Seagrass-Associated Molluscan and Fish Communities from the Early Pleistocene of the Island of Rhodes (Greece)

Efterpi Koskeridou¹, Danae Thivaiou¹, Christina Giamali², Konstantina Agiadi¹, Dimitra Mantzouka¹

¹ National and Kapodistrian University of Athens, Faculty of Geology and Geoenvironment, Department of Hist. Geology - Paleontology, Panepistimioupoli Zographou, 157 84 Athens, Greece
² Goulandris Natural History Museum, Levidou 13, 145 62, Kifissia, Greece

ekosker@geol.uoa.gr

Abstract. Well-preserved leaves and rhizomes of the Mediterranean endemic marine angiosperm Posidonia oceanica and the rich associated mollusc and fish fauna are contained in the early Pleistocene shallow siliciclastic sediments of the Kritika Formation of the island of Rhodes (Greece). The leaf moulds are preserved in fine-grained sands, whereas the rhizomes are found in situ within coarse-grained sediments. The associated molluscan fauna includes 79 species, 47 gastropods and 32 bivalves, most of them extant. The rhizome-associated community comprises 49 species and the leaves-associated community includes 30 species. Small gastropods grazing on microalgae (Rissoidae, Cerithiidae, Trochidae) are the most abundant elements of the fauna, however carnivorous gastropods (Nassariidae, Naticidae, Muricidae) are also diverse. Among the bivalves Lucinidae (e.g., Lucinella) numerically dominate the deeper infauna and other chemosymbiont bivalves, as Ungulinidae (Diplodonta) are also common. Although many species are not associated exclusively with this seagrass and they may occur in other environments as well, they generally thrive on P. oceanica leaves and rhizomes. The Posidonia oceanica meadows were also inhabited by several characteristic fish species which thrive in the seagrass meadows of the eastern Mediterranean until today. The studied fauna is the first reported from the early Pleistocene of Greece and shows similarities to the modern counterparts of Posidonia oceanica meadows, providing new data on the resilience of seagrass ecosystems to environmental change in general.

1. Introduction

Marine phanerogams appeared during the Late Cretaceous. Even though they have been important components of temperate to tropical shallow-water marine environments together with their associated communities until the Holocene, they are rarely fossilized due to easy disintegration. Extensive relevant literature is given in [1].

Posidonia oceanica (Linnaeus) Delile is a marine plant endemic to the Mediterranean Sea and grows in massive clumps. Its meadows, as all the seagrasses, constitute an ecologically highly valuable marine habitat, as they contribute significantly to the oceanic primary production [2] and also play an important role in nutrient cycling [3]. Furthermore, they are an important nursery habitat for different groups of organisms [4] and especially molluscs [5], [6], [7], [8]. Although this species is scarce in the fossil record and in the Mediterranean there are only two studies from Sicily [9] and northern Italy [10], exceptionally well-preserved moulds of the leaves and casts of the rhizomes are contained in the
early Pleistocene shallow-water siliciclastic deposits of the Greek Island of Rhodes. Associated with these fossil remains are abundant molluscs, among other organisms, which show a remarkable affinity with the modern biotic component of *Posidonia oceanica* biocoenosis.

The main goal of this work is to document the mollusc communities associated with the Early Pleistocene seagrass leaves and rhizomes from Rhodes and to compare them with those from the present-day Mediterranean *Posidonia oceanica* meadows.

2. Geological setting
Rhodes is a Dodecanese island in the Aegean Sea that belongs to the eastern end of the tectonically active Hellenic arc-trench subduction system marking the African-Eurasian plate boundary.

![Figure 1. Location of study area; a. Location of island of Rhodes b. Simplified geological map and location of the studied sections.](image)

The Pleistocene deposits of Rhodes record three major, transgressive-regressive cycles: The Trianda, Rhodes and Lindos-Acropolis Synthems [11, 12]. The Trianda Synthem comprises continental (Damatria Formation), then brackish to shallow marine (Kritika Formation) siliciclastic sediments deposited into a muddy deltaic setting [13-15]. Although these formations have been first considered of Piacenzian-Gelasian [16], [17] or Calabrian ages [18], biostratigraphic analyses based on calcareous nannofossils placed the shallow marine, uppermost part of the Kritika Formation in the late Gelasian (~2 Ma) [15].

Fossil seagrass remains were found in nine levels of two sections (Figure 2) of Kritika Formation situated near the coastal village of Kritika [13], [15], [19]. Numerous *Posidonia oceanica* leaf moulds has been recovered from the lower part of Kritika 2 section in the clayey and fine-grained sandy beds and reddish vertical branches of seagrass rhizomes were found in both sections in coarse-grained layers, as they have been figured by the previous authors.

3. Material and methods
The stratigraphic sections under study were logged and measured during fieldwork (Figures 1, 2). The samples were collected from each of the three coarse-grained sand beds containing seagrass rhizomes,
as well as from the six levels of fine-grained sand or silty clay containing leaf moulds. Molluscan fauna is well-preserved in all samples. Sediment bulks (3 kg each) were sieved using a column of three sieves with diminishing mesh size (from 1 cm to 250 mm). After drying, the molluscs were identified at the species level. Species identification and ecology was carried out using a vast literature dealing with molluscs, mainly [20–41]. Trophic information for all gastropod species was obtained from literature and each species was assigned to a trophic group following the classification of feeding modes as described in [42]: carnivores (C) feeding on mobile organisms; scavengers (SC); deposit feeders (D) feeding on organic particles contained in the sediment; ectoparasites and specialized carnivores (E) feeding on much larger organisms on which they live during their life cycle; filter feeders (F) intercepting nutrient particles with their gills and/or mucous strings; microalgal or periphyton grazers (MG). H is used for herbivores in general. An estimation of the number of specimens of each group was made. In order to give broad indications of relative faunal abundance, the following categories were used: rare (1–10 specimens), present (11–20), common (21–50), abundant (51–100), and very abundant (100 specimens).

Figure 2. Lithological sections under study. Samples: R1–R3 (Rhizomes), L1–L6 (Leaves)

The seagrass-associated fish fauna was identified by studying the fish otoliths contained in these deposits, since otoliths have species-specific morphology. Sediment samples (25 kg each) were taken from the same levels as for the molluscs. The samples were sieved using a 250-μm sieve, and the residues were dried in an oven. Fish otoliths were picked from the dry residues under a stereoscope, and identified through direct comparison with already identified fossil material and using the literature
We separated the functional guilds based on their present-day ecology in the eastern Mediterranean [45] and compared the fauna to the modern equivalent *Posidonia oceanica* seagrass-associated fish fauna along the eastern coast of Rhodes [47]: SR, seagrass residents; OV, occasional visitors; JM, juvenile migrants; SM, seasonal migrants.

### 4. Results and Discussion

Most molluscs come from the samples R1 and R2 with the rhizomes of *Posidonia* from the Kritika 1 section, while less from the samples of the section Kritika 2. There are 47 gastropods, 32 bivalves (Tables 1 and 2), one annelid and the chiton *Acanthochitona fascicularis* (in R1) [48]; among gastropods the most abundant are *Bittium reticulatum, Bittium latreillii, Cerithium vulgatum, Tricolla speciosa, Jujubinus striatus, Bolma rugosa, Barbatia barbata* with other species referable to the same type of environment, i.e. *Posidonia* prairies [8].

A total of 10 species of bivalves and 20 species of gastropods were found in the fine-grained and laminated sands and silts containing the fossil leaves. Each of the 6 sampled levels yielded from 3 to 10 bivalve species and 3 to 19 gastropod species (Table 1). Among the bivalves, with 10 species the infaunal and epibyssate taxa are the most diverse. The co-occurrence of bivalves, such as *Venus verrucosa, Flexopecten hyalinus, Lima inflata, Talochlamys multisiretria*, and *Mimachlamys varia*, characterize modern *Posidonia*-vegetated bottoms [7], [8]. The high abundance of the deep-burrowing *Loripinus fragilis*, suggests a transport of these shells during storms. Herbivore gastropods are dominating with 8 species and common presence over the carnivores, although the number of specimens is never abundant.

A total of 32 species of bivalves and 35 species of gastropods were found in the coarse-grained sediment containing the *Posidonia oceanica* rhizome casts (Table 2). Among the bivalves, infaunal forms dominate in number of species, but epibyssate forms are also abundant. Some filter-feeder bivalves as *Gouldia minima* and *Papilllicardium papillosum, Barbatia barbata, Mimachlamys varia* are dominating in R2 sample where a high proportion of *Venus verrucosa* and *Diplodonta rotundata* also occur. The most common species in the sample R3 are almost the same, but with *Lucinella divaricata* being the most abundant. This is reflective of a higher input of organic matter for the sample. Herbivore gastropods (most of them grazing on epiphytes) dominate in number of species and specimens over the carnivores, especially in sample R2. The most frequent species are *Gibbula fanulum, Jujubinus striatus, Bittium reticulatum, Rissosoa guerinii* and *Tricolla speciosa*. Gastropod/bivalve ratios (epifaunal/infaunal ratios) are considerably high. Scavengers are also present but scattered and connected to two species: *Nassarius musivus* and *Tritia incrassata*. An important element of the biodiversity of the assemblage is the presence of ectoparasites, namely the members of the family Triphoridae as *Monophorus perversus, Marshallora adversa, Metaxia metaxa*. The absence of nesting species, borers and encrusting bivalves from the leaves bearing sediment is due to the soft substratum conditions and their presence in sample R1 is due to the existence of hard substrate elements.

In modern *Posidonia* meadows many bivalves as reported upwards and also Lucinidae (e.g., *Loripinus, Lucinella*) can be abundant or may even numerically dominate the deeper infauna, and chemosymbiotic bivalves, as Ungulinidae (e.g., *Diplodonta*) are frequently reported. Common epiphytic gastropods include small cerithids that graze on microalgae, as *Bittium reticulatum*, rissoids and trochids (as *Calliostoma, Jujubinus, Bolma, Tricolla*) are often reported as significantly abundant on these meadows [5], [7], [8], [49], [50]. All the taxa recorded in the present material are not restricted to *Posidonia* meadows. The only obligate seagrass feeder, gastropod species *Smaragdia viridis* is missing from the studied seagrass beds.

The seagrass leaves were transported before accumulation and burial, unlike the rhizomes of *Posidonia oceanica* which were found in life position within the sediment. The molluscs associated with the rhizomes may thus be considered as having lived in the same environment. A rapid burial in coarse-grained siliclastic sediment is inferred, which also points towards a control by storms.
The mollusc assemblages of all the other samples in comparison with sample R2 suggests less than optimal environmental conditions, probably in shallow and turbid waters at depths of about 10–20 m. The siliciclastic facies and the sedimentary structures of the deposits containing the seagrass remains, point to such environmental conditions [13].

The otolith investigation yielded 35 species of Teleost fish, mostly Gobiidae and Sparidae, but also Myctophiidae, Bothidae, and other families in smaller concentrations. Among the identified species, several are known to inhabit Posidonia oceanica meadows along the eastern coast of Rhodes until today [47]. In terms of functional guilds, SR include Spicara smaris, Serranus cabrilla, and Boops boops; OV include Apogon imberbis, Gobius cobitis, Gobius paganellus, Scorpaena notata, and Trachinus draco; JM include Sardina pilchardus, Mullus barbatus, Mullus surmuletus, and Pagellus bogaraveo; and SM comprises only Chromis chromis.

Table 1. Bivalve species associated with fossil Posidonia oceanica leaves (samples L1–L6) and rhizomes (R1–R3). Faunal abundance: ● rare; ●●: present; ●●●: common; ●●●●: abundant.

| Species/ecology       | Leaves                    | Rhizomes       |
|-----------------------|---------------------------|----------------|
|                       | L1 | L2 | L3 | L4 | L5 | L6 | R1 | R2 | R3 |
| Deep infaunal          |    |    |    |    |    |    |    |    |    |
| Loripinus fragilis    | ●  | ●●| ●●●| ●●●|    |    |    |    |    |
| Ctena decussata       | ●  |    |    |    |    |    |    |    |    |
| Lucinella divaricata  |    | ● | ●●●| ●●●|    |    |    |    |    |
| Thracia phaseolina    |    |    |    |    |    |    |    |    |    |
| Shallow infaunal       |    |    |    |    |    |    |    |    |    |
| Ervillia castanea      |    |    |    |    |    |    |    |    |    |
| Glycymeris pilosa      | ●  |    |    |    |    |    |    |    |    |
| Gouldia minima        | ●  |    |    |    |    |    |    |    |    |
| Nucula nucleus        | ●  |    |    |    |    |    |    |    |    |
| Nucula sulcata A. Adams, 1856 | ●  |    |    |    |    |    |    |    |    |
| Papillicardium papillosum (Poli, 1791) | ●  |    |    |    |    |    |    |    |    |
| Spaniorinus sp.        |    |    |    |    |    |    |    |    |    |
| Timocelea ovata        |    |    |    |    |    |    |    |    |    |
| Venus verrucosa        |    |    |    |    |    |    |    |    |    |
| Parvicardium minimum   |    |    |    |    |    |    |    |    |    |
| Diplodonta rotundata   |    |    |    |    |    |    |    |    |    |
| Spisula subtruncata    |    |    |    |    |    |    |    |    |    |
| Epibyssate             |    |    |    |    |    |    |    |    |    |
| Barbatia barbata       |    |    |    |    |    |    |    |    |    |
| Acar clathrata        |    |    |    |    |    |    |    |    |    |
| Talochlamys multistriata (Poli, 1795) |    |    |    |    |    |    |    |    |    |
| Mimahlamys varia      |    |    |    |    |    |    |    |    |    |
| Limaria tuberculata    |    |    |    |    |    |    |    |    |    |
| Lima lima             |    |    |    |    |    |    |    |    |    |
| Lissoperctus haustorius (Poli, 1795) |    |    |    |    |    |    |    |    |    |
| Palliolum excisum      |    |    |    |    |    |    |    |    |    |
| Nestling species       |    |    |    |    |    |    |    |    |    |
| Cardita calciculata    |    |    |    |    |    |    |    |    |    |
| Striara lactea         |    |    |    |    |    |    |    |    |    |
| Irus Irus              |    |    |    |    |    |    |    |    |    |
| Borer                 |    |    |    |    |    |    |    |    |    |
| Hiatella rugosa       |    |    |    |    |    |    |    |    |    |
| Encrusting             |    |    |    |    |    |    |    |    |    |
| Anomia ephippium       |    |    |    |    |    |    |    |    |    |
| Ostrea lamellosa       |    |    |    |    |    |    |    |    |    |
| Mobile                 |    |    |    |    |    |    |    |    |    |
| Erycina sp.            |    |    |    |    |    |    |    |    |    |
| Notolimea sp.          |    |    |    |    |    |    |    |    |    |
Table 2. Gastropod species associated with fossil Posidonia oceanica leaves (samples L1–L6) and rhizomes (R1–R3). Faunal abundance: ● rare; ●●: present; ●●●: common; ●●●●: abundant

| Species/ecology | Trophic Group | Leaves | Rhizomes |
|-----------------|---------------|--------|----------|
|                 | L1 | L2 | L3 | L4 | L5 | L6 | R1 | R2 | R3 |
| Benthic         |    |    |    |    |    |    |    |    |    |
| Alvania cancellata (da Costa, 1778)  | MG |      |      |      |      |      |      |      |      |
| Rissoa membranacea (J. Adams, 1800)  | MG |      |      |      |      |      |      |      |      |
| Rissoa ventricosa Desmarest, 1814  | MG |      |      |      |      |      |      |      |      |
| Rissoa guerinii Recluz, 1843  | MG |      |      |      |      |      |      |      |      |
| Rissoa variabilis (Me格尔 von Muhfeld, 1824)  | MG |      |      |      |      |      |      |      |      |
| Homalopoma sanguineum (Linnaeus, 1758)  | MG |      |      |      |      |      |      |      |      |
| Tornus subcarinatus (Montagu, 1803)  |      |      |      |      |      |      |      |      |      |
| Cerithium vulgatum Bruguier, 1792  | MG |      |      |      |      |      |      |      |      |
| Gibbula magnus (Linnaeus, 1758)  |      |      |      |      |      |      |      |      |      |
| Gibbula ardens (Sais Marschlns, 1793)  | MG |      |      |      |      |      |      |      |      |
| Gibbula lancum (Gemlin, 1791)  | MG |      |      |      |      |      |      |      |      |
| Steromphala umbilicaris (Linnaeus, 1758)  | MG |      |      |      |      |      |      |      |      |
| Jujubinus striatus (Linnaeus, 1758)  | MG |      |      |      |      |      |      |      |      |
| Jujubinus exasperatus (Pennant, 1777)  |      |      |      |      |      |      |      |      |      |
| Clelandella miliaris (Brocchi, 1814)  | MG |      |      |      |      |      |      |      |      |
| Bittium lateritii (Paynadeuze, 1826)  | MG |      |      |      |      |      |      |      |      |
| Bittium reticulatum (da Costa, 1778)  | MG, DE |      |      |      |      |      |      |      |      |
| Bolma rugosa (Linnaeus, 1767)  | MG |      |      |      |      |      |      |      |      |
| Pusillina inconspicua (Alder, 1844)  | DE, MG |      |      |      |      |      |      |      |      |
| Tricola pullus (Linnaeus, 1758)  | MG |      |      |      |      |      |      |      |      |
| Tricola speciosa (Megerle von Muhfeld, 1824)  | MG |      |      |      |      |      |      |      |      |
| Calliostoma conulus (Linnaeus, 1758)  | C |      |      |      |      |      |      |      |      |
| Calliostoma ziczynphum (Linnaeus, 1758)  | C |      |      |      |      |      |      |      |      |
| Chausvetia turritellata (Deshayes, 1835)  | C |      |      |      |      |      |      |      |      |
| Gibberula miliaria (Linnaeus, 1758)  | C |      |      |      |      |      |      |      |      |
| Tritia incrassata (Sirem, 1768)  | SC |      |      |      |      |      |      |      |      |
| Nassarius musivus (Brocchi, 1814)  | SC |      |      |      |      |      |      |      |      |
| Naticarius stercusmuscuarum (Gmelin, 1791)  | C |      |      |      |      |      |      |      |      |
| Euspira catena (da Costa, 1778)  | C |      |      |      |      |      |      |      |      |
| Mitrella scripta (Linnaeus, 1758)  | C |      |      |      |      |      |      |      |      |
| Raphitoma linearis (Montagu, 1803)  | C |      |      |      |      |      |      |      |      |
| Muricopsis cristata (Brocchi, 1814)  | C |      |      |      |      |      |      |      |      |
| Pagodula echinata (Kiener, 1840)  | C |      |      |      |      |      |      |      |      |
| Mangelia scabrida (Méhos, 1803)  | C |      |      |      |      |      |      |      |      |
| Cerithiopsis tubercularis (Montagu, 1803)  | E, C |      |      |      |      |      |      |      |      |
| Metasia metaxa (Delle Chiaje, 1826)  | EC |      |      |      |      |      |      |      |      |
| Monophorus perversus (Linnaeus, 1758)  | E, H |      |      |      |      |      |      |      |      |
| Emarginula sicula J. E. Gray, 1826  | E, H |      |      |      |      |      |      |      |      |
| Diodora graeca (Linnaeus, 1758)  | E, C |      |      |      |      |      |      |      |      |
| Marshallora adversa (Montagu, 1803)  | E, C, DE |      |      |      |      |      |      |      |      |
| Chryssalida sp.  | E |      |      |      |      |      |      |      |      |
| Calyptraea chinensis (Linnaeus, 1758)  | F |      |      |      |      |      |      |      |      |
| Crepidula sp.  | F |      |      |      |      |      |      |      |      |

5. Conclusions

The Early Pleistocene molluscan and fish assemblages associated with the Posidonia oceanica in siliciclastic sediments of Kritika sections, display a composition and structure, similar to that observed from present-day meadows in the Mediterranean.

The molluscan species, although not associated exclusively with this marine phanerogam, generally thrive with its leaves and rhizomes. Gastropods dominate the fauna and exhibit a relatively high biodiversity (47 species) however bivalves are also diverse (32 species). A marked increase in number of species in coarse-grained layers relative to those in clayey and fine-grained sandy beds is observed.
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