelobatidae indet.							■		
	Bufonidae indet.							■		■
	Latonia sp.	■	■		■		■	■		
	Palaeobatrachidae indet.	■	■				■			
	Anura indet.	■								■
Reptilia	*Pseudopus* sp.	■								
	Ophisaurus sp.		■				■			■
	Anguis sp.									
	Anguinae indet.		■	■			■			■
	Lacertidae indet. 1									
	Lacertidae indet. 2						■		■	
	Lacertidae indet. 3						■	■		
	Lacertidae indet. 4								■	
	Lacertidae indet.						■		■	
	Lacertilia indet.	■					■			
	Blanidae indet. (?*Blanus* sp.)									
	Albaneryx sp.			■						
	Erycinae indet.				■					■
	Serpentes indet.						■		■	
	Crocodylia indet.	■	■	■	■		■		■	

8.   Appendix III: Supplementary material

This section includes supporting information in the cited order in the main text.

Capoeta buhsei   1 mm

Capoeta saadii   1 mm

Capoeta capoeta   1 mm

Capoeta sevangi   1 mm
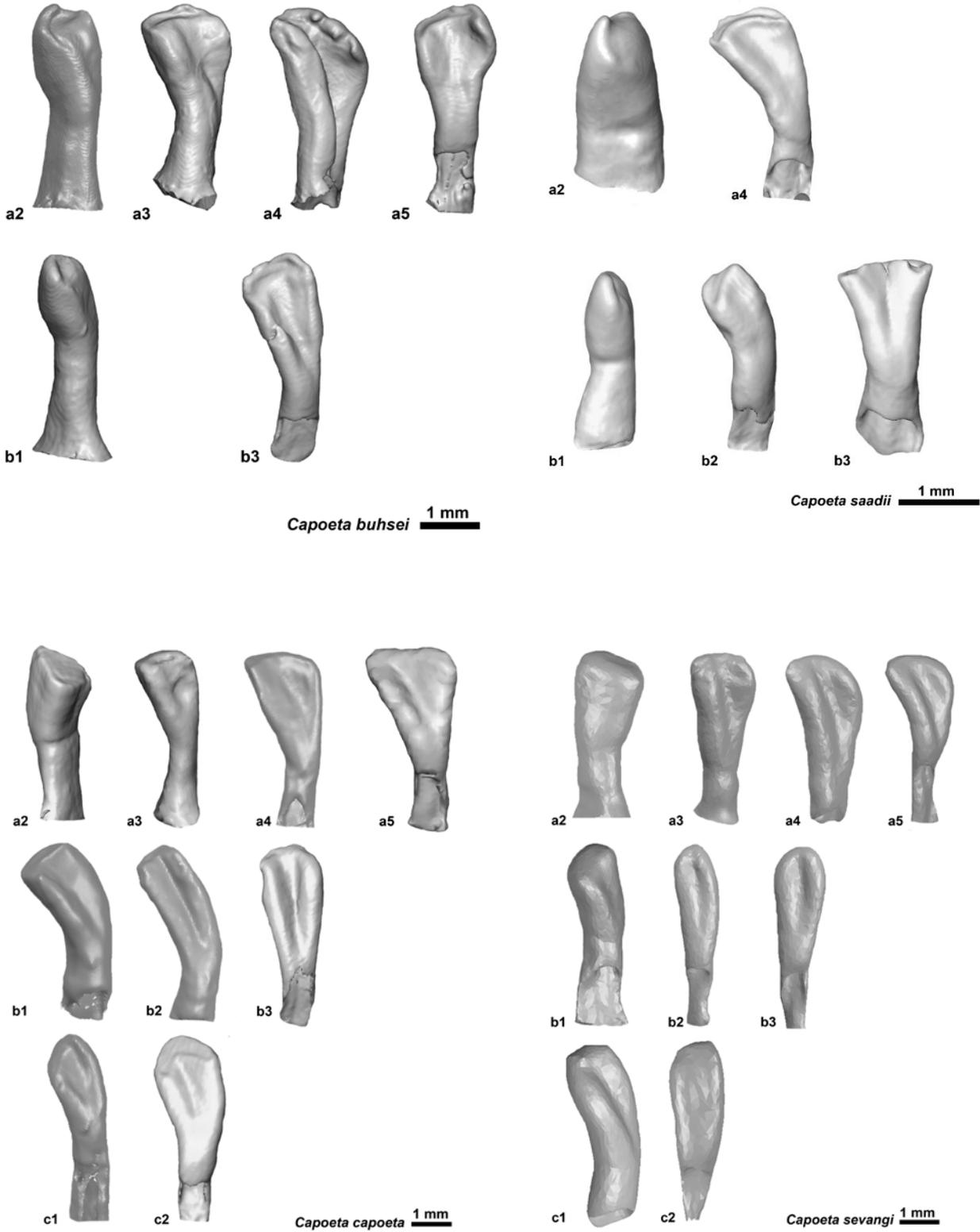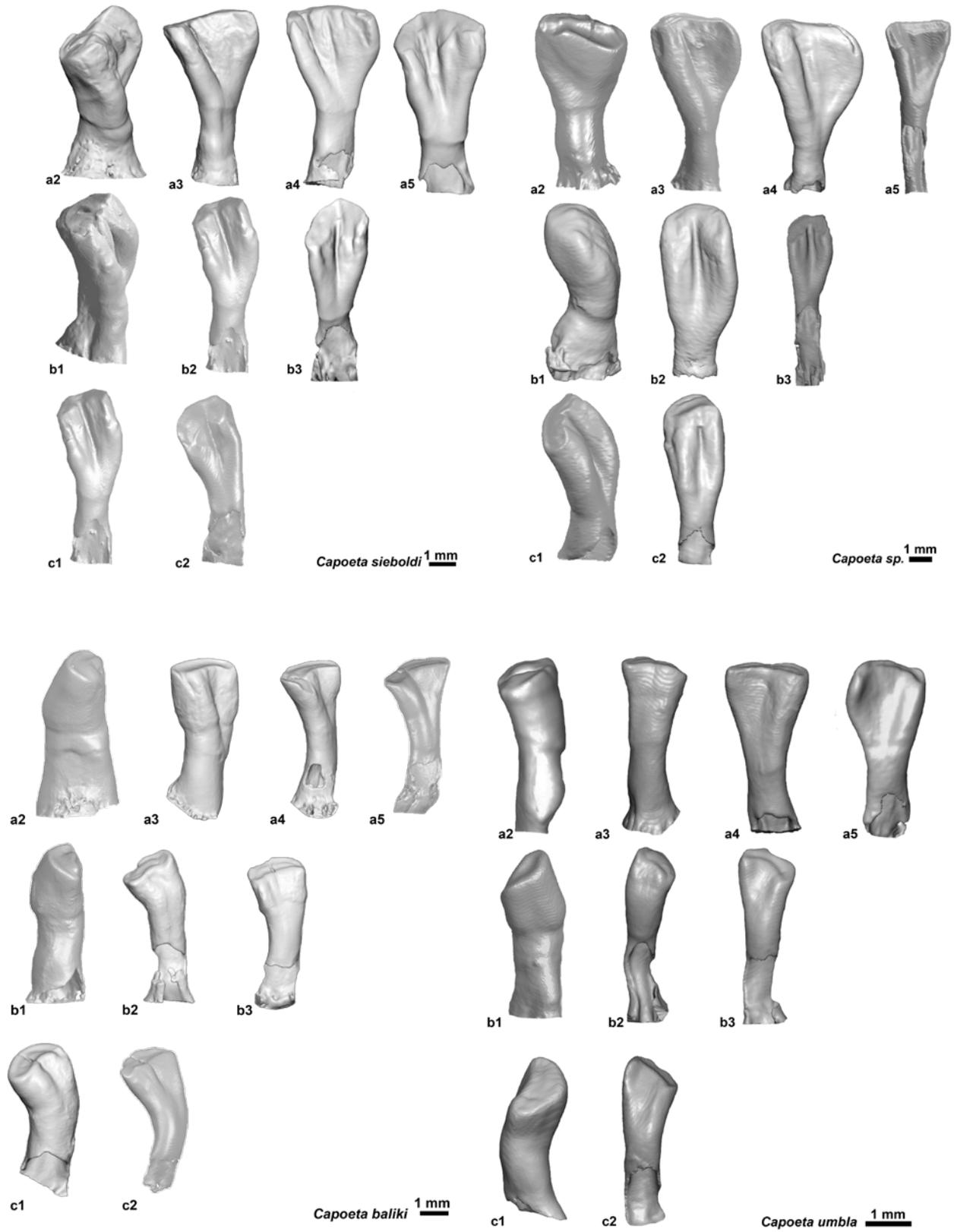
S1 Figure. Isolated pharyngeal teeth sets of the extant comparative material of *Capoeta*. Ayvazyan et al., 2018.
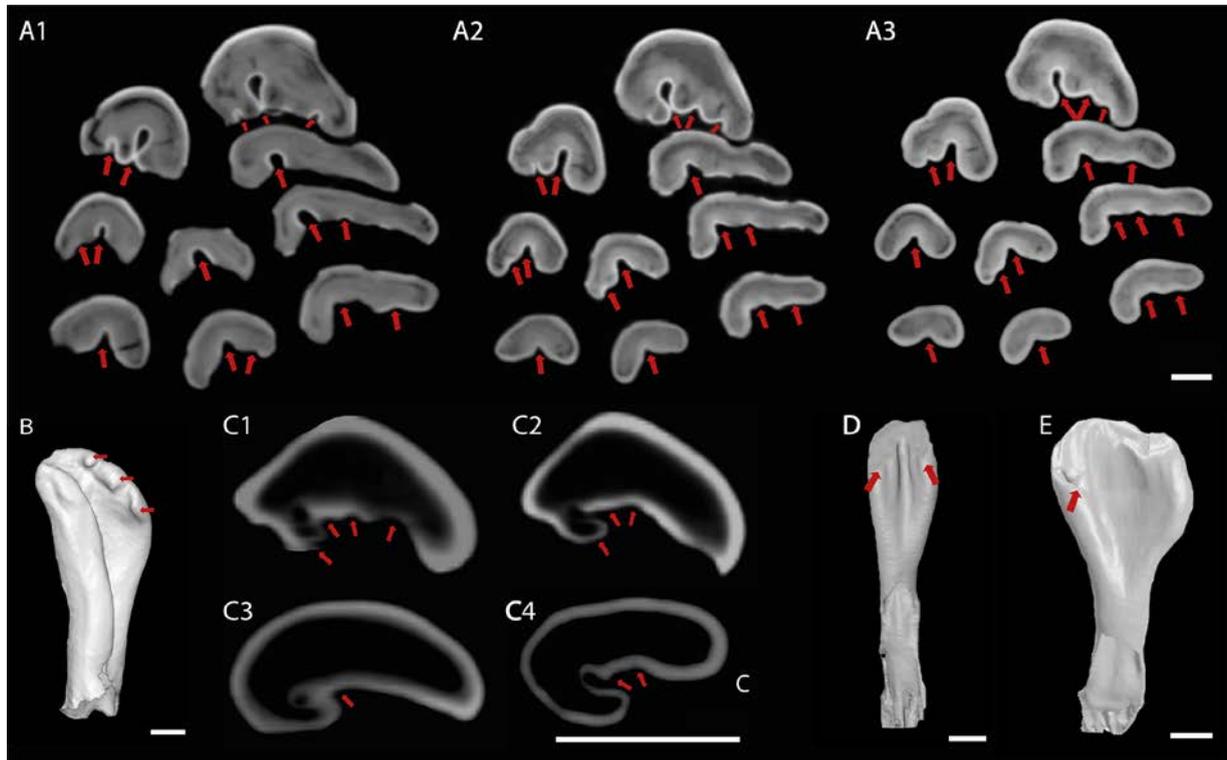
S2 Figure. Recorded variable morphologic characters of the grinding surface. (A) pharyngeal dentition of *C. sieboldi*, A1, A2, A3 correspond to the transverse cross-section of teeth at 0.57 mm, 0.87 mm and 1.42 mm below the top of the grinding surface. (B) *C. buhsei*, a4 tooth; C1, C2, C3, C4 correspond to 0,42 mm, 0,78 mm,1.31 mm and 1.87 mm below the top of the grinding surface of the a4 tooth of *C. buhsei*; (D) *Capoeat sp.*, b3 tooth; (E) *C. trutta*, a5 tooth. The scale bars equal to 1mm. Ayvazyan et al., 2018.

Table S1 Description of the shape characters. * molariform tooth morphology indicates/includes well-distinguished foot-crown border; spatulate - not well distinguished foot-crown border, margins widen distally and bent ventrally/laterally; oblong-longer than broad and with nearly parallel sides; reniform-kidney shape, concave dorsally/posteriorly and deeply convex ventrally/anteriorly.

Shape characters

Lateral outline (α)

α1	is molariform*. Foot is longer than crown. The crown is convex ventrally. The width at foot and crown section is nearly the same.
α2	is spatulate* in shape.
α3	is similar to α2, but widen rapidly and the foot section is nearly two times narrower than the crown section.
α4	is molariform but flower bud in shape and compressed on foot-crown border.
α5	is linear. The foot-crown border is differentiated, where the crown bents laterally. The foot is shorter than the crown, but the width of tooth is equal/constant along the body.
α6	is ablong*.
α7	is molariform, but bents ventrally. The foot and crown section are nearly same in length and width.
α8	is ablong, but unlike to α6 it bents dorsally and slightly widen distally.
α9	is molariform, but the foot-crown border is not well differentiated and it bents slightly dorsally/anteriorly. The crown is wider than the foot.
α10	is similar to α1, but it widen distally and bents dorsally.
α11	is similar to α1, but bents dorsally and unlike to other molariforms slightly narrows distally.
α12	is molariform, but is widen rapidly, foot is shorter and narrower than the crown.
α13	is similar to α11, but foot is shorter than the crown.
α14	is narrow ablong but the foot-crown border is slightly differentiated.

Transverse cross-section (β)

β1	is more or less rounded in shape.
β2	is slightly triangular in shape.
β3	is bean-shaped (concave dorsally and convex ventrally).
β4	is reniform.
β5	is comma-shaped and narrows laterodistally.
β6	is unciform (shaped like a hook).
β7	is reniform but gibbous (extremely convex ventrally) with the irregular folds on the dorsal edge of the grinding surface.
β8	is isosceles triangular, slightly convex ventrally with a cavity/fold on the dorsal edge of the grinding surface.
β9	is similar to β3 but gibbous and slightly convex dorsally.
β10	is more or less ellipsoid and slightly narrows laterodistally.
β11	is ovate, oblong but broader at one side (more or less oval in shape).

Table S2 Tooth shape classes in the studied recent *Capoeta* species.

Teeth shape classes	Tooth position	Shape characters	Species
A	a2	$\alpha8\beta1$	*Capoeta umbla*
B	a3	$\alpha2\beta5$	*Capoeta umbla*
	a3, a4		*Capoeta baliki*
	a3		*Capoeta buhsei*
	a3		*Capoeta damascina*
C	a4, a5	$\alpha3\beta6$	*Capoeta umbla*
	a5		*Capoeta baliki*
	a3,a4,a5		*Capoeta sp.*
	a3,a4,a5		*Capoeta trutta*
	a3,a4,a5		*Capoeta sevangi*
	a3,a4,a5		*Capoeta capoeta*
	a3,a4,a5		*Capoeta sieboldii*
	a4, a5		*Capoeta buhsei*
	a4		*Capoeta saadii*
	a4, a5		*Capoeta damascina*
D	a2	$\alpha4\beta7$	*Capoeta sieboldii*
E	b1	$\alpha7\beta8$	*Capoeta sp.*
	a2,b1		*Capoeta trutta*
F	b2,b3, c1,c2	$\alpha2\beta4$	*Capoeta sieboldii*
	b2,b3, c1, c2		*Capoeta trutta*
	b2,b3, c1, c2		*Capoeta sp.*
	b3, c1,c2		*Capoeta capoeta*
	b2,b3,c2		*Capoeta sevangi*
G	a2	$\alpha12\beta10$	*Capoeta sp.*
H	b1,c1	$\alpha1\beta2$	*Capoeta umbla*
	b1,c1		*Capoeta baliki*
	b1,c1		*Capoeta damascina*
I	b2, b3, c2	$\alpha2\beta3$	*Capoeta baliki*
	b2, b3		*Capoeta saadii*
	b2,b3,c2		*Capoeta damascina*
	b2, b3, c2		*Capoeta umbla*
	b3		*Capoeta buhsei*
J	a2	$\alpha11\beta9$	*Capoeta baliki*
K	b1	$\alpha1\beta11$	*Capoeta saadii*
	a2,b1		*Capoeta buhsei*
L	a2	$\alpha6\beta11$	*Capoeta saadii*
M	b1,b2	$\alpha5\beta4$	*Capoeta capoeta*
	b1,c1		*Capoeta sevangi*
N	a2	$\alpha9\ \beta10$	*Capoeta sevangi*
O	a2	$\alpha10\ \beta11$	*Capoeta capoeta*
P	a1	$\alpha14\ \beta1$	*Capoeta damascina*
Q	a2	$\alpha13\ \beta1$	*Capoeta damascina*
R	b1	$\alpha7\ \beta7$	*Capoeta sieboldii*

Table S3 The presence/absence of shape classes in the studied *Capoeta* species.

Shape classes / Species	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
Capoeta umbla	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Capoeta baliki	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
Capoeta trutta	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Capoeta sp.	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Capoeta capoeta	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0
Capoeta sevangi	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0
Capoeta sieboldii	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Capoeta saadii	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0
Capoeta buhsei	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Capoeta damascina	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0
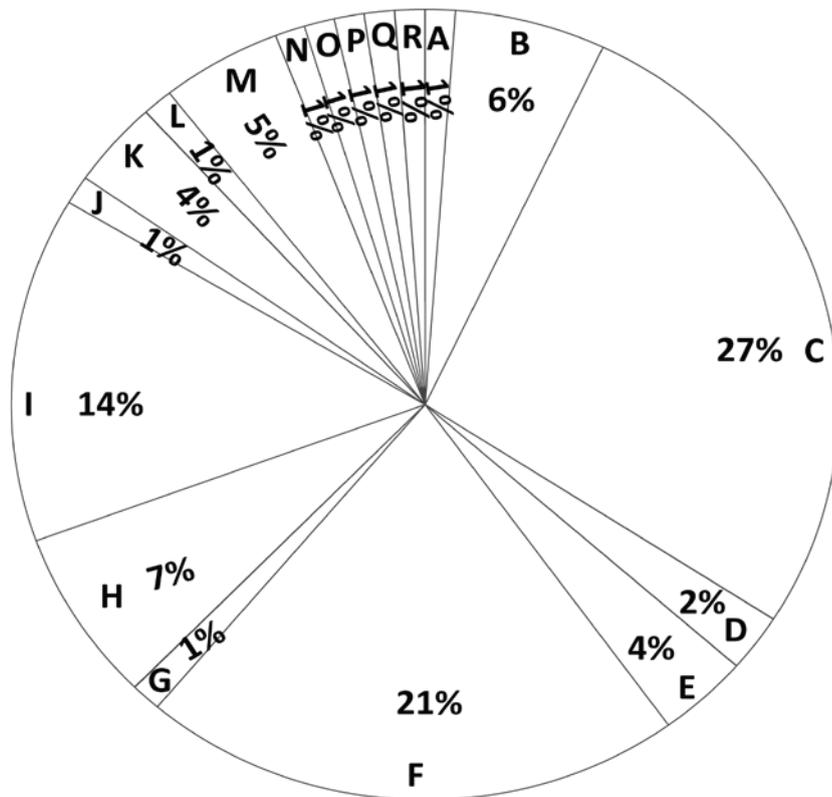
S3 Figure. The frequency (in % of all studied teeth, n=84) of the pharyngeal tooth shape classes in 10 studied species of the genus *Capoeta*. Ayvazyan et al., 2018.
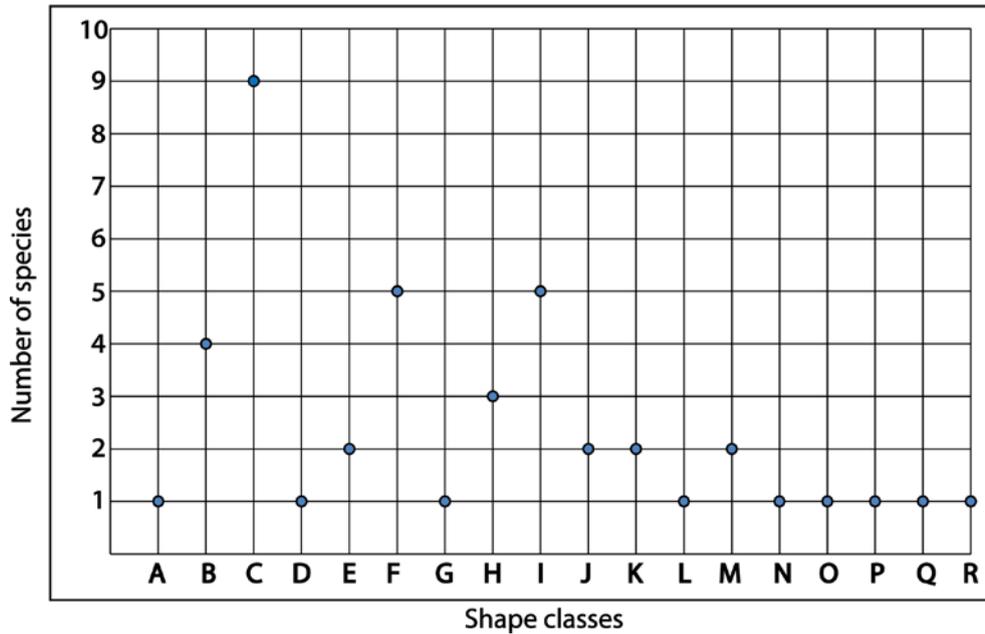
S4 Figure. The commonness of occurrences (Y axis) of the shape classes (X axis) in the studied *Capoeta* species, shows that most shape classes occur in one or two species only, whereas certain shape classes appear commonly in several species (e.g. shape classes F and I), or characteristic to all species as shape class C (except *C.buhs*ei, as the teeth are broken). Ayvazyan et al., 2018.

1 (8) Shape class F is present..2

2 (3) Shape classes D and R are present...*C. sieboldii*

3 (5) Shape class E is present..4

4 (4a) Shape class G is present...*C. sp.*

4a ....*C. trutta*

5 Shape class M is present..6

6 (7) Shape class N is present ....*C. sevangi*

7 Shape class O is present ....*C.capoeta*

8 Shape classes B and I are present...9

9 (13) Shape class H is present...10

10 (11) Shape class J is present ....*C.baliki*

11 (12) Shape Classes A is present...*C.umbla*

12 Shape classes P and Q are present ....*C.damascina*

13 Shape class K is present 14

14 (15) Shape class L is present ....*C. saadii*

15a...*C.buhsei*

S5 Figure. Identification key of the pharyngeal teeth for the genus *Capoeta*, according to the studied species, which all are provided by teeth of the shape class "C".*Capoeta*. Ayvazyan et al., 2018.

S6 Figure. Frequency of shape classes in relation to the tooth positions. Note that certain tooth positions can be characterized by few shape classes (e.g. at the tooth position a4 the shape class C occurs in nine species and the shape class B in one species), whereby other positions are quite heteromorphic among species (e.g. at the position a2, seven shape classes can occur). Similar to this, certain shape classes appear in only one species at one tooth position (e.g. shape classes G, J, and L), others appear in four or all species at many tooth positions (e.g. shape classes C and F). Ayvazyan et al., 2018.

Table S4 The scan settings of the scanned fossil material.

| Speciemns	Fossil locality/horizon	Depository	Resolution mm*	Tube voltage kV**	Electrical current of tube mA***
Capoeta sp.	JZ-1	JRD-15/01	0.028	58	355
Capoeta sp.	JZ-1	JRD-17/07	0.001	180	150
Capoeta sp.	JZ-1	JRD-17/08	0.046	89	181
Capoeta sp.	JZ-1	JRD-17/09	0.046	89	181
Capoeta nuntius	Kisatibi	GNM 8-1	0.035	71	228
Capoeta nuntius	Kisatibi	GNM 10-1	0.037	94	162
Capoeta nuntius	Kisatibi	GNM 11-1	0.040	89	662
Capoeta nuntius	Kisatibi	GNM 13-4	0.035	67	288

*mm resolution
**kV (the voltage or electrical potential applied to the tube)
***mA (the electrical current that flows through the tube)

Table S6 Scan settings of the pharyngeal bones of barbins.

Species	Coll. Numbers	Resolution (mm)	Tube voltage (kV)	Electrical current of tube (mA)
Luciobarbus comizo	MNCN 69304	0.038	150	64
Luciobarbus	MNCN E 54	0.026	83	99

longiceps				
Luciobarbus sclateri	MNCN 69331	0.03	64	150
Barbus barbus	SNSB SPAM-PI-00608	0.028	10	10
Barbus meridonalis	MNCN 19933	0.038	150	64
Barbus sacratus	MNCN GUI 17	0.026	83	99
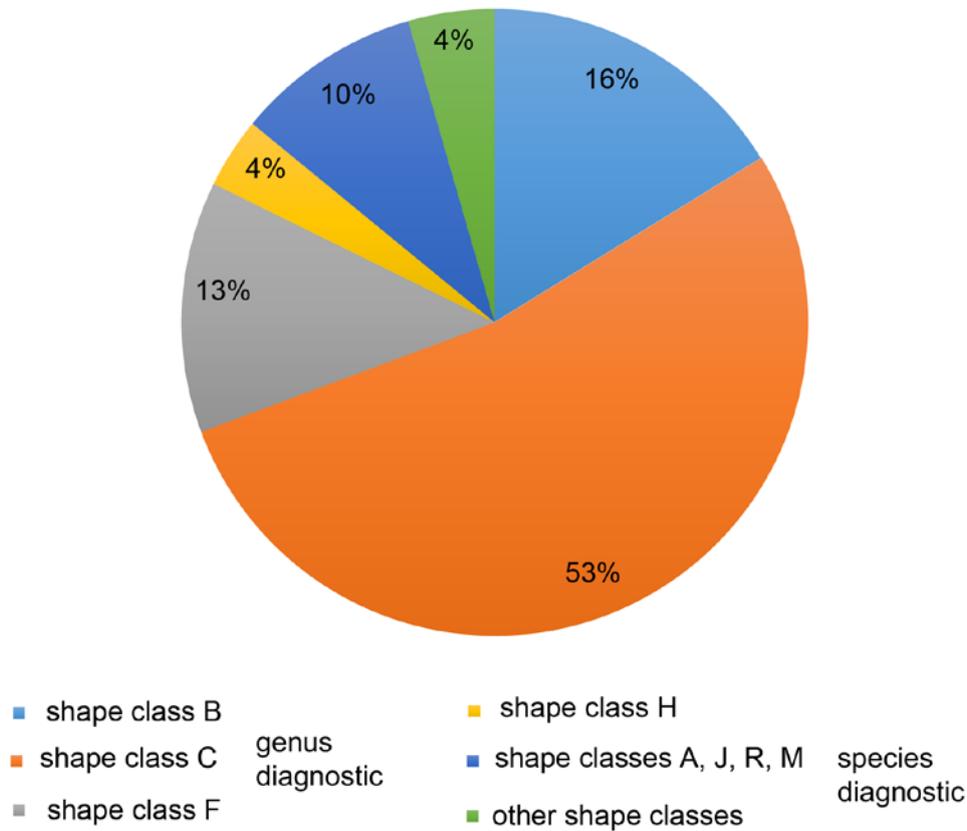
S7 Figure. Frequency distribution of recorded shape classes in the Çevırme sample (n=247). Ayvazyan et al., 2019.

Table S7 Fossil material from latest Oligocene to middle Miocene localities Kargı 1, Kargı 2, Harami1, Hancılı and Keseköy (Turkey).

Speciemens	Fossil locality	Number (n)	Morphotype	Depository
pharyngeal teeth				
Luciobarbus sp.	Hancılı	8	d3	UU HAN 5304, 5305, 5334
Luciobarbus sp.	Hancılı	4	d5	UU HAN 5332–5333
Luciobarbus sp.	Hancılı	1	d5	HAR1 5300

Luciobarbus sp.	Hancılı	21	d7	UU HAN 5313–5316
Barbus sp.	Hancılı	23	d4	UU HAN 5307, 5307-1, 5308, 5309
Barbus sp.	Hancılı	28	d6	UU HAN 5310-5312, 5321, 5335
Barbus sp.	Harami 1	1	d6	UU HAR1 5301
Luciobarbus vel *Barbus* sp	Hancılı	15	d1	UU HAN 5300, 5301, 5321
Luciobarbus vel *Barbus* sp	Hancılı	27	d2	UU HAN 5302, 5303, 5306
aff. *Capoeta* sp.	Hancılı	1	d8	UU HAN 5317
Barbini indet.	Kargı 1	15		UU KAR1 1300 – 1305
Barbini indet.	Kargı 2	19		UU KAR2 1301 – 1302, 1304-1306
Barbini indet.	Keseköy	116		UU KE 5305 – 5310
			dorsal fin spine	
Luciobarbus vel *Barbus* sp	Hancılı		s1 (7 unbranched last spine of the dorsal fin)	UU HAN 5322 – 5324
Luciobarbus vel *Barbus* sp	Hancılı		s2 (5 unbranched last spine of the dorsal fin)	UU HAN 5325 – 5328
Luciobarbus vel *Barbus* sp	Hancılı		s3 (2 unbranched last spine of the dorsal fin)	UU HAN 5329 – 5330
Barbini indet.	Kargı 2		one unbranched dorsal fin ray	UU KAR2 1303