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Pliocene and Pleistocene shallow-water chitons (Mollusca) from Rhodes Island, Greece

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With 11 figures and 1 table

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Abstract: The polyplacophoran faunas from the Pliocene and Pleistocene deposits of Rhodes Island (Aegean Sea, Greece) are described for the first time. Thirteen species are reported from five sections in three localities (Kritika, Faliraki and Ladiko) and their biostratigraphical position, faunal relationships and habitat specificity are investigated. The studied fauna developed in fully marine conditions and well-oxygenated waters from the shore to the detritic bottoms of the shelf edge. All these species are still living in the Mediterranean Sea and most of them also occur in the Atlantic Ocean. The following species have been identified: *Lepidopleurus cajetanus, Leptochiton cimicoides, Ischnochiton rissoi, Callochiton septemvalvis, Rhyssoplax corallina, R. olivacea, Lepidochitona* cf. *canariensis, L. caprearum, L. cinerea, L. furtiva, L. monterosatoi, Acanthochitona crinita*, and *A. fascicularis*.

Key words: Polyplacophora, Mollusca, Pliocene, Pleistocene, Rhodes, Greece, Mediterranean.

1. Introduction

Polyplacophorans, or chitons, are a class of exclusively marine molluscs, which characteristically have eight dorsal calcareous shell plates or valves surrounded by a girdle. Primarily they live in the intertidal zone, but range to depths of more than 7000 m (Sirenko 1997; Jones & Baxter 1987; Gowlett-Holmes et al. 1998). Recently, there has been an increase in the number of papers dealing with polyplacophoran evolution, phylogeny and comparative anatomy (Gowlett-Holmes et al. 1998; Okusu et al. 2003; Eernisse 2004), and many discussions on their taxonomy.

Compared to other mollusc groups, chitons are relatively scarce in the fossil record. After the death of the animal, the fragile skeletal plates are dissociated and often transported and winnowed by bottom currents. They are thus exposed to rapid decay and are consequently rarely fossilized. However, their fossil record scantily extends back to the Early Cambrian (Yochelson et al. 1965; Runnegar et al. 1979; Yates et al. 1992; Stinchcomb & Darrough 1995; Slieker 2000; Skovsted et al. 2004; Vendrasco & Runnegar 2004). The study of the fossil polyplacophorans has been based primarily on valve morphology (Van Belle 1983, 1985; Sirenko 1993, 1997; Dell'Angelo & Smriglio 1999).

In the Cenozoic of the Mediterranean and Paratethyan regions, diverse faunas of polyplacophorans have been found in the Middle Miocene of Austria (Sulc 1934; Kroh 2003), Poland (Baluk 1971, 1984; Macioszczyk 1988; Studencka & Studencki 1988) and Hungary (Dulai 2001, 2005), the Late Miocene of Italy (Dell'Angelo et al. 1999), the Pliocene of Spain (Dell'Angelo et al. 2004) and

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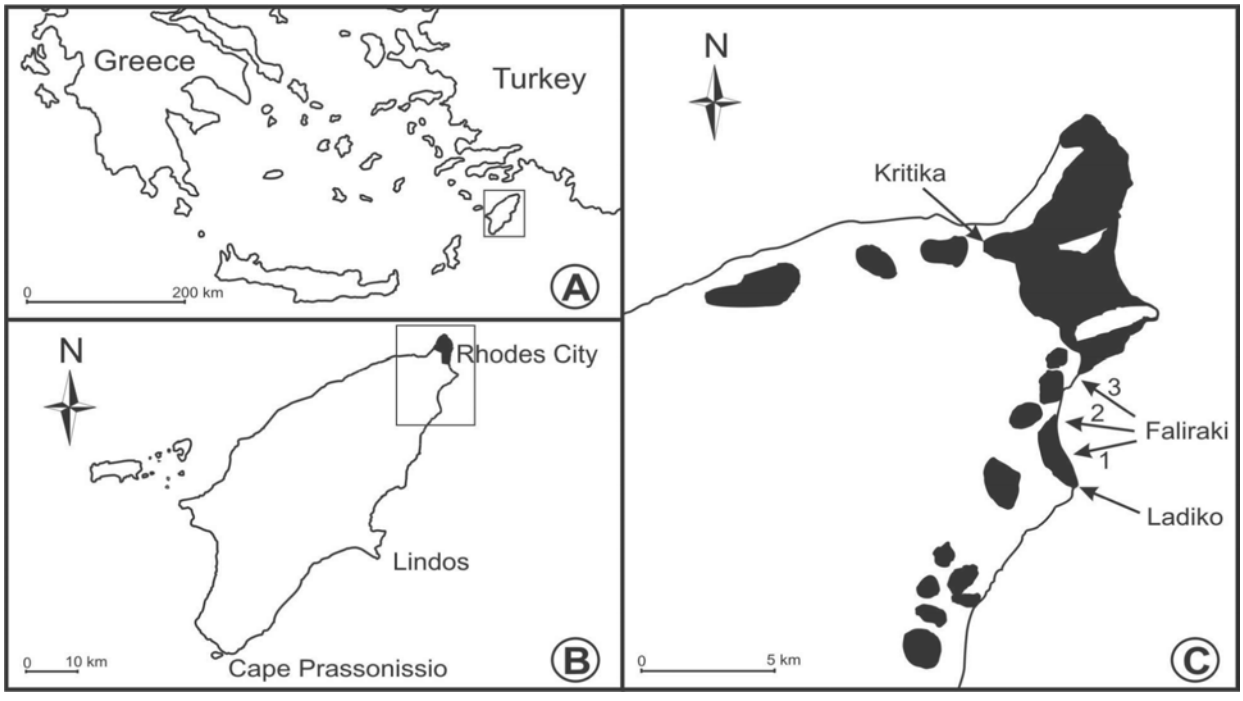

Fig. 1. A. Geographical location of the Island of Rhodes in the Aegean Sea. B. Map of Rhodes showing the location of the study area. C. Simplified geological map of the study area. Plio-Pleistocene marine outcrops are in black and stratigraphical sections are indicated with arrows.

Italy (Dell'Angelo & Forli 1996), and the Pleistocene of Italy (Sabelli & Taviani 1979; Dell'Angelo & Forli 1995; Garilli 1998).

Although the Pliocene and Pleistocene mollusc communities of Greece are very diverse and generally well studied, polyplacophorans are rare and poorly documented. They have been previously described from the Peloponnesus: Late Pliocene of Kallithea (Kleinhölter 1994), Pleistocene of Kyllini (Garilli et al. 2005) and Late Pleistocene of Perachora (Vardala-Theodorou 1998; Dell'Angelo & Vardala-Theodorou 2006). The first and only reference for polyplacophorans from the Pleistocene of Rhodes dates back to de Rochebrune (1883).

The main objectives of this paper are: 1) to describe the polyplacophoran species occurring in the Plio-Pleistocene siliciclastic deposits of Rhodes, 2) to use the ecological information provided by the extant chiton species and the accompanying molluscs, 3) together with sedimentological data, to reconstruct the depositional history of the beds where these organisms were found, and 4) to improve our knowledge of the spatial and temporal distribution of this scarcely known small group of molluscs in Greece.

2. Geological setting

The marine deposits of the Late Pliocene to Late Pleistocene of Rhodes are well exposed, notably in the northeastern part (Fig. 1). The general geology and stratigraphy of the island was studied by Mutti et al. (1970), Meulenkamp et al. (1972), Broekman (1973, 1974), Hanken et al. (1996), Hansen (1999), Titschack et al. (2005, in press), Cornée et al. (2006a-b), and Nielsen et al. (2006).

Three lithostratigraphical units have been recognized by Cornée et al. (2006a): the Rhodes Formation (Late Pliocene to Early Pleistocene: 2.5–1.3 Ma), the Ladiko-Tsampika Formation (Middle to Late Pleistocene: 1.3-0.3 Ma), and the Lindos Acropolis Formation (Late Pleistocene).

Polyplacophorans were found within the deposits of the basal Kritika Member and of the overlying Kolymbia Limestone of the Rhodes Formation and of the Ladiko Member of the Ladiko-Tsampika Formation. These mostly siliciclastic sediments contain abundant and diverse associations of coralline algae, foraminifers, corals, annelids, molluscs, bryozoans, crustaceans, and echinoids (Moissette & Spjeld-

naes 1995; Hanken et al. 1996; Hansen 1999; Titschack et al. 2005, in press; Cornée et al. 2006a; Nielsen et al. 2006; Moissette et al. 2007).

3. Material and methods

Fieldwork and sampling in the northeastern part of Rhodes was undertaken in three localities (Faliraki, Kritika, and Ladiko) where five sections were measured (Figs. 2-6). A total of 152 bulk samples were collected by the first and last authors, of which only 21 yielded identifiable polyplacophoran valves/plates. Valve fragments belonging to the same genera have been also found in other sections and levels of the Plio-Pleistocene of Rhodes, but they are very rare and poorly preserved and so are not included in this study.

The samples were washed on a column of six sieves (2 to 0.063 mm). For each sample, fractions between 2 and 0.5 mm were examined for chiton valves using a stereomicroscope (Leica MZ8 in the Department of Historical Geology-Paleontology, Athens University and Goulandris Natural History Museum, Kifissia). Scanning electron microscopes (Jeol JSM-5600 at the Faculty of Geology and Geoenvironment, Athens and Hitachi S-570 at UMR 5125, Lyon) were used for examination and photography of the plates and their sculpture. The fossil material has been compared with Recent material from the collections of the Goulandris Natural History Museum (Kifissia). Specimens have been placed in the repository of the Athens Museum of Palaeontology and Geology (AMPG), University of Athens, Greece (numbers 1500 to 1885).

Since many of the studied chitons are still living on modern shores and shallow shelves of the Mediterranean, the depth zonation established by Pérès & Moliner (1957), Pérès & Picard (1964) and Pérès (1967) for the present-day Mediterranean Sea has been used throughout the text: mediolittoral (0-1 m water depth), infralittoral (down to 40 m) and circalittoral (40-200 m).

4. Systematic palaeontology

The taxonomy used in this paper takes into consideration the works of Van Belle (1983, 1985), Sirenko (1993, 1997), Kaas & Van Belle (1998), and Dell'Angelo & Smirglio (1999), but is mainly based on Sirenko's paper (2006), which deals with extant and fossil species and relies on complex or aggregated characters of different attributes such as the shell and soft parts of the living chitons. The Polyplacophora are thus subdivided into the orders Paleoloricata and Loricata. The Loricata include two orders: Lepidopleurida and Chitonida. Accordingly, the subgenus *Leptochiton* Gray, which was previously included within the genus *Lepidopleurus* Risso, 1826 by Dell'Angelo & Palazzi (1989), now constitutes a separate genus. Also, *Rhyssoplax* Thiele, 1893 is regarded as a separate genus instead of a subgenus of *Chiton* Linnaeus, 1758. Even though Sirenko (2006) does not recognize subgenera, this taxonomic level is used here as it is accepted by many authors.

Subclass Loricata Schumacher, 1817
Order Lepidopleurida Thiele, 1909
Suborder Lepidopleurina Thiele, 1909
Family Leptochitonidae Dall, 1889
Genus *Lepidopleurus* Risso, 1826

Type species: *Chiton cajetanus* Poli, 1791, by subsequent designation, Herrmannsen, 1846.

Lepidopleurus cajetanus (Poli, 1791)
Fig. 7.1-7.3

1791 *Chiton cajetanus* Poli, p. 10, pl. 4, figs. 1-2.
1860 *Chiton decoratus* Reuss, p. 257, pl. 8, fig. 7.
1883 *Lepidopleurus cajetanus* Poli. – de Rochebrune, p. 72.
1934 *Lepidopleurus* (*Lepidopleurus*) *decoratus* (Reuss). – Sulc, p. 3.
1962 *Lepidopleurus* (*L.*) *cajetanus* (Poli). – Malatesta, p. 146, figs. 1-2.
1971 *Lepidopleurus decoratus* (Reuss). – Baluk, p. 453, pl. 1, figs. 1-4.
1985a *Lepidopleurus cajetanus* (Poli). – Kaas & Van Belle, p. 32, fig. 12.
1999 *Lepidopleurus* (*L.*) *cajetanus* (Poli). – Dell' Angelo & Smriglio, p. 38, pls. 6-7, figs. A-P, text-figs. 10-15.
2004 *Lepidopleurus* (*L.*) *cajetanus* (Poli). – Dell' Angelo et al., p. 26, pl. 7, figs. 4, 8.
2005 *Lepidopleurus* (*L.*) *cajetanus* (Poli). – Garilli et al., p. 129, pl. 1, figs. 1-2.

Material: 9 head, 5 intermediate and 5 tail valves (AMPG 1550-1552, 1574-1589).

Description: Valves with small and widely separated sutural laminae and without apophyses. Articulamentum without insertion laminae. Tegmentum sculptured with strong commarginal, terraced ribs in head valve (Fig. 7.2), lateral areas of intermediate valves (Fig. 7.3), and postmucronal area of tail valve (Fig. 7.1). Longitudinal chains (40-50) of united granules occur in central area of intermediate valves (Fig. 7.3) and in antemucronal area of tail valve (Fig. 7.1).

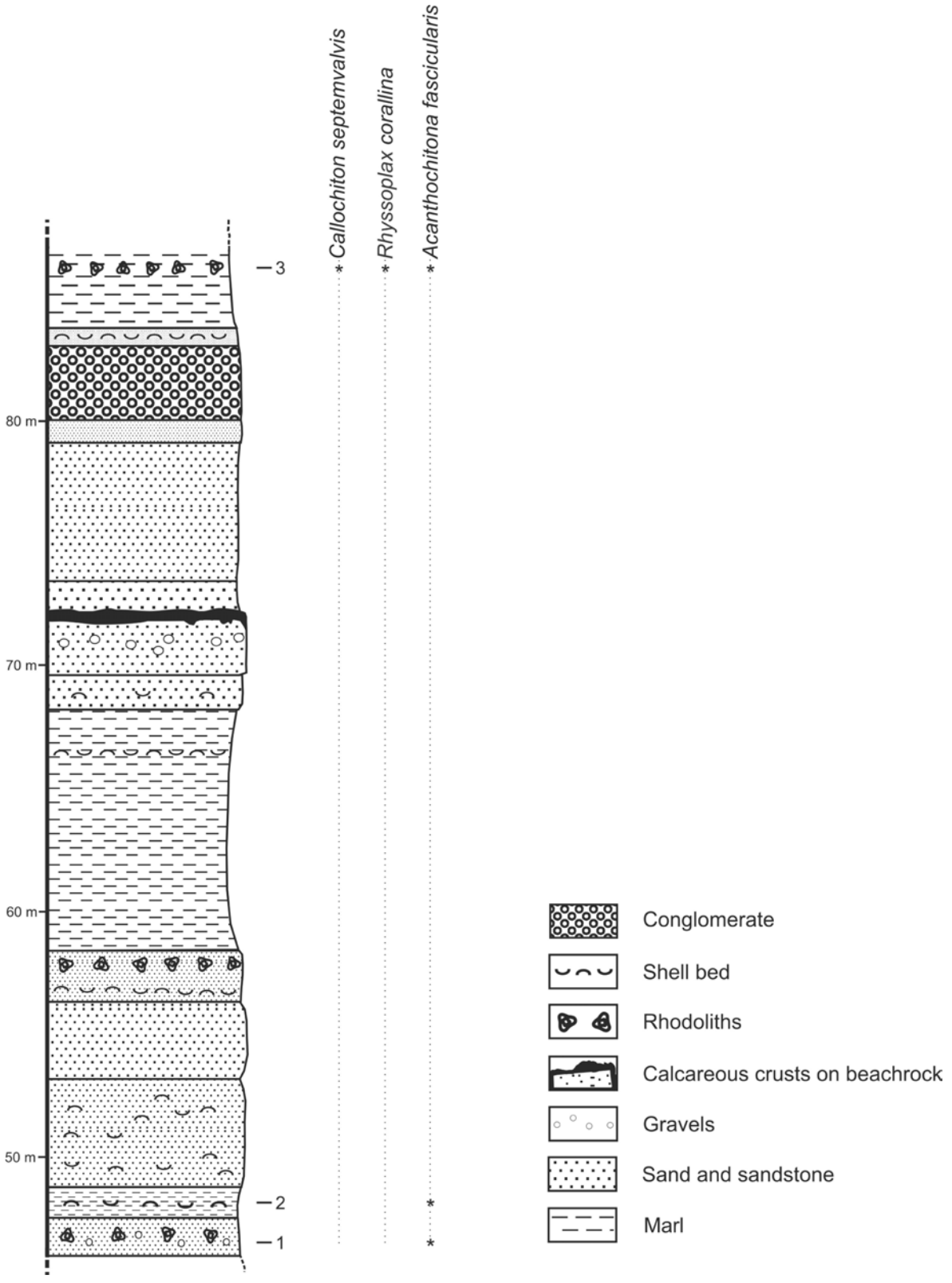

Fig. 2. Stratigraphical column of the Kritika section. Sample numbers and species of recovered polyplacophorans are displayed to the right of the column.

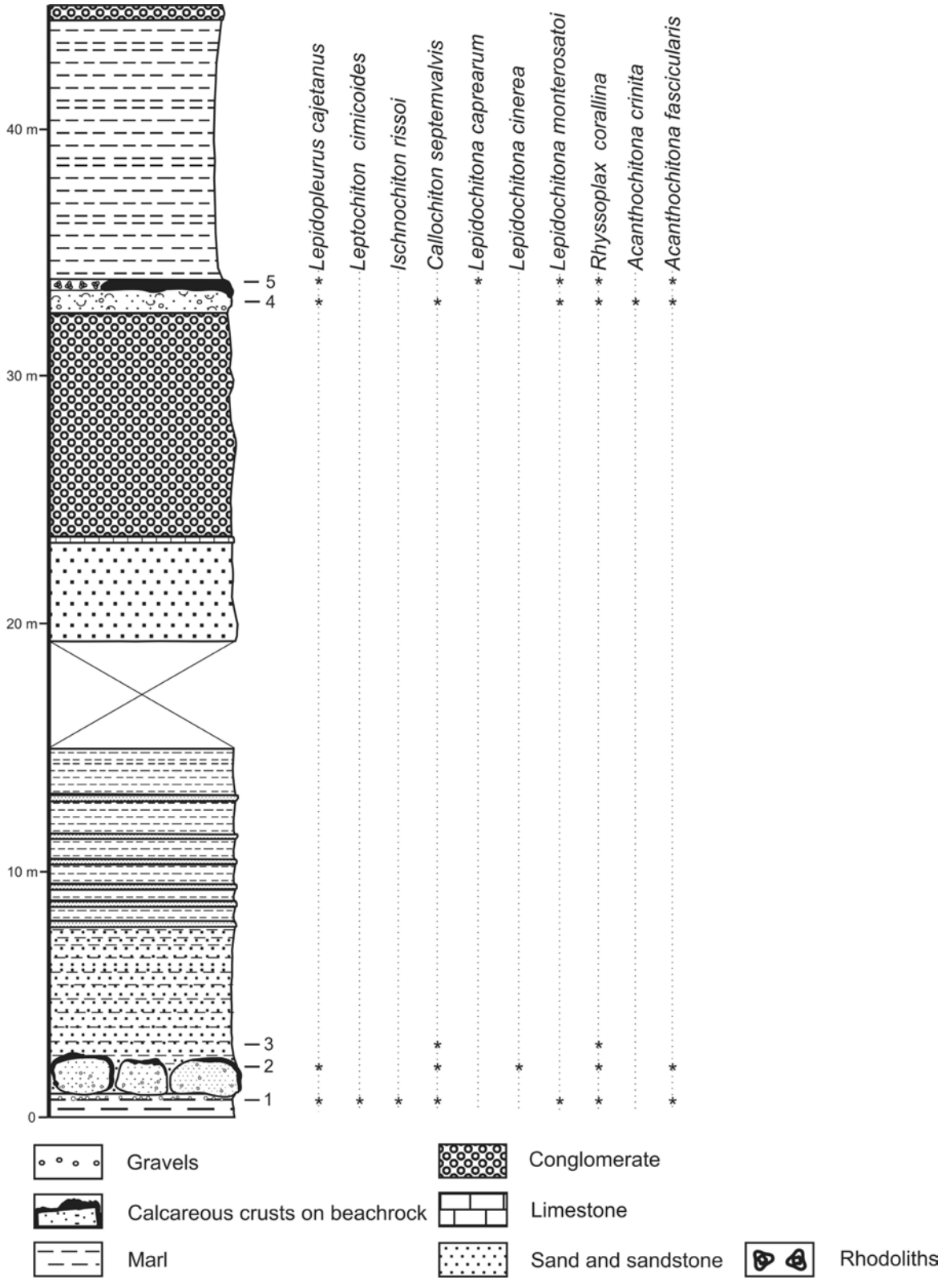

Fig. 3. Stratigraphical column of the Faliraki-1 section. Sample numbers and species of recovered polyplacophorans are displayed to the right of the column.

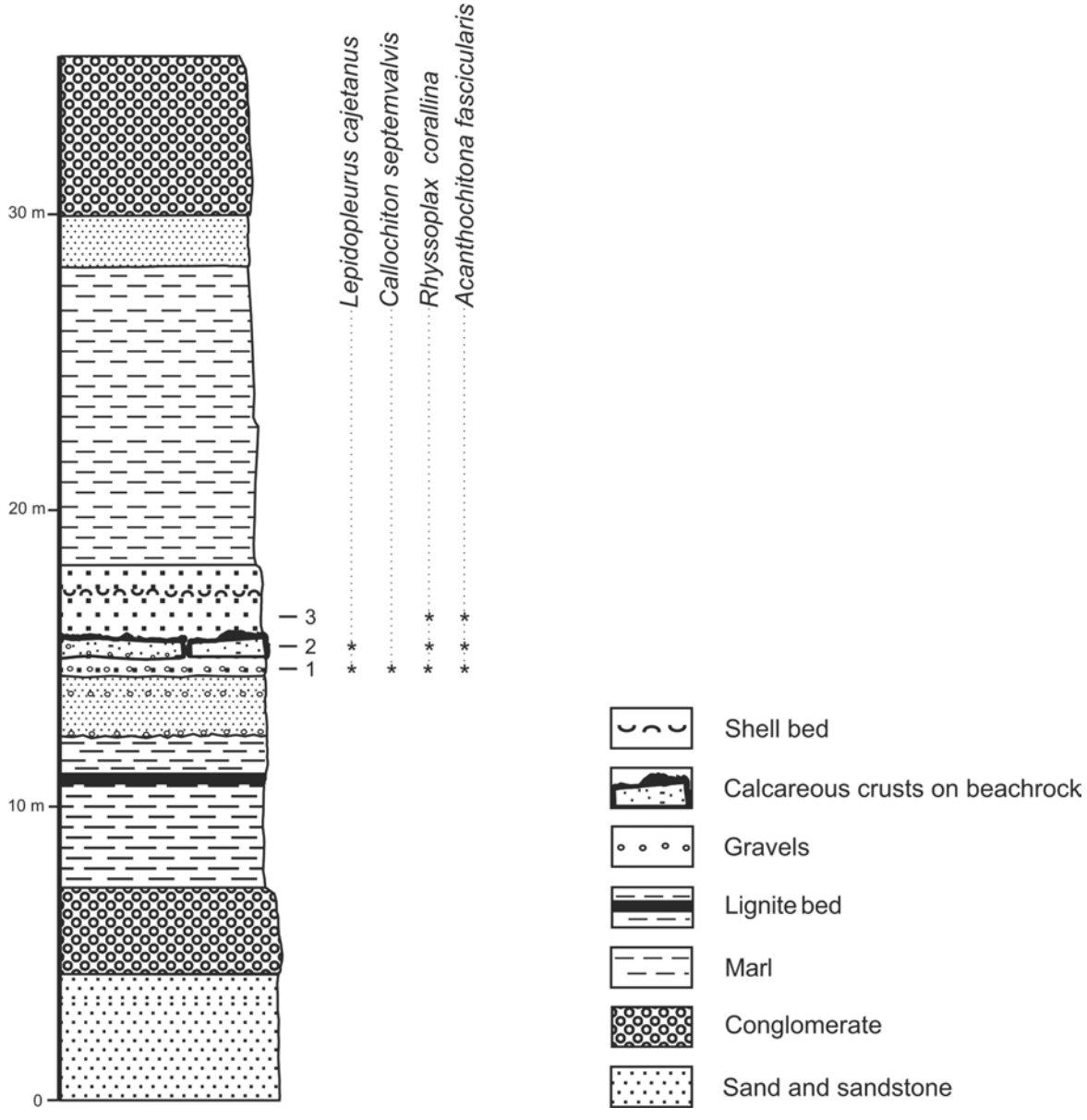

Fig. 4. Stratigraphical column of the Faliraki-2 section. Sample numbers and species of recovered polyplacophorans are displayed to the right of the column.

Remarks: Although only a few valves were recovered from Rhodes, their very good state of preservation shows that the studied specimens fully correspond to the description of the species given by Garilli et al. (2005) for material from the Peloponnesus.

Distribution: *L. cajetanus* has been reported from the Miocene of central Eastern Europe (under the name of *Chiton decoratus*: Reuss 1860; Baluk 1971) and a literature survey of this area is provided by Dulai (2005). It was described from the Miocene of northern Italy (Laghi 1977; Dell'Angelo et al. 1999). It is frequent in the Plio-Pleistocene of the Mediterranean region (Italy, France and Spain) (Sacco 1897; Malatesta 1962; Sabelli & Taviani 1979; Bellomo & Sabelli 1995; Dell'Angelo & da Silva 2003). It is known from the Pleistocene of Cyprus (Unger & Kotschy 1865) and Greece: Rhodes (de Rochebrune 1883) and Kyllini-NW Peloponnesus (Garilli et al. 2005). *L. cajetanus* is a common living species in the present-day Mediterranean Sea (Giovine & Dell'Angelo 1993). It occurs also in the Atlantic Ocean, from the Iberian Peninsula to Morocco, the Canary Islands, and Brittany (Dell'

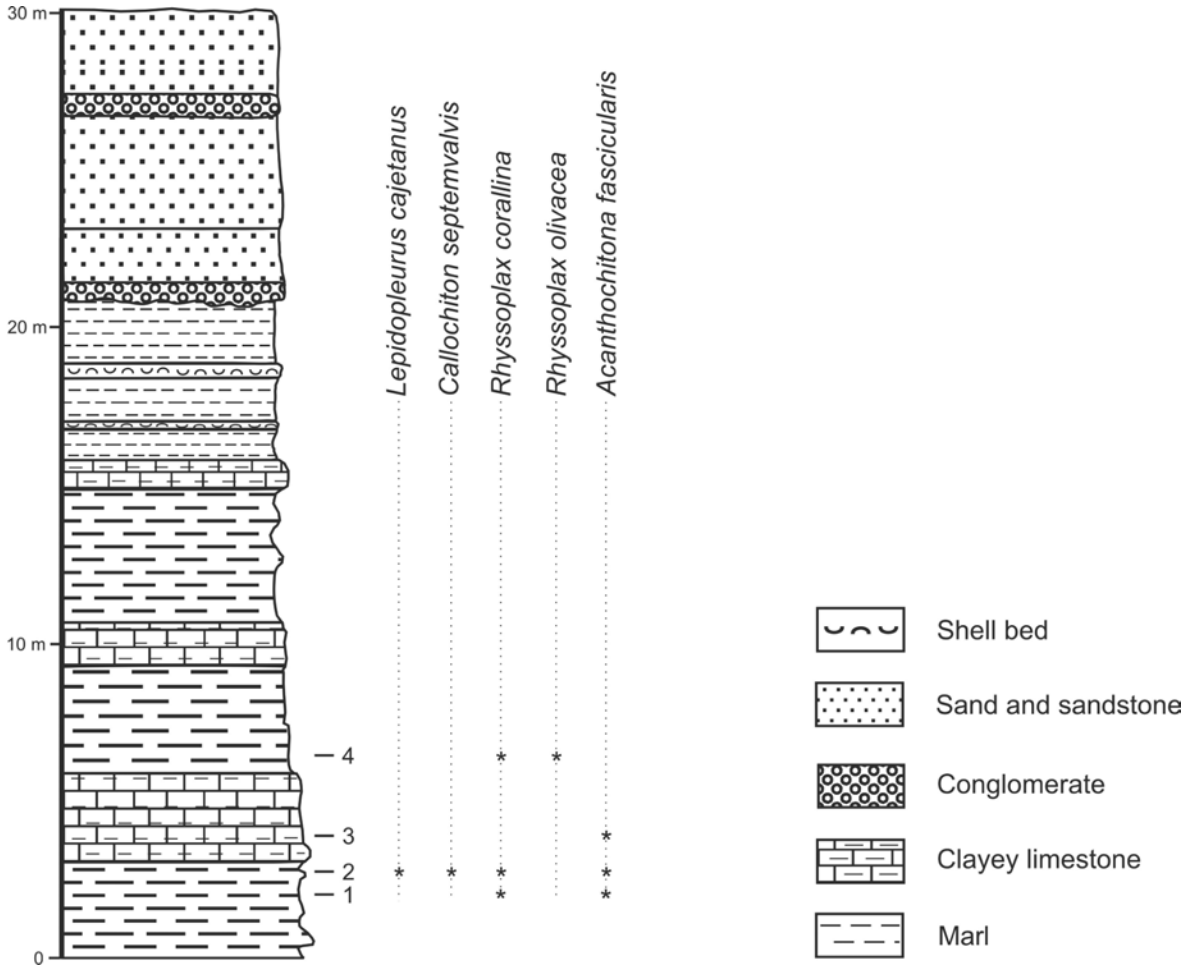

Fig. 5. Stratigraphical column of the Faliraki-3 section. Sample numbers and species of recovered polyplacophorans are displayed to the right of the column.

Angelo & Smriglio 1999). It has also been recorded from the coasts of Cyprus and Greece (Barash & Danin 1992; Delamotte & Vardala-Theodorou 2001; Koukouras & Karachle 2005). *L. cajetanus* is chiefly found living on stones, rocks and shells in shallow waters (Table 1). It occurs at depths of less than 40 m (Dell'Angelo et al. 1998).

Genus *Leptochiton* Gray, 1847

Type species: *Chiton cinereus* sensu Montagu, 1803 (non Linnaeus, 1767) = *Leptochiton asellus* (Gmelin, 1791), by subsequent designation, Gray, 1847.

Leptochiton cimicoides (Monterosato, 1879)
Fig. 7.4-7.8

1878a *Chiton minimus* Monterosato, p. 77 (nom. nud.).

1879 *Chiton cimicoides* Monterosato, p. 23 (nom. nov. *pro Chiton minimus* Monterosato, 1878, *non* Gmelin, 1791, *nec* Spengler, 1797).

1968 *Lepidopleurus intermedius* Salvini-Plawen, p. 251, pls. 6-8, figs. 44-57 [fide Dell'Angelo & Palazzi, 1987].

1985a *Leptochiton* (*Leptochiton*) *intermedius* (Salvini-Plawen). – Kaas & Van Belle, p. 54, fig. 22.

1987 *Leptochiton* (*L.*) *cimicoides* (Monterosato). – Dell'Angelo & Palazzi, p. 95, figs. 1-15.

1989 *Lepidopleurus* (*Leptochiton*) *cimicoides* (Monterosato). – Dell'Angelo & Palazzi, p. 64, pls. 14-15.

1990 *Leptochiton* (*Leptochiton*) *cimicoides* (Monterosato). – Kaas & Van Belle, p. 7-8, fig. 1.

1999 *Lepidopleurus* (*Leptochiton*) *cimicoides* (Monterosato). – Dell'Angelo & Smriglio, p. 58, pls. 14-15, figs. A-M, text-fig. 24.

2001 *Lepidopleurus* (*Leptochiton*) *cimicoides* (Monterosato). – Dell'Angelo et al., p. 147, fig. 6.

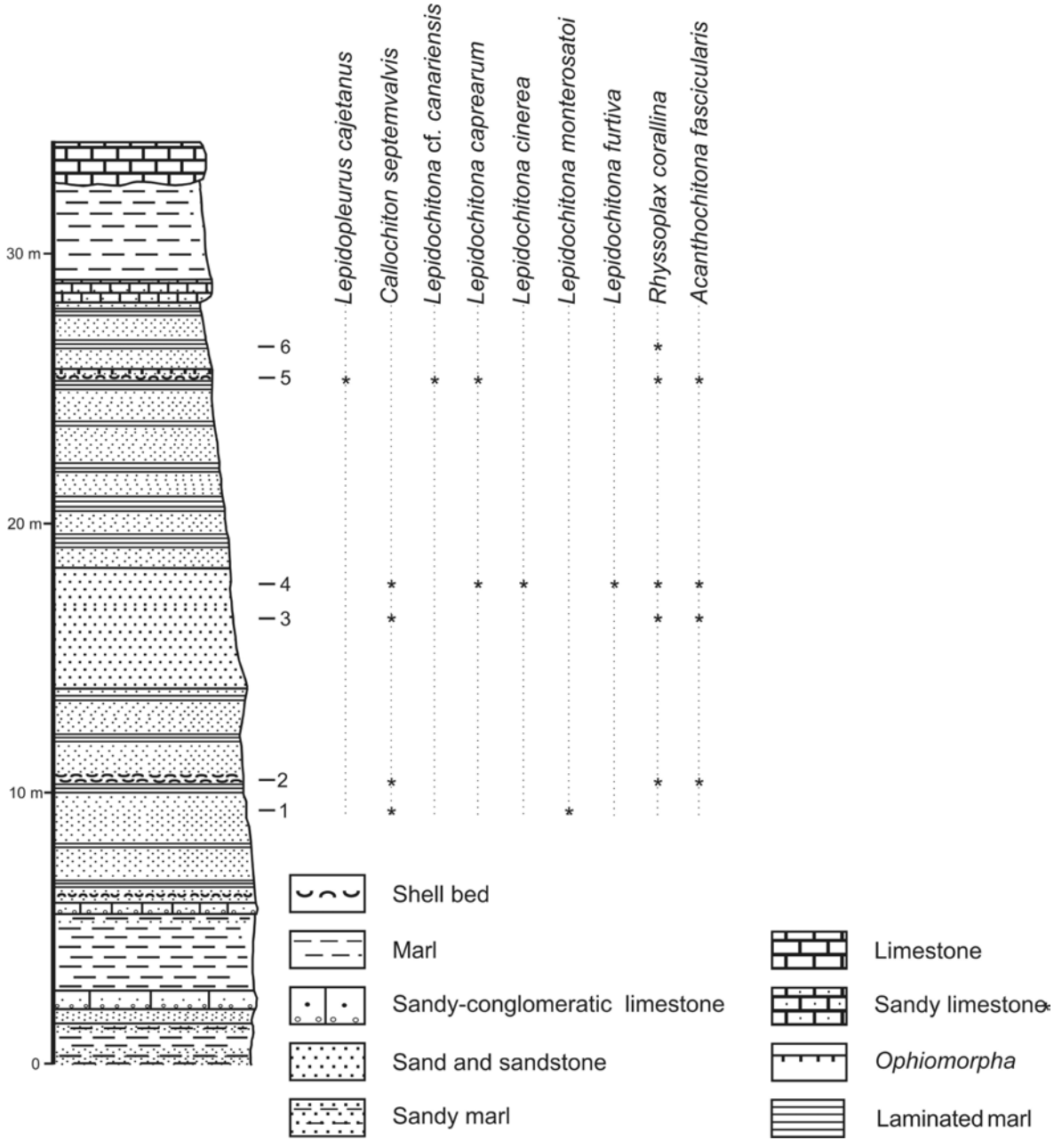

Fig. 6. Stratigraphical column of the Ladiko section. Sample numbers and species of recovered polyplacophorans are displayed to the right of the column.

Fig. 7. 1-3. *Lepidopleurus cajetanus* (Poli, 1791). 1, AMPG 1550, tail valve, dorsal view. 2, AMPG 1551, head valve, dorsal view. 3, AMPG 1552, intermediate valve, dorsal view. 4-8. *Leptochiton cimicoides* (Monterosato, 1879). 4-6, AMPG 1553, intermediate valve, dorsal view of central and lateral area (4), details of sculpture of lateral (5) and central area (6). 7-8, AMPG 1554, tail valve, dorsal view (7), detail of sculpture of antemucronal area (8).

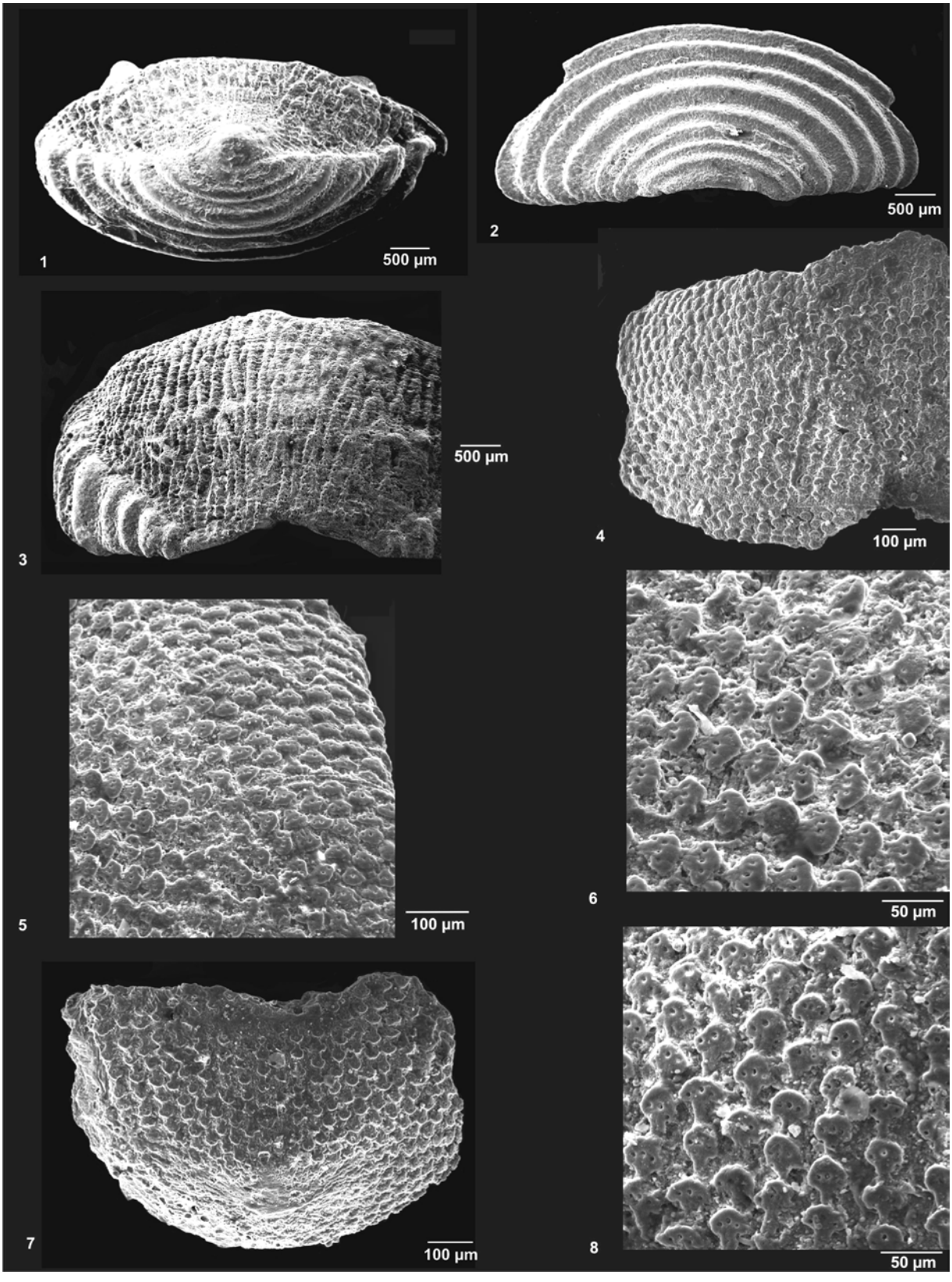

Fig. 7 (Legend see p. 310)

Table 1. Diversity of the studied polyplacophoran faunas and corresponding biotope assignment of sample sites (biotope nomenclature after PÉRÈS & PICARD 1964). Black squares indicate autochthonous and parautochthonous assemblages and open squares allochthonous assemblages.

Setting	Sections and sample numbers	*Acanthochitona crinita*	*Acanthochitona fascicularis*	*Callochiton septemvalvis*	*Ischnochiton rissoi*	*Lepidochitona* cf. *canariensis*	*Lepidochitona caprearum*	*Lepidochitona cinerea*	*Lepidochitona furtiva*	*Lepidochitona monterosatoi*	*Lepidopleurus cajetanus*	*Leptochiton cimicoides*	*Rhyssoplax corallina*	*Rhyssoplax olivacea*
Photophilous algae	Kritika (1), Faliraki-1 (3)		■	■				■			■		■	
Photophilous algae-gravely shore	Faliraki-1(1, 4), Faliraki-2 (1)	■	■	■	■					■	■	□	■	
Rhodoliths	Kritika (3)		■	■									■	
Posidonia meadows	Kritika (2)		■											
Posidonia meadows-transported	Ladiko (1, 2, 5, 6)		■	■		■	■			■	■		■	
Coralligenous	Faliraki-2 (3)		■										■	
Hard substrate-beachrock	Faliraki-1 (2, 5), Faliraki-2 (2)		■	■			■	■		■	■		■	■
Shelf-edge detritic bottoms	Faliraki-3 (1 - 6)		■	■							□		■	□
Delta front	Ladiko (3, 4)		■	■			■	■	■				■	

2005 *Lepidopleurus* (*Leptochiton*) *cimicoides* (MONTEROSATO). – GARILLI et al., p.129, pl. 1, figs. 3-10.

Material: 1 tail and 1 intermediate valve (AMPG 1553-1554).

Description: Tegmentum sculptured with thick, separated fungiform granules (with 4-6 aesthete pores), arranged randomly on head valve, on lateral areas of intermediate valves (Figs. 7.4, 7.5) and postmucronal area of tail valve. On central area of intermediate valves (Fig. 7.6) and antemucronal area of tail valve, granules arranged in parallel lines (Figs. 7.7, 7.8). Articulamentum without insertion laminae.

Remarks: DELL'ANGELO & PALAZZI (1987) after the examination of MONTEROSATO's type material accepted the synonymy with *Lepidopleurus intermedius* SALVINI-PLAWEN, 1968. This subject is still open: E. SCHWABE (personal communication), who studied material from SALVINI's type locality, considers *L. intermedius* SALVINI-PLAWEN as a valid species. On the recovered intermediate valve, the parallel lines in which the granules are arranged in the central area are about 30 vs. 50 for same size valves as reported by GARILLI et al. (2005) from the Peloponnesus.

Distribution: *L. cimicoides* occurs in the Pliocene and Pleistocene of Italy (DELL'ANGELO & PALAZZI 1989; DELL'ANGELO & FORLI 1995). In the Pleistocene of Greece it has been recorded for the first time from Kyllini in the NW Peloponnesus (GARILLI et al. 2005). *L. cimicoides* is found in the present-day western and central Mediterranean Sea (Italy, France, and Croatia) and in the Atlantic Ocean (Western Sahara) (DELL'ANGELO & SMRIGLIO 1999; KOUKOURAS & KARACHLE 2005). In the Mediterranean, it appears to prefer hard or soft substrates mixed with *Posidonia oceanica* meadows (Table 1) in the infralittoral zone and deeper in water depths of 20 to 110 m (DELL'ANGELO & SMRIGLIO 1999).

Fig. 8. 1-2. *Ischnochiton* (*Ischnochiton*) *rissoi* (PAYRAUDEAU, 1826), AMPG 1555, intermediate valve, dorsal view (1), detail of sculpture of lateral area (2). 3-4. *Callochiton septemvalvis* (MONTAGU, 1803). 3, AMPG 1556, intermediate valve, dorsal view. 4, AMPG 1557, tail valve, dorsal view. 5-8. *Rhyssoplax corallina* (RISSO, 1826). 5, AMPG 1565, intermediate valve. 6, 8, AMPG 1566, intermediate valve, dorsal view (6), sculpture of pleural and lateral area (8). 7, AMPG 1567, tail valve, dorsal view.

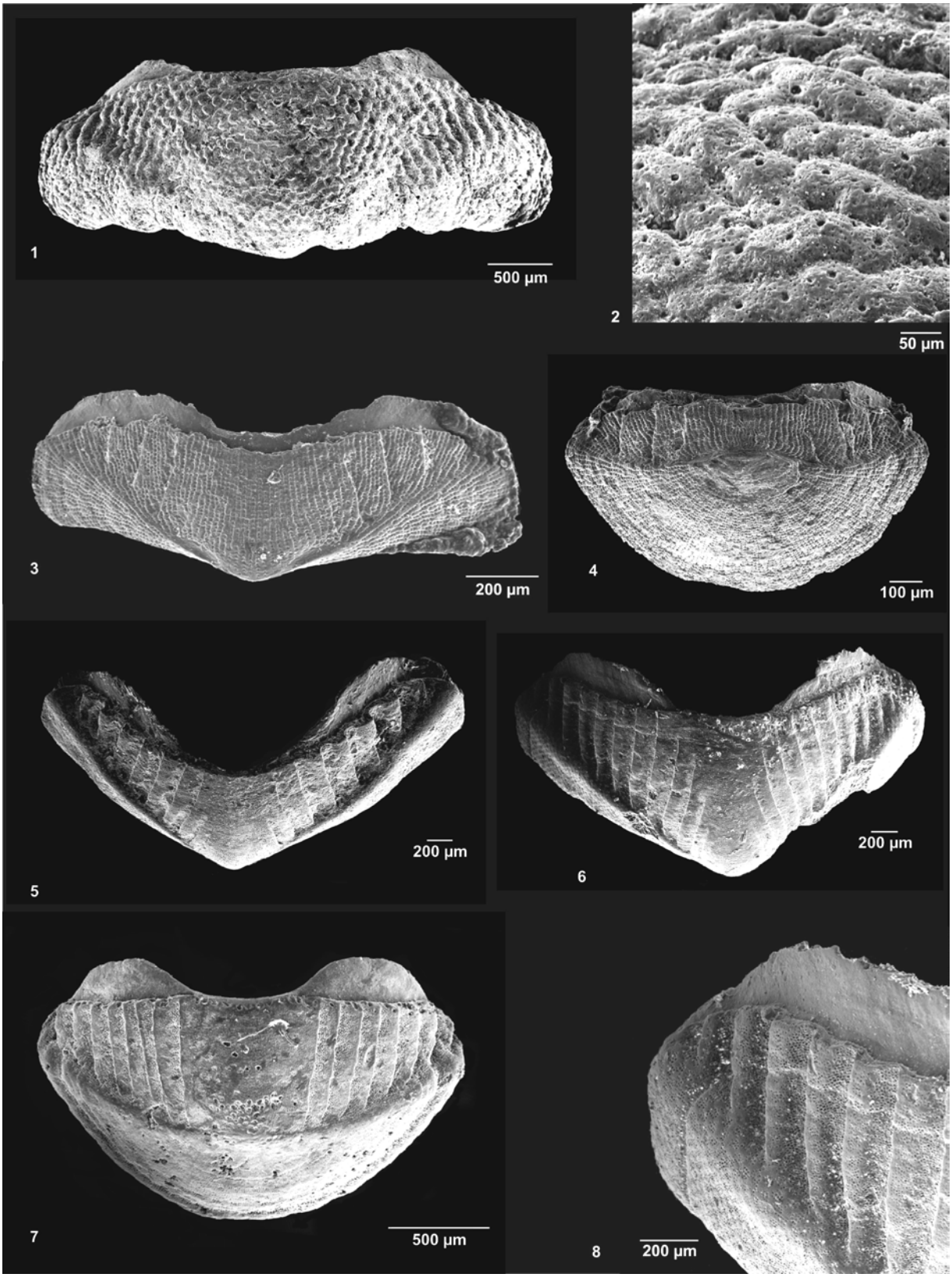

Fig. 8 (Legend see p. 312)

Order Chitonida Thiele, 1909
Suborder Chitonina Thiele, 1909
Superfamily Chitonoidea Rafinesque, 1815
Family Ischnochitonidae Dall, 1889
Genus *Ischnochiton* Gray, 1847

Type species: *Chiton textilis* 1828, by subsequent designation, Gray, 1847 Subgenus *Ischnochiton* s.s.

Ischnochiton (*Ischnochiton*) *rissoi* (Payraudeau, 1826)
Fig. 8.1-8.2

1826 *Chiton rissoi* Payraudeau, p. 87, pl. 3, figs. 4-5.
1847 *Chiton mediterraneus* Gray. – Reeve, pl. 23, fig. 157 [fide Garili et al. 2005].
1934 *Ischnochiton rudolticensis* Sulc, p. 23, pl. 2, figs. 41-43 [fide Garili et al. 2005].
1962 *Ischnochiton* (*I.*) *rissoi* (Payraudeau). – Malatesta, p. 160, figs. 16-17.
1971 *Ischnochiton rudolticensis* Sulc. – Baluk, p. 458, pl. 3, figs. 5-8.
1977 *Ischnochiton* (*Simplischnochiton*) *rissoi* (Payraudeau). – Laghi, p. 104, pl. 1, figs. 4-9.
1984 *Ischnochiton rissoi* (Payraudeau). – Baluk, p. 287, pl. 6, figs. 2a-b.
1990 *Ischnochiton* (*I.*) *rissoi* (Payraudeau). – Kaas & Van Belle, p. 78, fig. 32.
1999 *Ischnochiton* (*Ischnochiton*) *rissoi* (Payraudeau). – Dell'Angelo & Smriglio, p. 100, pls. 29-31, figs. A-U, text-figs. 40-48.
2004 *Ischnochiton* (*Ischnochiton*) *rissoi* (Payraudeau). – Dell'Angelo et al., p. 34, pl. 4, figs. 3-4.
2005 *Ischnochiton* (*Ischnochiton*) *rissoi* (Payraudeau). – Garilli et al., p.132, pl. 2, figs. 5-6.

Material: 2 intermediate and 1 tail valves (AMPG 1555, 1590-1591).

Description: Tail valve of semicircular outline and mucro slightly elevated. Tegmentum with a granulose aspect formed by commarginal vermicular ribs and fine radial grooves, on head valve, lateral areas of intermediate valves (Figs. 8.1, 8.2), and postmucronal area of tail valve. Ribs continue longitudinally on the antemucronal area of tail valve and central areas of intermediate valves, spaced on lateral areas (Fig. 8.1). Articulamentum characterized by slitted insertion plates.

Remarks: Our material bears the diagnostic characters of the species and the tegmental sculpture varies from faint to strongly marked.

Distribution: *I. rissoi* has been reported from the Middle Miocene (Badenian) of central Eastern Europe (Baluk 1971; Baluk 1984; Kroh 2003), the Tortonian, Messinian, Pliocene and Pleistocene of Italy, and the Pliocene of Spain (Laghi 1977; Sabelli & Taviani 1979; Dell'Angelo & Forli 1995; Dell'Angelo et al. 1999; Dell'Angelo et al. 2004; Dell'Angelo & Palazzi 1989). In Greece, the species has been recorded from the Pleistocene of Kyllini in the NW Peloponnesus (Garilli et al. 2005). *I. rissoi* is a common species in the Mediterranean Sea (Kaas & Van Belle 1987; Poppe & Goto 1991) and has been recorded from some Atlantic sites (Canary, Selvagens, and Azores Islands: Leloup 1934; Bergenhayn 1931, but according to Dell'Angelo & Smriglio (1999) these last records have to be confirmed). It is found in Greece where it occurs on hard substrates in shallow waters (1-5 m), rarely deeper (100 m) (Strack 1988, 1990; Delamotte & Vardala-Theodorou 2001; Koukouras & Karachle 2005). It is common under smooth stones on clean sand bottoms (Poppe & Goto 1991) and in crevices in shallow coastal areas (Riedl 1983).

Family Callochitonidae Plate, 1901
Genus *Callochiton* Gray, 1847

Type species: *Chiton laevis* Montagu, 1803, non Penant, 1777 (= *Chiton septemvalvis* Montagu, 1803), by subsequent designation, Gray, 1847.

Callochiton septemvalvis (Montagu, 1803)
Fig. 8.3-8.4

1803 *Chiton septemvalvis* Montagu, p. 3.
1985b *Callochiton septemvalvis* (Montagu). – Kaas & Van Belle, p. 11, fig. 2.
1995 *Callochiton septemvalvis* (Montagu). – Dell' Angelo & Forli, p. 226, figs. 10, 17.
1999 *Callochiton septemvalvis* (Montagu). – Dell' Angelo & Smriglio, p. 125, pls. 40-41, figs. A-P, text-figs. 55-63.
2004 *Callochiton septemvalvis* (Montagu). – Dell' Angelo et al., p. 34, pl. 3, figs. 2, 5.
2005 *Callochiton septemvalvis* (Montagu).– Garilli et al., p. 134, pl. 2, figs. 7-10.
2006 *Callochiton septemvalvis* (Montagu). – Dell' Angelo & Vardala-Theodorou, p. 325, figs. 1-2.

Material: 2 head, 28 intermediate and 7 tail valves (AMPG 1556-1557, 1592-1626).

Description: Tegmentum with threads of fine longitudinal ribs on central area of intermediate valves (Fig. 8.3) and antemucronal area of tail valve (Fig. 8.4), arranged radially in head valve, lateral areas of intermediate valves and postmucronal area of tail valve. Pleural areas of intermediate valves with 3-6 longitudinal grooves (Fig. 8.3). Articulamentum has connected laminae (Fig. 8.3).

Remarks: The opinion of Garilli et al (2005) was followed for the definition of *C. septemvalvis*, as Carmona Zalvide et al. (2002) give specific validity to both taxa *Chiton euplaeae* and *C. septemvalvis*, but they do not seem to take in consideration the discussion of Dell'Angelo & Palazzi (1994) suggesting to designate the species *Callochiton septemvalvis* as a whole, since *Chiton euplaeae* was clearly described by Costa (1829) as having a smooth

surface, without any scars. The recovered valves have the characteristics of living Mediterranean representatives of the species. The pleural areas of most of them show 3 longitudinal grooves. Kaas & Van Belle (1985b) recognize *Callochiton septemvalvis* (Montagu, 1803) *euplaeae* (Costa, 1829) as a formal subspecies for the Mediterranean Sea.

Distribution: *Callochiton septemvalvis* has been reported from the Miocene of central Eastern Europe and Northern Apennine (Dell'Angelo & Smriglio 1999). It is common in the Italian Plio-Pleistocene (Dell'Angelo et al. 2007) and was also recorded from the Portuguese (Dell'Angelo & da Silva 2003) and Spanish Pliocene (Dell'Angelo et al. 2004). It is also mentioned from the Pleistocene of NW Peloponnesus (Vardala-Theodorou 1998; Garilli et al. 2005; Dell'Angelo & Vardala-Theodorou 2006). *Callochiton septemvalvis* is a locally common species in the Mediterranean Sea and is also widely distributed in the northeastern Atlantic, from Norway to the Canary Islands (Dell'Angelo & Smriglio 1999). It also occurs in Greece (Strack 1988, 1990; Delamotte & Vardala-Theodorou 2001; Koukouras & Karachle, 2005) where it lives on rocks and coralline algae (Table 1). It is found from the upper subtidal zone to a depth of 500 m, more frequently on coralline algae (Dell'Angelo et al. 1998).

Family Chitonidae Rafinesque, 1815
Subfamily Chitoninae Rafinesque, 1815
Genus *Rhyssoplax* Thiele, 1893

Type species: *Chiton affinis* Issel, 1869, by subsequent designation, Thiele, 1909.

Rhyssoplax corallina (Risso, 1826)
Figs. 8.5-8.8, 9.1-9.2

1826 *Lepidopleurus corallinus* Risso, p. 268.
1844 *Chiton pulchellus* Phillipi, p. 83, pl. 19, fig. 14 (non Gray, 1828).
1860 *Chiton denudatus* Reuss, p. 259, pl. 8, figs. 14-15.
1870 *Chiton philippii* Issel, p. 5 (nom. nov. pro *Chiton pulchellus* Phillipi, 1844).
1934 *Chiton* (*Clathropleura*) *corallinus denudatus* Reuss. – Sulc, p. 24, pl. 2, figs. 44-45.
1962 *Chiton* (*Chiton*) *corallinus* (Risso). – Malatesta, p. 163, figs. 20-21.
1971 *Chiton denudatus* Reuss. – Baluk, p. 462, pl. 5, figs. 9-11.
1977 *Chiton corallinus* (Risso). – Laghi, p. 109, pl. 2, figs. 9-12.
1999 *Chiton* (*Rhyssoplax*) *corallinus* (Risso). – Dell' Angelo & Smriglio, p. 174, pls. 58-59, figs. A-N, text-figs. 97-107.
2001 *Chiton corallinus* (Risso). – Dell'Angelo et al., p. 152, fig. 25.
2004 *Chiton* (*Rhyssoplax) corallinus* (Risso). – Dell' Angelo et al., p. 39, pl. 3, figs. 4, 7.
2005 *Chiton* (*Rhyssoplax*) *corallinus* (Risso). – Garilli et al., p.139, pl. 4, figs. 6-10.

Material: 12 head, 167 intermediate, and 20 tail valves (AMPG 1565-1568, 1634-1828).

Description: Valves carinated. Intermediate valves wide, rectangular to slightly trapezoidal (Fig. 8.5, 8.6). Head valves, lateral areas of intermediate valves (Fig. 8.8) and postmucronal area of tail valves (Fig. 8.7) smooth. Pleural areas of intermediate valves with 7-10 longitudinal grooves that are actually small outward-leaning folds of tegmentum (Fig. 8.5, 8.6, 8.8). Aesthetes dense and randomly arranged (Fig. 9.1), more irregular on the jugal area of the valves than on lateral ones. Antemucronal area of tail valves smooth on the jugal area and with grooves on the pleural areas (Fig. 8.7).

Remarks: Baluk (1984) and subsequent authors accepted Laghi's (1977) considerations about *Chiton denudatus* Reuss, 1860, a species from the Miocene of the Vienna Basin, Bohemia and Central Poland (Baluk 1971), as a junior synonym of *Chiton corallinus*. As mentioned before, *Rhyssoplax* Thiele, 1893 is a separate genus from *Chiton* Linnaeus, 1758, after the new systematics of Sirenko (2006), which is based on the soft parts of living specimens.

Distribution: This species has been found in the Miocene of central Eastern Europe (Baluk 1971; Studencka & Studencki 1988; Kroh 2003) and Italy (Laghi 1977; Dell' Angelo & Smriglio 1999). It is very common in Italian Pliocene and Pleistocene deposits (Malatesta 1962; Laghi 1977; Dell'Angelo et al. 2007), and has also been reported from the Pliocene of Portugal (Dell' Angelo & da Silva 2003) and Spain (Dell' Angelo et al. 2004), and from the Pleistocene of NW Peloponnesus (Garilli et al. 2005). It is considered being an endemic Mediterranean species (Riedl 1983; Poppe & Goto 1991; Dell' Angelo & Smriglio 1999; Koukouras & Karachle 2005) that also occurs in the Sea of Marmara. It lives at depths of 0 to 100 m, on shells, calcareous algae, rocks, and stones, especially in coralligenous biocoenoses (Table 1).

Rhyssoplax olivacea Spengler, 1797
Fig. 9.3-9.4

1797 *Chiton olivaceus* Spengler, p. 73, pl. 6, fig. 8.
1828 *Chiton siculus* Gray, p. 5.
1883 *Gymnoplax bohemicus* de Rochebrune, p. 63.
1934 *Chiton bohemicus* (de Rochebrune).– Sulc, p. 25, pl. 2, figs. 48, 50-54.
1962 *Chiton* (*Chiton*) *olivaceus* Spengler. – Malatesta, p. 161, figs. 18-19.
1977 *Chiton olivaceus* Spengler. – Laghi, p. 109, pl. 2, figs. 5-8, 13.
1995 *Chiton* (*Rhyssoplax*) *olivaceus* Spengler. – Dell' Angelo & Forli, p. 231.
1999 *Chiton* (*Rhyssoplax*) *olivaceus* Spengler. – Dell' Angelo et al., p. 270, pl. 4, figs. 1-8.

1999 *Chiton* (*Rhyssoplax*) *olivaceus* Spengler. – Dell' Angelo & Smriglio, p.169, pls. 56-57, figs. A-P, text-figs. 86-96.
2005 *Chiton* (*Rhyssoplax*) *olivaceus* Spengler. – Garilli et al., p. 138, pl. 4, figs. 1-5.
2006 *Chiton* (*Rhyssoplax*) *olivaceus* Spengler. – Dell' Angelo & Vardala-Theodorou, p. 328, figs. 3-5.

Material: 1 intermediate valve (AMPG 1569).

Description: Valve carinated, with lateral areas elevated, prominent apex and radially sulcate tegmentum, three radial grooves on lateral areas and nine longitudinal grooves on pleural areas (Figs. 9.3, 9.4).

Remarks: The extant species is characterized by 6-15 longitudinal grooves in pleural areas of intermediate valves (Dell' Angelo & Smriglio 1999). The variability in the morphology and the sculpture of the valves of the fossil forms and the colour variations in the Recent material (Poppe & Goto 1991), gave rise to a rather extensive synonymy. Even though it is a very common species in the Aegean Sea (Koukouras & Karachle 2005), it is remarkably rare in the studied deposits.

Distribution: This species has been found in the Miocene of the Vienna basin, Poland, former Czechoslovakia, Romania, Ukraine, Hungary (Studencka & Studencki 1988; Kroh 2002; Dulai 2005) and Italy (Dell' Angelo et al. 1999). It also occurs in the Pliocene of Italy and France (Laghi 1977; Bellomo & Sabelli 1995; Dell'Angelo & Smriglio 1999) and the Pleistocene of Italy and Spain (Malatesta 1962; Dell'Angelo et al. 2004; Sabelli & Taviani 1979). In the Late Pleistocene it is mentioned from Greece (Vardala-Theodorou 1998; Garilli et al. 2005; Dell' Angelo & Vardala-Theodorou 2006) and Cyprus (Unger & Kotschy 1865). *R. olivacea* inhabits the Mediterranean; it is common in the Aegean Sea (Forbes 1844; Strack 1988, 1990) and in the Marmara Sea (Koukouras & Karachle 2005). It is also recorded from the Eastern Mediterranean (Haifa bay) in the infralittoral zone down to 26 m (Barash & Danin 1992). In the Atlantic Ocean it only occurs as far as Tangiers (Morocco), the southern coast of Portugal (Dell'Angelo & Smriglio 1999) and the Berlengas Islands (E. Schwabe personal communication). It lives on rocks, stones (Table 1), calcareous algae, sponges, and anthozoans such as *Eunicella singularis*, at depths from 0.5 to 62 m (Koukouras & Karachle 2005).

Suborder Acanthochitonina Bergenhayn, 1930
Superfamily Mopalioidea Dall, 1889
Family Tonicellidae Simroth, 1894
Subfamily Tonicellinae Simroth, 1894
Genus *Lepidochitona* Gray, 1821

Type species: *Chiton marginatus* Pennant, 1777 (= *Chiton cinereus* Linnaeus, 1767), by monotypy.

Subgenus *Lepidochitona* s. s.

Lepidochitona (*Lepidochitona*) cf. *canariensis* (Thiele, 1909)
Fig. 9.5-9.7

1909 *Trachydermon canariensis* Thiele, p. 15, pl. 2, figs. 14-25.
1931 *Trachydermon canariensis* Thiele. – Bergenhayn, p. 14, pl. 2, figs. 57-58.
1985b *Lepidochitona* (*L.*) *canariensis* Thiele. – Kaas & Van Belle p. 95, fig. 44.
1999 *Lepidochitona* (*L.*) *canariensis* Thiele. – Dell' Angelo & Smriglio, p.154, pl. 51, figs. A-H, text-fig. 78.
2004 *Lepidochitona* (*L.*) *canariensis* Thiele. – Dell' Angelo et al., p. 13, pl. 3., fig. 3.

Material: 1 fragment of intermediate valve (AMPG 1558).

Description: Valve rectangular with very prominent apex (Fig. 9.5). Lateral area separated from central area by a fold (Fig. 9.5, 9.6). Tegmentum covered with rough granules quincuncially arranged, not diamond-shaped as in *L. cinerea*, but coarser, forming faint longitudinal striae, less marked than in other *Lepidochitona* species, converging on pleural area (Fig. 9.7). Articulamentum with triangular apophysis (Fig. 9.5).

Remarks: Our valve fragment presents the main characteristics of the species, with valves rectangular in outline and a very prominent apex, more distinct than in *L. cinerea* and *L. caprearum*. However, until more material becomes available, we tentatively identified it as *Lepidochitona* cf. *canariensis* (B. Dell'Angelo personal communication).

Distribution: According to the available literature the first fossil record of this species is from the Pliocene of

Fig. 9. 1-2. *Rhyssoplax corallina* (Risso, 1826). 1, AMPG 1566, intermediate valve, dorsal view, detail of sculpture of left pleural area. 2, AMPG 1568, head valve, dorsal view. 3-4. *Rhyssoplax olivacea* Spengler, 1797, AMPG 1569, intermediate valve, dorsal view (3), sculpture of pleural and lateral area (4). 5-7. *Lepidochitona* (*Lepidochitona*) cf. *canariensis* (Thiele, 1909), AMPG 1558, fragment of intermediate valve, dorsal view (5), sculpture of pleural and lateral area (6), detail of sculpture of pleural area (7). 8-9. *Lepidochitona* (*Lepidochitona*) *caprearum* (Scacchi, 1836), AMPG 1559, intermediate valve, dorsal view (8), detail of sculpture of pleural area (9).

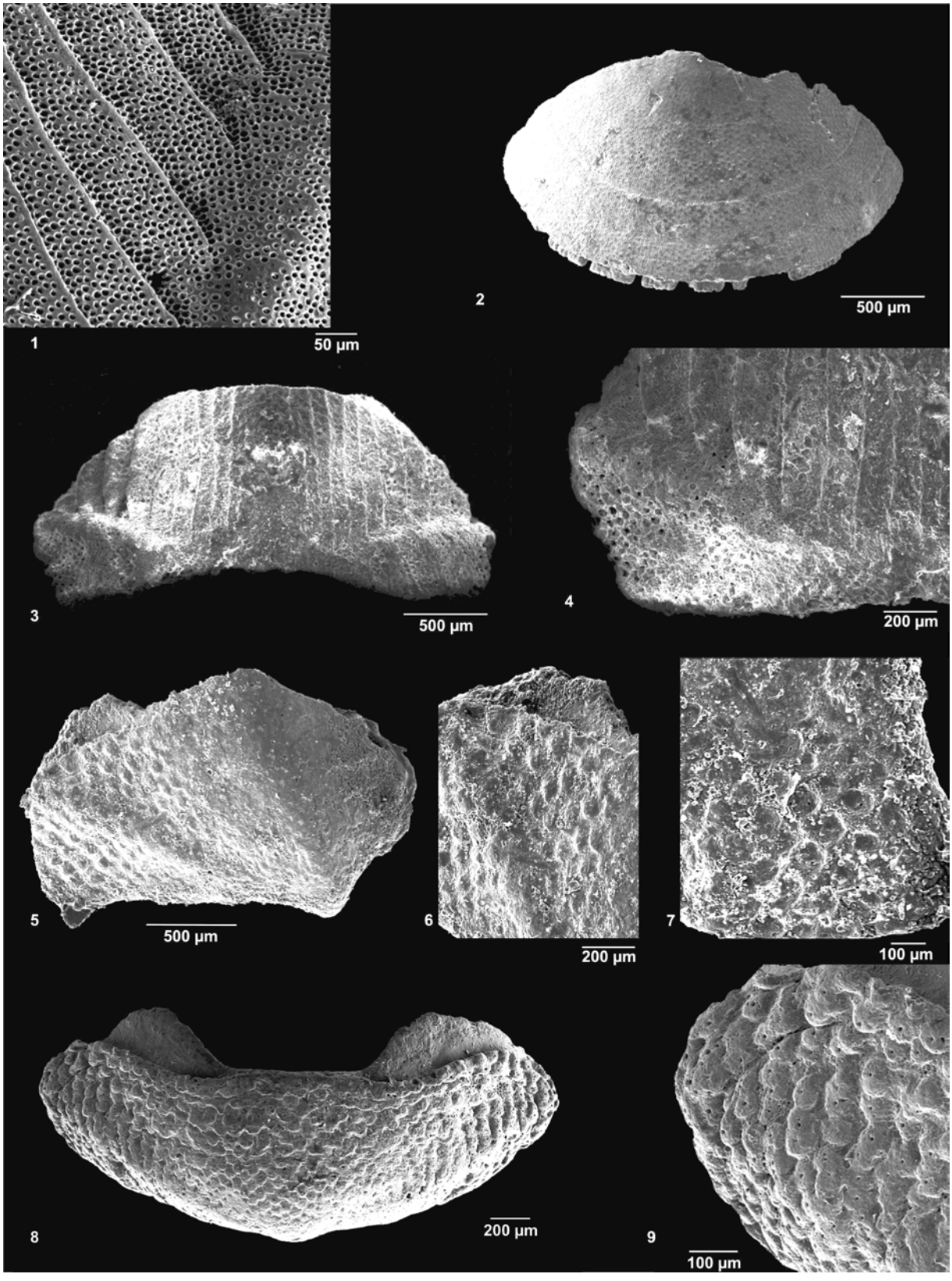

Fig. 9 (Legend see p. 316)

Estepona (Malaga, SW Spain) where two head valves were collected (Dell'Angelo et al. 2004). The valve presented herein is the first record from the Pleistocene. *L. canariensis* is a rare intertidal species found only in Madeira, the Canary Islands (Leloup 1968), and the Mediterranean (Morocco) (Dell'Angelo & Tringali 2000).

Lepidochitona (*Lepidochitona*) *caprearum* (Scacchi, 1836)
Figs. 9.8-9.9, 10.1-10.2

1836 *Chiton caprearum* Scacchi, p. 9.
1848 *Chiton corrugatus* Reeve, pl. 28, fig.185.
1877 *Chiton decipiens* Tiberi, p. 141.
1962 *Middendorffia caprearum* (Scacchi). – Malatesta, p.157, figs. 13-14.
1979 *Middendorffia caprearum* (Scacchi). – Sabelli & Taviani, pp. 160-161, pl. 1, figs. 8-9.
1981 *Lepidochitona* (*L.*) *caprearum* (Scacchi). – Kaas & Van Belle, p. 16, figs. 32-44.
1985 *Lepidochitona caprearum* (Scacchi). – Gaglini, pl. 1, figs. 1-2, pl. 3, fig. 3, pl. 7, figs. 3-4, pl. 13, fig. 6.
1995 *Middendorffia caprearum* (Scacchi). – Bellomo & Sabelli, p. 201.
1995 *Lepidochitona* (*L.*) *caprearum* (Scacchi). – Dell' Angelo & Forli, p. 228, fig. 12.
1999 *Lepidochitona* (*L.*) *caprearum* (Scacchi). – Dell' Angelo & Smriglio, p. 143, pls. 46-48, figs. A-S, text-figs. 73-76.

Material: 4 intermediate valves (AMPG 1559-1560, 1627-1628).

Description: Valves almost rectangular with small apex and two wide, rounded diagonal ribs (Fig. 9.8). Tegmentum with rough granules quincuncially arranged (Figs. 9.9, 10.2). Apophyses trapezoidal to subtriangular (Fig. 10.2). Articulamentum strongly slitted peripherically (Fig. 10.1).

Remarks. *L. caprearum* has a long nomenclatural history. Gaglini (1985) contributed to the establishment of the name. In our Recent material from Rhodes Island, the shell is oval to round in outline, not carinated, often eroded and encrusted with calcareous organisms.

Distribution: This species has been mentioned in the fossil records from the Pliocene and Pleistocene of Italy (Malatesta 1962). This is the first fossil record from the Eastern Mediterranean. *L. caprearum* is distributed in the supralittoral and mediolittoral zones, on rocky shores, in several areas of the Mediterranean Sea (Kaas 1989; Dell'Angelo & Smriglio 1999; Barash & Danin 1992), also in the Black and Marmara Seas (Raspaleff 1933 and Müller 1985 in Koukouras & Karachle 2005). There is one record from deeper water (70 m) (Koukouras & Karachle 2005). In the Atlantic, it occurs on the coasts of Northwest Africa, Spain, Portugal, and Selvagens Islands (Malatesta 1962; Kaas 1991).

Lepidochitona (*Lepidochitona*) *cinerea* (Linnaeus, 1767)
Fig. 10.3-10.5

1767 *Chiton cinereus* Linnaeus, p. 1107.
1962 *Lepidochitona* (*L.*) *cinereus* (Linnaeus). – Malatesta, p. 155, figs. 11-12.
1985b *Lepidochitona* (L.) *cinerea* (Linnaeus). – Kaas & Van Belle, p. 84, fig. 39.
1999 *Lepidochitona* (*L.*) *cinerea* (Linnaeus). – Dell' Angelo & Smriglio, p.138, pls. 44-45, figs. A-N, text-figs. 67-72.
2001 *Lepidochitona cinerea* (Linnaeus). – Dell' Angelo et al., p. 148, figs. 12, 15.
2004 *Lepidochitona* (*L.*) *cinerea* (Linnaeus). – Dell' Angelo et al., p. 36, pl. 3, fig. 6.
2005 *Lepidochitona* (*L.*) *cinerea* (Linnaeus). – Garilli et al., p.136, pl. 3, figs. 1-3.

Material: 2 intermediate valves (AMPG 1561, 1629).

Description: Valves rectangular, subcarinate, with an estimated wide/length ratio of about 0.32 (Fig. 10.3). Posterior margin almost straight with small apex not very prominent. Lateral areas not separated from the central one (Fig. 10.3). Tegmentum sculptured with fine diamond-shaped granules (Fig. 10.5), arranged in somewhat irregular quincunx pattern, apparently formed by oblique intersections of curved incised lines radiating in two directions towards the margins (Fig. 10.3, 10.4).

Remarks: Descriptions of this species are given by Kaas & Van Belle (1985b) and Dell'Angelo & Smriglio (1999), where the taxonomical history is also presented.

Distribution: There are doubtful records of this species from the Badenian of Poland and from the Miocene of Italy (Dell'Angelo et al. 1999). It is recorded from the Pliocene of Italy, Spain and Portugal (Malatesta 1962; Dell' Angelo et al. 2004; Dell'Angelo & da Silva 2003) and

Fig. 10. 1-2. *Lepidochitona* (*Lepidochitona*) *caprearum* (Scacchi, 1836), AMPG 1560, intermediate valve, ventral view (1), dorsal view of the sculpture of pleural and lateral area (2). 3-5. *Lepidochitona* (*Lepidochitona*) *cinerea* (Linnaeus, 1767), AMPG 1561, intermediate valve, dorsal view (3), details of sculpture of pleural area (4, 5). 6-7. *Lepidochitona* (Lepidochitona) *furtiva* (Monterosato, 1879), AMPG 1562, intermediate valve, dorsal view. 8-10. *Lepidochitona* (*Lepidochitona*.) *monterosatoi* Kaas & Van Belle, 1981. 8, AMPG 1563, intermediate valve, dorsal view. 9-10, AMPG 1564, intermediate valve, dorsal view (9), sculpture of pleural area (10).

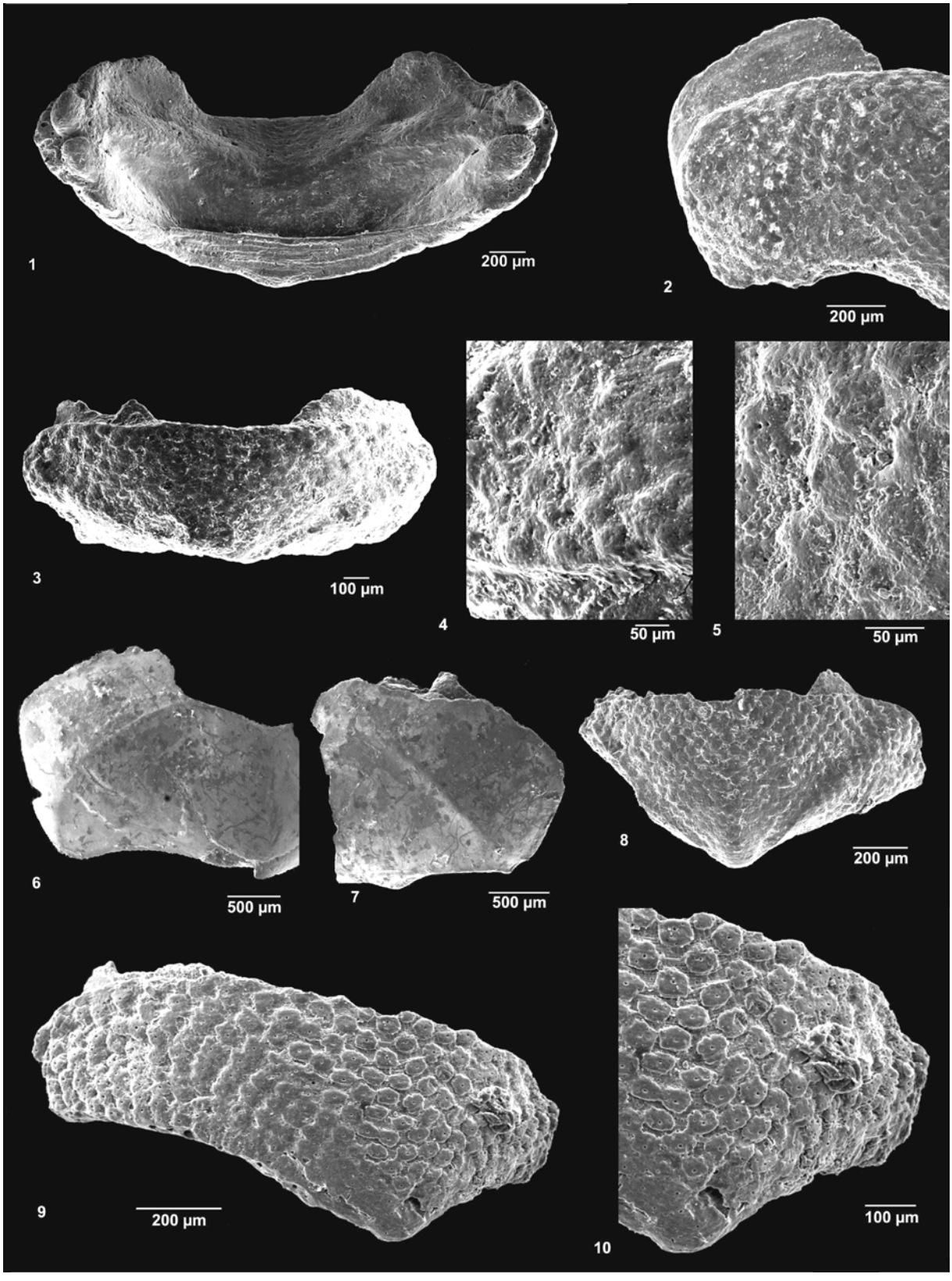

Fig. 10 (Legend see p. 318)

the Pleistocene of Italy and Norway (Antevs 1928). It was also found in the Pliocene and the Pleistocene of the NW Peloponnesus (Kleinhölter 1994; Garilli et al. 2005). *L. cinerea* is widely distributed in the present-day Mediterranean and Black Sea, also on the European Atlantic coasts (Malatesta 1962; Dell'Angelo et al. 1999; Dell'Angelo et al. 2004). The presence of this species on the North American Pacific coast (Dell'Angelo & Smriglio 1999) is doubtful as the detailed study of the genus in this area shows (Eernisse 1986). It occurs in Greece (Strack 1988; Delamotte & Vardala-Theodorou 2001; Koukouras & Karachle 2005). This species lives on rocks in the mediolittoral to infralittoral zones (Table 1) at depths of about 10 m (Koukouras & Karachle 2005), in the zone of photophilous algae (Dell'Angelo & Forli 1995). The only record from deeper water is one specimen found at about 70 m (Zenetos & Van Aartsen 1995).

Lepidochitona (*Lepidochitona*) *furtiva* (Monterosato, 1879)
Fig. 10.6-10.7

1872 *Chiton ruber* (Linnaeus) Lowe, var. = *C. furtivus* - Monterosato, p. 29 (nom. nud.).
1875 *Chiton furtivus* Monterosato, p. 21 [= *C. ruber* (L.) Lowe var. L.] (nom. nud.).
1878b *Chiton furtivus* Monterosato, p. 147 (nom. nud.).
1879 *Chiton furtivus* Monterosato, p. 19.
1909 *Trachydermon furtivus* (Monterosato). – Thiele, p. 15, pl. 2, figs. 6-13.
1985b *Lepidochitona* (*L.*) *furtiva* (Monterosato). – Kaas & Van Belle, p. 91, fig. 42.
1999 *Lepidochitona* (*L.*) *furtiva* (Monterosato). – Dell'Angelo & Smriglio, p. 150, pls. 49-50, figs. A-O, text-fig. 77.
2005 *Lepidochitona* (*L.*) *furtiva* (Monterosato). – Garilli et al., p. 136, pl. 3, figs. 4-8.

Material: 3 intermediate valves (AMPG 1562, 1630-1631).

Description: Valves rectangular, depressed. Articulamentum triangular to trapezoidal (Fig. 10.6, 10.7). Tegmentum nearly smooth, with weak radial striae on lateral areas. Lateral areas slightly elevated (Fig. 10.6).

Remarks. On one of the recovered valves (Fig. 10.6, 10.7) the tegmentum is smooth and there are no radial striae. An extensive nomenclatural history of *L. furtiva* has been given by Garilli et al. (2005).

Distribution: This is the second fossil record of *L. furtiva* after that of Garilli et al. (2005), also from the Pleistocene of Greece. The presence of this species in our samples and the fact that no fossil record was known so far except from Greece, indicate that it probably originated in the Pleistocene of the Mediterranean area. *L. furtiva* is considered being endemic in the Mediterranean Sea (Koukouras & Karachle 2005). It occurs in Italy (Sicily, Pontine Islands, Lampedusa Island) (Gravina et al. 1992), France, Corsica, Malta, Algeria (Dell'Angelo & Smriglio 1999), and Tunisia (Djerba, Bou Grara) (Kaas 1989). *L. furtiva* lives in association with *Posidonia oceanica* leaves and rhizomes from the subtidal zone to depths of about 30 m (Garilli et al. 2005; Boyer 2006; Delemarre 2007).

Lepidochitona (*Lepidochitona*) *monterosatoi* Kaas & Van Belle, 1981
Fig. 10.8-10.10

1981 *Lepidochitona* (*L.*) *monterosatoi* Kaas & Van Belle, p. 23, figs. 57-72.
1988 *Lepidochitona monterosatoi* Kaas & Van Belle. – Macioszczyk, p. 52, pl. 2, figs. 6-8a-b.
1995 *Lepidochitona* (*L.*) *monterosatoi* Kaas & Van Belle. – Dell'Angelo & Forli, p. 229, fig. 7.
1999 *Lepidochitona* (*L.*) *monterosatoi* Kaas & Van Belle. – Dell'Angelo & Smriglio, p. 158, pls. 52-53, figs. A-N, text-figs. 79-83.
2001 *Lepidochitona monterosatoi* Kaas & Van Belle. – Dell'Angelo et al., p. 148, fig. 14.

Material: 4 intermediate valves (AMPG 1563-1564, 1632-1633).

Description: Valves rectangular, subcarinated, with strongly protruding apex (Fig. 10.8, 10.9). Tegmentum sculptured with rounded convex granules quincuncially arranged on lateral and jugal areas, in curved and diverging longitudinal series on pleural areas (Fig. 10.9, 10.10). Articulamentum with triangular apophyses (Fig. 10.8).

Remarks: *L. monterosatoi* is distinguished from the other *Lepidochitona* species by its subcarinated valves and the eight radial depressions of the head valve that is missing in our material.

Distribution: *L. monterosatoi* has been found in the Middle Miocene of Poland (Macioszczyk 1988) and the Pliocene and Pleistocene of Italy (Dell'Angelo et al. 2001). This is the first fossil record from the Eastern Mediterranean. It is essentially a Mediterranean species

Fig. 11. 1-2. *Acanthochitona crinita* (Pennant, 1777), AMPG 1570, intermediate valve, dorsal view (1), detail of sculpture of lateropleural area (2). 3-8. *Acanthochitona fascicularis* (Linnaeus, 1767). 3-4, AMPG 1571, intermediate valve, dorsal view (3), detail of sculpture of lateropleural area (4). 5-6, AMPG 1572, tail valve, dorsal view (5), detail of sculpture of lateropleural area (6). 7-8, AMPG 1573, head valve, dorsal view (7), detail of sculpture (8).

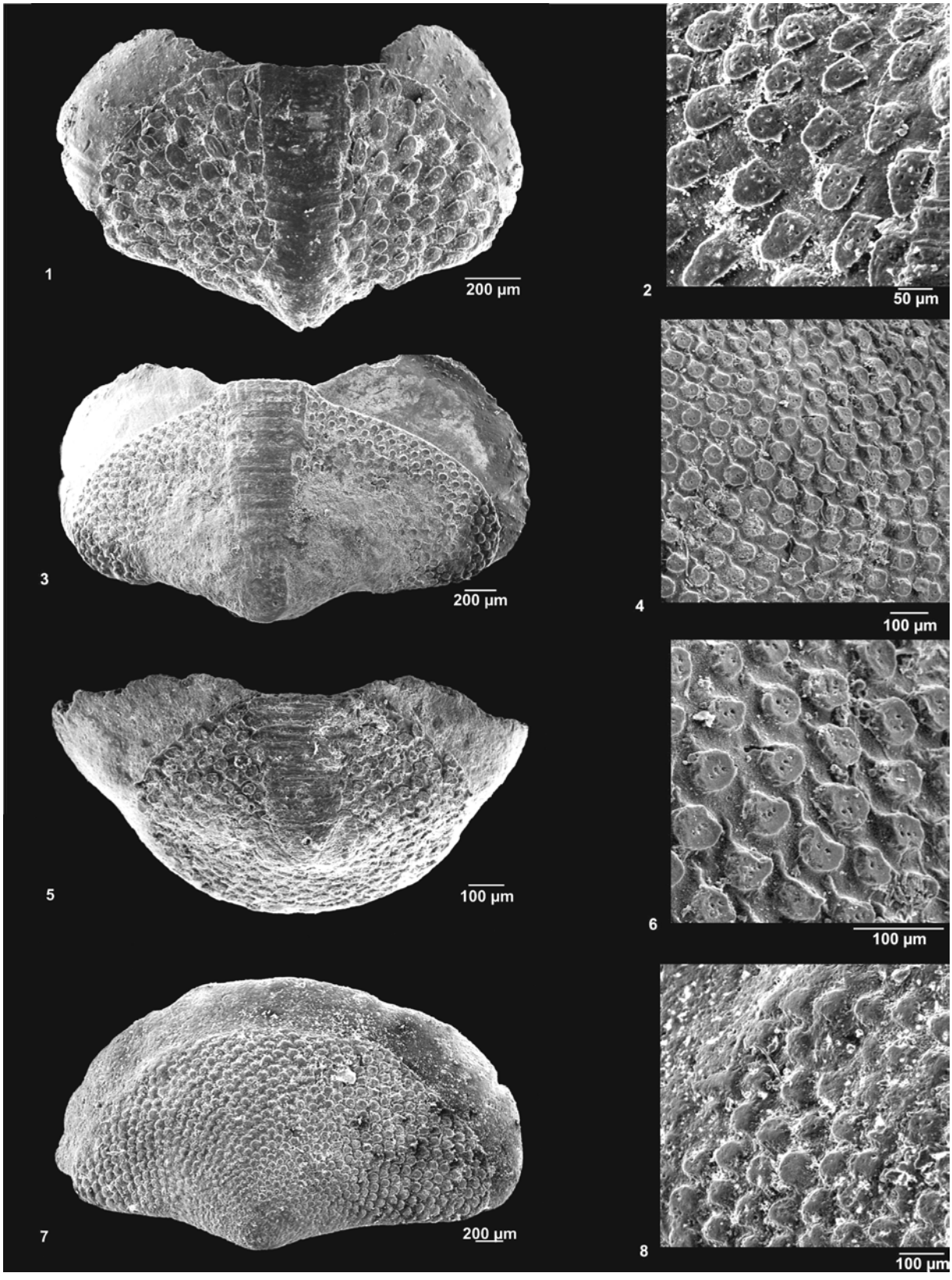

Fig. 11 (Legend see p. 320)

(Sardinia, France, Croatia, Turkey, Tunisia, Spain, Cyprus, Greece) (Koukouras & Karachle 2005), but it was also mentioned from the Red Sea (Strack 1993). According to Dell'Angelo & Smriglio (1999) in Greece it has been referred to *Chiton polii* Philippi, 1836 by Forbes (1844). It lives associated with calcareous algae in microcavities, on rocks, on *Posidonia oceanica* leaves (Table 1), and sponges (Koukouras & Karachle 2005).

Superfamily Cryptoplacoidea H. & A. Adams, 1858
Family Acanthochitonidae Pilsbry, 1893
Subfamily Acanthochitoninae Pilsbry, 1893
Genus *Acanthochitona* Gray, 1821

Type species: *Chiton fascicularis* Linnaeus, 1767, by monotypy.

Acanthochitona crinita (Pennant, 1777)
Fig. 11.1-11.2

1777 *Chiton crinitus* Pennant, p. 71, pl. 36, figs. 1, A 1.
1797 *Chiton onyx* Spengler, p. 95.
1962 *Acanthochitona fascicularis* (*L.*). – Malatesta, p. 164, fig. 22.
1971 *Acanthochitona lacrimulifera* Baluk, p. 464, pl. 2, figs. 6-9.
1977 *Acanthochitona fascicularis* (*L.*). – Laghi, p. 111, pl. 3, figs. 20-21.
1984 *Acanthochitona fascicularis* (*L.*). – Baluk, p. 291, pl. 9, fig. 2.
1985 *Acanthochitona crinita* (Pennant). – Kaas, p. 588, figs. 7-50.
1992 *Acanthochitona crinita* (Pennant). – Cavallo & Repetto, p. 30, fig. 4.
1995 *Acanthochitona crinita* (Pennant). – Dell'Angelo & Forli, p. 236, fig. 13.
1999 *Acanthochitona crinita* (Pennant). – Dell'Angelo & Smriglio, p. 198, pls. 66-68, figs. A-V, text-figs. 124-125.
2004 *Acanthochitona crinita* (Pennant). – Dell'Angelo et al., p. 41, pl. 4, figs. 2-5.

Material: 1 intermediate valve (AMPG 1570).

Description: Valve ellipsoidal, slightly pentagonal in shape. Jugal area wide, not very well separated from laterolateropleural area (Fig. 11.1). Tegmentum with oval to more or less elongated drop shaped granules, which bear a central megalaesthete and 8-10 micraesthetes (Fig. 11.2.). Articulamentum with quadrangular, strongly protruding apophyses (Fig. 11.1).

Remarks: *Acanthochitona crinita* is a very variable species in the morphology of the valves, less common than *A. fascicularis* (Dell'Angelo et al. 1998).

Distribution: This species has been found in the Miocene of central Eastern Europe (Dell'Angelo & Smriglio 1999) and the Miocene to Pleistocene of Italy (Dell'Angelo et al. 1999). This is the first fossil record from the Eastern Mediterranean. *A. crinita* occurs in the Mediterranean Sea, the Atlantic coasts of Europe, North America, the Canary Islands, Brazil, and Cape Verde (Kaas 1985; Dell'Angelo et al. 1999). It lives on rocks, stones and calcareous algae (Table 1) in the intertidal zone and at greater depths, down to 175 m (Dell'Angelo et al. 1989; Dell'Angelo & Smriglio 1999; Koukouras & Karachle 2005).

Acanthochitona fascicularis (Linnaeus, 1767)
Fig. 11.3-11.8

1767 *Chiton fascicularis* Linnaeus, p. 1106.
1826 *Acanthochites communis* Risso, p. 268.
1883 *Acanthochites Faluniensis* de Rochebrune, p. 60.
1934 *Acanthochiton faluniensis* de Rochebrune. – Sulc, p. 17, pl. 1, fig. 29, pl. 2, figs. 30-32, text-fig. 2.
1962 *Acanthochitona communis* (Risso). – Malatesta, p. 166, figs. 24-25.
1971 *Acanthochitona faluniensis* (de Rochebrune). - Baluk, p. 463, pl. 2, figs. 10-15.
1977 *Acanthochitona communis* (Risso). – Laghi, p. 110, pl. 3, figs. 13-19.
1977 *Craspedochiton* (*Pseudoacanthochitona*) *ambiguus* Laghi, p. 113, pl. 4, figs. 9-12.
1985 *Acanthochitona fascicularis* (Linnaeus). – Kaas, p. 585, figs. 1-6.
1999 *Acanthochitona fascicularis* (Linnaeus). – Dell' Angelo & Smriglio, p. 192, pls. 64-65, figs. A-P, text-figs. 113-123.
2004 *Acanthochitona fascicularis* (Linnaeus). – Dell' Angelo et al., p. 40, pl. 3, fig. 8, pl. 4, fig. 1.
2005 *Acanthochitona fascicularis* (Linnaeus). – Garilli et al., p. 139, pl. 5, fig. 1.
2006 *Acanthochitona fascicularis* (Linnaeus). – Dell' Angelo & Vardala-Theodorou, p. 331, fig. 6.

Material: 7 head, 94 intermediate and 8 tail valves (AMPG 1571-1573, 1829-1934).

Description: *A. fascicularis* is an extremely variable species in size and morphology. Intermediate valves with triangular to pentagonal shape. Jugal area elevated, distinctly separated from lateropleural area. Articulamentum with very protruding and quadrangular apophyses, delimiting a wide jugal sinus (Fig. 11.3). Tegmentum with small roundish granules arranged in orderly arched lines (except for the jugal area of intermediate and tail valve) and characterized by their flat or slightly concave surface (Fig. 11.3, 11.4, 11.5, 11.6, 11.7, 11.8). Articulamentum of tail valve surrounding the valve completely, except for the jugal margin (Fig. 11.5).

Remarks: *A. faluniensis* de Rochebrune, 1883, was reported from the Miocene of central Eastern Europe. It differs from *A. fascicularis* only by having a smaller number

of slightly larger granules; it was regarded as a synonym of *A. fascicularis* by Laghi (1977) and Dell'Angelo et al. (1999). This opinion was not accepted by Baluk (1984). The recovered specimens are characterised by a great variability of the size of the tegmentum granules, a fact that set questions for the investigation of which, more material is needed.

Distribution: *A. fascicularis* has been found in the Miocene of central Eastern Europe and Italy (Dell'Angelo et al. 1999), in the Pliocene of Spain (Dell'Angelo et al. 2004) and Italy (Laghi 1977; Dell'Angelo et al. 1999) and in the Pleistocene of Italy (Dell'Angelo et al. 2007). It is also recorded from the Pleistocene of NW Peloponnesus (Vardala-Theodorou 1998; Garilli et al. 2005; Dell' Angelo & Vardala-Theodorou 2006; Vardala-Theodorou & Nikolaidou 2007) and Cyprus (Unger & Kotschy 1865). This species has a vast geographical distribution: Mediterranean, Atlantic (from the British Channel and Brittany to the Azores and the Canary Islands) (Dell'Angelo & Smriglio 1999). It is a very common species in the Aegean Sea (Koukouras & Karachle 2005). It lives in shallow waters (0 to 73 m) under stones and rocks covered with algae (Table 1), often in association with sponges, anthozoans, and mollusc shells (Dell' Angelo & Smriglio 1999; Koukouras & Karachle 2005).

5. Palaeoecology

The ecological and geographical distribution of the polyplacophorans is controlled by their biology and by environmental parameters such as temperature, salinity, nutrients, substrate types, and water depth (even though many species have wide bathymetric ranges). To identify the ecological niches occupied by the collected specimens, we used field observation and sedimentological data, information from extant chiton species and the accompanying mollusc fauna, as well as the number of specimens of chitons and their state of preservation (taphonomic criteria). The main data on habitat specificity of polyplacophoran species per collecting site are presented in Table 1.

In the Kritika section (Kritika Member, Rhodes Formation, Late Pliocene), only three samples yielded chiton valves (Fig. 2). In levels 1 and 2 the sands with abundant coralline algal rhodoliths represent deposits of the infralittoral zone, with a well-preserved autochthonous to parautochthonous mollusc association. In level 1 the mollusc association is characteristic of gravely bottom settings of photophilous algae (*Bittium* spp., *Acinopsis cancellata*, and *Arca* sp.). In level 2, the sandy marls contain in *situ* rhizomes of the seagrass *Posidonia oceanica*; they are dominated by an association of bivalves such as *Arca noae, Striacra lactea, Nucula nucleus*, and *Acinopsis cancellata*, and the gastropod *Tricolia pullus*, which is characteristic for *P. oceanica* meadows (Moissette et al. 2007). In level 3, clays with some pebbles and numerous rhodoliths point to a shallow-water environment of the infralittoral zone and a transported *Posidonia*-meadow association of molluscs with *Gastrochaena dubia, Jujubinus exasperatus,* Rissoidae*, Bittium latreillei*, and *Clelandella milliaris*. The abundance of *Callochiton septemvalvis, Rhyssoplax corallina* and *Acanthochitona fascicularis* in these levels is in agreement with the inferred biotopes as mentioned above.

The Faliraki-1 section (Fig. 3) also belongs to the Kritika Member. This section comprises mostly fluviatile, brackish to marine infralittoral siliciclatic deposits. Two beds with calcareous crusts on drowned beachrock (levels 2 and 5) indicate different transgressive phases from a beach environment to a coralline algae horizon of the infralittoral zone. The sediments of levels 1 and 2 correspond to the first transgressive phase, occurring in medio to infralittoral settings in water depths of at most 20 m, swept by moderate currents, where a wide range of ecological niches occur. The mollusc association is dominated by herbivores, grazers and a few suspension feeders: *Rissoa variabilis, Acinopsis cancellata, Alvania cimex, A. lineata, Bittium reticulatum, B. latreillei, B. lacteum, Triphora perversa, Clelandella milliaris, Jujubinus exasperatus, Glycymeris glycymeris*, and *Arca tetragona*. In these sediments, eight species of chitons occur. The overall state of preservation of the bioclasts of these accumulations reflects rapid burial under high sedimentation rates. These assemblages are considered as autochthonous to parautochthonous. *Leptochiton cimicoides*, which occurs only in level 1, is represented by two poorly preserved valves. Since it lives today at depths of 20 to 110 m, we can assume that it has been transported from somewhat deeper water to shallower water. *Callochiton septemvalvis* and *Rhyssoplax corallina* were also found in the sandy marls of level 3 where solitary corals, *Nucula* sp., and *Parvicardium scriptum* dominate. The sediments of levels 4 and 5 correspond to the second transgressive phase. The mollusc association of level 4 is the same as in level 1, but the presence of *Theodoxus rhodiensis* indicates a freshwater influx. In level 5, *Lepidopleurus cajetanus, Lepidochitona caprearum, L. monterosatoi, Rhyssoplax corallina* and *Acanthochitona fascicularis* were collected from the calcareous crust of a drowned beachrock, associated with the biocoenosis of the

infralittoral rocks with distinctive calcareous algae, vermetid gastropods, *Bolma rugosa, Spondylus gaederopus*, and rissoids.

The Faliraki-2 section also belongs to the Kritika Member. It comprises fluviatile, brackish to marine infralittoral siliciclastic deposits, as in the previous section, but only one level with calcareous crust on drowned beachrock (Fig. 4). The polyplacophorans and their accompanying mollusc fauna found in three samples indicate a sea bottom characterized by fully marine conditions and well-oxygenated waters. Level 1 represents a mixing of parautochthonous faunas from neighbouring shallow rocky and sandy bottoms with disarticulated shells of endobenthic bivalves (e.g. *Glycymeris glycymeris* and *Tellina* sp.), gastropods of the mediolittoral zone (such as *Haliotis tuberculata* and *Diodora graeca*), epibenthic bivalves from rocky environments (such as *Chama gryphoides* and *Chlamys multistriata*), and molluscs from coralligenous biocoenosis (e.g. *Irus irus, Barbatia barbata, Rissoa ventricosa, R. splendida, R. mariae, Alvania reticulata, Acinopsis cancellata, Jujubinus exasperatus, Nassarius* sp., *Turbona cimex, Triphora perversa, Bittium reticulatum*, and *Clanculus corallinus*). Level 2 represents a drowned beachrock with organogenous crusts and molluscs from neighbouring rocky and sandy environments with seaweeds and seagrasses: *Anomia ephippium, Ostrea edulis, Spondylus gaederopus, Chama gryphoides, Vermetus* sp., *Bolma rugosa* living on rocky substrate, *Chlamys varia, Barbatia barbata* on substrate covered with algae, and *Coralliophila meyendorffii, Lunatia catena, Neverita josephinia, Bittium reticulatum, Tricolia pullus, Acinopsis cancellata* on substrate covered with *Posidonia*. In level 3 the accompanying mollusc fauna consists mainly of *Glycymeris glycymeris, Callista chione, Barbatia pulchella, B. barbata, Ostrea edulis, Spondylus* sp., *Chlamys varia, Gibbula magus, Lunatia catena, Neverita josephinia, Bittium reticulatum, Tricolia pullus, Acinopsis cancellata, Columbella rustica, Calliostoma conulum*, and *Rissoa mariae*, indicating also a mixing of elements from neighbouring rocky and sandy littoral environments. In this section we recognized *Rhyssoplax corallina, R. olivacea*, and *Callochiton septemvalvis*, which are generally associated with coralligenous biocoenoses (Dell' Angelo et al. 1998). Two other species, *Acanthochitona fascicularis* and *Lepidopleurus cajetanus* also occur; they are usually found between stones covered with seaweeds (Dell'Angelo et al. 1998) at depths of 0 to 73 m and 0.5 to 40 m respectively.

The basal part of the Faliraki-3 section (Fig. 5) from which chiton plates were collected, belongs to the Kolymbia Limestone Member of the Rhodes Formation and is Late Pliocene in age (Hanken et al. 1996; Titschack et al. 2005; Cornée et al. 2006a). The lime mud to argillaceous sediments contain abundant gravels and invertebrate communities. A mixed mollusc assemblage is observable with dominant infralittoral-circalittoral or shelf edge-detritic bottom ("Détritique du Large") elements, such as *Chlamys multistriata*, *Chlamys clavata, Venus casina, Striarca lactea, Timoclea ovata, Gregariella subclavata, Epitonium linctum*, and *Notolimea crassa*. The presence of *Callochiton septemvalvis, Rhyssoplax corallina, R. olivacea,* and *Acanthochitona fascicularis* in these sediments is in accordance with the aforementioned biotope, while shallow-water species, such as *Lepidopleurus cajetanus*, were transported downslope into coeval deeper-water environments (Titschack et al. 2005).

The Ladiko section (Fig. 6) belongs to the Ladiko-Tsampika Formation and is Early to Middle Pleistocene in age (Cornée et al. 2006a-b; Joannin et al. 2007). This section is composed of brackish, lagoonal, littoral and offshore siliciclastic deposits that accumulated in the vicinity of palaeocliffs (Hanken et al. 1996; Cornée et al. 2006a; Joannin et al. 2007). Samples 1, 2, 5 and 6 are characterized by accumulations of shell-sands. They correspond to a wave-dominated environment of the infralittoral zone where elements of the *Posidonia* parautochthonous assemblage were disarticulated and sorted. Samples 1 and 2 contain abundant Rissoidae, *Lima hians* and *Arca tetragona*. Sample 5 contains species from coastal detritic bottoms (*Tellina donacina, Timoclea ovata, Acanthocardia echinata*) and seagrass meadows (*Tricolia pullus,* Rissoidae*, Alvania cinex, Charonia* sp., *Granulina* cf. *boucheti*). The macrofaunal fossils of sample 6 correspond to shallow-water sandy bottoms (abundance of Rissoidae, *Rissoa guerinii, Bittium reticulatum, Cerithiopsis tubercularis*). On the basis of the known bathymetric ranges of the extant polyplacophoran species, *Lepidochitona* cf. *canariensis* (0-1 m) and *L. caprearum* (living mostly in the intertidal to mediolittoral zone), a very shallow depth of deposition is assumed for this part of the section. Samples 3 and 4 correspond to sandy bottoms of the delta front in high-energy conditions with turbid water. This is indicated by the abundance of the serpulid worm-tube *Ditrupa arietina* and the accumulation of parautochthonous endobenthic bivalves

(*Divaricela divaricata, Ctena decussata, Abra alba, Dosinia lupinus*), together with fragmented endobenthic and epibenthic gastropods (*Bittium reticulatum,* Rissoidae*, Cylichna cylindracea, Ringicula* sp.). The constant association of shallow-water molluscs with *Lepidochitona cinerea*, suggests deposition at depths of up to 10 m. The only specimen of *Lepidochitona caprearum* found in these sediments was probably transported.

6. Conclusion

The material described in this paper represents 385 valves of polyplacophorans, including well-preserved head, intermediate and tail valves.

The studied Plio-Pleistocene fauna was established in fully marine conditions and well-oxygenated waters from the shore to the detritic bottoms of the shelf edge (Table 1). The most diverse communities correspond to the biocoenoses of the infralittoral rocks with the characteristic vegetal cover of calcareous algae and *Posidonia oceanica* meadows.

The polyplacophoran fauna from Rhodes comprises 13 species, all are still living in the Mediterranean Sea and most of them also occur in the Atlantic Ocean.

Among these species, *Lepidochitona caprearum, L.* cf. *canariensis, L. monterosatoi* and *Acanthochitona crinita* are identified for the first time in the fossil record of the Eastern Mediterranean, whereas *Lepidopleurus cajetanus, Leptochiton cimicoides, Ischnochiton rissoi, Callochiton septemvalvis, Lepidochitona* cf. *canariensis, L. monterosatoi, Rhyssoplax corallina, R. olivacea* and *Acanthochitona fascicularis* are here reported for the first time from the Pliocene of the Eastern Mediterranean. Another species, *Lepidochitona cinerea* has a wide stratigraphical and geographical distribution. *Lepidochitona furtiva* seemingly appeared in the Pleistocene of the Mediterranean Sea, as no fossil record was known so far except from Greece.

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