

## SPECTACULAR PRESERVATION OF SEAGRASSES AND SEAGRASS-ASSOCIATED COMMUNITIES FROM THE PLIOCENE OF RHODES, GREECE

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### ABSTRACT

An exceptionally well-preserved fossil seagrass community occurs in the late Pliocene of the Greek Island of Rhodes. The siliciclastic deposits of the Kritika section (Kritika Member, Rhodes Formation) contain several beds of clay and fine-grained sand with abundant remains of the leaves of *Posidonia oceanica*. A coarser sand bed with *in situ* rhizomes of the same endemic Mediterranean phanerogam also was found. Samples yield a diverse skeletal assemblage of 121 species of crustose coralline algae, foraminifers, annelids, gastropods, bivalves, encrusting bryozoans, and ostracodes, some of which also live exclusively on the leaves of present-day *P. oceanica*. The community of organisms associated with the rhizomes is slightly poorer (57 species), with bivalves appearing as distinctively abundant components of this assemblage (21 species). An analysis of the relationships between skeletal organisms and fossil leaves and rhizomes shows that the majority of them lived together in the same seagrass-vegetated environment, were transported a short distance from their natural habitat, and buried very rapidly in fine-grained sediments, thus preserving this remarkable assemblage almost intact. The rhizomes were preserved in growth position within a coarse-grained sand trapped by their horizontal and vertical network. The fossil assemblage compares well in terms of major skeletal components with modern shallow-water *P. oceanica* meadows. This study also provides evidence for the presence during the Pliocene of an already well-established and widespread seagrass community with biotopes comparable to those of the present-day Mediterranean.

### INTRODUCTION

Seagrasses and their associated communities have been important components of temperate to tropical marine shallow-water environments since the appearance of the marine phanerogams during the Late Cretaceous (den Hartog, 1970; Brasier, 1975; Larkum and den Hartog, 1989). Seagrasses also play a significant role in sediment baffling and trapping and in the production of carbonate benthic biogenic particles (e.g., Wanless, 1981; Canals and Ballesteros, 1997; Gacia and Duarte, 2001; Perry and Beavington-Penney, 2005). Due to their poor preservation potential, however, marine phanerogams rarely are found in the fossil record. The few studies dealing with unequivocal fossil seagrass occurrences are from the Cretaceous of the Netherlands (Voigt and Domke, 1955; Voigt, 1981), the Eocene of the Paris Basin (Fritel, 1909, 1913) and Florida (Lumbert et al., 1984; Ivany et al., 1990), the Miocene of Sulawesi (Laurent and Laurent, 1926) and Hungary (Radócz, 1972), the Pleistocene of Sicily (Di Geronimo, 1984), and the Holocene of Florida (Froede, 2002).

On the Greek Island of Rhodes (Fig. 1), late Pliocene deposits of the Kritika Member (base of the Rhodes Formation) contain clayey and fine-

grained sandy horizons with abundant and exceptionally well-preserved molds of the leaves of *Posidonia oceanica*, an endemic Mediterranean phanerogam. This material is characterized by its spectacular preservation, not only of the seagrass leaves, but also of some of the epiphytes (=epiphytobionts of Taylor and Wilson, 2003) that are otherwise rarely fossilized. In addition, a coarser sand lens containing well-preserved, essentially *in situ* rhizomes of *P. oceanica* was found, together with a number of skeletal organisms.

The main objectives of this paper are to: (1) document the paleontological characteristics of the marine organisms associated with *Posidonia oceanica* leaves and rhizomes (Table 1); (2) examine the relationships between this community and the fossil plants; (3) gain insight into the mode of preservation of the various seagrass remains; (4) use this information to reconstruct the paleoenvironment and depositional conditions; and (5) compare the results obtained for the main skeletal components of the Pliocene of Rhodes with those reported from the present-day Mediterranean (Table 1).

### STRATIGRAPHIC AND GEOLOGIC SETTING

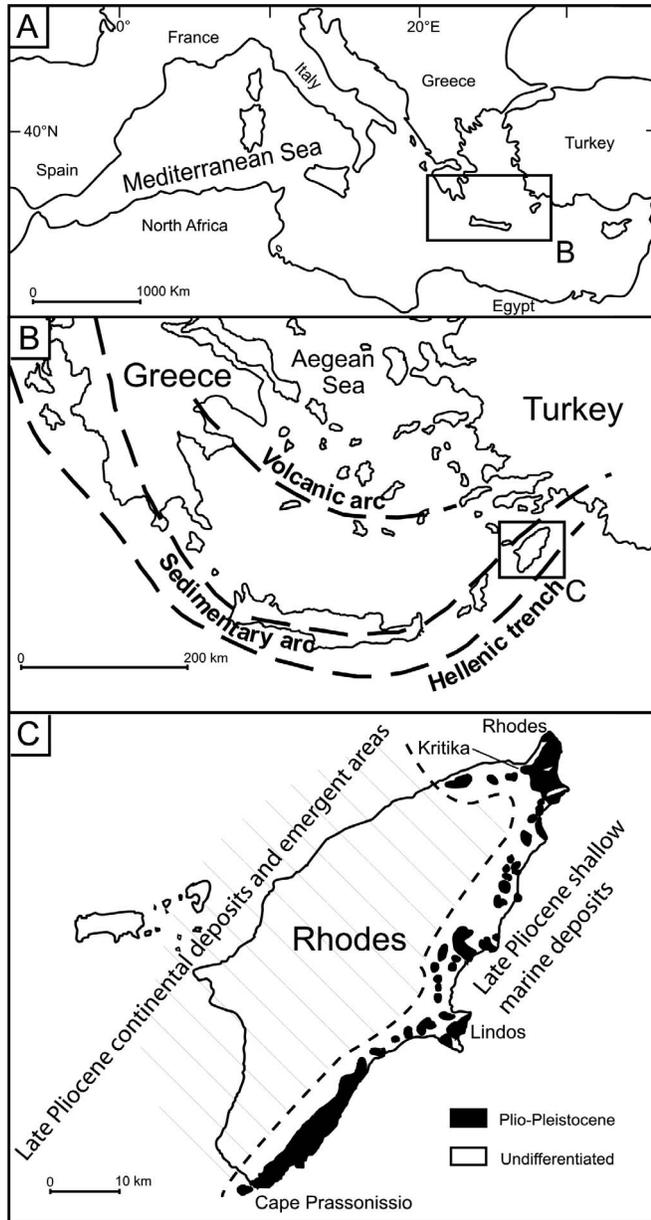
Rhodes, a Dodecanese island in the Aegean Sea (Figs. 1A–B), belongs to the eastern end of the tectonically active Hellenic arc-trench subduction system marking the African-Eurasian plate boundary. The basement rocks are mainly Mesozoic and Tertiary carbonate and siliciclastic deposits folded and faulted during the Alpine orogeny (Mutti et al., 1970a).

Pliocene-Pleistocene sediments (Fig. 1C) cover a large part of the northern and eastern margin of the island (Meulenkamp et al., 1972; Hanken et al., 1996). They were deposited with complex facies patterns within a series of micrograbens developed along the coast of Rhodes since the late Pliocene (Pirazzoli et al., 1989; Hanken et al., 1996). The basement rocks for these small basins are mostly metamorphosed Mesozoic limestones.

Hedenborg (1837) was the first to provide a detailed stratigraphy for these Cenozoic beds. Bukowski (1899) and other authors regarded all these beds as Pliocene. The first lithostratigraphic subdivisions of the Plio-Pleistocene deposits were proposed by Mutti et al. (1970b) and Meulenkamp et al. (1972). Hanken et al. (1996), appreciating the complexity of the Plio-Pleistocene successions, have shown that the stratigraphic scheme developed by the previous authors was too simplified and have recognized three main formations (Kritika, Rhodes, and Lindos Acropolis), each including several informal facies groups. Cornée et al. (2006a) revised the tectono-sedimentary organization of these deposits and defined a new formation (the Ladiko-Tsampika Formation) between the Rhodes Formation (now including three members: Kritika, Kolymbia, and Lindos Bay clay) and the Lindos Acropolis Formation.

The Pliocene-Pleistocene boundary was positioned within the Lindos Bay clay facies group of Hanken et al. (1996), based on the limited biostratigraphical studies of bivalves (Keraudren, 1970), ostracodes, and palynomorphs (Sissingh, 1972; Benda et al., 1977), and the paleomag-

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**FIGURE 1**—General location of study area. A) Location of island of Rhodes in Mediterranean Sea. B) Enlargement indicating position of Rhodes in Aegean Arc. C) Simplified geological map showing distribution of Plio-Pleistocene deposits (modified after Hanken et al., 1996). Location of sedimentary section under study is also shown (GPS coordinates: N 36°25.507', E 28°12.065').

netic studies by Løvlie et al. (1989). On the basis of calcareous nannofossils, ostracodes, and foraminifers, however, Thomsen et al. (2001) assigned an early Pleistocene age to the whole marine sequence. Cornée et al. (2006a, 2006b) established that these three formations range from late Pliocene (Kritika to base of the Lindos Bay clay) to middle Pleistocene in age.

The Kritika Member consists of estuarine to marine terrigenous deposits (pebbles, gravels, sands, clays) that are considered as coeval with the continental sediments to the west (Fig. 1C; Meulenkamp et al., 1972). The marine succession preserves diversified assemblages of organisms corresponding to those found in paralic and nearshore environments.

The studied section is part of the Kritika Member and is situated about 5 km southwest of Rhodes, near the road leading from the coastal village of Kritika to the hospital (Fig. 1C). The section is about 80 m thick (Fig. 2) and comprises only marine deposits dominated by sand, clay, gravel,

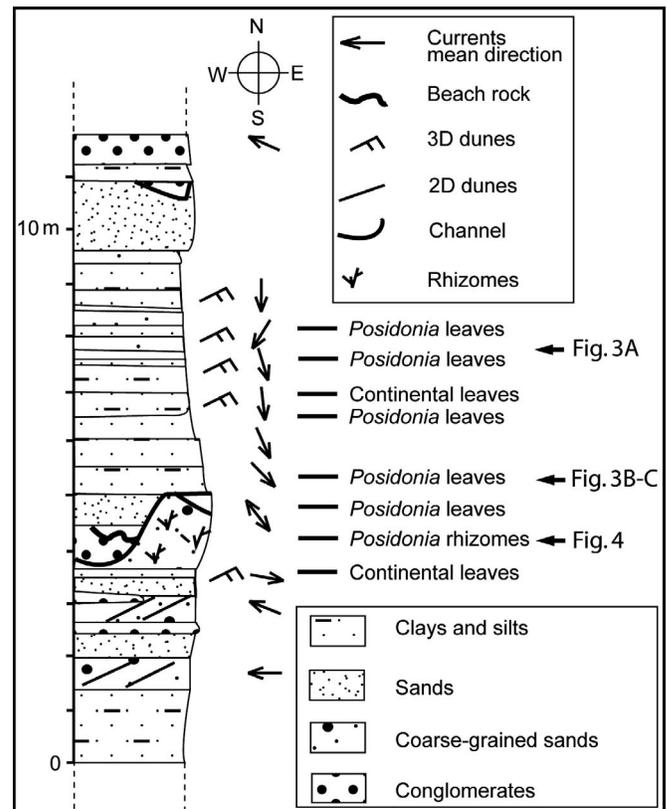
**TABLE 1**—Taxonomic diversity of major groups of organisms associated with recent *Posidonia oceanica* meadows. Numbers of potentially fossilizable species indicated in parentheses.

Taxonomic groups	Leaves	Rhizomes
Sponges	9 (0)	29 (0)
Cnidarians	27 (0)	26 (0)
Annelids	20 (1)	111 (1)
Gastropods	20 (18)	47 (40)
Bivalves	2 (2)	28 (28)
Bryozoans	73 (61)	108 (97)
Brachiopods	0	2 (2)
Ostracodes	15 (15)	30 (30)
Other crustaceans	0	84 (10?)
Echinoderms	3 (3)	20 (15?)
Tunicates	13 (0)	21 (0)
<b>Total</b>	<b>182 (100)</b>	<b>506 (223)</b>

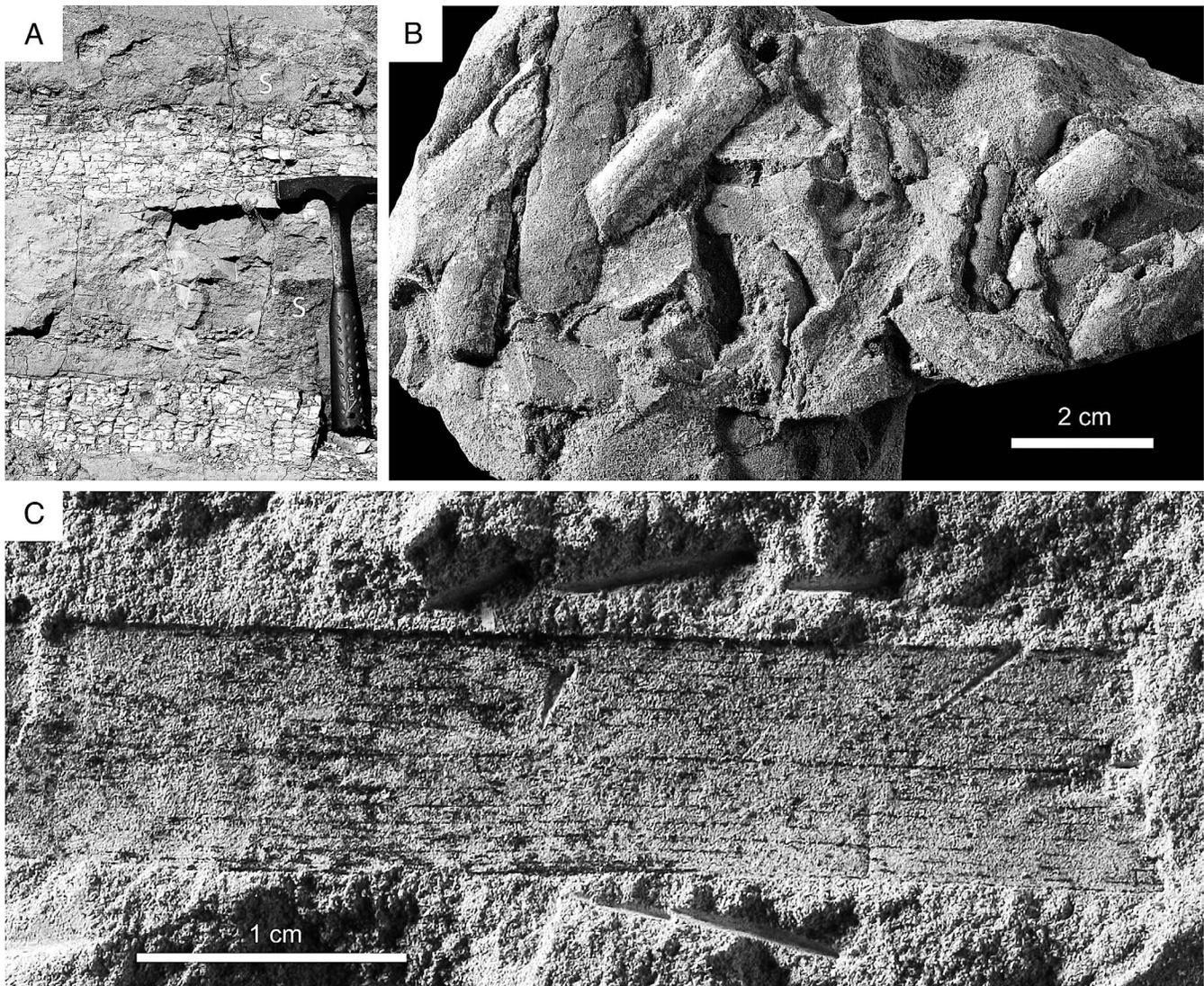
and pebble, with rare drowned beachrock blocks encrusted by various calcareous organisms. Most of the clastic material originates from the basement rocks found around Rhodes, which consist mostly of Mesozoic carbonates and ophiolites (Mutti et al., 1970b). Individual beds are a few centimeters to several decimeters thick, well stratified, and dip 5°–10° toward the SW. Some of the clayey and fine-grained sandy beds near the base of the section (Figs. 2, 3A) yield numerous seagrass remains in the form of leaf molds on which several types of epiphytic organisms are observable (Figs. 3B–C). Underlying these beds is a coarse-grained layer, some 80 cm thick, where rhizomes of *Posidonia oceanica* are fairly well preserved in the form of reddish to brownish horizontal and vertical branches (Fig. 4, arrows).

**MATERIAL AND METHODS**

The stratigraphic section at Kritika was first logged and measured. Eight blocks of ~2 kg each of poorly indurated sediment containing the



**FIGURE 2**—Detail log of seagrass-yielding beds in Kritika Bay.



**FIGURE 3**—Seagrass-leaf beds of Kritika Member. A) Outcrop photograph of one of sedimentary intervals containing fossil seagrass leaves within fine-grained sandy levels (S). Hammer shaft is 33 cm long. B) Photograph showing molds of *Posidonia oceanica* leaves with their numerous epiphytes (light-colored patches). Scale bar = 20 mm long. C) Detail view of a *P. oceanica* blade showing parallel carbonaceous marks of ribs.

seagrass-leaf molds and the rhizomes were collected from the outcrop and wrapped for transport and subsequent preparation. Photographs of the outcrop were made during fieldwork and macrophotographs of some of the seagrass leaves and rhizomes taken in the laboratory.

Fifteen sediment samples (clay and sand) also were collected to be washed and sieved on a column of 6 sieves with diminishing mesh size (from 2 mm to 0.063 mm). After drying, fossils were picked, isolated from each residue, and 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). For the bryozoans, each colony fragment was counted as one specimen, although some morphotypes may break into numerous pieces (erect growth forms), whereas others (encrusting and nodular) are mostly preserved as whole colonies. The results (faunal lists, abundances, and ecological groups) are summarized in Tables 2–6.

A simple grain-size distribution analysis was also performed on 10 sediment samples by weighing each granulometric fraction after sieving. The weight of the <0.063 mm fraction was obtained by subtracting the total weight of the six sieved residues from the dry weight of each treated sample. The averaged results for the sediments containing the leaves (N

= 5) and the rhizomes (N = 5) are summarized graphically in two histograms (Fig. 5).

The epiphytic organisms are found on the indurated matrix of the leaf molds, with the adaxial surfaces in the sediment and only the abaxial surface exposed (Figs. 3B–C). The material was prepared by first splitting the blocks of indurated sediment with a knife and then peeling off the specimens from the molds with double-sided adhesive tape. This procedure worked reasonably well in most cases, even if some of the specimens were incomplete. Attempts also were made with silicone rubber and epoxy resin, but the bonding substance was too strong and embedded a lot of sedimentary clasts together with the fossils. The best results, especially for fossils with comparatively pronounced relief, were obtained with methyl acetate gel glue. Well-preserved examples were mounted on pieces of cardboard or directly affixed to SEM mounts. After examination and identification of the fossils to genus or species level, some specimens were observed and photographed with a scanning electron microscope.

#### PRESENT-DAY SEAGRASSES AND THEIR ASSOCIATED COMMUNITIES

Recent seagrasses inhabit shallow depths on the continental platform of most temperate and warm-water oceans. Three associations are rec-



FIGURE 4—Field photograph of *Posidonia oceanica* rhizomes (arrows) within a coarse siliciclastic bed.

ognized among the recent marine phanerogams: *Cymodocea*, *Thalassia*, and *Zostera* (Brasier, 1975). The *Zostera* association consists predominantly of temperate-water forms and includes several genera in addition to *Posidonia*. Extant *Posidonia* is found only in the Mediterranean Sea and on the southern coasts of Australia. In the Mediterranean Sea, all three seagrass associations occur, but *Posidonia* is by far the most abundant genus, represented by one species, *P. oceanica* (L.) Delile.

*Posidonia oceanica* is a Mediterranean endemic species that lives from surface waters down to depths of ~30–40 m. As documented by numerous authors (e.g., Molinier and Picard, 1952; Kerneis, 1961; Peres and Picard, 1964; Eugène, 1978; Lepoint et al., 2000) *Posidonia* rhizomes and leaves provide numerous microenvironments for both sessile and vagile organisms. Covering the leaves and rhizomes are numerous and diverse bacteria and epiphytic algae including diatoms, Rhodophyta, Phaeophyta, and Chlorophyta (Boudouresque, 1968; Panayotidis, 1980; Boudouresque and Meinesz, 1982; Cinelli et al., 1984; Novak, 1984; Piazzini et al., 2002). Abundant filter-feeding protozoans and invertebrates also are attached to the leaves and the rhizomes. These range from foraminifers, sponges, cnidarians, and serpulid worms to mollusks, bryozoans, and ascidians. Vagile organisms (annelids, gastropods, polyplacophorans, crustaceans, and echinoderms) live on the rhizomes or climb and feed on the leaves but more often graze on the attached organisms and their detritus (Eugène, 1978; Mazzella and Russo, 1989; Lepoint et al., 2000). Soft-bottom epifaunal and infaunal elements also occur on and in the sediment where seagrasses grow, including mollusks, crustaceans, echinoderms, and fish (Harmelin, 1964; Harmelin-Vivien, 1984; Valle et al., 2001).

Detailed studies of the organisms associated with *Posidonia oceanica* show that biodiversity is always high (Kerneis, 1961; Reys, 1964; Harmelin, 1976; Hayward, 1976; Eugène, 1978; Boudouresque and Meinesz,

1982; Mazzella and Russo, 1989; Lepoint et al., 2000). In France and Italy, for example, 166 species of invertebrates have thus been identified on the leaves (Table 1). With a total of 506 species, the fauna associated with the rhizomes is still more diverse (Table 1). Many of these organisms are nonskeletal, and their preservation potential is extremely poor. With an estimated total number of at least 140 species, the bryozoans are probably the most diverse group of metazoans associated with the rhizomes and leaves of *Posidonia oceanica*. They have been the subject of various taxonomic and ecological studies, and, since most of them are skeletal, there is greater potential for preservation as fossils (Kerneis, 1961; Gautier, 1962; Harmelin, 1973, 1976; Hayward, 1976; Eugène, 1978; Geraci and Cattaneo, 1980; Zabala, 1986). The number of benthic foraminifers recorded from *Posidonia* meadows (rhizomes, leaves, and sediment) of the western and eastern Mediterranean reaches about 160 species (Blanc-Vernet, 1957, 1967, 1984; Langer, 1988, 1993; Ribes and Gracia, 1991). A few planktonic foraminifer species also live within the *Posidonia* beds (Blanc-Vernet, 1957; Ribes and Gracia, 1991).

## RESULTS

### Sediments

The deposits examined in this study (Fig. 2) are organized in siliciclastic sequences several meters in thickness, delimited by emersive surfaces marked by beachrock beds. The sediments have been assigned to three facies: (1) conglomerates characterized by 2D subaqueous dunes and channels prograding ESE to WNW; (2) sands and silts with asymmetrical current ripples and decimeter-sized 3D dunes indicative of deposition from currents with a general N-S to NW-SE direction; and (3) clays with planar lamination draping the sedimentary structures of the silty and sandy facies.

**TABLE 2**—Foraminifer species associated with fossil seagrass leaves and rhizomes (ecological data from Langer, 1993). Relative faunal abundance: x = rare; xx = present, xxx = common. See text for further explanation.

Species-Ecology	Leaves	Rhizomes
Sessile:		
<i>Nubecularia lucifuga</i> DeFrance	xxx	—
<i>Planorbulina acervalis</i> (Brady)	xx	—
<i>Planorbulina mediterraneensis</i> d'Orbigny	xx	—
<i>Sorites</i> sp.	x	—
Temporarily motile:		
<i>Asterigerinata mamilla</i> (Williamson)	x	x
<i>Asterigerinata planorbis</i> (d'Orbigny)	xx	—
<i>Cibicides lobatulus</i> (Walker & Jacob)	xxx	x
<i>Cibicides refulgens</i> de Montfort	xx	—
<i>Discorbis</i> sp.	x	—
<i>Rosalina bradyi</i> (Cushman)	xx	x
<i>Rosalina globularis</i> d'Orbigny	xxx	xx
Permanently motile:		
<i>Anomalinoidea ornatus</i> (Costa)	—	x
<i>Discorbinella bertheloti</i> (d'Orbigny)	x	—
<i>Gavelinopsis lobatulus</i> (Parr)	x	—
<i>Globulina fissicostata</i> Cushman & Ozawa	—	x
<i>Globulina gibba</i> (d'Orbigny)	—	x
<i>Elphidium crispum</i> (L.)	xx	x
<i>Elphidium macellum</i> (Fichtel & Moll)	xxx	x
<i>Miliolinella elongata</i> Kruit	x	—
<i>Nonion depressulum</i> (Walker & Jacob)	x	x
<i>Peneroplis</i> sp.	x	—
<i>Pyrgo depressa</i> (d'Orbigny)	x	—
<i>Quinqueloculina agglutinans</i> d'Orbigny	x	—
<i>Quinqueloculina lamarciana</i> d'Orbigny	x	x
<i>Quinqueloculina oblonga</i> (Montagu)	x	—
<i>Quinqueloculina seminulum</i> (L.)	x	—
<i>Spiroloculina</i> sp.	x	—
<i>Triloculina austriaca</i> d'Orbigny	x	—
<i>Triloculina gibba</i> d'Orbigny	x	—
<i>Triloculina</i> sp.	x	—
Shallow infaunal:		
<i>Ammonia beccarii</i> (L.)	xxx	xxx
<i>Lenticulina</i> cf. <i>peregrina</i> (Schwager)	x	—
<i>Reussella spinulosa</i> (Reuss)	x	—
<i>Valvulineria complanata</i> (d'Orbigny)	x	x

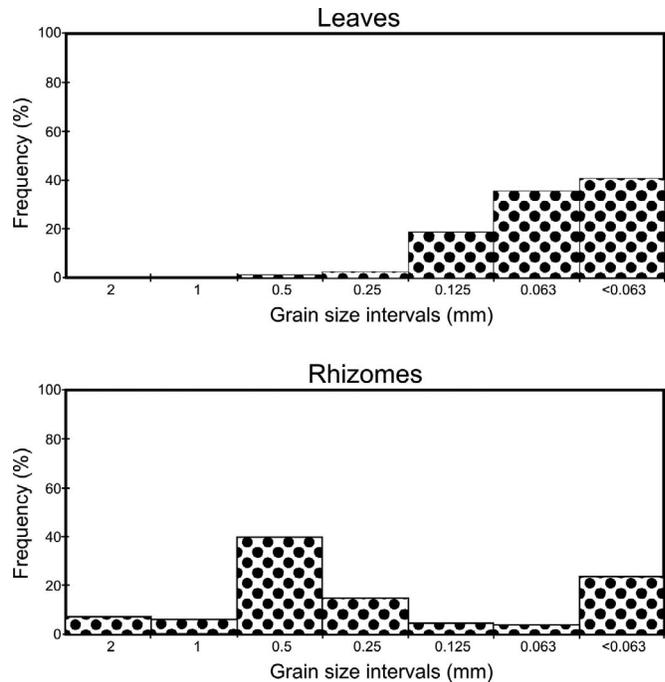
The *Posidonia* leaves are preserved mostly within beds of fine-grained laminated sand containing a high proportion of silt and clay; these are intercalated with thin argillaceous horizons (Fig. 3A). The alternation of high-energy sands with clayey horizons suggests that sedimentation was predominantly controlled by storms.

The *Posidonia* rhizome-bearing bed is a lens of coarse-grained sandstone that is eroded at the top and covered by conglomerate or sandstone (Fig. 4). This siliciclastic sediment contains a skeletal component and has a pronounced bimodal grain-size distribution (Fig. 5) typical of facies associated with recent seagrass meadows (Wanless, 1981; Jeudy de Gris-sac, 1984; Canals and Ballesteros, 1997; De Falco et al., 2003; Pomar et al., 2004; Perry and Beavington-Penney, 2005).

On the whole, the sediments are poorly sorted and contain a significant proportion of clay. The deposit types and their spatial organization suggest that sedimentation took place on a wide, flat, and muddy shallow shelf and was affected by high-energy events (floods and tempests). Sediment input came from the continent situated to the SW (Fig. 1C), with local re-sedimentation events triggered by WNW-ESE-trending flood currents, whereas marine currents with a general N-S to NW-SE direction transported the material from the open sea toward the shore.

#### Seagrass Leaves

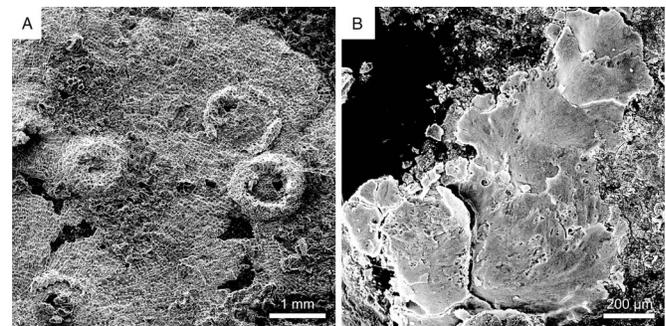
Molds of seagrass leaves are abundant in several clayey and fine-grained sandy beds of the studied exposure. The diverse assemblage of



**FIGURE 5**—Histograms displaying percentage of each grain-size group for sediments with leaf and rhizome samples.

calcareous algae, foraminifers, mollusks, tube worms, and bryozoans (preserved on the leaves or in the associated sediment) points to a community of organisms adapted to the unique conditions existing on *Posidonia* leaves. Allochthonous minor components include organisms transported from other marine environments and to a lesser extent from the continent.

**Preservation State.**—The fossil leaves of *Posidonia oceanica* are preserved on the bedding planes as molds a few centimeters long and approximately 1 cm wide. They are unordered and densely packed upon one another (Fig. 3B), although a slight preferred orientation is sometimes observable (N30°E to N300°E, N = 40). The surface of the molds is generally colored red by iron oxides (possibly due to groundwater flow after deposition). The characteristic venation of the bladelike leaves is preserved under the form of parallel carbonaceous lines (Fig. 3C). On the basis of the width of the blades (~1 cm) and the number of ribs (mean = 14), the fossil leaves were identified as belonging to *P. oceanica*. The seagrass leaves are absent to rare in the clay intervals, whereas they are rare, present, or abundant in the fine-grained sandy beds. Thin crusts of calcareous coralline algae are often observed, whereas encrusting foraminifers and invertebrates (serpulid worms and bryozoans) are found attached to the molds (Figs. 6–8) and preserved in their original calcitic mineralogy.



**FIGURE 6**—Encrusting calcareous algae on seagrass blades. A) *Dermatomolithon littorale*. B) *Pneophyllum fragile*.

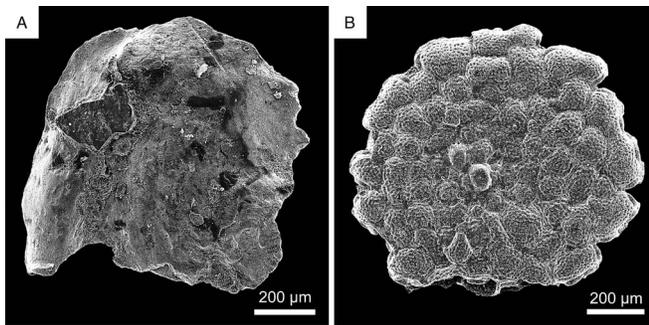


FIGURE 7—Encrusting foraminifers found in sediment containing seagrass leaves. A) *Nubecularia lucifuga*. B) *Planorbulina mediterraneensis*.

All encrusting fossils are fairly well preserved, but always upside down with their upper surface buried into the poorly indurated sediment of the molds and only their under surface visible (Figs. 3B–C). This peculiar mode of fossilization made the preparation of the specimens somewhat more difficult but also had the great advantage of allowing very fragile organisms to be preserved. The upper surfaces of these specimens were imbedded in the fine-grained sediment and protected. As a consequence, four species of bryozoans (*Collarina balzaci*, *Electra posidoniae*, *Fenestulina joannae*, and *Haplopoma impressum*) are reported for the first time in the fossil state, their skeleton being otherwise too thin and fragile to be fossilized. This is also the case for two crustose calcareous red algae: *Pneophyllum fragile* and *Dermatolithon litorale*.

**Associated Organisms.**—Among the sessile organisms, the algal epiphytes are represented by thin calcified encrusting Rhodophyta (Corallinaceae, Melobesioideae). These constitute a large part of the leaf epiphytic biomass, with *Pneophyllum fragile* Kützing (= *Fosliella lejolisii* (Rosanoff)) and *Dermatolithon litorale* Suneson (Fig. 6) being very abundant. Both are very characteristic epiphytes on leaves of extant *Posidonia oceanica* (Peres and Picard, 1964; Panayotidis, 1980).

Numerous benthic foraminifers assigned to 31 species have been recognized, either attached to the seagrass blades or in the associated sediment (Table 2; Fig. 7). Among the most frequent are taxa that belong to the disc-shaped sessile (encrusting) or temporarily motile forms. These include *Cibicides lobatulus*, *Discorbis* sp., *Nubecularia lucifuga*, *Planorbulina acervalis*, *P. mediterraneensis*, *Rosalina bradyi*, *R. globularis*, and *Sorites* sp. Permanently motile species, especially elphidiids and miliolids, and rare infaunal species also occur. Planktonic foraminifers are, however, conspicuously absent. Although species of disc-shaped sessile or temporarily motile foraminifers do not live exclusively on seagrass leaves, they are common inhabitants. In addition, there are also many reports of epiphytic foraminifers (for example, elphidiids, miliolids, and rotaliids) commonly associated with present-day seagrass beds (Blanc-Vernet, 1957, 1984; Wright and Murray, 1972; Brasier, 1975; Eva, 1980; Langer, 1988, 1993; Ribes and Gracia, 1991). The presence of the above-mentioned microfauna in the Pliocene sediments is thus indirect evidence of a fossil seagrass community.

The serpulid worms are only represented by the small encrusting coiled tubes of *Spirorbis* sp. They are relatively common on the seagrass blades. This species does not live only on *Posidonia oceanica* leaves but is extremely common on modern seagrass leaves (Kerneis, 1961; Peres and Picard, 1964). It has also been reported from several fossil seagrass occurrences (Radócz, 1972; Ivany et al., 1990).

The bivalves are represented by 10 species (Table 3). The most abundant are the deep infaunal *Anodontia fragilis*, three epibyssate forms, and the temporary epibyssate *Lima inflata*. Shallow sediment dwellers also occur. All these species are suspension feeders, except for *Anodontia fragilis*, which has a mixotrophic or chemosymbiotic diet. The co-occurrence of bivalves, such as *Venus verrucosa*, *Lissopecten hyalinus*, *Lima inflata*, *Chlamys multistriata*, and *C. varia*, distinctively characterize *Posidonia*-vegetated zones today (Harmelin, 1964; Peres and Picard,

TABLE 3—Bivalve species associated with fossil seagrass leaves and rhizomes. Relative faunal abundance: x = rare; xx = present, xxx = common; xxxx = abundant. See text for further explanation.

Species-Ecology	Leaves	Rhizomes
Deep infaunal:		
<i>Anodontia fragilis</i> (Philippi)	xxx	x
<i>Ctena decussata</i> Costa	—	x
<i>Divaricella divaricata</i> (L.)	—	x
<i>Thracia papyracea</i> (Poli)	—	x
Shallow infaunal:		
<i>Ervillia</i> sp.	—	x
<i>Glycymeris pilosa</i> (L.)	—	xx
<i>Gouldia minima</i> (Montagu)	x	—
<i>Nucula nucleus</i> (L.)	—	xx
<i>Nucula sulcata</i> Bron	—	xx
<i>Plagiocardium papillosum</i> (Poli)	x	—
<i>Spaniorinus</i> sp.	—	xx
<i>Timoclea ovata</i> (Pennant)	x	x
<i>Venus verrucosa</i> (L.)	x	xxx
Epibyssate:		
<i>Barbatia barbata</i> (L.)	—	xx
<i>Barbatia pulchella</i> (Reeve)	—	x
<i>Chlamys multistriata</i> (Poli)	xxx	xxxx
<i>Chlamys varia</i> (L.)	x	xxxx
<i>Lima inflata</i> (Chemnitz)	x	—
<i>Lissopecten hyalinus</i> (Poli)	x	xxxx
<i>Palliolium excisum</i> (Bronn)	x	xxx
Encrusting:		
<i>Anomia ephippium</i> L.	—	xx
<i>Ostrea lamellosa</i> Brocchi	—	x
Mobile:		
<i>Erycina</i> sp.	—	x
<i>Notolimea</i> sp.	—	x

1964). The abundance of the deep-burrowing *Anodontia fragilis* suggests exhumation and transport of the shells during storms.

The benthic gastropod assemblage of 19 species (Table 4) is dominated by small climbing herbivorous forms, most of them grazing on epiphytes. Very rare planktonic species also occur (pteropods and *Janthina fragilis*). The great abundance of the herbivorous forms *Gibbula fanulum*, *G. umbilicaris*, *Jujubinus striatus*, and *Tricolia speciosa*, together with the carnivorous *Calliostoma laugierii* and *C. zizyphinum*, also typify the environment of modern *Posidonia oceanica* meadows, as their recent representatives usually live on these seagrass leaves (Russo et al., 1984; Mazzella and Russo, 1989).

With a total of 25 species, the bryozoans are the more diverse group of invertebrates. Encrusting morphotypes were observed on most of the leaves and are very abundant (Table 5; Fig. 8). Segments of erect articulated bryozoans (*Crisia* spp.) and colonies or fragments of other encrusting forms also were found in the sediment. Three extant species are obligate epiphytes of *Posidonia oceanica* leaves: *Collarina balzaci*, *Electra posidoniae*, and *Fenestulina joannae* (Gautier, 1954, 1962; Kerneis, 1961; Peres and Picard, 1964; Eugène, 1978; Geraci and Cattaneo, 1980). These species may be considered as truly diagnostic of seagrass leaves. A fourth species, *Haplopoma bimucronatum*, lives either at depths of ~10–30 m on *Posidonia oceanica* leaves or ~80–90 m on deep-water kelps (Gautier, 1962). Several other species, although not associated exclusively with seagrass communities, generally thrive on the leaves and rhizomes of this marine phanerogam; these include *Aetea sica*, *Calpensia nobilis*, *Crisia* spp., *Disporella hispida*, *Schizomavella aicularata*, *Tubulipora liliacea*, *Tubulipora plumosa*, and *Watersipora subovoidea* (Kerneis, 1961; Gautier, 1962; Peres and Picard, 1964; Harmelin, 1973, 1976; Hayward, 1976; Eugène, 1978; Geraci and Cattaneo, 1980).

The ostracodes are relatively abundant in the sediment associated with

**TABLE 4**—Marine gastropod species associated with fossil seagrass leaves and rhizomes. Relative faunal abundance: x = rare; xx = present, xxx = common. See text for further explanation.

Species-Ecology	Leaves	Rhizomes
Herbivorous:		
<i>Bittium reticulatum</i> (da Costa)	xx	—
<i>Circulus</i> sp.	x	—
<i>Gibberula miliaria</i> (L.)	xx	—
<i>Gibbula ardens</i> (von Salis)	xxx	xx
<i>Gibbula fanulum</i> (Gmelin)	xxx	—
<i>Gibbula umbilicaris</i> (L.)	xxx	—
<i>Hydrobia</i> sp.	x	—
<i>Jujubinus striatus</i> (L.)	xxx	xxx
<i>Tornus</i> sp.	xxx	—
<i>Truncatella subcylindrica</i> L.	xx	—
<i>Tricolia pullus pullus</i> (L.)	xx	—
<i>Tricolia speciosa</i> (von Mühlfeldt)	xx	—
Carnivorous:		
<i>Calliostoma laugierii</i> (Payraudeau)	xxx	—
<i>Calliostoma zizyphinum</i> (L.)	xxx	—
<i>Nassarius limatus</i> Deshayes	xx	—
Suspension feeder:		
<i>Calyptraea chinensis</i> L.	x	—
Planktonic:		
<i>Cavolinia gibbosa</i> (Rang)	x	—
<i>Clio</i> sp.	x	—
<i>Janthina fragilis</i> (Lamarck)	xxx	—

the leaves (Table 6). Nevertheless, this group is not very diverse (only 12 species identified), and no species can be considered as specific to seagrass meadows. The exceptional abundance of *Xestoleberis communis*, together with *Aurila convexa*, *Bairdia longevaginata*, *Loxoconcha affinis*, and *L. stellifera*, may, however, be used as an indicator for the presence of seaweeds or seagrasses (Reys, 1964; Lachenal, 1989; Hajjaji et al., 1998; Saint Martin et al., 2000).

Always rare, various skeletal remains of other groups of marine organisms are present in the associated sediment: segments of geniculate calcareous algae, echinoid spines, and crab claws. The fossil assemblage also includes organisms transported from continental areas, including extremely rare freshwater charophycean oogonia and ostracodes (*Candona* sp., *Ilyocypris* sp.), rare plant remnants (*Quercus* sp. and other angiosperms), and some terrestrial gastropods (*Isthmia* cf. *villafanchiana*).

#### Seagrass Rhizomes

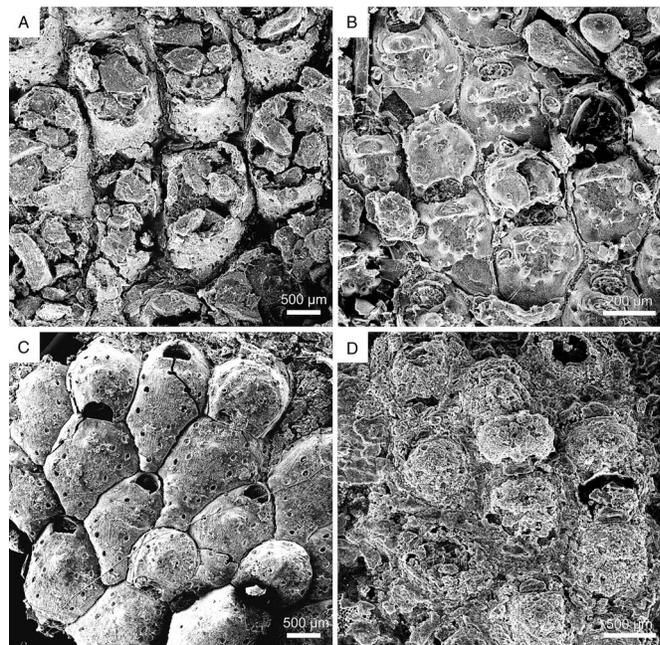
Unlike the leaves, the rhizomes were buried in life position within a fine- to coarse-grained argillaceous, sandy, gravely, and fossiliferous bed (Fig. 4). The associated thanatocoenosis is formed of a single autochthonous community consisting of organisms that lived either on the rhizomes (foraminifers, bivalves, gastropods, bryozoans, ostracodes) or in connection with the sediment (foraminifers, bivalves, ostracodes).

**Preservation State.**—The fossil rhizomes occur as connected horizontal and vertical branches several decimeters long and approximately one centimeter in diameter (Figs. 4, 9). The stratigraphic position of the rhizomes provides evidence that this material was preserved *in situ*, probably after severe scouring of the top of the bed, immediately followed by rapid burial in coarse-grained sediments (Fig. 10). Like the leaf molds, the fossil rhizomes are colored red by iron oxides. Careful scrutiny reveals that they consist of a carbonate core on which short (0.5 to 2 mm) internodes are visible (Fig. 9).

As noted by Molinier and Picard (1952) and Peres and Picard (1964), *Posidonia oceanica* rhizomes have a life span of several centuries and, once embedded in the sediment, do not decay easily. In the study site, this may explain their relatively good preservational state and *in situ*

**TABLE 5**—Bryozoan species associated with fossil seagrass leaves and rhizomes. Relative faunal abundance: x = rare; xx = present, xxx = common; xxxx = abundant; xxxxx = very abundant. See text for further explanation.

Species-Growth forms	Leaves	Rhizomes
Encrusting:		
<i>Aetea sica</i> (Couch)	x	—
<i>Annectocyma major</i> (Johnston)	xx	x
<i>Calpensia nobilis</i> (Esper)	x	x
<i>Collarina balzaci</i> (Audouin)	xxx	—
<i>Cryptosula pallasiana</i> (Moll)	x	—
<i>Disporella hispida</i> (Fleming)	xx	—
<i>Electra posidoniae</i> Gautier	xxx	—
<i>Escharina vulgaris</i> (Moll)	x	—
<i>Fenestulina joannae</i> (Calvet)	x	—
<i>Haplopoma impressum</i> (Audouin)	xx	—
<i>Patinella radiata</i> (Audouin)	xx	x
<i>Rhynchozoon</i> sp.	x	—
<i>Schizomavella auriculata</i> (Hassall)	x	—
<i>Schizoporella longirostris</i> Hincks	x	x
<i>Trypostega rugulosa</i> (Reuss)	—	x
<i>Tubulipora liliacea</i> (Pallas)	x	x
<i>Tubulipora plumosa</i> Harmer	xx	x
<i>Umbonula ovicellata</i> (Hastings)	—	xx
<i>Watersipora complanata</i> (Norman)	—	x
<i>Watersipora subovoidea</i> (d'Orbigny)	x	—
Erect articulated:		
<i>Crisia fistulosa</i> Heller	xxxxx	xx
<i>Crisia</i> cf. <i>occidentalis</i> Trask	xxxxx	—
<i>Crisia sigmoidea</i> Waters	xxxx	xx
<i>Crisia</i> sp. 1	xxx	—
<i>Crisia</i> sp. 2	xx	x
<i>Margaretta cereoides</i> (Ellis & Solander)	x	xx
Erect bilaminar:		
<i>Metrarabdotos moniliferum</i> (Milne Edwards)	x	xxxxx
Erect cylindrical:		
<i>Entalophoroecia deflexa</i> (Couch)	x	x
Nodular:		
<i>Celleporina costazi</i> (Audouin)	—	x



**FIGURE 8**—Encrusting bryozoans on seagrass blades. A) *Electra posidoniae*. B) *Collarina balzaci*. C) *Haplopoma impressum*. D) *Fenestulina joannae*.

**TABLE 6**—Marine ostracode species associated with fossil seagrass leaves and rhizomes. Relative faunal abundance: x = rare; xx = present, xxx = common; xxxx = abundant. See text for further explanation.

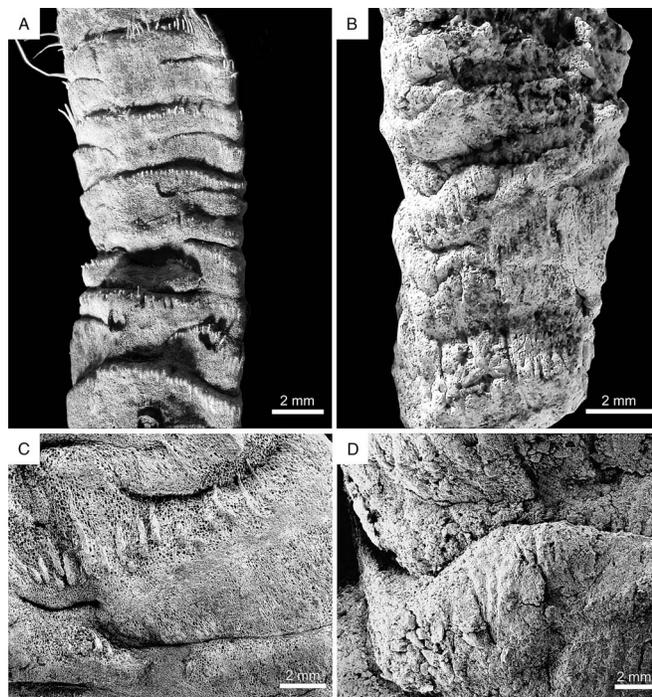
Species-Ecology	Leaves	Rhizomes
Phytic:		
<i>Bairdia longevaginata</i> Müller	x	x
<i>Loxoconcha</i> cf. <i>affinis</i> (Brady)	x	—
<i>Loxoconcha stellifera</i> Müller	xx	—
Opportunistic:		
<i>Acanthocythereis</i> sp.	x	—
<i>Aurila convexa</i> (Baird)	xx	x
<i>Aurila</i> sp.	x	x
<i>Carinocythereis</i> sp.	x	—
<i>Pontocythere elongata</i> (Brady)	x	—
<i>Urocythereis</i> sp.	xx	x
<i>Xestoleberis communis</i> Müller	xxxx	x
Opportunistic euryhaline:		
<i>Cyprideis torosa</i> (Jones)	x	—
<i>Loxoconcha elliptica</i> Brady	x	—

growth position within the coarse siliciclastic and calcareous material trapped by the network of horizontal and vertical rhizomes.

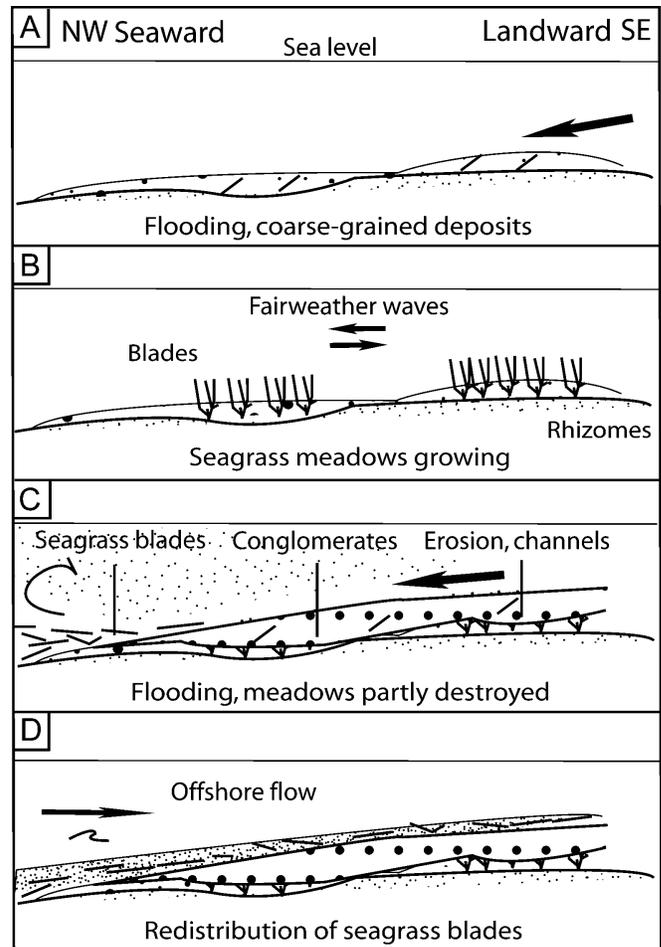
Despite their life position and the preservation of fine surficial details, *Posidonia oceanica* rhizomes do not compare in preservational quality with that of the leaves. For instance, neither roots nor *in situ* epiphytic organisms are recognizable. As shown on Figure 9, however, fine details are discernible that closely resemble those observable on living plants.

**Associated Organisms.**—Only 13 foraminifer species were found in the sediment preserving the rhizomes of *Posidonia oceanica*. All taxa are permanently or temporarily motile, and some are infaunal (Table 2). Although impoverished, this foraminiferal assemblage is relatively typical of Mediterranean seagrass rhizomes and sediments (Blanc-Vernet, 1957, 1967, 1984; Langer, 1988, 1993; Ribes and Gracia, 1991).

The bivalves (Table 3) are relatively numerous and diverse (21 species



**FIGURE 9**—Macrophotographs and SEM images of living (water depth of about 2 m off Rhodes, A, C) and fossil (B, D) rhizomes of *Posidonia oceanica*.



**FIGURE 10**—Reconstruction of depositional settings at different stages of seagrass bed formation. After A) initial flood event, B) seagrass community was established; C) it was subsequently destroyed and D) redistributed following another flood and storm event.

compared to only 10 species associated with the leaves). The most common taxa are the shallow infaunal *Glycymeris pilosa*, *Nucula*, *Spaniorinus* sp., *Venus verrucosa*, the epibyssate *Barbatia*, *Chlamys*, *Lissopecten hyalinus*, *Palliolium excisum*, and the encrusting *Anomia ephippium*. *Venus verrucosa* is regarded as specific to the Mediterranean *Posidonia* meadows (Harmelin, 1964). *Lissopecten hyalinus*, *Anomia ephippium*, and *Barbatia barbata* also are considered usually as characteristic members of the epiphyte fauna living on *Posidonia* rhizomes. Finally, *Chlamys*, *Palliolium excisum*, and *Ctena decussata* often are found in the same environment.

The most abundant skeletal organisms are bryozoans (Table 5). They are represented by an assemblage of 16 species where the erect rigid bilaminar *Metrarabdotos moniliferum* is probably the most distinctive. This species belongs to a tropical genus (Cheetham, 1967), and its occurrence in abundance points to warmer seawater temperatures than in the present-day Mediterranean. Although not occurring solely in the seagrass environment, *M. moniliferum* probably found favorable sheltered conditions within *Posidonia oceanica* meadows. Several other colonial morphotypes also occur: encrusting (nine species), erect articulated (*Crisia* spp. and *Margaretta cereoides*), erect rigid cylindrical (*Entalophoroecia deflexa*), and rare nodular colonies of a small celeropod (*Celleporina costazi*). None of these taxa can be considered as characteristic of the epiphytic bryozoan fauna.

The ostracodes (Table 6) are represented by a small number of

individuals and species, among which only *Bairdia longevaginata* may be considered as truly epiphytic (Lachenal, 1989; Hajjaji et al., 1998).

The sediment also preserves gastropods (only 2 species: Table 4), rare fragments of calcareous coralline algae, echinoid plates and spines, and decapod crustacean articles and claws.

## DISCUSSION

### Comparison with Recent Mediterranean *Posidonia* Meadows

A detailed comparison with the present-day community of organisms associated with *Posidonia oceanica* meadows is hampered by the fact that: (1) published studies of the recent analogues encompass a much wider area; (2) sampling was stretched over several decades by many researchers; (3) the number of samples is clearly much higher; and (4) samples were routinely collected from water depths ranging from 0 to 60 m. Moreover, most published research has been descriptive with little or no quantitative information available.

The recent *Posidonia oceanica* meadows provide habitats for a diverse biota estimated at some 350 potentially fossilizable (well-calcified) taxa (Table 1). Although relatively poor by comparison (121 species), the taxonomic diversity of the fossil skeletal assemblage recovered from the upper Pliocene of Rhodes shows a variety of distinctive characters that compare well in terms of major skeletal components with present-day seagrass communities. For example, within the foraminiferal assemblage of 34 taxa (Table 2), of the 29 identified to species level, 27 are extant and 18 occur in both fossil and recent *P. oceanica* beds. Benthic gastropods are represented by 16 taxa (3 left in open nomenclature, Table 3), with 11 species common to both communities. Among the bivalves, 20 taxa identified to species level (Table 4) are extant, and 9 occur in both fossil and extant seagrass meadows. Bryozoans are represented by a total of 29 species (Table 5), including 3 in open nomenclature. Of the total, 2 occur as fossils, and only 1 extant species has never been reported from present-day *P. oceanica* meadows. The fossil ostracode assemblage of 12 species (Table 6) is much poorer, and only 3 species occur in both communities. The general composition of the fossil assemblage is relatively characteristic of modern Mediterranean *P. oceanica* meadows. A number of species may even be considered as distinctively specific to the seagrass leaves, especially among the sessile disc-shaped foraminifers, the small herbivorous gastropods, and the encrusting bryozoans.

A comparison between the fossils from the late Pliocene of Rhodes and present-day *Posidonia oceanica* communities suggests that some of the elements belonging to the original biocoenosis are absent. Not preserved are many soft-bodied or poorly calcified sessile epibionts such as macrophytic algae, sponges, hydroids, sea anemones, ctenostome bryozoans, and tunicates (Table 1). A number of skeletal vagile and sessile invertebrate groups are also uncommon or totally lacking: polyplacophorans, brachiopods, echinoids, and ophiuroids. Fish skeletal remains were not recovered, although numerous species inhabit present-day *Posidonia oceanica* meadows (e.g., Harmelin-Vivien, 1984; Valle et al., 2001). The lack of these organisms may be explained by detrimental environmental conditions (see below).

These *Posidonia*-rich beds testify to the presence on the shelf of Rhodes of an already well-established and widespread seagrass community with biotopes comparable to those of the present-day Mediterranean. It also suggests that no significant change occurred within this community for the last two million years.

### Depositional Settings and Reconstruction of the Paleoenvironment

Based on comparisons with modern *Posidonia oceanica* meadows and more generally on seagrass beds, the Kritika seagrasses were probably living in nearshore shallow water, normal salinity environments. Although planktonic foraminifers were not recovered, relatively open marine conditions are indicated by the occurrence of pteropod remains.

An analysis of the organisms associated with *Posidonia* leaves shows

that the studied thanatocoenosis is in fact a mixture of paleocommunities, as evidenced by the presence of organisms that normally live in seagrass meadows, along with those from other shallow-water marine environments and some that were transported from the continent. Numerous invertebrates found living in the same environment as seagrasses can also occur in other habitats. Among these are foraminifers (e.g., *Elphidium*, *Globulina*, *Peneroplis*, *Quinqueloculina*, and *Triloculina*), gastropods (*Truncatella subcylindrica*), bivalves (e.g., *Anodontia fragilis*, *Gouldia minima*, *Chlamys multistriata*, and *C. varia*), and bryozoans (e.g., *Annectocyma major*, *Patinella radiata*, *Schizomavella auriculata*, and *Schizoporella longirostris*). In the late Pliocene of Rhodes, these organisms could have lived within the *Posidonia oceanica* biotope or could have been transported from nearby habitats and deposited with the leaves. Leaf fragmentation and a predominantly chaotic spatial distribution (Fig. 3B) also indicate that deposition occurred after transport. The leaves of seagrasses are shed annually, especially as a result of trauma during autumn and winter storms, and are commonly transported outside the environment of growth, either offshore or onshore to beaches where they accumulate (Peres and Picard, 1964; De Falco et al., 2003). The vulnerability of the leaves to wave disturbance may be increased by the growth of the epiphytes (Peres and Picard, 1964; Eugène, 1978), even though the majority are of small size (maximum of 1 cm). Together with the sedimentary evidence, these features indicate that most of the organisms lived as epibionts on the seagrass blades and were transported with the leaves, probably during storms or floods, before accumulation and rapid burial in a shallower setting (Fig. 10). Distance of transport was probably not very great, because the diversity of associated mollusks is relatively high, despite their small size and the fact that most were not cemented to the leaves. A small number of remains from other environments (terrestrial and pelagic) were, however, incorporated into the same sediment. A number of well-calcified bryozoan taxa that are not strictly epiphytic but which commonly occur on recent *P. oceanica* leaves (and in numerous Plio-Pleistocene deposits in Rhodes), however, are missing (e.g., *Cellaria salicornioides*, *Chorizopora brongniarti*, *Fenestulina malusi*, *Puellina gattyae*, *Scrupocellaria* spp.). Their absence suggests less than optimal environmental conditions, for example, in shallow and turbid waters at a depth of ~10 meters (Harmelin, 1976; Eugène, 1978).

With only 57 species, the autochthonous skeletal assemblage associated with the fossil rhizomes is less diverse (except for the bivalves) than that seen in the leaf levels. This number is also considerably smaller than the several hundred species reported from the present-day Mediterranean, even taking into account that many of the extant species are nonskeletal and the samples much larger (Kerneis, 1961; Reys, 1964; Harmelin, 1976; Hayward, 1976; Eugène, 1978; Boudouresque and Meinesz, 1982; Mazzella and Russo, 1989; Lepoint et al., 2000). The relatively impoverished fossil assemblage, together with the absence of taxa commonly occurring in *Posidonia* meadows, probably indicates shallow and turbid waters where rapid rates of sediment accumulation eliminated most of the species usually associated with this environment. Moreover, the bed containing the rhizomes is truncated at the top, suggesting that some of the flora and fauna may have been removed and deposited elsewhere.

Based on sedimentological and paleontological characteristics together with biological data from the literature, the strata at the study site are interpreted as deposited on a wide and shallow muddy shelf where *Posidonia*-vegetated patches developed in a shoreface setting, only to be destroyed during high-energy events. The environment was further disturbed by a temporary influx of terrestrial material (and possibly fresh water) during flood season, causing greater turbidity and a concomitant reduction in diversity within the seagrass community. Increased stress on marine organisms would also occur during storms. This interpretation is corroborated by the high siliciclastic content of the fine-grained sediments, the sedimentary structures, and the presence of continental and freshwater organisms among the biogenic components associated with *Posidonia* leaves.

### Recognizing Seagrass Beds in the Fossil Record

Direct evidence of seagrass beds is extremely rare in the fossil record, but their former presence can be deduced by the occurrence of characteristic biological components. Thus, several groups of organisms have been proposed as possible indicators of seagrass-vegetated environments in the rock record: calcareous algae (Beavington-Penney et al., 2004; Perry and Beavington-Penney, 2005), foraminifers (Brasier, 1975; Hoffman, 1979; Eva, 1980; Blanc-Vernet, 1984; Langer, 1993; Clarke et al., 1996; Betzler et al., 1997; Haunold et al., 1997; Lukasik et al., 2000; Saint Martin et al., 2000; Cann et al., 2002), mollusks (Baluk and Radwanski, 1977; Hoffman, 1979; Lukasik et al., 2000), bryozoans (Voigt, 1981; Lukasik et al., 2000), ostracodes (Hajjaji et al., 1998; Saint Martin et al., 2000), and even herbivorous marine mammals (Domning, 2001). Taphonomic features observable on mollusk shells (encrustation, bio-erosion, dissolution, abrasion) have also been suggested as a proxy for recognizing fossil seagrass beds (Leonard-Pingel, 2005). Various sedimentary characteristics, especially a bimodal grain-size distribution with abundant silt, coarser siliciclastics, and biogenic carbonate material, may also hint at the presence of seagrass beds (Wanless, 1981; Jeudy de Grissac, 1984; Fornos et al., 1992; Pomar, 2001; Pomar et al., 2002; De Falco et al., 2003).

In Rhodes, with the exception of one bed in a nearby section of the same formation where rhizomes have been found, seagrass leaves or rhizomes are not preserved in other levels of the Kritika Member. Some evidence indicates, however, that similar communities existed during the late Pliocene. The co-occurrence of geniculate coralline red algae, discoidal foraminifers (*Cibicides*, *Discorbis*, *Nubecularia*, *Planorbulina*, *Peneroplis*, *Rosalina*, *Sorites*), infaunal and epibyssate bivalves (*Chlamys*, *Lissopecten hyalinus*, *Lima inflata*, *Venus verrucosa*), small herbivorous (*Gibbula*, *Jujubinus*, *Tricolia*) and carnivorous (*Calliostoma*) gastropods, encrusting and articulated bryozoans (*Calpensia nobilis*, *Crisia*, *Disporrella hispida*, *Patinella radiata*, *Tubulipora*), and ostracodes (*Aurila*, *Bairdia*, *Loxocochlea*), within poorly sorted terrigenous sediments, may possibly point to the existence of other ancient *Posidonia* meadows.

### CONCLUSIONS

This study documents an exceptionally well-preserved example of fossil seagrass rhizomes, leaves, epiphytic algae, foraminifers, and invertebrates. A diverse skeletal assemblage of 121 species belonging to 7 main groups was recovered from the sampled interval of the late Pliocene Kritika section of Rhodes, with the organisms still preserved in their original aragonitic or calcitic mineralogy. Among the organisms associated with the fossil leaves, a number are found consistently on leaves of present-day *Posidonia oceanica* and some are even obligative epiphytes of this marine phanerogam.

The fortuitous preservation of the leaves with their associated community indicates that the assemblage underwent minimal postmortem transport before rapid burial in fine-grained sediment, probably occurring during flooding events or storms. A rapid burial in coarse but poorly sorted sediment and the slow decay of the rhizomes may explain their preservation *in situ* with some of the associated organisms.

Although lower in diversity than modern communities, the Pliocene skeletal assemblage shows distinctive characters that compare well with recent *Posidonia oceanica* meadows. A number of species, especially among the foraminifers, gastropods, and bryozoans, are even considered specific to seagrass leaves. The occurrence of these distinctive components in the geologic record could potentially be used to identify additional fossil seagrass beds.

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