ARISTOTLE UNIVERSITY OF THESSALONIKI
Interinstitutional Program of Postgraduate Studies in
PALAEONTOLOGY – GEOBIOLOGY

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EARLY PLEISTOCENE CONTINENTAL GASTROPODS FROM THE SEDIMENTARY BASIN OF SOUSAKI AG. THEODOROI, GREECE

MASTER THESIS

DIRECTION: Macropalaeontology
Directed by: Aristotle University of Thessalokini

ATHENS/PATRAS
2023

[λευκή σελίδα]

Interinstitutional
Program of
Postgraduate
Studies in
PALAEONTOLOGY – GEOBIOLOGY

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ΔΗΜΗΤΡΗΣ ΠΡΩΤΟΠΑΠΑΣ
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EARLY PLEISTOCENE CONTINENTAL GASTROPODS FROM THE SEDIMENTARY BASIN OF SOUSAKI AG. THEODOROI, GREECE

ΗΠΕΙΡΩΤΙΚΑ ΓΑΣΤΕΡΟΠΟΔΑ ΤΟΥ ΚΑΤΩΤΕΡΟΥ ΠΛΕΙΣΤΟΚΑΙΝΟΥ ΑΠΟ ΤΗΝ ΙΖΗΜΑΤΟΓΕΝΗ ΛΕΚΑΝΗ ΤΟΥ ΣΟΥΣΑΚΙΟΥ ΑΓ. ΘΕΟΔΩΡΟΙ, ΕΛΛΑΔΑ

Υποβλήθηκε στο ΔΠΜΣ Παλαιοντολογία-Γεωβιολογία

Ημερομηνία Προφορικής Εξέτασης: 06/10/2023
Oral Examination Date: 06/10/2023

Three-member Examining Board

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EARLY PLEISTOCENE CONTINENTAL GASTROPODS FROM THE SEDIMENTARY BASIN OF SOUSAKI AG. THEODOROI, GREECE – *Master Thesis*

ΗΠΕΙΡΩΤΙΚΑ ΓΑΣΤΕΡΟΠΟΔΑ ΤΟΥ ΚΑΤΩΤΕΡΟΥ ΠΛΕΙΣΤΟΚΑΙΝΟΥ ΑΠΟ ΤΗΝ ΙΖΗΜΑΤΟΓΕΝΗ ΛΕΚΑΝΗ ΤΟΥ ΣΟΥΣΑΚΙΟΥ ΑΓ. ΘΕΟΔΩΡΟΙ, ΕΛΛΑΔΑ – *Μεταπτυχιακή Διπλωματική Εργασία*

Citation:
Protopapas D., 2023. Early Pleistocene continental gastropods from the sedimentary basin of Sousaki Ag. Theodoroi, Greece, Interinstitutional Program of Postgraduate Studies in Palaeontology-Geobiology. School of Geology, Aristotle University of Thessaloniki, 92 pp.

Cover Figure: A sketch of the Pleistocene freshwater gastropod of genus Islamia from Sousaki basin.

Περιεχόμενα

ABSTRACT

This work involves the study of a Lower Pleistocene freshwater malacofauna from the Sousaki sedimentary Basin and contributes towards the better understanding of the relationship between modern and fossil species. The studied area lies next to the Sousaki volcano, which is the westernmost end of the South Aegean volcanic arc, about 15 Km west of Corinth, in southern Greece. Four samples were collected from a section, consisting of alternations of marly and conglomeratic layers and located in the area of the youngest group of volcanic rocks, which comprises the substrate of the respective deposits. As a result, 24 different species were determined, belonging to 10 families and 20 genera, namely Neritidae, Planorbidae, Lymnaeidae, Acroloxidae, Geomitridae, Hydrobiidae, Bithyniidae, Viviparidae, Melanopsidae, Thiaridae. At least, *Islamia* n. sp., *Bania* n. sp., *Prososthenia* n. sp., *Graecamnicola* n. sp., could be new species as they were not detected in the literature. The similarities of the studied malacofauna with other lower Pleistocene ones, of which (60 %) of extinct taxa, seem to verify this age as suggested by other studies. Caenogastropoda are dominate, whereas the most diverse family is Hydrobiidae and second the Planorbidae. Representatives of the Superfamily Lymnaeoidea (i.e., Lymnaeidae, Planorbidae, Acroloxidae) appear in the study area as well, including extant species, such as *Armiger crista,* or widespread extinct species in various Pliocene & Pleistocene basins like *Lymnaea megarensis.* In the family Hydrobiidae, observed a probably a new species of the extinct genus *Graecamnicola*. Species of this genus have been known only from the Pleistocene sediments of the Atalanti Basin and it has been recorded for the first time in the study area. Two representatives of the genus *Islamia* and *Bania* refer here for the second time in the Greek fossil record, with *Bania* n. sp., represent the chronologically youngest species of the genus. The statistical analysis, groups the samples into two association groups, based on the abundance gastropod species. According to the ecological preferences of the studied taxa, a lacustrine palaeoenvironment could be inferred. The first group includes species that prefer the most stagnant aquatic environment rich in aquatic vegetation, such as several species of Lymnaeoidea. The second group lacks species that prefer mainly stagnant water and is dominated by species that prefer more stony substrates, especially by the genus *Theodoxus*, which could perhaps signal a change in the hydrological or water chemical conditions of this environment. This palaeofauna eventually disappeared from the study area, due to the collapse of the ecosystem after the loss of this freshwater environment.

Key words: Systematics, Palaeoecology, Palaeobiogeography, Lower Pleistocene, Non-marine gastropods, Greece

ΠΕΡΙΛΗΨΗ

Η μελέτη αυτή αφορά μια πανίδα μαλακίων γλυκού νερού του κατωτέρου Πλειστόκαινου από την ιζηματογενή λεκάνη του Σουσακίου, με στόχο να συμβάλλει στην καλύτερη κατανόηση της σχέσης μεταξύ σύγχρονων και απολιθωμάτων ειδών. Η περιοχή μελέτης γειτνιάζει με το ηφαίστειο του Σουσακίου, το οποίο είναι το δυτικότερο άκρο του ηφαιστειακού τόξου του Νοτίου Αιγαίου, περίπου 15 Km δυτικά της Κορίνθου στη νότια Ελλάδα. Συνολικά συλλέχθηκαν τέσσερα δείγματα από γεωλογική τομή η οποία αποτελείται από εναλλαγές μαργών και κροκαλοπαγών και βρίσκεται στην περιοχή της νεότερης ομάδας ηφαιστειακών πετρωμάτων τα οποία αποτελούν το υπόβαθρο της. Ως αποτέλεσμα, προσδιορίστηκαν 24 διαφορετικά είδη, που ανήκουν σε 10 οικογένειες και 20 γένη, συγκεκριμένα Neritidae, Planorbidae, Lymnaeidae, Acroloxidae, Geomitridae, Hydrobiidae, Bithyniidae, Viviparidae, Melanopsidae, Thiaridae. Τα είδη *Islamia* n. sp., *Bania* n. sp., *Prososthenia* n. sp., *Graecamnicola* n. sp., μπορεί να επρόκειτο για νέα είδη καθώς δεν αναγνωρίστηκαν βιβλιογραφικά. Οι ομοιότητες της μελετηθείσας μαλακοπανίδας με άλλες του κατώτερου Πλειστόκαινου, εκ των οποίων το (60 %) να αποτελείτε από εξαφανισμένα είδη, φαίνεται να επιβεβαιώνουν αυτή την ηλικία. Κυριαρχούν τα Caenogastropoda, ενώ η πιο ποικιλόμορφη οικογένεια είναι τα Hydrobiidae και δεύτερη τα Planorbidae. Εκπρόσωποι της υπεροικογένειας Lymnaeoidea (δηλαδή, Lymnaeidae, Planorbidae, Acroloxidae) εμφανίζονται επίσης στην περιοχή μελέτης και περιλαμβάνουν είδη που διαβιούν και σήμερα όπως το *Armiger crista*, αλλά και εξαφανισμένα ευρέως διαδεδομένα είδη σε διάφορες λεκάνες του Πλειόκαινου και του Πλειστόκαινου, όπως το *Lymnaea megarensis*. Στην οικογένεια Hydrobiidae, παρατηρήθηκε ένα πιθανά νέο είδος του εξαφανισμένου γένους *Graecamnicola*. Είδη αυτού του γένους είναι γνωστά μόνο από τα ιζήματα του Πλειστόκαινου της Λεκάνης της Αταλάντης και έχει καταγραφεί για πρώτη φορά στην περιοχή μελέτης. Δύο εκπρόσωποι του γένους *Islamia* και *Bania* αναφέρονται εδώ για δεύτερη φορά στο ελληνικό αρχείο απολιθωμάτων, με το *Bania* n. sp., αντιπροσωπεύουν το χρονολογικά νεότερο είδος του γένους. Η στατιστική ανάλυση ομαδοποιεί τα δείγματα σε δύο ομάδες συσχέτισης με βάση την αφθονία των γαστερόποδων. Σύμφωνα με τις οικολογικές προτιμήσεις των ειδών που μελετήθηκαν, θα μπορούσε να συναχθεί ένα λιμναίο παλαιοπεριβάλλον. Η πρώτη ομάδα περιλαμβάνει είδη που προτιμούν το πιο στάσιμο υδάτινο περιβάλλον πλούσιο σε υδρόβια βλάστηση, όπως αρκετά είδη Lymnaeoidea. Η δεύτερη ομάδα στερείται ειδών που προτιμούν κυρίως λιμνάζοντα νερά και κυριαρχείται από είδη που προτιμούν περισσότερα πετρώδη υποστρώματα, ειδικά από το γένος *Theodoxus*, το οποίο θα μπορούσε ίσως να σηματοδοτήσει μια αλλαγή στις υδρολογικές ή χημικές συνθήκες του νερού αυτού του περιβάλλοντος. Αυτή η παλαιοπανίδα τελικά εξαφανίστηκε από την περιοχή μελέτης, λόγω της κατάρρευσης του οικοσυστήματος μετά την απώλεια αυτού του περιβάλλοντος γλυκού νερού.

Λέξεις κλειδιά: Συστηματική, Παλαιοοικολογία, Παλαιο-βιογεωγραφία, Κατώτερο Πλειστόκαινο, Μη-θαλάσσια γαστερόποδα, Ελλάδα

1. INTRODUCTION

1.1 Threatened non-marine molluscs and gastropods

Biodiversity in freshwater biomes, offer valuable ecosystem to maintain human health, fresh water supplies and nutrition. (Neubauer et al., 2021). The Balkan peninsula, including Greece, hosts one of the world's freshwater biodiversity hotspots (Glöer et al., 2007; Strong et al., 2008). Continental gastropods comprise an important part of this local biodiversity (Strong et al., 2008), being present in the region since the Pleistocene. Many are today critically endangered, especially due to human activities on the environment, e.g., global warming, extraction, invasive species (Bae and Park, 2020; Czaja et al., 2020; Neubauer et al., 2021; Neubauer and Georgopoulou, 2021).

According to research of Bae and Park (2020), anthropogenic disturbance has reduced the distribution of endemic species in Korea and increased the spatial distribution of invasive species. In North America of all aquatic biota, freshwater molluscs (especially gastropods and mussels) are the most endangered (Brown and Lydeard, 2010; Czaja et al., 2020). About the continents, the Palearctic region (including Europe) characterized with peculiar freshwater gastropod fauna (1,408–1,711 valid species) with the other continental regions to have comparable diversity, about 350–600 species (Strong et al., 2008).

Already from the 1996 edition of the IUCN (The World Conservation Union) which listed a measure of the animal biodiversity crisis, the Red List of Threatened Animals, reported 641 species that have become extinct or extinct in the wild since 1600 AD, i.e., in the last 400 years (IUCN 1996). Of these, 239 was mollusc extinctions, i.e., more than mammals, birds, amphibians and reptiles together (Bouchet et al., 1999). Today, the latest data of IUCN, (2022), indicate 265 extinct species, that belong only to gastropods. The current European freshwater gastropod extinction rates, are three times greater than those from the Cretaceous, with the 92.5% of all species to disappear at that period. (Neubauer et al., 2021). Caenogastropoda are more prone than Hygrophila to become extinct, a fact related to their lifestyle (Neubauer and Georgopoulou, 2021). The future, looks ominous for many spring endemic species, because freshwater molluscs have already experienced a series of local and maybe worldwide extinctions, especially as result of the lower water levels (Bouchet et al., 1999; Smith et al., 2014).

For the reasons mentioned above, it is necessary to get any information, even from the fossil record, to contribute to the better understanding and for protection of modern species. In this thesis, emphasis was given on the systematic classification and palaeoecological analysis of a gastropod macrofauna, from deposits of an early Pleistocene tectonically controlled volcanic lake, from the basin of Sousaki, Ag.

Theodoroi, Greece. The stratigraphy, tectonic and the palaeoenvironmental analysis of the study area, have been already recorded by Papadopoulou et al., (2019). Sampling for this work, was focusing at the base of the sedimentary sequence, because there were the most well-preserved specimens. The purpose of this work is to reassess the existing data and establish this fauna as a useful tool for new studies.

1.2 General view of Molluscs and Freshwater Gastropods

Molluscs are a very old monophyletic invertebrate phylum, originating before the Cambrian (Barker, 2009). They are distributed worldwide and they are highly diverse, living in a variety of aquatic and terrestrial habitats at varying depths and elevations, enabling them to act as proxies for (palaeo)environmental and climate change studies (Fortunato, 2016). Furthermore, molluscs have proven useful tool for palaeogeographical studies, e.g., fossil gastropods of inland waters (Neubauer et al., 2015b) in order to define biogeographical units in the European Neogene. Also have constituted the object of evolutionary palaeontology studies, locally (e.g., the fauna of the island of Kos Willmann, 1985), even on a global scale (e.g., distribution of Melanopsidae, from the late Cretaceous period to the present Neubauer et al., 2016).

Molluscs evolved in the sea and for this reason all their classes are characterized by a broad body plan. It is of no surprise that their representatives from continental waters, despite diversity, display some broad points of resemblance (Dillon, 2000). Head, foot, visceral mass, and mantle are the parts of a gastropod's soft tissues. Having both a univalve shell and specifically for freshwater gastropods a radula for feeding on the periphyton coverings of rocks or plants (Brown and Lydeard, 2010).

Gastropods make up over 75 percent of the approximately 110,000 species of known molluscs, making them the most varied class within the phylum (Brown and Lydeard, 2010). A total of 721 gastropod families have been recognized, 245 of them are known exclusively as fossils and 476 are extant with or without a fossil record (Bouchet et al., 2017). This can be considered as a low overall proportion, taking into consideration that the duration of the Cambrian-Cretaceous interval constitutes 88 % of the 570 million years of the gastropod fossil record (Hausdorf and Bouchet, 2005). This fossil record together with the molecular clock analysis, shows that the Cambrian explosion was accompanied by a rapid radiation of molluscs, while the Ordovician Biodiversification event, was characterized by a slower radiation of bivalves and gastropod crown families (Vinther, 2015). Most of these gastropod species—over 50,000—belong to the Caenogastropoda subclass consisting mostly marine and freshwater organisms (previously known as Prosobranchia), while another 20,000 species—most of which are terrestrial—belong to the informal subclass Pulmonata (Brown and Lydeard, 2010).

Of the 409 families of extant currently recognized gastropods, based upon Strong et al., (2008) and Bouchet and Rocroi (2005), three marine groups have colonized freshwaters, with isolated genera [Rivomarginella (Marginellidae), Clea (Buccinidae), Cremnoconchus (Littorinidae)]. According to the same authors, twenty-six are composed of taxa that are entirely or mostly restricted to freshwater, while four are significantly taxonomically represented in freshwater biotopes (Assimineidae, Neritidae, Stenothyridae, Hydrobiidae).

More specifically, Caenogastropoda and Hygrophila make up the majority of the continental water's gastropods in the world (Strong et al., 2008). Caenogastropoda reflects a number of distinct colonization events and independent lineages and including several clades, e.g, Cerithioidea (Pleuroceridae,Pachychilidae, Paludomidae) and Rissooidea (Pomatiopsidae, Hydrobiidae), have produced endemic radiations (Strong et al., 2008). Also, a lot Heterobranchs lineages invaded continental water systems (Acochlidiida, Valvatidae, Glacidorbidae) and some Neritimorpha (Neritidae, Neritiliidae) (Strong et al., 2008). Also, according to Strong et al., (2008), of the superfamilial (or above) groupings, only the Viviparoidea, Glacidorboidea, and nearly all Hygrophila have members that are only found in continental water systems.

According to Brown and Lydeard (2010), the corneous or calcareous operculum, which is drawn in after the foot to protect the animal, and the gill (ctenidium) are features of Caenogastropods. In contrast, according to the same authors, the Pulmonates, having lost their operculum and secondary colonized freshwaters from the terrestrial environments occupied by their progenitors. These forebears often employed a modified part of the mantle cavity as a lung (Brown and Lydeard, 2010).

Freshwater gastropods also have a calcareous shell for protective reasons (Fig.1), and each species' characteristics varies in detail (Burch, 1989). According to Brown and Lydeard, (2010), the characters of shell structure, are important for the systematics taxonomy and can be conical tube like as for the family Ancylidae, with the new development of the shell to secreted at the margin. Additionally, as the pulmonate family Planorbidae demonstrates, the shell can be planospiral, meaning that the whorls are all in one plane. (Brown and Lydeard, 2010).

The gastropods shells of continental waters (Fig.1), according to Vermeij and Covich, (1978), comparing the majority of marine snails', are in general thin with dull colour pattern. The sculpture usually it is not intense, while it may be absent. The same authors mention also that, the basins of big rivers and lakes contain several exceptions to this general rule, exhibiting significant morphological variation between continental water’s gastropods as in Lakes Ohrid and Tanganyika etc. Many authors have taken a look upon the snails of the Rift Valley lakes of east Africa, as forms convergent to marine shelled gastropods and generally such similarities are attributed to the exposure to specific physical conditions, high levels of calcium carbonate concentration, rapid speciation rates or trophic specialization within the lakes (Vermeij and Covich, 1978).

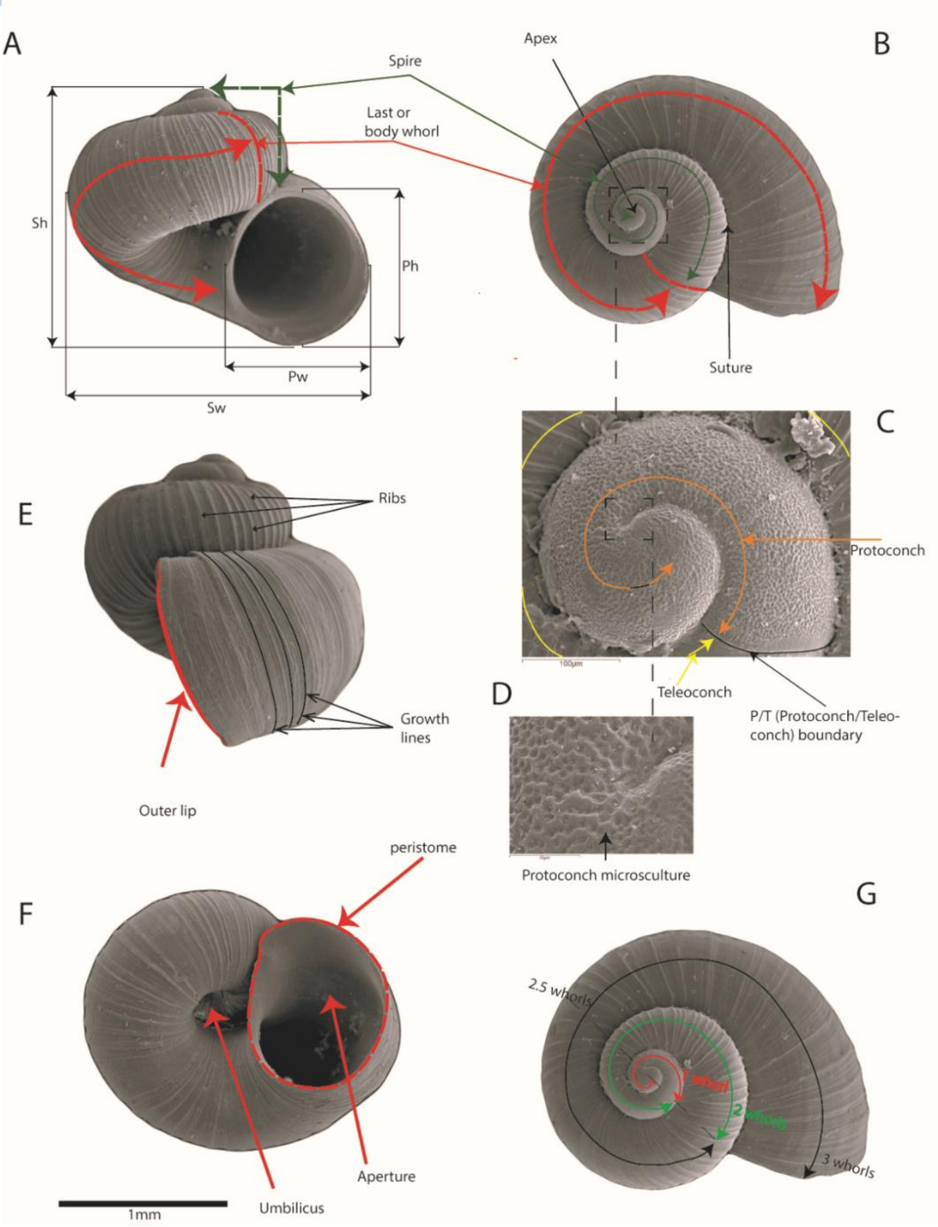


Fig. 1. A. Basic morphometric parameters, **A-G.** Basic morphological characters are depicted on the shell of *Islamia* sp. The terminology is based mainly on the works of (Burch, 1989; Neubauer et al., 2018; Ruiz-Cobo et al., 2018; Verduin Rijksmuseum van Natuurlijke Historie, 1977).

A great number of unanswered questions regarding the evolution of gastropods persist, as in any diverse taxon. In systematics, it is still unclear whether or if adult shell characteristics preserve any evolutionary information (Wagner, 2001). For instance the fresh water family gastropod Melanopsidae, demonstrate an example of "morphostatic radiation" (Falniowski et al., 2020). That is a radiation with low morphological and anatomical differentiation and little specialized differentiation. When based purely on morphology in such a characteristic, the identification of various species will always be probably questionable (Clark et al., 2003).

1.2.1 Caenogastropoda

Caenogastropods are often dioecious and have the female and male reproductive organs in separate individuals (Brown and Lydeard, 2010). Publicly available sex ratios often differ significantly between conspecific populations of prosobranch taxa and with time (Dillon, 2000). Some members of the genus Campeloma in Viviparid are parthenogenetic while family Valvatidae is one hermaphrodite group of native freshwater snails (Brown and Lydeard, 2010). Potamopyrgus antipodarum, a New Zealand mud snail is a parthenogenetic hydrobiid and males are either rare or nonexistent in the populations (Brown and Lydeard, 2010). The gonochoristic families that brood their eggs exhibit the highest expression of prosobranch endemism, such as the Baicallidae, Hydrobiidae, Thiaridae and Benedictiidae (Frogley and Preece, 2004).

Prosobranchs typically deposit tiny (1 mm) eggs singly or in small clusters on solid substrates, covering them with mud, sand or excrement (Dillon, 2000). Freshwater Caenogastropods breathe with the use of a single ctenidium or gill (Brown and Lydeard, 2010; Frogley and Preece, 2004), permitting them to live in habitats with deeper water as well as shallow water, which can have more stable environmental conditions in terms of salinity and temperature (Frogley and Preece, 2004). The ten operculates that are found in England are primarily found in flowing water noted; they probably need of oxygenated water because they are gill breathers and cannot ascend to the surface like pulmonates which they breathe with air (Dillon, 2000). The water is also free from particles that could choke their gills, but a number of prominent exceptions could be immediately noted (Dillon, 2000).

Acording to Dillon, (2000) the group of families of the old polyphyletic group of Prosobranchs, which includes the families Neritidae, Pleuroceridae, Pomatiopsidae, Hydrobiidae, Ampullariidae, Viviparidae, Bithyniidae, Valvatidae, tend to grow more slowly, comparing to those of the five pulmonate families, Planorbidae, Physidae Lymnaeidae, Acroloxidae, and tend to be found more often in lotic environments.

Frogley and Preece, (2004) they mention that the compared to pulmonates, the poorly dispersing prosobranchs prefer a comparatively more stable habitat. Lineage divergence, speciation, and endemism are the results of this environment's promotion of ecological and environmental specialization. (Frogley and Preece, 2004).

1.2.2 Pulmonata

Pulmonates, on the other hand, are all monoecious and have both the male and female reproductive organs in the very same individual, (hermaphrodite) (Dillon, 2000). Additionally, they can self-fertilize, despite frequently coming at the expense of fitness for both parents and offspring (Dillon, 2000).

Because of their basic "lung" mechanism for breathing, pulmonates are limited to shallower habitats, which are typically marshy or littoral (Brown and Lydeard, 2010). According to Brown and Lydeard, (2010), Pulmonates have to regularly adapt to extremely unstable environmental conditions due to their physiological restriction and vulnerability to dispersal (living mostly in marginal environments makes them more likely to be dispersed passively by animal vectors than the deeper living prosobranchs). It is most likely because of this that tropical pulmonates can tolerate temperatures close to 40°C, while temperate pulmonates, for example, can tolerate temperatures close to 0°C for several months (Brown and Lydeard, 2010).

Rarely do pulmonates exhibit three generations or two years per generation, but typically only two while Prosobranchs rarely exhibit two generations annually and typically exhibit generation times every two to three years (Dillon, 2000). Their sexual and reproductive practices also demonstrate this need (Frogley and Preece, 2004). In these circumstances, there is little chance of finding a partner, giving monoecy a selective advantage (Brown and Lydeard, 2010). It seems that not reproducing at all is more harmful than inbreeding depression (Brown and Lydeard, 2010). Because this strategy demands stable conditions, Pulmonates do not brood; instead, they create eggs that are frequently hard and resistant (Frogley and Preece, 2004). Eggs are fertilized by the two following ways, by the sperm from another individual near the junction of the hermaphroditic duct and the oviduct or either in the hermaphroditic duct by the same individual’s sperm (Dillon, 2000). Gelatinous egg casings in which eggs are placed are attached to plants or rocks (Dillon, 2000).

Parthenogenesis are able to have a similar possess an analogous adaptive value for caenogastropod snails which isolated in tiny headwater streams (Brown and Lydeard, 2010). Since most pulmonate gastropods have shorter life cycles and the ability for air-breathing juveniles to disperse passively, these adaptations have led to their abundance and widespread distribution (Brown and Lydeard, 2010).

1.3 Current taxonomy

The taxonomic traditions and practices of several generations of workers across numerous continents have combined to form the current taxonomy (Strong et al., 2008). A small number of widely dispersed species with varying conchology were recognized as a result of early research on some taxa, or the opposite occurred, leading to an unjustified large inflation of nominal taxa (Strong et al., 2008). This can be understood if we consider the high plasticity of some taxa such as the genus *Radix* (Pfenninger et al., 2006). A more in-depth understanding of the genera and species has been achieved, through the use of modern analytical methods, incorporating molecular and newly interpreted morphological characters, in combination with an increased understanding of geographic and ecological patterns (Strong et al., 2008). There are currently many recognized clades that are well-supported, Caenogastropoda (with the majority of the former Mesogastropoda and all Neogastropoda); its sister group, Heterobranchia (encompassing the former Pulmonata and Opisthobranchia, along with a few groups of Mesogastropods); Vetigastropoda (Including a great deal of the former Archaeogastropoda) and Neritimorpha (Previously, a subgroup of Archaeogastropods) (Bouchet et al., 2017). As for the systematic study In Europe, Quaternary freshwater gastropod assemblages have been intensively studied during the last 150 years (Georgopoulou et al., 2015).

1.4 Autecology of aquatic continental gastropods

Freshwater gastropods, with a few obvious exceptions, generally have comparable ecological requirements (Dillon, 2000). The significant intraspecific variety in freshwater snails' life cycles, productivity, feeding patterns, morphology, permits them to endure in erratic freshwater environments (Brown and Lydeard, 2010). Freshwater molluscs often appear immobile in small spatial scales. According to Dillon, (2000), on a coarse geographic scale, the possibility that the distributions of freshwater molluscs are the result of random colonization could be figured high. Biotic interactions in large lakes, like predation or interspecific competition are of great importance in the determination of the gastropod diversity and abundance (Brown and Lydeard, 2010). In reference to the competition, some data indicate that freshwater snails rarely engage in it (Brown and Lydeard, 2010).

Gastropod report significant similarities in the gut contents of various snails’ species, the distinction between diet and habitat is subtle, particularly in regard to the proportions of filamentous algae and macrophytes in their diet (Brown and Lydeard, 2010, Dillon, 2000). Gastropods frequently control the quantity and periphyton composition in lentic and lotic environments (Brown and Lydeard, 2010). Based on Dillon, (2000) this seems to result from differences in habitat selection as well as variations in the size and strength of different radula of the gastropods, rather than from the selective retention of food. As a result, little snails, like small species of Planorbidae and Ancylids, do not feed on aquatic vegetation, in contrast to the big snails, such as the ampullariids, that do so (Dillon, 2000). Furthermore, evidence suggests that habitat selection occurs at the species level and that snails routinely migrate between different habitats (Brown and Lydeard, 2010, Dillon, 2000). Migrations occur in the fall in the deeper lake waters and return to the littoral zone in the spring, whereas Pond pulmonates, burrow into the substrate as temperatures decline (Brown and Lydeard, 2010).

About biogeographic scale, a determining factor on the distribution of gastropods, is the dispersal ability (Brown and Lydeard, 2010). High gastropod diversity in a lake environment, according to Frogley and Preece (2004), is more likely to be caused by a confluence of various interrelated causes, than it is to be the result of numerous invasions of unrelated taxa. These factors comprise: (a) presence and the ecological preferences of certain gastropod lineages; (b) the physical attributes of the basin of lakes (e.g., areal extent, bathymetry, depth, longevity); (c) external factors (e.g., the climate); and (d) local abiotic and biotic conditions. The first two of these factors are thought to be the most significant, according to the same authors. Research has also indicated that the number of lakes and ponds increases diversity, according to Brown and Lydeard, (2010), and they also mention as habitat size increases, immigration rates rise, and extinction rates fall. Consequently, larger habitats are most important, all else being equal, often offer support more species (Brown and Lydeard, 2010). It is also interesting to mention some information of Brown and Lydeard, (2010) below. Successful colonization, following the dispersal, depends on suitability of the present substrata. Admittedly, substrate preferences that are determined in the laboratory constitute good predictors of the types of ponds that the snails are found commonly in. There is also a positive relation between gastropod diversity and macrophyte biomass, most probably due to the increase of the surface area for periphyton colonization by the macrophytes (Brown and Lydeard, 2010).

According to Bae and Park, (2020), the primary factor affecting how gastropod assemblages are distributed throughout South Korea, was determined to be the ratio of cobble in the substrate composition. Based upon the same authors, depending on the habitat preference and environmental tolerance of each species, different environmental factors affect its distribution. (Bae and Park, 2020).

Disturbance is another factor that could impact the snail assemblage. (Brown and Lydeard, 2010, Dillon, 2000). Because temporary ponds frequently dry out, their diversity is diminished. Consequently, when these habitats become hypoxic, macrophyte and gastropod populations will also experience diebacks (Brown and Lydeard, 2010). In areas that are prone to disturbance, a limitation of some species can occur, e.g., littoral zones of reservoirs, wave-swept shores, etc., (Brown and

Lydeard, 2010, Dillon, 2000). In streams, current velocity may also affect distribution and growth (Brown and Lydeard, 2010, Dillon, 2000).

1.5 Diversity in continental water systems

The main hotspots nowadays are associated with long-lived lakes in preglacially formed, permanently subsiding geological basins or to isolation of existing inland basins and embayments from the marine realm dynamics (Neubauer et al., 2015a). The evolution of fauna within hotspots is highly depended on warm climates and on the surface area although in some cases, climate might only be a secondary or indirect cause for the varying richness of the species (Neubauer et al., 2015a). The tectonic processes can greatly influence the climate conditions and cause closing or opening of seaways or orogenesis. These configurations control the dynamics of the oceanic and atmospheric circulation, thus affecting climatic dynamics (Neubauer et al., 2015a). Ancient lakes have played a crucial role, to enhance comprehension of the processes of radiation and speciation in space and time (Hauswald et al., 2008). They are frequently viewed as confined geographical areas with distinct histories within a particular hydrological setting (Albrecht et al., 2008). It is very clear according to Albrecht et al., (2008), that through geological time scales, they do not remain constant; instead, some of these lakes went through a repeated subdivision and reconnection in the past. It has been suggested that such conditions in ancient lakes, could trigger allopatric speciation (Albrecht et al., 2008).

Despite the divergent hypotheses that have been proposed in order to explain the diversity and speciation, based on the interaction of various biotic and abiotic parameters, a new study by Neubauer et al., (2022) based on a biotic (diversity) and nine abiotic parameters (tectonic complexity index, annual precipitationovel, ter-rain ruggedness index, number of basins, average basin size, mean annual temperature, mean elevation range, continental area, mean geographical distance among fossil occurrences) has been published and showed that both diversity dependence and topography are consistently important in geological time.

1.6 Pleistocene in Europe and fossil record in Greece

According to Neubauer et al., (2015b), in European region, at the Pleistocene the successive decline in species wealth coincided with global cooling. Large systems with high diversity and endemism disappeared at the end of the Pliocene, including Lakes Dacia, Slavonia, and Lake Transylvania. The formerly hotspots vanished and were replaced by a scattering of smaller hotspots, such Lake Bresse in France, Lake Tiberino in Italy, and Lake Kos in Greece. Such a small spot could also be called the area of Sousaki as can be seen from the study of (Papadopoulou et al., 2019).

In Greece according to Esu and Girotti, (2015), during the Quaternary, changes in palaeogeography and palaeobiogeography were brought on by Crustal Uplift and sea level oscillations due to climate changes, particularly in tectonically active coastal areas. The authors also state that flatlands may experience very widespread coastal withdrawal due to glacial sea level reductions, which promotes the creation of more or less broad non-marine sedimentary basins that can remain isolated in the event of tectonic uplift. This process really seems quite important in the case of Greece, which is surrounded by the Mediterranean, where successive isolated basins could be potentially important habitats for freshwater gastropods during the Pleistocene.

In Greece there are several works since the 19th century and modern ones, that concern the Pleistocene freshwater mollusc faunas, as well as from older geological periods. However, few works are those that analyze the whole fauna and not parts of it.

More detailed research on lake invertebrates has been done in the past in the wider study area and in other places of Greece. An older work from the study area is that of Fuchs (1877), where he records a variety of gastropods and bivalves from the Isthmus of Corinth, from Kalamaki, from Megara and Atalanti basin. Also, there are the records of Gaudry (1862) from Megara of Attica, of Bukowski, from Rhodes and later works for example of Willmann (1981) from Kos, of Koskeridou and Ioakim, (2009) from Atalanti basin, of Esu & Girotti, (2015) from Achaia, of Vasileiadou et al. (2017) from Lesvos and more.

2. GEOLOGICAL & STRATIGRAPHICAL SETTINGS OF STUDY AREA

The South Aegean Volcanic Arc extends from the Gulf of Saronikos to the west with the volcanoes of Sousaki, Aegina, Poros, Methana, to Kos, Nisyros and some minor islands to the East, through Milos and Santorini island groups at the central part (Fig.2.A)(Francalanci et al., 2005; Innocenti et al., 1981, 1979; Pe-Piper and Piper, 2003; Piper and Perissoratis, 2003). It records a complex history of volcanic activity during Pliocene and Quaternary, triggered both by extensional and subduction-related tectonics (Calvo et al., 2012; Kokkalas and Aydin, 2013; Pe-Piper and Piper, 2003; Piper and Perissoratis, 2003).
Sousaki comprises the westernmost end of the South Aegean Volcanic arc located about 15 km east of Corinth, Central Greece (Fig.1). It is found at the Northeastern part of the Corinth gulf, one of the most tectonically and seismically active areas in Europe (Leeder et al., 2008; Roberts and Koukouvelas, 1996; Tsodoulos et al., 2008). It can merely be considered as a volcanic centre, as the only thing remaining today is some volcanic outcrops of limited extension with a total volume less than 1 km which is scattered in a relatively large area and its active though hydrothermal activity (Francalanci et al., 2005; Pe-Piper and Hatzipanagiotou, 1997). Despite this fact,

Sousaki is of great interest as it is the most westerly, late Cenozoic volcanic activity in the arc. Two volcanic outcrops of different ages are present in Sousaki. The older one is found at the western part of the Sousaki basin (north of Kalamaki), and has an age of 3.6-4 Ma. The younger one, found at the eastern part of the basin (between Sousaki village and Agioi Theodoroi), has an age of 2.2-2.8 Ma (Francalanci et al., 2005; Fytikas et al., 1976; Pe-Piper and Hatzipanagiotou, 1997; Schroeder, 1976). The majority of the sediments in the basin are marls, which may reach a thickness of 400 m and present a swift transition laterally and vertically into sandy conglomerates that can reach a thickness of 250 m (Papadopoulou et al., 2021). Both the palaeogeographic complexity and the strong tectonic activity are evidenced by the various and frequent shifts in the sedimentary facies that can be seen across the region (Papadopoulou et al., 2021). Distinct geomorphological characteristics were developed in the Sousaki Basin that supported various sub-environments, including marginal lakes, marshes, and delta fans, as occurs in the related geotectonic settings (Papadopoulou et al., 2019).

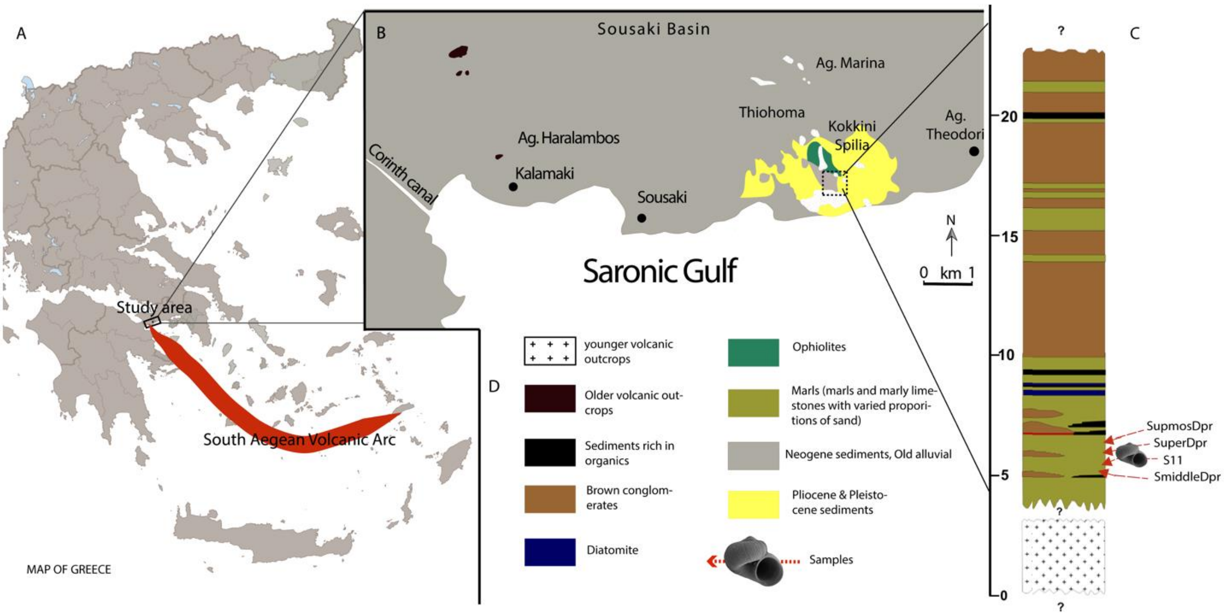


Fig. 2. A. Map of Greece with the Aegean volcanic arc. **B.** Sousaki Basin with the two volcanic outcrops C., synthetic stratigraphic column of the studied section, modified after Papadopoulou et al., (2019).

The studied section is artificial (90m long) and was made accessible during the construction of the escape exit tunnel of the suburban Athens-Corinth railway track line (coordinates EGSA: 421735.55,4197108.42). It lies next to the Sousaki volcano in the area of the younger volcanic rocks group (Fig. 2. B). The younger group of volcanics, are autobrecciated dacitic to rhyolithic lava flows. The studied sediments that consist by marly and conglomeratic layers have been deposited on them (Papadopoulou et al., 2021) (Fig.2. C).

The section is severely tectonised by a group of normal faults. Tectonism created a graben near a coastal zone after the emplacement of the volcanic material in the study area (Papadopoulou et al., 2019). Stratigraphic, tectonic and micropalaeontological analyses have been already carried out by Papadopoulou et al. (2019). The authors found out that the section consisted deposits of a tectonically controlled volcanic lake from the early Pleistocene (Gelasian). The micropalaeontological analysis of the studied section revealed a rich fauna of mostly oligohaline ostracods, gastropods, fishes and Testate amoebae. However, a complete description of this well-preserved gastropod fauna was not given, and this is the object of this study.

3. MATERIAL AND METHOD

All material comes from, Ag. Theodoroi, Sousaki Basin. Three samples, ten kg each, and one the S11 almost 2 kg, were collected from a lacustrine beige marls layer. The layer was rich in gastropod shells from the same stratigraphic horizon as sample S10, Fig. 4, reported in the work of Papadopoulou et al. (2019). The Early Pleistocene (Gelasian) age is estimated by the same authors for the study area. The sampling was performed by the members of the Laboratory of Palaeontology & Stratigraphy department of Geology University of Patras and the samples are part of the collections of this Laboratory.

Following the collection, the samples were wet sieved through 500 μm and 63 μm sieves, preparing the samples for the collection of otoliths. After the fish otoliths were firstly handpicked, the remaining material from the 500 μm sieve was examined by the author. From the 63 μm sieve each sample was split in quarters and part of the total material was thoroughly examined and gastropod shells were handpicked. The rest of the material was checked as well macroscopically. Handpicked almost 21,400 shells, with the use of a Bresser Advance ICD 10x-160x Stereo Microscope (fig. 3), when necessary.

The systematic classification was based on MolluscaBase eds. (2023) and Bouchet et al. (2017). Historical works like the one of Fuchs (1877) who was the first to examine the fossil continental gastropods in the wider study area, and additional similar works in Greece, e.g., (G. v. Bukowski, 1893; Esu and Girotti, 2015a; Gaudry, 1862; Willmann, 1981), as well as from the wider European area, e.g, (Brusina, 1882, 1874) we are taken into account. Also a multitude works from modern species, e.g., (Glöer, 2019; Welter-Schultes, 2012) were also examined.

Photographs of the studied taxa are also provided at the end of this work as plates. The presented views follow the work of (Callomon, 2019). Scanning Electron Microscope (SEM) photographs were taken with a JEOL 6300 SEM at the Laboratory of Electron Microscopy and Microanalysis (L.E.M.M.) of University of Patras. Color images were taken under a Leica M165 C stereoscope, with a LEICA IC90 E camera, at the Department of Historical Geology – Palaeontology, Faculty of Geology and Geoenvironment, National and Kapodistrian University of Athens.

The descriptions of the shells were mostly based on the work of Burch, (1989). The terminology of the protoconch follows the work of Neubauer et al., (2018). The method for the whorl counting follows the method of Verduin, (1977). Basic shell measurements follow Ruiz-Cobo et al., (2018). The terminology of the morphological features of the shell and operculum of the genus *Theodoxus* follows Sands et al., (2020). The measurements for the genus *Acroloxus* follow Glöer (2019). For research of the fossil species of the genus *Melanopsis* we also follows Neubauer, (2016). Measurements were made in Photoshop using the respective photographs and where necessary for larger taxa and shells with a caliper.

For statistical analysis, all gastropods that were identifiable up to the family-level were used processed using PAST v. 3.19 (Hammer et al., 2001). A set of Individual Rarefaction curves was constructed for the four samples, with richness index S, the data used are given in (Tab. 1). The method is suitable for abundance data for several taxa, using a log Gamma function to calculate combination terms. Thus, the effect of sample size on taxonomic diversity can be investigated. In this way it was checked whether statistically the samples are satisfactory and carry all available taxonomic information (Hammer et al., 2001). Relative abundances of gastropods were calculated in excel; the data are given in (Table 2), in the appendix of the images. This data used for Cluster analysis, because is suitable method for comparing associations (columns) based on abundances of individuals/taxon. Cluster analysis was performed on the samples, using unweighted pair-group average (UPGMA), and the Bray-Curtis similarity index because it is appropriate for abundance data and has a strong monotonic relationship with ecological distance (Beals, 1984; Hammer et al., 2001; Papadopoulou et al., 2019). Correspondence analysis (Fig. 10), used to identify groups of samples and the taxa in that define the assemblages, so these assemblages could be interpreted ecologically based on the ecological preferences of the species (Hammer et al., 2001; Papadopoulou et al., 2019).

Additionally for comparative material, the following collections were assessed: Museum of Geology, Palaeontology and Palaeoanthropology of the Aristotle University of Thessaloniki, Laboratory of Palaeontology and Stratigraphy, Department of Geology, University of Patras. Department of Historical Geology – Palaeontology, Faculty of Geology and Geoenvironment, National and Kapodistrian University of Athens, in which the material is kept of Koskeridou and Ioakim, (2009).

As a result, detected *Theodoxus micans* (Gaudry & Fischer in Gaudry, 1867), *Lymnaea megarensis* Gaudry in Gaudry & Fischer, 1867, *Graecamnicola euomphalus* (T. Fuchs, 1877) and some other different species from Pleistocene or from different geological ages.

Abbreviations and other used in the text:

Max: Maximum, Min: minimum, Sh: shell height, Sw: shell wide, Ph: peristome height = aperture height, Pw: peristome width = aperture width width width width.
SL: Shell length (for genus *Acroloxus*).
SEM: Scanning electron microscope.

4. SYSTEMATIC PALAEONTOLOGY

Phylum Mollusca Cuvier, 1795
Class Gastropoda Cuvier, 1795
Subclass Neritimorpha Koken, 1896
Order Cycloneritida Frýda, 1998
Family Neritidae Rafinesque, 1815
Genus *Theodoxus* Montfort, 1810

Type species: *Theodoxus lutetianus* Montfort, 1810 (Synonym of *Theodoxus fluviatilis* (Linnaeus, 1758)); Recent; Europe.

Theodoxus micans (Gaudry & Fischer in Gaudry, 1867)

Pl. 4, J-U.

1867, *Neritina micans*, Gaudry & Fischer in Gaudry, p. 445, pl. 61, fig. 11-13.
1877, *Neritina micans*, Fuchs, p. 14, pl. 3. fig. 5-16.
1947, *Theodoxus* (*Calvertia*) *micans micans*, Papp, p. 117, pl. 9, fig. 2a, b.
2019, *Theodoxus* sp., Papadopoulou et al., p. 52, fig. 7a-c.

Material. 3916 specimens, very well preserved, of all stages of development, from the samples SmiddleDpr, SuperDpr, SupmostDpr and S11.

Dimensions. Max., Sh 7.5-8 mm, Sw 9 mm.

Description. Variable species with solid shells. Dominant morphology characterized by an almost globose shape, with 2.7 rapidly increasing whorls. Spire slightly protruding, body whorl increasing fast. Body whorl attains 90 % of the total spire height. Whorls are convex, separated by a shallow suture. Protoconch consists of 0.6-0.7 whorls, has a smooth surface without colour pattern. Microsculpture decorate by an irregular network of wrinkled lines. The P/T boundary is usually faint, because the protoconch and more than half of the first whorl of the teleoconch have smooth surfaces. After that, the teleoconch has a smooth shell surface with thin growth lines and rich colour patterns, ranging from white to black or brown shells, with more or less zig zag lines, white splotches on dark background or combinations of those already mentioned above. Imperforate shell. Aperture shape semi-circular, inner margin almost straight, weakly denticulate. Outer margin simple, columellar plate thick, almost rectangular.

Operculum. The apophysis is slightly convex, with the rib shield touching the apical part of the apophysis and lowering at an angle of 60°. Diagonal pseudo-apophysis. In the middle of the calcareous base appears a slightly elevated banded area, starting from the middle of the upper margin and ending after bending to the right adductor, under the apophysis. Left adductor angular, with an angle of about 60-70°. Its bad preservation does not allow the description of other characters.

Remarks. The studied material is considered to belong to the genus *Theodoxus* Montfort, 1810, which is characterized by a D-shaped operculum with a strong apophysis and also does not have a planktotrophic larvae (Bandel, 2008; Glöer, 2019). The morphology of the operculum has suitable characters to identify species (Glöer, 2019; M. Alba et al., 2016; Sands et al., 2020), but it is usually rarely preserved. In contrary, shell shape, periostracum colouration and patterning, might be influenced by environmental factors according to Sands et al. (2020). The elongated spherical shape, the absence of embossed sculpture and the plethora of colour patterns is consistent with observations made by Fuchs, (1877) for *Theodoxus micans* (Gaudry & Fischer in Gaudry, 1867). Also, the size (Sw 9 mm) and geographical distribution, indicate this species. In addition, based on the shell, it differs from other fossil *Theodoxus* species of Greece; *Theodoxus macedonicus* Wenz, 1943 whose parietal callus has intense thickness, *T. doricus* (Neumayr, 1880) and their subspecies and *T. hellenicus* (Bukowski, 1896) which the shape of the shells is not spherical as that of *T. micans*. The following species (*T. patrae* Esu & Girotti, 2015, *T. milessii* A. Papp, 1979*, T. atticus* Kühn, 1963*, T. morulus* Kühn, 1963), have relief sculpture and not smooth like *T. micans*. In addition *Theodoxus rhodiensis* (Tournouër in P. Fischer, 1877) [= *Neritina micans* var. *rhodiensis* Tournouër in Fischer, (1877)] from Pliocene to Quaternary deposits of Rhodes island, seems to be related to *T. micans*, according to the remarks of Tournouër in P. Fischer (1877). This was also observed by comparing the material to Willmann (1981), (pl. 3, fig. 1-7), which morphologically in terms of their shell they are quite similar and might indicate a close relationship.

Few similarities with older representative species from Lago-Mare deposits of Mediterranean region, such as the colour pattern and the general smooth spherical shell as *T. micansit* has are: *T. mutinensis* (D’Ancona, 1869), which recorded in many Messinian localities of Italy, Sicily and Spain and *T. doderleini* (D’Ancona, 1869) from the Messinian of Italy, (pl. 1, fig. 1-4), as depicted by Harzhauser et al. (2015).

Concerning modern species and judging by the geographical distribution, the size and morphological characteristics of the shell and operculum (see Glöer, 2019; 2018) reminds *Theodoxus callosus* [= *Theodoxus baeticus* (Lamarck, 1822)].

Ecology and geographic/stratigraphic distribution. The genus *Theodoxus*, occurs in freshwater to mesohaline aquatic environments and possibly it is suggestive of high quality waters (Alhejoj et al., 2017; Bandel, 2008; Glöer, 2019; Sands et al., 2020). Individuals, live in the littoral zone of lakes, also in rivers and canals (Glöer, 2019). Animals are found adhering to stones, as well as under stones, in depths of up to 6 meters (Welter-Schultes, 2012), feeding on algae, detritus and preferable diatoms (Dillon, 2000; Glöer, 2019). Due to the lack of jaws, *Theodoxus* requires rough surfaces, in order to crush its food against them, therefore a stony substrate is necessary (Glöer, 2019; Welter-Schultes, 2012). First record for *T. micans,* was from the Pliocene deposits of Megara basin by Gaudry & Fischer in Gaudry, 1867 and existed at least until the late Early Pleistocene (Esu and Girotti, 2015a). Also it has been found in the Early Pleistocene sediments of an oligotrophic lake from the Sousaki basin (Papadopoulou et al., 2019; this study), the Pliocene-Pleistocene deposits of the Magoula-Karatoulas basin (Pyrgos, Peloponnesus) by (ΣΙΝΕΚΟΓΛΟΥ et al., 2018), Early Pleistocene Basin of Atalanti (Koskeridou and Ioakim, 2009) and Cythera (Papp, 1947).

Subclass Caenogastropoda Cox, 1960
Order Littorinimorpha Golikov & Starobogatov, 1975
Superfamily Truncatelloidea Gray, 1840
Family Hydrobiidae Stimpson, 1865
Genus *Prososthenia* Neumayr, 1869

Type species: *Prososthenia schwartzi* Neumayr 1869

Prososthenia cf. *attica* (Fuchs, 1877)

Pl.1, A-O.

1877, *Hydrobia attica*, Fuchs, p. 13, pl. 2, figs. 36-44.
1981, *Prososthenia attica* (Fuchs, 1877), Willman, p. 204, fig. 68, A.
2019, *Prososthenia* sp., Papadopoulou et al., p. 52, fig. 7p-q.

Material. 1733 very well-preserved specimens, of all ontogenetically stages, from the samples (SmiddleDpr, SuperDpr, SupmostDpr, S11).

Dimensions. Shell measurements as depicted in fig. 1 G., Sh 4.7 mm, Sw 2.59 mm, PW 1.48 mm, PH 2.11 mm, L., Sh 5.6 mm, Sw 2.49 mm, PW 1.51 mm, PH 1.77 mm., J., PW1.78 mm, PH 1.2mm.

Description. Small shell, shape elongate conical. Five and a half to six, whorls, slowly increasing spire whorls and faster increasing body whorl, as it has a height greater than the spire. The whorls are mildly convex, separated by a shallow suture. Imperforate to remotely perforate shell, with a slit-like umbilicus, with straight columella. Protoconch whorl, with smooth wall surface, microsculpture with granulate surface. The P/T boundary is not strongly discernible because the protoconch and the teleoconch have smooth surfaces, but the distinction is made by a series of growth lines at the beginning of the teleoconh. After that the teleoconch is characterized by a smooth and glossy surface with thin growth lines and less or more visible spiral striae. Aperture is broadly ovate with a complete peristome. Aperture profile sigmoid with convex aperture lips. When the outer lip starts to become mature, a point is visible, where the outer lip begins to go downwards, at the base of the whorl and growth lines become sharper and more visible. Then it starts to rise again, and the upper part of the aperture turns backwards from the direction of coiling and creates an earlike aperture shape. But most commonly is seen as in Pl. 1., F. The characters of the population are not uniform for all specimens, may vary more in width and less in height. Also, it can appear a slight angulation, especially on the last two whorls or to be absent and its windings to be perfectly convex.

Remarks. The genus *Prososthenia*, distinguish by the broadly (ovately) conical shell, the large body whorl, the oval aperture, wider at the base, with an angle and slightly thickened at the top, with a typical sinuate outer lip. The microsculpture of protoconch is weakly granular (Neubauer et al., 2020, 2013a). The species of this work coincides morphologically with the typical characteristics of the genus. Is greatly similar to *Prososthenia neutra* Brusina, 1897 from the middle Miocene Lake Gacko of southern Bosnia and Herzegovina, as depicted by Mandic et al., (2011), however it resembles a Miocene species and therefore it is not the same species. In Greece the species of this study, it could be associated with *P. gregaria* (Fuchs, 1877) from East Attica (late Miocene), and probably from late Early Pleistocene of Achaia, Greece (Esu and Girotti, 2015a; Fuchs, 1877; Willmann, 1981). It has a smooth shell, with more or less obvious spiral lines, which resembles *P. gregaria* but also to *P. attica* from Pliocene of Megara basin. Both species agreeing with the descriptions of (Fuchs, 1877; Willmann, 1981). Despite that *P. attica* characterized by an angulation at the base of each whorl, Fuchs in his description has noticed that, the angulation sometimes disappears on the last whorl, even the entire shell. This occurs in the majority in most of our samples (PL.1, B). For this reason, the species of this study, is temporarily attributed to *Prososthenia attica* (Fuchs, 1877), as although less often, in its widest morphological range can appear a slight angulation (PL.1, B), coinciding with the observations of Fuchs, (1877).

Ecology and geographic/stratigraphic distribution. An extinct genus, common interpretations attribute it to low-energy, shallow freshwater lakes and ponds, need stable water bodies. (Neubauer et al., 2013a). This species has been found in Lower

Pleistocene lacustrine sediments, of the Sousaki basin by (Papadopoulou et al., 2019; this study), also Pliocene-Pleistocene deposits of Megara basin by (Fuchs, 1877).

?*Prososthenia* n. sp.

Pl.1, P-U.

Diagnosis. Elongate conical shape with five and a half to six whorls. Aperture ovate with a complete peristome. Shell surface with a corrugated carina which runs through the middle of each whorl and spiral striae lines and sigmoid growth lines.

Material. 21 specimens, of which only one adult with broken outer lip from all the samples (SmiddleDpr, S11).

Type locality. Ag. Theodoroi, Sousaki Basin.

Type horizon. Lacustrine beige clays rich in gastropod shells, early Pleistocene (Gelasian).

Dimensions. Only from one adult shell, the measurement PW could not be accurate because of the broken outer lip. Sh 4.7 mm, Sw 2.27mm, PW 1.33 mm, PH 1.62 mm**.**

Description. Small shell, elongate conical shape, five and a half to six whorls are distinguished, slowly increasing spire whorls, faster increasing body whorl and larger height than the spire. The whorls are mildly convex, separated from shallow suture. Imperforate to remotely perforate shell, with slit-like umbilicus and straight columella (the adult shell can be characterized as Imperforate). Protoconch 1 whorl, with smooth wall surface, microsculpture probably characterized by an granulate surface, when the periostracum is preserved. The P/T boundary is not strongly discernible because the Protoconch and more than a half of the first whorl of the teleoconch have smooth surfaces. After that the teleoconch has unique shell surface characters, a corrugated carina which runs through the middle of each whorl, but this is seen on the body whorl, in the previous whorls it seems to be found at the base. In addition, spiral striae lines and sigmoid growth lines intersect with each other all over the surface. Aperture is broken but broadly is rather ovate with a complete peristome. Aperture profile probably sigmoid with convex aperture lips.

Remarks. Regarding the existing species in the Hellenic area, *Prososthenia lakonica* Schütt, 1988 is the oldest record of the genus from Miocene of Laconia (Schütt, 1988) and therefore not related chronological. In general contexts, *Prososthenia attica* (Fuchs, 1877) from the Pliocene of Megara, resembles in terms of shell shape with *Prososthenia* n. sp., but differs in term of morphology of carina. *Prososthenia gregaria* (Fuchs, 1877), also differs, has a smooth shell surface. Additionally, in

Rhodes, *Prososthenia sturanyi* (Bukowski, 1896) as well species of the genus from other localities also differs from the described species. A similar morphological genus in term of shell surface pattern, is *Goniochilus* F. Sandberger, 1875. Many species of this genus, e.g., *Goniochilus rissoina* (Brusina, 1878), *Goniochilus breviformis* (A. Papp, 1953), are decorate by nodular "keel" and spiral lines, but thiese characters appear in many other genera like *Pyrgula crispata* Brusina, 1881. Also, the shell shape of the genus *Goniochilus*, is more tower-shaped, and usually is more elongate. In case of *Prososthenia* n. sp., the broadly (ovately) conical shell with the large body whorl and the oval aperture, leads us to classify it with some doubts in the genus *Prososthenia* Neumayr, 1869. The corrugated carina distinguishes *Prososthenia* n. sp., from the other species and for these reasons it could be considered as a new species.

Ecology and geographic/stratigraphic distribution. This species has been found in the lower Pleistocene lacustrine strata of the oligotrophic volcanic lake of Sousaki, (Papadopoulou et al., 2019; this study).

Genus *Goniochilus* Sandberger, 1875

Type species: *Pleurocera costulatum* Fuchs, 1870

***Goniochilus graecus* (Wenz, 1919)**

Pl. 2, A-E.

***1877** *Melania elegans* Fuchs, p. 15, pl. 3, fig. 30-32.

Material. 1396 specimens very well preserved, of all developmental stages, from the samples (SmiddleDpr, SuperDpr, SupmostDpr, S11).

Dimensions. Sh min-max 5.74-6.05 mm, Sw min-max 2.22-2.34 mm, PW min-max 1.17-1.3mm, PH 1.62-1.78mm.

Description. Small shell, shape elongated conical. Seven to seven and a half strong walled, slowly increasing, mildly convex whorls are distinguished, separate by deep suture. Each whorl is almost twice as high as the previous one. Imperforate shell, with straight columella. Protoconch with smooth wall surface, microsculpture characterized by a granulate surface when the periostracum is preserved. The P/T boundary is not strongly discernible. The microsculpture of the protoconch, gradually goes over to a smooth microsculpture surface of the teleoconch, with thin growth lines and ribs, which are gradually becoming stronger. The ribs of the teleoconch, start from the previous suture and are cut by the next. On the body whorl, the ribs are simply lost just before the base of the maneuver. The ribs are parallel to each other, convex to the right, with a distance between them twice their width. Ribs have also smooth surface and are slightly thicker in the centre. Rarely, mainly at the end of the body whorl or much rarer on part of the whorls, ribs can thicken and give the impression of intense growth lines. Aperture broadly ovate with complete peristome, with the columellar lip slightly reflected. Usually thin, rarely thicker, parietal callus covers the base of the body whorl. Aperture profile opisthocline and convex apertural lip. The characters of the population are almost uniform for all specimens.

Remarks. This genus includes at least 23 extinct freshwater species from Europe. The type species of the genus fits well to the characteristics of *G. graecus* in terms of elongate and tower-shaped shell, arched whorls almost the first two whorls smooth, teleoconch with ribs, rounded elliptical aperture, in more mature shells the aperture profile is very clear opisthocline. The following species have been recorded from Greece: *Goniochilus aegaea* (Schütt in Schütt and Besenecker, 1973) from the late Miocene of Chios, *G. graecus* (= Melania elegans Fuchs, 1877, non Benson, 1836) from Megara, *Goniochilus pauli* (Fuchs, 1877) from the late Miocene of Attica, *Goniochilus achaiae* Esu & Girotti, 2015 from the late Early Pleistocene of Achaia. The most similar one to our species is *Goniochilus achaiae* and *G. graecus* (Wenz, 1919). The morphology of the species of this work, resembles fairly to the two species but is morphometrically and morphologically more alike to *G. graecus*. The morphological differentiation of both species given by (Esu and Girotti, 2015a).

Ecology and geographic/stratigraphic distribution. It has been found in Pliocene lacustrine sediments from Megara basin (Fuchs, 1877), and was found in the Lower Pleistocene oligotrophic lake sediments, of the sedimentary basin of Sousaki by (Papadopoulou et al., 2019; this study).

?*Goniochilus* sp.

Pl. 2, F-H.

Diagnosis. Elongated conical shell, whorls very convex, with thin growth lines and almost 18 ribs per whorl. Ribs are parallel to each other, convex to the right, with a distance between them, the width of a rib. Aperture broadly ovate with a complete peristome.

Material. 2 specimens (S11).

Dimensions. Measurements of shell Fig.8, Sh 3.9 mm, Sw 2.1 mm.

Description. Small shell, shape elongated conical. Four and a half to five strong-walled, slowly increasing whorls (faster increasing the body whorl). The whorls are very convex, separated from the deep suture, which rotates almost perpendicularly to the central axis and collides to the right. Each whorl increases a little more in height than the previous one, e.g., 0.33mm, 0.48 mm, 0.77mm but the body whorl increases much more, by 1.8 mm. Imperforate shell, with straight columella. Protoconch not preserved. Teleoconch with very thin growth lines and almost 18 ribs per whorl. The ribs are uniformly thin, sigmoid, start from the previous suture and are cut by the next one. On the body whorl the ribs are simply lost just before the base. The ribs are parallel to each other, convex, to the right, with a distance between them, the width of a rib. Aperture broadly ovate with a complete peristome. Thin parietal callus covers the base of the body whorl. Aperture profile, most likely opisthocline and convex, apertural lip.

Remarks. Only two specimens have been found and identified with uncertainty, in the genus *Goniochilus* Sandberger, 1875. The first two whorls and basal lip were not preserved. Nevertheless, this species could be clearly distinguished by the morphologically two closest species, *G. graecus* (Wenz, 1919) and *G. achaiae* Esu & Girotti, 2015. Mostly in regard to the deep suture and the almost perpendicular to the central axis direction of coiling and not with a small angle as in the other two species. It has more ribs and almost circular whorls. Judging by the material that is complete in *G. graecus* and the variations that exist, we theorize that the ?*Goniochilus* sp., does not belong to any of those and it consists a different species. However, further conclusions would not be safe due to lack of material.

Subfamily Pyrgulinae Brusina, 1882
Genus *Pyrgula* de Cristofori & Jan, 1832

Type species: *Turbo annulatus* Linnaeus, 1758

Pyrgula cf. *nikosi* Esu & Girotti, 2015

Pl.2, I-T.

2015, *Pyrgula nikosi*, Esu & Girotti, p. 74, fig. 23, 24.
2019, *Pyrgula nikosi*, Papadopoulou et al., p. 52, fig. 7. L-O.

Material. 1092 specimens, some of them adults with a not well-preserved aperture (SmiddleDpr, SuperDpr, SupmostDpr, S11).

Type horizon. Lacustrine beige clays rich in gastropod shells, lower Pleistocene.

Dimensions. Measurements of mature shell, max. Sh 3.9 mm, Sw 2.19 mm, PW 1.07 mm, PH 1.4 mm, Indicative measurements of shell with four whorls. Sh 2.74mm, Sw1.8mm, PW 0.99mm, PH 1.11mm.

Description. Small shell, shape elongated conical (for the most elongated forms) or more broadly (ovately) conical (for the less elongated shells). Distinguished five and a half to six whorls, slowly increasing the spire whorls and faster the body whorl. The whorls are mildly convex, separated by a shallow suture which can turn a little or more, towards the base of the carina of the previous whorl. Imperforate to remotely perforate shell, with slit-like umbilicus. Protoconch with smooth wall surface, microsculpture characterized by an irregular network of pores, when the periostracum is preserved. The P/T boundary is distinguished for the first growth lines on the teleoconch, but with difficulty if the periostracum is not well maintained, because the protoconch and more than a half of the first whorl of the teleoconch have smooth surfaces. After that the teleoconch has a carina which run through the middle of each whorl, but this is seen on the body whorl (rarely the carina can weaken enough there). In previous whorls, carina it seems to be found at about their base. In addition, straight growth lines intersect all over the surface of the whorls and the carina, and when the periostracum is preservable there are distinct spiral striae lines. Aperture is broadly ovate, touches the base of the previous whorl, sometimes touches the base of the carina. Straight columella. Peristome continuous, columellar lip and basal lip reflected. Aperture profile, sigmoid. The characters among the population are not uniform, shorter and thicker to more elongated shells can be found.

Remarks. The moderately conical elongate carinate shell, with the small apex and the aperture shape suggests placement in Pyrgulinae. This taxon seems to be rather variable. It would be possible to classify it as two different species, but this would exclude specimens with intermediate transitional characteristics, which have to do with the way of coiled of the shell. A good example of Intraspecific variation is given for the type species of the genus, *Pyrgula annulata* (Linnaeus, 1758) (Riedel et al., 2001), which confirms the morphological plasticity of shell in representatives of this genus. This morphological variation is spotted and to our species, mostly in all the samples except from the sample (SuperDpr), in which were found mainly smaller shells of intermediate forms. Rather that shell shape is extremely variable, ranging from stout, trochiform (fig.3, A-D), to slender, elongate forms (fig.2, M-R). The trochiform shells looks like the depiction of (Fuchs, 1877) for *Prososthenia attica* (Fuchs, 1877) from the region of Megara, however, it is a different genus, and it was rejected due to the morphology of aperture and body whorl. The elongate forms could be attributed for example to *Xestopyrguloides heldreichii* (Fuchs, 1877), in this species the keel is at the base and the whorls are pretty straight sided and for that doesn't belong to this genus. The *Pyrgula nikosi* Esu & Girotti, 2015 from Achaia, of late Early Pleistocene age, is similar with trochiform shells of the species from Sousaki as to dimensions and the morpholgy. For this reason, Papadopoulou et al., (2019) classified it as Pyrgula nikosi. The similarities of *Pyrgula nikosi* to the genus *Falsipyrgula* Radoman, 1973 are multiple, especially to *Falsipyrgula sieversi* (O. Boettger, 1881) as is has been depicted by Vasilyan et al., (2014). However, according to Anistratenko, (2008) the direction of the introduction of the ancestors of

Falsipyrgula is obvious – from the Black Sea Basin into the lakes of southern Turkey and subsequently are most probably not related palaeogeographically. The majority of the collected shells for this thesis, leads us to two possible scenarios for this species. The time being, attribute the species as *Pyrgula* cf. *nikosi*, as we might probably have in our possession most mature shells, in comparison with the samples of (Esu and Girotti, 2015a), consequently more complete picture of this species. Or the species from Sousaki could be different species but very similar to*Pyrgula nikosi*. This uncertainty lies in the fact that Esu and Girotti, (2015a), they do not record elongated forms of this species.

Ecology and geographic/stratigraphic distribution. Found in the late early Pleistocene Fluvio-lacustrine deposits from Synania Formation (Achaia, Greece) and in the early Pleistocene Lacustrine beige clays from Sousaki (Gelasian) (Esu and Girotti, 2015a; Papadopoulou et al., 2019).

Subfamily Islamiinae Radoman, 1973
Genus *Islamia* Radoman, 1973

Type species: *Horatia servaini* Bourguignat, 1887

***Islamia* n. sp.**

Pl. 3, A-E.

2019 *Islamia* cf. *corinthica,* Papadopoulou et al., p. 52, fig. 7. L-O.

Diagnosis. Valvatoid shape. Shell surface has messy axial ribs and strong growth lines. Reduction of protoconch pores at the P/T boundary. Sh min-max 1.43-1.74 mm, Sw min-max 1.49-1.9 mm.

Material. 448 specimens, very well preserved, of all stages of development, from the samples SmiddleDpr, SuperDpr, SupmostDpr and S11.

Type locality. Ag. Theodoroi, Sousaki Basin.

Type horizon. Lacustrine beige clays rich in gastropod shells (the stratigraphic horizon lays on the base of the stratigraphic column, given by Papadopoulou et al., (2019) from whom the sample with the name S11 was taken. This sample is included in this thesis and was one of the four samples that are studied.

Dimensions. Sh min-max 1.43-1.74 mm, Sw min-max 1.49-1.9 mm, PW min-max 0.8-0.9 mm, PH 0.86-1mm.

Description. Shape depressed (valvatoid). 3-3.5 thin walled rapidly increasing whorls, separated from deep suture line. The spire is slightly prominent, the height of it, is usually 1/3 of the body whorl's height. Body whorl very wide, with circular circumference, occupying more than 3/4 of total shell length. Protoconch rounded and slightly raised, with one whorl, its surface with microsculpture, characterized by an irregularly dense network of almost polygonal shaped pores. P/T boundary is strongly discernible. Teleoconch has strong growth lines, rarely are finer and usually have irregular axial ribs. Umbilicated, the previous whorls are distinguished through a large and deep umbilicus. Aperture round to broadly ovate with complete peristome, with columellar lip and basal lip, that may be slightly reflected. The upper part of the aperture touches the base of the body whorl. Aperture profile prosocline with convex to straight apertural lip. The characters among the population are almost uniform for all the specimens.

Remarks. A variety of valvatiform hydrobiids that can be found in the freshwater fauna of the Mediterranean Basin. Because their identification was based on shell features, which are frequently convergent, many of them still have an ambiguous taxonomic classification (Radea et al., 2016). Because of their small size, the shell could be characterized by a pattern with no distinct features of which some morphological data may be misleading because they contain just a few features, the states of which are susceptible to homoplasies that are difficult to identify (Falniowski et al., 2007; Yildirim et al., 2017). At present, among the European valvatoid hydrobiids, nine taxa have been found in Greek lotic and lentic environments, the genera *Islamia* Radoman 1973, *Daphniola* Radoman 1973, *Pseudoislamia* Radoman 1978, *Fissuria* Boeters 1981, *Prespolitorea* Radoman P, 1983, *Graecoarganiella* Falniowski & Szarowska 2011, and *Isimerope* Radea & Parmakelis in Radea et al. 2013 (Esu and Girotti, 2015a; Radea et al., 2016). The genera *Daphniola*, *Graecoarganiella*, *Isimerope*, *Myrtoessa* Radea, 2016 and *Pseudoislamia*, are endemic to Greece (Radea et al., 2021). Other genera of similar morphology that are found in the Balkan Penninsula and the broader region of the Mediterranean, according to Radea et al. (2016) are *Zaumia* Radoman, 1983, *Tarraconia* Ramos & Arconada, 2000, *Strugia* Radoman, 1973, *Spathogyna* Arconada & Ramos, 2002, *Sardohoratia* Manganelli, Bodon, Cianfanelli, Talenti & Giusti, 1998, *Pseudohoratia* Radoman, 1967, Pezzolia Bodon & Giusti, 1986, *Ohrigocea* (*Karevia*) Hadžišče, 1959, *Ohridohauffenia* Hadžišče, 1959, Milesiana Arconada & Ramos, 2006, *Lyhnidia* Radoman, 1959, *Kerkia* Radoman, 1978, Josefus Arconada & Ramos, 2006, *Iberhoratia* Arconada & Ramos, 2007, *Heraultiella* Bodon, Manganelli & Giusti, 2002, *Gocea* Hadžišče, 1956, Dabriana Radoman, 1974, *Corbellaria* Callot-Girardi & Boeters, 2012, *Chondrobasis* Arconada & Ramos, 2001, *Boetersiella* Arconada & Ramos, 2001, *Arganiella* Giusti & Pezzoli, 1980 and *Docleiana* Delicado & Pešić, 2021, whereas two relatively new genera from Morocco, *Ifrania* Glöer, Mabrouki & Taybi, 2020 and *Fessia* Glöer, Mabrouki & Taybi, 2020 are also added in the long list.

As can be seen, the differentiation of the genera and species is not an easily accomplished task and most workers consider necessary the detailed study of anatomical characters and/or molecular data. Taking into consideration Bodon et al., (2001) who examined in detail the shell morphology of the European valvatiform hydrobiids, we conclude that *Islamia* of this study (*Islamia* n. sp.), is exhibiting the greatest similarity to the genus *Islamia* Radoman, 1973 morphologically, morphometrically and geographically. Radoman (1973), provides both morphometric and morphological characters for some of the species of the genus, with which *Islamia* n. sp., exhibits similarities. A substantial description of the genus, that is in alignment with the one for *Islamia* n. sp., is provided by Esu and Girotti (2015a) and it is the following 'the valvatiform shape, spire raised, convex whorls, last whorl large, dilated, aperture roundish-ovoid, prosocline, peristome slightly thickened at columellar margin and slightly reflected at lower and columellar margin'. Glöer and Reuselaars (2020) mention that the aperture of *Pseudoislamia* is not circular, it has a convex outer lip and a concave inner lip. The umbilicus of *Daphniola* is not as open as genus *Islamia*, distinguishing these morphologically similar genera from Greece. According to Szarowska (2006), the protoconch habitus may characterise a species, but rather not a genus. Indeed the apex morphology of *Islamia* n. sp., looks like the apex of *Islamia* as shown by Szarowska (2006). Moreover, the P/T boundary, based on bibliography is similar to *Islamia* n. sp. According to Harzhauser et al. (2013) *Islamia* has a pitted protoconch with a very distinct demarcation of the teleoconch. Another important character is that *Daphniola* and *Horatia* have circular opercula with a central nucleus without a peg (Szarowska, 2006, Glöer and Grego, 2015). However, no operculum of *Islamia* n. sp., was found.

The genus *Islamia* has been found in the following regions: Iberian peninsula, Croatia, Bosnia and Herzegovina, Greece, Italy, Western Europe and Turkey, and *Islamia* spp., are usually endemic to their type locality (Glöer et al., 2020; Yildirim et al., 2017). This genus is widely distributed in the Balkans. All other valvatiform hydrobiids are locally restricted (Glöer and Grego, 2015). Most of the 47 known *Islamia* species occur in Spain and Italy, 5 in Bosnia and Hercegovina, one in Montenegro and 4 species in the Greek mainland and Peloponnese (Glöer and Reuselaars, 2020), at least one from Cyprus, described by Radea et al. (2017), which is significantly smaller than the species described in this thesis. After MolluscaBase eds, (2023), de Jong et al., 2014 and IUCN (2022), in Greece the following species are recorded: *Islamia bendidis* Reischütz, 1988 from the island Samothrace, the dimensions of which are different from *Islamia* n. sp., leading to its differentiation. *Islamia graeca* Radoman, 1973 is endemic to Lake Amvrakia in the south Adriatic-Ionian region (IUCN, 2022). *Islamia hadei* (Gittenberger, 1982) that now is accepted as *Daphniola hadei* (Gittenberger, 1982), is also greatly different than *Islamia* n. sp., as it is certainly smaller with a smoother shell. *I. epirana* (Schütt, 1962) is not sufficiently documented and at present is being perceived as a different species by the IUCN (2022). It is mentioned that it could consist as synonym to *D. hadei*, thus if this is the case, then it is a different species than *Islamia* n. sp. The species *Islamia papavasileioui* Glöer & Reuselaars, 2020 and *Islamia skalaensis* Glöer & Reuselaars, 2020 from southern continental Greece and southern Peloponnese respectively, even though they resemble morphologically with *Islamia* n. sp., they are smaller in size, and they do not have so strong growth lines. *Islamia trichoniana* Radoman, 1979, endemic to Greece from Lake Trichonis, is fairly differentiated than *I.* sp., as it does not have strong growth lines, it has a low spire, and the aperture is almost parallel with the body whorl. Lastly, *Islamia edlingeri* (A. Reischütz & P. L. Reischütz, 2004) which originally was described as *Hauffeniü edlingeri* from Arkadia Peloponnese, is characterized by a nearly depressed spire, distinguishing it easily from *Islamia* n. sp. According to Neubauer et al. (2014), *Islamia hecki* (Kadolsky, 2008) is the oldest fossil of this genus from the Late Oligocene of Rhön Mountains, Germany. Moreover the species *Islamia amiatae* Esu & Girotti, 2015 from the Early Messinian and *Islamia bambolii* Esu & Girotti, 2015 from the Late Tortonian of Tuscany, Italy (Esu and Girotti, 2015b). In Greece, the only fossil species found and recorded so far is *Islamia corinthica* Esu & Girotti, 2015 from the late early Pleistocene of Neos Erineos, Ahaia. In addition, the same species is reported to have been also found in the location of the present thesis by Papadopoulou et al, (2019), however the determination is not considered as accurate herein. The morphology is different, such as the intense growth lines, the smaller spire, the curvature of the whorls and the parietal callus of *Islamia corinthica* which is thicker. Also, historical works like Fuchs, (1870), Bukowski (1896) and Fischer (1877) describe valvatoid shells which, however, most belong to the family Valvatidae according to Neubauer et al. (2014). An example is *Pseudamnicola welterschultesi* Neubauer, Harzhauser, Kroh, Georgopoulou & Mandic, 2014 (= *Valvata minima* Fuchs, 1877, non Hislop, 1860) from Pliocene sediments of Megara basin, the description is also given by Willmann, (1981), fig. 74. p 212), but our specimens doesn't belong to the genus *Pseudamnicola* although the descriptions are similar. Finally, from the literature, we conclude that *Islamia* n. sp., is most likely a new species, as it is different from the fossil species of the genus, as well as the living species from Greece, Cyprus and Mediterranean.

Ecology and geographic/stratigraphic distribution. *Islamia* Radoman, 1973 is a genus of minute hydrobiid gastropods inhabiting springs, rivers, lakes and subterranean waters (Radea et al., 2017). Living representatives in Greece, *I. graeca* Radoman, 1973 and *I. trichoniana* Radoman, 1979, are restricted to lakes (Boeters et al., 2013). Some species, like *I. sulfurea* from Italy, are able to live also in sulfidic waters, which are toxic to most animals (Bodon and Cianfanelli, 2012).

Subfamily Pseudamnicolinae Radoman, 1977
Genus *Graecamnicola* Willmann, 1981

Type species: *Valvata euomphalus* Fuchs, 1877.

Graecamnicola n. sp.
Pl. 3, F-J.

Diagnosis. Diagnosis. Very small valvatoid to planispiral shell, with 2.8 whorls. Umbilicated, with shallow umbilicus. The spire is flat, with almost sinker apex. Protoconch with diameter almost 0.28 mm, with 0.9 -1 whorls decorated with pores. P/T boundary is strongly discernible. Teleoconch has straight growth lines and almost 11 spiral raised lines per whorl. Ornament consists of two median apical keels one at the apex view and one and base. Also decorated by smoother spiral ribs. Aperture almost round with complete peristome.

Material. 448 specimens, well preserved, of all stages of development, from samples SmiddleDpr, SuperDpr and SupmostDpr, S11

Type locality. Ag. Theodoroi, Sousaki Basin.

Type horizon. Lacustrine beige clays rich in gastropod shells (the stratigraphic horizon lays on the base of the stratigraphic column, given by Papadopoulou et al., (2019) from whom the sample with the name S11 was taken. This sample is included in this thesis and was one of the four samples that are studied.

Dimensions. Maximum measurment as given in Pl.3 F., Sh 0.87 mm, Sw 1.71 mm, PW 0.68 mm, PH 0.68 mm.

Description. Very small right-coiling shell, shape depressed to discoidal (valvatoid to planispiral), with a few rapidly increasing whorls. 2.8 whorls are distinguished separated by a shallow suture. Umbilicated, the previous whorls are distinguished through the large and shallow umbilicus. The spire is flat. Protoconch with 0.9-1 whorls, surface with microsculpture characterized by an irregularly dense network of shaped pores. The P/T boundary is strongly discernible. The microsculpture of the protoconch, directly goes over to a smooth microsculpture surface of teleoconch. Teleoconch has straight growth lines and spiral raised lines. Aperture round with complete peristome, with columellar lip slightly reflected. The position of aperture where the parietal callus is found, touches the base of the body whorl. Aperture profile sigmoid and straight apertural lip. The characters of the population are almost uniform for all specimens.

Remarks. The samples have similarities with two genera. The first genus is *Graecamnicola* Willmann, 1981 from upper Pliocene to Pleistocene of Greece. The second is *Muellerpalia* Bandel, 2010, with the most morphological similar species to our specimens to be the *Marinescugyra varians* (T. Fuchs, 1870) [= *Muellerpalia varians* (FUCHS 1870)], *Muellerpalia tabensis* Bandel, 2010, *Muellerpalia striata* Bandel, 2010, all from late Miocene to early Pliocene of Hungary. These species although very similar morphological to our specimens, differ in terms of protoconch, especially P/T boundary and their slightly smaller size. The main difference between the two genera is that mature specimens of *Muellerpalia* has about half the size of *Graecamnicola* (Bandel, 2010). Further research could clarify the relationships between these two similar genera, but in this particular work, we classify our specimens in the *Graecamnicola*, taking in addition apart from the description of the type species and the palaeogeographical and stratigraphic distribution. Particularly aafter comparison with the type species *Graecamnicola euomphalus* by (Fuchs, 1877; Willmann, 1981) with diagnosis; small and short shell, smooth protoconch, flat cone-shaped shape or almost disc-shaped, two spiral keels that influence the shape of the aperture, leads us to the genus *Graecamnicola* Willmann, 1981. We could add additional diagnosis about this poorly known genus is considering the potential presence of a new species *Graecamnicola* n. sp.; the valvatiform to planispiral carinate to lirate shell, with an almost circular aperture and a characteristic protoconch (like many other Hydrobiidae), with porous microsculpture. In addition to the type species, only one other species has been described in the genus, i.e., *Graecamnicola graeca* (Fuchs, 1877). This species, also described from the Atalanti Basin (Central Greece), differs from the present taxon in the raised spire. According to Koskeridou and Ioakim, (2009) the age is estimated to be early Pleistocene, therefore of the same age as the fauna under study. From the description given by Fuchs (1877), for *G. euomphalus*, we detect four differences. First is the size, according to Fuchs (1877) the maximum dimensions are Sw 3mm and Sh 1 mm and by Willmann (1981), maximum diameter is 3.1mm and height 1.3mm. Second is the number of whorls which are three and a half. Third is the downwards bending of the aperture. Fourth is the two strong carinas that affect the mouth opening, which are less visible in the samples we studied. *Graecamnicola* n. sp., has Sw 1.71 mm, Sh 0.87 mm, 2.8 whorls, aperture opening parallel to the body whorl, and a teleoconch with uniform and equidistant spiral raised lines. Taking into consideration the above, we consider that this is probably a new species with a similarity to *G. euomphalus*.

Ecology and geographic/stratigraphic distribution. Representatives of the genus, so far only known from Pliocene to lower Pleistocene deposits of Atalanti Basin (Central Greece) (Fuchs, 1877; Koskeridou and Ioakim, 2009). Taking into account the accompanying fauna, e.g., *Theodoxus carinatus*, *Valvata piscinalis*, *Pyrgula incisa*, where the species of the genus *Graecamnicola* were found together by Fuchs, (1877), conclude that the age of the species probably dates to the Lower Pleistocene. Also this fauna indicate the freshwater phases of sedimentary basin of Atalanti, as it results from the work of (Koskeridou and Ioakim, 2009). The species of this study, has been found in the Lower Pleistocene oligotrophic lake sediments, of the sedimentary basin of Sousaki by (Papadopoulou et al., 2019; this study). Accordingly, the geographic distribution of this genus during the Lower Pleistocene, expand further than the Atlanti’s basin.

Genus *Bania* Brusina, 1896

Type species: *Stalioa prototypica* Brusina, 1872

***Bania* n. sp.**

Pl. 3, K-T.

Diagnosis. Globose conical (valvatoid) shape, with four mild convex whorls. Protoconch 0.8 whorls, microsculpture with dense network of pores. The body whorl is very large, it has almost the height of the spire or more. The aperture, if it belongs to a mature shell, has an almost rectangular (oblique rectangle) shape. Aperture profile, sigmoid.

Material. 170 specimens, some of those mature and of significantly smaller size.

Dimensions. Maximum measurement, Sh 1.84 mm, Sw 1.33 mm, PW 0.76 mm, PH 0.82 mm.

Description. Small shell, shape globose conical or more globose conical. Four mild convex and rapidly increasing whorls are distinguished, separated by a shallow suture. Remotely perforate shell, with straight columella. Protoconch consists by 0.8 whorl, microsculpture characterized by a well-ordered dense network of pores when periostracum is preserved, like a honeycomb. The P/T boundary is strongly discernible and the microsculpture of the protoconch goes over to a smooth microsculpture surface of teleoconch, with thin prosocline growth lines. Usually but not always it is visible from apex view that the whorls are slightly flattened on the top and slightly sunk in the middle, convex curve on the side. Intersected by dense and soft sigmoid growth lines. Maybe this character has to do with sexual dimorphism, because there are more plump and thinner shells, making this character more or less visible. From the aperture view the upper part of each whorl bends sharply and curves. The body whorl is very large, it has almost the height of the spire or more and seems to be compressing its upper part of aperture. The aperture, if it belongs to a mature shell (Pl. 3, P), has an almost rectangular (oblique rectangle) shape, with a posterior aperture and anterior aperture angle of about 70o, the upper side near the body whorl is straight and the lower parallel more convex. If the shell is smaller, than the aperture is more circular at the anterior end of the shell, but on the posterior end creates a right angle (Pl. 3, T, V). Peristome continuous, aperture profile, sigmoid.

Remarks. This genus has been already discussed by (Neubauer et al., 2013b). Characterized mainly by a reticulate protoconch, a small broad ovoid shell, and convex to step-like whorls (Neubauer et al., 2013a, 2013b), characters presented in *Bania* n. sp. Despite the fact, that the shell shape of *Bania* n. sp, is similar to genus

Pseudamnicola Paulucci, 1878, it has not a smooth protoconch (Neubauer et al., 2013b), also differ in aperture. With the exception of the thickening of the margin of aperture, the description of the type species *Bania prototypica* as given by Brusina, (1874), is similar to the species of this work. Also, *Bania* n. sp., bears similarities with other species of the genus; It shows similarities in the morphology of the aperture with the *Bania goehlichae* (p. 7, fig. 5, a─j, m, n), however, it differs, in the shape of the shell and the more opening umbilicus. The microsculpture of Protoconch of *Bania torbariana* (Brusina, 1874), (p. 230, pl. 4, fig. 8-11, 13) in work of (Neubauer et al., 2011) it's very similar, however the morphology of opening differentiates them easily. Another quite similar species relative to the shape of the shell, is *Bania stosiciana* (Brusina, 1874) (fig. E, F, G) and *Bania torbariana* (Brusina, 1874) (fig. H, I, J) as illustrated by (Neubauer et al., 2015c), but the variation in suture and the shape of the opening, also differentiates the *Bania* of this work. From the Greek area, there is a reference for this genus from the Miocene deposit of the island of Lesvos by Vasileiadou et al., (2017). However, the poor preservation of the specimens of ?*Bania* sp., (p. 4, fig. 3, j–o) from Lesvos, led authors to classify it with some uncertainty to this genus. In any case, the species of this work differed in terms of the apex, the suture and especially in aperture, which is more oblique rectangle from the species of Lesvos, as well as from another species of the genus *Bania*, which are not mentioned here. For this reason, that species could be new in science.

Ecology and geographic/stratigraphic distribution. Species of this genus have been found in freshwater systems like in Dinaride Lake System (Miocene). Also, from Germany in Steinheim basin, (Early Serravallian), Vienna basin (Tortonian), probably Lesvos island in Greece (Miocene), with the youngest age record, the Pliocene of Slavonia (Neubauer et al., 2013b; Vasileiadou et al., 2017). The *Bania* n. sp., is possibly the youngest record of this genus, and was found in the Lower Pleistocene oligotrophic lake sediments, of the sedimentary basin of Sousaki by (Papadopoulou et al., 2019; this study).

Family Bithyniidae Gray, 1857
Genus *Bithynia* Leach, 1818

Type species: *Helix 39arbara39ria* Linnaeus, 1758

Bithynia candiota Westerlund, 1886
Pl.4, A-I.

?1877, *Bithynia rubens* Fuchs, p. 39., pl. 4, fig. 32-34 (non Menke, 1830).
2009, *Bithynia candiota,* (Westerlund, 1886), Glöer and Maassen, p.42, fig. 2.
2010, *Bithynia 39arbara39r,* Kobelt, 1892, Glöer et al., p. 181, fig.2.
2019, *Bithynia 39arbara39r,* Kobelt, 1891, Glöer, p. 100, fig. 105.

2019, *Bithynia candiota* Westerlund, 1891, Glöer, p. 94, fig. 96.

Material. 418 specimens, 1 adult shell well maintained, many smaller and opercula from SmiddleDpr, SuperDpr, SupmostDpr and S11.

Dimensions. Maximum dimension, Sh 6 mm, Sw 3.84 mm, PW 2.3 mm, PH 2.5 mm.

Description. Small shell, broadly (ovately) conic, with few rapidly increasing whorls. 4-4.5 whorls separate from deep suture are distinguished. Perforated shell. The microsculpture of the protoconch is characterized by a smooth surface with very thin spiral raised lines and thin growth lines. The P/T boundary is not detected. Teleoconch (with the help of SEM pictures) has straight growth lines and spiral striae, which may not be detectable with the naked human eye. Straight columella. Aperture broadly ovate with complete peristome, with columellar lip slightly reflected. Parietal callus touches the base of the body whorl. Aperture profile sigmoid and straight apertural lip. The characters of the population are almost uniform for all specimens. Operculum ovate with a dent before the top and nucleus shifted down.

Remarks. This species presents all the typical morphological and metric characters of *B. candiota* as described by Glöer, (2019), Glöer et al., (2010) and Glöer and Maassen, (2009). It has been found in the Greek mainland, e.g., Nafpaktos, as well as in Crete (de Jong et al., 2014; Glöer, 2019; Glöer et al., 2010). The fossil species from the Atalanti Basin (Central Greece) described by Fuchs (1877, pl. 4, fig. 32-34) as *Bithynia rubens* most likely refers to the species *Bithynia candiota*, as it is morphologically similar to it. Also recorded from the Middle Pleistocene of Megalopolis Basin (Konidaris et al., 2023).

Ecology and geographic/stratigraphic distribution. These freshwater gastropods are, grazing, e.g., over macrophytes or on hard substrates during the growing season or filter feeding with detritus and from the water. Could be buried in the mud during winter (Dillon, 2000; Glöer et al., 2010, 2007).

Family Viviparidae Gray, 1847
Genus *Viviparus* Montfort, 1810
Type species: *Helix vivipara* Linnaeus, 1758

Viviparus sp.

Pl. 5, M-O.

Material. 96 specimens broken near the protoconch and only an adult shell almost destroyed (SmiddleDpr, SuperDpr, SupmostDpr, S11).

Dimensions. Height of the body whorl (suture of body whorl -basal lip) almost 12.5 mm. Maximum width, almost 12 mm.

Description. Medium to large, glossy shell, depressed conic shape, with few rapidly increasing whorls. 4-4.5 whorls separate from deep suture are distinguished. In adults no umbilicus is seen, in previous broken whorls, a primarily perforate shell appears. Smooth protoconch, with more or less visible three spiral raised lines. The P/T boundary not detected. Teleoconh like the protocnch, characterized by a smooth surface with more or less three visible spiral raised lines and smaller ones. These three spiral raised lines also appear on the body whorl, but at the end of the outer lip they get weaken.

Remarks The more accurate determination of this taxon is problematic, as there are no intact shells preserved. We hypothesize that the shell fragments were formed partially during the process of sieving which in combination with the sensitive shells, led to the lack of intact shells. The morphology of the body whorl has a shape like the one of the extant *Viviparus hellenicus* and not as circular as the one of *Viviparus contectus* (Millet, 1813), but it is not one of those two species, as they do not exhibit spirally raised lines. Moreover it is not alike to any other extant species from the European continent according to Glöer, (2019). From the Greek fossil species, it seems that it is different from the *Viviparus* from Kos island according to (Willmann, 1985, 1981). It differentiates from *Viviparus clathratus* from the Neogene of Rhodes (Deshayes, 1835 and Bukowski,1893) as its shell is smooth and we don’t observe longitudinal folds, perhaps it exhibits some similarities to *Viviparus rhodensis* Bukowski, 1892. Regarding the closest to the study area, *Viviparus megarensis* Fuchs, 1877, has been found in Megara basin but it’s probably not the same species. Also, our specimens, don’t have a nodular keel like *Viviparus graecus* Fuchs, 1877. It seems to be more similar to *Viviparus spratti* Fuchs, 1877, in terms of the morphology of the carina, but also to *Viviparus incertus* Fuchs, 1877. The *Paludina* (*Vivipara*) *41arbar* Fuchs, 1877 is now accepted as *Holandriana fuchsi* (Wenz, 1928) so doesn’t belong to this species. The *Viviparus mitzopoulosi* Psarianos, 1953, seems to have similarities, in more than the two spiral raised lines that *V. megarensis* has, but it is larger and has a more conical shell. In any case this species is problematic and new sampling and comparison with the aforementioned species are necessary for its precise identification.

Ecology and geographic/stratigraphic distribution. Rivers, lakes, ponds, swamps, canals (Glöer, 2019; Strong et al., 2008). Species of *Viviparus* are ctenidial suspension feeders, often graze, but may also remain motionless for weeks at a time, and filter debris from the water current (Strong et al., 2008; Welter-Schultes, 2012).

Superfamily Cerithioidea J. Fleming, 1822
Family Melanopsidae H. Adams & A. Adams, 1854

Genus *Melanopsis* A. Férussac, 1807

Type species: *Melania costata* Olivier, 1804.

Melanopsis cf. *bittneri* Fuchs, 1877

Pl.7., A-G.

***1877**, *Melanopsis bittneri*, Fuchs, p. 40, pl. 4, fig. 12-17.

Material. 6081 specimens (SmiddleDpr, SuperDpr, SupmostDpr, S11).

Dimensions. Max. Sh 1.6 cm, Sw 0.8 cm.

Description. Medium shell with an elongated conic shape. Eight to eight and a half, whorls are distinguished, slowly increasing at the spire and faster at the body. The whorls separate by a very shallow suture which covers them above the base. P/T boundary distinguished by a line, but with difficulty, because the protoconch until the second whorl or little more of the teleoconch, has a smooth surface. Protoconch with smooth microsculpture, nucleus raised, inflated and rounded (less often the protoconch appears flat), after that the protoconch rotates almost horizontally around the central axis like the other whorls. First and second whorl, have a smooth surface (rarely at more whorls), after those ribs start to appear. Imperforate shell, with straight columella. The surface of the teleoconch usually shows a coloured pattern of brown spots, with more intense or less intense convex axial ribs. Sometimes these ribs are thicker, sometimes not, denser in distance or a little further apart but always equidistant. In addition, may be more or less visible, spiral parallel zoned areas, slightly elevated, at the point they intersect with the ribs, they form small nodules. In addition, specimens are found that are shorter or slightly longer at height, with the same number of whorls. Aperture shape broadly ovate, with siphonal notch at the anterior end of the shell. Parietal callus, smooth and relatively thick. Outer lip, broken but rather prosocline, with convex aperture lip.

Remarks. The medium to large oval shell, with acute-oval aperture, with siphonal notch and the broad distinct parietal callus, leads us to the genus *Melanopsis* (Glöer, 2019; Welter-Schultes, 2012). This species is not similar to the extant European species, e.g., (Glöer, 2019). We are led to fossil species, mostly found in Greece where according to Neubauer et al., (2016) and MolluscaBase eds. (2023), approximately 70 species and subspecies and varieties are found. Among them few were similar and were recorded from the Miocene to the Pleistocene. A variety of works was taken into consideration (Esu and Girotti, 2015a; Willman 1981; Oppenheim, 1891; Papp, 1953; Bukowski, 1893; Fuchs, 1877; Gaudry, 1862; Deshayes, 1835) including the rich electronic collection of the National Museum of

Natural History, France, which includes many species from Greece, in order to cover most of the mentioned species.

According to the literature, we concluded that the described species do not belong in the fossil fauna that has been found in Rhodes and Kos. They are associated morphologically more to the species from Megara and Peloponnese, and perhaps phylogenetically they are associated to the even older species of the Miocene and Pliocene found in Attiki and Peloponnese.

The most important species that may belong to the same species of this work are, *Melanopsis anceps* var. *crassicosta*, *Melanopsis anceps* Gaudry & Fischer in Gaudry, 1867, *Melanopsis costata* as given by Fuchs, 1877, *Melanopsis bittneri* Fuchs, 1877 and *Melanopsis revelata* Pallary, 1920. There seems to be differences with the rest of the species.

More specifically, this species is relatively smaller than the other two species, mentioned in this work and is distinguished mostly due to the protoconch, that has a raised nucleus and the smooth second whorl, and to the spiral parallel zoned areas, that are slightly elevated and create a wavy surface. The closest species could be *M. revelata* Pallary, 1920 from Megara basin or *M. bittneri* Fuchs, 1877 Livanates, Late Pleistocene (Neubauer, 2016a). If it is not related to these species, then we could say that this is probably a new species, the geological age and geographical distance could agree with that scenario. We conclude that it is probably about *Melanopsis bittneri*, the number of sigmoid axial ribs, (about 24 ribs in body whorl), is quite characteristic and distinguishes it from *Melanopsis incerta*. Also, the short notch, the type of suture and the oval aperture also, agree with the description of Fuchs, (1877) about this species.

Ecology and geographic/stratigraphic distribution. *Melanopsis* is a generalist, grows in freshwater rivers, ponds, springs, small lakes with flooded marshes, mud and gravel coasts of estuaries, and oases. It can tolerate high temperatures and brackish conditions and needs stable waterbodies (Neubauer et al., 2013a).

***Melanopsis* sp.**

Pl.7, H-M & Y.

Material. 1444, (SmiddleDpr, SuperDpr, SupmostDpr, S11).

Dimensions. Max. Sh 2.1cm, Sw 1.2cm.

Description. A variable species in terms of width and height and how intense the nodules are, which are found in ribs. Nodules always appear to any morphotypes of this species. Nine and a half to ten whorls are distinguished separated by a very superficial suture. Whorls slowly increasing at the spire and faster increasing at the body whorl. P/T boundary distinguished with difficulty because the first 1,5 -1, 8 whorls have smooth surfaces and usually after that point the ribs started growing. Protoconch inflated and rounded, probably almost 0.5 -0.6 whorls with smooth microsculpture with wrinkle like structures. The surface of the teleoconch usually shows a coloured pattern of brown spots, thin growth lines and mildly convex axial ribs, that could be more or less elevated and thicker or thinner. Usually at the beginning of the suture, each rib has a nodule and at the middle of it but could have three nodules on the body whorl. The nodules could be blunt or more angular. Rarely can be observed, mainly in the first whorls, a few spiral lines like striae and shells with strong growth lines. Aperture shape broadly ovate, with siphonal notch at the anterior end of the shell, which is wide and slightly shorter in the adult specimens. Parietal callus smooth and relatively thick. Aperture profile sigmoid with almost straight apertural lip.

Remarks. This species is extensively discussed in the remarks of *Melanopsis* cf. *gearyae*, perhaps it is associated to *Melanopsis costata* as shown by Fuchs, (1877) but it is not clear if this is the same species with *Melanopsis anceps var. crassicosta* Gaudry & Fischer, 1867.

Ecology and geographic/stratigraphic distribution. This species has been at least found in the Lower Pleistocene oligotrophic lake sediments of the sedimentary basin of Sousaki by Papadopoulou et al., (2019).

Melanopsis cf. *gearyae* Neubauer, Harzhauser, Georgopoulou, Mandic & Kroh, 2014

Pl.7, N-S.

1986, *Melanopsis* cf. *eleis* posterior Schütt, p. 342, pl. 4, fig. 8, 9.

Material. 2407 (SmiddleDpr, SuperDpr, SupmostDpr, S11).

Dimensions. Max. Sh 2.6 cm, Sw 1.1cm.

Description. The characters of the population are almost uniform for all specimens of this species. Nine and a half to ten whorls are distinguished, separated by a very superficial suture. Whorls slowly increasing at the spire and faster increasing at the body whorl. P/T distinguished with difficulty because the first 1.5-1.8 whorls have smooth surfaces and usually after that the ribs start growing. Protoconch inflated and rounded, probably almost 0.5-0.6 whorls with smooth microsculpture, with wrinkled like structures. There is no colour decoration on the surface of the teleoconch, except for a monochrome pattern that in some points can be darkened slightly with thin growth lines and parallel, almost equidistantly, to mildly convex axial ribs. The ribs could be more or less elevated and thicker or wider at the beginning (close to the suture) and are overlapping by the suture of the next whorl. No nodules present on the shell. Aperture shape broadly ovate, with siphonal notch at the anterior end of the shell, which is elongated narrow and slender. Parietal callus smooth and relatively thick. Aperture profile sigmoid with convex apertural lip.

Remarks. The *Melanopsis* cf. *gearyae,* is distinguished from *Melanopsis* cf. *bittneri* of this work regarding its apex, shell surface characters and the size. However, distinction between it and the *Melanopsis* sp, can be at times difficult. *Melanopsis* cf. *gearyae*, and *Melanopsis* sp., are difficult to be distinguished, especially regarding the first whorls which are not substantially distinguished (Pl. 7, K, Q). Both are characterized by a relatively similar protoconch, but *Melanopsis* sp., has shell with nodules, after the third whorl, unlike *Melanopsis* cf. *gearyae,* which has in all its developmental stages a shell without nodules. Even though this character is not stable as it is changeable for this genus, according to Glöer, (2019) and Neubauer et al., (2013), we cannot ignore this fact, when in all the developmental stages of *Melanopsis* cf. *gearyae,* the absence of nodules is a characteristic, in contrast to *Melanopsis* sp., especially when this is accompanied by other characters. Moreover, these two species are different in terms of the siphonal notch, which is thinner and elongated in Melanopsis cf. *gearyae*, while in *Melanopsis* sp., is shorter and thicker (Pl.7, H, N, C, J) and the single-coloured shell of *Melanopsis* cf. *gearyae*, compared to the blotchy *Melanopsis* sp. The distinction is more apparent in the more mature specimens. As the categorization of all the specimens of the various developmental stages, in two different groups was achieved, we conclude that they are different species. More specifically, *Melanopsis* cf. *gearyae* and *Melanopsis* sp., seem to be more related morphologically to species from the Pliocene of Megara. Fuchs, 1877, reports that he does not know the description of the species *Melanopsis anceps* Gaudry & Fischer in Gaudry, 1867, but he accepts shells he found in Megara, to belong to this species, while one additional distinctive species, *M. costata*, which is more likely associated to *M. anceps*. A third species from Megara, *Melanopsis incerta* Fuchs, 1877, is also mentioned which is now accepted as *Melanopsis revelata* Pallary, 1920. Comparison to *M. anceps*, from the digital collection of the National Museum of Natural History, France, showed that *Melanopsis* sp, *Melanopsis* cf. *gearyae* are different from that species. Moreover, according to descriptions by Fuchs, (1877), they are differentiated also from *Melanopsis revelata* Pallary, 1920, which has18 mm height and 9 mm width. Finally, this species may be *Melanopsis gearyae*, through exclusion, as well as the smooth surface with the axial ribs characterizes our samples.

Ecology and geographic/stratigraphic distribution. A lower Pleistocene species, from Aetolia-Acarnania, Greece (T. Neubauer et al., 2014). This species has been found in the Lower Pleistocene oligotrophic lake sediments of the sedimentary basin of Sousaki (Papadopoulou et al., 2019; this study).

Family Thiaridae Gill, 1871 (1823)
Subfamily Thiarinae Gill, 1871 (1823)
Genus *Melanoides* Olivier, 1804

Type species: *Melanoides fasciolata* Olivier, 1804 accepted as *Melanoides 46arbara46ria* (O. F. Müller, 1774) (type by monotypy)

Melanoides curvicosta **(Deshayes, 1835)**
Pl.7, T-X.

1835, *Melania curvicosta*, Deshayes, p. 149, pl. 25, fig. 7-9.
1877, *Melania curvicosta*, Fuchs, p. 40, pl. 4, fig. 18-21.
1893, *Melania rhodensis*, Bukowski, p. 281, pl. 2, figs 11-13.
1934, *Melania* (*Melanoid.*) *rhodiensis* v. Bukowski. Picard, p. 281, fig. 47-50.
1981, *Melanoides 46arbara46ria curvicosta* (Deshayes, 1832), Willmann, p. 123, pl. 10, Fig. 9-11.
2015, *Melanoides curvicosta* (Deshayes, 1835), Harzhauser et al., p. 9, pl. 1, fig. 5-7.
2018, *Melanoides curvicosta* (Deshayes, 1832), Bizzarri et al., p. 12, fig. 6, k. p. 12.
2019, *Melanoides curvicosta* (Deshayes, 1835), Papadopoulou et al., p. 52, fig. 7i.

Material. 586 (SmiddleDpr, SuperDpr, SupmostDpr, S11).
Dimensions. Max. Sh 16mm, Sw 6mm.

Description. Medium shell, shape elongate conical. At least nine to nine and a half slowly increasing whorls, little faster on the body whorl. Mild or slightly more convex whorls are separated by a shallow or little deeper suture. Imperforated shell, with straight columella. P/T boundary is not discernible. Protoconch with a nucleus without spiral raised line, after almost 0.5 whorls a spiral raised line appears in the middle of the whorl and continues appearing until the second whorl. During the third whorl two spiral raised lines appear, one in the middle of the whorl and the other one close to the suture, the ribs start appearing at this whorl. At the point where the ribs intersect with the spirally raised lines, nodules are formed, sometimes intensely, sometimes not, with the presence of growth lines. This spirally raised lines may or may not appear at all, on the first two whorls they resemble smooth. From the third whorl to the fourth, up to seven spiral raised lines appear, but usually are covered by the next whorl and only three appear. After that, more and more spirally raised lines are visible, with ribs and more or less appeared nodules, variable intensity. Aperture shape, broadly ovate with complete peristome. Aperture profile probably sigmoid with convex aperture lips. Characteristic at the base of the body whorl is the spirally raised lines without ribs.

Remarks. This species is characterized by a high intraspecific variation inside its population. We observe variations mainly in the intensity of the shell's surface character but with the constant presence of a rib, growth lines and spiral lines. It fairly resembles the extant species of *Melanoides 47arbara47ria* (O. F. Müller, 1774), a subspecies of which, *Melanoides 47arbara47ria dadiana* (Oppenheim, 1919), had been reported as a fossil in Kos by Willmann, (1985), who also reported *Melanoides 47arbara47ria* ssp., which resembles more of *Melanoides curvicosta* (Deshayes, 1835), also mentioned from Megara and Atalanti Basin (Central Greece) (Fuchs, 1877). The original description of *M. curvicosta* is complete and given by Deshayes, (1835) who among other things states that the living analogue of this species is not known, but the fossil analogue exists around Siena in Italy. The same species is mentioned in the Neogene of Rhodes (Bukowski, 1893) as *Melania rhodiensis* and from the Pliocene deposits of Jordan Valley (Picard, 1934). In any case, morphologically, the species reported in this thesis is more alike to *M. curvicosta* (Deshayes, 1835) depicted by Fuchs (1877), but taking into consideration the high intraspecific variation of this species, it could be also considered as a subspecies of *M. 47arbara47ria* (O. F. Müller, 1774). An interesting paper that reveals some aspects of the phenotypic plasticity of *M. 47arbara47ria* (O. F. Müller, 1774), by Abdelhady et al., (2018) indicated that metal concentrations are a main predictor of the shell shape.

Ecology and geographic/stratigraphic distribution. Prefer warm temperatures, (Bizzarri et al., 2018) it was fairly widespread species during the Pliocene to Lower Pleistocene in Greece, e.g., Kos, Rhodes, Peloponnese, and ubiquitous in many Messinian sections of Mediterranean (Bukowski, 1893; Fuchs, 1877; Harzhauser et al., 2015; Papadopoulou et al., 2019; Willmann, 1981). According to Fuchs (1877), it has been found in Pliocene freshwater and brackish deposits of Megara basin. Also in the Early Pleistocene sediments of an oligotrophic lake from the Sousaki basin Sousaki Basin (Papadopoulou et al., 2019; this study).

Subclass Heterobranchia Burmeister, 1837
Infraclass Euthyneura Spengel, 1881
Superorder Hygrophila Férussac, 1822
Superfamily Lymnaeoidea Rafinesque, 1815
Family Planorbidae Rafinesque, 1815
Subfamily Planorbinae Rafinesque, 1815
Genus *Armiger* Hartmann, 1843

Type species: *Nautilus crista* Linnaeus, 1758

Armiger crista (Linnaeus, 1758)

Pl.6, A-E.

1758, *Nautilus crista*, Linnaeus, p. 709.
1964, *Armiger crista* (L.), Ložek, p. 189, pl. 5, fig. 4a-c.

1981, *Gyraulus* (*Armiger*) *crista*, Willmann, p. 97, fig. 39.
1992, *Armiger crista* L., Gorthner, p. 161, pl. 4, fig. 7, 8.
2012, *Gyraulus crista*, Welter-Schultes, p. 62.
2013, *Gyraulus crista nautileus,* Spyra and Strzelec, p. 691, fig. 1c.
2013, *Armiger crista*, Vinarski and Khokhutkin, p. 95, fig. 38a.
2014, *Armiger crista*, Vasilyan et al., p. 297, fig. 2c.
2016, *Gyraulus crista*, Danukalova et al., p. 17, fig. 1.
2019, *Gyraulus crista*, Glöer., p. 301, p. 337, fig. 373.
2021, *Gyraulus crista*, Kobe et al., p. 150, fig. 9 A1-A3.
2022, *Gyraulus crista*, Koskeridou et al., p. 9, fig. 3, b1-b3.

Material. 116 specimens, very well preserved, of all stages of development, from the samples SmiddleDpr and S11.

Dimensions. Max. Sw 2.74 mm, Sh 1.09.

Description. Small shell, thin-walled, discoidal shape, with two and a half to three rapidly increasing whorls. The whorls are almost flattened, separated by a shallow suture at the spire, deeper suture on the body whorl. Umbilical side with wide umbilicus and apex side with a flat spire. Protoconch is almost 0.5 whorls, with microsculpture spiral lines. The P/T boundary is discernible, protoconch interrupted by a convex sharp line. Teleoconch has a smooth surface with convex thin growth lines and the thin spiral striae (can hardly be distinguished). Aperture is almost ovate. The posterior aperture touches the base of the body whorl. Aperture profile, prosocline with a convex aperture lip.

Remarks. As type species, *Armiger crista* (Linnaeus, 1758) differentiates this genus from other genera. Last whorl not embracing the penultimate whorl, but it is almost loosely attached to the upper side of the latter, for this reason peristome being continuous (Meier-Brook, 1983). Is an extant species, very widespread in many European countries, the Balkan Penninsula, Turkey, Central Anatolia region with records of it also in Canada (Glöer, 2019; Welter-Schultes, 2012). Moreover, it has been found as a fossil and as subfossil in Greece, for example from the Pliocene of Apolakkia formation (Bukowski, 1896; Willmann, 1981), the Middle Pleistocene of Megalopolis Basin (Konidaris et al., 2023), lake Lerna in NE Peloponnese (Koskeridou et al., 2022) and elsewhere, e.g., the Early Pleistocene of the Pasinler Basin, north-eastern Turkey (Vasilyan et al., 2014).

Ecology and geographic/stratigraphic distribution. Lakes, especially ponds and rich in plant ditches. Shady waters are typical environments in which *A. crista* lives. It avoids flowing waters and can be seen on aquatic plant leaves and vegetated lake margins (Glöer, 2019; Spyra and Strzelec, 2013; Welter-Schultes, 2012). In Greece *G. crista* seems to be dominant in stagnant to slow-moving freshwater environments of an ancient coastal lake called Lerna, from Peloponnese, Greece (Koskeridou et al., 2022).

It is tolerant of soft water and prefers a Ph of 5.6-9.6, while its passive dispersion qualities are good (Spyra and Strzelec, 2013; Welter-Schultes, 2012). According to Spyra and Strzelec, (2013), *A. crista* is more common in soft waters with low calcium levels and a wide Ph range. Also, the species is known for its large morphological variability according to the same authors and they recognize three types of shell shapes of *A. crista*.

Type species: *Planorbis albus* O. F. Müller, 1774

Gyraulus parvus (Say, 1817)
Pl.6, N-W.

1817, *Planorbis parvus*, Say, pl. 1, fig. 5**.**
1838, *Planorbis laevis*, Alder, p. 337.
1964, *Gyraulus laevis*, Ložek, p. 188, pl. 5, fig. 2a-c.
1983, *Gyraulus laevis*, Meier-Brook, p. 34, fig. 46, 47, 49.
1992, *Gyraulus parvus*, Gorthner, p. 165, pl. 6, fig. 1, 2.
2012, *Gyraulus laevis*, Welter-Schultes, p. 63.
2013, *Gyraulus laevis*, Vinarski and Khokhutkin, p. 92, fig. 37.
2016, *Gyraulus laevis*, Danukalova et al., p. 17, fig. 2.
2019, *Gyraulus* (*Torquis*) *leavis*, Glöer, p. 324, fig. 403.
2019, *Gyraulus* (*Torquis*) *parvus*, Glöer, p. 325, fig. 404.
2019, *Anisus* sp., Papadopoulou et al., p. 52, fig. 7, d-f.
2021, *Gyraulus laevis*, Kobe et al., p. 150, fig. 9 B1-B3.
2021, *Gyraulus parvus*, and *Gyraulus* (*Torquis*) *leavis*, Lorencová et al., p. 3, fig.1 A–D, E–F.

Material. 432 specimens, (SmiddleDpr, S11).

Dimensions. Max. diameter 3.8 mm, Max height 1.2 m, but fragments indicate that it can reach a diameter of 4-4.5 mm and a height of 1.3.

Description. Small shell thin-walled, discoidal shape. Distinguished three to three and a half whorls (could be little more), which increasing slowly. The whorls are flattened in both sides, apex side more umbilicated than the umbilical side. The outer circumference of the whorls is almost semicircular. Protoconch almost 0.5 whorls, with microsculpture of very thin parallel raised spiral lines and absence of growth lines. The teleoconch has a smooth surface, with very thin convex growth lines and a spiral stria that is almost difficult to be seen. The P/T boundary is hardly discernible. The distinction (umbilical side) can be made from the thin almost indistinguishable growth lines, that seem to shift slightly the spiral lines of the protoconch. Aperture lunate to semicircular (rarely found inside of the thickening of the walls Pl. 6, O), turns slightly to the left. Anterior aperture semicircular, on the umbilical side the outer lip is more extensive than the apex side. At the posterior aperture, the body whorl appears slightly and is covered with parietal callus. The body whorl does not increase sharply in width, and from the apertural view it appears to be slightly deflected to the apex side but not like *A. crista*.

Remarks. A full description is given by Meier-Brook, (1983) for this genus, an always planispiral shell with more or less oval aperture, it is some standard characters. This species could be confused with the genus *Planorbis*, cause has a nearly smooth shell. However, some specimens had thin spiral striae, which is a character for many species of the genus *Gyraulus* Charpentier, 1837 according to (Meier-Brook, 1983; Welter-Schultes, 2012). The species is matching with the original description for the type species *Gyraulus albus* which given by Müller (1774). Moreover, based on the studied fragments, the shell's size can reach at least 4-4.5 mm in width. Additionally, the semi-circular perimeter of whorls is also presented in *G. albus* (Müller, 1774). The broad expansion of the species, could justify its existence in the area under study, in contrast to highly endemic species, which could resemble those from distant areas. However, our specimens do not have intense decoration like *G. albus* the body whorl is not abruptly wide, and the aperture is not elliptical in shape. This species resembles more modern species, like *Gyraulus shasi* Glöer & Pešić, 2007, but this species is endemic and has been found only in the Skadar lake Basin, in Montenegro (Glöer and Pešić, 2007) and additionally our specimens are more umbilicated from the apex side. Non keeled form of *Gyraulus albidus* Radoman, 1953, is similar to our specimen according to the descriptions of Glöer, (2019) and Glöer and Pešić, (2007), but this species is endemic from lake Ohrid and the Drim river. Another similar species is *Gyraulus argaeicus* (Sturany, 1904) found only in the type locality, the Lake of Soysali village, Turkey (Glöer, 2019). It has thinner whorls and does not appear to be directly related to our species. *Gyraulus ehrenbergi* (Beck, 1837) is endemic in the lower part of the Nile River and it has 1.00 mm height (Glöer, 2019), while *Gyraulus* cf. *aegaeus* is over 1.2 mm. Another extant similar species is *Gyraulus riparius* (Westerlund, 1865) but its aperture is quite different from our species. Finally, *Gyraulus laevis* (Alder, 1838) [= *Gyraulus parvus* (Say, 1817)], is the most morphologically similar to our species and the descriptions of (Glöer et al., 2020; Meier-Brook, 1983; Welter-Schultes, 2012) are compatible. The periphery is rounded without carina, with smooth surface, spiral striae almost not visible, also general shape of shell and the roundish aperture, safely directs us to this species.

Regarding the fossil record of Greece, the morphologically closest fossil species is *Gyraulus* (*Gyraulus*) *aegaeus*, from Kos and Rhodes and reported by Willmann (1981). Description consists of a dwarf *Gyraulus* taxon with whorls strongly convex, both above and below; without spiral lines, keel formations are absent. Most likely the holotype is not a fully adult shell, thus making it quite uncertain and was rejected.

Ecology and geographic/stratigraphic distribution. According to Strong et al., (2008) the ecology of family Planorbidae usually characterises low energy temporary and permanent ponds, streams, rivers, springs, lakes. Many examples of extant *Gyraulus* spp., suggest freshwater environments (Glöer, 2019). The species lives in shallow water zones, of clean and low hydrodynamics waters bodies, in lakes and ponds rich in vegetations, while it can tolerate slightly brackish water. Especially the *Gyraulus parvus* prefer, pools and lakes, with shallow standing waters of various sizes rich in vegetation, mostly on muddy bottom, abundant (Glöer, 2019; Welter-Schultes, 2012).

Genus *Segmentina* J. Fleming, 1818

Type species: *Nautilus lacustris* [Lightfoot], 1786

Segmentina cf. *nitida* (O. F. Müller, 1774)

Pl.6, F-J.

1774, *Planorbis nitidus,* Müller, p. 163.
1964, *Segmentina nitida* (Müll.), Ložek, p. 190, pl. 5, fig. 3a-3c.
2012, *Segmentina nitida,* Welter-Schultes, p. 70.
2013, *Segmentina nitida,* Vinarski and Khokhutkin, p. 109, fig. 43, a.
2018, *Segmentina nitida,* Graham Oliver and Morgenroth, p. 285, fig. 9.
2019, *Segmentina nitida* (O.F Müller), Glöer, p. 328, fig. 407.

Material. 8 broken specimens, two and a half whorls mostly preserved (SmiddleDpr, S11)

Dimensions. Max. Sw 1.9 mm, Sh 0.6 mm.

Description. Small shell with thin-walled, discoidal shape. Two and a half, increasing rapidly canted- carinate whorls. The whorls are almost flattened from the apex side, more convex at the right and separate from a shallow suture, which covers almost 70 % of each previous whorl. Right side with a very circular small and deep umbilicus. Apex side with a submerged spire. Protoconch almost 1 whorl, smooth, with microsculpture spiral lines. The P/T boundary is not discernible. Teleoconch with a smooth glossy surface, with convex thin growth lines. Aperture is almost equilateral triangle, anterior aperture angular, at the posterior aperture the body whorl emerges. In some shells, detected a transversal septen inside the aperture.

Remarks. This species can be found throughout the temperate regions of Europe, including Greece (Glöer, 2019; Hobbs et al., 2021). Our samples contained only a poorly number of specimens which are almost broken. Fragments, indicate that it can be reach larger size from the measurements, as we report. Our descriptions in combination with the distribution of extant species, lead us to classify this taxon with some hesitation, as *S. nitida*. *Segmentina* sp., has been reported by Willmann (1981), but its bad preservation did not allow him to a more accurate identification to the species level, it is most probably the same species. It was also mentioned from the Middle Pleistocene of Megalopolis Basin (Konidaris et al., 2023).

Ecology and geographic/stratigraphic distribution. It inhabits in shallow water bodies, that are both still and permanent, having a high humic content, such rich vegetated ponds, lakes with black mud, small pools, ditches and water bodies on meadows (Glöer, 2019; Vinarski and Khokhutkin, 2013; Welter-Schultes, 2012). Periodical drought is occasionally tolerated (Welter-Schultes, 2012). Its existence might suggest a high biodiversity and conservation importance in a location (Hobbs et al., 2021).

Genus *Planorbarius* Duméril, 1805

Type species: *Helix cornea* Linnaeus, 1758

***Planorbarius* sp.**

Pl.6, K-M.

Material. 5 specimens, only broken near of protoconch (SmiddleDpr).

Dimensions. Max. diameter of the first whorl, 0.93 mm.

Description. First whorl with a maximum diameter of 0.93 mm. Protoconch almost 0.5 whorls, with microsculpture spirally arranged pits lines. P/T is almost indistinguishable, after almost 0.5 whorl of the protococh, the spirally arranged pits lines are intersected by indistinguishable growth lines. After 1 whorl, the spirally arranged pits lines close and give way to spiral raised lines. Then are intersected by relatively more straight growth lines, this microsculpture characterizes the teleoconch. Also, the fragments indicate a large shell with a deep umbilicus. No other character can be described safely.

Remarks. Taking under consideration the relatively large protoconch, that has a distinctive microsculpture of spirally arranged pits lines (Pl. 6, M), as also shown by Gorthner, (1992), Harzhauser et al., (2014), Vasileiadou et al., (2017) and parts of the fragments, that indicate a deep umbilicus, leads us to *Planorbarius* Duméril, 1805. According to Gaudry, (1862), Fuchs (1877), Glöer (2019), Wesselingh et al., (1999), Willmann (1981), Vasileiadou et al. (2014) and MolluscaBase eds. (2023), the following fossils and extant species, reported in Greece; *Planorbarius corneus* (Linnaeus, 1758), an unidentified *Planorbarius* sp., by Vasileiadou et al., (2017), *Planorbarius thiollieri* (Michaud, 1855) recorded by (Gaudry, 1862), also in the

Kozani Basin, N. Greece by Wesselingh et al., (1999), *Planorbarius arabatzis* A. Reischütz, P. L. Reischütz & W. Fischer, 2008, from Lake Prespa, *Planorbarius grandis* (Dunker, 1850), also from lake Prespa, *Planorbarius solidus* (Thomä, 1845) which mentioned by Gaudry (1862). Also reported from Megara basin by (Fuchs, 1877) the *Planorbarius cornu* (Brongniart, 1810), but this belong probably to another species, as it is an Early Miocene taxon (Harzhauser et al., 2014). Possibly our specimens belong to one of the species mentioned above, but as there were no complete shell, we therefore suggest *Planorbarius* sp., as the most plausible determination.

Ecology and geographic/stratigraphic distribution. In general contexts, Planorbidae and modern species of *Planorbarius* Duméril, 1805, e.g., *P. corneus* (Linnaeus 1758), prefer areas with rich aquatic vegetation and low energy waters (Dillon, 2000; Glöer, 2019; Welter-Schultes, 2012)**.**

Genus *Planorbis* O. F. Müller, 1773

Type species: *Helix planorbis* Linnaeus, 1758

Planorbis planorbis (Linnaeus, 1758)

Pl.6, X-b.

1758, *Helix planorbis*, Linnaeus, p. 769.
1964, *Planorbis planorbis* (L), Ložek, p. 181, pl. 4, fig. 1a-1c.
1981, *Planorbis planorbis* (L.), Willmann, p. 198, pl. 12, fig. 1.
1985, *Planorbis planorbis* (L.), Willmann, p. 300, fig. 3, x.
2010, *Planorbis planorbis* (L.), Glöer and Pešić, p. 255, fig. 8, 1.
2012, *Planorbis planorbis* (L.), Welter- Schultes, p. 69.
2016, *Planorbis planorbis* (L.), Danukalova et al., p. 14, fig. 9,7a-e, p. 17, fig.11 3a-e
2019, *Planorbis planorbis* (L.), Glöer, p. 281, fig. 352.

Material. 109 specimens, most of them broken, with a maximum diameter 4,5 mm and height 1.44 (SmiddleDpr, S11).

Dimensions. Max. diameter 4.5 mm, Max height 1.47, but fragments of this specimen (about 7 mm long) from the apex side, suggest that the diameter may reach at least 9 mm, compared to extant samples of *P. planorbis* (personal collection of the author) from Achaia, Greece.

Description. Thin-walled shell, discoidal shape. Three to three and a half slowly increasing whorls. Umbilical side flat, separated by a deep suture. Apex side with mild submersion, separate by a little deeper suture. Each whorl covers almost ¼ of each previous whorl from the umbilical side, less on the apex side, which has submerged spire. Protoconch almost with one smooth whorl, with microsculpture spiral lines. The outer perimeter of the whorls at the Basal side, a carina can be distinguished, and this becomes more evident in the third whorl. Especially below the third whorl, it looks like other similar species, and this is because the keel usually does not appear. Protoconch 0.5 whorls, microsculpture with very thin raised spiral lines, without growth lines. The raised spiral lines of the protoconch gradually weaken in the teleoconch. Teleoconch with a smooth surface and very thin growth lines. The P/T boundary is not discernible on the apex side, because both have smooth surfaces and the very thin growth lines appear very discreetly in the teleoconch. On the umbilical side, the growth lines are more distinct. Aperture lunate almost parallel to the body whorl, bends slightly to the apex side. Anterior aperture semicircular, at the umbilical side the outer lip is more extensive than the apex side. At the posterior aperture the body whorl appears slightly and is covered with a parietal callus.

Remarks. Nowadays this species is quite widespread, at least in Europe, from Greece to W. Siberia (Glöer and Pešić, 2010). In addition it has been reported in various areas as a fossil, e.g. in Kos island, Middle Pleistocene of Megalopolis Basin (Konidaris et al., 2023; Willmann, 1985, 1981). Fragments of it indicate a shell that exceeds 9 mm, thus it is separated from the smaller *Planorbis atticus* Bourguignat, 1852 (Glöer, 2019; Glöer and Pešić, 2010).

Ecology and geographic/stratigraphic distribution. Occur in stagnant and slow-moving waters, with dense vegetation and muddy substrate, or at the muddy shore areas of bigger lakes to depth of 1 meter. Also appear in muddy ponds, periodic swamps and temporarily drying flood grooves. Normally *P. planorbis* prefers smaller water bodies and intense water motions are not tolerated. It is common in shallow pools that are prone to drying out in hot weather (Glöer, 2019; Kotsakis et al., 2011; Ložek, 1964; Welter-Schultes, 2012). Relatively resistant to eutrophic conditions, salt tolerance up to 0.4 %, Ph preference 6.6-6.9, temperature optimum 19°C, and drought resistance (Glöer, 2019; Welter-Schultes, 2012).

Family Lymnaeidae Rafinesque, 1815
Subfamily Lymnaeinae Rafinesque, 1815
Genus *Lymnaea* Lamarck, 1799

Type species: *Helix stagnalis* Linnaeus, 1758

Lymnaea megarensis Gaudry in Gaudry & Fischer, 1867

Pl.6, A-D.

1867, *Limnaea megarensis*, Gaudry in Gaudry & Fischer, p. 445, pl. 61, figs 14-17.
1877, *Lymnaeus megarensis,* Fuchs, p. 12, pl. 2, fig. 36-37.
1891, *Lymnaeus* (*Acella*) *megarensis,* Oppenheim, p. 461, pl. 26, fig. 6.
1943, *Acella* (*Acella*) *megarensis,* Wenz, p. 148, fig. 10.

1981, *Lymnaea megarensis*, Willmann, pl. 12, fig. 11-15.
1985, *Lymnaea megarensis*, Willmann, p. 300, fig. 3, u.
2016, *Lymnaea* (*Lymnaea*) *megarensis*, Vinarski & Frolov, p. 6, fig. 6 a-d.
2019, *Lymnaea megarensis*, Papadopoulou et al., p. 52, fig. 7, k.

Material. 209 well preserved, but almost all of them broken at the aperture, from the samples SmiddleDpr and S11.

Dimensions. Max. Sh 13.92 mm, Sw 3.89 mm, Pl. 5. A.

Description. Medium sized shell, shape narrowly conic. Five and a half to six, very mildly convex and slowly increasing whorls are distinguished, (little faster the body whorl), separate from characteristic groove-like suture. Imperforate shell, with mildly twisted columella. The P/T boundary is not discernible, smooth protoconch, probably almost 0.7 whorls without growth lines, ends gradually to a teleoconch with a smooth surface, with more or less strongly visible growth lines. Aperture D-shaped. Aperture profile prosocline, with an almost straight apertural lip.

Remarks. The elongated conical shell, with the acute apex and the long spire, characterizes the genus *Lymnaea* (Glöer, 2019). Vinarski and Frolov, (2016) found a groove-like suture, resembling that of *L. bogatschevi* in a sample of *L. megarensis* from the Pliocene of Greece. This unique character is also found in our samples that we have been identified as *Lymnaea megarensis*. Except Pliocene deposits of Megara (Attica), this species is recorded also in the islands of Kos and Rhodes, and material from both islands resembles this of Sousaki. This is the first record of the species from the early Pleistocene in the study area.

Ecology and geographic/stratigraphic distribution. The amphibious Lymnaeidae are distributed worldwide and live in all kind of habitats, preferably in rich vegetated waters (Dillon, 2000; Glöer, 2019). Also occasionally inhabit lotic environments (Dillon, 2000). The extinct *L. megarensis* has been widespread during the Pliocene-Pleistocene. Willmann (1985) reported that *L. megarensis* was found in the upper Pliocene Gurniati Formation, which consists of fluviatile and terrestrial sediments deposited in central Kos. In this place repeatedly small, stagnant, and ephemeral waters were formed. We can therefore assume that it lived in such environments. Also known from the Pliocene-Pleistocene deposits of Megara basin recorded by Gaudry (1867) and Fuchs (1877), Ptolemaida basin (Wenz, 1943), from the Lower Pleistocene of the sedimentary basin of Sousaki (Papadopoulou et al., 2019; this study).

Subfamily Amphipepleinae Pini, 1877
Genus *Radix* Montfort, 1810

Type species: *Radix auriculatus* Montfort, 1810 [unnecessary substitute name for *Helix 55arbara55ria* Linnaeus, 1758]

***Radix* sp.**

Pl.5, E-H.

Material. 675 specimens, most of them broken (SmiddleDpr, SuperDpr, SupmostDpr, S11).

Dimensions. Measurements of larger specimen Pl. 5., E., Sh 5.54 mm, Sw 3.42, PW 2.48 mm, PH 3.97 mm.

Description. Small Shell thin-walled, globular ovoid shape. Three and a half, slightly convex increasing whorls, (faster in the body, which is almost seven times higher than the spire), separate from the deep suture. Imperforate to remotely perforate shell, with a Slit-like umbilicus, with twisted in the middle columella. The P/T boundary is not strongly discernible, distinguished by a smooth protoconch almost 0.8 whorls, and a teleoconch with a smooth surface, with more or less strongly visible growth lines. From the apex view, it is difficult to be distinguished with the naked eye or not at all can a spiral line in the middle of the winding, and two other less distinctive ones. The height of the spire can be less or more elevated. Aperture shape, D-shaped. The outer lip with the body whorl at the upper part of the aperture, creates an angle of almost 45^{o} and after that the outer lip curves downwards abruptly. The parietal wall and the columellar lip give the feeling of a sloping straight line, which is just twisted in the middle. The basal lip wide, almost semi-circular and convex. Columellar lip slightly reflected. Aperture profile sigmoid, with an almost straight to mildly convex apertural lip.

Remarks. General determination solely on shell morphology is difficult and unreliable, due to the high level of morphological variability and presence of numerous cryptic taxa in the cosmopolitan family Lymnaeidae (Aksenova et al., 2018; Pfenninger et al., 2006). Taking into consideration the distinctive morphology of the genus, by Welter-Schultes, (2012) 'the shell short, last whorl considerably enlarged' we are led to the genus *Radix*, also see diagnosis by Aksenova et al., (2018). Modern representatives of the genus, according to Glöer, (2019), exhibit in their majority a relatively large shell, with a height of 1 cm and above, in the case of mature specimens, while the largest shell we found was 5.54 mm high. This perhaps indicates that it concerns an almost immature shell or a tiny species. The second scenario indicates a possible different species, compared to modern ones. In modern Greece, the following species can be found according to Glöer (2019): *Radix 56arbara56ria* (Linnaeus, 1758), *Ampullaceana balthica* (Linnaeus, 1758), *A. lagotis* (Schrank, 1803), *A. relicta* (Poliński, 1929), and *Peregriana 56arbara* (Rossmässler, 1835) (genus names updated according to latest systematics). Comparisons to the afore mentioned species and more to those found in Europe, outside Greece, indicate some differences regarding the aperture, the height of the spire and several more, show that perhaps it concerns an old, fossilized, extinct species. In the fossil record of

Greece, in Athens recorded by Gaudry (1867), (pl. 61, fig. 24-25) the fossil species *Limnaea voisine* a species close to *L. cylindrica*, possible a wrong identification species. This species judging by the depiction of it, we observe some differences regarding the wider whorl and the higher spire, thus most probably it cannot be related with our specimens. The "*Lymnaeus*" sp. Fuchs (1877, pl. 1, fig. 5), from the region of Corinth, resembles to the genus *Radix*, however a description is not given, as most of the findings were the internal mold of the gastropods and any comparison is uncertain. The species *Corymbina 57arbara57ri* Fuchs, (1877, pl. 4, fig. 7-8),), *Lymnaeus adelinae* Cantr = *Corymbina elegans* (Cantraine, 1841) (pl. 4, fig. 1-6), also differ from *Radix* sp. The species *Lymnaea obtusissima* (Deshayes, 1838) (now belonging to the genus *Radix*) as mentioned by Fuchs (1877, p. 38, pl. 4, fig 31) from the Atalanti Basin (Central Greece), differs in the nearly circular body whorl, the wider and more oval aperture, the lower height of the spire and its larger size (compare original description by Deshayes 1838, p. 63, pl. 5, fig. 10-11). Moreover, the taxon described by Fuchs (1877) as "*Lymnaeus*" *obtusissimus* should not be considered as a synonym with *Radix obtusissima* (Deshayes, 1838) as it could be a different species. The morphological differences can also be perceived from the depictions of the authors. Deshayes' depiction shows a more inflated body whorl that come almost to the height of the apex, while in this of Fuchs, the position of the spiral you come above the body whorl. In addition, the grow lines are also different underlining different development of both shells. Lastly, *Radix calavardensis* Bukowski, (1896, pl. 8. Fig.1) is mentioned in Rhodes, and Willmann (1981) confirms its existence and depicts it as *Radix calavardensis* (Bukowski, 1896) (pl.11, fig.12). This species according to Willmann (1981) is reported also from Athens and Chios, but it is probably not the same species from Rhodes. In this work, no species from Chios was taken into consideration. According to reports by Willmann (1981), a younger specimen is depicted. The comparison shows some similarities but especially for this genus, it is uncertain. On the other hand, Bukowski (1896) described a greatly larger in size shell, that consisted of three whorls, while our shell is made of three and a half and is significantly smaller, which differentiates it from this species. In conclusion and taking in account all data that have been mentioned above, it should be considered as a distinct species, but the small number of mature specimens cannot confirm us if surely *Radix* sp., is a new species.

Ecology and geographic/stratigraphic distribution. The genus *Radix* generally indicate shallow, low-energy settings, with aquatic vegetation, e.g., *Radix auricularia* (Linnaeus, 1758) (Glöer, 2019; Neubauer et al., 2013a; Welter-Schultes, 2012)**.**

Family Acroloxidae Thiele, 1931
Genus *Acroloxus* Beck, 1838

Type species: *Patella lacustris* Linnaeus, 1758

Acroloxus lacustris (Linnaeus, 1758)

Pl.5, I-J.

1758, *Patella lacustris*, Linnaeus, p. 778.
1964, *Segmentina nitida* (Müll.), Ložek, p. 191-192, texfig. 37.
1981, *Acroloxus lacustris* (L.), Willmann, p. 198, pl. 12, fig. 9.
1985, *Acroloxus lacustris* (L.), Willmann, p. 300, fig. 3, v.
2012, *Acroloxus lacustris,* Glöer and Pešić, p. 39, fig. 15. C-d.
2012, *Acroloxus lacustris,* Welter-Schultes, p. 46.
2013, *Acroloxus lacustris,* Vinarski and Khokhutkin, p. 38, fig. 15.
2019, *Acroloxus lacustris,* Glöer, p. 337, fig. 419.
2019, *Acroloxus lacustris,* Papadopoulou et al., p. 52, fig. 7. G-H.

Material. 11 specimens most of them broken, (SmiddleDpr, S11).

Dimensions. Max. measurements of the biggest shell (pl. 7, g-h., Papadopoulou et al., 2019) is, SH 1.5 mm, SL 5.59 mm, SW 3.33.

Description. Small shell, oval limpet shaped. Aperture continuous almost elliptical. From the apex view, the anterior end is wider than the posterior end, both with semicircular margins. At the posterior, appears a small depressed conic apex, which turns left. The anterior slope is wide with a slight slope. The posterior slope has a smaller surface area and a steeper slope. To the naked eye, the shell surface is smooth with thin central growth lines. Under the SEM, the microsculpture of the protoconch has no growth lines, on the top is flat and perimetrically has only axial arranged pits lines. After that, the P/T is distinguished because the axial lines and the growth lines show a mesh surface of the teleoconch.

Remarks. Apex shifts to the left, leading us to this genus. Moreover, the morphology of the shell in combination with the dimensions of the shell and its geographical distribution, indicate *A. lacustris* (Linnaeus, 1758). A species mentioned in the Neogene of Kos & Rhodes by Willmann (1981), has been reported from the early Pleistocene of Sousaki Basin (Papadopoulou et al., 2019).

Ecology and geographic/stratigraphic distribution. *A. lacustris* is limnophilous and found in stagnant waters or rarely slowly running clean waters with well oxygenated content and always associated with macrophytes, preferring small closed ponds (Dillon, 2000; Glöer, 2019; Kotsakis et al., 2011). The Ph tolerance range is 6-8.9, is sensitive to water pollution and feeds on algae cover and microorganisms (Glöer, 2019; Welter-Schultes, 2012).

Superorder Eupulmonata Haszprunar & Huber, 1990
Family Geomitridae C.R. Boettger, 1909
Genus *Cochlicella* A. Férussac, 1821

Type species: *Helix conoidea* Draparnaud, 1801

Cochlicella cf. *conoidea* (Draparnaud, 1801)

Pl.5, K-L.

1801, *Helix conoidea*, Draparnaud, p. 69.
2012, *Cochlicella conoidea* (Draparnaud, 1801), Welter-Schultes, p. 498.

Material. 4 broken specimens (SmiddleDpr, S11).

Description. Shell conic. P/T distinct. Protoconch with 1.5 whorls, smooth, vaulted and circular without growth lines. Teleoconch smooth, with thin growth lines.

Remarks. Compared to the extant *Cochlicella conoidea* (Drap Arnaud, 1801) and *Cochlicella barbara* (Linnaeus, 1758) from Peloponnese (personal collection of the author from Peloponnese), the species has a more inflatable protoconch, resembling much to *C. conoidea*. We are not sure if this is a fossil or an extant shell, rather impossible to be extant as the samples were taken from unweathered sediments. This species was found in sandy habitats, in beaches (Welter-Schultes, 2012), but the study area is far away from the sea and its colour is similar to the other freshwater fossil gastropods that were found.

Ecology and geographic/stratigraphic distribution. In coastal vicinity on sandy and dry habitats (Welter-Schultes, 2012)**.**

5. RESULTS

5.1 Summary of the data

A total of four samples were studied, from the 21.411 collected specimens, 24 morphospecies belonging to 20 genera and 10 families were identified (Table 1). The majority of the specimens were well-preserved gastropods of all developmental stages, with predominance of juvenile stages. There was a lot of broken shells. Due to the fragile nature of the shells, some of them broke during wet sieving. Sample S11 and SmiddleDpr are closest to the base of the stratigraphic sequence, as shown in the synthetic stratigraphic column (Fig. 2., C). The samples SuperDpr and lastly SupmostDpr follow. About species richness of the studied samples of the whole fauna, Caenogastropoda is the dominant taxon with 14 species, against Heterobranchia with 9 and Neritimorpha with 1.

Table 1 Results of gastropod counts in the studied samples.

Subclass	Family	Species	Samples			
			SmiddleDpr	SuperDpr	SupmostDpr	S11
Neritimorp	Neritidae	*Theodoxus micans* (Gaudry & Fischer in Gaudry, 1867)	14	1176	2713	13
Heterobranchia	Planorbidae	*Planorbis planorbis* (Linnaeus, 1758)	81			27
		Gyraulus parvus (Say, 1817)	143	2		287
		Armiger crista (Linnaeus, 1758)	70			46
		Planorbarius sp.	5			
		Segmentina nitida (O. F. Müller, 1774)				7
	Lymnaeidae	*Lymnaea megarensis* Gaudry in Gaudry & Fischer, 1867	158	1	1	49
		Radix sp.	494	19	55	107
	Acroloxidae	*Acroloxus lacustris* (Linnaeus, 1758)	4			7
	Geomitridae	*Cochlicella ? conoidea* (Draparnaud, 1801)	4			1
Caenogastropoda	Hydrobidae	*Prososthenia cf. attica* (Fuchs, 1877)	77	588	1055	13
		Prososthenia n. sp.	12			9
		Goniochilus graecus (Wenz, 1919)	291	396	641	68
		Goniochilus sp.				2
		Pyrgula cf. *nikosi* Esu & Girotti, 2015	169	226	624	73
		Islamia n. sp.	254	4	1	189
		Graecamnicola n. sp.	16	3	5	9
		Bania n. sp.	44	81	27	18
	Bithynidae	*Bithynia candiota* Westerlund, 1886	258	12	18	130
	Viviparidae	*Viviparus* sp.	46	10	31	9
	Melanopsidae	*Melanopsis* sp.	1912	107	8	380
		Melanopsis bittneri ? Fuchs, 1877	200	4039	1813	29
		Melanopsis cf. *gearyae* Neubauer, Harzhauser, Georgopoulou, Mandic & Kroh, 2014		240	1204	
	Thiaridae	*Melanoides curvicosta* (Deshayes, 1835)	64	207	300	15

The richest family in number of species are Hydrobiidae with 8 species (*Prososthenia* cf. *attica*, *Prososthenia* n. sp., *Goniochilus graecus*, ?*Goniochilus* sp., *Pyrgula* cf. *nikosi*, *Islamia* n. sp., *Graecamnicola* n. sp., *Bania* n. sp.), followed by Planorbidae with 5 species (*Planorbis planorbis*, *Gyraulus parvus*, *Armiger crista*, *Planorbarius* sp., *Segmentina nitida*, then Melanopsidae with 3 species (*Melanopsis* sp., *Melanopsis* cf. *bittneri*, *Melanopsis* cf. *gearyae*), the Lymnaeidae with two species (*Lymnaea megarensis*, *Radix* sp.), while the rest of the families are represented by one species each; Neritidae (*Theodoxus micans*), Acroloxidae (*Acroloxus lacustris*), Geomitridae (*Cochlicella* cf. *conoidea*), Bithyniidae (*Bithynia candiota*), Viviparidae (*Viviparus* sp.), Thiarinae (*Melanoides curvicosta*).

Below in (Fig. 3), they are presented with pie charts, the relative abundance per family. The most abundant and stable family in number of shells, is Melanopsidae in all samples. The rest of the other families varies in the number of individuals and also in terms of their presence or absence in the samples. In (Table 2) the appendix of images, presents the percentages of each species, that have been used for the statistical analysis. Further information per sample is presented below.

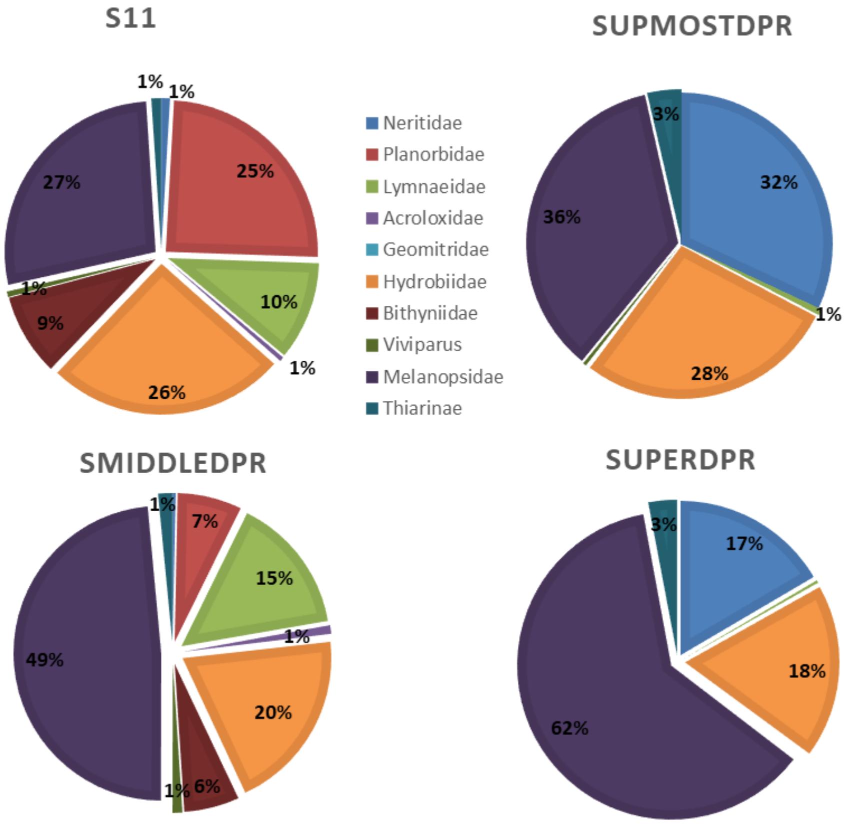


Fig. 3 Number of shells per family for the four samples.

Sample S11: Collected 1488 specimens, with number of species per Subclass to be (Neritimorpha 1, Heterobranchia 8, Caenogastropoda 13). The biophase includes (*Theodoxus micans*, *Planorbis planorbis*, *Gyraulus parvus*, *Armiger crista*, *Segmentina nitida*, *Lymnaea megarensis*, *Radix* sp., *Acroloxus lacustris*, *Cochlicella* cf. *conoidea*, *Prososthenia* cf. *attica*, *Prososthenia* n. sp., *Goniochilus graecus*, *Pyrgula* cf. *nikosi*, *Islamia* n. sp., *Graecamnicola* n. sp., *Bania* n. sp.,?*Goniochilus* sp., *Bithynia candiota*, *Viviparus* sp., *Melanopsis* sp., *Melanopsis* cf. *bittneri*, *Melanoides curvicosta*). A bar graph is given below (Fig. 4) with percentage of abundance per species in the sample, also see (Tab 2). *Melanopsis* sp., *Gyraulus parvus* are the most abundance species.

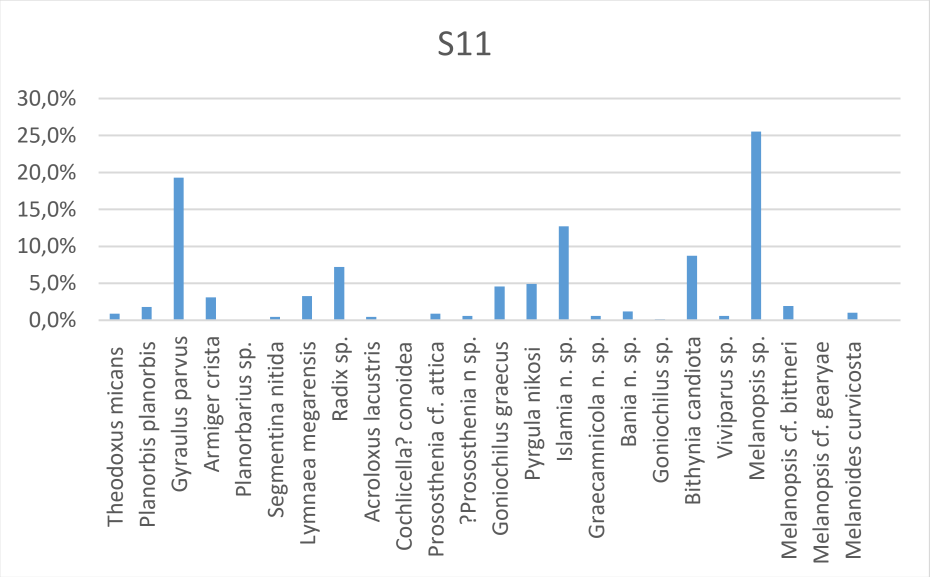


Fig. 4 The percentage of abundance per species on sample S11.

Sample SmiddleDpr: Collected 4316 specimens, with number of species per Subclass to be (Neritimorpha 1, Heterobranchia 8, Caenogastropoda 12). The biophase consists of (*Theodoxus micans*, *Planorbis planorbis*, *Gyraulus parvus*, *Armiger crista*, *Planorbarius* sp., *Segmentina nitida*, *Lymnaea megarensis*, *Radix* sp., *Acroloxus lacustris*, *Cochlicella* cf. *conoidea*, *Prososthenia* cf. *attica*, *Prososthenia* n. sp., *Goniochilus graecus*, *Pyrgula* cf. *nikosi*, *Islamia* n. sp., *Graecamnicola* n. sp., *Bania* n. sp., *Bithynia candiota*, *Viviparus* sp., *Melanopsis* sp., *Melanopsis* cf. *bittneri*, *Melanoides curvicosta*. A bar graph is given below (Fig. 5), the percentage of abundance per species in the sample are given, also see (Tab 2). The *Melanopsis* sp., *Radix* sp., are the most abundance species.

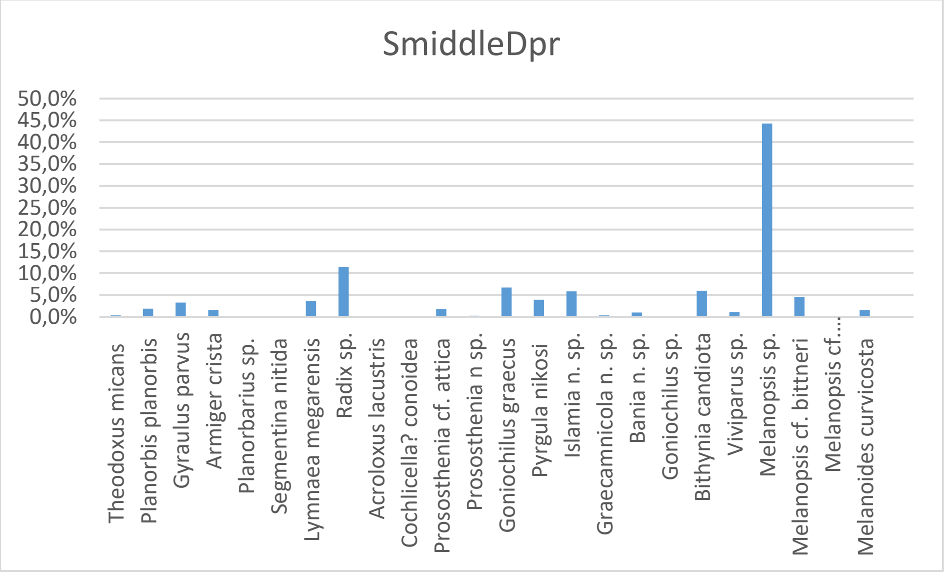


Fig. 5 The percentage of abundance per species in the sample SmiddleDpr.

Sample SuperDpr: Collected 7111 specimens, with number of species per Subclass to be (Neritimorpha 1, Heterobranchia 3, Caenogastropoda 12). The biophase consists of (*Theodoxus micans*, *Gyraulus parvus*, *Lymnaea megarensis*, *Radix* sp., *Prososthenia* cf. *attica*, *Goniochilus graecus*, *Pyrgula* cf. *nikosi*, *Islamia* n. sp., *Graecamnicola* n. sp., *Bania* n. sp., *Bithynia candiota*, *Viviparus* sp., *Melanopsis* sp., *Melanopsis* cf. *bittneri*, *Melanopsis* cf. *gearyae*, *Melanoides curvicosta*. A bar graph is given below (Fig. 6) with percentage of abundance per species in the sample, also see (Tab 2). *Melanopsis* cf. *bittneri*., *Theodoxus micans* are the most abundance species.

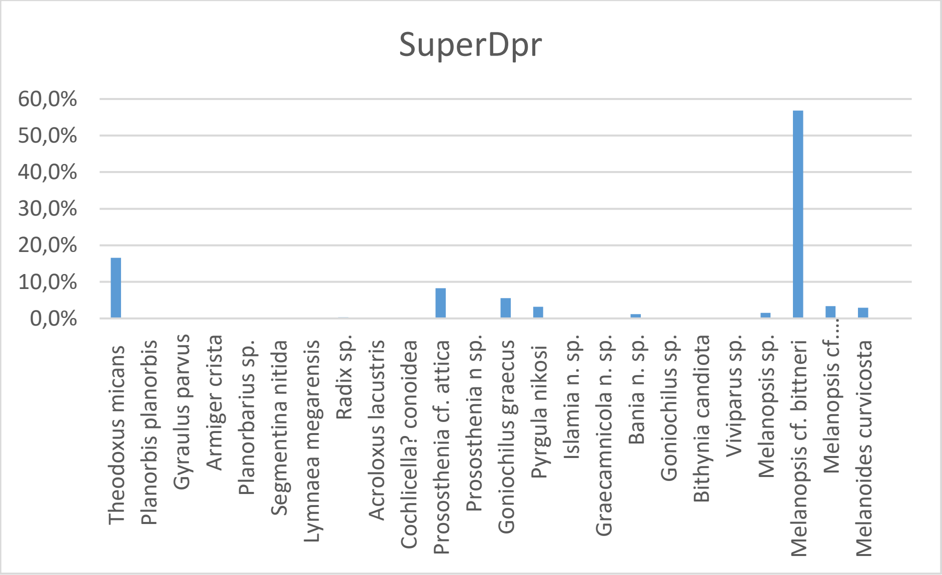


Fig. 6 The percent of abundance per species in the sample SuperDpr.

Sample SupmostDpr: Collected 8497 specimens, with number of species per Subclass to be (Neritimorpha 1, Heterobranchia 2, Caenogastropoda 13). The biophase consists of (*Theodoxus micans*, *Lymnaea megarensis*, *Radix* sp., *Prososthenia* cf. *attica*, *Goniochilus graecus*, *Pyrgula* cf. *nikosi*, *Islamia* n. sp., *Graecamnicola* n. sp., *Bania* n. sp., *Bithynia candiota*, *Viviparus* sp., *Melanopsis* sp., *Melanopsis* cf. *bittneri*, *Melanopsis* cf. *gearyae*, *Melanoides curvicosta*). A bar graph is given below (Fig. 7) with percentage of abundance per species in the sample, also see (Tab 2). The *Theodoxus micans* and *Melanopsis* cf. *bittneri*, are the most abundance species.

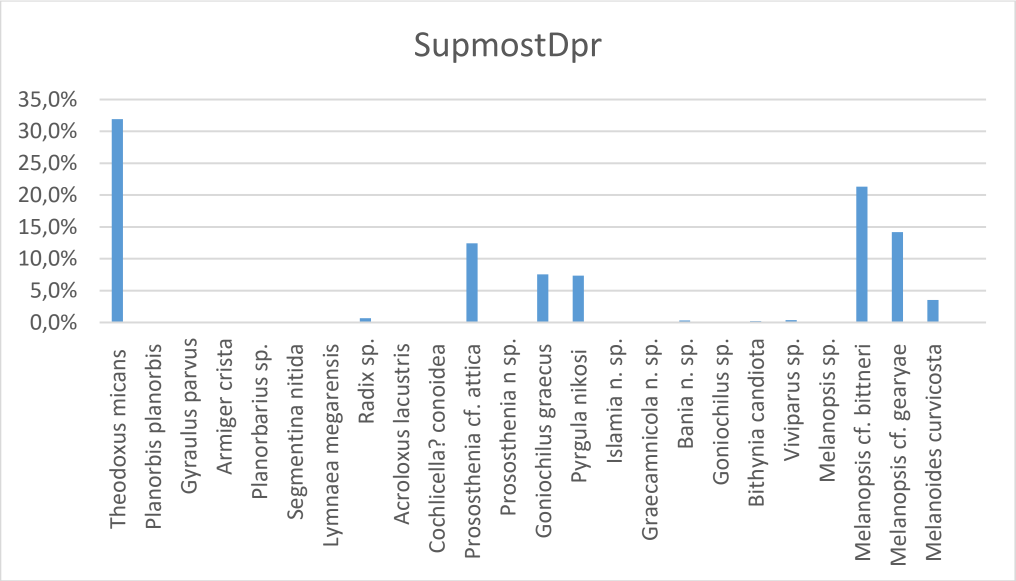


Fig. 7 The percentage of abundance per species in the sample SupmostDpr.

5.2 Statistical analysis

According to the Individual Rarefaction diagram (Fig. 8), which compares the number of taxa in samples of different sizes, the flattening of the diagram curves for the four samples (S11, SmiddleDpr, SuperDpr & SupmostDpr) has already reached approximately 300 to 500 specimens, exceeding so, in all samples, the limit of statistical safety and allowing further analysis, as we do not expect any greater increase in species numbers in the samples. This is also evident from the material of the samples, where 3 species that were found, were not well preserved or statistically safe, due to the low number of individuals per species. As a result, these species were not finally recognized at the species level and, statistically, were not considered in the interpretations of the palaeoenvironment. Specifically, ?*Goniochilus* sp. *Cochlicella* cf. *conoidea*, *Planorbarius* sp., probably were transferred from another palaeoenvironment for example a river, because both the number of individuals was low and in poorly preserved condition (broken and usually the periostracum was worn). *Viviparus* sp., *Radix* sp., are considered in situ but the fragile nature of their shells, did not allow the retention of mature individuals and so we did not end up determining them at the species level. Finally, it is important to note that some species may be underrepresented, as smaller shells like some Hydrobiidae could have a higher number of individuals overall in the samples. As the material was monotonous after a point, it was considered that the palaeoecological interpretation would not change with further collection of specimens. For this reason, for the samples SuperDpr & SupmostDpr from the material of the 63 μm sieve, our study was based on a part of the sample, after it was firstly split in quarters.

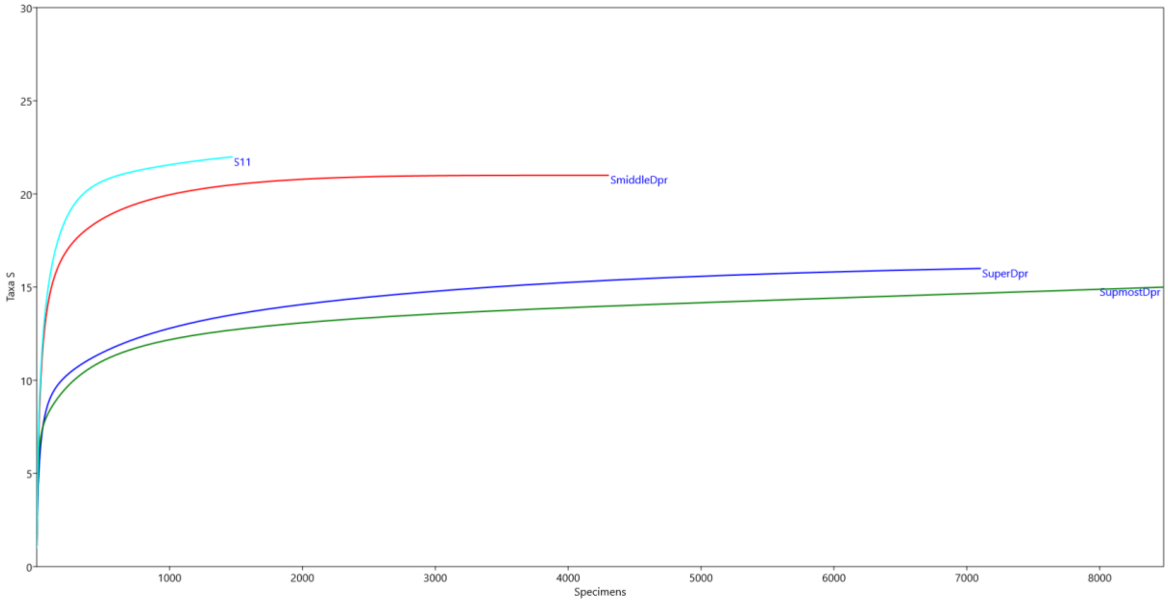


Fig. 8 Individual Rarefaction for the four samples.

Hierarchal cluster analysis grouped the samples into two groups based on species abundance. Group 1 includes the samples (S11, SmiddleDpr) which are the two successive lower layers as distinguished in the synthetic stratigraphic column (Fig. 2, C). The second group includes the Samples (SuperDpr, SupmostDpr) which successively follow the strata of Group 1.

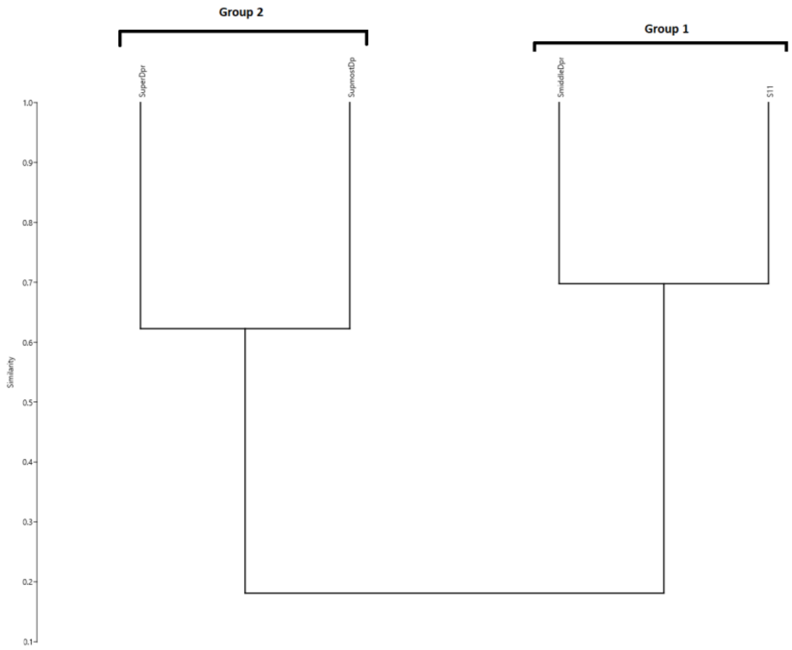


Fig. 9 Hierarchal cluster analysis based on Gastropod abundances. Used UPGMA algorithm and Bray-Curtis similarity index.

The Correspondence analysis (Fig. 10), also through the Gastropod abundances separate the samples in the same Groups like Hierarchical cluster analysis. Group 1 is more affected by *Gyraulus parvus*, *Lymnaea megarensis*, *Melanopsis* sp., *Bithynia cadiota*, *Radix* sp., while the Group 2, seems to be more affected by the abundance of *Theodoxus micans*, *Melanopsis* cf. *bittneri*.

The ecological interpretation, together with the statistical analysis data, can be found in subsection 6.2.

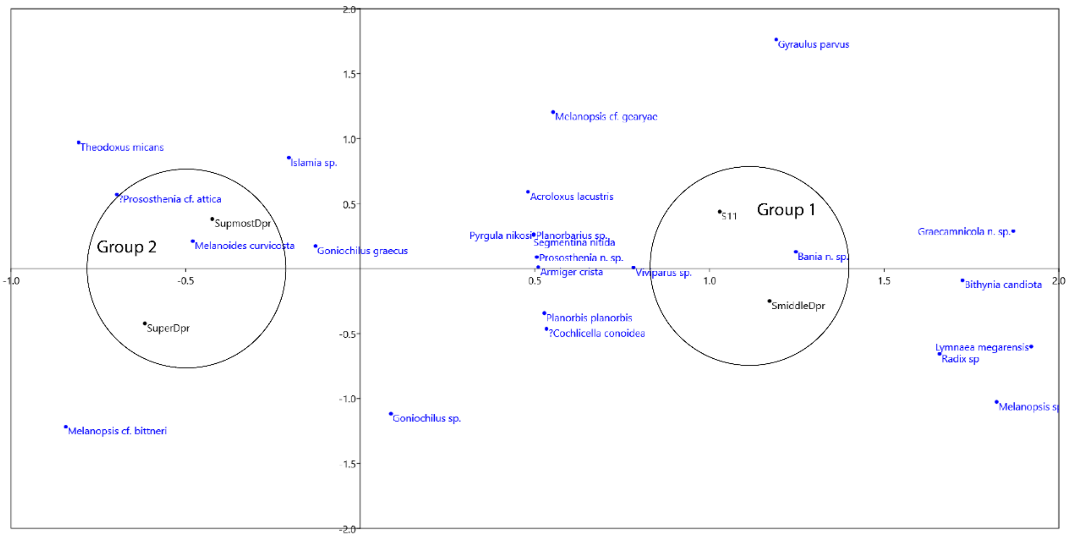


Fig. 10 Correspondence analysis based on Gastropod abundances.

6. DISCUSSION

6.1 Endemicity and palaeobiogeography of the malacofauna

The mollusk fauna of Sousaki sedimentary basin, was represented by 24 species, of which 14 are extinct taxa [(*Prososthenia* cf. *attica* (Fuchs, 1877), ?*Prososthenia* n.sp., *Goniochilus graecus* (Wenz, 1919), ?*Goniochilus* sp., *Pyrgula* cf. *nikosi*, Esu & Girotti, 2015, *Islamia* n. sp., *Graecamnicola* n. sp., *Bania* n. sp., *Theodoxus micans* (Gaudry & Fischer in Gaudry, 1867), *Lymnaea megarensis* Gaudry in Gaudry & Fischer, 1867, *Melanopsis* cf. *bittneri* Fuchs, 1877, *Melanopsis* sp., *Melanopsis* cf. *gearyae*, *Melanoides curvicosta* (Deshayes, 1835)], i.e., (60 %) of the total fauna. Most belong to extinct genera or do not coincide morphologically with modern species. Exceptions were the *Lymnaea megarensis* which belongs to Hygrophila, and one from Neritimorpha, all other extinct species belong to Caenogastropoda.

More specifically, regarding the extinct species identified in the Sousaki basin, *Prososthenia* cf. *attica*, *Goniochilus graecus*, *Pyrgula* cf. *nikosi*, *Theodoxus micans*, *Lymnaea megarensis*, *Melanopsis* cf. *bittneri*, *Melanoides curvicosta*, were not endemic to the basin of Sousaki, as they have been found in other locations. However, most of them were limited to the continental part of Greece such as Megara basin, Atalanti basin, and Achaia, except *Melanoides curvicosta*, *Lymnaea megarensis*, which had larger distribution, including the Greek islands of Kos and Rhodos (Esu and Girotti, 2015a; Fuchs, 1877; Gaudry, 1862; Harzhauser et al., 2015; Koskeridou and Ioakim, 2009; Neubauer, 2016b; T. A. Neubauer et al., 2014; Schütt, 1986; Vinarski and Frolov, 2016; Willmann, 1981, 1985). Was not observed in the study area, same species from the families Melanopsidae and Hydrobidae, with those that have been found in the eastern Aegean islands such as Rhodes and Kos (Bukowski, 1896; G. von Bukowski, 1893; Willmann, 1985, 1981).

Moreover, *Islamia* n. sp., *Bania* n. sp.,?*Prososthenia* n. sp., *Graecamnicola* n. sp., could possibly be new species, as these morphotypes were not detected in the literature. In the family Hydrobiidae, we observed a species of the extinct genus *Graecamnicola*. To date, species of this genus [*Graecamnicola euomphalus* (T. Fuchs, 1877), *Graecamnicola graeca* (T. Fuchs, 1877)], have been known only from the late to middle Pleistocene sediments of the Atalanti Basin (Fuchs, 1877; Koskeridou and Ioakim, 2009; Willmann, 1981), and they have been recorded for the first time in the study area. The fossil species of the genus *Islamia* and *Bania* are reported in the Greek fossil record for the second time. The first record was *Islamia corinthica* Esu & Girotti from the late early Pleistocene of Achaia (Esu and Girotti, 2015a) and ?*Bania* sp., from Miocene of Lesvos island (Vasileiadou et al., 2017). Today, the genus *Islamia* has been found in the following regions: Iberian Peninsula, Croatia, Bosnia and Herzegovina, Greece, Italy, Western Europe and Turkey, and

Islamia spp., are usually endemic to their locality type (Glöer et al., 2020; Yildirim et al., 2017). The extinct genera *Bania* and especially *Prososthenia* are represented by several endemic species in European Neogene, e.g, Dinaride Lake System (Neubauer et al., 2013b). Taking into account the information above, the species (*Islamia* n. sp., *Bania* n. sp.,?*Prososthenia* n. sp., *Graecamnicola* n. sp), could be endemic of the wider study area.

The other seven species, *Acroloxus lacustris* (Linnaeus, 1758), *Cochlicella* cf. *conoidea* (Draparnaud, 1801), *Gyraulus parvus* (Say, 1817), *Armiger crista* (Linnaeus, 1758), *Segmentina nitida* (O. F. Müller, 1774), *Planorbis planorbis* (Linnaeus, 1758), *Bithynia candiota* Westerlund, 1886, are extinct and quite widespread today, especially in the European region (Glöer, 2019; Welter-Schultes, 2012). Also, many of them was widespread in many Pliocene - Pleistocene localities, such as *Acroloxus lacustris*, *Armiger crista*, *Planorbis planorbis*, *Segmentina nitida*, and was common both in the mainland of Greece and the islands, like Kos and Rhodes (Bukowski, 1896; Konidaris et al., 2023; Koskeridou et al., 2022; Willmann, 1985, 1981). Of course they were not limited only in Greece during the Pleistocene, but like the *Armiger crista*, which has been found in the Pleistocene of Turkey (Vasilyan et al., 2014), they have been found in many other locations as well. If we exclude from the mollusk fauna of Sousaki, the extinct *Lymnaea megarensis* and the extinct *Bithynia candiota*, and *Cochlicella* cf. *conoidea* which is a terrestrial species, all other extinct species are widespread and belong to Hygrophila. The *Viviparus* sp., *Planorbarius* sp., *Radix* sp., are taxonomically uncertain species and were not included in the overall conclusion.

Summarizing, based on the data we have, we observe that the mollusk fauna of the Sousaki basin, consisted of an assemblage of extinct Caenogastropoda. The majority of them, were limited to the continental part of Greece, with possible endemics to Sousaki basin, *Islamia* n. sp., *Bania* n. sp.,?*Prososthenia* n. sp., *Graecamnicola* n. sp. The exception is the probably parthenogenetic, *Melanoides curvicosta*, which has been found also outside the Greece, e.g., Italy (Harzhauser et al., 2015). The only representative from Neritimorpha was *Theodoxus micans*, with first record being from the Pliocene deposits of Megara basin by Gaudry, (1867), that existed at least until the late Early Pleistocene (Esu and Girotti, 2015a). Also it has been found from the Pliocene-Pleistocene deposits of the Magoula-Karatoulas basin (Pyrgos, Peloponnesus) (Sinekoglou et al., 2018), Early Pleistocene Basin of Atalanti (Koskeridou and Ioakim, 2009) and Cythera (Papp, 1947). And this seems to have been limited to the continental of Greece, but probably had a larger spread. In contrast, Hygrophila that were found in the Sousaki basin, still live today and are quite widespread, for example in Europe. The only exception is the large species of *Lymnaea megarensis*, which has extinct but was widespread during the Pliocene-Pleistocene, at least in the geographical part of the eastern Mediterranean. Kos, Megara, Ptolemaida, Sousaki, are some of the locations it was found (Gaudry, 1862;

Papadopoulou et al., 2019; Wenz, 1943; Willmann, 1985, 1981). According to Neubauer et al. (2015), in the European region, in the Pleistocene, the successive decline in species richness coincided with global cooling. Large systems with high diversity and endemism disappeared at the end of the Pleistocene, including the lakes of Dacia, Slavonia and Transylvania. The former major hotspots disappeared and were replaced by a scattering of smaller foci, such as Lake Bresse in France, Lake Tiberino in Italy and Lake Kos in Greece. Such a small foci could also be the area of Sousaki. The area was a wetland that allowed species to survive. The local tectonic factor in the area is known and contributed to the creation of suitable habitats such as the tectonic volcanic lake of Sousaki (Papadopoulou et al., 2019). However, sedimentation prevailed, and habitats disappeared resulting in the extinction of this mollusc fauna.

As inferred from the general ecology of freshwater gastropods (Brown and Lydeard, 2010; Dillon, 2000; Frogley and Preece, 2004) the proportion of extinct Caenogastropoda against the majority of living Hgrophyla, is in a sense justified due to their lifestyle, sexual strategy and the habitats that they live in. Maybe it's not a coincidence that the only parthenogenetic species found in the area, *Melanoides curvicosta*, had the greatest spread, in contrast to the other Caenogastropoda found, which in their majority have male and female individuals and cannot be favored in a random passive their dispersion. The hermaphrodites Hygrophila of this work, that still live today, are quite small and easier to passively transport and occupy ecological niches that are more susceptible to environmental change. Also they are quite common in many Pleistocene locations in the Greek area. In Greece according to Esu and Girotti, (2015), during the Quaternary, changes in palaeogeography and palaeobiogeography were brought by Crustal Uplift and sea level oscillations due to climate changes, particularly in tectonically active coastal areas. The authors also state that flatlands may experience very widespread coastal withdrawal due to glacial sea level reductions, which promotes the creation of more or less broad non-marine sedimentary basins that can remain isolated in the event of tectonic uplift. This process really seems quite important in the case of Greece, which is surrounded by the Mediterranean, where successive isolated basins could be potentially important habitats for freshwater gastropods during the Pleistocene. Evaluation of the effect of this factor on the evolution of freshwater gastropods needs study.

6.2 Palaeoenvironmental analysis

The studied samples, dominated by the genus *Melanopsis* although it's representatives, *Melanopsis* sp. *Melanopsis* cf. *bittneri*, *Melanopsis* cf. *gearyae* are extinct, therefore their ecology is unknown. In general, members of the genus live in a plethora of freshwater environments, such as freshwater rivers, ponds, springs, and consequently stable water bodies are needed, while they can tolerate both brackish and high temperature conditions (Neubauer et al., 2013a).

Two association groups were recognized through statistical analysis (Fig. 9, 10), based on the relative abundances of the species. Group 1 includes S11, SmiddleDpr which are closer to the base of the stratigraphic sequence (Fig. 2) and are characterized by a high number of species 21-22 and a high presence of Pulmonata, with percentages of 35.62 % and 22.62 % respectively. The most abundant Pulmonata are the *Radix* sp. with 7.19 % - 11.44 %, *Gyraulus parvus* 3.31 % - 19.29 %, *Lymnaea megarensis* 3.29 % - 3.66 %, and which indicate shallow, low-energy settings with rich vegetated waters (Dillon, 2000; Neubauer et al., 2013a; Willmann, 1981).

The presence of modern Pulmonata species gives us a more detailed interpretation of the environment. Specifically, both samples show well-preserved extant Pulmonata, *Gyraulus parvus*, *Planorbis planorbis*, *Armiger crista*, *Segmentina nitida*, *Acroloxus lacustris* with a total percentage of almost 8-25 %. They prefer to live in lakes, especially ponds on shallow and slow-moving waters, rich in vegatation on muddy substrates. Most of these species tolerate short periodical drought, with a salt tolerance up to 0.4 %, pH preference 6.6-6.9, and optimum temperature 19 ℃ (Dillon, 2000; Glöer, 2019; Koskeridou et al., 2022; Kotsakis et al., 2011; Ložek, 1964; Spyra and Strzelec, 2013; Vinarski and Khokhutkin, 2013; Welter-Schultes, 2012). Also, the extinct amphibious *L. megarensis* has been found in similar environments by Willmann (1981; 1985) in the upper Pliocene of Gurniati Formation, which consists of fluviatile and terrestrial sediments, which were deposited in central Kos. In this place repeatedly small, stagnant, and ephemeral waters were formed. The only living Caenogastropoda that is in this association Group 1, in a percentage of 8.7-6 % against the association group 2, that did not exceed 1 %, and can give us with greater safety ecological information is *Bithynia candiota.* These freshwater gastropods are, grazing, e.g., over macrophytes or on hard substrates, or filter feeding with detritus from the water. Could be buried in the mud during winter (Dillon, 2000; Glöer et al., 2010, 2007). The *Hydrobiidae* also take part in smaller amounts, but the only one that can be conclude out is that Hydrobiidae, e.g., *Prosothenia* spp., likely they preferred low-energy, shallow freshwater lakes and ponds (Neubauer et al., 2013a). However, what we can say with certainty is that Hydrobiidae and Melanopsidae needed stable water bodies (Dillon, 2000; Neubauer et al., 2013a).

In contrast Group 2 included the samples SuperDpr, SupmostDpr which succeed Group 1. They are characterized by a lower number of 16 taxa in total, the Pulmonata are almost absent and their place was occupied by the species *T. micans* (Neubauer et al., 2013a).

The genus *Theodoxus* occurs on freshwater to mesohaline aquatic environments and possibly it is suggestive of high quality water (Alhejoj et al., 2017; Bandel, 2008; Glöer, 2019; Sands et al., 2020). They live in the littoral zone of lakes, but also in rivers and canals (Glöer, 2019). Animals are found adhering to stones, as well as under stones, in depths of up to 6 meters (Welter-Schultes, 2012). Feeding with algae, detritus and preferable Diatomeae (Dillon, 2000; Glöer, 2019). Due to the lack of jaw, to digest its meal, such as Diatoms, *Theodoxus* requires rough surfaces, hence a rocky substrate is required (Glöer, 2019; Welter-Schultes, 2012). *T. micans*, also has been found in the Pliocene to Pleistocene basin of Magoula- Karatoulas (Pyrgos, Peloponnese), in a brackish environment according to Sinekoglou et al. (2018). Its increase compared to Pulmonata from Group 1 is not entirely clear. The reason could be the increase in the hydrodynamicity of water, e.g., supply of water from a river, it is known that it is not tolerated by the Pulmonata of this work, such as the *P. planorbis.* Another reason may be the chemical changes in the water due to evaporation, as both *Melanopsis* and *Theodoxus micans* can tolerate more brackish waters. On the other hand stratigraphically, according to (Papadopoulou et al., 2019), we have the appearance of diatom layers almost above the studied samples (Fig.2, C), e.g., due to SiO2 supply from some springs, as there was a history of volcanism in the area due to the volcano of Sousaki. An increase in this component could trigger the growth of diatoms and consequently the increased presence of *Theodoxus*, which fed on them (Dillon, 2000; Glöer, 2019). The presence of springs in the area cannot be ruled out, as several species of Hydrobiidae today live in springs such as the like *Islamia sulfurea* from Italy, are able to live also in sulfidic waters, which are toxic to most animals (Bodon and Cianfanelli, 2012). However, the most abundant genus from the family Hydrobiidae in this samples, is the *Prososthenia,* with 8.3 - 12.4 %. According to Neubauer et al., (2013), interpretations assign it to shallow freshwater lakes and ponds with low-energy regimes and requiring stable water-bodies. General, most abundant are Melanopsidae with 50 - 60 %, and the only thing we can say for sure is that stable water bodies are needed.

The Lake of Sousaki according to Papadopoulou et al., (2019), was a tectonic lake, with a volcanic origin basement in the early stages. As can be inferred from the gastropods, it was indeed a depositional lake environment. Group 1 includes the initial stages of development of the lake as it consists of the older samples, S11, and the little younger SmiddleDpr, which presents a similar ecology. Possibly these samples indicate the littoral zone of the lake. In any case, we do not know full extent of this Paleoenvironment. Dominated by rich vegetation with shallow, slow flowing fresh waters and a high presence of Pulmonata and Melanopsis. The waters were probably fed by springs or a river system.

The samples SuperDpr and SupmostDpr follow stratigraphically, which make up group 2, both samples, suggesting similar ecologies. *Theodoxus micans, Melanopsis* spp., *Prososthenia gregaria*? begin to prevail at this level, probably due to a change in the hydrodynamics of this system, e.g., an increase of water supply from the river systems due to the tectonic regime or change in the chemical composition of the water through springs or both. As mentioned by Papadopoulou et al., (2019), this fauna survived in the overlaying strata as well, but it was in the form of moulds and did not allow the systematic taxonomy to the species level, but it has been clear that the assemblage was still dominated by *Theodoxus* and *Melanopsis*. The end of the stratigraphic sequence and mollusc faunal assemblages is marked by the deposition of a conglomerate layer. This palaeofauna eventually disappeared from the study area due to the collapse of the ecosystem after the loss of this freshwater ecosystem.

6.3 Research restrictions and future work

For this work, the inability to visit and study corresponding museum material, resulted to non-identification or non-confirmation of *Radix* sp., *Melanopsis* sp., and *Prososthenia* cf. *attica* respectively. Especially the family Melanopsidae, Lymnaeidae, is characterized by morphological plasticity. This reason had as a possible result, incorrect taxonomic estimates by previous researchers. Should constitute a more systematic work for the future, as we have identified bibliographically incomplete or incorrect identifications. For example, Theodoxus, works like Bukowski, (1896) and Fuchs, (1877) and does not include operculums, which are very important taxonomic elements for this genus Glöer, (2019).

Another issue that arose, is the high number of fragments in some fragile species such as Viviparus sp. Probably caused during the wet sieving process, has led to inadequate identification of individuals at species level and for these species additional sampling is proposed for the future. A larger and denser sampling also could be able to provide palaeogeographical data of these gastropods and data of ecophenotypic variation, if the geological record allows it.

This research is a traditional taxonomic study which, although not wrong, could be enriched with techniques, like geometric morphometrics method, to study the shape variability of gastropods. However, more comparative studies based on material from the region need to be conducted in the future.

Despite the research restrictions and the extent of sampling, because of the complexity of the tectonic and the natural conservation of the fossils, we provide the first complete record of the freshwater fauna of Sousaki basin, Ag. Theodoroi, Greece. This is the first step to a more detailed review that needs to be conducted. This fauna provided new data, for the chronological gap between the faunas of the upper Pliocene, for example, the Megara basin, and younger ones, like the late Early Pleistocene non-marine molluscan fauna from the Synania Formation (Achaia), from continental Greece. Further study will be able to give information about the existing relations of the fauna of Sousaki and other known locations like the Atalanti basin. Some similarities observed in some species from the basin of Sousaki, with some older species of the continental trunk of the Helladic area, perhaps further studies will provide new data regarding their phylogeny. This could also contribute to a better understanding of the evolutionary trends and their adaptation to the environment, helping to better understand them and the contemporary representatives of this endangered group of organisms, like the genus *Islamia*.

Finally, it would be important after highlighting it, to protect such geological sections. The deposition of small area deposits, such as small Pleistocene freshwater basins provide important data, which can be easily lost, especially from human intervention.

7. CONCLUSIONS

1. The study area demonstrated an interesting composition of Gastropods. This allowed us to extract ecological information about the fossil taxa, which lived in a freshwater lake with rich aquatic vegetation. This lake, in its initial stages, was probably dominated by slow-flowing water, while later, it had an increased supply of water, probably from river systems.
2. The volcanic basement of the lake does not seem to have negatively affected the distribution of gastropods, but was inhabited by at least 23 species of gastropods, if we exclude *Cochlicella* cf. *conoidea*, which has been transferred from a terrestrial environment.
3. The molluscan fauna of the sedimentary basin of Sousaki overall, bears more similarities with Atalanti and Megara Basins and Achaia from the Pleistocene deposits. Less than the islands of Kos, Rhodes, in terms of species of the families Melanopsidae, Hydrobiidae.
4. Most diverse family was the Hydrobiidae, with eight species, of which, *Islamia* n. sp., *Bania* n. sp., *Prososthenia* n. sp., *Graecamnicola* n. sp., could be new for the science.
5. The *Bania* n. sp., represent the chronologically youngest species of the genus (Lower Pleistocene).
6. The reported species of the genera *Islamia* and *Bania* are the second species of the genera reported in the Greek fossil record. Also, these genera, are recorded for the first time in the study area.
7. Sousaki basin hosted a high number of invertebrate species and can be characterized as an important wetland of the Lower Pleistocene.
8. The existence of genera that live even today, especially the threatened ones like those of the genus *Islamia*, offered a new dimension to the understanding of the evolution of modern fresh water gastropods in Greece.
9. The studied samples contained extant and extinct species. The large percentage of the extinct species (60 %) indicates a lower Pleistocene age (e.g *Melanopsis* cf. *bittneri*, *Pyrgula* cf. *nikosi*).
10. Most of Caenogastropoda, of this study, appeared to be restricted at the continental part of Greece, while most of Hygrophila in this work, were widespread during the Pleistocene in many parts of Europe and on islands, including the Aegean Islands of Kos and Rhodes.

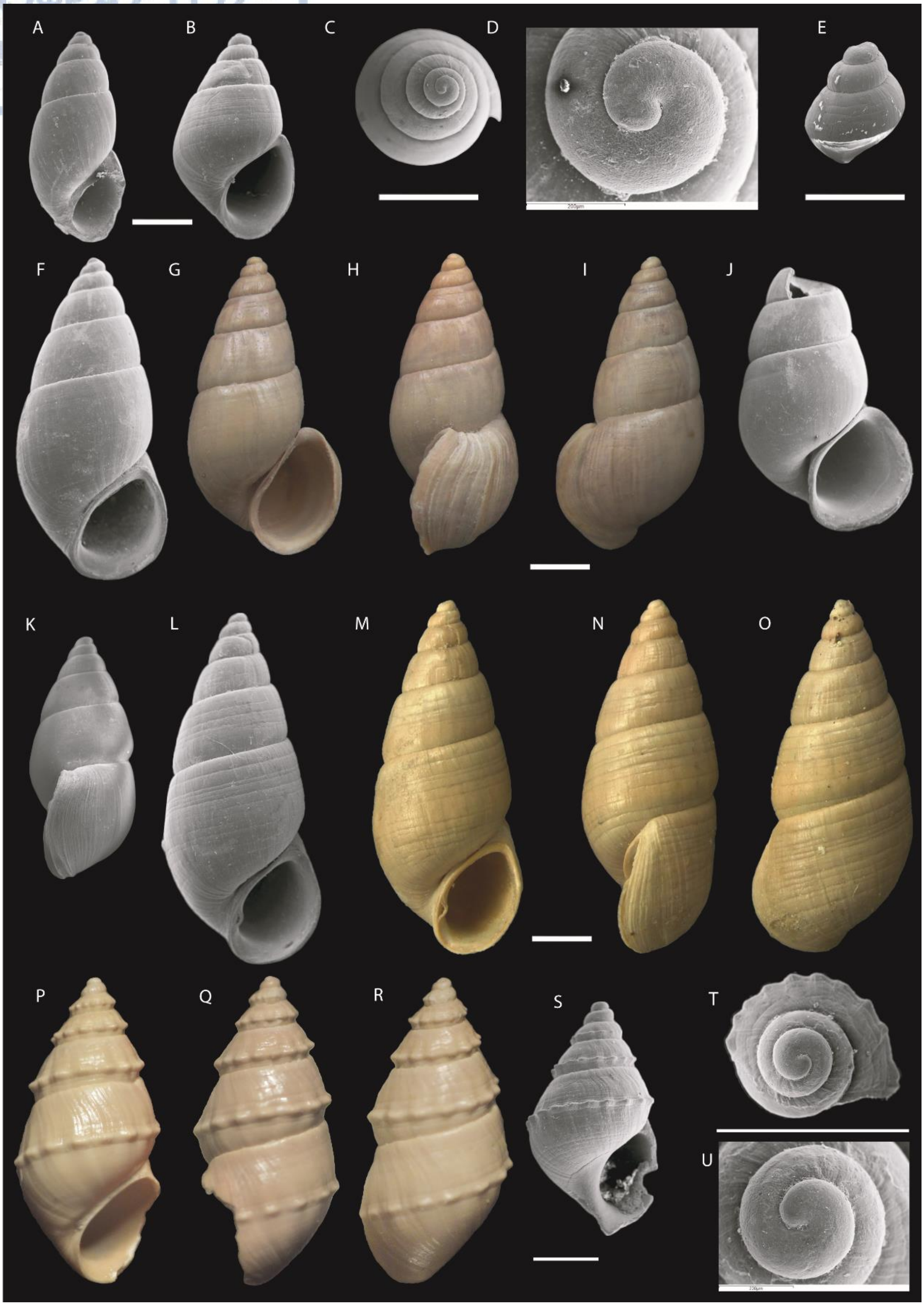
11. The studied paleofauna eventually disappeared from the study area, due to the collapse of the ecosystem after the loss of this freshwater environment.

ACKNOWLEDGMENTS

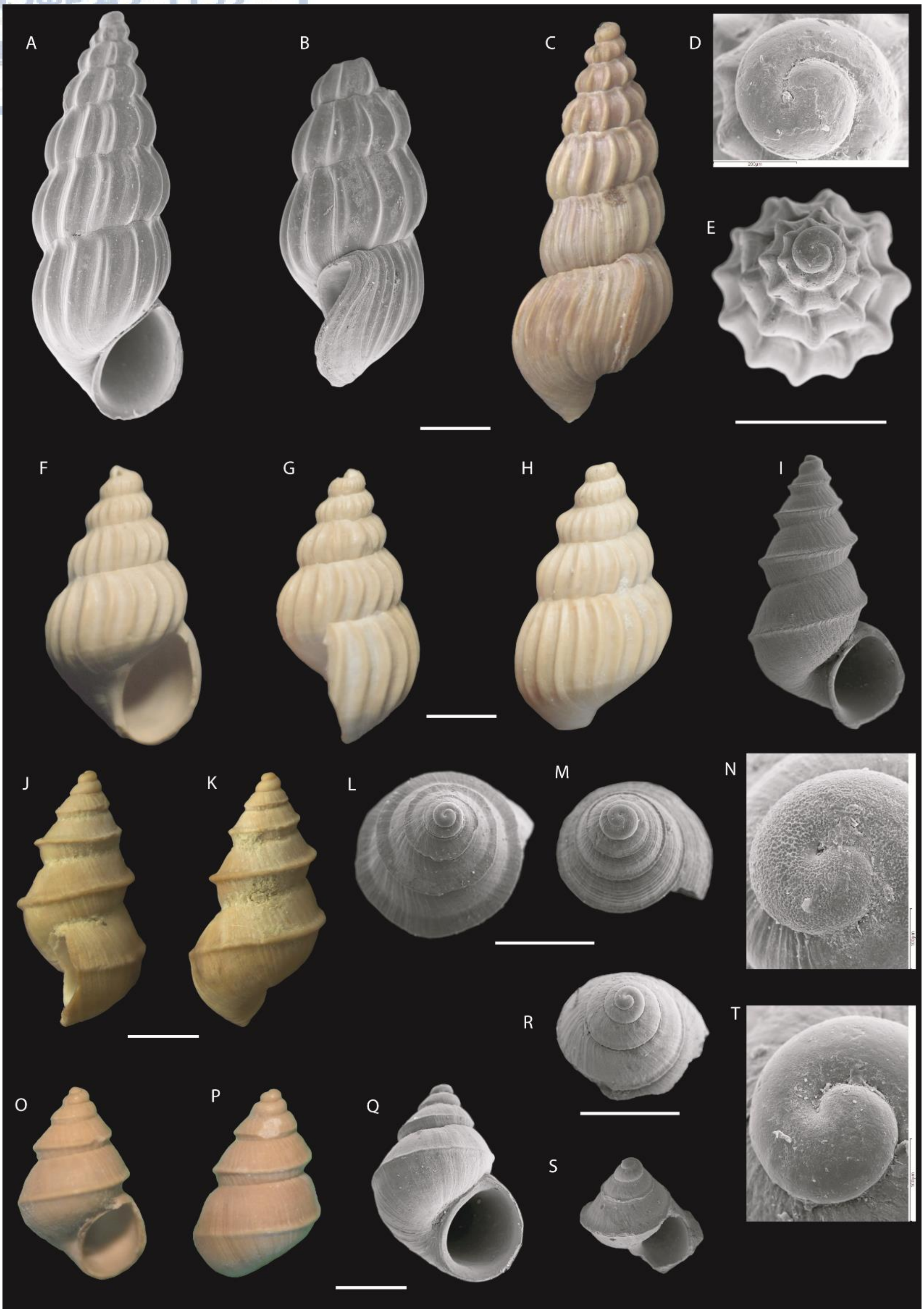
I am grateful to the three-member examining board, the supervisor Prof. Efterpi Koskeridou, Prof. George Iliopoulos, Dr. Mathias Harzhauser, and the external =advisor Dr. Thomas A. Neubauer for their contribution to this work. Lots of thanks to Penelope Papadopoulou, doctor of the Department of Geology of the University of Patras, for her assistance in matters relating to the geology of the study area, sampling and processing of samples for the SEM pictures. Also, the PhD candidate in the same department Spyridon Spyropoulos is thanked for processing the samples and Elisavet Georgopoulou for sending studied material. In addition, I appreciate the Laboratory of Electron Microscopy and Microanalysis (L.E.M.M.) of University of Patras, for the immediate service in photography. At this point I also want to thank Danae Thivaiou, Christos Psarras, Evangelia Rentoumi from the Department of Historical Geology – Palaeontology, Faculty of Geology and Geoenvironment, National and Kapodistrian University of Athens, who demonstrated to me the use of Leica M165 C stereoscope with which the colour images were taken. I would like to thank all the professors of the Interinstitutional course of postgraduate studies in Palaeontology- Geobiology, for helping me to delve into palaeontology. This work is dedicated to my family Odysseus, Alexandra, Ifigeneia and my good friend Chara Rekoumi, to which I dedicate this work their support to me was invaluable.

APPENDIX OF IMAGES

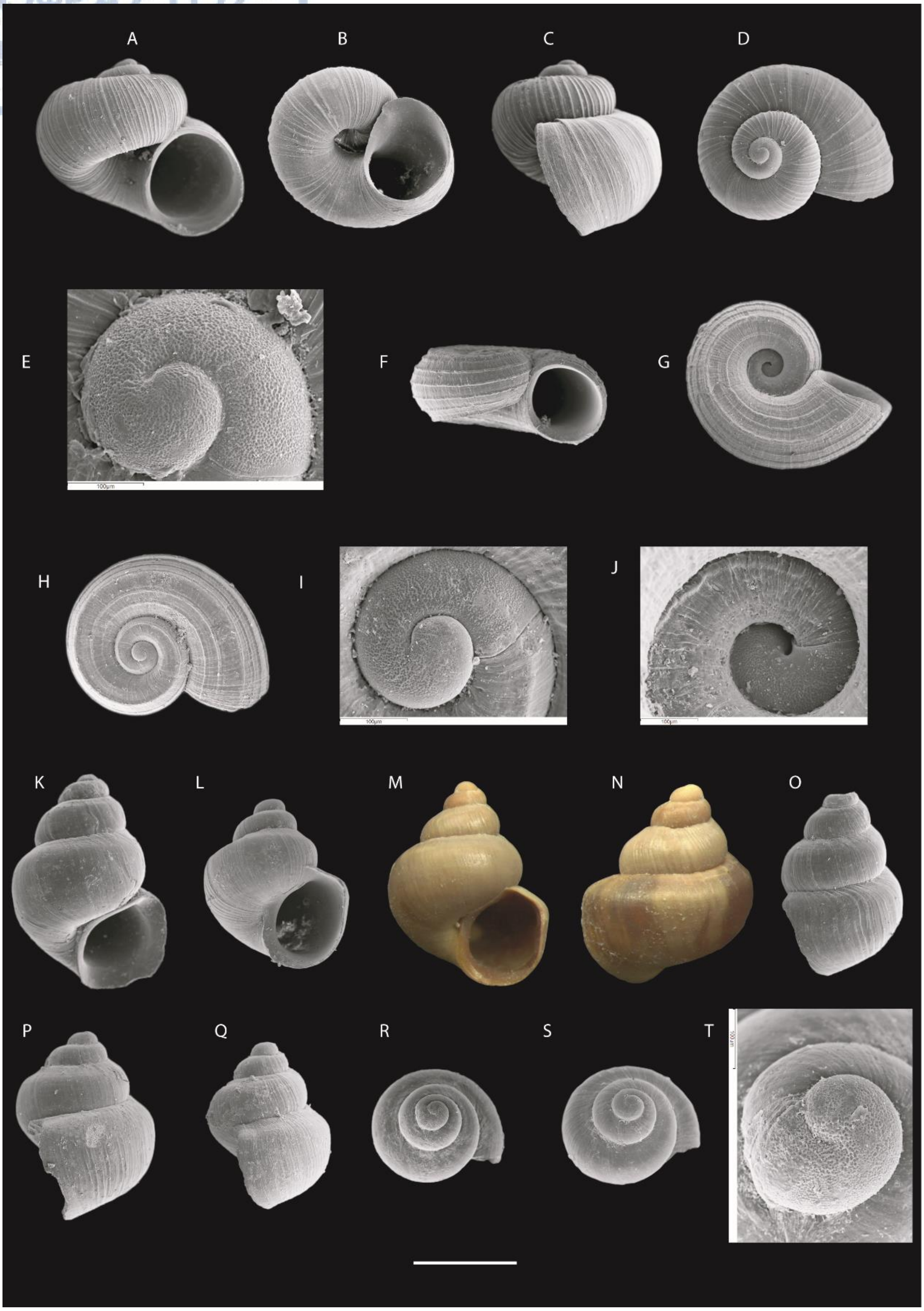
All pictures are grouped per view (Apertural, Apical = apex view, Lateral, Dorsal, Basal = umbilical view). For family Planorbidae apex side = apical view, right side= basal view. Scalebars correspond to 1 mm, while for pictures of protoconch view, the size and unit of measurement are given with the scale bar inside the plate.



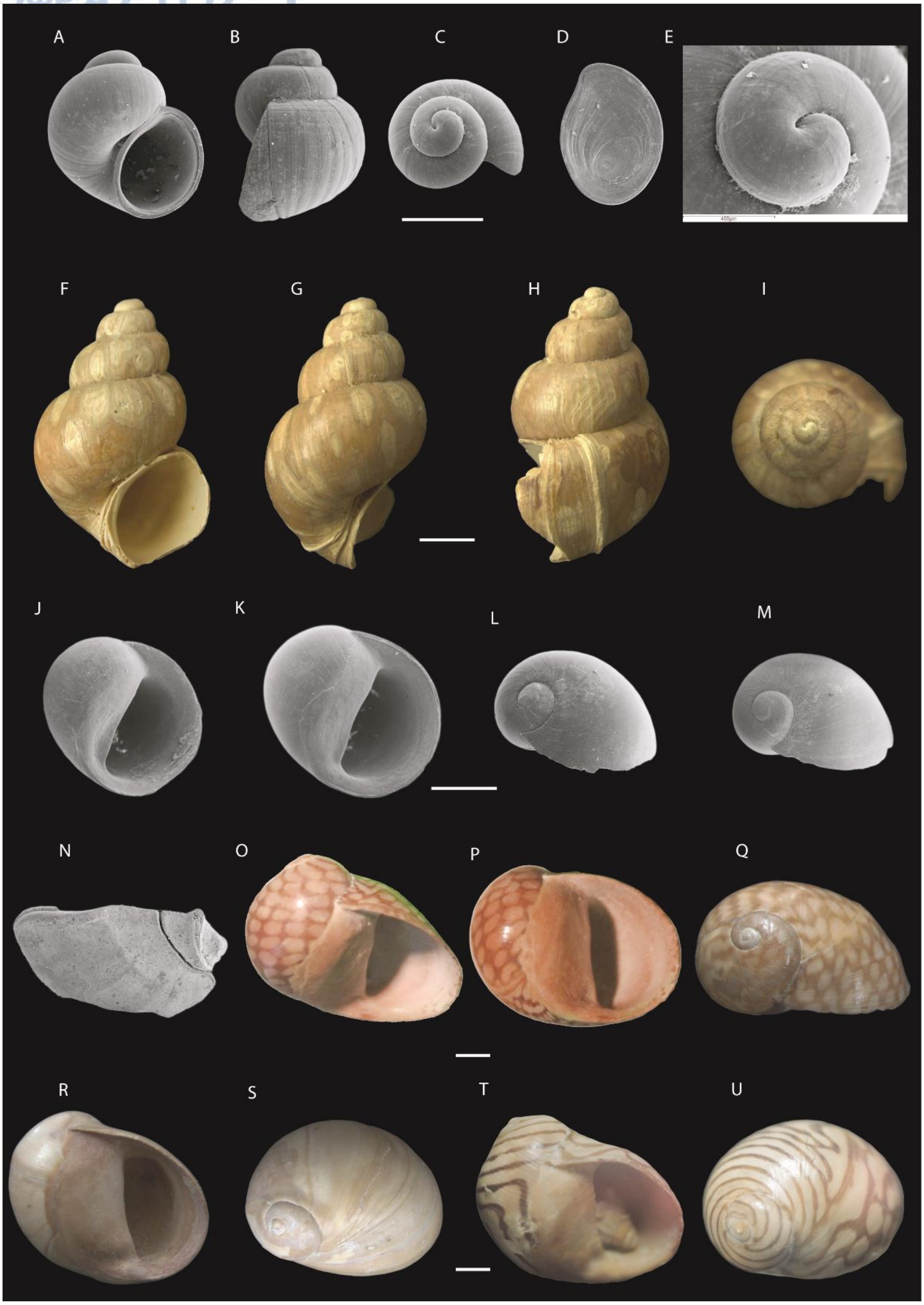
Pl. 1: A-O *Prososthenia* cf. *attica* (Fuchs, 1877), P-U ***Prososthenia* n. sp.**, Apertural view (A, B, F, G, J, L, M, P, S). Apical view (C, D, T, U). Dorsal view (E, I, O, R). Lateral view (H, K, N, Q).



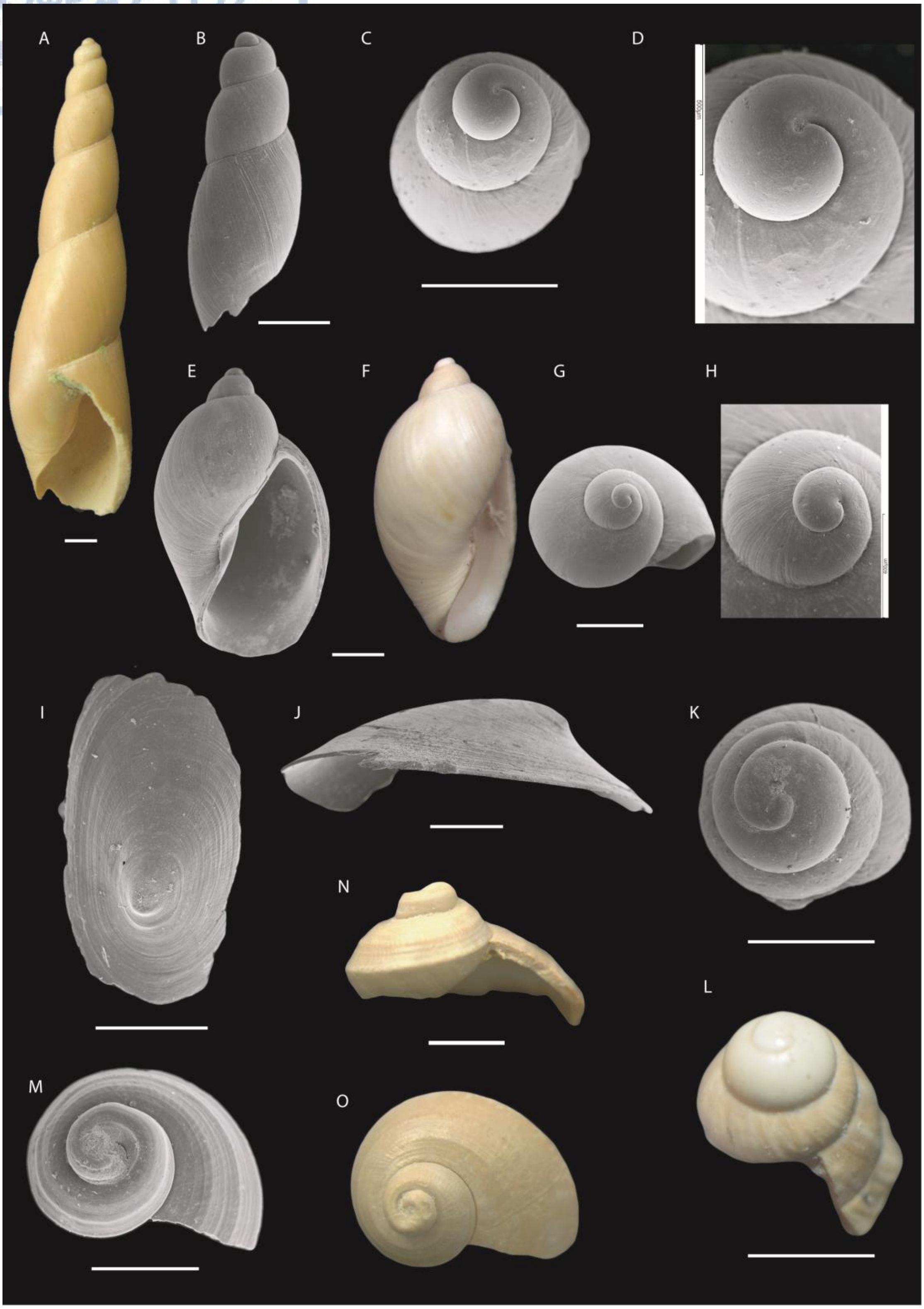
Pl. 2: A-E *Goniochilus graecus* (Wenz, 1919), **F-H ?*Goniochilus* sp.**, **I-T *Pyrgula* cf. *nikosi*** Esu & Girotti, 2015. Apertural view (A, F, I, O, Q, S). Apical view (D, E, L, M, N, R, T). Dorsal view (C, H, K, P). Lateral view (B, G, J).



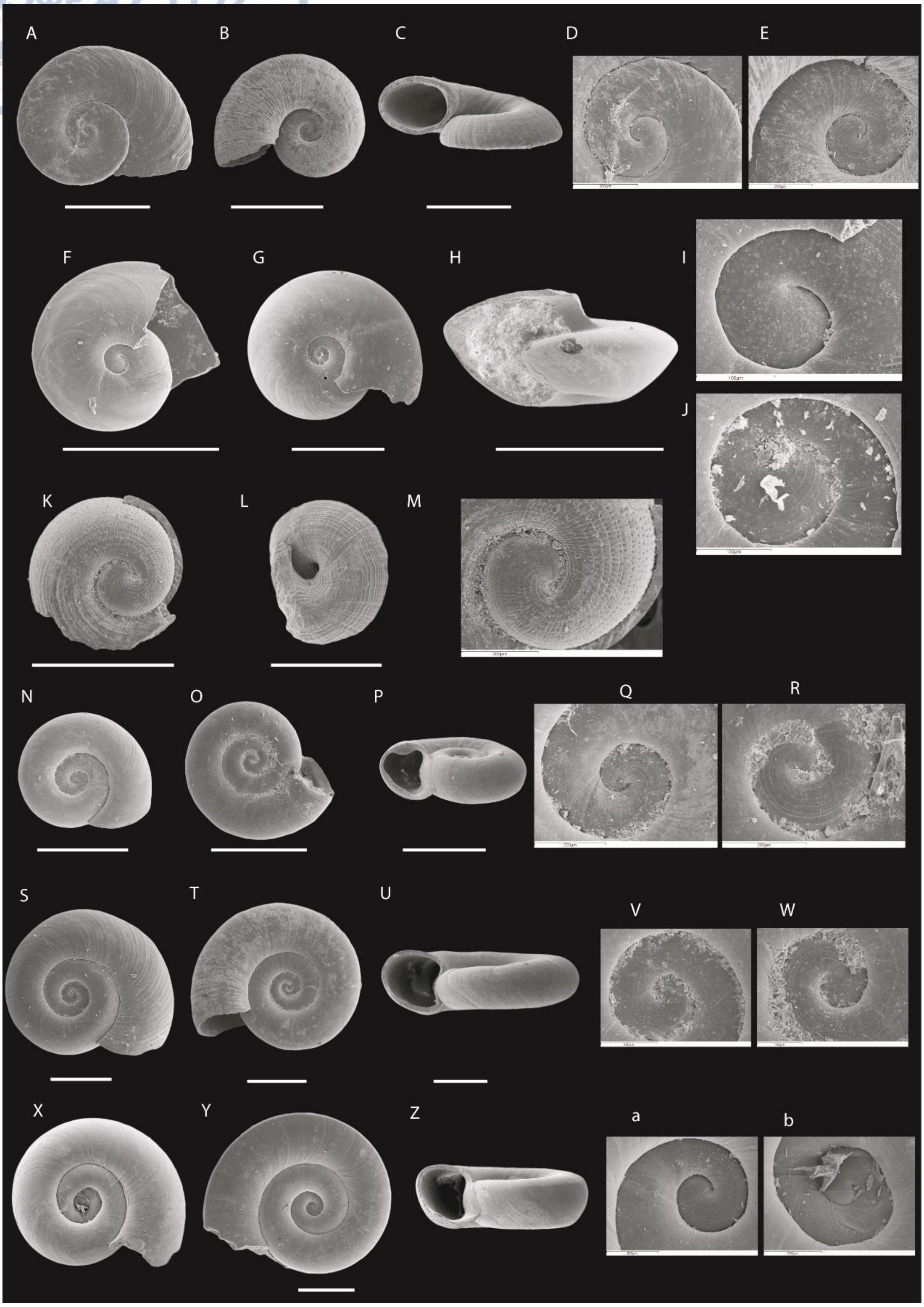
Pl. 3: A-E *Islamia* n. sp., **F-J *Graecamnicola n.* sp**., **K-T *Bania* n. sp**. Apertural view (A, F, K, L, M). Apical view (D, E, H, I, R, S, T). Dorsal view (N). Lateral view (C, O, P, Q). Basal (B, J).



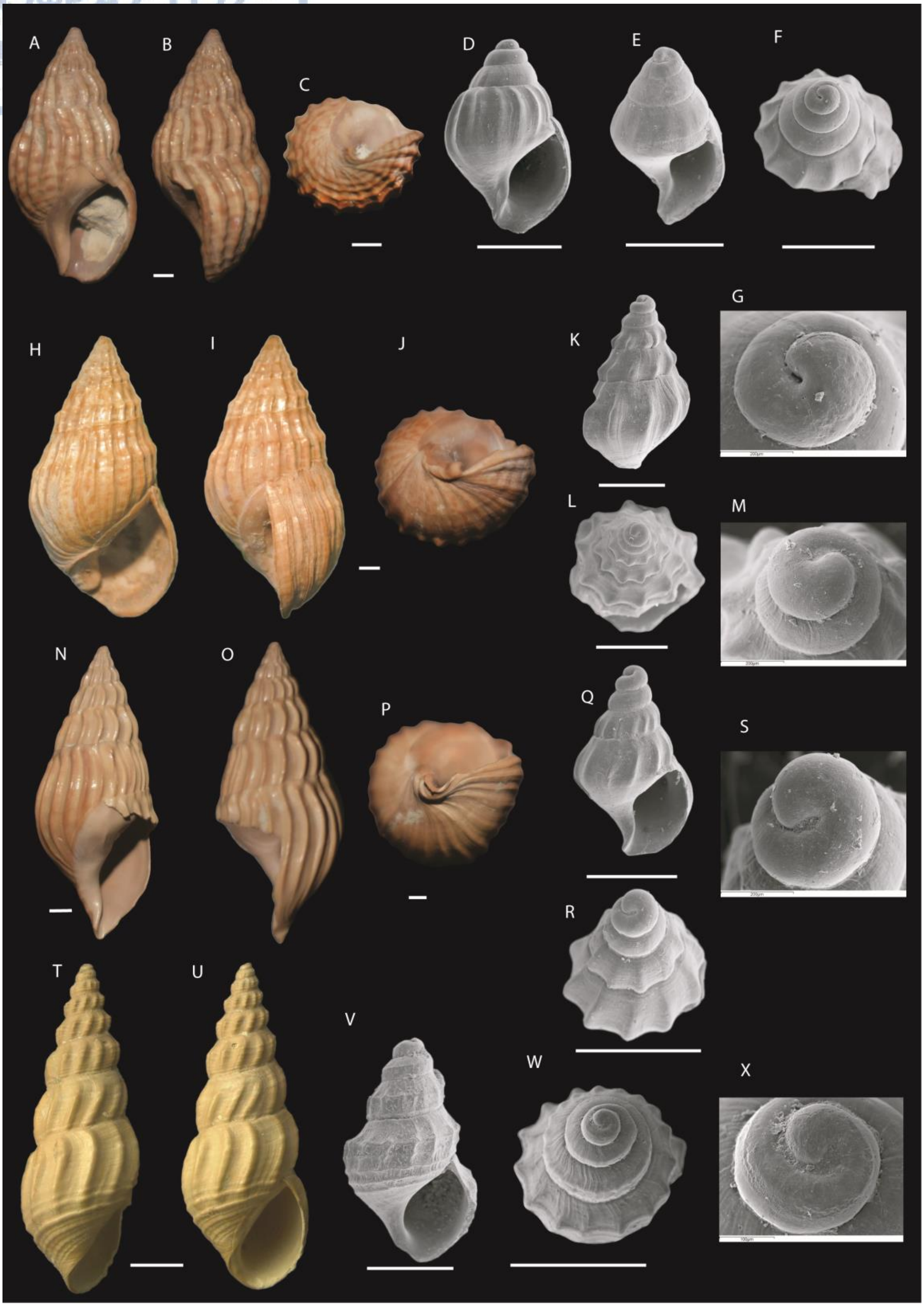
Pl. 4: A-I *Bithynia candiota* Westerlund, 1886, **J-U *Theodoxus micans*** (Gaudry & Fischer in Gaudry, 1867). Apertural view (A, F, J, K, P, R). Apical view (C, E, I, L, M, Q, S, U). Lateral view (B, G, H, O, T).



Pl. 5: A-D *Lymnaea megarensis* Gaudry in Gaudry & Fischer, 1867, **E-H *Radix* sp.**, **I-J *Acroloxus lacustris*** (Linnaeus, 1758), **K-L *Cochlicella*? *conoidea*** (Draparnaud, 1801), **M-O *Viviparus* sp.** Apertural view (A, E, N). Apical view (C, D, G, H, I, K, L, M, O). Lateral view (B, F, J).



Pl. 6: A-E ***Armiger crista*** (Linnaeus, 1758), **F-J** ***Segmentina nitida*** (O. F. Müller, 1774), **K-M** ***Planorbarius*** **sp**., **N-W** ***Gyraulus parvus*** (Say, 1817), **X-b** ***Planorbis planorbis*** (Linnaeus, 1758). Apertural view (C, H, P, U, Z). Apical view (A, D, K, M, N, Q, S, V, X, a). Basal (B, E, F, G, I, J, L, O, R, T, W, Y, b).



Pl. 7: A-G *Melanopsis* cf. *bittneri* Fuchs, 1877, **H-M *Melanopsis* sp.**, **N-S *Melanopsis* cf. *gearyae*** Neubauer, Harzhauser, Georgopoulou, Mandic & Kroh, 2014, **T-X *Melanoides curvicosta*** (Deshayes, 1835). Apertural view (A, D, E, H, N, Q, U, V). Apical view (F, G, L, M, R, S, W, X). Basal (C, J, P), Dorsal view (K). Lateral view (B, I, O, T).

Table 2
Relative abundances (%) of Gastropods in the studied samples.

Sample	S11	SmiddleDpr	SuperDpr	SupmostDpr
Theodoxus micans	0.9	0.3	16.5	31.9
Planorbis planorbis	1.8	1.9	0	0
Gyraulus parvus	19.3	3.3	0	0
Armiger crista	3.1	1.6	0	0
Planorbarius sp.	0	0.1	0	0
Segmentina nitida	0.5	0.1	0	0
Lymnaea megarensis	3.3	3.7	0	0
Radix sp	7.2	11.4	0.3	0.6
Acroloxus lacustris	0.5	0.1	0	0
?*Cochlicella conoidea*	0.1	0.1	0	0
Prososthenia cf. attica	0.9	1.8	8.3	12.4
Prososthenia n. sp.	0.6	0.3	0	0
Goniochilus graecus	4.6	6.7	5.6	7.5
Pyrgula nikosi	4.9	3.9	3.2	7.3
Islamia sp.	12.7	5.9	0.1	0
Graecamnicola n. sp.	0.6	0.4	0	0.1
Bania n. sp.	1.2	1	1.1	0.3
?*Goniochilus* sp.	0.1	0	0	0
Bithynia candiota	8.7	6	0.2	0.2
Viviparus sp.	0.6	1.1	0.1	0.4
Melanopsis sp.	25.5	44.3	1.5	0.1
Melanopsis cf. *bittneri*	1.9	4.6	56.8	21.3
Melanopsis cf. *gearyae*	0	0	3.4	14.2
Melanoides curvicosta	1	1.5	2.9	3.5

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