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An Integrated Paleoenvironmental Reconstruction of the Early Pleistocene Hominin-Bearing Site of Dursunlu (Türkiye)

Àngel H. Luján [1,*], Václav Paclík [2], Elvan Demirci [3,4], Andrea Villa [1], Thomas A. Neubauer [5,6,7], Alaettin Tuncer [8], Martin Ivanov [2], Àngel Blanco-Lapaz [9,10], Kelly Ann Vega-Pagán [1] and Josep Sanjuan [3]

1 Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA), Universitat Autònoma de Barcelona, C/Columnes, s/n, Cerdanyola del Vallès, 08193 Barcelona, Spain; andrea.villa@icp.cat (A.V.); kelly.vega@icp.cat (K.A.V.-P.)
2 Department of Geological Sciences, Faculty of Science, Masaryk University, Kotlářská 267/2, 611 37 Brno, Czech Republic; 358290@mail.muni.cz (V.P.); mivanov@sci.muni.cz (M.I.)
3 Departament de Dinàmica de la Terra i de l'Oceà, Facultat de Ciències de la Terra, Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, 08028 Barcelona, Spain; edemirde116@alumnes.ub.edu (E.D.); josepsanjuan@ub.edu (J.S.)
4 MSA Geological Engineering, Maltepe Mahallesi G.M.K. Bulvarı No:51/24, 06570 Ankara, Türkiye
5 SNSB—Bavarian State Collection for Paleontology and Geology, Richard-Wagner-Straße 10, 80333 Munich, Germany; neubauer@snsb.de
6 Department of Earth and Environmental Sciences, Palaeontology & Geobiology, Ludwig-Maximilians-Universität München, Richard-Wagner-Str. 10, 80333 Munich, Germany
7 Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, The Netherlands
8 Graduate School of Science and Engineering, Hacettepe University, 06800 Ankara, Türkiye; tunceralaettin@gmail.com
9 Senckenberg Centre for Human Evolution and Paleoenvironment (SHEP), Hölderlinstrasse 12, 72074 Tübingen, Germany; angel.blanco-lapaz@uni-tuebingen.de
10 Institute for Archaeological Sciences, University of Tübingen, Hölderlinstrasse 12, 72074 Tübingen, Germany
* Correspondence: angel.lujan@icp.cat

Abstract

The fossiliferous Dursunlu Lignite Quarry (DLQ) is highlighted prominently in the archeological and paleontological literature because of the study of Pleistocene fauna and lithic artifacts, being considered the oldest Paleolithic site in Türkiye. Although the fauna and flora assemblage from DLQ are reasonably well known, taxonomic studies devoted to some groups, such as ostracods, mollusks, reptiles, and amphibians, have never been carried out. Here, we describe, illustrate, and study the taxonomic composition and ecological implications of the unpublished material of said groups, together with the aquatic plants and fish, recovered from six samples taken from the palustrine and peat bog facies of the sedimentary sequence. In addition, the recovered charophytes and cyprinids refine our taxonomical knowledge of both aquatic plants and fish. Our results concur with previous paleoenvironmental inferences based on flora and fauna composition—with DLQ representing a very shallow eutrophic lake with a dense palustrine vegetation belt during the cold (glacial) stage of the late Early Pleistocene—as well as highlight the study of all available groups as pivotal for better understanding the paleolake biota. We further conclude that the wetland areas of Dursunlu and surrounding steppe areas appear to have been an excellent environment for sporadic settlement of hominins during the Early Pleistocene, given the availability of food resources and easy access to water.

Keywords: Dursunlu paleolake; Günz glaciation; paleoecology; hominins sporadic settlement; Central Anatolia

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1. Introduction

1.1. The Hominin-Bearing Site of Dursunlu Lignite Quarry

1.1.1. Historical Background

The fossil site of Dursunlu Lignite Quarry (DLQ) in the Konya Province, Central Anatolia region, Ilgın Basin (Figure 1) has stood out in the study of Pleistocene mammals from Eurasia and lithic artifacts, being considered the oldest known Paleolithic site (Early Pleistocene) in Türkiye [1,2]. It was discovered in 1986 ([3]; and references therein) during a mapping project of the General Directorate of Mineral Research and Exploration of Turkey and gained more importance with the discovery of human artifacts by the latter team, together with the Ankara University (Türkiye) and the University of California, Berkeley (USA) within the project "Vertebrate Fossils of Turkey" in 1993–1994 [4]. The DLQ was opened and abandoned several times during the 1980s and early 90s because of the low quality of coal, until it was declared as a "protected area" in 1994. Although it used as a power plant in 2024, it is currently not in service and was filled with groundwater and wetlands (e.g., [3,5,6]).

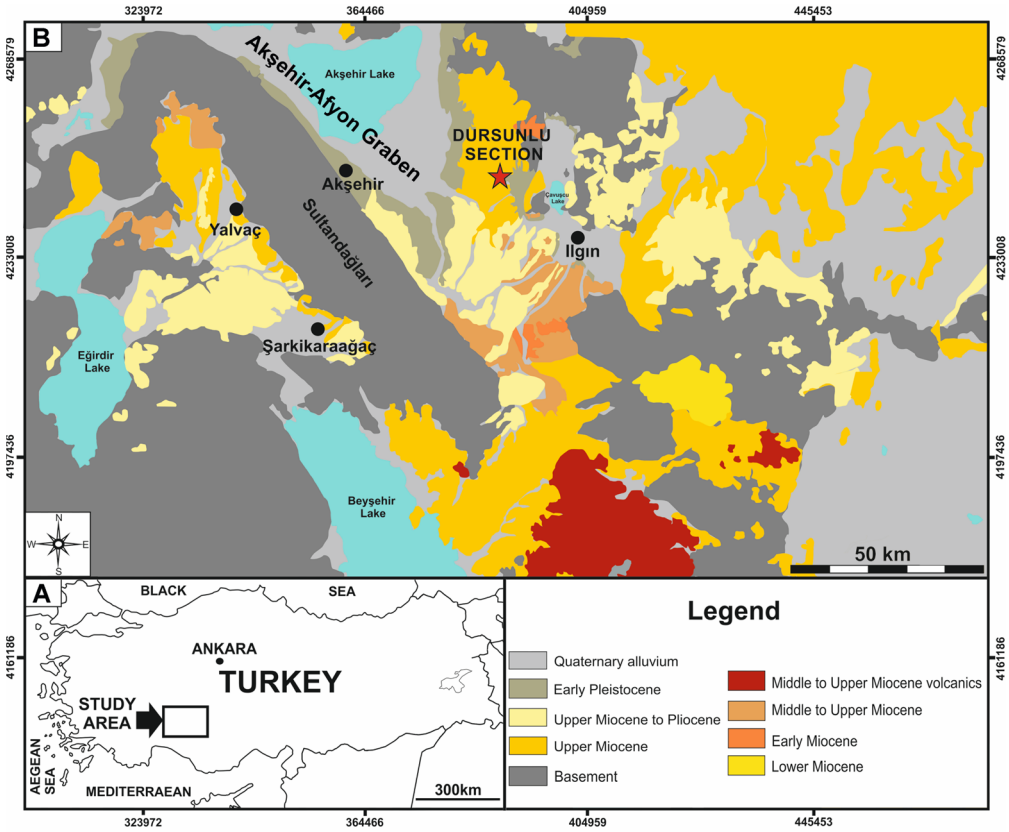

Figure 1. (**A**) Geographic location of the Ilgın Basin within Türkiye. (**B**) Simplified geological scheme of the study area: the red star denotes the location of the studied section. Modified from (Koopman [7]: Figure 3) and (Demirci et al. [5]: Figure 2).

Mammal remains, assigned to proboscideans, artiodactyls, perissodactyls, and carnivorans, were found by the miners in 1986 from the bioturbated, gastropod-rich clays and silt layers, as well as from the overlying lignite layer, also called upper lignite [3,4]. Moreover, small mammals, such as eulipotyphlans, lagomorphs, and rodents, were recovered from the clay layer by wet sieving more than ten tons of sediment [4]. Additional remains of mammals, reptiles, amphibians, birds, and fish were subsequently recovered during 1993 and 1994, and reported in several publications (e.g., [2,4,8–10]). Paleontological studies conducted at DLQ increased significantly when several fragments of mammal

bones were found associated with lithic artifacts, including chipped stone tools [1]. This not only attested the presence of hominin at that site, but further, they represented the oldest evidence of hominins ever found in Türkiye. The significance of the site grew further during the next years, with the recovery of more than 100 modified lithic artifacts produced with the bipolar technique, including quartz flakes, as well as cut-marked bones [2,11,12]. The first palynological studies were published by Yavuz-Işık [13], indicating a pollen community dominated by different kinds of herbs, abundant arboreal components, and moist-adapted aquatic plants, which suggested a humid-temperate climate during the Early Pleistocene. More recently, a Ph.D. thesis focused on the revision of Miocene-Pleistocene ostracod fauna from Southwest Anatolia and recovered up to 18 ostracod taxa from Dursunlu Formation [14]. Similarly, Demirci et al. [5] studied the aquatic plant assemblage (mainly charophytes) along with gastropods and bivalves recovered from 50 samples taken from all exposed strata at the DLQ (about 18 m thick). These authors also conducted a sedimentological analysis in order to assess the environmental evolution of the paleolake. Subsequently, fish remains (cyprinids and cobitids) from the same samples were published by Blanco-Lapaz et al. [6]. Finally, Yavuz et al. [3] restudied the pollen assemblage of freshwater algae, herbs, hydrophytes ferns, and *Pinus*, together performing a reconstruction of the paleovegetation and paleoenvironmental conditions.

1.1.2. Chronological Background and Aims

Recovered macromammals from DLQ are diverse, including felids, bovids, cervids, and equids. Ünay et al. [4] mentioned faunal similarities of the Pleistocene faunas of Monte Peglia (Italy) and Les Valerots (France) with DLQ, and more specifically they used the presence of the vole *Allophaiomys nutiensis* to assign an age of ca. 0.9 Ma to the latter. Howell et al. [9] revised the entire micromammal assemblages from DLQ under a strictly biostratigraphic approach, concluding that the presence of the arvicolid rodents *A. nutiensis* and *Lagurus arankae* fit well with zone MNQ-20. Güleç et al. [2] went a step further and combined both magnetostratigraphic—two 50 m cores— and biostratigraphic data. In fact, they correlated the sedimentary sequence of DLQ to the reverse polarity of the upper Matuyama chron (0.773–0.99 Ma) but further proposed an interpolated age (0.85 to 0.90 Ma) for the lithic assemblage bearing layer (LAL) based on the micromammal assemblage.

Despite many detailed studies on fish, birds, macro- and micromammals, pollen, and aquatic plants, other groups from DLQ have received little (i.e., seeds and ostracods) to no (reptiles, amphibians, and mollusks) attention. Here, we study the above-mentioned groups to update the faunal record and complete the paleoenvironmental reconstruction of the DLQ during the cold (glacial) stage of the late Early Pleistocene (Günz glacial period).

2. Geographical and Geological Setting

The DLQ is located on the Lycaonian Plateau (31°46′10.7″ N, 38°22′38.3″ E), on the northern front of the Taurus Mountains (Figure 1), and more specifically, about 1.5 km southwest of the homonymous village in the Ilgın district, Konya province (Central Anatolia, Türkiye). As stated by Koçyiğit et al. [15], the western half of Central Anatolia is dominated by a series of horst and graben structures bounded by active normal faults. Among them, the Akşehir-Afyon Graben is one of the most important active rifts, which is W–NW to E–SE-oriented, and bordered North–South by the Emir and Sultan Mountains, respectively. This graben contains both Eber and Akşehir Lakes, as well as sedimentary infills ranging from Miocene to Quaternary. From a geological viewpoint, the DLQ is placed on the eastern border of the Isparta Angle and further represents the Southeast extension of the larger Akşehir-Afyon Basin [7].

In the Dursunlu area, the bedrock basement of the Akşehir Basin consists of Early Cambrian–Late Cretaceous metavolcanic (quartzite, schist, and ophiolites) and metasedimentary (marble, dolomite, and nodular cherty limestones) rocks (e.g., [3,16–19]). The Akşehir-Afyon Basin is filled by two main sedimentary sequences, Miocene and Pleistocene in age, respectively, separated by an angular unconformity. During the Miocene, alluvial fans of the Belekler (conglomerates, sandstones, siltstones, and mudstones) and Aşağıçiğil (mainly coal, marls, conglomerates, sandstones, siltstones, and mudstones) Formations were deposited discordantly on the older Paleozoic/Mesozoic deposits ([20]; and references therein). An alternation of coals (with up to three m-thick layers) with claystones, marls, and mudstones (Dursunlu Fm.; Figure 2A–C) overlies the Miocene alluvial fan deposits [21]: this formation has a total thickness of 320 m and is composed of fine-grained horizons and peatlands littered with vertebrate and mollusk remains. Quaternary sedimentation in the Akşehir-Afyon Basin terminates with the uppermost colluvial and alluvial sediments.

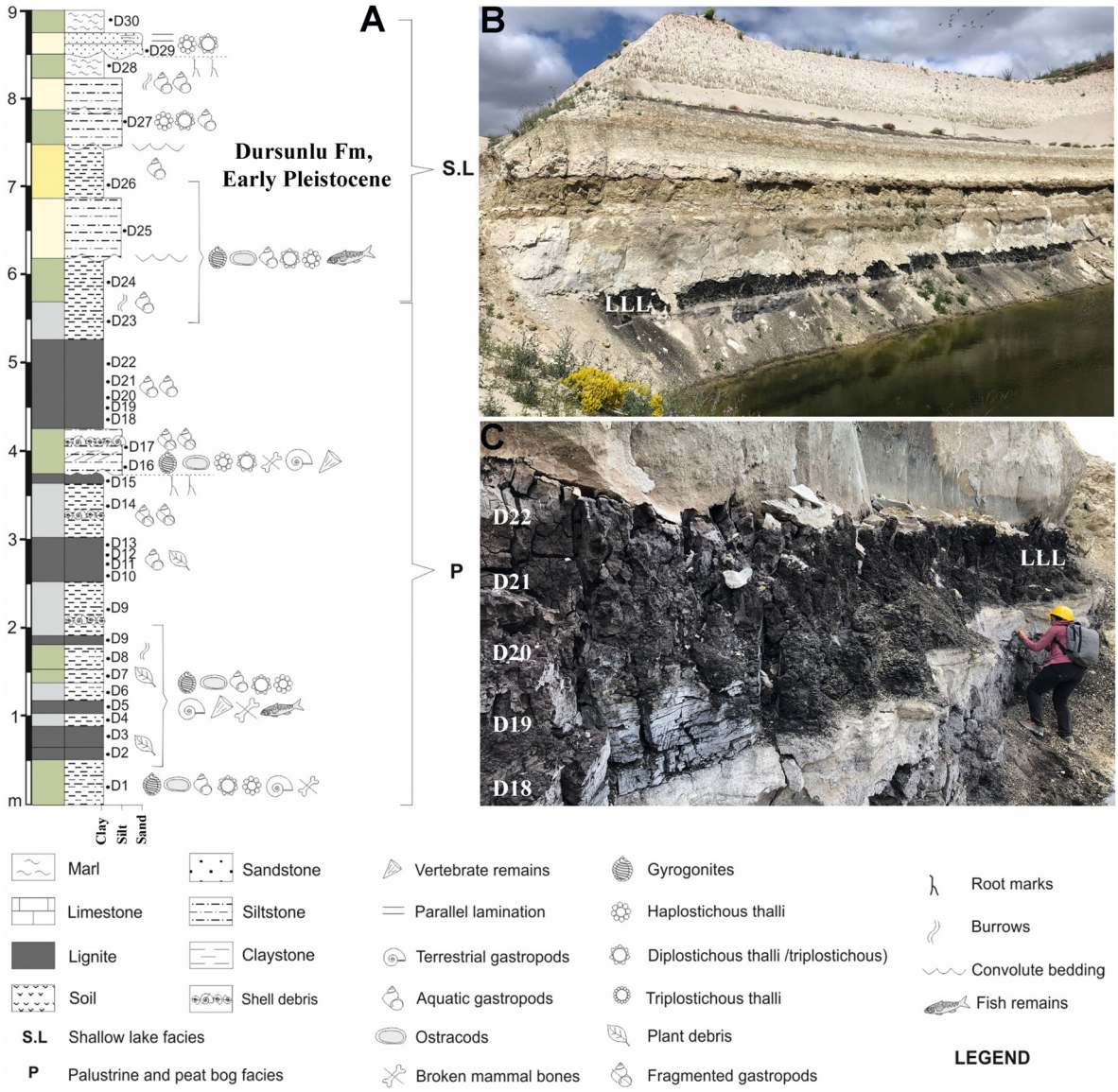

Figure 2. (**A**) Stratigraphic section of the first nine m at DLQ (SE of Ilgın Basin, Türkiye). (**B**) Field photo showing the palustrine (where the largest lignite layer is denoted by LLL), peat bog, and lake facies; (**C**) detailed field photo of the bottom of the stratigraphic column (between four and six m) showing the samples D18–D22. D1 indicates sample 1: the same applies for D2 until D30.

The six samples studied herein belong to the Dursunlu Formation [21], including the upper lignite member also described by Güleç et al. [2]. According to Demirci et al. [5], the entire sequence exposed in the DLQ consists of two facies associations: the base is formed by approximately six m of organic-rich siltstones/claystones (dark brown to grayish layers with root marks: Figure 2B,C; samples D1–D23), which are rich in invertebrate, vertebrate, and floral remains (i.e., palustrine and peat bog facies = also corresponding to lithic assemblage bearing layer); and the upper part of the section, from 6 to 18 m (samples D24–D50 in [5]: Figure 2), which consists of light gray-yellowish fossiliferous marls, marly siltstones, and a limestone bed (Figure 2B) with abundant charophyte flora, ostracods, and mollusk remains.

3. Material and Methods

The samples studied were extracted from soft rocks (marls, siltstones, and claystones) in the DLQ: coordinates 38.37519130 N, 31.77109127 E (Figure 1A,B). Six samples (D2–D3, D16–D17, and D22–D23), each weighing 3 kg, were extracted and processed to recover the material of interest: flora (including seeds), arthropods, and mollusks in the Paleontology Laboratory of the Department of Geological Engineering, Hacettepe University (Ankara, Türkiye), and in the Department of Earth and Ocean Dynamics (Faculty of Earth Sciences), University of Barcelona (Catalonia, Spain), and vertebrate remains in the Paleontology Unit, Department of Geology, Universitat Autònoma de Barcelona (Catalonia, Spain). Soft rocks were disaggregated in a solution of 12 L of water, hydroxide peroxide (150 mL), and sodium carbonate (7 g) for 72 h. Once the clayed component had been dissolved, sediments of the different samples were washed with a regulated stream of running water in sieves of varying mesh sizes (2, 1, 0.5, 0.35, and 0.2 mm). All fossils were sorted under a light binocular microscope. The most complete gyrogonites, seeds, and fish bones were selected and photographed using a scanning electron microscope (Quanta 200 at the Centres Científics i Tecnològics, Universitat de Barcelona: CCiTUB; Tescan Gaia3 + at Hacettepe University: HÜNİTEK), whereas photos of selected herpetofauna and mollusk specimens were mainly taken with a Leica M80 stereomicroscope (Wetzlar, Germany) and a Nikon D7500 camera (Tokyo, Japan). All illustrated remains presented here are currently housed in the Ege University Natural History Museum (Izmir, Türkiye) under the catalogue number EUNHM PV–KID-1-45 (KID = Konya, Ilgın, Dursunlu). To estimate whether the mollusk taxa composition was accurately sampled, conducted rarefaction analyses for the assemblages of four of the six samples (D2, D16, D17, D22) using R v4.3.2 [22] with the iNEXT v3.0.1 package was performed [23] and 500 calculation knots. For bivalves, the higher number of left or right valves was used as the number of specimens.

Taxonomic analysis follows the systematics of Horn af Rantzien [24] and Feist et al. [25] for gyrogonites, Neubauer et al. [26] for mollusks, Schönhuth et al. [27] and Küçuk et al. [28] for cyprinids, Dubois et al. [29] for anurans, de Broin [30] for turtles, and Szyndlar [31] for snakes.

4. Results

The Floral and Faunal Assemblage

The following sections report on the fossil flora, arthropods, mollusks, and vertebrates identified in the faunal assemblages of samples D2, D16–D17, and D22–D23 (Table 1).

Charophytes: Up to three gyrogonite species of the genus *Chara* (Characeae) have been found in the sample D-2. *Chara hispida* gyrogonites are large and prolate to perprolate in shape (Figure 3A–C: EUNHM PV–KID-1). The morphometrical parameters and the presence of a psilocharoid-type apex allow us to refer them to genus *Chara*, and more particularly, to *C. hispida* on the basis of the tapering base and periapical thinning and swollen apex (e.g., [32,33]; and references therein). The second species is attributed to *Chara vulgaris* (Figure 3D–G:

EUNHM PV–KID-2) based on having a smaller size, prolate shape, pointed and psilocharoid apex, a rounded and tapered base, and a higher number of convolutions in lateral view (see [5,32]). The third species fits well with *Chara globularis* (Figure 3H–J: EUNHM PV–KID-3) since it displays a characteristic prominent and protruding psilocharoid apex, forming a hat-like shape. The base is slightly pointed and shows a large pore within a shallow pentagonal funnel [5,34]. These charophyte taxa have been recently described and depicted in detail by Demirci et al. [5] in the same stratigraphical column from Dursunlu.

Table 1. List of fossil taxa of flora, invertebrates (arthropods and mollusks), and vertebrates (teleosts, anurans, testudines, and squamates) recovered at Dursunlu site. '•' Denotes which taxa were previously reported in other publications, whereas 'This work' denotes the taxa described in this article.

Order/Suborder/ Family	Taxa	Demirci et al. (2023) [5]	Blanco-Lapaz et al. (2024) [6]	This Work	Figure
Characeae	*Sphaerochara intricata*	•			-
Characeae	*Sphaerochara prolifera*	•			-
Characeae	*Chara hispida*	•		•	Figure 3A–C
Characeae	*Chara vulgaris*	•		•	Figure 3D–G
Characeae	*Chara globularis*	•		•	Figure 3H–J
Characeae	*Chara* cf. *molassica* var. *notata*	•			-
Characeae	*Chara* cf. *pappii*	•			-
Characeae	*Chara* sp. 1	•			-
Characeae	*Chara* sp. 2	•			-
Characeae	*Lychnothamnus barbatus* var. *antiquus*	•			-
Characeae	*Nitellopsis obtusa*	•			-
Hydrocharitaceae	*Najas marina* s. str.			•	Figure 3K,L
Ranunculaceae	*Ranunculus* sp.	•			-
Potamogetonaceae	*Zannichellia palustris*	•		•	Figure 3M,N
Cyprididae	*Heterocypris salina*			•	Figure 4A,B
Cyprididae	*Prionocypris zenkeri*			•	Figure 4C
Cyprididae	*Neglecandonaangulata*			•	Figure 4D,E
Ilyocyprididae	*Ilyocypris* cf. *bradyi*			•	Figure 4F,G
Candonidae	*Cyclocypris* sp.			•	-
Candonidae	*Pseudocandona* sp.			•	-
Valvatidae	*Valvata cristata*			•	Figure 5A
Valvatidae	*Valvata* cf. *kebapcii*			•	Figure 5B
Bithyniidae	*Bithynia* s.l. sp.			•	Figure 5C
Hydrobiidae	*Tefennia* sp.			•	Figure 5D,E
Lymnaeidae	Lymnaeidae gen. et sp. indet.			•	Figure 5F
Lymnaeidae	?*Radix* s.l. sp.			•	Figure 5G
Planorbidae	*Anisus* sp.			•	Figure 5H
Planorbidae	?*Gyraulus* sp.			•	Figure 5I
Planorbidae	Planorbidae gen. et sp. indet.			•	Figure 5J
Planorbidae	*Armiger crista*			•	Figure 5K
Planorbidae	*Segmentina nitida*			•	Figure 5L
Sphaeriidae	*Euglesa obtusalis*			•	Figure 5M
Sphaeriidae	*Euglesa pseudosphaerium*			•	Figure 5N

Table 1. *Cont.*

Order/Suborder/ Family	Taxa	Demirci et al. (2023) [5]	Blanco-Lapaz et al. (2024) [6]	This Work	Figure
Ellobiidae	*Carychium minimum*			•	Figure 5O
Vertiginidae	*Vertigo angustior*			•	Figure 5P
Vertiginidae	*Truncatellina* sp.			•	Figure 5Q
Valloniidae	*Vallonia* cf. *enniensis*			•	Figure 5R
Teleostei	Teleostei indet.		•	•	Figure 6A
Cyprinidae	Cyprinidae indet.		•		-
Cyprinidae	*Capoeta* sp.		•		-
Cyprinidae	*Squalius* sp.		•	•	Figure 6B–D
Cyprinidae	*Chondostroma* sp.		•	•	Figure 6E–G
Cyprinidae	*Barbus* sp.		•	•	Figure 6F
Cobitidae	Cobitidae indet.		•		-
Anura	Anura indet.			•	Figure 7A,B
Bufonidae	Bufonidae indet.			•	Figure 7C–G
Ranidae	Ranidae indet.			•	Figure 8A–H
Testudines	cf. Geoemydidae indet.			•	Figure 9A,B
Squamata	Squamata indet.			•	Figure 9C
Squamata	Serpentes indet.			•	Figure 9D,E
Natricidae	cf. *Natrix* sp.			•	Figure 10A–F

From a paleobiogeographic viewpoint, *Chara hispida* probably originated during the Late Miocene in Western Europe and expanded quickly towards Asia during the latest Miocene–Pliocene. This species became fully cosmopolitan during the Quaternary (e.g., [35,36]), thriving in lakes in Europe (Spain and Poland: [37]), the Middle East (Western Türkiye: [38]), Africa (Morocco, Sudan: [39,40]), and South America (Argentina: [35]). Currently, it is a common taxon growing in permanent lakes in Europe, Siberia, and North Africa [36]. In turn, *C. vulgaris* is a cosmopolitan taxon that thrives in a wide array of shallow freshwater habitats (see [36,41]; and references therein). The fossil record suggests it originated during the Late Miocene in Western Europe as well and achieved a cosmopolitan distribution during the Pleistocene (see [33]). Pleistocene populations of this species have been found in lacustrine deposits in Eastern Europe (Cluj Basin, Romania: [42]), Western Türkiye (Söke region: Tuncer and Tunoğlu [43]), India (Kashmir and Bangong Co Basin: [44]), Africa (Chad, Algeria, and Sudan: [36]), and Argentina (Puna Plateau: [35]). Likewise, *C. globularis* appeared during the late Neogene, when its geographic distribution was restricted to the Northern hemisphere. This species has been reported in the Late Miocene–Pliocene of the Middle East (Bekaa Valley, Lebanon: [45]), India (Haiti, Guajart, and Jammu: [34]) and North America (Kansas, USA: [46]). However, its Pleistocene record is limited to the West of Türkiye (Söke area: [43]).

Other aquatic plants: EUNHM PV–KID-4 (Figure 3K,L) is a longer seed measuring more than 2 mm. *Najas marina* is an aquatic, annual, dioecious plant with notable morphological variability, especially in leaf shape, spine presence, and seed size (e.g., [47,48]. It typically has slender, branching, submerged stems with leaves that possess marginal teeth on the sheaths (see [47]; and references therein). The species adapts well to diverse freshwater habitats [48]. The revision of 29 herbarium specimens and recent field collections confirmed that all samples from the study area belong to *Najas marina* s. str. (Figure 3K,L), based on key morphological traits [47,48]. Despite size variations, the features fall within the species'

known range. New populations were discovered in the Sharypovskii District, extending the species' known range 240–250 km northwest in Southern Siberia [49]. These new localities are endorheic post-glacial lakes developed on Devonian and Neogene formations, underscoring the long-term persistence of *N. marina* s.str. in the region [49]. *Najas marina* is a submerged macrophyte found in Turkish wetlands such as Lakes Mogan, Eber, and Beyşehir (e.g., [50,51]). It thrives in shallow, nutrient-rich freshwater habitats with stable sediments and high light penetration. It supports water clarity, sedimentation, and aquatic biodiversity, and indicates ecological status through changes in its distribution ([50]; and references therein).

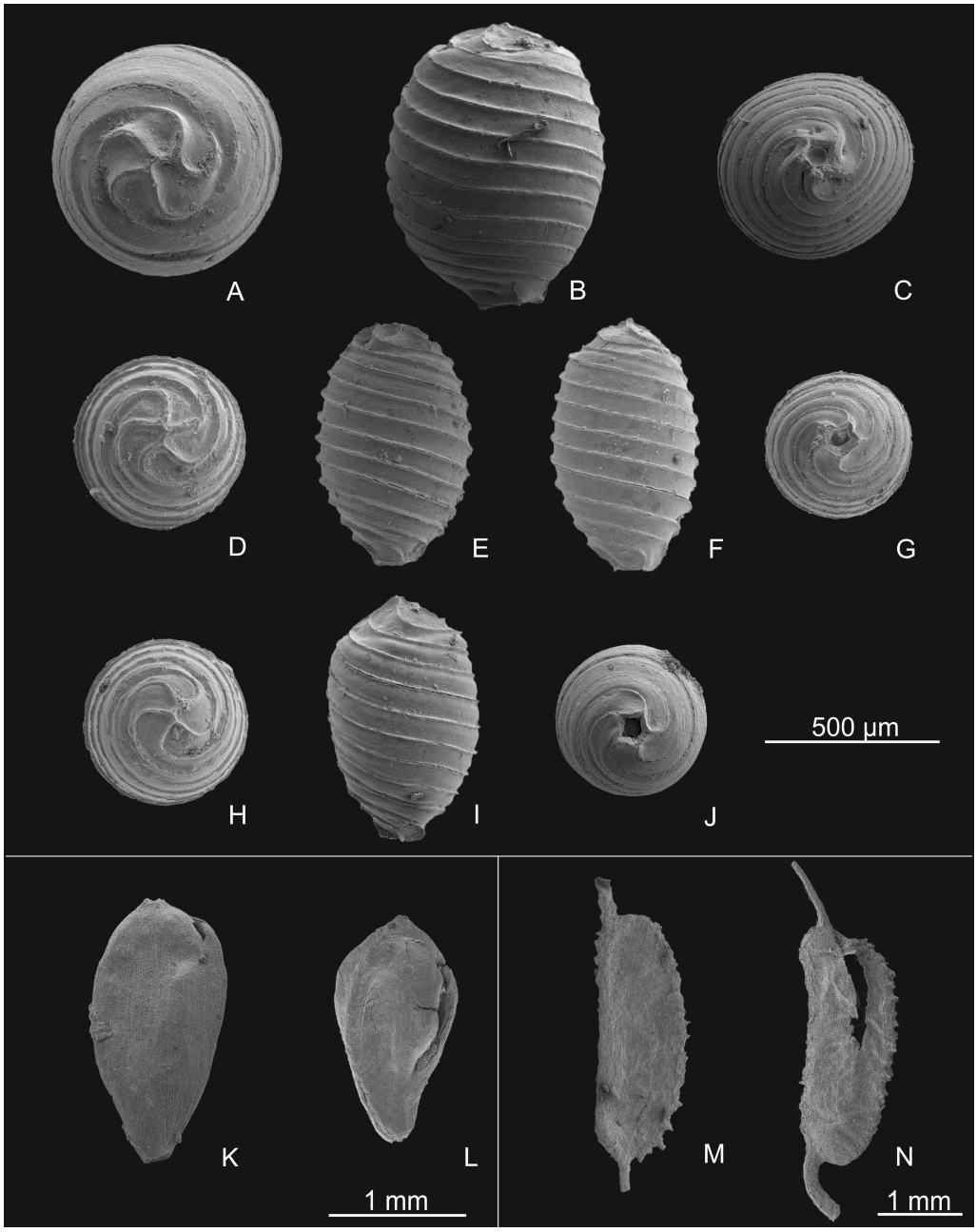

Figure 3. Remains of aquatic plants from DLQ (Ilgın Basin, Türkiye). (**A**–**C**) Gyrogonites of *Chara hispida* (EUNHM PV–KID-1) from sample D2. (**A**) Apical view; (**B**) lateral view; (**C**) basal view. (**D**–**G**) Gyrogonites of *Chara vulgaris* (EUNHM PV–KID-2) from sample D2: (**D**) apical view; (**E**,**F**) lateral views; (**G**) basal view. (**H**–**J**) Gyrogonites of *Chara globularis* (EUNHM PV–KID-3) from sample D2: (**H**) apical view; (**I**) lateral view; (**J**) basal view. (**K**,**L**) Lateral views of seeds attributed to *Najas marina* s. str. (EUNHM PV–KID-4) from sample D17. (**M**,**N**) Lateral views of seeds of *Zannichellia palustris* (EUNHM PV–KID-5) from sample D17.

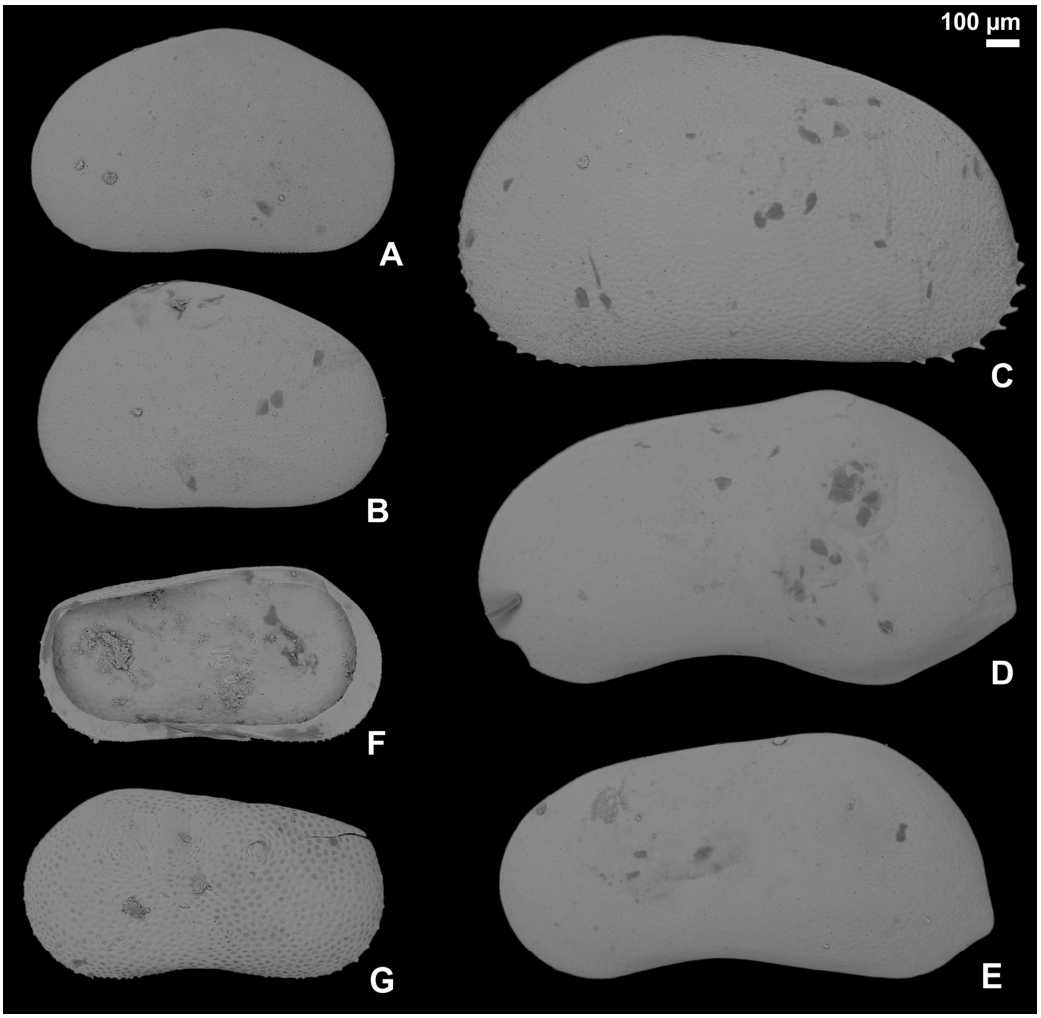

Figure 4. Ostracod carapaces recovered from samples D2–D3 and D16–D17, DLQ (Ilgın Basin, Türkiye). All images are external views of the carapaces, except for F, which is in internal view. S. (**A**,**B**) *Heterocypris salina* (EUNHM PV–KID-6): (**A**), external view of the right valve (l: 1094 µm; h: 680 µm); (**B**) external view of the left valve (l: 1057 µm; h: 689 µm). (**C**) *Prionocypris zenkeri* (EUNHM PV–KID-7): external view of the left valve (l: 1705 µm; h: 996 µm). (**D**,**E**) *Neglecandona angulata* (EUNHM PV–KID-8): (**D**) external view of the left valve, male (l: 1617 µm; h: 891 µm); (**E**) external view of the left valve, female (l: 1487 µm; h: 743 µm). (F,G) *Ilyocypris* cf. *bradyi* (EUNHM PV–KID-9): (**F**) internal view of the left valve (l: 1085 µm; h: 574 µm); (**G**) external view of the left valve (l: 1032 µm; h: 533 µm). Abbreviations: l = length, h = height.

EUNHM PV–KID-5 (Figure 3M,N) is a seed with a morphological appearance resembling a bean pod and measuring around 2 mm length. *Zannichellia* is a genus of submerged aquatic plants living in freshwater to brackish habitats [52,53]. According to Van Vierssen [52], *Zannichellia palustris* occurs in Northern to Western Europe, tolerates up to 3.5% salinity, and requires cold water for germination. It has short shoots, narrow leaves, and grows in shallow, temporary freshwater environments [52,53]. In the Baltic region, it is found in both brackish and freshwater environments [52]. *Zannichellia palustris* has been observed in several lakes across Türkiye, including Işıklı, Gökgöl, Eğirdir, Eber, Gölhisar, and Beyşehir ([51]; and references therein). It has a broad and subcosmopolitan distribution across temperate, subtropical, and tropical regions, including Europe, Asia Minor, Northern Africa, and parts of North America. It thrives in lakes, ponds, and slow-moving waters, demonstrating significant ecological flexibility (e.g., [49,52,53]).

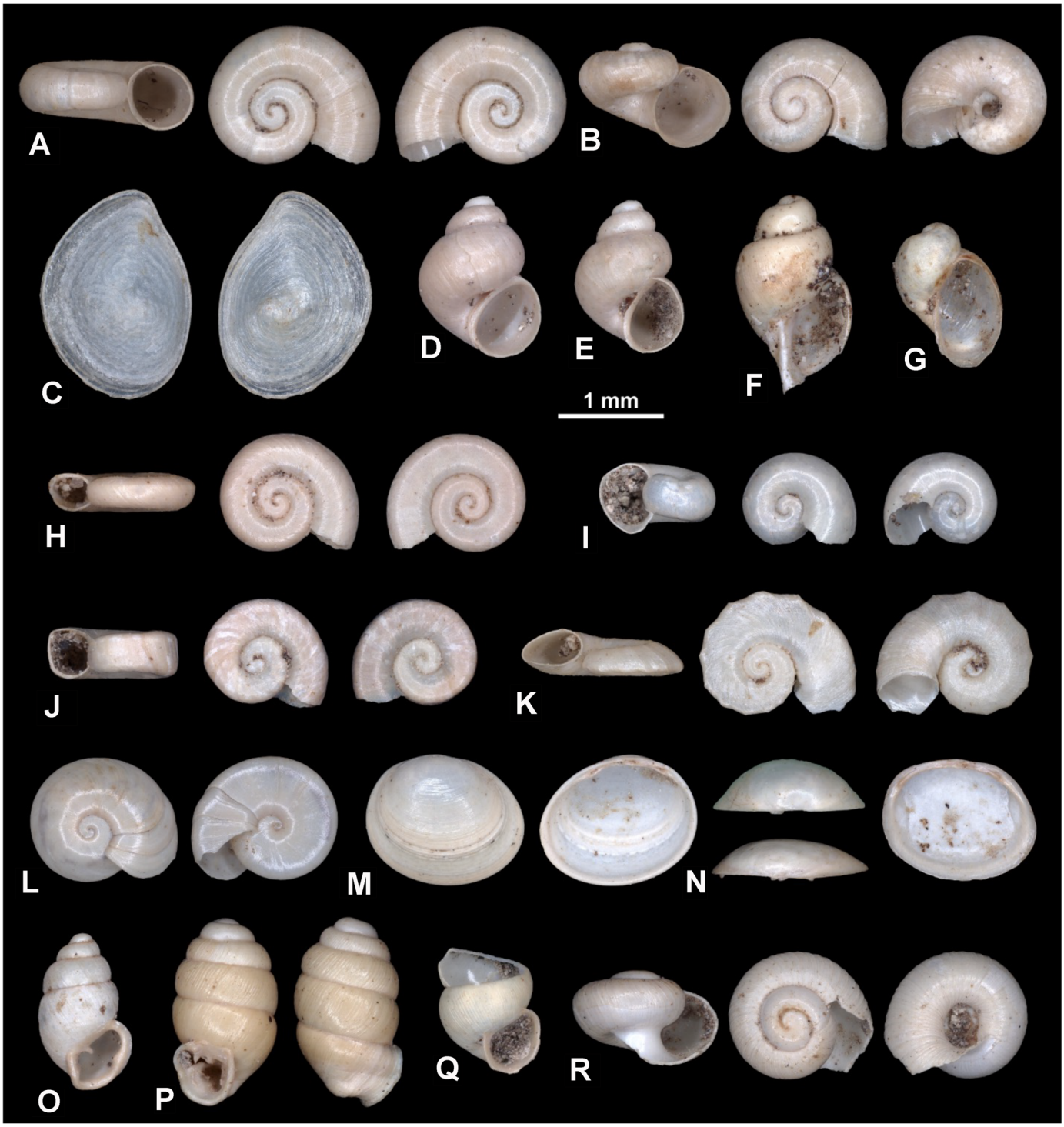

Figure 5. Representatives of the mollusk taxa retrieved from sample D2 from DLQ (Ilgın Basin, Türkiye). (**A**) *Valvata cristata* (EUNHM PV–KID-10). (**B**) *Valvata* cf. *kebapcii* (EUNHM PV–KID-11). (**C**) Opercula of *Bithynia* s.l. sp. (EUNHM PV–KID-12). (**D**,**E**) ?*Tefennia* sp. (EUNHM PV–KID-13 and EUNHM PV–KID-14). (**F**) Lymnaeidae gen. et sp. indet. (EUNHM PV–KID-15). (**G**) ?*Radix* s.l. sp. (EUNHM PV–KID-16). (**H**) *Anisus* sp. (EUNHM PV–KID-17). (**I**) ?*Gyraulus* sp. (EUNHM PV–KID-18). (**J**) Planorbidae gen. et sp. indet. (EUNHM PV–KID-19). (**K**) *Armiger crista* (EUNHM PV–KID-20). (**L**) *Segmentina nitida* (EUNHM PV–KID-21). (**M**) *Euglesa* sp. (EUNHM PV–KID-22) right valve, convex form. (**N**) *Euglesa* sp. (EUNHM PV–KID-23) left valve, low-convex form. (**O**) *Carychium minimum* (EUNHM PV–KID-24). (**P**) *Vertigo angustior* (EUNHM PV–KID-25). (**Q**) *Truncatellina* sp. (EUNHM PV–KID-26). (**R**) *Vallonia* cf. *enniensis* (EUNHM PV–KID-27).

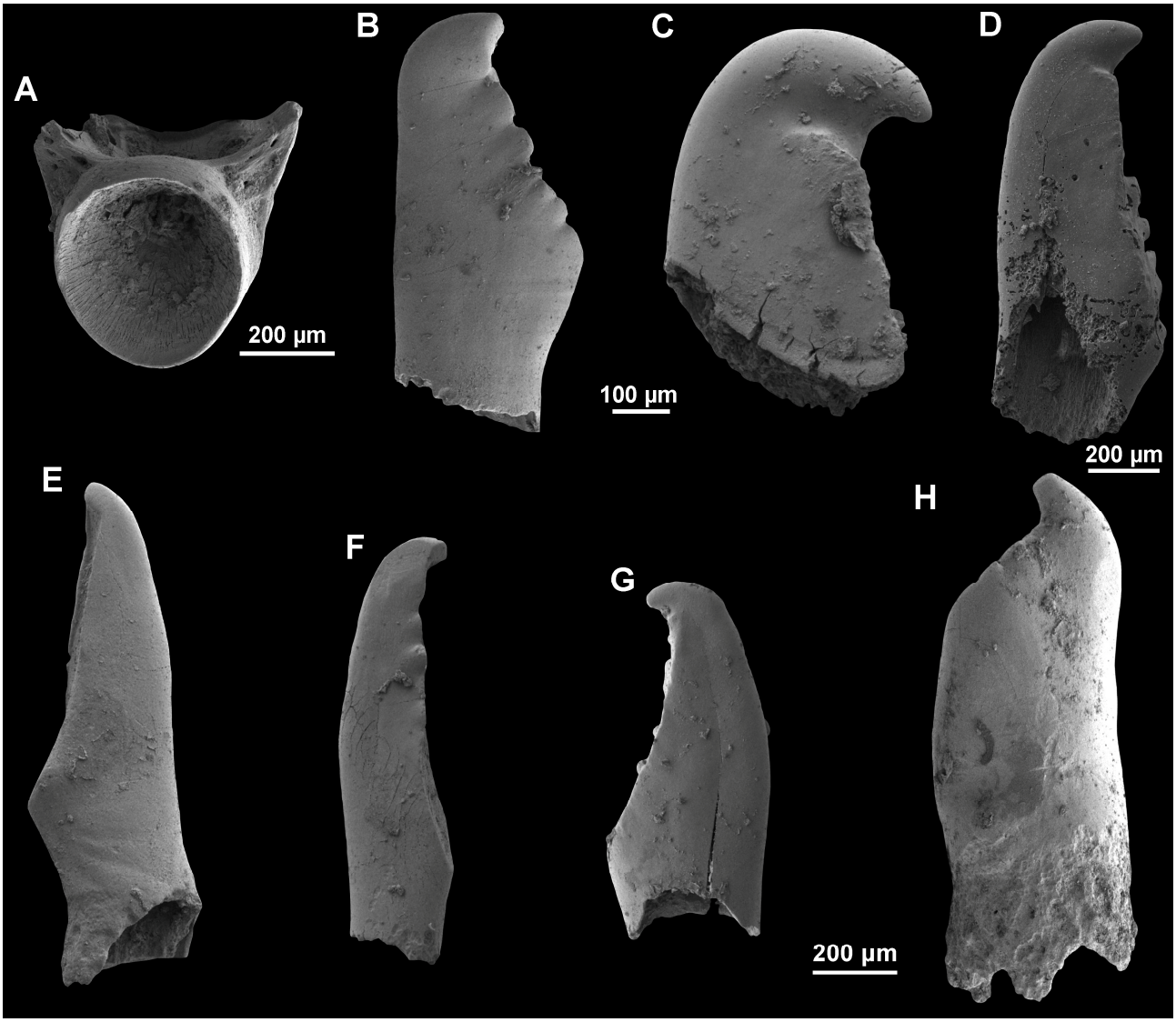

Figure 6. Fish remains recovered from samples D2–D3, D16, and D23 from DLQ (Ilgın Basin, Türkiye). (**A**) Partial vertebra of Teleostei indet. (EUNHM PV–KID-28) from D3. (**B**–**D**) Isolated pharyngeal teeth of *Squalius* sp. (EUNHM PV–KID-29, EUNHM PV–KID-30 and EUNHM PV–KID-31) from D2 (see also [6]; Figure 3B), D3 (see also [6]; Figure 3C3), and D16 (see also [6]; Figure 3M), respectively. (**E**–**G**) Isolated pharyngeal teeth of *Chondrostoma* sp. (EUNHM PV–KID-32, EUNHM PV–KID-33 and EUNHM PV–KID-34) from D3 (see also [6]; Figure 3C1–C2). (**H**) Isolated pharyngeal teeth of *Barbus* sp. (EUNHM PV–KID-35) from D23 (see also [6]; Figure 3N).

Ostracods. In this study, ostracod fauna (Cyprididae, Ilyocyprididae, and Candonidae) of the palustrine and coal-bearing lower parts of the Dursunlu Formation are determined by three samples (D2, D16, and D17): six ostracod taxa belonging to six genera were identified. The most abundant and diverse ostracod assemblage was recovered in the sample D2: *Heterocypris salina* (53 valves), *Ilyocypris* cf. *bradyi* (52 valves), *Neglecandona angulata* (33 valves and two carapaces), *Prionocypris zenkeri* (16 valves), *Cyclocypris* sp. (one valve), and *Pseudocandona* sp. (one valve).

Heterocypris salina. The valves, particularly the dorsal margins, exhibit a sub-triangular shape in lateral view (e.g., [54–57]). The left valve overlaps the right valve. Posteroventral and anteroventral rims of the right valve are covered by some small denticles (see [14]) that are apparent along the latter (Figure 4A,B: EUNHM PV–KID-6).

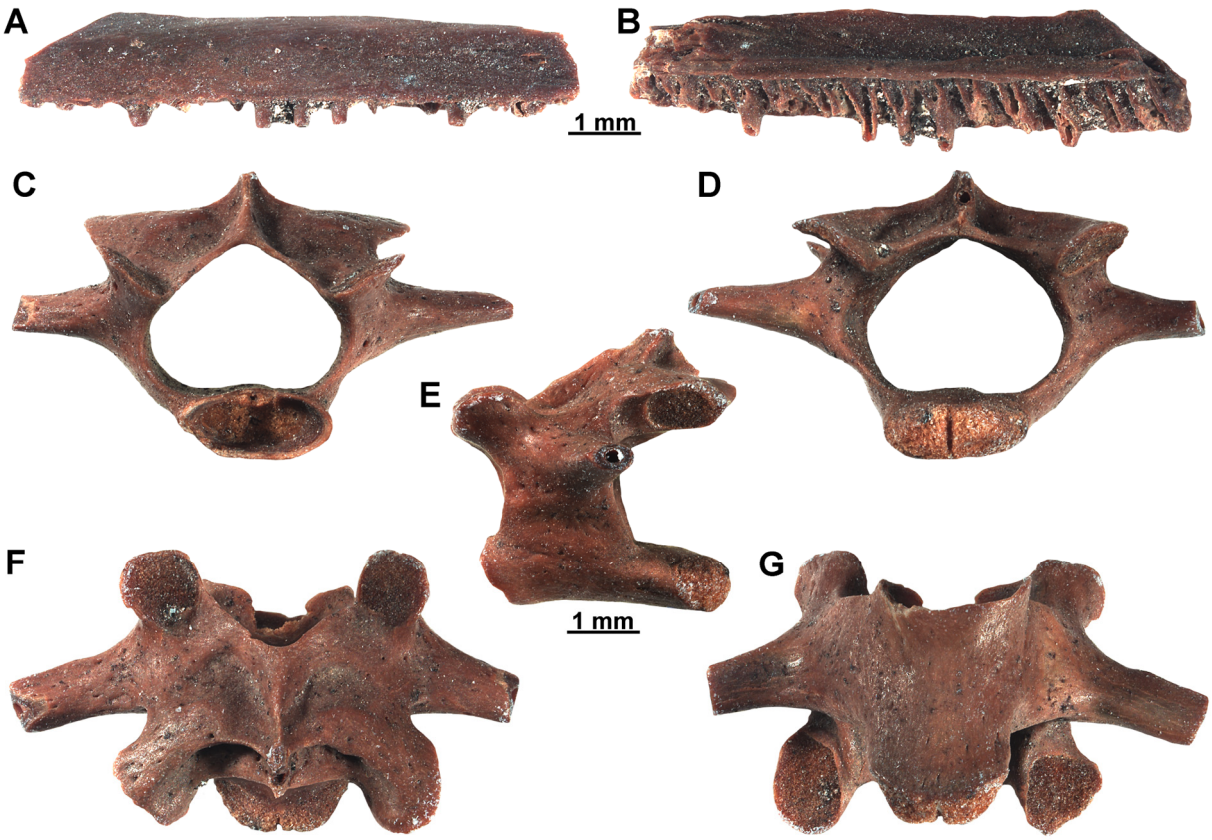

Figure 7. Indeterminate anuran and bufonid remains recovered from sample D16, DLQ (Ilgın Basin, Türkiye). (**A**,**B**) Partial maxilla (EUNHM PV–KID-36) of Anura indet. in lateral (**A**) and medial (**B**) views. (**C**–**G**) Trunk vertebra (EUNHM PV–KID-37) of Bufonidae indet. in anterior (**C**), posterior (**D**), left lateral (**E**), dorsal (**F**), and ventral (**G**) views.

Prionocypris zenkeri. The valves are claviform in lateral view. Well-developed 7–8 bigger denticles are arranged in a row along the posteroventral margin of the left valve, whereas the anteroventral margin displays comparatively smaller ones (e.g., [14,55,58]). These diagnostic characteristics make it simple to distinguish this salient species from other taxa (Figure 4C: EUNHM PV–KID-7).

Neglecandona angulata. The valves are elongated in lateral view and exhibit sexually dimorphic variations in both lateral and dorsal views (e.g., [58,59]). Lobe-like expansion, the diagnostic character of the species, is visible in the posteroventral margin of the adult left valves [58–61]. Moreover, particularly in adult forms, the posterior area of the valve surfaces is reticulated (Figure 4D,E: EUNHM PV–KID-8).

Ilyocypris cf. *bradyi*. The valves are sub-rectangular in lateral view (e.g., [14,54,56,62]). The dorsomedian part of both valves contains two vertically oriented sulci (grooves). The anterior and posterior margins have a few tiny denticles, with the latter being particularly noticeable [54,62]. Although it is unclear, marginal ripplets of the left valve resemble *bradyi*-type ripples. According to the above-mentioned features, they are here referred to *I.* cf. *bradyi* (Figure 4F,G: EUNHM PV–KID-9).

Cyclocypris sp. and *Pseudocandona* sp.: Due to the limited number of forms obtained, detailed diagnoses enabling the way for species-rank identification could not be performed. Therefore, these are left in open nomenclature.

The new ostracod fauna studied here from DLQ resembles those determined by Tuncer [14], who thoroughly examined this group but from laterally equivalent levels of our samples of the same Dursunlu Formation. Unlike sample D2, the abundance of *H. salina* in D16 level strikingly decreases, being represented by only two valves and one carapace. The

rest of taxa are composed by *I.* cf. *bradyi* (38 valves and two carapaces), *N. angulata* (29 valves and one carapace), and *P. zenkeri* (14 valves). As for the diversity and abundance of ostracod assemblage in D17 sample, it is relatively low: the most abundant species is *P. zenkeri* (14 valves of adults and larger juveniles), while species common in other samples, like *N. angulata* and *H. salina*, become extremely rare (two and one valves respectively, in this sample).

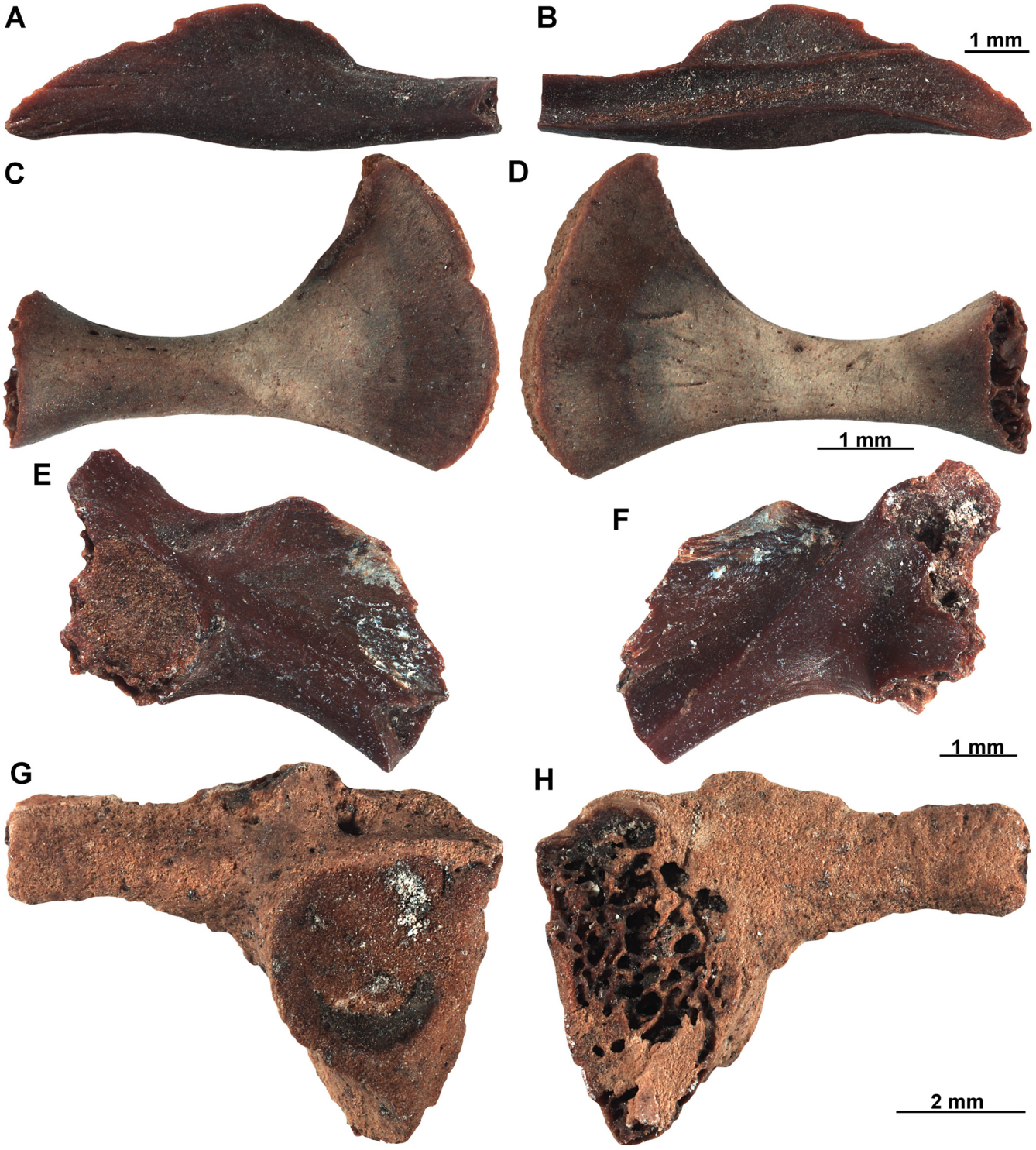

Figure 8. Ranid remains recovered from sample D16, DLQ (Ilgın Basin, Türkiye). (**A**,**B**) Partial angular (EUNHM PV–KID-38) of Ranidae indet. in ventral (**A**) and dorsal (**B**) views. (**C**,**D**) Coracoid (EUNHM PV–KID-39) of Ranidae indet. in dorsal (**C**) and ventral (**D**) views. (**E**,**F**) Partial ilium (EUNHM PV–KID-40) of Ranidae indet. in lateral (**E**) and medial (**F**) views. (**G**,**H**) Partial ilium (EUNHM PV–KID-41) in ventral (**G**), and medial (**H**) views.

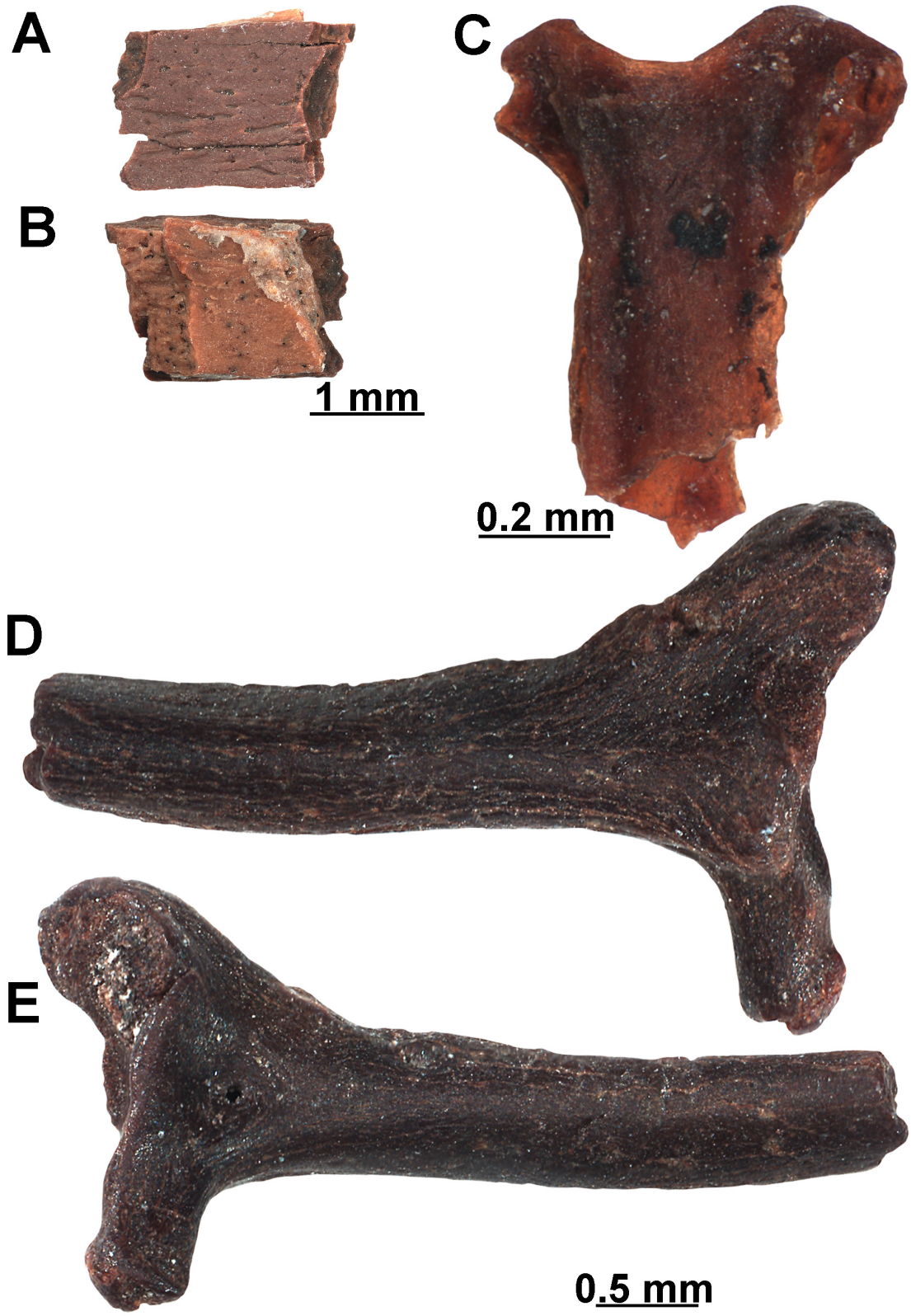

Figure 9. Turtles and squamate remain recovered from sample D16, DLQ (Ilgın Basin, Türkiye). (**A**,**B**) Shell fragment (EUNHM PV–KID-42) of cf. Geoemydidae indet. in dorsal (**A**) and ventral (**B**) views. (**C**) Trunk vertebra (EUNHM PV–KID-43) of Squamata indet. in ventral view. (**D**,**E**) Partial rib of Serpentes indet. (EUNHM PV–KID-44) of Serpentes indet. in anterior (**D**), and posterior (**E**) views.

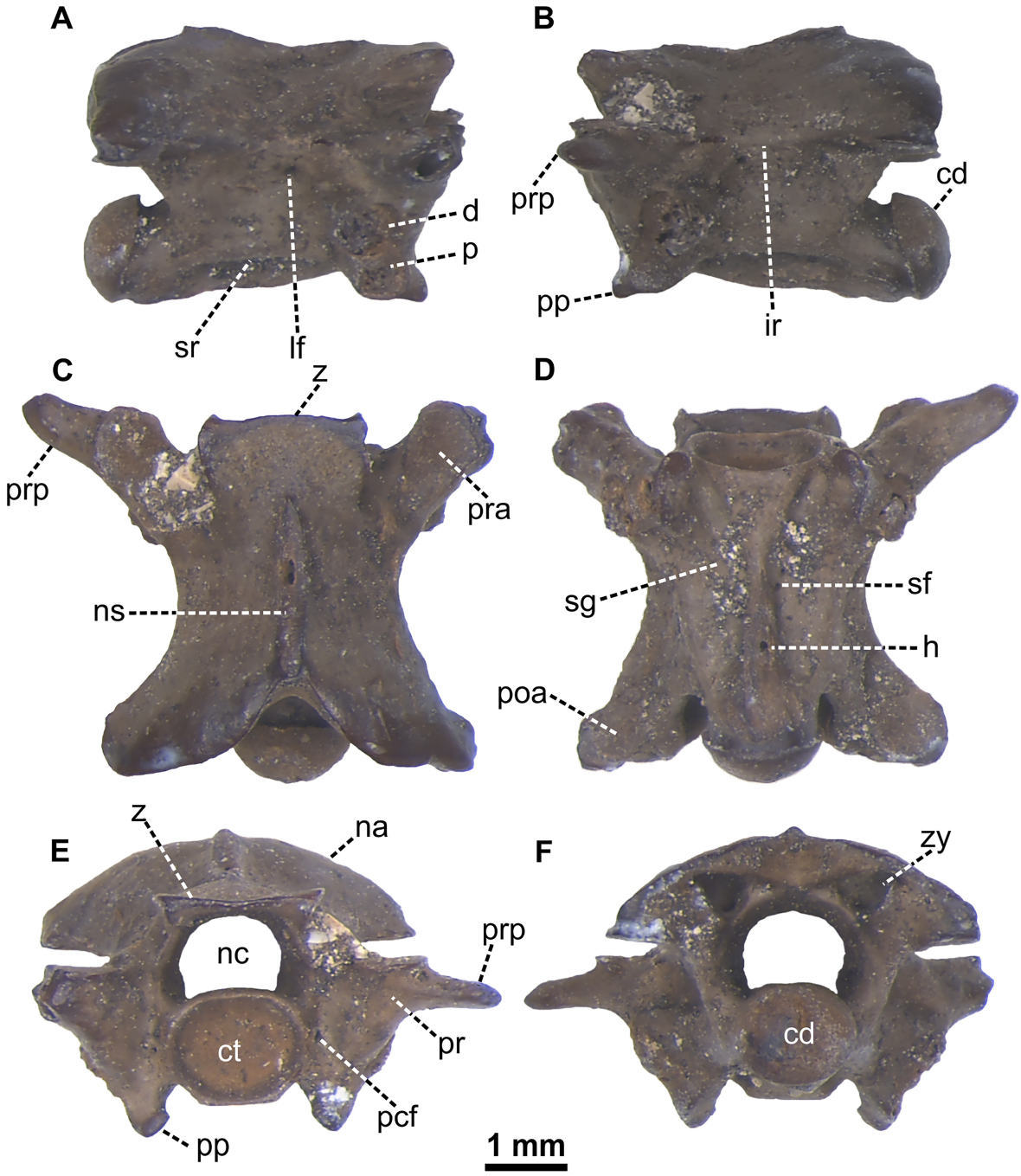

Figure 10. Cf. *Natrix* sp. remains recovered from sample D16, DLQ (Ilgın Basin, Türkiye). (**A**–**F**) Trunk vertebra (EUNHM PV–KID-45) in right lateral (**A**), left lateral (**B**), dorsal (**C**), ventral (**D**), anterior (**E**), and posterior (**F**) views. Abbreviations: cd, condyle; ct, cotyle; d, diapophysis; h, hypapophysis; ir, interzygapophyseal ridge; lf, lateral foramen; na, neural arch, nc, neural canal; ns, neural spine; p, parapophysis; pcf, paracotylar foramen; poa, postzygapophyseal articular facet; pp, parapophyseal process; pr, prezygapophysis; pra, prezygapophyseal articular facet; prp, prezygapophyseal process; sf, subcentral foramen; sg, subcentral groove; sr, subcentral ridge; z, zygosphene; zy, zygantrum.

The earliest known records of *H. salina* are from the Early Miocene sequences of Anatolia [63] and surrounding regions. Particularly, the species became common in Pleistocene-Holocene deposits of Central and Southwestern Anatolia and the Mediterranean region (e.g., [43,54,57,62,64]). The living representatives of the species are worldwide distributed, particularly in the Northern hemisphere [60]. The fossil forms of *N. angulata* became prevalent since Late Pliocene-Pleistocene in the Mediterranean region [61] and have been

also documented in several Pliocene-Quaternary strata from Central and Southwestern Anatolia [58,59]. Recent occurrences of the species are observed in the Palearctic zone [60]. *Ilyocypris bradyi* was previously reported from numerous Neogene-Quaternary sequences of Mediterranean and Balkan areas [64,65]. In Central and Southwestern Anatolia, it is known from Neogene [14,56] and particularly Pleistocene-Holocene [43,54,57,58,62] deposits. The living forms of this taxon are also widely distributed, like *H. salina* [60]. The oldest record of *P. zenkeri* in Europe is reported from Lower Pleistocene strata of Liri Valley, Italy (see [14]; and references therein). On the other hand, this species is significantly more common in the Anatolian fossil record and was discovered from Upper Miocene–Pleistocene [14,55] and Holocene [58] deposits. The distribution of the recent representatives is relatively narrow and reported in the Palearctic like *N. angulata* [60].

Mollusks. The mollusk fauna was recovered from samples D2, D16–D17, and D22. It is moderately diverse, containing at least 17 taxa, including 12 freshwater gastropods, four terrestrial gastropods, and at least one freshwater bivalve. The complete list of studied material is given in Supplementary Table S1. Most shells are juvenile specimens or fragments, sometimes not allowing the identification at the genus or species rank. All taxa that could be identified are still living in Europe and Asia Minor today. Since most of them are well-known taxa, we refrain from a detailed systematic assessment, but instead briefly summarize notes on taxonomy.

Two valvatids could be identified, i.e., the widespread European species *Valvata cristata* (Figure 5A: EUNHM PV–KID-10) and the Turkish endemic *Valvata* cf. *kebapcii* (Figure 5B: EUNHM PV–KID-11). The latter species resembles *Valvata macrostoma*, but the characteristic, weak angulation at the aperture suggests *V. kebapcii*. It is worth noting that *V.* cf. *kebapcii* represents the second most common taxon found at the Dursunlu site. Bithyniids are represented by a high number of apices and opercula with a subcentral nucleus (Figure 5C: EUNHM PV–KID-12): not a single complete shell could be obtained. The morphology suggests that all specimens may belong to a single species, which is here classified cautiously as *Bithynia* s.l. sp. A rather unusual find is the record of a minute, pseudamnicoline-like hydrobiid from sample D2, here attributed tentatively to the genus *Tefennia* (Figure 5D,E: EUNHM PV–KID-13 and EUNHM PV–KID-14). This genus is so far only known from a single extant species, *Tefennia tefennica*, endemic to the headwaters of a spring system in the Tefenni depression 60 km SW of Burdur [66]. Classification of hydrobiids is exceptionally difficult and, for extant material, primarily based on molecular and soft anatomical data. The identification of our material as *Tefennia* relies on the strong morphological similarity with an unpublished extant shell from Western Anatolia referred to this genus based on anatomical and molecular data (D. Delicado, pers. comm. in 2024). Further research is needed to substantiate this attribution. Two species of lymnaeids are recorded at Dursunlu, but both are represented by juvenile specimens only. The first taxon exhibits a broader spire and is here, tentatively attributed to the genus *Radix* (Figure 5G: EUNHM PV–KID-16). The second one has a more elongated shell resembling the genera *Galba* or *Stagnicola*, but without more complete shells, we provisionally place the taxon in open nomenclature (Figure 5F: EUNHM PV–KID-15) as an indeterminate member of the family.

Planorbidae are the dominant gastropod family at Dursunlu, represented by at least five taxa. Of these, only common *Armiger crista* (Figure 5K: EUNHM PV–KID-20) and rare *Segmentina nitida* (Figure 5L: EUNHM PV–KID-21) could be identified to the species rank. In addition, one species of *Anisus*, one ?*Gyraulus* sp., and one Planorbidae gen. et sp. indet. were found. *Anisus* sp. is characterized by a rather slow increase in whorl diameter and pronounced convexity above the whorl center (Figure 5H: EUNHM PV–KID-17). It resembles juveniles of *Anisus spirorbis*, but the shell is more flattened and the ratio between

shell height and width is less than in typical *A. spirorbis*. ?*Gyraulus* sp. shows an inflated early teleoconch whorl with spiral striae (Figure 5I: EUNHM PV–KID-18), which is found in several living species of the genus. Juvenile *Planorbarius* shows a similar morphology but has a usually immersed umbilical side. For the fifth taxon, even the genus could not be identified with certainty. The comparatively fast whorl expansion rate, and broadly rounded to subangulate whorl cross-section, matches several extant species of *Planorbis* and *Gyraulus* (Figure 5J: EUNHM PV–KID-19). Terrestrial gastropods were only detected in sample D2. Among them is a single specimen of *Carychium minimum* (Figure 5O: EUNHM PV–KID-24). It differs from its congener *Carychium tridentatum* in being bulkier. The sinistral *Vertigo angustior* is the most common terrestrial species (Figure 5P: EUNHM PV–KID-25). It can be distinguished from the generally similar *Vertigo pusilla* by its smaller and narrower shell, the presence of 5–6 apertural teeth that do not almost fill the aperture and a long and lamella-like palatal tooth. *Truncatellina* is represented by a single fragment of the last whorl containing the aperture (Figure 5Q: EUNHM PV–KID-26). The general shape as well as the delicate riblets suggest placement in *Truncatellina*. Finally, a taxon of *Vallonia* was detected that is tentatively identified as *Vallonia* cf. *enniensis* (Figure 5R: EUNHM PV–KID-27). The type and frequency of the ribs as well as the width of the umbilicus match well with *V. enniensis*. Another similar species is *Vallonia chinensis*, which is, however, geographically an unlikely candidate [67,68]. The common species *Vallonia costata* has fewer and typically stronger ribs. *Valvata asiatica* differs in a broader umbilicus, while *Vallonia tenuilabris* has a higher spire [69]. Moreover, the species *V. enniensis* has frequently been reported in the fossil record [70].

Among freshwater bivalves, several juvenile valves of the sphaeriid *Euglesa* sp. were found. The specimens cover a large range of variability and may include more than a single species; however, due to their juvenile state, identification is difficult. Specimens with a more angulate morphology, slender hinge, and low convexity (Figure 5N: EUNHM PV–KID-23) are similar to *Euglesa pseudosphaerium*, as described and illustrated by Gittenberger et al. [71]. This species is also known from other Pleistocene Turkish localities [72]. A more convex specimen (Figure 5M: EUNHM PV–KID-22) may represent *Euglesa obtusalis*.

Fishes. Up to eight fish remains belonging to four taxa (one unidentified Teleostei plus three cyprinids) have been identified in Dursunlu samples (D2, D3, D16, and D23), including a vertebra and pharyngeal bones. The single vertebra coming from the sample D3 displays an amphicoelous morphology and both neural arches are broken off. Although the vertebral morphology is compatible with that of Cyprinidae, due to its poor preservation, here, it is attributed to a Teleostei indet. (Figure 6A: EUNHM PV–KID-28). Three isolated and broken pharyngeal teeth were recovered from samples D2, D3, and D16 (Figure 6B–D: EUNHM PV–KID-29, EUNHM PV–KID-30, and EUNHM PV–KID-31). All of them are elongated and compressed mesiodistally on their entire length. The tip of the tooth is a short, sharp, and hook-directed mesial. The grinding surface is narrow and serrated with wrinkled surface patterns. The teeth have an elongated, narrow, labial grinding surface, serrated with marked wrinkled surface patterns. In two teeth (Figure 6B,D), several small bumps with rounded tips, which decrease in size towards the basal margin of the tooth, are discerned. In all recovered teeth, both the neck and the pedicle are not preserved. On the basis of the above-mentioned features, these pharyngeal teeth are referred to the cyprinid genus *Squalius*, which is widely distributed in the Western Palearctic, and more specifically in Türkiye (e.g., [6,73,74]). Regarding the third taxon, three isolated and broken teeth were recovered from samples D3 (Figure 6E–G: EUNHM PV–KID-32, EUNHM PV–KID-33, and EUNHM PV–KID-34). All available teeth are slim and compressed throughout their entire mesiodistal axis. The grinding surface is elongated and knife-shaped: in three specimens, a short hook is preserved (Figure 6F–H). The neck is poorly developed and slightly curves

inward below the grinding surface. According to Çiçek et al. [74], up to fourteen species of the genus *Chondrostoma* are present in the Türkiye fossil record, of which eleven are endemic. Lastly, one isolated and broken pharyngeal tooth of *Barbus* is available (Figure 6H: EUNHM PV–KID-35). The tooth crown is slightly narrower than the tooth base, being the latter compressed at the foot-crown boundary (Figure 6H). It has a robust crown with a hook on its top, and a smooth grinding surface. According to Çiçek et al. [74]; and references therein), ten endemic species of the genus *Barbus* are present in Türkiye.

Amphibians. This clade is represented by six remains that belong to three taxa (see Table 1), all of them recovered from sample D16. Due to the fragmentary nature of the bones, they have only been identified between the order and family level. Anurans are represented by one partial maxilla, EUNHM PV–KID-36, which is small and rather lightly built (Figure 7A,B). In particular, this maxilla cannot pertain to a bufonid, given the presence of teeth (in contrast to toothless maxillae in toads; [75]). Since this element is quite fragmentary and poorly significative for a more precise identification, it is here referred to Anura indet. Anurans are previously identified in Plio-Pleistocene deposits of Türkiye, and more specifically in Central Anatolia (e.g., [76,77]). EUNHM PV–KID-37 (Figure 7C–G) is a middle sized and moderately robust procoelous trunk vertebra. The centrum is well individualized and distinctly dorsoventrally compressed. The neural canal is wide. The transverse processes are robust, directed laterally and located posteriorly to the prezygapophyses. The dorsal surface of the neural arch is wide and rather short, with a strongly concave anterior margin. The arch displays a sharp carina neuralis, originating a very short point posteriorly. The large and well-extended zygapophyses are tilted dorsally with an angle of about 30°. The prezygapophyseal facets are circular, whereas the postzygapophyseal ones are subelliptical. According to Bailon [75], the attribution of this vertebra to a bufonid is supported by: procoelous morphology; short neural arch; transverse processes located posterior to the prezygapophyses; well individualized centrum; and overall robust structure. Isolated vertebrae of these anurans are not diagnostically significant enough for a more precise identification at the genus rank, because of a general homogenous morphology. In Europe, bufonids are known since the Early Miocene (MN4) of Spain, whereas in Türkiye, the oldest remains were reported from the Pliocene locality of Çalta [78,79].

Specimen EUNHM PV–KID-38 is a slender angular bone, with a well-developed processus coronoideus. The process is wide, rounded, and almost vertically oriented (Figure 8A,B). Specimen EUNHM PV–KID-39, a coracoid, is lightly built and straight, very narrow at mid-length, but expanding towards the medial and lateral ends (Figure 8C,D). The pars epicoracoidalis is strongly more expanded in anteroposteriorly length than the pars glenoidalis, being more than twice the width of the latter. The first ilium is very small and lightly built, probably representing a very young individual (EUNHM PV–KID-40: Figure 8E,F). A second ilium (EUNHM PV–KID-41) is notably larger and much more robust (Figure 8G,H). All two ilia are fragmentary, but they clearly display the presence of a dorsal crest (always damaged), a dorsal tubercle (poorly marked in the small ilium, but well distinct in the largest one), a supraacetabular fossa, a wide acetabular fossa with a raised anteroventral portion of the acetabular rim, and a smooth medial surface of the ilial body with no evidence of an interiliac tubercle or groove. The supraacetabular fossa is much deeper in the largest ilium, compared to the smallest one. The angle between the dorsal tubercle and the short dorsal acetabular expansion is very obtuse in the small ilium. The same feature cannot be evaluated in the largest one as both the tubercle and the expansion are almost completely broken off (Figure 8G,H: EUNHM PV–KID-41). The largest ilium is the only specimen in which the morphology of the ilioischiatic juncture can be observed. The latter is rather narrow in posterior view. All these remains show ranid features. As far as the angular and the coracoid are concerned, diagnostically significant

are the vertical processus coronoideus and the strongly expanded pars epicoracoidalis, respectively [75]. The two ilia are comparable in morphology to the genus *Rana*, but they are referred tentatively to Ranidae indet. We avoid an attribution to brown frogs, though. The obtuse angle in the two small individuals may indeed suggest *Rana* affinities, but this feature is similar in very young green frogs [80]. Adding to this, the narrow ilioischiatic juncture of the largest specimen may also hint towards *Rana* for this other specimen [81], but identification to genus rank of such a fragmentary fossil would be far from confident in our opinion (especially without clear information on the dorsal tubercle/acetabular expansion angle).

Reptiles. A single shell fragment of a testudinoid (EUNHM PV–KID-42) coming from D16 sample is available (Figure 9A,B). This specimen corresponds most likely to a portion of plastron as it is lightly built, but it is difficult to confirm this with certainty. The maximum width of the preserved plate fragment is 4,5 cm. As a rule, both geoemydids and testudinids have dermal scutes, which can or not be ornamented (e.g., [82,83]); however, the external portion of this preserved shell is smooth and without ornamentation, and, further, it is not crossed by any sulcus (Figure 9A). Nonetheless, on the basis of the minimal thickness of the plate, observed in EUNHM PV–KID-42, we refer it to cf. Geoemydidae indet. Another reptilian specimen (EUNHM PV–KID-43) consists of a notably small and poorly preserved procelous trunk vertebra. Only the centrum and the right wall of the neural arch (with the right prezygapophysis) are preserved (Figure 9C: EUNHM PV–KID-43). The posterior condyle broke off during manipulation, but it is still available as very small, separated bone fragments. The centrum is anteroposteriorly elongated and dorsoventrally compressed. The ventral surface of the centrum is gently convex and displays no evident ventral keel. The right synapophysis is dorsoventrally elongated. The prezygapophysis is slightly tilted dorsally in anterior view and ovoid in dorsal view. This isolated vertebra can be ascribed to Squamata indet. Referral to both snakes and amphisbaenians can be discarded given the morphology of the synapophysis (i.e., not separated into para- and diapophysis as in most snakes and not massive and rounded as in amphisbaenians). The dorsoventrally elongated shape is more comparable with that of a lizard, to which this vertebra here is tentatively referred. The small size, the compressed centrum, as well as the gently convex ventral surface are somehow reminiscent of vertebrae of scincids, such as *Ophiomorus* [84], suggesting that this fossil may belong to a taxon related to this group of lizards. However, we herein deem this potential identification to be too speculative, given the very poor preservation of the specimen and absence of more informative material. Therefore, this vertebra is only referred to as an indeterminate lizard (Squamata indet.).

Snakes are represented by a single small partial rib (EUNHM PV–KID-44; Figure 9D,E) and one middle trunk vertebra (EUNHM PV–KID-45; Figure 10A–F). EUNHM PV–KID-44 is an elongated element, medially curved, and with its distal end broken. Given the poor information provided by this bone, here, we refer it to an indeterminate snake i.e., Serpentes indet. The incomplete procoelous vertebra (EUNHM PV–KID-45; Figure 10A–F) is rather small and almost complete, with elongated centrum. The neural spine and hypapophysis are not preserved and the diapophyses are also slightly damaged. In the lateral view, the broken-off neural spine rose at the posterior end of suboval zygosphenal facets. Large lateral foramina are situated close under the rather sharp interzygapophyseal ridges. Synapophyses are well divided into para- and diapophyses, with the latter situated slightly behind the former. The short parapophyseal processes are anteriorly rather than antero-ventrally. Subcentral ridges are long and moderately arched dorsally. The preserved base of the hypapophysis starts to rise behind the posterior level of the diapophyses. In dorsal view, the zygosphene has two sharp and short lateral lobes oriented anteriorly and a wide, but indistinct median lobe. The prezygapophyseal articular facets are subtriangular

in outline. Only the left prezygapophyseal process is preserved; it is about as long as the prezygapophyseal facet and oriented anterolaterally. The epizygapophyseal ridges are moderately developed. The caudal notch is rather deep. In the ventral view, the vertebral centrum is triangular. Subcentral grooves are relatively deep and small; marked subcentral foramina are present close to the base of the hypapophysis and situated at midlength of the subcentral grooves. The anterior keel of the thin hypapophysis is triangular. The postzygapophyseal articular facets are roughly circular in outline. In the anterior view, the neural arch is moderately vaulted, with slightly developed epizygapophyseal ridges. The neural canal is rounded with two short lateral sinuses. The zygosphene is thin and nearly straight. Prezygapophyses are horizontal, with prezygapophyseal facets situated high above the base of the neural canal. The obtuse parapophyseal processes are oriented medially. On the sides of the subcircular cotylar rim, there are small, yet well visible paracotylar foramina. In caudal view, small zygantral foramina are situated within the rather deep zygantrum. The condyle is suborbicular. Measurements are as follows: central length (cl) = 3.72 mm; narrow anterior width (naw) = 2.61 mm; cl/naw: or = 1.42. The sole snake vertebra from Dursunlu undisputedly displays an hypapophysis. Because of the rather deep subcentral ridges, it can be excluded that it comes from the anterior trunk section of a colubrid snake. The vaulted neural arch and horizontal prezygapophyses in anterior view also excludes its classification as a viperid snake. This vertebra could be easily attributed to *Natrix*, if the two most important structures, neural spine and hypapophysis, were not broken. Therefore, the vertebra is attributed rather as cf. *Natrix* sp. on the basis of the following combination of features: (1) the vertebral centrum is elongated; (2) the hypapophysis is present with triangular anterior keel; (3) parapophyseal processes are directed anteriorly; (4) vaulted neural arch with rather indistinct, yet present epizygapophyseal ridges; (5) subcentral ridges are strong and marked; and (6) neural arch is moderately vaulted [85–87]. Two species of *Natrix* can be considered as survivors through the Pliocene-Pleistocene transition: *Natrix longivertebrata* and *Natrix rudabanyaensis*. Specifically, *N. longivertebrata*, which is documented mainly from Hungary and Poland [85,88,89], shares with the Dursunlu specimen a narrow zygosphene, well delimited subcentral ridges, and a broad triangular anterior hypapophyseal keel. However, EUNHM PV–KID-45 differs in less prominent centrum length, a sharper prezygapophyseal process, and shorter parapophyseal processes. *Natrix rudabanyaensis*, known mostly from Hungary, but also from Romania and Greece [90–92], shares with EUNHM PV–KID-45 the elongated vertebral centrum, long prezygapophyseal processes, and moderately developed subcentral ridges. EUNHM PV–KID-45 differs in a more vaulted neural arch with less prominent epizygapophyseal ridges, and horizontal prezygapophyses with triangular facets. It is up to discussion if *Natrix* aff. *rudabanyaensis* from the Greek locality of Maramena (Miocene-Pliocene transition; [92]) could share affinities with *Natrix* occurrences from the Pleistocene of Anatolia, such as the one from Dursunlu. From these Greek specimens, EUNHM PV–KID-45 differs in shorter parapophyseal processes, pezygapophyseal facets being triangular in outline, smaller subcentral foramina, and wider lateral sinuses of the neural canal. During the Pleistocene, two species of *Natrix* are reported from Eastern Europe: *N. natrix* ([31,93–97]; and references therein) and *N. tessellata* [81,85]. EUNHM PV–KID-45 differs from *Natrix natrix* in a longer prezygapophyseal process, less prominent lateral lobes of the zygosphene, and shorter parapophyseal processes [31,81], while *Natrix tessellata* has shorter prezygapophyseal processes and smaller diapophyses [85]. The studied vertebra closely resembles *Natrix* sp. from the Turkish Pasinler Basin, but in contrast to that, it has a straight zygosphene and a cotyle without subcotylar tubercles [98]. In lateral view, it differs from *Natrix* cf. *natrix* from the Emirkaya-2 locality only in straighter subcentral ridges [76]. While the preserved long prezygapophyseal process differs from most of the Pleistocene *Natrix* taxa, it is not possible to attribute the vertebra beyond

(tentatively) the genus rank as the highly diagnostic hypapophysis and neural spine are broken. Several snake taxa have been described from the Pleistocene localities of Türkiye. Specifically, from the Early Pleistocene, the only properly documented snake taxon is *Natrix* sp. from the Pasinler Basin [98]. Alternatively, the Middle Pleistocene locality of Emirkaya-2 provides the richest snake assemblage, including the following taxa: Scolecophidia indet., *Coluber caspius* (now referred to as *Dolichophis caspius*; see [99]), *Coluber* (s.l.) sp., *Elaphe* cf. *quatuorlineata* (*Elaphe* cf. *E. quatuorlineata* sensu [76]), cf. *Telescopus* sp., Colubridae indet., *Natrix* cf. *natrix* (sensu [76]) and *Vipera* sp. [76]. Also of Middle Pleistocene age, locality Yenisarbademli yielded only a fragmentary vertebra each of Natricinae indet. and Colubrinae indet. [100].

5. Discussion

5.1. Paleoenvironmental Reconstruction of Dursunlu Paleolake

Most of the identified taxa from DLQ are still present in Türkiye and Central Anatolia and; therefore, we use an actualistic approach to infer conditions that prevailed in the lake during the Early Pleistocene. The presence of well-preserved gyrogonites of *Chara hispida*, *C. vulgaris*, and *C. globularis* not only confirms those remains were deposited in situ but further denotes a fully lacustrine conditions of the studied section. It is noteworthy that both *C. vulgaris* and *C. globularis*, display wide ecological amplitude, thriving in many kinds of shallow aquatic environments from small eutrophic temporary ponds to oligotrophic permanent lakes, at depths of up to one meter (see [5]; and references therein). Among the charophyte flora, the most remarkable and informative taxa is *C. hispida*, mainly recovered from samples D2–D3 and D22–D23 of the stratigraphical column, which indicates that stable oligohaline and meso-oligotrophic conditions prevailed in these intervals [5,6]. According to Van Vierssen [52], *Zannichellia palustris* is a fresh-brackish water cosmopolitan taxon, which commonly lives in eutrophic temporary water bodies, and seeds of this taxon germinate at relatively low temperatures (8–12 °C). The abundance of macrophyte seeds, such as *Zannichellia palustris* and *Najas marina*, the abundance of planorbid gastropods, the high organic content, and the strongest decrease in charophytes in the middle part of the series (D17), denotes very shallow and highly eutrophic conditions in a fully palustrine context. Such reconstruction is also reinforced by the fragments of halophytic plants (reeds) and the presence of rootlet marks at the base of the lignite intervals.

Regarding ostracods, the presence of *Heterocypris salina* and *Neglecandona angulata* throughout all samples supports a palustrine paleoenvironment, but more specifically, the abundance of those ostracods in the lower samples (i.e., D2–D3) would suggest shallow water conditions and very little saline. In contrast, the ostracod fauna recovered from middle levels (samples D16–D17) is dominated by *Ilyocypris* cf. *bradyi*: *N. angulata* and *H. salina* are poorly represented in these samples, which implies almost zero salinity conditions. Although it is difficult to assess with confidence the conditions of the paleolake in detail for D16-D17 samples, it seems that the prevalence of *P. zenkeri* and *I.* cf. *bradyi* in the assemblage may indicate that the stream recharges to the basin were still effective. The ostracod assemblage presented here resembles those studied by Tuncer [14], who thoroughly examined a similar fauna coming from laterally equivalent levels of the Dursunlu Formation.

As for mollusks, *Valvata cristata* is a calciphile species known from springs, slowly flowing waters, lakes, ponds and, rarely, temporary water bodies. It prefers eutrophic habitats with rich vegetation, muddy substrate, and well-oxygenated water [70,101]. *Valvata* cf. *kebapcii*, which is the second-most common species found at DLQ, prefers to inhabit shallow streams and brooks with lush vegetation and sandy substrate [102]. Considering the uncertainty of the systematic classification and the wide range of environments extant bithyniids dwell in, we refrain from inferring any ecological preference for this

taxon. Though lymnaeid snails occur in all types of habitats, they prefer richly vegetated waters [101]. Planorbids are the dominant gastropod family at Dursunlu, but species classification was possible only in two cases: *Armiger crista* and *Segmentina nitida*. The former dwells today in lentic, permanent water bodies with rich vegetation, often on the leaves of water plants or at the vegetated fringes of lakes [70], whereas the latter is known to live in lentic waters such as ponds, pools, ditches, and lakes with rich vegetation and high humic contents throughout most of the Palearctic [70,101]. The terrestrial snail *Carychium minimum* favors wet habitats, such as swamps, river plain woods, and wet meadows, and usually occurs near silent water bodies on stones, plants, tree branches, or submerged wood. It does not tolerate drought but can withstand flooding periods [70]. *Vertigo angustior* is a small terrestrial and calciphile species typically found in litter. It occurs in a variety of environments, ranging from open dry habitats and sandy dunes in coastlands with low vegetation, to areas with high humidity or permanently moist, open habitats [70]. The genus *Truncatellina* is known from a variety of habitats but is much more common in dry, often calcareous environments [70]. The species *Vallonia enniensis* dwells today in humid and wet habitats in lowlands, on meadows, and on calcareous swamps, and sunny hills with springs in the highlands [70]. Among freshwater bivalves, today, both *E. pseudosphaerium* and *E. obtusalis* live in swamps or lentic waters with abundant vegetation, sometimes even occurring together [70].

From a mollusk diversity point of view (Figure 11, ST1), the number of taxa generally decreases from the oldest to the youngest sample. While in sample D2, almost all taxa were recorded, samples D16, D17, and D22 each contain a smaller subset. The rarefaction analysis indicates that only D17 captures the mollusk fauna well, while for D2 and D16, one additional species each may be recovered with more intensive sampling. Note, however, that the sphaeriids may already include more than a single species. For D22, the rarefaction curve was even steeper: according to the analysis, approximately three more species may be found with doubling the sampling effort.

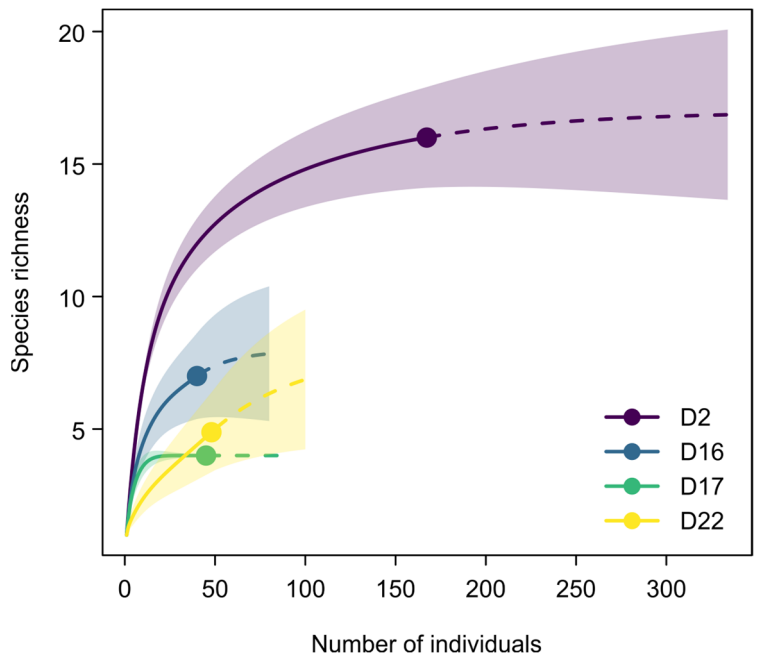

Figure 11. Rarefaction analysis of the mollusk samples (D2, D16, D17, and D22) from DLQ.

Sample D2 is dominated by pulmonate taxa (Planorbidae, Lymnaeidae), followed by truncatelloids (Hydrobiidae, Bithyniidae), valvatids, and sphaeriids. Especially, the pulmonates, valvatids, and sphaeriids indicate the presence of a richly vegetated habitat.

The pulmonates and sphaeriids furthermore point towards a permanent, lentic environment. *Valvata cristata* indicates well-oxygenated water, and *Valvata* cf. *kebapcii* and ?*Tefennia* sp. suggest at least some water movement. It may be noted that studied samples contain many juvenile and fragmented shells, which signals of transport, and further suggests that taxa may not have all dwelled in the same habitats. In any case, the rather pristine shell matter makes a bias from reworking unlikely. The fringes of the water body were inhabited by terrestrial snails: *Vertigo angustior*, *Truncatellina* sp., and *Vallonia enniensis* suggest the presence of calcareous soils near the water. The remaining samples consist of similar assemblages. All four samples (D2, D16, D17, D22) contain *Bithynia* s.l. sp. and *Valvata* cf. *kebapcii*, along with few planorbids and sphaeriids. In the case of D16, rare lymnaeids also occur. Despite being much less diverse assemblages, the paleoecological conditions were probably similar to D2. Apart from absent hydrobiids and terrestrial snails, the same groups (bithyniids, pulmonates, valvatids, and sphaeriids) are present. The lack of *Valvata cristata* may point towards poorly oxygenated waters, whereas the absence of terrestrial snails perhaps indicates deposition further away from the shore. Note that compared to the other samples, shells in sample D22 are poorly preserved, possibly indicating some transport or reworking. In any case, the mollusk association is congruent with a mixture of palustrine and shallow lake facies at DLQ.

The fish assemblage recovered from the six samples is low diverse, including three genera Cyprinidae (*Squalius*, *Chondrostoma*, and *Barbus*) and the unidentified remains of another teleost taxa. The three cyprinind genera are still present in Türkiye and Central Anatolia in particular (Figure 12). The fish composition from the bottom of the sequence fits well with palustrine freshwater environment, following previous interpretations based on charophytes and fish [5,6]. The presence of *Squalius* and *Chondrostoma*, together with the family Cobitidae reported by Blanco-Lapaz et al. ([6]; samples D4, D6–D9), would suggest the presence of some water movement (e.g., fast/slow-moving waters). The same authors further reported in the lowermost samples (i.e., D6–D7) the genera *Barbus* (here in sample D23) and *Capoeta*: the former are generalist and benthonic but prefer fast-flowing rivers or streams with sandy and pebbly bottoms and well-oxygenated waters, whereas the latter preferred either slow-flowing or oxygen rich waters (e.g., [28,103,104]).

Due to the low precision to which remains were identified, anurans and lizards provide only limited paleoecological information. Today, amphibians inhabit most types of freshwater bodies—such as rivers, lakes, swamps, and ponds—as they need water to lay their eggs and/or for other physiological needs. As a rule, frogs always need to be near water to keep the skin moist, while toads spend more time out of the water and have adapted more efficiently to thrive in drier environments. However, bufonids and ranids of the genus *Rana* include species with wide ecological preferences (e.g., [105]) and so they can only be used to confirm the presence of water bodies in Dursunlu. Affinities of the lizard vertebra with *Ophiomorus* skinks may support the presence of rocky microenvironments in the surroundings of the lake, where extant Western species of this lizard genus live [84,106,107]. However, this cannot be stated with certainty given that preservation of the fossil hampers a confident identification even at genus rank. Moreover, most geoemydids are classified as semiaquatic turtles and only leave the water for a few hours to either thermoregulate or lay their eggs. However, some species of this family show some ecological flexibility (e.g., genera *Rhinoclemmys*, *Cuora*, and *Geoemyda*) and could be considered semiterrestrial, which implies that they spend a significant amount of time on land as well, mainly for feeding ([108–110]; and references therein). Though members of the genus *Natrix* spends time thermoregulating on land or diving in shallow water, this group of natricines is well adapted to wet areas, such as rivers, lakes, ponds, and wetlands (Figure 12), as they depend on them for both food (mainly fish and amphibians) and reproduction (e.g., [111]). The

fact that only amphibians and reptiles have been recovered in sample D16 reinforces the idea that this level deposited under extremely shallow conditions, and particularly at the lake margins. In this paleoenvironment, extensive stands of halophytic plants would have thrived, forming local peat swamps, being ideal for the proliferation of herpetofauna, mollusks, and fish fingerlings.

Figure 12. Life reconstruction of the most relevant flora and fauna from the Early Pleistocene site of DLQ. Reconstruction artwork by Roc Olivé.

5.2. Potential Resources for Homo During the Early Pleistocene

During the Early Pleistocene, the area of Dursunlu had two peculiarities: a high elevation and an unfavorable climate. As pointed out by Kuhn et al. [12], the high elevation (i.e., altitudes above 1000 m above sea level) of the most productive sites of Central Anatolia, such as KD3, Dursunlu, and Göllüdağ, was an important challenge for early hominins in Eurasia during the Early Pleistocene (see also [112]). Thereby, attempts by hominins to inhabit the Dursunlu area at the time would have been affected by the continental climate of Central Anatolia with harsh winters at those elevations and even more so during glacial periods. Previous studies (e.g., [113]) have suggested that sites in Anatolia would not have been an inhospitable environment for the early hominins who dispersed from Africa and Asia (see also [112,114,115]).

The steparian conditions around wetland areas of Dursunlu appear to have been an excellent environment to support sporadic settlement of hominins, who would make stone tools and obtain food resources [1,2,8]. One may assume that early hominins at Dursunlu have exploited alluvial plains and nearby areas that provided access to quartz rocks, enabling tool production and supporting a mobile foraging subsistence strategy, i.e., scavenging, gathering, and small to medium-scale hunting (e.g., [116–118]). Although

more than a hundred stone tools have been recovered at Dursunlu, this sample of artifacts does not provide a complete account of the tool-making technologies and, therefore, does not allow to confirm the idea of a continuous settlement in Central Anatolia [1,2,8,112].

As far as we know, many African and Eurasian Lower Paleolithic sites are located near freshwater sources, serving as potential meeting points or hotspots during the early dispersal routes of hominins (e.g., [119,120]). Early hominins certainly exploited available resources provided by the lacustrine system of Dursunlu, offering with clear and well-oxygenated water and at the same time attracting potential prey [1,2,5,6,8,121]. Even though detailed taphonomical analyses are required, the herpetofauna and fish recovered from Dursunlu could have been part of the potential resource for early *Homo* during the Early Pleistocene. Particularly, fossils recovered from sample D17 were deposited at the lake margins under extremely shallow conditions, further indicating a very short transportation of the fish and some herpetofauna remains [5,6]. Although there is no evidence of reptile and amphibian consumption by early humans in Dursunlu, the extensive stands of halophytic plants and peat swamp environments would have facilitated the capture of these animals. Previous authors also reported on the consumption of turtles in other Eurasian and African Early Pleistocene contexts, such as testudinids (e.g., [122]), geoemydids (e.g., [123]), trionychids (e.g., [124]), and pelomedusids (e.g., [125]). While the consumption of turtles by hominins is considered a rather sporadic event, small animals—i.e., birds, reptiles, amphibians, fishes, and others—inhabiting the surrounding areas of the Dursunlu paleolake would have been an important component of small game, and more specially, during the cold (glacial) stage of the late Early Pleistocene (Günz glaciation) when large prey and carrion would have become scarce.

6. Conclusions

The DLQ assemblage stands out as one of the most abundant and diversified floras and faunas from the Early Pleistocene documented thus far in Central Anatolia (Türkiye), enhancing our understanding of the past ecosystem of the Dursunlu paleolake and surrounding steppe areas during the Günz glaciation.

The charophyte association recovered from the six samples herein studied coming from palustrine and peat bog facies, includes three (*Chara hispida*, *Ch. vulgaris*, and *Ch. globularis*) of the 11 taxa already reported in previous studies. Two taxa of seeds have been identified (i.e., *Najas marina* and *Zannichellia palustris*), which refine our knowledge of aquatic plants from the paleolake. Ostracods are scarcely represented in DLQ by six taxa, which resemble those studied in Tuncer's PhD Thesis: *Heterocypris salina*, *Prionocypris zenkeri*, *Neglecandona angulata*, *Ilyocypris* cf. *bradyi*, *Cyclocypris* sp., and *Pseudocandona* sp. On the other hand, mollusks are moderately diverse (17 taxa), including one freshwater bivalve, four terrestrial gastropods, and 12 freshwater gastropods. Fish are underrepresented with only four taxa (Teleostei indet., *Squalius* sp., *Chondostroma* sp. and *Barbus* sp.); however, this is most probably due to the few samples included in the present study. Among amphibians, Anura indet., Bufonidae indet., and *Rana* sp. have been identified. The reptile assemblage, in turn, comprises cf. Geoemydidae indet., Squamata indet, Serpentes indet., and cf. *Natrix* sp.

The fauna and flora reported from DLQ in our study is in line with the Early Pleistocene age, estimated based on the rodent assemblage. The ecological requirements of flora, ostracods, mollusks, fish, amphibians, and reptiles presented here are congruent with previous paleoenvironmental inferences, indicating a very shallow eutrophic lake with a dense palustrine vegetation belt at the margins, surrounded by steppe areas, under glaciation conditions in the Ilgın Basin, Central Anatolia, Türkiye. The present study further adds new data to the potential role played by the Dursunlu wetland and the surrounding steppes for sporadic settlements of hominins during the Early Pleistocene: the

paleolake would have provided easy access to water and a variety of food resources, such as the fish, amphibians, and reptiles described here for the first time.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d17090631/s1, Table S1: Composition of the studied mollusk assemblages at DLQ. The numbers for *Bithynia* refer to number and apices and opercula, respectively; only opercula (including fragments) containing nucleus were counted. For *Euglesa*, the higher number of left or right valves was used to calculate the total number of specimens.

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