Pliocene–Pleistocene Unionida from Rhodes (Dodecanese, Greece): insights into the evolution of Eastern Mediterranean freshwater mussels

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Abstract. The island of Rhodes (eastern Greece) is devoid of large freshwater mussels today, but during the Pliocene and earliest Pleistocene, while still connected to Anatolia, it hosted a diverse fauna of Unionida, comprising 6 species in total. Two species, *Unio pseudatavus* Bukowski, 1896, which has its type locality on Rhodes, and *Unio* sp., co-occur in the Pliocene Salakos Formation; both are assigned to the *Unio pictorum* group here. *Potomida semirugata* (Lamarck, 1819) (Lamprotulini) occurs in fluvial deposits of the Late Pliocene Damatria Formation. The overlying lower Kritika Formation, dated as close to the Pliocene–Pleistocene boundary, has yielded *Unio bruguierianus* Bourguignat, 1853 (*Unio crassus* group), *Leguminaia hedenborgi* n. sp. (Gonideini), the margaritiferid *Pseudunio auricularius* (Spengler, 1793) and potentially additional specimens of *P. semirugata*. The new species *Leguminaia hedenborgi* is described, and lectotypes for *Unio pseudatavus* Bukowski, 1896 and *Unio prusii* Bourguignat, 1856 (a junior synonym of *U. bruguierianus*) are designated. The fossil records of the 4 genera involved reliably date back to the Eocene, Oligocene or Miocene of the Mediterranean and Paratethys regions. At tribe level, European Unionidae likely have their origins in Asia and migrated westward during several Cenozoic dispersal events. Mesozoic Unionidae in Europe thus may represent extinct clades.

Key words. Unionidae, Margaritiferidae, *Pseudunio*, *Unio*, *Leguminaia*, *Potomida*, Mediterranean, biogeography, fossil record.

Introduction

Today, the Mediterranean region is home to a number of critically endangered species of freshwater mussels in the Unionidae and Margaritiferidae and forms a centre of biodiversity for several genera in these 2 families (e.g. ARAUJO et al. 2009a, b, 2017a, b, 2018, FROUFE et al. 2016a, b, 2017, VIKHREV et al. 2018, LOPES-LIMA et al. 2021). Whereas the investigation of the phylogeny of these bivalves is rapidly advancing, knowledge of their historical and fossil distribution is relatively poor (e.g. ARAUJO & RAMOS 2000, SCHNEIDER & PRIETO 2011, LYUBAS et al. 2019). This gap in knowledge is predominantly a function of the scant fossil record of freshwater mussels (NIELSEN et al. 2008, ARAUJO et al. 2017b) but also results from a lack of comprehensive descriptions of material present in scientific collections. Similarly, information on the ecology of unionid species, particularly of those whose populations are in rapid decline, is

often deficient, which hampers their conservation. The fossil record helps to improve our understanding of the evolution, propagation and palaeobiogeography of the Unionida and enables reliable calibration of molecular-clock models. In addition, the environmental information accessible from autochthonous or parautochthonous fossil shells and their substrates provides clues about their ecology and may ultimately inform conservation efforts to preserve freshwater-mussel diversity today.

The island of Rhodes (Dodecanese Archipelago, eastern Greece) has no extant occurrence of large freshwater bivalves (PAGET 1976, FRANK 1997). Fossil unionids, however, have been known since the 19th century. DESHAYES (1836) and BOURGUIGNAT (1856a) independently reported fossil shells of *Unio littoralis* Cuvier, 1798 from Rhodes. BOURGUIGNAT (1856a) further described a new species, *Unio prusii*, which "was collected as a fossil from modern strata of this island" (BOURGUIGNAT 1856a: 76, translated from French; re-published by BOURGUIGNAT

1856b), most probably indicating that he proposed a Holocene age for these shells. Tournouër (1877) studied material in the collections of Deshayes (École des Mines, Paris) and d'Orbigny (Laboratoire de Paléontologie, Muséum d'Histoire naturelle, Paris) and confirmed the presence of these 2 species. None of these scientists ever visited the outcrops where the fossils were collected. Thus, the observations of Swedish amateur scientist Johan Hedenborg, who started to explore the Cenozoic strata of Rhodes in the early 1830s, provide a valuable resource. In 1837, Hedenborg published a first description of the "Tertiary formations" of Rhodes, where he characterized marine sediments with their typical fossils, but also mentioned a stratum of marls containing freshwater gastropods and bivalves attributed to "*Myo* [sic] or *Unio*" (Hedenborg 1837: 245). He had sent these specimens, together with other fossils, to the Swedish Museum of Natural History in Stockholm (NRMS), but, although numerous marine taxa from Hedenborg's collection are present at the NRMS, no fossil unionids from Rhodes could be located there (see Materials below).

In the 1850s, Hedenborg established a correspondence with Moritz Hörnes, the curator of the K.K. Hofmineralienkabinett in Vienna, to discuss the stratigraphy of Rhodes, and donated fossils from the island in several instalments in 1853 and 1859; these are curated in the Natural History Museum Vienna (NHMW) today. Two undated letters of Hedenborg to Hörnes are preserved (Hedenborg 1850s) and provide details of the writer's observations regarding the freshwater sediments of the island. In his first letter, Hedenborg described the geology between the towns of Ialysos (formerly Trianda) and Kremasti, where freshwater sediments extend along the slopes of Mount Filerimos and over the plain to the north (Fig. 1). From 2 successive layers at the base of his schematic cross-section of these strata he reported freshwater bivalves: *U. littoralis* and "*Anodonta* (fragment), which seems analogue to *Anatina*" (= *Anodonta* cf. *anatina*; Hedenborg 1850s; translated from German). Slightly higher in the same log, a first horizon with marine or brackish-water fauna followed, indicating the onset of the Kritika Formation as presently defined (see the section "Geological setting" below).

In his subsequent letter, Hedenborg (1850s) described a second freshwater unit from the Filerimos area, which occurs higher in the succession than the first one and is intercalated between marine strata. He mentioned a well-preserved specimen of *Unio* from the "greensands" in this succession, which he considered different from the previously collected *U. littoralis*. Again, the text of his letter is accompanied by schematic logs of the successions described, and the horizon that yielded the unionid is annotated as greyish-green sand in the respective drawing. While Hedenborg left no published record of his exploration of the freshwater deposits on Rhodes, his 2 letters to Hörnes demonstrate that he was aware of the alternating freshwater and marine conditions of the studied succession, which mark the transition from the Damatria Formation into the Kritika Formation (see the

"Geological setting" section below). Furthermore, the letters provide clues about the origins of the specimens he collected, which are studied here.

Bukowski (1889, 1892, 1894, 1896, 1898) was the first to investigate the freshwater deposits of Rhodes in detail and to monograph their fossil mollusc fauna. Although he travelled the entire island, he did not find any of the unionid species previously mentioned. However, he studied the fossil unionid shells collected earlier by Hedenborg in the Natural History Museum in Vienna (Bukowski 1892). Later, Bukowski (1896) reported 2 additional species of unionids from Rhodes. One of these, *Unio pseudatavus* Bukowski, 1896, with its varieties *dorica* and *calavardensis*, was described as new. Furthermore, a single, poorly preserved valve was addressed as "*Unio* f. indet. cfr. *Unio Vardinicus* Fontannes" (Bukowski 1896: 57) but not figured. Magrograssi (1928) subsequently described an additional variety, *Unio pseudatavus* var. *elongata*. It should be noted that, due to a printing error, all photographs on the single plate of her study are mirror-inverted. While research on the fossil freshwater gastropods from Rhodes continued (e.g. Willmann 1981), the bivalves received no further attention thereafter, apart from Willmann (1981: 92) mentioning indeterminate unionids from several outcrops, including a coastal section of the Apolakkia Formation.

Based on historical and newly collected material, the present study reassesses the taxonomic status of the fossil unionids previously reported from Rhodes, and 3 additional species are recorded. The biogeography and evolutionary relationships of these bivalves are evaluated in the context of the Neogene and Quaternary geological evolution of the Aegean region, and their ecology is discussed.

Geological setting

Rhodes is the largest island of the Dodecanese, located in the Eastern Mediterranean Sea, only 20 km off the south coast of Turkey (Fig. 1), to which it was joined until the latest Pliocene or earliest Pleistocene (Daams & van de Weerd 1980). The island is part of the easternmost Hellenic Forearc and is comprised of a stack of crustal nappes and ophiolites, collectively termed the Hellenic Basement. These accreted from the Cretaceous onward, due to the subduction of the African plate beneath Eurasia (e.g. van Hinsbergen et al. 2005, 2007, 2020), and they are overlain unconformably by Oligocene to questionably Early Miocene molasse-type sediments of the Vati Group (Mutti et al. 1970, Meulenkamp et al. 1972). Since the Eocene, adversely directed rotations within the forearc increased its curvature, causing various motions of smaller blocks (e.g. ten Veen & Kleinspehn 2002, van Hinsbergen et al. 2007, 2020, van Hinsbergen & Schmid 2012). Meanwhile, the opening of the Rhodes Basin east of the island, which commenced in the Late Miocene, triggered further, rapid movements (Woodside et al. 2000, van Hinsbergen et al. 2007, Hall et al.

2009, CORNÉE et al. 2019). Fossil mammals from Karpathos and Rhodes show that Rhodes became isolated from Anatolia during the latest Pliocene or earliest Pleistocene (DAAMS & VAN DE WEERD 1980). Presumably, this disconnection also was tectonic in nature, and Rhodes has remained an island since. The documented movements of Rhodes include counter-clockwise rotation of the order of 25° during 2 intervals, as well as Pleistocene tilting of the island by up to 2 degrees, first south-eastward (2.5–1.8 Ma), then back towards the northwest (1.6–1.1 Ma) (VAN HINSBERGEN et al. 2007). This tilting caused the present-day eastern coast of the island to drown (to 500–600 m water depth) and re-emerge, leading to the deposition and subsequent exposure of shallow to deep marine Pleistocene sediments on Rhodes (e.g. VAN HINSBERGEN et al. 2007, TITSCHACK et al. 2013, QUILLÉVÉRÉ et al. 2019).

BUKOWSKI (1889, 1892, 1894, 1898), who produced the first geological map of Rhodes, advocated an Early Pliocene age for the majority of the widespread freshwater deposits on the island but also recognised the presence of a separate unit of younger freshwater strata, which transition into the marine Pleistocene strata in northern Rhodes. These observations were largely confirmed by MUTTI et al. (1970), who emphasised the gradual transition from freshwater to marine deposits. MEULENKAMP et al. (1972) established 4 Neogene depositional phases for Rhodes and subdivided the respective strata into several formations. While all of these formations lacked stratotypes and formal definitions, their general characteristics and lateral extent were outlined.

Only the depositional phases 2 and 3 of MEULENKAMP et al. (1972) are relevant to the present study. During Phase 2 (~ Late Miocene? to early Late Pliocene), Rhodes was part of Anatolia. Two separate lake basins formed north and south of a central mountain range. Their proximal parts were gradually filled with braided-river and alluvial-fan deposits consisting of polymict conglomerates, sandstones, siltstones and clays; these are assigned to the Maritsa Formation in the north and the Istrios Formation in the south. In more distal areas, lake sediments composed of alternating clays, marls, siltstones and lignites were deposited; these are termed the Salakos Formation in the north and the Apolakkia Formation in the south (Figs 1, 2). As sediment supply waned, the lacustrine strata gradually overstepped the fluvial deposits. In south-eastern Rhodes, the coastline was close to its present-day position during phase 2, and shallow marine strata of the Cape Vigli Formation were deposited (SCHNEIDER et al. 2022). Phase 3 (~ late Late Pliocene to earliest? Pleistocene) is characterised by much lower sedimentation rates. Travertines and lacustrine limestones of the Monolithos Formation deposited during this phase are restricted to a small area in the west. In the northeast of the island, fluvial and lacustrine siliciclastic strata of the coeval Damatria Formation are more widespread. These grade laterally and upward into the brackish-water to shallow-marine siliciclastics of the Kritika Formation (Fig. 2). During this widespread transition from freshwater to marine conditions, Rhodes became an island

(DAAMS & VAN DE WEERD 1980). Given that none of the published geological maps of Rhodes depicts separate marine Pleistocene units, the Kritika Formation is integrated with the overlying marine deposits in Figure 1.

Age attributions of the non-marine Neogene succession on Rhodes rely on relatively sparse mammal faunas, corresponding to the Neogene European Land Mammal Zones MN15 and MN16 (MEULENKAMP et al. 1972, BENDA et al. 1977, VAN DE WEERD et al. 1982, KOUFOS 2016). The Apolakkia Formation is dated as MN15 (late Zanclean to mid Piacenzian) based on mammals (*Hipparion*), which is supported by magnetostratigraphy (VAN HINSBERGEN et al. 2007). The Salakos Formation correlates with the lower part of MN16 (BENDA et al. 1977). The Damatria Formation is broadly assigned to MN16 (mid to late Piacenzian); the first occurrence of *Equus* (modern horse) near the top of the unit marks the Pliocene–Pleistocene transition (BENDA et al. 1977). The overlying Kritika Formation is thought to be broadly Gelasian in age, which is supported by the ^{40}Ar/^{39}Ar age of a volcaniclastic layer slightly above the unit, but its precise age range is still poorly constrained (CORNÉE et al. 2006, MOISSETTE et al. 2016, SCHNEIDER et al. 2022).

Materials and Methods

The materials studied here are derived from 5 independent collections:

(1) Shells of *Pseudunio auricularius* (Spengler, 1793) and *Unio bruguierianus* Bourguignat, 1853 were collected by the second author in 1999, from the lower part of a steep, west-facing hill slope near the northern end of Kritika village, north-east Rhodes (36.4395° N, 028.2071° E; WGS84 datum) (Fig. 1). On its higher part, the hillside exposes richly fossiliferous, shallow-marine, fine- to medium-grained sands of the Kritika Formation. Like most of the slope, the transition from the fluvial deposits to the nearshore sands is densely overgrown with shrubs and is thus not documented in detail. The specimens occurred in situ, with closed valves, at the base of a fluvial channel (Fig. 3A, B). The sediment is best classified as a diamictite, consisting of poorly sorted, poorly rounded, fine-gravel-size conglomerate and coarse-grained sand, embedded in a silty matrix. When revisited in September 2018, the locality was overgrown and inaccessible, and no further shells were found. The specimens are curated at the Bavarian State Collection for Palaeontology and Geology (**BSPG**), Munich, Germany, under accession numbers BSPG 2020 CI 46 and 47 (*P. auricularius*) and BSPG 2020 CI 58 to 62 (*U. bruguierianus*).

The locality is within the type area of the Kritika Formation (HANKEN et al. 1996) but occurs in a lower position, stratigraphically, than the succession documented and described in detail by FERRY et al. (2001); its precise relationship with this succession is unclear. Here we provisionally assign the locality to the Kritika Formation,
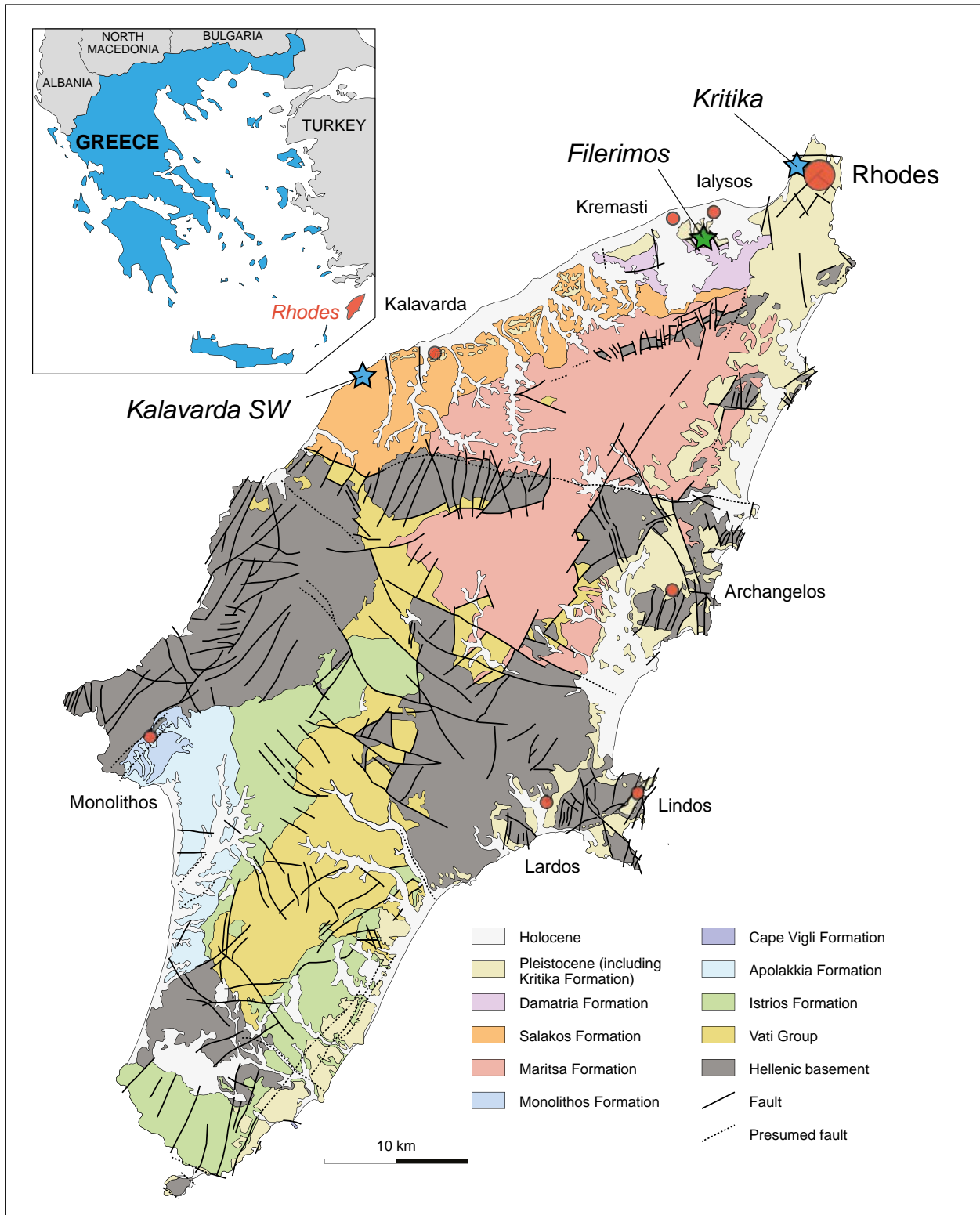
Figure 1. Geological map of the island of Rhodes, based on Lekkas et al. (2000), with Pliocene freshwater units adapted from Meulenkamp et al. (1972); modified from Schneider et al. (2022). The Kritika Formation is included in the Pleistocene strata (light yellow). The locations of Kritika and Kalavarda SW, where we collected freshwater bivalves, are marked by blue stars. Mount Filerimos, where specimens were collected by Johan Hedenborg and by us, is marked by a green star.

which reportedly elsewhere has fluvial deposits intercalated (Willmann 1981, Moissette et al. 2016). Should it turn out that there are no marine sediments below, the strata may be better placed in the Damatria Formation. In any case, the fluvial channel likely is close to the lower boundary of the Kritika Formation, and we suppose the shells to be latest Pliocene or earliest Pleistocene in age.

(2) *Unio pseudatavus* occurs in abundance in lacustrine and fluvial deposits of the Salakos Formation southwest of Kalavarda, north-western Rhodes (Fig. 1),
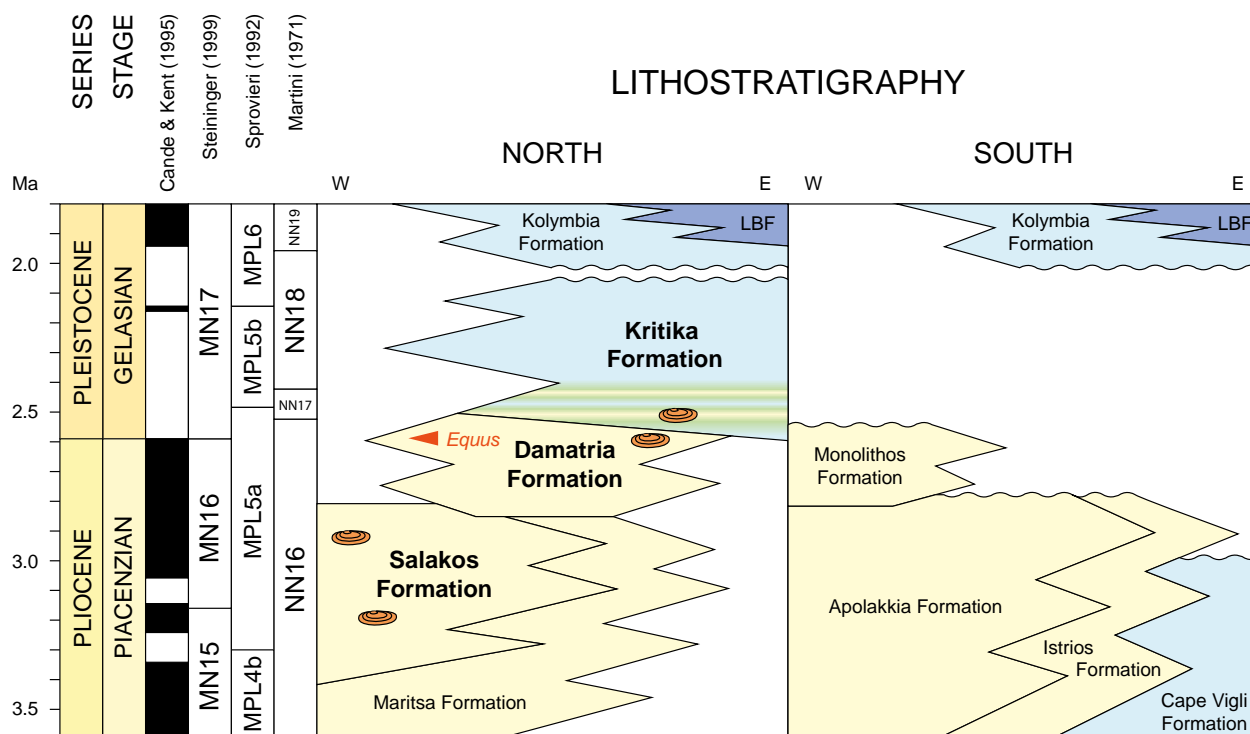
Figure 2. Pliocene–Pleistocene lithostratigraphy of Rhodes, modified from SCHNEIDER et al. (2022). Columns to the left display international chronostratigraphic series and stages, palaeomagnetic polarity timescale (CANDE & KENT 1995), mammal zones (STEININGER 1999), planktic foraminifer zones (SPROVIERI 1992) and calcareous-nannofossil zones (MARTINI 1971). Note that the precise positions of most unit boundaries are unsettled. Representative occurrences of the studied freshwater bivalves are indicated by orange symbols. LBF = Lindos Bay Formation. Colours: light yellow = freshwater; light green = brackish water; light blue = shallow marine; dark blue = deep marine.

which are easily accessible along the coastal road. Unionid shells often occur in situ, with closed valves, in silt or fine-grained sand, but also disarticulated, as part of rich parautochthonous mollusc assemblages in coarser-grained beds (Fig. 3C, D). The same deposits contain abundant Dreissenidae as well as Viviparidae, Melanopsidae, Neritidae and other freshwater gastropods (BUKOWSKI 1894, 1896, MAGROGRASSI 1928, WILLMANN 1981). In September 2018 we collected numerous shells of *Unio pseudatavus* from 2 closely adjacent outcrops (Locality A at 36.3333° N, 027.8991° E; Locality B at 36.3303° N, 027.8951° E). The shell assigned to *Unio* sp. below comes from Locality B. These specimens are curated at the BSPG, under accession numbers BSPG 2020 CI 45 (*Unio* sp.) and BSPG 2020 CI 48 to 57 (*U. pseudatavus*). Additionally, we re-figure part of BUKOWSKI's (1896) type material, which is curated at the Department of Geology, University of Vienna under accession numbers IGUW 1895 XII/48 to 52 and 55 to 60; photographs were kindly provided by Alice Schumacher (Natural History Museum Vienna).

(3) In the early 1850s, the French vice-consul on Rhodes, Monsieur Prus, collected fossils on the island, which he donated to Alcide d'Orbigny in Paris in 1855 (FISCHER et al. 1877). These specimens, studied by TOURNOUËR (1877), are now held by the Muséum national d'Histoire naturelle (**MNHN**), Paris, France, and include 4 specimens labelled as *U. prusii* (MNHN.F.B41267, MNHN.F.

A89391–A89393) and another 4 specimens labelled as *U. littoralis* (MNHN.F.B41266a–d). BUKOWSKI (1896) studied in detail most of the older freshwater strata, and they did not yield any of these taxa. Thus, it is likely that the specimens were collected from either the Damatria Formation or the Kritika Formation, as also suggested by BUKOWSKI (1892). WILLMANN (1981: 70) claimed that the material studied by TOURNOUËR (1877) was derived from the Kritika Formation at Mount Filerimos south of Ialysos (Fig. 1), but there is no written evidence to support this claim.

We are convinced that the 4 specimens numbered MNHN.F.B41267 and MNHN.F.A89391 to A89393 represent the type series of *U. prusii*. BOURGUIGNAT (1856a, b) did not provide any information regarding the whereabouts of the material he studied, and no specimens of *U. prusii* are preserved in his own collection, held by the Muséum d'histoire naturelle de Genève (pers. comm. Lionel Cavin and Emmanuel Tardy, Geneva, 21.vi.2021). However, given that Bourguignat was one of d'Orbigny's disciples and was employed at the Muséum national d'Histoire naturelle, Paris, when he described *U. prusii*, it seems likely that the specimens held by d'Orbigny represent the actual syntypes. A further indication as to that is that the new species was named after the collector Monsieur Prus (FISCHER et al. 1877). Photographs of the specimens were kindly provided by Philippe Loubry and Didier Merle (MNHN).

Figure 3. Outcrop photographs. **A, B.** Fluvial deposits of the lower Kritika Formation (?) at Kritika. **A.** Numerous unionid specimens in life position near the base of a fluvial channel fill. **B.** Close-up of a *Pseudunio auricularius* specimen in life position. **C, D.** Outcrops of the Salakos Formation SW of Kalavarda. **C.** Fluvial channel fill of poorly sorted coarse-grained components in silt-to-sand-grade matrix, including numerous shells of *Unio pseudatavus*. **D.** Thin shell lag, containing abundant *Unio pseudatavus* and gastropods.

(4) Johan Hedenborg, who was a freelance medical doctor on Rhodes in the 1850s and served as the Norwegian and Swedish vice-consul on the island in the early 1860s (LINSE 2011), studied the geology of the island and also collected fossils, some of which he donated to the Kaiserliche Akademie der Wissenschaften (in 2 instalments in 1853) and the K.K. Hofmineralienkabinett (in 1859) in Vienna, Austria. All 3 instalments were subsequently transferred to the Natural History Museum in Vienna (**NHMW**; accession numbers NHMW 1853/0036/0040, NHMW 1854/0015/0021, NHMW 1859/0030/0257–262). The freshwater mussels contained in this collection were studied by BUKOWSKI (1892) and identified as *U. littoralis* and *U. prusii*. For the present study, the fossils were re-examined by the first author, and several of them were photographed. Based on HEDENBORG's (1850s) letters to curator Moritz Hörnes in Vienna, specimens of *Potomida semirugata* (Lamarck, 1819) (identified as *U. littoralis* by Hedenborg) are here assigned to the uppermost Damatria Formation, while the single specimen of *Leguminaia hedenborgi* n. sp. is attributed to the lower Kritika Formation. For both species, Mount Filerimos serves as only a broad indication of locality; the exact positions of the collection sites remain unknown. In the large collection donated by Hedenborg to the Swedish Museum of Natural History in the early 1830s, no Unionidae could be identified (pers. comm. Steffen Kiel, Stockholm, xi.2022).

(5) Two fragments of *Pseudunio auricularius* (Spengler, 1793) were collected by the first author on the north-eastern slope of Mount Filerimos south of Ialysos (36.3993° N, 028.1529° E) (Fig. 1) in 2023. The respective strata are poorly exposed but seem to occur above a horizon with marine molluscs and are thus provisionally

assigned to the lower Kritika Formation. These specimens are curated at the BSPG under accession number BSPG 2020 CI 63.

All shells studied by us were cleaned with water, needle and brush only. Fossils from the Salakos Formation are entirely free from sediment after this treatment. Some of the specimens from Kritika remain partly encrusted with sand. However, forcibly removing the crusts would also damage the shell surface, and we refrained from further cleaning. For photographs, most specimens were whitened with ammonium chloride.

The following abbreviations of repositories apply: **BSPG** = Bavarian State Collection for Palaeontology and Geology, Munich, Germany; **IGUW** = Department of Geology, University of Vienna, Austria; **MNHN** = Muséum national d'Histoire naturelle, Paris, France; **NHMW** = Natural History Museum, Vienna, Austria.

Systematic Palaeontology

Order Unionida J.E. Gray, 1854

Superfamily Unionoidea Rafinesque, 1820

Family Margaritiferidae Henderson, 1929

Subfamily Margaritiferinae Henderson, 1929

Genus *Pseudunio* F. Haas, 1910

Type species. *Unio sinuatus* Lamarck, 1819, by original designation.

Remarks. In the literature, *Pseudunio* has been variably treated as a valid genus, a junior subjective synonym of *Margaritifera* Schumacher, 1815, or a subgenus of the latter. The most recent phylogeny of the Margaritiferidae by Lopes-Lima et al. (2018) re-established the validity of *Pseudunio* as a genus. *Unio sinuatus* Lamarck, 1819 is a junior subjective synonym of *Pseudunio auricularius* (Spengler, 1793).

***Pseudunio auricularius* (Spengler, 1793)**

Figures 3B, 4A, B

Unio auricularius Spengler 1793: 54, no. 21 [referring to Lister 1686: 149, fig. 4].
Pseudunio auricularius—Lopes-Lima et al. 2018: 112.

Type locality. Spengler (1793: 54) did not designate a type locality for *Unio auricularius*, and the origins of the specimen referred to, which was figured by Lister (1686: 149, fig. 4), are unknown. Spengler's (1793) vernacular name, "East Indian River Pearl Mussel" (translated from Danish), suggests an origin in Southeast Asia, which is far outside the geographic distribution of the species and thus clearly erroneous (see discussion by Araujo & Ramos 2000). Spengler (1793: 55) also assigned fossil shells from "Berlingen at the Untersee in Switzerland" (translated from Danish) to *Unio auricularius*. The

locality name refers to Überlingen at Lake Constance in Germany, close to the Swiss border. These fossil shells most likely represent *Pseudunio flabellatus* (Goldfuss, 1837), which occurs in Miocene strata of the Lake Constance area (cf. Schneider & Prieto 2011).

Materials. Right and left valve of a single individual; lower Kritika Formation (?); Kritika, N Rhodes. BSPG 2020 CI 46, 47. Fragments of a single left and a single right valve; lower Kritika Formation (?); NE slope of Mount Filerimos S of Ialysos, N Rhodes. BSPG 2020 CI 63.

Description. Shell 133 mm long and 61 mm high, solid, relatively thick; elongate-ovate, faintly kidney-shaped in outline. Anterior shell margin well rounded, curving into rather straight ventral margin with broad, shallow incurvature in its central part. Dorsal margin gently rounded; posterior part sloping towards bluntly rounded, slightly tapering posterior end, positioned at approximately ⅓ of shell height. Umbo broad, poorly inflated, barely projecting; positioned at approximately 25% of shell length.
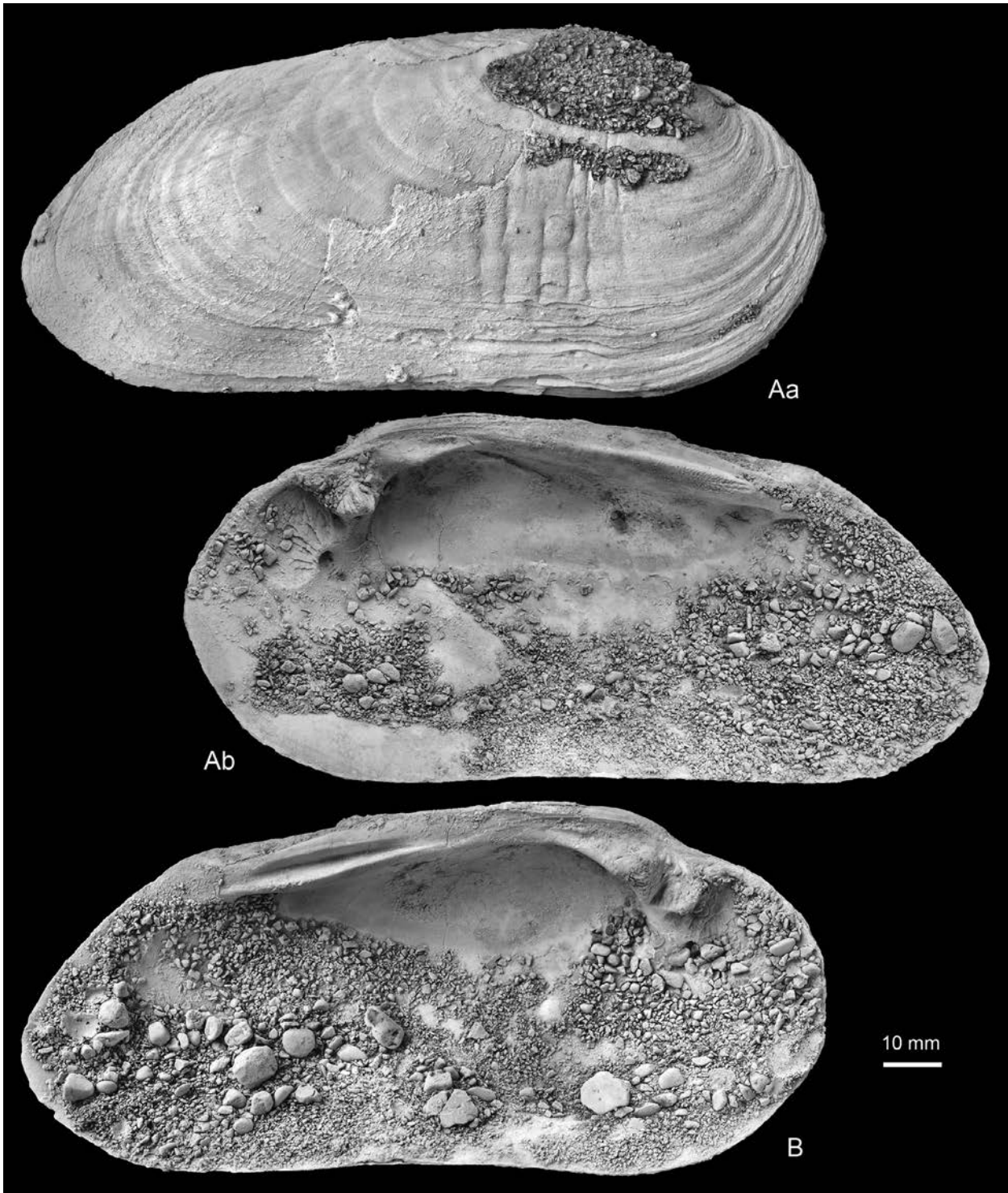
Only parts of outermost shell layer preserved, showing ornament of rugose, irregular growth lines. Weakly developed oblique flabellae deflected in posterior-dorsal direction from imaginary line between umbo and posterior end of shell. Several relatively distinct, vertical, undulating incisions of at least 30 mm length occur slightly anterior to shell centroid. Umbonal ornament obscured by encrusted sediment.

Left valve hinge. Massive pseudocardinal tooth with 2 prominent cusps, separated by deep, relatively wide socket; supported by strong, but not down-sloping, buttress. Anterior cusp short-tongue-shaped, pointing forward; situated anterior to umbo. Posterior cusp prominent, with several subradial grooves; oblique-elongate-triangular in outline, its base curving gently upward posteriorly; situated behind umbo. Wide gap to 2 prominent, sharply raised, rather short posterior lateral teeth, paralleling posterior-dorsal shell margin.

Right valve hinge. Massive pseudocardinal tooth with prominent anterior and relatively weak posterior cusp. Anterior cusp short, peg-like, with several subradial grooves; flanked by deep sockets; situated anterior to umbo. Posterior cusp a rounded, elongate, posteriorly tapering swelling; situated behind umbo. Wide gap before onset of 1 relatively short, prominent posterior lateral tooth; posterior part of ventral facet faintly crenulated. Nymphs long, slightly raised, extending backward to approximately ½ length of lateral teeth.

Anterior adductor-muscle scar large, short-kidney-shaped, deep, internally textured; in anterior-ventral position to pseudocardinal tooth. Posterior adductor-muscle scar relatively shallow (largely obscured by encrusted sediment). Anterior pedal-retractor-muscle scar very deep, circular, positioned directly behind, but separate from, anterior adductor-muscle scar. Pallial line and mantle attachment scars obscured by encrusted sediment.

Remarks. Although the pallial line and mantle-attachment scars are obscured, the overall morphology of the specimens leaves no doubt as to the generic assignment

Figure 4. *Pseudunio auricularius* (Spengler, 1793). Lower Kritika Formation (?); Kritika, Rhodes. **Aa.** Right valve, with part of outermost shell layer preserved; BSPG 2020 CI 46. Note weak posteriorly directed oblique flabellae behind umbo, as well as vertical furrows near centroid of shell. **Ab.** Same valve as in Aa. **B.** Left valve of same individual; BSPG 2020 CI 47.

to *Pseudunio*. Weak dorsal flabellae are known to occur in some individuals of all extant representatives of *Pseudunio* (e.g. Araujo et al. 2009b: fig. 4) but are much more strongly expressed in fossil *Pseudunio flabellatus* (Goldfuss, 1837) and its predecessors (Schneider & Prieto 2011). Likewise, the shallow vertical incisions on the shell flanks occur in some individuals of modern representatives (e.g. Araujo et al. 2009a: fig. 2E).

As demonstrated by Vikhrev et al. (2018: fig. 6), the shapes of the shell outlines of the 3 very closely related modern species of *Pseudunio* overlap. Typical adult shells of western European *P. auricularius* are usually more elongate, with more subdued umbos than in its Levant sister species *Pseudunio homsensis* (I. Lea, 1865). Typical specimens of North African *Pseudunio marocanus* (Pallary, 1918) can be identified by their more trapezoidal

shells, which are highest in their posterior third. However, outliers occur in all 3 species (VIKHREV et al. 2018: fig. 6). At a length of 133 mm, the specimen from Rhodes is adult, with a rather elongate shell that is highest at its umbo, while the posterior-dorsal shell margin is gently sloping. This shape conforms closely to the typical shell outline of *P. auricularius*.

Hinge morphology in the 3 extant species of *Pseudunio* is similar. However, specimens of *P. auricularius* that we studied show a distinct, elongate posterior pseudocardinal cusp in the right valve. In contrast, in *P. homensis* this cusp is reduced to a number of short, rather low ridgelets. In the figured specimen from Rhodes, the posterior cusp forms a contiguous, elongate swelling (Fig. 4Ab), resembling the condition in typical adult *P. auricularius*, to which the material from Rhodes is here assigned.

Family Unionidae Rafinesque, 1820

Subfamily Unioninae Rafinesque, 1820

Tribe Unionini Rafinesque, 1820

Genus *Unio* Philipsson, 1788

Type species. *Mya pictorum* Linnaeus, 1758, by subsequent designation; Opinion 495, INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE (1957).

Unio pseudatavus Bukowski, 1896

Figures 3C, D, 5A–D, 6A–F, 7A–C

Unio pseudatavus BUKOWSKI 1896: 51, pl. 10 figs 4–8, pl. 11 figs 1–7.
Unio pseudatavus var. *dorica* BUKOWSKI 1896: 53, pl. 11 figs 4, 5.
Unio pseudatavus var. *Calavardensis* BUKOWSKI 1896: 53, pl. 11 figs 6, 7.
Unio pseudatavus var. *elongata* MAGROGRASSI 1928: 256, pl. 6 fig. 2.

Type locality and stratum. Kalavarda, NW Rhodes, Greece; Salakos Formation, Piacenzian (Pliocene).

Types. BUKOWSKI (1896) did not select types for his taxa. As far as we are aware, no lectotypes have been designated since. The specimen figured in plate 10 fig. 7 of BUKOWSKI (1896), IGUW 1895 XII/51, is hereby designated as the lectotype of *Unio pseudatavus* Bukowski, 1896 (Fig. 5A). The specimen in plate 11 fig. 5a, b, IGUW 1895 XII/59, is hereby designated as the lectotype of *Unio pseudatavus* var. *dorica* Bukowski, 1896 (Fig. 5B). The specimen in plate 11 fig. 6a, b, IGUW 1895 XII/55, is hereby designated as the lectotype of *Unio pseudatavus* var. *calavardensis* Bukowski, 1896 (Fig. 5D). Additional specimens from Kalavarda figured by BUKOWSKI (1896) thereby become paralectotypes; specimens from Langonia valley are originals, but not types. The specimen figured by MAGROGRASSI (1928), plate 6 fig. 2, is hereby designated as the lectotype of *Unio pseudatavus* var. *elongata* Magrograssi, 1928.

Additional materials. More than 30 specimens; Salakos Formation; W of Kalavarda, localities A and B, NW Rhodes. BSPG 2020 CI 48 to 57.

Description. Shells up to 70 mm long and 40 mm high, very solid and thick, elongate-ovate to trigonally ovate in outline; individuals gradually becoming more elongate with age. Anterior shell margin well rounded, curving into fairly straight, faintly rounded ventral margin; dorsal margin almost straight, backward sloping, curving into further sloping, slightly tapering, gently curved posterior margin. Umbo moderately inflated, distinctly incurved, prosogyrate, relatively narrow and prominent, in near-terminal position. Shell with a relatively narrow, short, lanceolate lunule.

Shell ornamented with rugose, irregular, commarginal growth lines. Umbonal ornament of 2 rows of small, arcuate tubercles preserved in 1 juvenile specimen and in 1 of Bukowski's syntypes; posterior row comprising 4 tubercles, anterior row 2 minute ones (Figs 5Ba, 7Ca, Cc). In some specimens, several delicate, short, oblique, posteriorly extending wrinkles occur behind umbo, on dorsal side of shell.

Left valve hinge. Pseudocardinal tooth with short, blade-like, subvertical anterior cusp, curving into massive, elongate-triangular posterior cusp dorsally; both cusps flanking deep central socket. Tapering end of posterior cusp joined to ventral one of 2 long, prominent posterior lateral teeth.

Right valve hinge. Prominent, peg-like single cusp of pseudocardinal tooth flanked by deep, slit-like socket anterior-dorsally, and wide, deep socket posteriorly. Single, long, prominent posterior lateral tooth arising behind socket. Nymphs low, extending to approximately ½ shell length.

Hinge plate supported by massive, broad, subvertical buttress. Anterior adductor-muscle scar very deep, rounded-quadrate, situated in front of buttress. Posterior adductor-muscle scar also relatively deep, roundish to short-ovate, situated below posterior end of laterals. Anterior pedal-retractor-muscle scar deep, slit-like, oblique, situated at ventral base of buttress. Pallial line distinct, entire.

Remarks. BUKOWSKI (1896) characterised *U. pseudatavus* as a highly variable species and provided an extensive description of the shells. Unlike many other scientists of his time, he regarded most of the variability he observed as truly intraspecific and erected 2 varieties beside the typical form. His variety *dorica* refers to specimens with a less inflated posterior part and a slightly more curved posterior-dorsal shell margin. Moreover, the umbonal ornament and posterior-dorsal wrinkles described above were said to occur only in this variety (BUKOWSKI 1896). We have observed that these less elongate, less inflated specimens tend to be smaller and less thick-shelled than the elongate individuals and thus are generally younger. Consequently, their umbos are less corroded and still preserve details of the ornament, as is also the case in a single young adult specimen in our collection (Fig. 6A). In contrast, BUKOWSKI's (1896) variety *calavardensis* is characterised
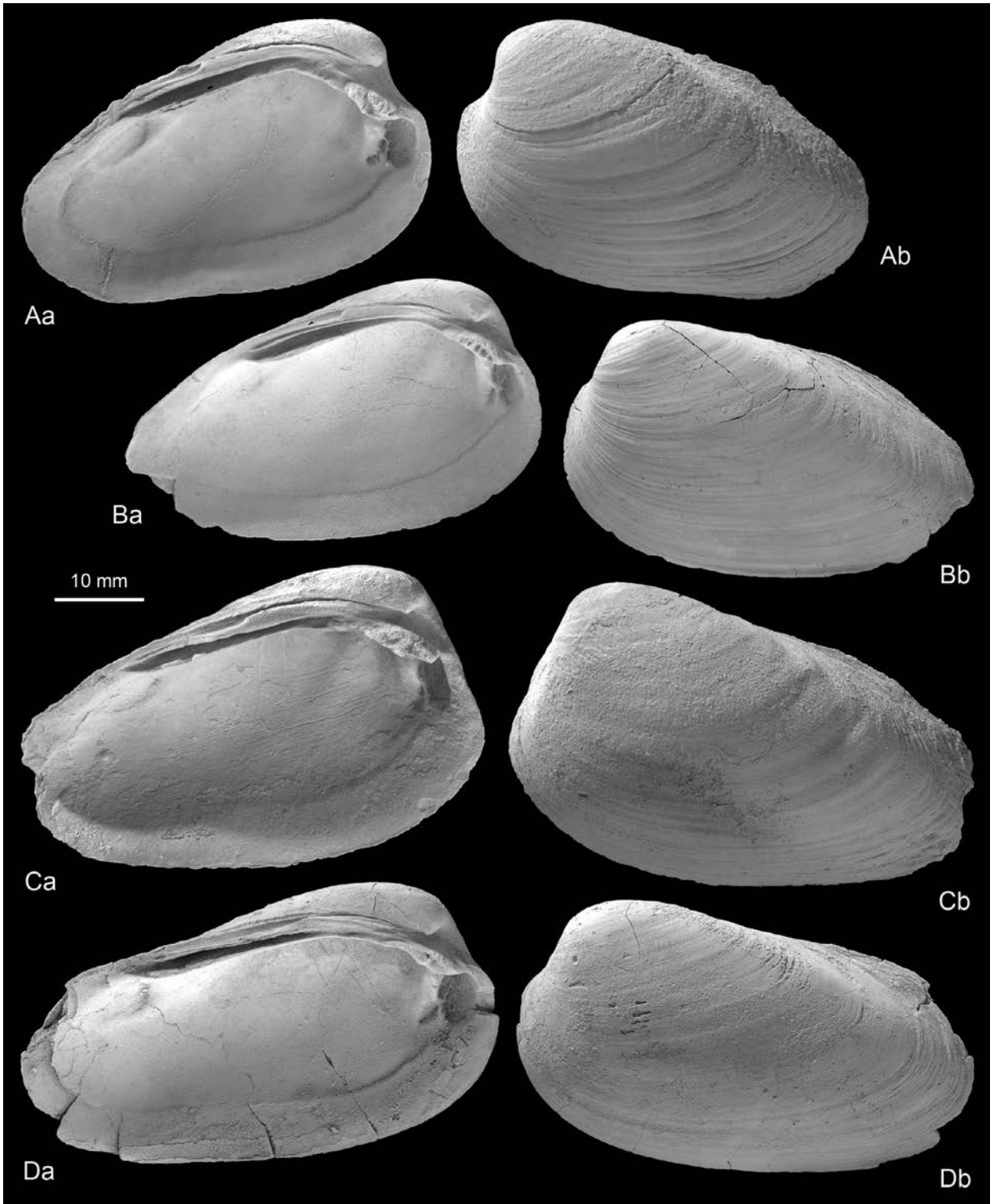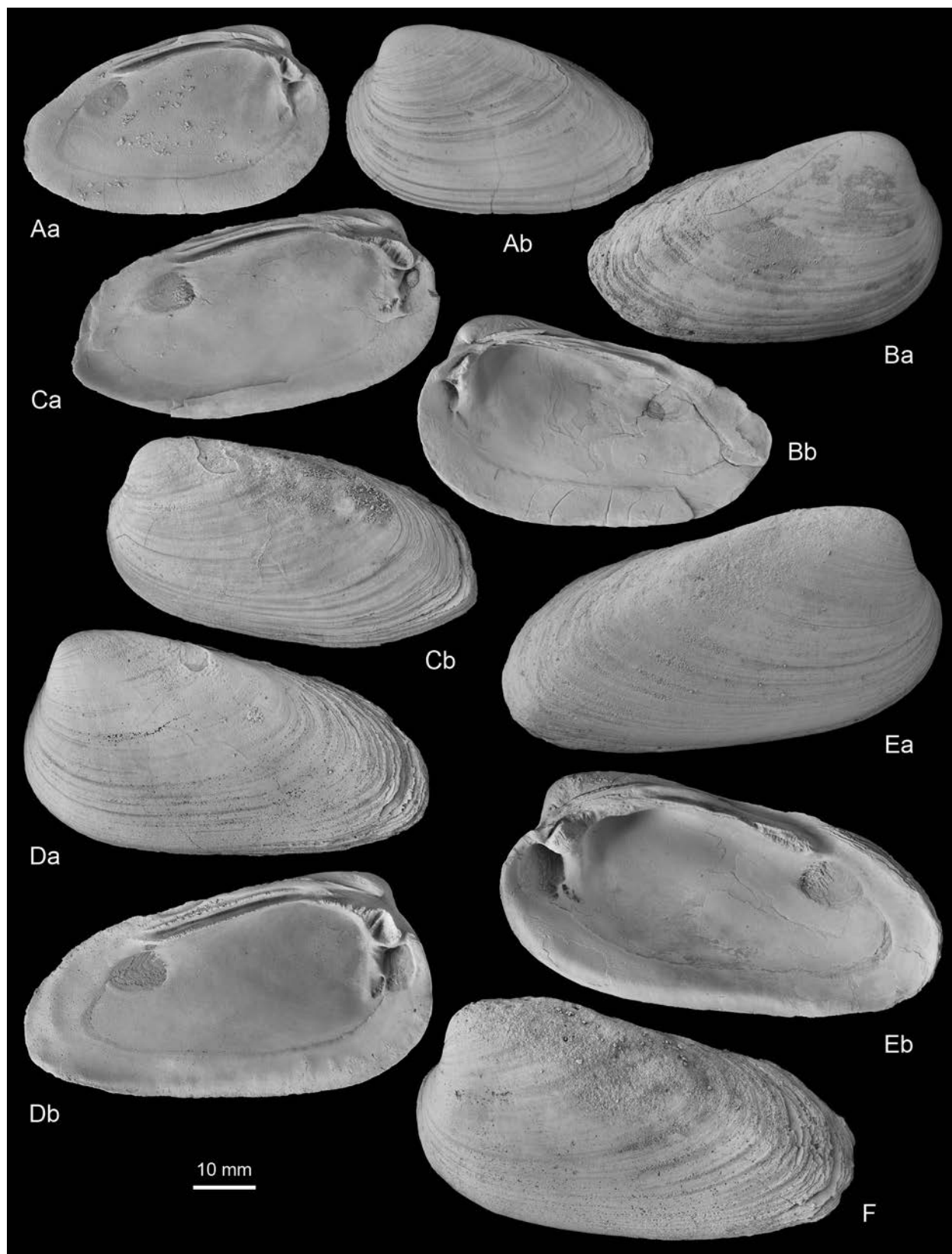
Figure 5. *Unio pseudatavus* Bukowski, 1896. Salakos Formation. **A.** *Unio pseudatavus* Bukowski, 1896 (pl. 10 fig. 7), lectotype designated here; Kalavarda; IGUW 1895 XII/51. **B.** *Unio pseudatavus* var. *dorica* Bukowski, 1896 (pl. 11 fig. 5), lectotype designated here; Kalavarda; IGUW 1895 XII/59. **C.** *Unio pseudatavus* Bukowski, 1896 (pl. 10 fig. 8); Langonia valley; IGUW 1895 XII/52. **D.** *Unio pseudatavus* var. *calavardensis* Bukowski, 1896 (pl. 11 fig. 6), lectotype designated here; Kalavarda; IGUW 1895 XII/55.

by more elongate, posteriorly more tapered shells. Exactly the same characteristics, a more elongate and posteriorly more tapered shell, are given by MAGROGRASSI (1928) for her variety *elongata*. As pointed out by BUKOWSKI (1896), these varieties represent extremes of a continuum and thus, in our opinion, do not warrant nomenclatorial

separation; they are listed in synonymy above.

We refrain from repeating BUKOWSKI's (1896) detailed comparison of *U. pseudatavus* with similar species. *Unio pseudatavus* differs from other species in *Unio* in its near-terminal, prominent, distinctly prosogyrate umbos, combined with a very solid shell and relatively small but

Figure 6. *Unio pseudatavus* Bukowski, 1896. Salakos Formation SW of Kalavarda. **A, C, D.** Locality A. **B, E, F.** Locality B. **A.** BSPG 2020 CI 51. **B.** BSPG 2020 CI 50. **C.** BSPG 2020 CI 52. **D.** BSPG 2020 CI 53. **E.** BSPG 2020 CI 54. **F.** BSPG 2020 CI 55.

deep adductor-muscle scars. The heavy shell is further reflected in rather prominent hinge teeth. Due to its rather slender shell and its umbonal ornament of 2 rows of small tubercles, which is similar to those of *Unio pictorum*, *U. mancus* and *U. elongatulus* (pers. obs.; Zieritz et al. 2014), *U. pseudatavus* is here assigned to the *Unio pictorum* group (see Araujo et al. 2018 and Lopes-Lima et al. 2021 for composition).
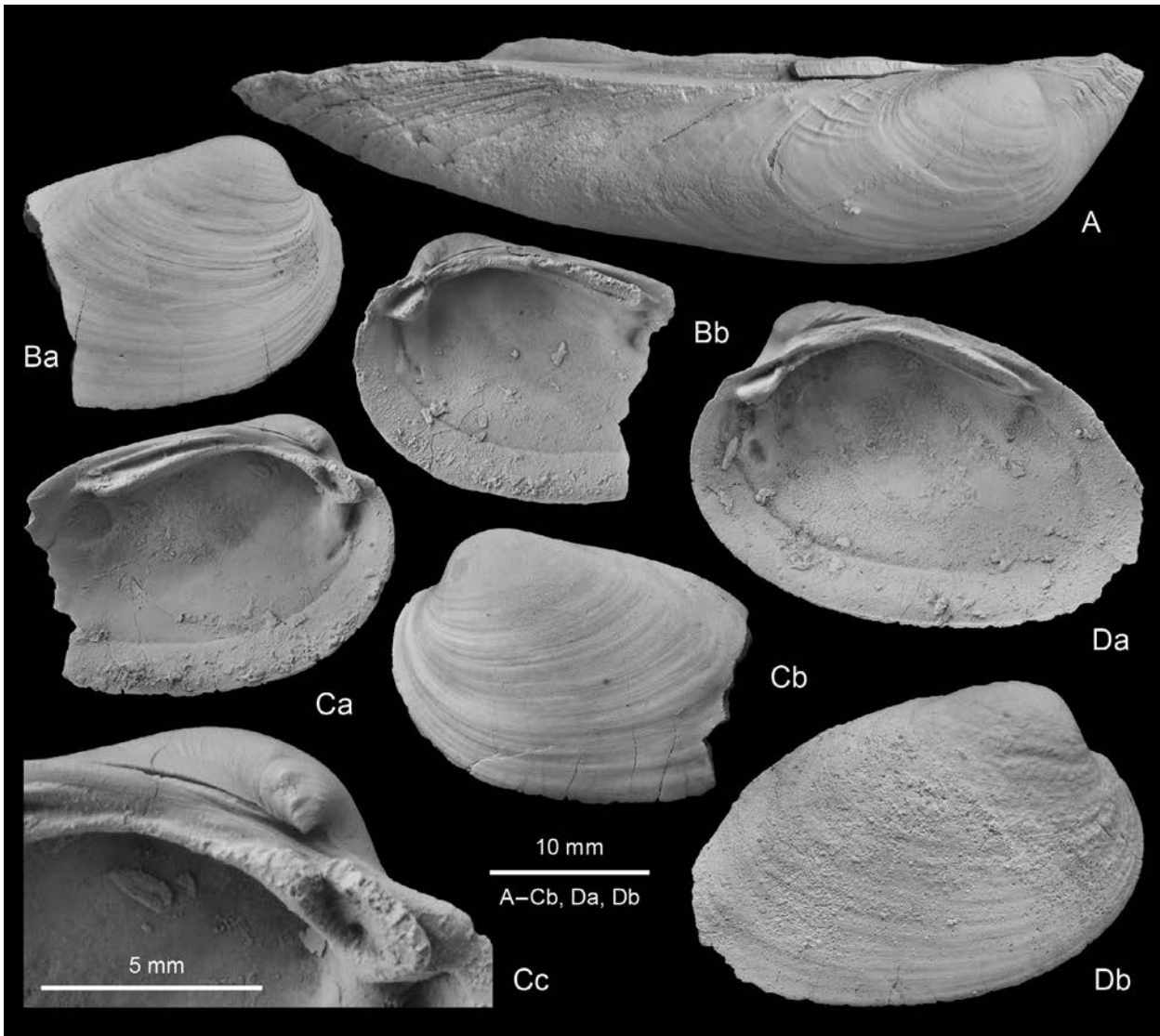
Figure 7. A–C. *Unio pseudatavus* Bukowski, 1896. Salakos Formation; SW of Kalavarda, Rhodes; Locality B. **A.** Adult right valve, showing posterior-dorsal ornamentation; BSPG 2020 CI 50. **B, C.** Fragmentary juvenile right and left valves of same individual; BSPG 2020 CI 48, 49. **Cc.** Close-up of left valve, showing umbonal ornament. **D.** *Unio* sp., right valve; Salakos Formation; SW of Kalavarda; Locality B; BSPG 2020 CI 45.

Unio sp.

Fig. 7D

Material. A single small right valve; Salakos Formation; W of Kalavarda, Locality B, NW Rhodes. BSPG 2020 CI 45.

Description. Shell 27.5 mm long and 20 mm high, solid, moderately thick, ovate in outline. Anterior-dorsal shell margin straight to slightly concave; all other parts of shell margin well rounded. Umbo relatively broad, prominent, distinctly prosogyrate. Outside of shell ornamented with growth lines only; umbonal and anterior portion markedly corroded.

Single short-ovate cusp of pseudocardinal tooth flanked by deep, slit-like socket dorsally, and wide socket posteriorly. Single, prominent, rather sharp posterior lateral tooth emerging behind socket. Nymph relatively short, prominent, faintly projecting above shell margin.

Hinge plate supported by distinct but low buttress. Moderately deep, roundish anterior adductor-muscle scar situated in front of buttress. Posterior adductor-muscle scar short-ovate, moderately deep, situated below posterior end of lateral tooth. Anterior pedal-retractor-muscle scar deep, ovate, situated at lower end of buttress. Pallial line distinct, entire.

Remarks. The single left valve differs from *U. pseudatavus*, which occurs in abundance in the same horizon, by its short-ovate outline, less prominent buttress, ovate rather than slit-like anterior pedal-retractor-muscle scar and more prominent nymph. The specimen may thus represent a distinct species rather than an extreme morph of *U. pseudatavus*. However, given that only 1 slightly corroded, probably juvenile valve was collected, we refrain from specific assignment.

"*Unio* f. indet. cfr. *Unio Vardinicus* Fontannes", described but not figured by Bukowski (1896: 57), was

either collected from the Apolakkia Formation or from the Monolithos Formation. *Unio vardinicus* Fontannes, 1883 was originally described from Pliocene strata in the Rhône Valley in southwest France. This is another rather elongate, moderately inflated species of the *pictorum* group, similar to *U. pseudatavus*, but with a much more rounded, non-tapering posterior end and less terminal umbos, resulting in a more ovate shell outline. Bukowski (1896) mentioned these distinguishing characters but refrained from a conclusive determination of his 2 rather poorly preserved specimens. Whether the material collected by Bukowski and our specimen belong to the same species remains uncertain.

Unio bruguierianus Bourguignat, 1853

Figures 8, 9

Unio bruguierianus Bourguignat 1853: 78, pl. 2 figs 54–56.
Unio prusii Bourguignat 1856a: 76, pl. 3 figs 1–4.
Unio prusii—Bourguignat 1856b: 160, pl. 12 figs 1–4.
Unio prusi—Tournouër 1877: 48.
Unio crassus bruguierianus—Haas 1940: 132.
Unio crassus bruguierianus—Haas 1969: 54.
Unio bruguierianus—Lopes-Lima et al. 2021: appendix 1: 4.

Type locality. "In the streams around Smyrna, Anatolia" (Bourguignat 1853: 78, translated from French) = İzmir area, Aegean coast of Turkey.

Materials. Five right valves, 1 left valve, 2 double-valved specimens; lower Kritika Formation (?); Kritika, NE Rhodes. BSPG 2020 CI 58 to 61. Syntypes of *U. prusii*: 2 right valves, 2 left valves, without indication of locality; Damatria or Kritika formations in N Rhodes. The specimen illustrated in Figure 8D (MNHN.F.B41267) is hereby designated as the lectotype of *U. prusii*, whereby the remaining 3 specimens (MNHN.F.A89391 to 89393) become paralectotypes.

Description. Shells up to 56 mm long and 37 mm high; solid, moderately thick; rounded-subrectangular in outline. Anterior shell margin and transition to ventral margin well rounded; ventral margin rather straight, with a feeble, more or less central incurvature in some specimens; posterior margin truncated, steeply sloping to subvertical, meeting ventral margin at bluntly rounded angles of 75–88°; dorsal margin nearly straight. Two faintly accentuated bends extending from umbo to posterior shell margin, flanking the truncated shell portion. Umbo low, broadly rounded, positioned at 25–28% of shell length. Shell ornamented with rather rugose, irregular, commarginal growth lines, anteriorly and posteriorly more pronounced than in central part of shell. No umbonal ornament preserved.

Left valve hinge. Pseudocardinal tooth with 2 prominent cusps, both situated anterior to umbo; anterior cusp lobe-shaped, protruding forward; posterior cusp rounded-triangular; deeply incised socket between cusps. Two strong, gently rounded posterior lateral teeth lie parallel to dorsal margin, emerging from hinge plate distinctly behind the umbo.

Right valve hinge. Pseudocardinal tooth with 1 prominent, narrow cusp, flanked by deep anterior socket and relatively shallow posterior socket. One strong, gently rounded posterior lateral tooth. Hinge plate in both valves supported by broad, rounded anterior buttress. Nymphs low, relatively long, extending from shortly behind umbo approximately halfway towards posterior end of shell.

Anterior and posterior adductor-muscle scars deep, rounded to subcircular, nearly equal in size, not internally structured. Anterior adductor-muscle scar posteriorly bounded by buttress. Anterior pedal-retractor-muscle scar deep, but faintly demarcated; situated posterior-ventrally to anterior adductor-muscle scar. Anterior pedal-elevator-muscle scar deep, point-like, situated at anterior dorsal end of buttress, just below anterior ends of pseudo-cardinal cusps. Pallial line distinct, entire.

Remarks. As recently confirmed by Lopes-Lima et al. (2021), *U. bruguierianus* inhabits several river basins in mainland Greece, Turkey, Armenia, Azerbaijan, Iran and Iraq, and some populations sampled for their study live less than 200 km north of Rhodes. The subrectangular, rather than ovate, shells studied here, with their rather low umbos positioned rather distant from the anterior margin, closely match the morphology of *U. bruguierianus*. The rather prominent hinge teeth and deep, roundish anterior and posterior adductor-muscle scars are also typical of this species, as well as of the *Unio crassus* group in general (see Araujo et al. 2018 and Lopes-Lima et al. 2021 for composition). Note that, unlike in the present species, the posterior adductor-muscle scar in *Potomida semirugata* is faint, shallow and elongate (see below). As far as we are aware, this is the first fossil record of *U. bruguierianus*. However, given the taxonomic confusion in *Unio*, there may be other fossil shells with erroneous taxonomy.

Bourguignat (1856a) erected a new species, *U. prusii*, for fossil shells from Rhodes. He provided relatively accurate drawings of a specimen with closed valves in left lateral, frontal and dorsal view, and of the hinge regions of a pair of left and right valves. As outlined in the Materials and Methods section above, we regard the 4 specimens preserved in the d'Orbigny collection at MNHN Paris as the type series of Bourguignat's (1856a) species, and the right valve depicted in Figure 8D, which is well-preserved externally and internally, is here designated as the lectotype of *U. prusii*; the paratype depicted in Figure 8E best shows the configuration of the hinge.

Tournouër (1877) maintained Bourguignat's (1856a) determination; he remarked that *Unio littoralis* (see below) and *U. prusii* quite certainly came from the same deposits. While Lea (1870: 51), in his "*Synopsis of the family Unionidae*" still considered *U. prusii* a valid species, Simpson (1900: 694, 1914: 563) regarded it as a junior synonym of *Unio durieui* Deshayes, 1847. Haas (1940: 132, 1969: 54) listed the species in the synonymy of *Unio crassus bruguierianus*. Lopes-Lima et al. (2021: Appendix 1 and fig. 4), who have given the latest taxonomic opinion on *U. prusii*, confirmed it as a synonym of *U. bruguierianus*.
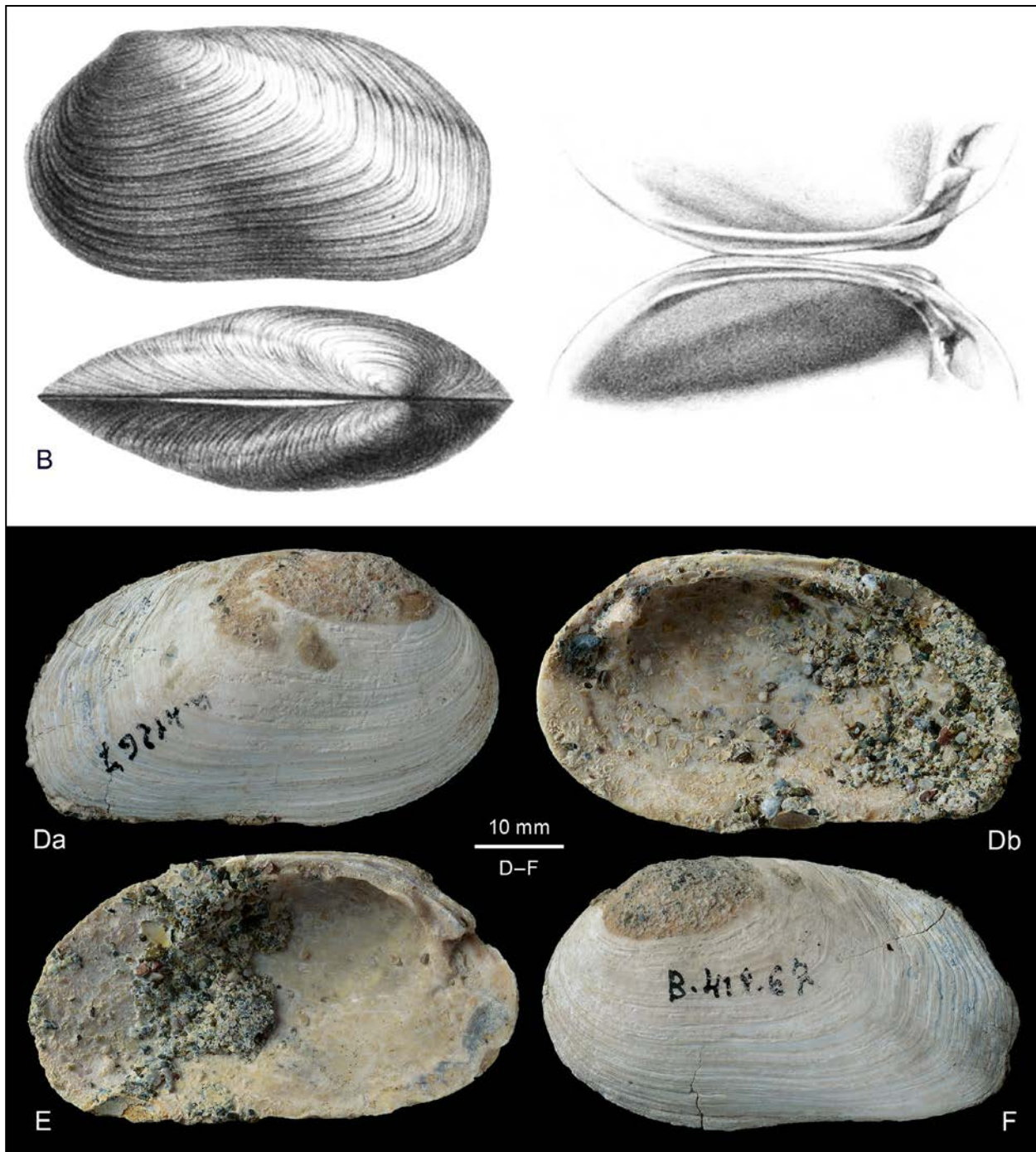
Figure 8. *Unio bruguierianus* Bourguignat, 1853. Lower Kritika Formation (?). **A–C.** Original figures of *Unio prusii*, reproduced from Bourguignat (1856a, pl. 12 figs 1, 3, 4); shell length is stated to be 65 mm. **D–F.** Type specimens of *Unio prusii* Bourguignat, 1856; d'Orbigny collection, MNHN Paris. **D.** Lectotype designated here; MNHN.F.B41267. **E.** Paralectotype; MNHN.F.A89391. **F.** Paralectotype; MNHN.F.A89392.

Some of the newly collected specimens from Kritika (Fig. 9) are slightly shorter than Bourguignat's (1856a) types (Fig. 8), but the individual displayed in Figure 9A is almost identical in shape. We thus agree with Haas (1940, 1969) and Lopes-Lima et al. (2021) and place *U. prusii* in the synonymy of *U. bruguierianus*.

Subfamily Gonideinae Ortmann, 1916
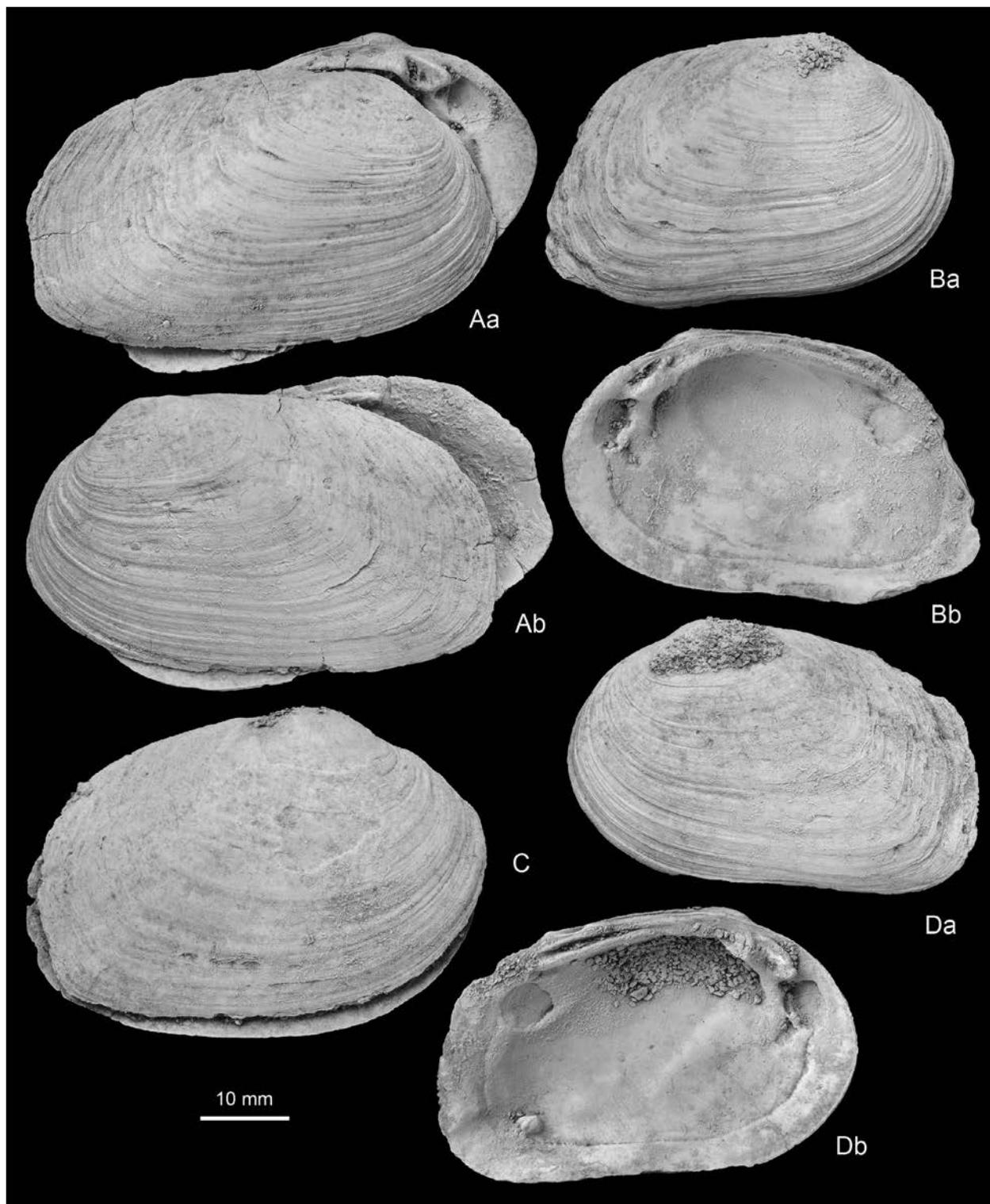
Tribe Gonideini Ortmann, 1916

Genus *Leguminaia* Conrad, 1865

Type species. *Monocondyloea mardinensis* I. Lea, 1865; by monotypy.

***Leguminaia hedenborgi* n. sp.**

Figure 10A, B

ZooBank registration. urn:lsid:zoobank.org:act:6ED66 422-F48E-4B18-A68A-4077F0E49B65

Figure 9. *Unio bruguierianus* Bourguignat, 1853. Lower Kritika Formation (?); Kritika, Rhodes. **A.** Double-valved specimen; BSPG 2020 CI 58. **B.** Right valve; BSPG 2020 CI 60. **C.** Double-valved specimen, right-valve view; BSPG 2020 CI 59. **D.** Left valve; BSPG 2020 CI 61; in Db, note the blister pearl just inside posterior ventral corner of pallial line.

Type locality and stratum. Slopes of Mount Filerimos S of Ialysos, N Rhodes; lower Kritika Formation; specimen labelled "Insel Rhodus; im Grünsand unter dem Mergel" = Island of Rhodes; in the greensand below the marl, corresponding to the upper freshwater unit intercalated with marine strata, as described in the second letter of HEDENBORG (1850s).

Type. Left and right valve of the holotype, the only known individual; length = 49 mm, height = 28 mm, width = 16 mm; NHMW 1854/0015/0021.

Diagnosis. Small, short-trapezoid–ovate *Leguminaia* with faint posterior rim; highest near its posterior end. Two very weak pseudocardinal cusps in the left valve, and a single spoon-shaped one in the right valve. Each

Figure 10. *Leguminaia hedenborgi* n. sp. Lower Kritika Formation. Left (**A**) and right (**B**) valves of the holotype (same individual); NHMW 1854/0015/0021. **C.** Original note by Hedenborg.

valve with a single weak, lamellar posterior lateral tooth.

Derivation of name. Named after Johan Hedenborg (*1787; †1865), Swedish physician, devoted amateur scientist and explorer, and Norwegian and Swedish vice-consul on Rhodes in the early 1860s (Linse 2011), who collected and donated the type specimen (Hedenborg 1850s).

Description. Shell rather small (length = 49 mm), thin and fragile; poorly inflated; short-trapezoid–ovate in outline, highest in posterior third of shell. Anterior shell margin well rounded, curving into oblique, but rather straight, ventral margin. Posterior shell margin gently rounded, with a slight angulation at the posterior end, well below mid-shell height. Posterior-dorsal shell margin faintly rounded, meeting posterior shell margin in well-rounded corner. Umbo broad, barely projecting, positioned at approximately ⅓ of shell length.

Outside of shell with a faint rim extending from umbo to posterior end of shell. Ornament consisting of marked, irregular growth lines only. Outer shell layer in umbonal region delaminated.

Left valve hinge. Two very weak, slightly elongate, lamellate pseudocardinal cusps, 1 in front of and 1 behind umbo; the latter one merely transitioning into single, long, rather weak posterior lateral tooth.

Right valve hinge. Single, smooth, slightly spoon-shaped pseudocardinal cusp, situated directly in front of umbo; flanked posteriorly by wide gap in hinge plate. Single, long, rather weak posterior lateral tooth rising behind gap. Nymphs low, sunken, almost as long as lateral teeth.

Anterior adductor-muscle scar obliquely D-shaped, moderately deep, posteriorly bounded by a weak buttress.

Posterior adductor-muscle scar much larger but shallow, elongate-trapezoidal in outline. Anterior pedal-retractor-muscle scar faint, roundish, situated below buttress. Pallial line faint, entire.

Remarks. The shell from Rhodes is most similar to the recently described *Leguminaia anatolica* Gürlek, Kebapçı & Lopes-Lima, 2021 (in Lopes-Lima et al. 2021) from the Murat River near Tutak in east-central Turkey, in the upper Euphrates catchment. However, the Rhodes fossil differs in being highest near its posterior end, rather than shortly behind the umbo. Unfortunately, *L. anatolica* is insufficiently described and illustrated by Lopes-Lima et al. (2021); the shell interior is not depicted, and the condition of the hinge is unknown. Given the different morphology, together with the occurrence of the modern species at a distance of more than 1300 km, in an unrelated river catchment, we assign the specimen from Rhodes to a new species, *Leguminaia hedenborgi*.

Shells of *Leguminaia wheatleyi* (I. Lea, 1862) and *L. saulcyi* (Bourguignat, 1852), from the Euphrates/Tigris and Orontes catchments, respectively, are more sturdy, more inflated and have more prominent umbos. Moreover, they lack the faint posterior rim, which is present both in *L. hedenborgi* and *L. anatolica*.

Tribe Lamprotulini Modell, 1942

Genus *Potomida* Swainson, 1840

Type species. *Mysca* (*Potomida*) *corrugata* Swainson, 1840, by original designation; see Araujo (2008) for details on nomenclature.

Potomida semirugata (Lamarck, 1819)

Figures 11A–H, 12

Unio semi-rugata LAMARCK 1819: 76.
Unio littoralis?—DESHAYES 1836: 108.
Unio littoralis—BOURGUIGNAT 1856a: 77 [excluding specimens from 'Toudja' = Tundzha/Tunca River, near Edirne, European part of Turkey].
Unio littoralis—BOURGUIGNAT 1856b: 161 [excluding specimens from 'Toudja' = Tundzha/Tunca River, near Edirne, European part of Turkey].
Unio littoralis—TOURNOUËR 1877: 47.
Potomida semirugata—FROUFE et al. 2016b: 325.

Type locality. No type locality was indicated by LAMARCK (1819).

Materials. NHM Vienna: shells of approximately 20 individuals, all labelled "Rhodos" or "Rhodus", without further indication of locality; slopes of Mount Filerimos S of Ialysos, N Rhodes, uppermost Damatria Formation, based on HEDENBORG's (1850s) letters. NHMW 1853/0036/0040; NHMW 1859/0030/0257 to 0262. MNHN Paris: 2 left valves and 2 right valves, without indication of locality; Damatria Formation or lower Kritika Formation, N Rhodes. MNHN.F.B41266a–d.

Description. Shells up to 56 mm long and 41 mm high, moderately thick, moderately inflated, short-ovate, rounded-subrectangular or rounded-trapezoidal in outline. Anterior shell margin well rounded; ventral margin well rounded to almost straight; posterior dorsal margin gently rounded. Posterior margin slightly or markedly obliquely truncated, forming blunt corner with posterior-dorsal margin and well-rounded or slightly truncate transition to ventral margin. Umbo rather pointed in juveniles; in more mature specimens broad, prosogyrate, low, barely projecting; positioned at approximately ⅓ of shell length.

Outside of shell ornamented with irregular, rugose growth lines. Umbonal ornament consisting of numerous densely arranged, rather smooth, double-looped costae sensu ZIERITZ et al. (2014), extending up to shell heights greater than 10 mm, with the posterior loop rather pointed ventrally (Fig. 11C, E, G). Umbos in the Paris material corroded (Fig. 12Aa, Bb, Ca).

Left valve hinge. Pseudocardinal tooth with 2 cusps, with marked subradial grooves in some specimens. Anterior cusp a prominent, short, oblique blade, nearly joining posterior cusp. Posterior cusp prominent, oblique-elongate-triangular, tapering posteriorly, followed by short, rather smooth portion of hinge plate. Two moderately long, distinct posterior lateral teeth emerging behind this smooth gap.

Right valve hinge. Prominent elongate-ovate anterior pseudocardinal cusp, with marked subradial grooves in some specimens, followed by a short gap in hinge plate and a faint, elongate posterior cusp, subparallel to dorsal shell margin. Single, moderately long, distinct posterior lateral tooth emerging above posterior end of posterior pseudocardinal cusp. Nymphs low, relatively long.

Hinge plate supported by broad, moderately prominent buttress. Anterior adductor-muscle scar deep, high-subovate, positioned in front of buttress. Posterior adductor-muscle scar rather faint, large, elongate-ovate. Anterior pedal-retractor-muscle scar deep, pointed to slightly ovate, situated at anterior base of buttress.

Remarks. The divergence events of the 3 extant species of *Potomida* were estimated at 8.1 Ma (late Tortonian; separation of *P. littoralis* from *P. acarnanica* + *P. semirugata*) and 5.9–5.3 Ma ago (mid to late Messinian; separation of *P. acarnanica* from *P. semirugata*) by FROUFE et al. (2016b). The shells from Rhodes, broadly assigned to the Pliocene–Pleistocene transition (2.58 Ma), are significantly younger than these events and would thus likely belong to one of the modern species of *Potomida*; these are difficult to distinguish on morphological grounds alone. However, *P. semirugata* generally has shorter, more roundish shells than its 2 congeners, and its umbonal ornament is much more extensive and pronounced. We are thus confident in assigning the Vienna specimens (Fig. 11) to *P. semirugata*. The case of the Paris specimens is more difficult, given that their umbos are corroded, and they are generally more elongate and angular (Fig. 12), thus more closely resembling the other 2 species in outline shape; as a result, DESHAYES (1836), BOURGUIGNAT (1856a) and TOURNOUËR (1877) all assigned the fossil shells from Rhodes to *Unio littoralis* (i.e. the basionym of *Potomida littoralis*). We assume that allometric growth and intraspecific variability account for these shapes, and, with some reservation, also assign the Paris specimens to *P. semirugata*. This decision is further informed by the modern distribution of *P. semirugata* in Anatolia and the Levant (FROUFE et al. 2016b, LOPES-LIMA et al. 2021).

Discussion

Palaeoecology

Unio pseudatavus (along with *Unio* sp.) seems to have lived under rather lentic fluvial conditions. This is suggested by the silty to fine-sandy substrate, which yielded abundant shells in life position, but also by the composition of the autochthonous to parautochthonous mollusc association found in numerous beds of the Salakos Formation (Fig. 3C, D). Besides *U. pseudatavus*, this association comprises small dreissenid bivalves, as well as abundant viviparid, melanopsid, valvatid, neritid and hydrobioid gastropods (BUKOWSKI 1894, 1896, WILLMANN 1981, pers. obs.). The rather broad channels, extending beyond outcrop scale, as well as the fauna of moderately thick-shelled, often ornamented gastropod taxa, demonstrate that these molluscs lived in a distal fluvial environment. Channel bases often cut into laminated lacustrine clays and silts (Fig. 3C), suggesting that alternations of fluvial and lacustrine sedimentation were driven by fluctuations in run-off and/or lake level.

For *Leguminaia hedenborgi* and the *Potomida semirugata* curated at Vienna, precise outcrop information is
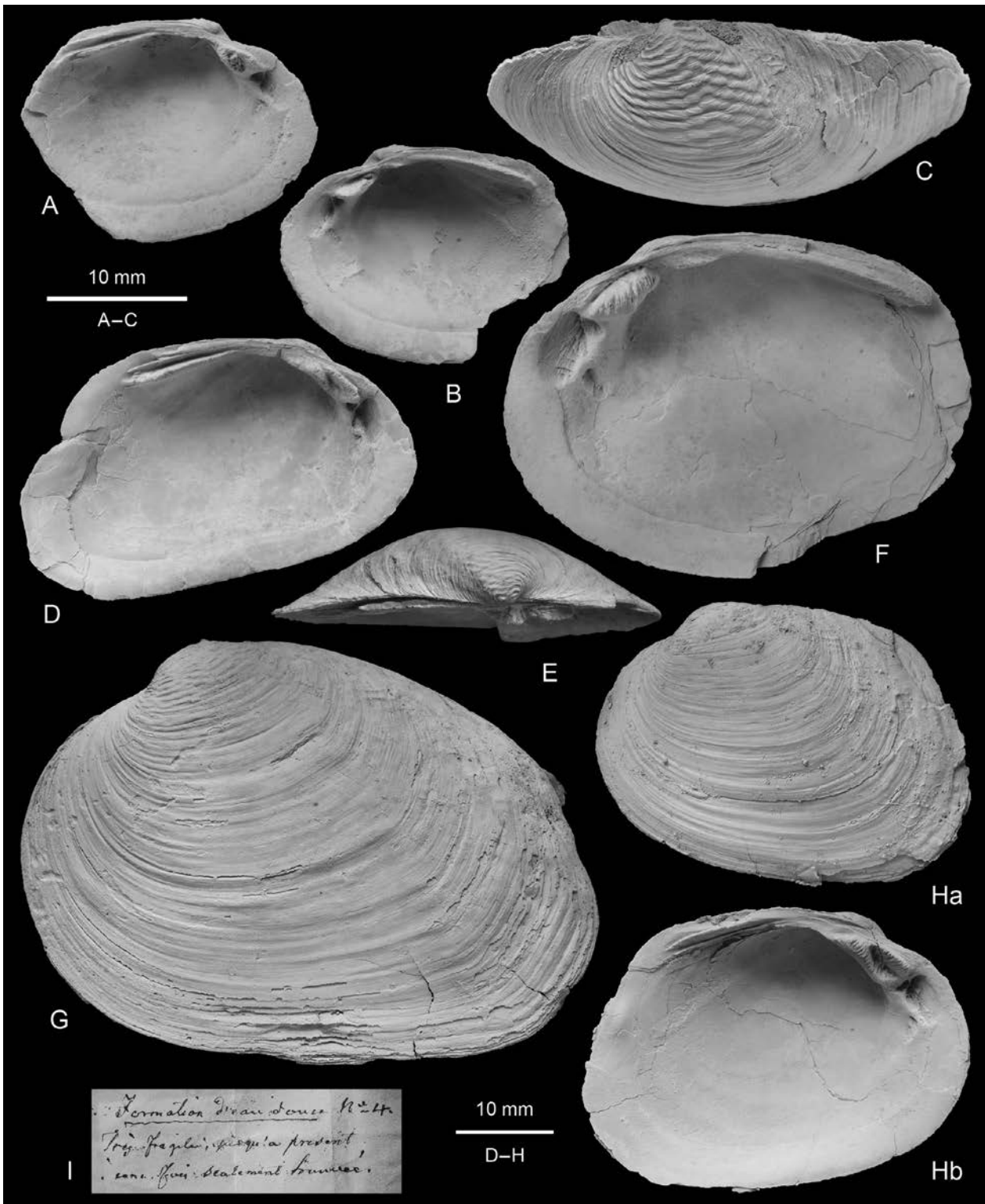
Figure 11. *Potomida semirugata* (Lamarck, 1819). Lower Kritika Formation. Left (**A**) and right (**B**) valves of the same juvenile individual from inside; NHMW 1853/0036/0040a. **C.** Oblique-dorsal view of umbonal ornament of left valve; NHMW 1859/0030/0261a. **D.** Elongate-trapezoidal left valve; NHMW 1859/0030/0262a. **E.** Left valve; NHMW 1859/0030/0262b. **F.** Ovate right valve; NHMW 1859/0030/0262c. **G.** Left-lateral view of double-valved specimen; NHMW 1859/0030/0260. **H.** Two views of right valve; NHMW 1859/0030/0258a. **I.** Original note by Hedenborg.

lacking, but HEDENBORG (1850s) provided information on the sampled horizons. He characterised the stratum with *Potomida* as a friable greyish marl, but the matrix adhering to some of the specimens consists of medium- to coarse-grained, polymict sand with admixture of common small pebbles. The coarse sediment indicates a rather lotic fluvial habitat, probably in a small channel, similar to the one inhabited by *P. auricularius* and *U. bruguierianus* (see below). However, weathering colours are brownish-greenish rather than yellowish, suggesting

Figure 12. *Potomida semirugata* (Lamarck, 1819). Lower Kritika Formation (?). Original material reported by Bourguignat (1856a, b) and Tournouër (1877); d'Orbigny collection, MNHN Paris. **A.** Two views of right valve; MNHN.F.B41266a. **B.** Two views of left valve; MNHN.F.B41266b. **C.** Two views of right valve; MNHN.F.B41266c.

that these shells are not from the same strata. Melanopsid, neritid and thiarid gastropods, as well as fragments of "*Anodonta*", are documented from the layer with *Potomida* and support the interpretation of a well-oxygenated, lotic habitat. As outlined in the Materials and Methods section above, these specimens come from the Damatria Formation.

Hedenborg's (1850s) letters demonstrate that the single individual of *L. hedenborgi* came from a different horizon, which can be attributed to the lower Kritika Formation. The substrate of *L. hedenborgi* is classified as "greyish green sand" in the letter and as "greensand" on Hedenborg's label (Fig. 10C), and no additional fauna is recorded from that horizon. The specimen is free of matrix, thus providing no further clues about the habitat.

In the context of Hedenborg's finds, it should be emphasised that the lower Kritika Formation records fluctuating salinities and alternating marine, brackish and freshwater sediments (Fig. 2; Willmann 1981, Ferry et al. 2001, Moissette et al. 2016). Thus, while the lower boundary of the Kritika Formation is placed at the onset of brackish or marine conditions (cf. Mutti et al. 1970, Meulenkamp et al. 1972), the general nature of the boundary interval of the Damatria and Kritika formations is transitional, with a transgressional trend.

Pseudunio auricularius and *Unio bruguierianus* from Kritika formed a community in a small fluvial channel, probably in close proximity to the coast, considering that shallow marine sediments occur in the same outcrop section only a few metres above. The channel is filled with a fining-upward clastic succession, starting with a thin

layer of rather coarse gravel at the base, but quickly transitioning into pebbly sand with admixture of silty to fine-sandy matrix, where the bivalves had settled (Fig. 3A). These sediments suggest that the bivalves lived in a relatively lotic, well-oxygenated habitat, where most clay and silt particles would have stayed in suspension. The bivalves were trapped in life position, most probably by a minor flash-flood event, which deposited poorly sorted sediment consisting of pebbly sand in a silt and clay matrix. Materials of *U. bruguierianus* (syn. *U. prusii*) and *P. semirugata* curated in the MNHN in Paris seem to have come from very similar deposits. The shells have the same yellowish weathering colour and are incrusted with coarse-grained, pebbly, polymict sand on the insides (Figs 8, 12).

Both the Salakos and Damatria to basal Kritika formations were deposited in lowlands characterised by a patchwork of perennial lakes, swamps and meandering rivers (Meulenkamp et al. 1972), indicating higher levels of rainfall and a more humid climate in the Pliocene and earliest Pleistocene than today. This is supported by the occurrence of a wet woodland mammal fauna in the Pliocene Apolakkia Formation, including beavers, rhinoceroses and elephants (van de Weerd et al. 1982). Fossils of large bovines, horses, pigs and porcupines from the Damatria Formation (Meulenkamp et al. 1972) probably indicate slightly dryer conditions. Moreover, progressive Pliocene–Pleistocene cooling of the Mediterranean Region is well documented from both the marine and terrestrial realms (e.g. Monegatti & Raffi 2001, 2007, Suc et al. 2018). The freshwater strata of Rhodes are not precisely dated, which precludes detailed reconstruction of climate change, but the broad palaeoclimatic tendencies associated with the onset of the Pleistocene are evident. The climate, together with the isolation of the island, the concurring demise of the lake systems, as well as the drowning of parts of Rhodes during the Early Pleistocene (e.g. Cornée et al. 2019), must have altered the available freshwater habitats significantly. These alterations may have caused the local extinction of *U. pseudatavus* and several of the associated gastropods and led to the establishment of a mollusc fauna of modern character. However, it is unknown at which precise time the rivers and streams on the island became too seasonally unstable, causing unionids to go extinct on Rhodes.

Evolutionary relationships

The fossil freshwater mussel fauna of Rhodes is closely linked to the modern fauna of Anatolia, to which the island was joined until the latest Pliocene or earliest Pleistocene (e.g. Daams & van de Weerd 1980, van Hinsbergen et al. 2007). *Unio bruguierianus* and *P. semirugata* still live in close proximity to Rhodes, near the southern coast of Turkey, and *L. hedenborgi* has its likely closest relative, *L. anatolica*, in eastern Anatolia (Lopes-Lima et al. 2021). *Pseudunio auricularius* is restricted to France and Spain today, but its close sister species, *P. homsensis*,

occurs in Syria and adjacent Turkey. However, the Cenozoic history of the 4 genera involved is more intricate.

The *Pseudunio* clade

The origin of *Pseudunio* is still a matter of debate. Lopes-Lima et al. (2018) considered Hauterivian–Barremian *Unio idubedae* Palacios & Sánchez, 1885 from Spain the earliest crown group member of the *Pseudunio* clade and assigned it to *Paraheudeana* Starobogatov, 1970. Barremian *Unio valdensis* Mantell, 1844 from southern England, which is the type species of *Paraheudeana*, has well-developed posterior lateral teeth. However, in *Unio idubedae* the state of this character is unknown, given that all specimens known to date are fragmented (Delevene & Araujo 2009). As a result, the generic assignment to *Paraheudeana* is arbitrary. Whether earlier, Mesozoic representatives from Europe or Africa, potentially including some of the Late Jurassic species from Portugal described by Choffat (1885–1885), are closely related to *Pseudunio* remains unknown.

To our knowledge, no definite Late Cretaceous to Eocene Margaritiferidae are known from Europe, northern Africa or the Middle East, where *Pseudunio* occurs today (e.g. Munt et al. 2012, Van Damme et al. 2015). As remarked on in the original description, *Margaritifera* (*Pseudunio*)? *Modelli* Čtyroký, 1965 from the Turonian to Santonian Klikov Formation of southern Bohemia (Czech Republic; Knobloch 1985) is too poorly preserved to be assigned to a genus with certainty. As a result, there is a greater than 80 Ma gap in the fossil record of the Margaritiferidae in Europe and the wider Mediterranean region.

From the Oligocene onward, *Pseudunio* has a continuous and remarkably comprehensive presence in Europe (Schneider & Prieto 2011). The oldest unquestionable representative of the genus is "*Unio* aff. *flabellatus* Goldf." from the Early Oligocene (late Rupelian) Sulzheim Formation at Offenbach near Frankfurt am Main in central Germany, figured by Zinndorf (1901) (Schneider & Prieto 2011). As noted by Modell (1931), margaritiferids with fully developed dentition (i.e. pseudocardinal and posterior lateral teeth) also occur in Late Oligocene (Chattian) strata of the North Alpine Foreland Basin. These shells, which all show more or less strongly developed flabellae, are assigned to several species by Modell (1931, 1934, 1938). Modell (1931) was the first to comment on the evolutionary significance of flabellae in *Pseudunio*. While he acknowledged that this feature was variable already in Oligocene forms (and, following a rather narrow taxonomic concept, assigned these to several different species), he remarked on a gradual decline in the extent and strength of the flabellae, leading to the entirely smooth shells of most modern specimens. This general tendency has been acknowledged by subsequent authors (Chepalyga 1967, Schneider & Prieto 2011, Lyubas et al. 2019) and is undisputed. The Oligocene to Holocene shells of *Pseudunio* seem to form a continuum with regard to shell shape and ornament, rather than a

series of sharply delimited species. However, 3 main shell types, linked to chronostratigraphy, can be distinguished.

(1) Shells with 2 divergent sets of pronounced flabellae are known only from Oligocene (earliest available name: *Unio inaequiradiatus* Gümbel, 1861) and Miocene strata (earliest available name: *Unio flabellatus* Goldfuss, 1837). The clade reliably dates back to the Early Oligocene north of the Alps and expanded to its present-day range and beyond in the Miocene.

(2) In Pliocene strata, only shells with dorsal flabellae occur (earliest available name: *Unio flabellatiformis* Grigorovich-Beresovskiy, 1915), and so far, they have been recorded only from the Paratethys region (Austria, Moldova, Ukraine). Given the scant record of Pliocene freshwater strata in Western Europe, it is unclear whether the range of *Pseudunio* contracted to the Paratethys region during the Pliocene and subsequently expanded again.

(3) From the Pleistocene onward, shells of *Pseudunio* are generally smooth, with some specimens retaining faint dorsal flabellae, as discussed in the context of *P. auricularius* above. The fossil record of Pleistocene *Pseudunio* is scant, and our specimen from the Pliocene–Pleistocene transition on Rhodes is probably the oldest Pleistocene record.

If the assignment to *P. auricularius* is correct, our specimen is also the earliest representative of this species. Its occurrence on Rhodes is interesting in light of the very close molecular relationships of *P. auricularius* and *P. homsensis*, whose closest common ancestor must have had a contiguous range before the lineages diverged. During Pleistocene to Holocene times, *P. auricularius* occurred in several large Atlantic river basins in Spain, France, Germany and England, as well as in Mediterranean rivers in Spain, France and Italy (PRIÉ et al. 2019, ARAUJO & RAMOS 2000, BIDDITTU & GIROD 2005). In addition, a fragmentary left valve tentatively identified as *P. auricularius* was found in an archaeological excavation site on Cyprus, dated at 600–500 years B.C. (LIGNEREUX et al. 2008).

Pseudunio marocanus is known exclusively from Atlantic rivers in Morocco (ARAUJO et al. 2009a) and has no fossil record. *Pseudunio homsensis* occurs only in Mediterranean rivers in southeast Turkey and Syria (VIKHREV et al. 2018). Fossil shells conforming to the typical morphology of *P. homsensis* occur in poorly dated strata of the Orontes valley near Jisr ash-Shugur in Syria and were regarded as Pliocene in age (BLANCKENHORN 1897) but are probably younger, also given the readjustment of the Pliocene–Pleistocene boundary to base Gelasian. Early and Middle Pleistocene *Margaritifera* (*Pseudunio*) *moldavica* Chepalyga, 1964 and *Margaritifera* (*Pseudunio*) *robusta* Chepalyga, 1964 (with 3 subspecies), from the lower Dniester catchment near Tiraspol in Moldova, are very similar to modern *P. homsensis* with regard to shell shape. Only the shell interior was depicted by CHEPALYGA (1964), but LYUBAS et al. (2019) studied similar Middle Pleistocene shells from the area and illustrated 6 individuals, which all lack posterior

ornament. They synonymised CHEPALYGA's (1964) species with *Pseudunio flabellatiformis* (Grigorovich-Beresovskiy, 1915), which is based on Pliocene shells from the lower Prut and Danube catchments in southernmost Moldova (Slobozia Mare) and adjacent Ukraine (Kyslytsya). However, the syntypes of *P. flabellatiformis*, despite being incomplete, are more elongate than the specimens of LYUBAS et al. (2019); they also show broad, prominent dorsal flabellae (GRIGOROVICH-BERESOVSKIY, 1915, pl. 4 figs 7, 8, pl. 5 figs 1, 2), which are much more pronounced than those occasionally seen in modern *Pseudunio*. The Pliocene and Pleistocene shells are thus clearly not conspecific.

In summary, these data suggest that *Pseudunio* originated in Central or Eastern Europe in the Oligocene, its ancestor being unknown. Early representatives had 2 divergent sets of flabellae, which gradually became reduced during the Neogene and Pleistocene, and younger representatives usually have smooth shells. In the Pleistocene, *P. homsensis* diverged from *P. auricularius*, and both species occurred in the Eastern Mediterranean region, before contracting to their present-day ranges.

The *Unio* clade

A comprehensive assessment of fossil *Unio* is still far beyond reach, and even the taxonomy and phylogeny of extant representatives seems not settled. Established more than 200 years ago, and characterised by rather simple, commonplace unionid shell characters, *Unio* remains a wastebasket taxon. The genus comprises several hundred fossil and extant species that are currently considered valid, or which often simply have not been reassessed applying up-to-date methodology (MOLLUSCA BASE EDS 2023). Molecular-clock estimates yielded a broadly defined early Eocene age for the common ancestor of western Palaearctic *Unio* (FROUFE et al. 2016a, ARAUJO et al. 2018), suggesting that significantly stratigraphically older species retained in *Unio* may be misplaced. Several divergence events occurred, supposedly during the Miocene, and modern species in the genus are now referred to 4 informal species-groups (e.g. FROUFE et al. 2016a, ARAUJO et al. 2018, LOPES-LIMA et al. 2021). Of these, 3 occur in the Eastern Mediterranean region, and 2 are represented in the fossil fauna of Rhodes: *Unio pseudatavus* and *Unio* sp. of the *pictorum* group, and *U. bruguierianus* of the *crassus* group. Generally, the *pictorum* group is characterised by more slender, posteriorly tapering shells with subterminal umbos, while shells in the *crassus* group are shorter, often with a bluntly truncated posterior margin. However, there is a considerable degree of morphological overlap, and, even at the species-group level, shell-based taxonomy is not always straightforward.

Modern representatives of *Unio* have expanded over nearly all of Europe south of the Arctic Circle. They further occur in most of those Asian and African river basins that drain into the Mediterranean Sea and the Moroccan

Atlantic, in the Euphrates and Tigris catchments, which drain into the Persian Gulf, and, broadly speaking, in the eastern half of Africa (e.g. GRAF & CUMMINGS 2021). Molecular data currently suggest a western Mediterranean origin of the clade, with species from Iberia and Northwest Africa in basal positions (e.g. ARAUJO et al. 2018). However, as pointed out by LOPES-LIMA et al. (2021), the tribe Unionini quite certainly has its origin in Asia, where numerous more basal genera of that clade thrive today.

The *Leguminaia* clade

The genus *Leguminaia* comprises 3 extant species, occurring in Iran, Iraq, Lebanon, Syria and Turkey (LOPES-LIMA et al. 2021). Pleistocene shells from near Antakya in southernmost Turkey were assigned to *Leguminaia mardinensis* (I. Lea, 1865) and *L. bourguignati* Locard, 1883 by BLANCKENHORN (1897); these are both junior subjective synonyms of *Leguminaia wheatleyi* (I. Lea, 1862) (MODELL 1951). Another fossil species, *Leguminaia poratica* Chepalyga, 1967, occurs in Late Pliocene deposits of the lower Prut River near Slobozia Mare in southernmost Moldova. GOZHIK (2006) described 2 additional fossil species, *Leguminaia (Microcondylea) bachtynica* Gozhik, 2006 (Middle Miocene, Sarmatian) and *L.* (*M.*) *prysjazhnjuki* Gozhik, 2006 (Late Miocene, Meotian) from Ukraine. He also transferred *Leguminaia poratica* Chepalyga, 1967 to *Leguminaia (Microcondylaea)*. *Microcondylaea* Vest, 1866 has been treated as a synonym or subgenus of *Leguminaia* by some authors (e.g. CHEPALYGA 1967, GOZHIK 2006) but is genetically distinct at the genus level; *Microcondylaea bonellii* (Férussac, 1827) is the only extant species, (historically) occurring in Adriatic drainages of the Alps and the Balkans, from Switzerland and Italy in the northwest to Albania and Greece in the southeast (MODELL 1951, FISCHER et al. 1999, FROUFE et al. 2017, LOPES-LIMA et al. 2021). The appropriate assignment of the fossils described by CHEPALYGA (1967) and GOZHIK (2006) thus needs to be clarified by restudy of the type material. A third genus in the Gonideini, *Pseudodontopsis* Kobelt, 1912, consists of a single species, *Pseudodontopsis euphratica* (Bourguignat, 1852), from Iran and Iraq, and has no fossil record.

Together with the 3 genera mentioned above, MODELL (1942, 1951, 1964) classified a fourth, fossil-only genus, *Leptanodonta* Wenz, 1927 (in KREJCI & WENZ 1927), in his Pseudodontinae. Recently, HARZHAUSER & MANDIC (2010) reassigned the type species of *Leptanodonta*, *Dreissenomya unioides* Fuchs, 1870, to *Dreissenomya* (family Dreissenidae), which makes *Leptanodonta* Wenz, 1927 a junior subjective synonym of *Dreissenomya* Fuchs, 1870. However, when erecting *Leptanodonta*, WENZ (1927) had studied material from Câmpina in the Dacian Basin of southern Romania, which he assigned to FUCHS' (1870) species from Tihany in the Pannonian Basin of western Hungary. In our opinion, WENZ (1927) correctly assigned the Romanian material to the Unionidae (he explicitly remarked on a non-sinuate pallial line in his specimens) but chose the wrong species name for his fossils and consequently also an inappropriate type species for his new genus. Interestingly, WENZ (1942) himself later remarked on these issues, but, having not studied any material from Hungary, came to no final conclusion; he thus introduced a new species name, *Leptanodonta rumana* Wenz, 1942, for the Romanian material. We conclude that (1) *D. unioides* is correctly placed in the Dreissenidae. (2) *Leptanodonta rumana* is a unionid, and should be placed in the Gonideini; restudy of the type material is required to decide whether the species should be placed in a new genus, or rather in *Leguminaia* or *Microcondylea*.

To summarise, the *Leguminaia* clade presumably arose in the (Middle) Miocene in the Eastern Paratethys region. From there it expanded to the eastern and central Mediterranean and the Middle East during the Pliocene and Pleistocene, to reach its present-day distribution. Politically, the new species extends the range of *Leguminaia* into Greece; geographically, Rhodes was still in the process of becoming detached from Anatolia during the species' lifetime. Like for the Unionini, the origins of Gonideini likely are farther to the east, given that most other genera in the tribe occur in East and Southeast Asia (MODELL 1951, GRAF & CUMMINGS 2021, LOPES-LIMA et al. 2021).

The *Potomida* clade

Potomida comprises 3 morphologically similar extant species (FROUFE et al. 2016b). In addition, more than 50 fossil species are currently attributed to this genus (MOLLUSCABASE EDS 2023), which are probably not all correctly assigned, given that some of the relevant literature is dated. While a comprehensive assessment is beyond our scope here, the spatial and stratigraphic distribution of fossil and extant species is interesting. *Potomida littoralis* (Cuvier, 1798) ranged as far north as England during the Pleistocene (ELLIS 1962) and is currently distributed throughout France and the Iberian Peninsula, as well as northern Morocco, Algeria and Tunisia (FROUFE et al. 2016b). Within this range, only 2 fossil species, *Potomida capellinii* (Fontannes, 1880) and *P. nicolasi* (Fontannes, 1883), occurred, in southern France. Extant *Potomida acarnanica* (Kobelt, 1878) is restricted to the Peloponnese and the Achelous drainage in mainland Greece, while *P. semirugata* currently occurs in Syria and southern Anatolia, with additional historical records from Lebanon and Israel (FROUFE et al. 2016b, LOPES-LIMA et al. 2021); its occurrence in the Pliocene–Pleistocene of Rhodes, reported here, is its only fossil record. In addition, numerous fossil *Potomida* are recorded from the Eastern Mediterranean region (Greece, Turkey, Syria and Israel) but also from drainage basins associated with the Eastern Paratethys (Romania, Moldova, Ukraine and Russia) and the Dinaride palaeo-lakes (Croatia) (MOLLUSCABASE EDS 2023). As far as we are aware, Italy and

Slovenia on the northern Mediterranean margin, as well as Libya and Egypt in the south have no fossil or extant records of *Potomida* (see also MODELL 1951).

In both the western and eastern regions, the oldest representatives of the genus are Late Miocene (Tortonian) in age: *Potomida capellinii* (Fontannes, 1880) from the Rhône valley in southeast France, and *Potomida transylvanica* Lubenescu, 1985 from central Romania. All other records of the genus are Pliocene or younger (MOLLUSCABASE EDS 2023). It thus seems that the current, disjunct distribution pattern persisted since the Miocene, which is in line with molecular-clock estimates (FROUFE et al. 2016b). The eastward migration of *Potomida* via the Danube proposed by MODELL (1951) would thus have occurred in the Miocene or earlier. This is in conflict with modern reconstructions of the Danube system, which indicate that the river reached the Black Sea only in the Pliocene or later (MAGYAR et al. 2013, DE LEEUW et al. 2017). As a result, the origin of *Potomida* remains enigmatic. However, given that *Potomida* is the only representative of Lamprotulini occurring outside East and Southeast Asia, it seems likely that the genus arrived and expanded from the east.

Conclusions

Six species of Unionida occurred on Rhodes during the Pliocene and earliest Pleistocene, when the island was still part of the Anatolian mainland. Three successive lithostratigraphic units in the north of the island host fossil freshwater mussels: (1) *Unio pseudatavus* Bukowski, 1896 and *Unio* sp. co-occur in the Late Pliocene (Piacenzian) Salakos Formation. (2) *Potomida semirugata* (Lamarck, 1819) occurs in the latest Pliocene Damatria Formation. (3) *Pseudunio auricularius* (Spengler, 1793), *Unio bruguierianus* Bourguignat, 1853, *Leguminaia hedenborgi* n. sp. and potentially also *P. semirugata* occur in the lower Kritika Formation, straddling the Pliocene–Pleistocene boundary. These species provide evidence of wetter climate conditions on Rhodes in the past, with perennial, more extensive water bodies providing habitats for bivalves. Preferred habitats in the Salakos Formation were rather lentic, broad, distal fluvial channels. In the Damatria and Kritika formations, most mussels are reported from more lotic habitats, in rather small coastal rivers and streams.

Pseudunio has its evolutionary origins in the Oligocene of Central or Eastern Europe. Plesiomorphic ornament of 2 divergent sets of posterior flabellae gradually became reduced during the Neogene, and Quaternary representatives have smooth shells. *Pseudunio homsensis* diverged from *P. auricularius* in the Pleistocene, likely in the Eastern Mediterranean. The specimen from Rhodes represents the earliest fossil record of *P. auricularius*.

Unio remains a poorly resolved clade, due to its common use as a wastebasket taxon. Molecular data point to an Eocene origin of the genus in its modern sense,

suggesting that stratigraphically older species may represent different genera. The tribe Unionini likely has its origins in East and Southeast Asia. The fossil shells from Rhodes represent the earliest and only fossil record of *U. bruguierianus*. *Unio pseudatavus* is extinct and endemic to Rhodes.

Leguminaia likely has its origins in the Miocene of the Eastern Mediterranean and Paratethys regions. The newly described species from Rhodes, *Leguminaia hedenborgi*, is most closely related to *L. anatolica* from east-central Anatolia.

The stratigraphically oldest species of *Potomida* occur in Middle Miocene deposits of southern France and Romania. The origins of the genus, however, are likely in the east, since closely related genera occur in East and Southeast Asia.

There is growing evidence for an Asian origin of modern European Unionidae, likely involving several out-of-Asia dispersal events during the Cenozoic. This would suggest that Mesozoic European Unionidae represent extinct clades.

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