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Biogeography of northeastern Atlantic Neogene chitons (Mollusca, Polyplacophora): New data from the Pliocene of Portugal

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Abstract.—Based on extensive new material, 2088 valves resulting from search sampling of ~500 kg of sediment, the Pliocene chiton biodiversity of the Mondego Basin (Portugal) is reassessed. Twelve species were identified, assigned to seven genera. Eight species are new for the Pliocene of Portugal, as well as two of the genera: *Hanleya*, *Acanthochitona*. Two taxa are described as new: *Ischnochiton loureiroi* n. sp. and *Lepidochitona rochae* n. sp. Until now, the polyplacophoran European Neogene record was too poorly known to be of help in generating a clear picture of the Miocene to present-day biogeography of the group. This new wealth of data from western Iberia, in conjunction with recent data from the Loire Basin Upper Miocene assemblages (France), allows clarification the Late Miocene to Recent eastern Atlantic and Mediterranean biogeography of the Polyplacophora. The northern range of warm-water northeast Atlantic and Mediterranean Polyplacophora experienced a sharp contraction since, at least, Late Miocene to Early Pliocene times. Warm-water chiton species represented in the Upper Miocene of the Loire Basin of NE France (European-West African Province) and the Pliocene of the Mondego Basin of central-west Portugal (Pliocene French-Iberian Province) are today confined to the southern Mediterranean-Moroccan Molluscan Province.

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Introduction

The Portuguese Pliocene marine fossil assemblage from the Mondego Basin, and the one from the Vale de Freixo site in particular, which is the sole Pliocene assemblage known between the Atlantic Guadalquivir Basin (southwestern Spain) and the Loir Basin (northwestern France), is key for understanding of biodiversity and biogeography of the northeastern marine Pliocene Franco-Iberian Atlantic mollusks (Silva et al., 2006, 2010; Silva and Landau, 2007, Landau et al., 2020). The chiton paleobiodiversity from Vale de Freixo was initially studied by Dell'Angelo and Silva (2003), who reported five species, including the endemic *Ischnochiton zbyi* Dell'Angelo and Silva, 2003, based on the scant material then available. Prior to Dell'Angelo and Silva (2003), the sole reference to the presence of Polyplacophora in the Pliocene of Portugal was that of Morais (1941), who reported *Chaetopleura fulva* (Wood, 1815), a junior synonym of *Chaetopleura angulata* (Spengler, 1797), from the Pliocene of Marinha Grande (Fig. 1).

Whereas the biogeography of Neogene northeastern Atlantic and Mediterranean gastropod mollusks has been extensively analyzed in the last three decades by several authors (e.g., Raffi and Monegatti, 1993; Monegatti and Raffi, 2007; Silva and

Landau, 2007; Silva et al., 2011; Vermeij, 2012; Lozouet, 2014; Ávila et al., 2016; Landau et al., 2020), the biogeography of northeastern Atlantic Polyplacophora has not been studied. In this paper, based on extensive new material, the chiton assemblage of Vale de Freixo is revisited, and new taxa are added to the Pliocene Atlantic fauna of western Iberia. Moreover, two new species of Atlantic Pliocene chitons are described. Based on the novel data obtained, an original approach to the Pliocene to present biogeographical evolution of the group in the northeastern Atlantic is presented and discussed.

Geological and paleoecological setting

Vale de Freixo is situated in central-west Portugal, near Pombal, 20 km east of the present-day coastline, with the geographical coordinates 39°53'02.1"N, 8°43'52.9"W (Fig. 1). The Neogene sequence exposed at this locality (Fig. 2) is part of the Cenozoic Mondego Basin, the fossiliferous Pliocene sediments corresponding to the basal beds of the Carnide Formation (Cachão, 1990; Diniz et al., 2016). The calcareous nannofossil assemblage in them indicates placement in biozone CN12a of Okada and Bukry (1980). Based on calcareous nannofossils and gastropods, these beds have been assigned to the uppermost Zanclean to lower Piacenzian (Cachão, 1990; Silva, 2001; Diniz et al., 2016). The marine molluscan assemblage of Vale de Freixo, as well as all the remaining marine Pliocene Atlantic

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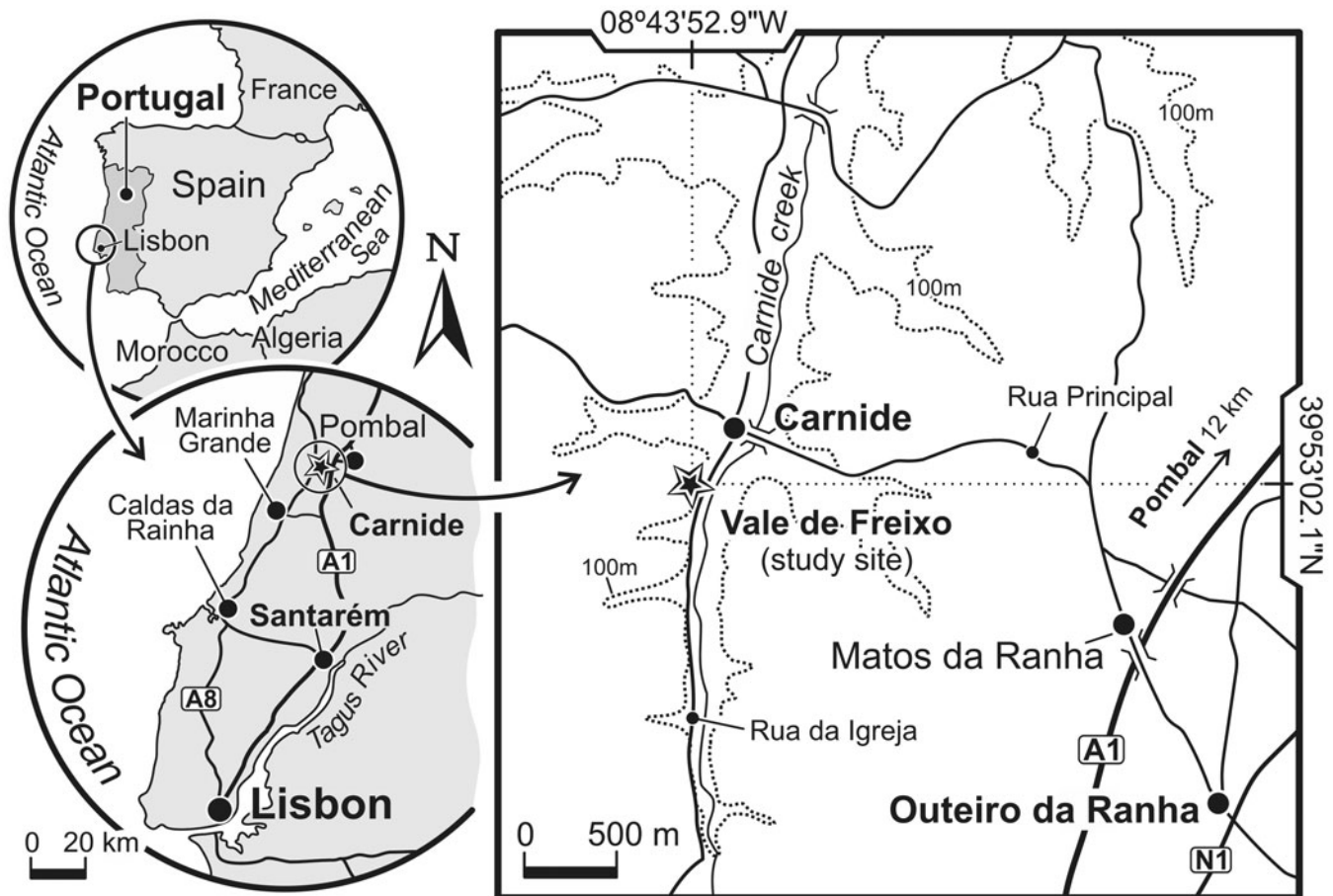


Figure 1. Location of the Pliocene Vale de Freixo site in the Pombal region of central-west Portugal.

assemblages of the Mondego Basin, correlate to the Mediterranean Pliocene Molluscan Unit 1 (MPMU1) of Monegatti and Raffi (2001) for the Mediterranean (Silva et al., 2010). For more information on the general geological setting and the stratigraphy of the Vale de Freixo site, as well as additional references, please refer to Silva et al. (2006, 2010) and Diniz et al. (2016).

During the very end of the Zanclean and the beginning of the Piacenzian, in times of global high sea level (Dowsett and Cronin, 1990; Chandan and Peltier, 2017), the area of present-day Caldas da Rainha-Pombal region of western Portugal was inundated and partially occupied by shallow marine environments of normal salinity, somehow protected from direct influence of the open Atlantic Ocean (Nolf and Silva, 1997; Silva et al., 2010). Based on the Pliocene gastropod assemblage, the mid-Pliocene Sea Surface Temperatures (SST) along the western Iberian coast at that latitude were subtropical, akin to those recorded today off western Africa at the latitude of Cape Blanc (northern Mauritania, 21° N), with maximum Mean Monthly SST (MMSST) of ~23.5°C in September and minimum MMSST of 19°C in January–March (Silva et al., 2010). The gastropod fauna was part of the Pliocene French-Iberian subtropical Province of Silva and Landau (2007) and Landau et al. (2020).

The fossil assemblage of Vale de Freixo indicates a local infralittoral environment in which the gastropods were the

most diverse molluscan group (Silva, 2001, 2002), followed by bivalves (Pimentel, 2018) and polyplacophorans (Dell'Angelo and Silva, 2003). Other benthic invertebrate groups (e.g., bryozoans [Carvalho, 1961], echinoids [Silva, 2001; Pereira, 2010], and barnacles [Ferreira et al., 2019]) were also well represented in the local ecosystem. In the assemblage the vertebrates are represented by bony fish otoliths and rare shark teeth (Nolf and Silva, 1997; Silva, 2001). Frequent terrestrial plant remains—plant debris, poorly preserved pine needles, and the occasional small conifer cone—are also present in the assemblage, confirming the proximity to emerged land (Silva, 2001). The palynoflora was studied by Diniz (1984), Vieira et al. (2006), and Diniz et al. (2016).

Material and methods

The recent sampling of the Pliocene of Vale de Freixo (“bed 3” in Gili et al., 1995, and Dell'Angelo and Silva, 2003) yielded 2088 chiton valves. In this extensive sample, seven genera and 12 species are represented, two of which are described as new. The new material herein discussed was obtained by means of search sampling under a binocular microscope from extensive wet sieving of ~500 kg of fine sandy sediment using a 1 mm mesh sieve, primarily intended for collecting microgastropod fossils. For comparison, for the Dell'Angelo and Silva (2003)

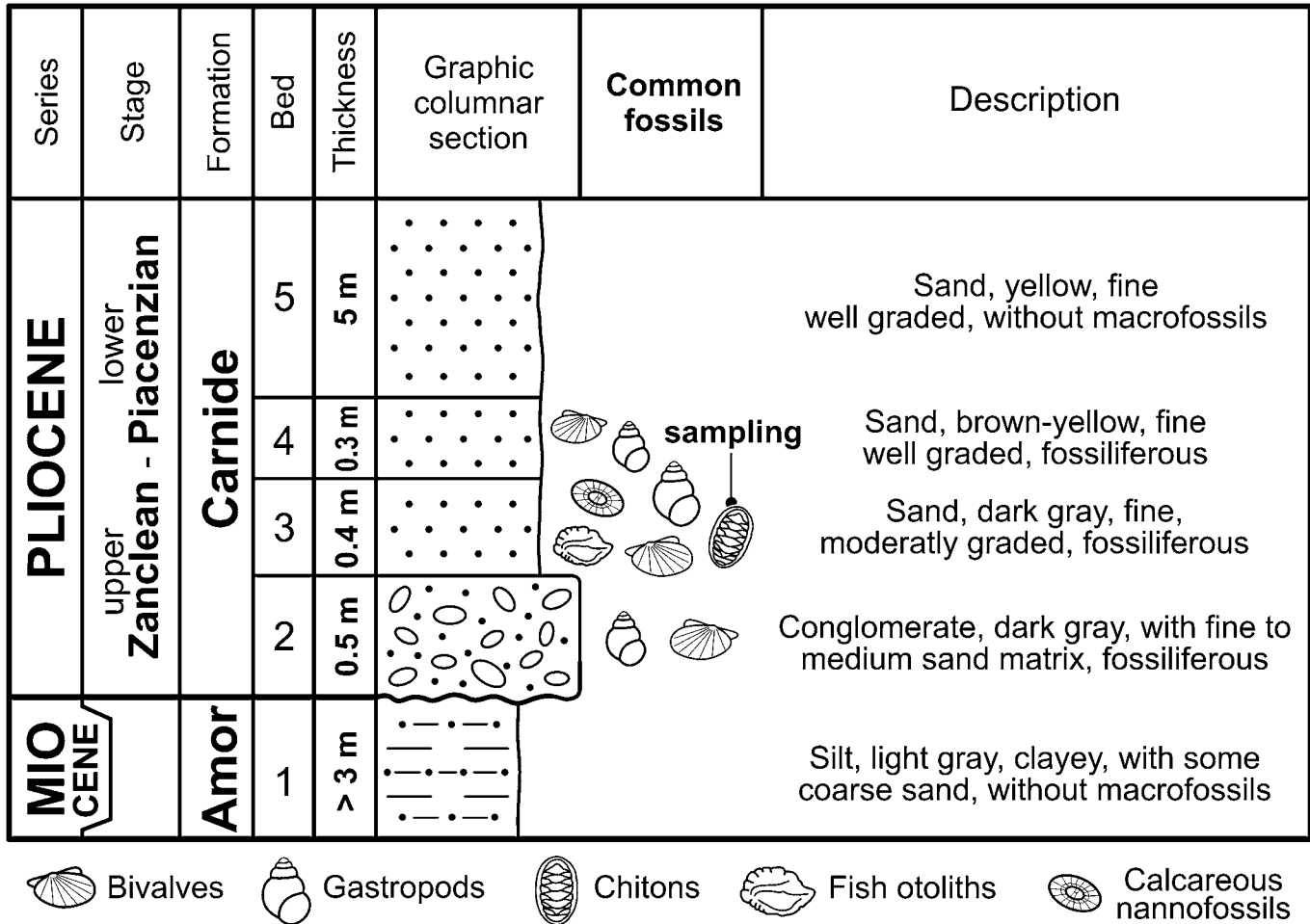


Figure 2. Stratigraphic column of the Vale de Freixo Neogene section in the Pombal region of central-west Portugal.

paper, 37 valves were collected from a 10 kg bulk sample using a 1 mm mesh sieve.

The maximum width (maximum left-right dimension perpendicular to the longitudinal body axis) of complete valves (head, intermediate, and tail, presented as: Maximum width: 0.0 | 0.0 | 0.0 mm) of each species is given, as well as the width/length ratio (W/L). The type materials of the new taxa, *Ischnochiton loureiroi* n. sp. and *Lepidochitona rochae* n. sp., were deposited in the Naturalis Biodiversity Center, Fossil Mollusca collection, Leiden, The Netherlands.

Usually, non-scientific circumstances are irrelevant when it comes to publishing paleontological works. Unfortunately, this is not the case here. This work was prepared at the height of the COVID-19 pandemic in spring 2020. Part of the material photographed was sent from the Netherlands to Italy by registered post. Regrettably, regardless of registration, part the material was lost in the chaos and the Dutch Post Office was unable to trace the material despite numerous attempts. Material lost was replaced in museum collections by similar specimens of the same species and locality. This unusual circumstance is explained on the museum label attached to each replacement specimen. Thankfully, all type material illustrated here is deposited safely at the Naturalis Biodiversity Center. In the text and in the plate captions, the figured lost specimens are identified as

such and a replacement museum number is given for the substitute specimen.

Repositories and institutional abbreviations.—Types, figured, and other specimens examined in this study are part of the following collections and/or deposited in the following institutions: Department of Geology of the Faculty of Sciences of the University of Lisbon, Portugal (GeoFCUL), Carlos Marques da Silva, Vale de Freixo (VFX) PhD Collection; The Linnean Society of London (LSL), London, UK; Muséum National d’Histoire Naturelle (MNHN), Paris, France; Museu Nacional de História Natural da Universidade de Lisboa (MNHN/UL), Lisbon, Portugal; Museo di Zoologia dell’Università di Bologna (MZB), Bologna, Italy; The Natural History Museum [formerly British Museum (Natural History)] (NHMUK), London, UK; Natural History Museum Wien (NHMW), Austria; Naturalis Biodiversity Center, Fossil Mollusca collection (RGM), Leiden, The Netherlands; Royal Scottish Museum of Natural History (RSMNH), Edinburgh, UK; United States National Museum of Natural History (USNM), Washington, D.C., USA; Zoologisches Museum an der Humboldt Universität (ZMHU), Berlin, Germany; Bruno Dell’Angelo Collection (BD), these specimens will be deposited in the Museo di Zoologia dell’Università di Bologna, Italy.

Systematic paleontology

In this paper, the taxonomy of Sirenko (2006) is followed. Many of the chiton species represented in the study assemblage are well known from Mediterranean Neogene deposits and have been previously illustrated and discussed in detail (e.g., Dell'Angelo et al., 2004, 2012, 2013, 2015, 2016, 2018a, b, 2020; Garilli et al., 2005). For these species, only a short chresonymy, some comments, and stratigraphic ranges are given. The geographic ranges and habitats of extant species were compiled based on Kaas and Van Belle (1985a, b, 1988, 1990, 1994), Dell'Angelo and Smriglio (1999), and Kaas et al. (2006).

Class Polyplacophora Gray, 1821
 Subclass Loricata Schumacher, 1817
 Order Lepidopleurida Thiele, 1909
 Family Leptochitonidae Dall, 1889
 Genus *Leptochiton* Gray, 1847

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

Occurrence.—Known from the Triassic of Italy, *L. davolii* (Laghi, 2005). Today, it has a worldwide distribution, being common in the northeastern Atlantic and the Mediterranean Sea (Kaas and Van Belle, 1985a).

Leptochiton cancellatus (Sowerby, 1840)
 Figure 3.1–3.9

- 1840 *Chiton cancellatus* Sowerby, figs. 104, 104a, b, 105.
 1985a *Leptochiton (Leptochiton) cancellatus*; Kaas and Van Belle, p. 43, fig. 16.
 1986 *Leptochiton (Leptochiton) cancellatus*; Dell'Angelo and Palazzi, p. 10, figs. 6–8, 41, 51, 65, 67, 69.
 1987 *Leptochiton (Leptochiton) cancellatus*; Cesari, p. 6, pl. 1, figs. 1–7.
 1999 *Lepidopleurus (Leptochiton) cancellatus*; Dell'Angelo and Smriglio, p. 48, pl. 10, 11, figs. 18, 19.
 2002 *Lepidopleurus (Leptochiton) cancellatus*; Marquet, p. 12, pl. 2, fig. 1.
 2003 *Lepidopleurus (Leptochiton) cancellatus*; Dell'Angelo and Silva, p. 9, figs. 3, 4.
 2010 *Leptochiton cancellatus*; Studencka and Dulai, p. 260, text-fig. 2A–D.
 2013 *Leptochiton cancellatus*; Dell'Angelo et al., p. 70, pl. 1, figs. N–T.
 2015 *Leptochiton cancellatus*; Dell'Angelo et al., p. 226, pl. 3, figs. 1–6.

Holotype.—Unknown, probably lost. Northeastern Atlantic, Great Britain, probably from Oban, Scotland (Kaas and Van Belle, 1985a).

Occurrence.—Middle Miocene: Paratethys in Poland (Macioszczyk, 1988; Studencka and Studencki, 1988) and Ukraine (Studencka and Dulai, 2010). Upper Miocene:

Proto-Mediterranean in Italy, Po Basin (Tortonian, Dell'Angelo and Palazzi, 1989; Dell'Angelo et al., 2015). Lower Pliocene: North Sea Basin in Belgium (Marquet, 1984, 2002); Mediterranean, Italy, Liguria (Dell'Angelo et al., 2013), Tuscany (Dell'Angelo et al., 2001; Chirli, 2004). Lower to Upper Pliocene: northeastern Atlantic in Portugal, Mondego Basin (MPMU1, Dell'Angelo and Silva, 2003); Mediterranean in Italy, Sicilia (MPMU1, Dell'Angelo et al., 2012). Pleistocene: North Atlantic in Sweden and Norway (Brogger, 1901; Antevis, 1917); Mediterranean in Italy, Calabria, and Sicilia (BD unpublished data). Present: Atlantic Ocean, from Great Britain and Ireland (Light and Baxter, 1990) to France, Spain, Portugal, and Madeira archipelago (Kaas, 1979; Rolán Mosquera et al., 1990; Macedo et al., 1999; Segers et al., 2009; Urgorri et al., 2017); Mediterranean Sea in Spain (Moreno and Gofas, 2011), Italy (Dell'Angelo and Smriglio, 1999), Malta, Greece; and Aegean Sea (Mifsud et al., 1990; Zenetos and Van Aartsen, 1995; Koukouras and Karachle, 2005), Turkey (Öztürk et al., 2014), Tunisia (Cecalupo et al., 2008), and Israel (Barash and Danin, 1977).

Materials.—265 valves (37 head, 159 intermediate and 69 tail). One intermediate valve lost (Fig. 3.4–3.6) and replaced by specimen GeoFCUL VFX.03.349, RGM.1363997 (1 valve) (Fig. 3.1–3.3), GeoFCUL VFX.03.339 (1 valve) (Fig. 3.7–3.9), RGM.1363998 (40 valves), GeoFCUL VFX.03.346 (40 valves), MNHN.F.A81981 (40 valves), BD 237 (142 valves). Maximum width: 2.5 | 3.2 | 3.8 mm.

Remarks.—This species is characterized by having rounded intermediate valves, and the tegmentum sculptured with very dense granules arranged in radial series on the head valve, the lateral areas of the intermediate valves, and the postmucronal area of the tail valve, in longitudinal series on the central area of the intermediate valves, and the antemucronal area of the tail valve, with reduced intercostal spaces. Detailed description and discussion of *L. cancellatus* were given by Kaas and Van Belle (1985a) and Dell'Angelo and Smriglio (1999).

Dell'Angelo and Silva (2003) reported two valves (one intermediate and one tail) from Vale de Freixo. In the material now available, there are hundreds of small and fragile valves, most of which are incomplete and poorly preserved. The shape and the sculpture of the valves are consistent with the diagnostic characters of this species.

The Middle Miocene (lower Badenian) Paratethys (Korytnica, Poland) specimens assigned to *Leptochiton sulci* (Bałuk, 1971) were considered conspecific with *L. cancellatus* by Laghi (1977), Dell'Angelo and Palazzi (1989), Dell'Angelo and Smriglio (1999), and Dell'Angelo and Silva (2003). However, as reported by Dell'Angelo et al. (2013), these Paratethian specimens represent a distinct species, following Bałuk (1971, 1984) and Studencka and Dulai (2010).

Leptochiton cancellatus was reported from Scandinavian coasts and from the northern Pacific (Kaas and Van Belle, 1985a). However, the European records were assigned by Kaas (1981) to *L. sarsi* Kaas, 1981, occurring from the Swedish coasts of the Skagerrak arm of the North Sea (Bohuslän) to Finmark in northern Norway (Kaas, 1981). Ferreira (1979) recognized two separate species on the west coast of North

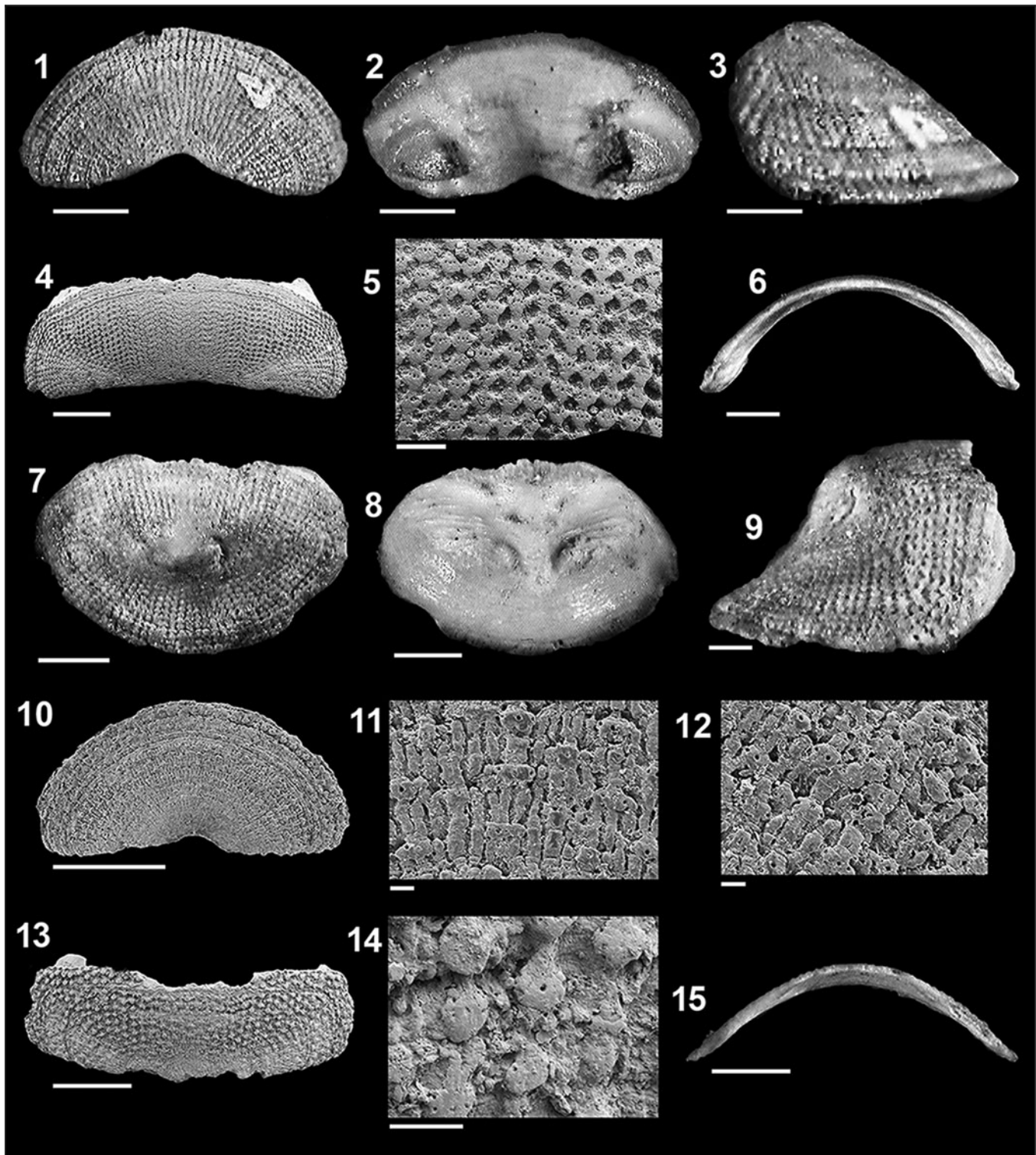


Figure 3. (1–9) *Leptochiton cancellatus* (Sowerby, 1840) from the Carnide Formation, Pliocene, Portugal: (1–3) RGM.1363997, (1) head valve in dorsal, (2) ventral, and (3) lateral views; width 2.2 mm; (4–6) intermediate valve (4) in dorsal view, (5) close-up of ornamentation of central area, and (6) frontal view; width 3 mm (valve lost, replaced by specimen GeoFCUL VFX.03.349); (7–9) GeoFCUL VFX.03.339, (7) tail valve in dorsal, (8) ventral, and (9) lateral views; width 2.2 mm. (10–15) *Leptochiton scabridus* (Jeffreys, 1880) from the Carnide Formation, Pliocene, Portugal: (10–12) RGM.1363999, (10) head valve in dorsal view and (11, 12) close-up of ornamentation width 1.4 mm; (13–15) intermediate valve (13) in dorsal view, (14) close-up of ornamentation of central and lateral areas, and (15) frontal view; width 2.1 mm (valve lost, replaced by specimen GeoFCUL VFX.03.350). Scale bars = 0.5 mm (1–4, 6–10, 12, 13, 15), or 100 μ m (5, 11, 14).

America: *L. rugatus* (Carpenter in Pilsbry, 1892), restricted to California and Mexico, and the northern '*L. cancellatus*.' The Pacific specimens of '*L. cancellatus*' have been assigned to a

recently described northeastern Atlantic species, *L. cascadiensis* Sigwart and Chen, 2018, occurring along the coasts of North America, from Oregon to Alaska (Sigwart and Chen, 2018).

Leptochiton scabridus (Jeffreys, 1880)
Figure 3.10–3.15

- 1880 *Chiton scabridus* Jeffreys, p. 33.
1894 *Lepidopleurus scabridus*; Sykes, p. 35, pl. 3, figs. 4, 7.
1985a *Leptochiton (Leptochiton) scabridus*; Kaas and Van Belle, p. 49, fig. 19.
1986 *Leptochiton (Leptochiton) scabridus*; Dell'Angelo and Palazzi, p. 11, figs. 11–14, 19–22, 32–34, 45–48, 54, 55, 60.
1987 *Leptochiton (Leptochiton) scabridus*; Cesari, p. 7, pl. 2, figs. 1–8, pl. 3, figs. 1–10, pl. 4, figs. 1–6, pl. 5, figs. 1–11, pl. 11, figs. 4–6.
1989 *Lepidopleurus (Leptochiton) scabridus*; Dell'Angelo and Palazzi, p. 65, pl. 16, 17.
1999 *Lepidopleurus (Leptochiton) scabridus*; Dell'Angelo and Smriglio, p. 63, pl. 16, 17, figs. 25, 26.
2005 *Lepidopleurus (Leptochiton) scabridus*; Garilli et al., p. 130, pl. 2, figs. 1–4.
2013 *Leptochiton scabridus*; Dell'Angelo et al., p. 71, pl. 2, figs. E–G.
2015 *Leptochiton scabridus*; Dell'Angelo et al., p. 226, pl. 3, figs. 7–11.

Holotype.—Unknown, probably lost.

Syntypes.—Known type material, syntypes: one specimen (USNM 177391) from Goodrington, Torbay (England); 15 specimens (USNM 177392) from Jersey (Channel Islands) (Warén, 1980).

Occurrence.—Upper Miocene: Proto-Mediterranean Sea in Italy, Po Basin (Tortonian, Dell'Angelo and Palazzi, 1989; Dell'Angelo et al., 2015). Lower Pliocene: central Mediterranean in Italy (Dell'Angelo and Palazzi, 1989; Dell'Angelo et al., 2013). Lower to Upper Pliocene: northeastern Atlantic in Portugal, Mondego Basin (MPMU1, Dell'Angelo and Silva, 2003). Middle to Upper Pleistocene: central Mediterranean in Greece (Garilli et al., 2005). Present: Atlantic Ocean from southwestern Great Britain and the English Channel (Light and Baxter, 1990) to France, Bretagne (Van Belle, 1972), northern Spain (Urgorri et al., 2017), Portugal (Macedo et al., 1999), Canary Islands (Hernández and Rolán, 2011), Cape Verde Islands (Kaas, 1991), and Angola (Dell'Angelo and Smriglio, 1999); Mediterranean Sea in Italy (Dell'Angelo and Smriglio, 1999), Greece and Aegean Sea islands (Strack, 1988; Koukouras and Karachle, 2005), Malta (Mifsud et al., 1990), and Turkey (Öztürk et al., 2014).

Materials.—Fourteen valves (1 head, 10 intermediate and 3 tail): one intermediate valve lost (Fig. 3.13–3.15) and replaced by specimen GeoFCUL VFX.03.350, RGM.1363999 (1 valve) (Fig. 3.10–3.12), RGM.1364000 (1 valve), GeoFCUL VFX.03.333 (1 valve), MNHN.F.A81982 (1 valve), BD 238 (9 valves). Maximum width: 1.4 | 3.7 | 2 mm.

Remarks.—Detailed descriptions and discussion of specimens of this species were given by Kaas and Van Belle (1985a) and

Dell'Angelo and Smriglio (1999). The tegmentum surface is rough, the sculpture granules are extended into a body that usually is formed by two or three longitudinal varices that merge into one along the external margin of the valve (Dell'Angelo and Palazzi, 1986, fig. 34; Garilli et al., 2005, pl. 2, figs. 2, 4). This characteristic feature is well preserved in the study material.

Family Hanleyidae Bergenhayn, 1955
Genus *Hanleya* Gray, 1857

Type species.—*Hanleya debilis* Gray, 1857 (= *Chiton hanleyi* Bean in Thorpe, 1844), by monotypy.

Occurrence.—Known from the Lower Oligocene to present. Today, it is represented by *H. hanleyi* (Bean in Thorpe, 1844), occurring in the northern and central Atlantic and the Mediterranean, and by *H. mediterranea* Sirenko, 2014, circumscribed to the Mediterranean Sea (Dell'Angelo et al., 2015, 2018b, 2021; Sirenko et al., 2016).

Hanleya hanleyi (Bean in Thorpe, 1844)
Figure 4

- 1844 *Chiton hanleyi* Bean in Thorpe, p. 263, fig. 57.
1846 *Chiton nagelfar* Lovén, p. 158.
1962 *Hanleya hanleyi*; Malatesta, p. 153, figs. 9, 10.
1977 *Hanleya hanleyi*; Laghi, p. 99, figs. 5–9.
1984 *Hanleya hanleyi*; Marquet, p. 336, pl. 1, fig. 3.
1985a *Hanleya hanleyi*; Kaas and Van Belle, p. 193, fig. 91, map 18.
1995 *Hanleya nagelfar*; Bellomo and Sabelli, p. 201, text-fig. 1.
1997 *Hanleya hanleyi*; Dell'Angelo and Giusti, p. 51, fig. 2.
1998 *Hanleya nagelfar*; Dell'Angelo et al., p. 244, pl. 1, fig. 10.
1999 *Hanleya hanleyi*; Dell'Angelo et al., p. 262, pl. 1, fig. 1 (part).
1999 *Hanleya hanleyi*; Dell'Angelo and Smriglio, p. 85, pl. 25–26, figs. 34–36 (part).
2002 *Hanleya hanleyi*; Marquet, p. 13, pl. 2, fig. 2.
2014 *Hanleya nagelfar*; Sirenko, p. 2931, figs. 9–19.
2015 *Hanleya nagelfar*; Dell'Angelo et al., p. 231, pl. 4, figs. 10–12.
2016 *Hanleya hanleyi*; Sirenko et al., p. 58, figs. 1–10.
2018b *Hanleya hanleyi*; Dell'Angelo et al., p. 20, fig. 10.
2021 *Hanleya hanleyi*; Dell'Angelo et al., p. 125, fig. 1.

Holotype.—Scarborough Museums Trust, Scarborough, England (Sirenko et al., 2016).

Occurrence.—Upper Miocene: northeastern Atlantic in France (Tortonian, Dell'Angelo et al., 2018b). Proto-Mediterranean Sea in Italy, Po Basin (Tortonian, Dell'Angelo et al., 1999, 2015). Lower to Upper Pliocene: northeastern Atlantic in England (Wood, 1848; Reid, 1890), Belgium (Marquet, 1984, 2002), Portugal, Mondego Basin (MPMU1, this paper); central Mediterranean in Italy, Liguria (Dell'Angelo et al., 2013). Upper Pliocene to Lower Pleistocene: northeastern

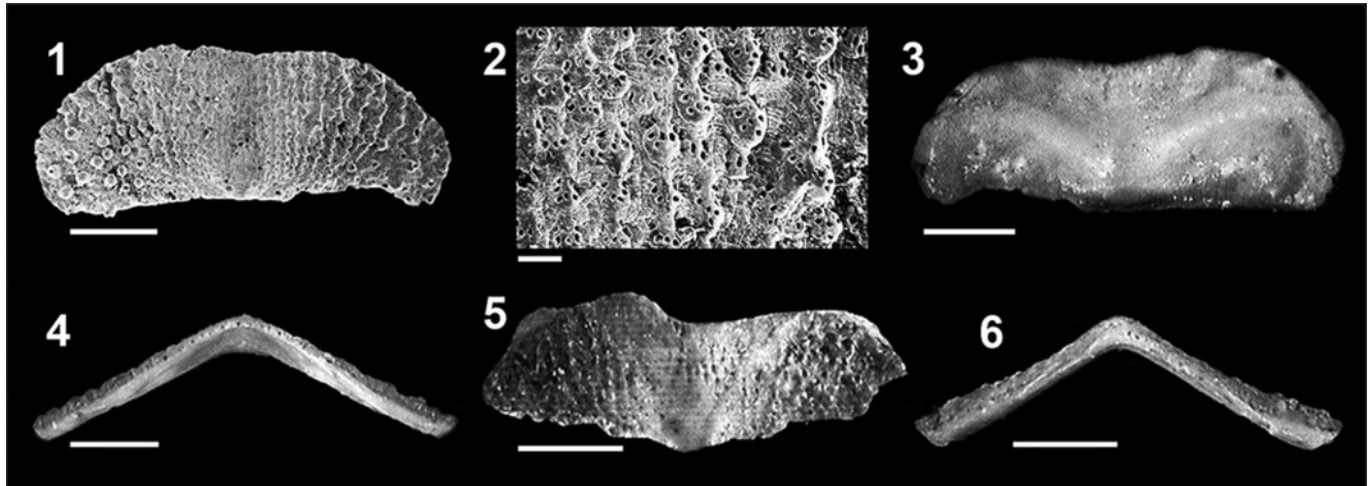


Figure 4. *Hanleya hanleyi* (Bean in Thorpe, 1844) from the Carnide Formation, Pliocene, Portugal: (1–4) RGM.1364001, (1) intermediate valve in dorsal view, (2) close-up of ornamentation of central area, (3) ventral, and (4) frontal view; width 2.4 mm; (5, 6) GeoFCUL VFX.03.364, intermediate valve (5) in dorsal and (6) frontal views; width 2 mm. Scale bars = 0.5 mm (1, 3–6), or 100 μ m (2).

Atlantic in France, Anjou (Dell'Angelo et al., 2018b). Pleistocene: central Mediterranean in Italy (questionable, many reports in need of revision). Present: Atlantic Ocean from southern Greenland (Hansson, 1998; Sneli and Gudmundsson, 2018) to North America, Europe (Kaas, 1979; McKay and Smith, 1979; Macedo et al., 1999; Urgorri et al., 2017), Madeira (Kaas, 1991; Segers et al., 2009), the Canary Islands (Kaas, 1991; Hernández and Rolán, 2011), and northern Africa; Mediterranean Sea in Italy (Dell'Angelo and Smriglio, 1999), Aegean Sea islands (Zenetos and Van Aartsen, 1995), and Turkey (Öztürk et al., 2014).

Materials.—Two intermediate valves, RGM.1364001 (Fig. 4.1–4.4), and GeoFCUL VFX.03.364 (Fig. 4.5, 4.6). Maximum width: 2.4 mm.

Remarks.—Detailed descriptions and discussion of specimens of this species were given by Kaas and Van Belle (1985a) and Sirenko et al. (2016). This species has an intricate taxonomic history, with several accepted synonyms (Sirenko et al., 2016). Recently, *H. mediterranea* Sirenko, 2014, has been described from the Mediterranean Sea. *Hanleya hanleyi* is characterized by the sculpture of pleural areas of intermediate valves and antemucronal area of the tail valve consisting of longitudinal series of small, roundish to oval granules, while *H. mediterranea* is distinguished by the lack of longitudinal series of granules across the entire pleural area, and by the presence of large granules comprising two or more small granules. Both species are represented in the Italian Neogene fossil record, sometimes occurring simultaneously, as in the Upper Miocene of Borelli (Dell'Angelo et al., 2015). *Hanleya* was not reported by Dell'Angelo and Silva (2003), being an addition to the Pliocene chiton biodiversity of western Iberia.

Order Chitonida Thiele, 1909
Suborder Chitonina Thiele, 1909
Superfamily Chitonoidea Rafinesque, 1815

Family Ischnochitonidae Dall, 1889
Genus *Ischnochiton* Gray, 1847

Type species.—*Chiton textilis* Gray, 1828, by subsequent designation (Gray, 1847).

Occurrence.—Known from Eocene to present. Today it has a worldwide distribution, except for the northern Atlantic and Arctic oceans (Kaas and Van Belle, 1990).

Ischnochiton zbyi Dell'Angelo and Silva, 2003
Figures 5, 6

2003 *Ischnochiton zbyi* Dell'Angelo and Silva, p. 10, figs. 5–11.

2005 *Ischnochiton zbyi*; Schwabe 2005, p. 105.

2012 *Ischnochiton zbyi*; Dell'Angelo et al., p. 60.

2019 *Ischnochiton zbyi*; Cherns and Schwabe, p. 688.

2019 *Ischnochiton zbyi*; Dell'Angelo et al., p. 48.

Holotype.—Holotype: MNHN/UL.II.406 (intermediate valve, width 5.8 mm, Fig. 5.1, 5.2).

Paratypes.—MNHN/UL.II.407–408 (head valve, width 3.4 mm, Fig. 5.3, 5.4, and tail valve, width 3.6 mm, Fig. 5.5, 5.6); MZB 12692 (3 valves); BD (3 valves); GeoFCUL VFX.03.312–332 (21 valves). Vale de Freixo, near the village of Carnide, Pombal municipality, central-west Portugal (Fig. 1). Pliocene, upper Zanclean to lower Piacenzian, Carnide Formation, basal fossiliferous gray sands, “Bed 3” in Gili et al. (1995), Dell'Angelo and Silva (2003), and herein (Fig. 2). Equivalent to the Mediterranean MPMU1 of Monegatti and Raffi (2001).

Occurrence.—Pliocene: northeastern Atlantic in Portugal, Mondego Basin (MPMU1, Dell'Angelo and Silva, 2003; this paper).

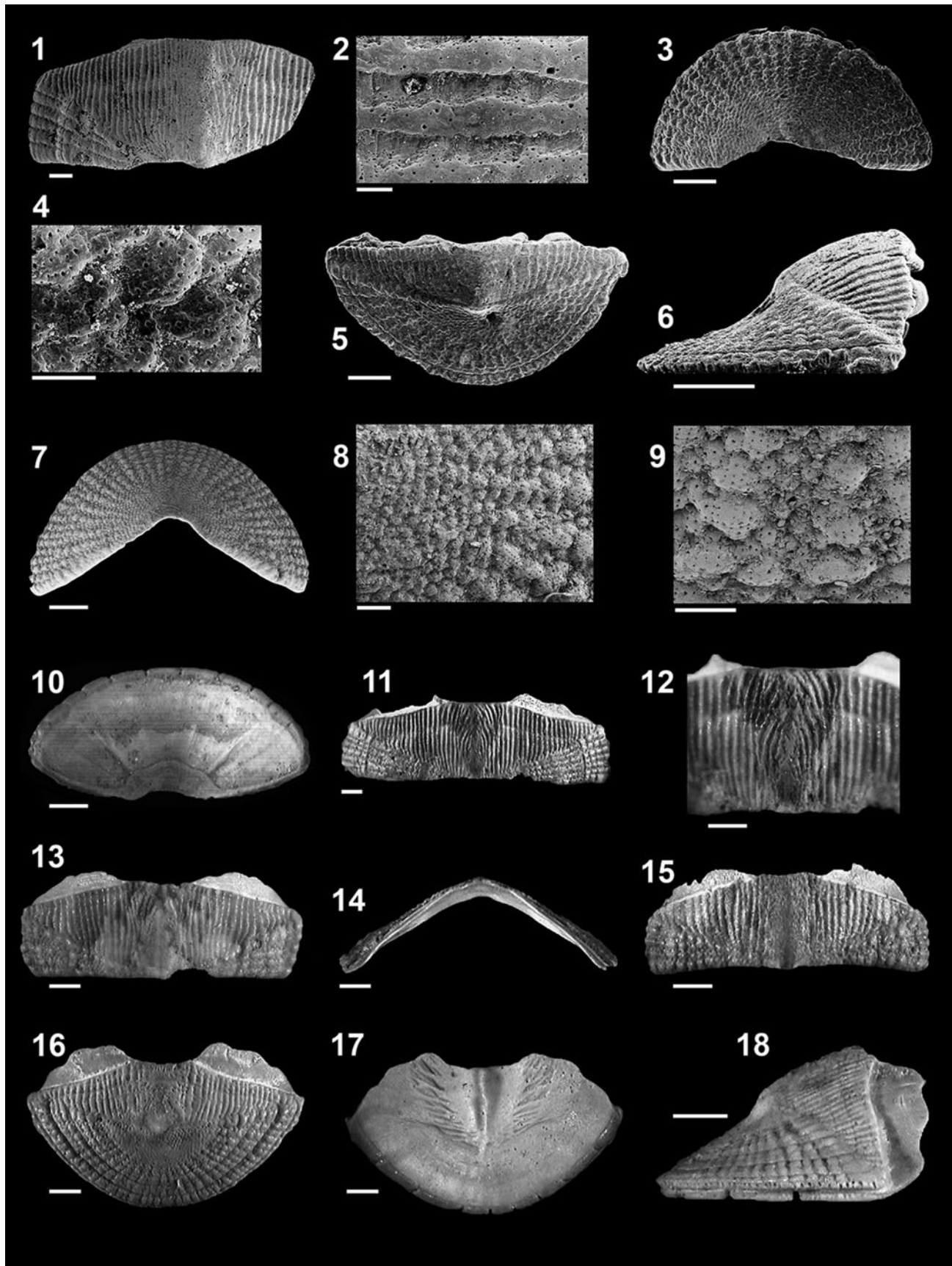


Figure 5. *Ischnochiton zbyi* Dell'Angelo and Silva, 2003 from the Carnide Formation, Pliocene, Portugal: (1, 2) holotype, MNHN/UL.II.406, (1) intermediate valve in dorsal view and (2) close-up of ornamentation of longitudinal ribs; width 5.8 mm (Dell'Angelo and Silva, 2003, figs. 5, 6); (3, 4) paratype, MNHN/UL.II.407, (3) head valve in dorsal view and (4) close-up of ornamentation; width 3.4 mm (Dell'Angelo and Silva, 2003, figs. 7, 8); (5, 6) paratype MNHN/UL.II.408, (5) tail valve in dorsal and (6) lateral views; width 3.6 mm (Dell'Angelo and Silva, 2003, figs. 9, 10); (7–10) head valve (7) in dorsal view, (8) close-up of ornamentation of microgranules and granules, (9) close-up of radiating ribs, and (10) ventral view; width 3.6 mm (valve lost, replaced by specimen GeoFCUL VFX.03.351); (11, 12) RGM.1364002, (11) intermediate valve in dorsal view and (12) close-up of ornamentation of jugal area; width 6.5 mm; (13, 14) GeoFCUL VFX.03.334, intermediate valve (13) in dorsal and (14) frontal views; width 4.4 mm; (15) MNHN.F.A81983, intermediate valve in dorsal view; width 3.6 mm; (16–18) RGM.1364003, tail valve in (16) dorsal, (17) ventral, and (18) lateral views; width 4.2 mm. Scale bars = 0.5 mm (1, 3, 5–7, 10–18), or 100 μ m (2, 4, 8, 9).

Revised description.—Head valve semi-circular, posterior margin widely V-shaped, notched in middle, slope straight to slightly concave; tegmentum with microgranulose sculpture showing random roundish/squarish granules up to 30–40 μ m, with 3–5 aesthetes of equal size on surface, and 19–24 granulose radiating ribs, not starting from apex, but from mid-valve, concentrically crossed by numerous growth lines,

some ribs splitting towards anterior margin, ribs formed by larger granules (up to 100 μ m, with 10–15 or more aesthetes of equal size), with microgranules present in all rib interspaces, surface between microgranules rough.

Intermediate valves broadly rectangular, three times wider than long or more (W/L = 3.0–3.5), moderately elevated (H/W = 0.26–0.36), anterior profile carinate, anterior margin

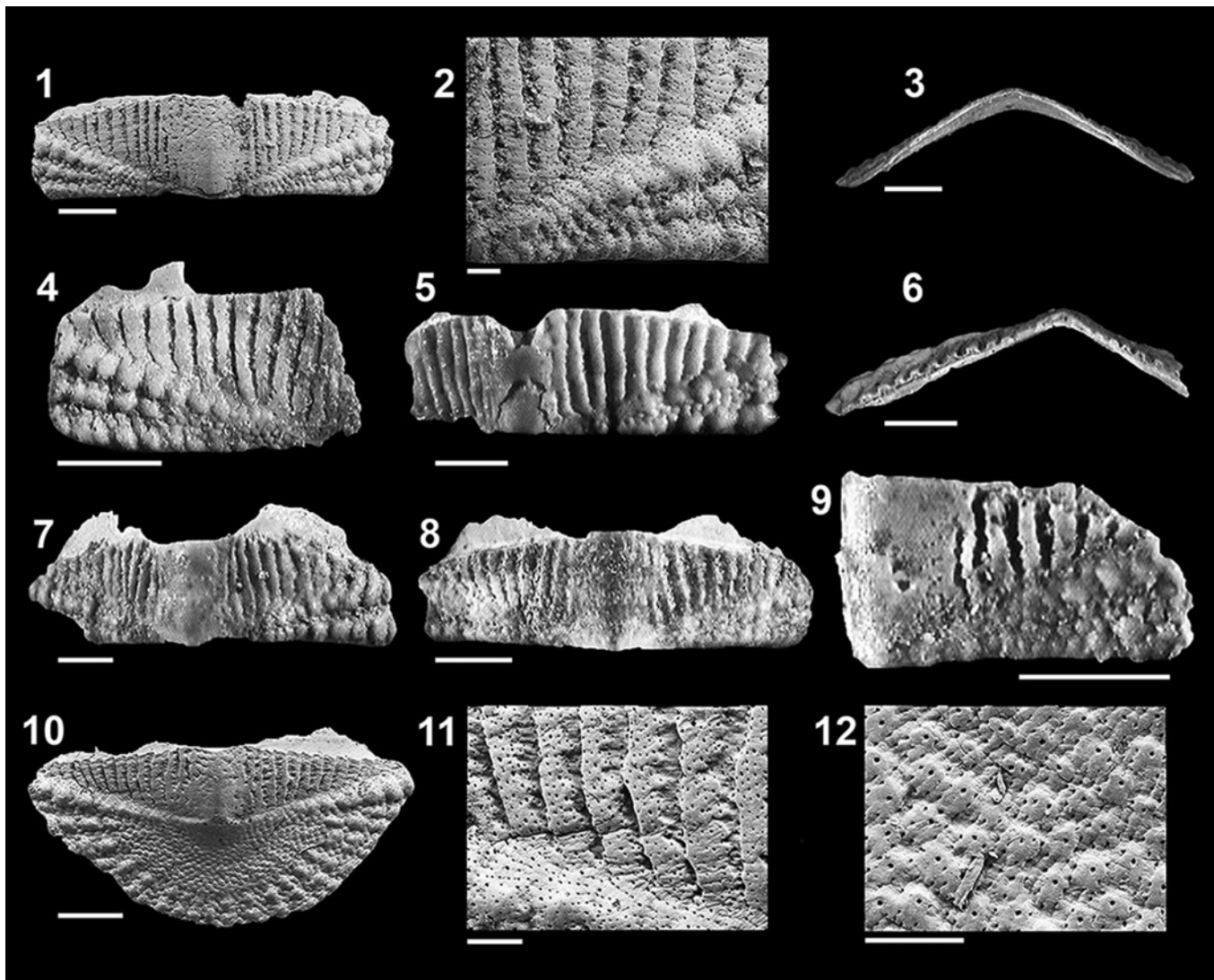


Figure 6. *Ischnochiton zbyi* Dell'Angelo and Silva, 2003, from the Carnide Formation, Pliocene, Portugal: (1–3) intermediate valve (1) in dorsal view, (2) close-up of ornamentation, and (3) ventral view; width 3.1 mm (valve lost, replaced by specimen GeoFCUL VFX.03.352); (4) RGM.1364004, intermediate valve in dorsal view; width 1.7 mm (estimated width just over 3 mm); (5, 6) RGM.1364005, intermediate valve in (5) dorsal and (6) frontal views; width 2.6 mm; (7) GeoFCUL VFX.03.335, intermediate valve in dorsal view; width 3.2 mm; (8) MNHN.F.A81984, intermediate valve in dorsal view; width 2.5 mm; (9) intermediate valve (estimated width ~2.5 mm), dorsal view; width 1.2 mm (valve lost, replaced by specimen GeoFCUL VFX.03.353); (10–12) tail valve (10) in dorsal view, (11) close-up of ornamentation of longitudinal ribs of antemucronal area, and (12) microgranules of postmucronal area; width 3 mm (valve lost, replaced by specimen GeoFCUL VFX.03.354). Scale bars = 0.5 mm (1, 3–10), or 100 μ m (2, 11, 12).

straight, slightly concave in jugum, side margins straight to slightly rounded, posterior margin straight, with apex not evident, lateral areas moderately elevated, with microgranulose sculpture and 2–8 radiating granulose ribs starting from apex, with microgranules always present between ribs and structure of granules same as head valve, pleural areas with longitudinal granulose ribs (10–26 on either side), with granules coalescent forming uninterrupted ribs, interstices narrower than ribs with subobsolete microgranulose sculpture, jugal area triangular with longitudinal striae converging towards center on both sides in wider valves, forming larger, irregular granules; not arranged in longitudinal striae in smaller valves.

Tail valve depressed, wider than long ($W/L = 1.9–2.1$), anterior margin straight or slightly concave in jugal tract, mucro subcentral, slightly raised; antemucronal slope straight, postmucronal slope slightly concave directly behind mucro, antemucronal area sculptured like central area of intermediate valves, postmucronal area sculptured like head valve.

Articulamentum whitish, apophyses wide, triangular in intermediate valves, trapezoidal in tail valve, jugal sinus narrow, slit formula 10–11/1/7–11, slits inequidistant.

Materials.—Type material and 505 valves (100 head, 346 intermediate and 59 tail): Four valves lost (Figs. 5.7–5.10, 6.1–6.3, 6.9, 6.10–6.12) and replaced by specimens GeoFCUL VFX.03.351–354, RGM.1364002–1364005 (Figs. 5.11, 5.12, 5.16–5.18, 6.4, 6.5, 6.6), GeoFCUL VFX.03.334, VFX.03.335 (Figs. 5.13, 5.14, 6.7), MNHN.F.A81983, MNHN.F.A81984 (Figs. 5.15, 6.8), RGM.1364006 (50 valves), GeoFCUL VFX.03.336 (50 valves), MNHN.F.A81985 (50 valves), BD 240 (343 valves). Maximum width: 5.8 | 6.5 | 4.3 mm.

Remarks.—We provide a revised description of *I. zbyi*, because the abundant material now at hand, representing the complete growth series from juvenile to adult, allows a more detailed description of some shell features and a better understanding of intraspecific variability. The number of granulose ribs in the lateral areas of the intermediate valves is variable, from 5–8 in the larger valves (Fig. 5.11, 5.13) to 2–3 in smaller valves (Fig. 6.1, 6.4, 6.5, 6.7, 6.9), with microgranules always present in the rib interspaces. The number of longitudinal ribs in the pleural areas of the intermediate valves is also variable, from 22–26 on either side in the larger valves (Fig. 5.11, 5.13) to 10–15 in juveniles (e.g., 12 in Fig. 6.1).

Taken individually, the intermediate valves shown in Figures 5 and 6 (shown sequentially in decreasing width to illustrate valve variability) could give the impression of belonging to two distinct species, but the intraspecific variability in *I. zbyi* is very high and the variations occur continuously without clear separation between the characters examined.

Ischnochiton loureiroi new species
Figure 7.1–7.6

Holotype.—Holotype RGM.1364007, intermediate valve (Fig. 7.1–7.3).

Paratype.—Paratype RGM.1364008, intermediate valve (Fig. 7.4–7.6). Maximum width: 3.4 mm. Vale de Freixo site,

near the village of Carnide, Pombal municipality, central-west Portugal (Fig. 1). Pliocene, upper Zanclean to lower Piacenzian, Carnide Formation, basal fossiliferous gray sands, “Bed 3” in Gili et al. (1995), Dell'Angelo and Silva (2003), and herein (Fig. 2). Equivalent to the Mediterranean MPMU1 of Monegatti and Raffi (2001).

Diagnosis.—Intermediate valves broadly rectangular, elongated, slightly elevated, carinate, posterior margin straight with prominent apex, lateral areas poorly elevated, with microgranulose sculpture and three radiating irregular granulose ribs, with scattered elevated granules irregularly distributed on striae, pleural areas with longitudinal irregular granulose ribs (9–11 on either side), interstices smooth, large smooth triangular jugal area, weak growth lines. Articulamentum with large, triangular apophyses, insertion plate short with a single slit.

Occurrence.—Pliocene: northeastern Atlantic in Portugal, Mondego Basin (MPMU1, this paper).

Description.—Intermediate valves broadly rectangular, width four times length or a little less, slightly elevated ($H/W = 0.20–0.24$), anterior profile carinate, anterior margin straight, side margins rounded, posterior margin straight on both sides of prominent apex, lateral areas poorly elevated, sharply delimited, with microgranulose sculpture and three radiating irregular granulose ribs originating at apex, some ribs splitting towards anterior margin, with scattered elevated granules irregularly distributed on striae, pleural areas with longitudinal irregular granulose ribs (9–11 on either side), with granules coalescent forming uninterrupted ribs, interstices smooth, equal in width to ribs, ribs not reaching anterior margin in jugal area, large smooth triangular jugal area, weak growth lines.

Articulamentum with large, triangular apophyses, insertion plate short with a single slit, slit rays scarcely visible.

Etymology.—Named after João de Loureiro (1717–1791), a Portuguese Jesuit missionary in the Far East and botanist, author of the “Flora Cochinchinensis.” He published what is considered the first Portuguese paleontological paper on “a kind of animal petrification,” discussing petrified crabs from present-day Vietnam (Loureiro, 1799). According to the International Phonetic Alphabet (IPA) norm, the word loureiro (meaning laurel tree in Portuguese, also a surname) is pronounced /low.'rej.ru/.

Other materials.—One intermediate valve, width 2.7 mm (specimen lost).

Paleoecology.—Epibenthic vagile mollusks living in coastal, infralittoral, subtropical marine environments (estimated maximum mean monthly SST, MMSST, of ~23.5°C in September and minimum MMSST of 19°C in January–March; Silva et al., 2010) of normal salinity and sand-pebble shelly substrates.

Remarks.—The material at hand is quite worn and some morphological features are not preserved, but the sculpture of the valves is different from that of any other *Ischnochiton*

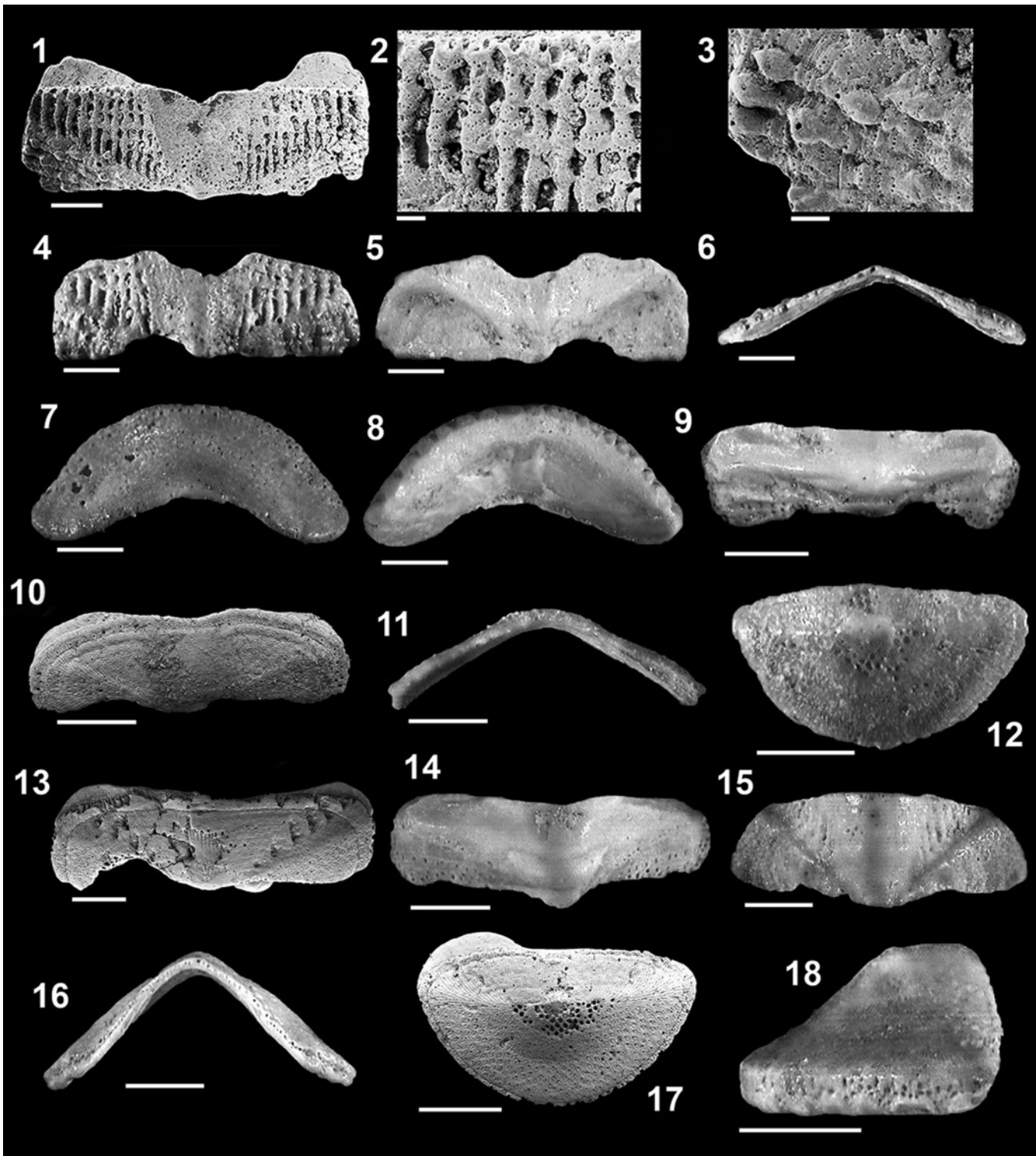


Figure 7. (1–6) *Ischnochiton loureiroi* n. sp. from the Carnide Formation, Pliocene, Portugal: (1–3) holotype, RGM.1364007, intermediate valve (1) in dorsal view and (2) close-up of ornamentation of central and (3) lateral area; width 3.4 mm; (4–6) paratype, RGM.1364008, intermediate valve in (4) dorsal, (5) ventral, and (6) frontal views; width 2.4 mm. (7–12) *Callochiton septemvalvis* (Montagu, 1803) from the Carnide Formation, Pliocene, Portugal: (7, 8) RGM.1364009, head valve in (7) dorsal and (8) ventral views; width 2.3 mm; (9) RGM.1364010, intermediate valve in dorsal view; width 1.9 mm; (10, 11) intermediate valve in (10) dorsal and (11) frontal views; width 2 mm (valve lost, replaced by specimen GeoFCUL VFX.03.355); (12) GeoFCUL VFX.03.337, tail valve in dorsal view; width 1.5 mm. (13–18) *Callochiton doriae* (Capellini, 1859) from the Carnide Formation, Pliocene, Portugal: (13) intermediate valve in dorsal view; width 3 mm (valve lost, replaced by specimen GeoFCUL VFX.03.356); (14) RGM.1364012, intermediate valve in ventral view; width 2 mm; (15, 16) GeoFCUL VFX.03.340, intermediate valve in (15) dorsal and (16) frontal views; width 2 mm; (17, 18) tail valve in (17) dorsal and (18) lateral views; width 1.7 mm (valve lost, replaced by specimen GeoFCUL VFX.03.357). Scale bars = 0.5 mm (1, 4–18), or 100 μ m (2, 3).

species known from the European Neogene and distinct enough to warrant description as a new species. *Ischnochiton loureiroi* n. sp. (Fig. 7.1) markedly differs from *I. zbyi* (Figs. 5.11, 6.1) by the shape of the intermediate valves, being more elongated (width about four times the length or slightly less, versus $W/L = 3.0\text{--}3.5$ in *I. zbyi*) and less elevated ($H/W = 0.20\text{--}0.24$ versus $0.26\text{--}0.36$ in *I. zbyi*), the different sculpture of the central area (9–11 very irregular granulose ribs on both sides and a large smooth triangular jugal area versus 10–26 granulose ribs and a striated jugal area in *I. zbyi*) and the lateral areas of the valves (three radiating irregular granulose ribs with some elevated granules irregularly distributed on striae versus 2–8 in *I. zbyi*).

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

Type species.—*Chiton laevis* Montagu, 1803, non Pennant, 1777 [= *Callochiton septemvalvis* (Montagu, 1803)], by subsequent designation (Gray, 1847).

Occurrence.—Known from lower Oligocene to present. Today it occurs in the Indo-Pacific (including Japan, but is absent from the northeastern Pacific) and in the eastern and sub-Antarctic Atlantic Ocean (Kaas and Van Belle, 1985b).

Callochiton septemvalvis (Montagu, 1803)
Figure 7.7–7.12

- 1803 *Chiton laevis* Montagu, p. 2 (non Pennant, 1777).
1803 *Chiton septemvalvis* Montagu, p. 3.
1985b *Callochiton septemvalvis septemvalvis*; Kaas and Van Belle, p. 11, fig. 2.1, 2.4–2.6, 2.8–2.15, part (non fig. 2.2, 2.3, 2.7 = *Callochiton doriae*).
non *Callochiton septemvalvis* (non Montagu); Dell'Angelo and Smriglio, p. 125, pl. 40, figs. A–H, pl. 41 figs. I–P, color figs. 61–63 (= *Callochiton doriae*).
1999 *Callochiton septemvalvis*; Dell'Angelo and Silva, p. 11, part (only one of the two intermediate valves).
non *Callochiton septemvalvis* (non Montagu); Dell'Angelo et al., p. 60, fig. 4L (= *Callochiton doriae*).
2012 *Callochiton septemvalvis* (non Montagu); Dell'Angelo et al., p. 83, pl. 5, figs. N–P (= *Callochiton doriae*).
2013 *Callochiton septemvalvis*; Dell'Angelo et al., p. 73, pl. 1, figs. 1–4.

Holotype.—Holotype NHMUK (Kaas and Van Belle, 1985b). Northeastern Atlantic, English Channel, Salcomb Bay, Great Britain.

Occurrence.—Upper Miocene: Proto-Mediterranean Sea in Italy, Po Basin, (Tortonian, Laghi, 1977; Dell'Angelo et al., 2016). Lower to Upper Pliocene: northeastern Atlantic in Portugal, Mondego Basin (MPMU1, Dell'Angelo and Silva, 2003); western Mediterranean in Spain, Estepona Basin (Dell'Angelo et al., 2004). Upper Pliocene to Lower Pleistocene: Mediterranean in Greece, Rhodes (Koskeridou et al., 2009). Pleistocene: North Atlantic in Sweden and

Norway (Brogger, 1901; Antevs, 1917, 1928). Present: northeastern Atlantic, from northern Norway (Dons, 1934; Hansson, 1998) to the Iberian Peninsula (McKay and Smith, 1979; Rolán Mosquera et al., 1990; Macedo et al., 1999; Urganorri et al., 2017) and the Canary Islands (Hernández and Rolán, 2011; Dell'Angelo and Smriglio, 1999).

Materials.—269 valves (216 intermediate and 53 tail): one intermediate valve lost (Fig. 7.10, 7.11) and replaced by specimen GeoFCUL VFX.03.355, RGM.1364009, 1364010 (2 valves) (Fig. 7.7–7.9), GeoFCUL VFX.03.337 (Fig. 7.12), RGM.1364011 (30 valves), GeoFCUL VFX.03.338 (30 valves), MNHN.F.A81986 (30 valves), BD 241 (175 valves). Maximum width: 2.3 | 2.8 | 1.5 mm.

Remarks.—Detailed description and discussion of *C. septemvalvis* was given by Kaas and Van Belle (1985b). Its complicated taxonomic history was discussed by Dell'Angelo and Smriglio (1999) and Dell'Angelo et al. (2016, 2017). Herein, following Dell'Angelo et al. (2016, 2017), *Callochiton* valves without longitudinal grooves on the pleural areas are assigned to *Callochiton septemvalvis*, and the ones with longitudinal grooves to *Callochiton doriae* (Capellini, 1859).

The material at hand consists of small, incomplete, and abraded valves, in which diagnostic characters are often difficult to discern (e.g., the incisions in the articulamentum), sometimes making specific attribution (to *C. septemvalvis* or *C. doriae*) difficult, particularly for the head valves. That is why head valves were not included in the study material.

Callochiton doriae (Capellini, 1859)
Figure 7.13–7.18

- 1829 *Chiton euplaeae* O.-G. Costa, p. i, iv, pl. 1, fig. 3 (nomen dubium).
1859 *Chiton doriae* Capellini, p. 325, pl. 12, fig. 2.
1879 *Chiton laevis* var. *doriae*; Monterosato, p. 26.
1985b *Callochiton septemvalvis euplaeae*; Kaas and Van Belle, p. 11, fig. 2.2, 2.3, 2.7, part (non fig. 2.1, 2.4–2.6, 2.8–2.15 = *Callochiton septemvalvis*).
1999 *Callochiton septemvalvis* (non Montagu); Dell'Angelo and Smriglio, p. 125, pl. 40, figs. A–H, pl. 41, figs. I–P, color figs. 61–63.
2003 *Callochiton septemvalvis* (non Montagu); Dell'Angelo and Silva, p. 11, part (only one of the two intermediate valves).
2012 *Callochiton septemvalvis* (non Montagu); Dell'Angelo et al., p. 60, fig. 4L.
2013 *Callochiton septemvalvis* (non Montagu); Dell'Angelo et al., p. 83, pl. 5, figs. N–P.
2016 *Callochiton doriae*; Dell'Angelo et al., p. 74, pl. 1, figs. 5–9.
2017 *Callochiton doriae*; Dell'Angelo et al., p. 243, fig. 5A–C.

Holotype.—Unknown, probably lost. Mediterranean, northern Ligurian Sea, Gulf of La Spezia, Italy (Capellini, 1859).

Occurrence.—Lower Miocene: Proto-Mediterranean Sea in Italy, Sciolze (Burdigalian, Dell'Angelo et al., 2016). Middle

Miocene: Proto-Mediterranean Sea in Italy, Po Basin (Langhian, Dell'Angelo et al., 2016); Paratethys in Slovakia (Ruman and Hudáčková, 2015), Czech Republic (Šulc, 1934), Poland (Bałuk, 1971, 1984; Studencka and Studencki, 1988), and Austria (Šulc, 1934). Upper Miocene: northeastern Atlantic in France, Anjou (Tortonian, Dell'Angelo et al., 2018b); Proto-Mediterranean Sea in Italy, Po Basin (Tortonian, Laghi, 1977; Dell'Angelo et al., 2016). Lower Pliocene: central Mediterranean in Italy, Liguria (Dell'Angelo et al., 2013), and Tuscany (Dell'Angelo et al., 2001). Lower to Upper Pliocene: northeastern Atlantic in Portugal, Mondego Basin (MPMU1, Dell'Angelo and Silva, 2003); central Mediterranean in Italy, Sicily (Dell'Angelo et al., 2012), western Mediterranean in Spain, Estepona Basin (Dell'Angelo et al., 2004). Upper Pliocene to Lower Pleistocene in the central Mediterranean, Greece, Rhodes (Koskeridou et al., 2009). Lower Pleistocene: central Mediterranean in Italy (Sabelli and Taviani, 1979; Dell'Angelo et al., 2001). Middle to Upper Pleistocene: central Mediterranean in Greece (Garilli et al., 2005). Pleistocene: central Mediterranean in Italy (Dell'Angelo and Giusti, 1997). Present: Atlantic Ocean, from Spain, Galicia (Carmona Zalvide et al., 2002), south to Madeira (Segers et al., 2009), Morocco (Kaas, 1991), and Canary Islands (Kaas, 1991); Mediterranean Sea in France, Italy (Leloup, 1934; Dell'Angelo and Smriglio, 1999), Croatia (Dell'Angelo and Zavodnik, 2004), Greece and Aegean Sea islands (Strack, 1988, 1990; Koukouras and Karachle, 2005), Lebanon (Crocetta et al., 2014), Israel (Barash and Danin, 1977), Algeria (Pallary, 1900), and Tunisia (Kaas, 1989; Cecalupo et al., 2008).

Materials.—213 valves (154 intermediate and 59 tail): one intermediate and one tail valve lost (Fig. 7.13, 7.17, 7.18) and replaced by specimens GeoFCUL VFX.03.356, VFX.03.357, RGM.1364012 (one valve) (Fig. 7.14), GeoFCUL VFX.03.340 (one valve) (Fig. 7.15, 7.16), RGM.1364013 (20 valves), GeoFCUL VFX.03.341 (20 valves), MNHN.F.A81987 (20 valves), BD 242 (149 valves). Maximum width: – | 3 | 1.8 mm.

Remarks.—Prior to Sigwart et al. (2013) a single *Callochiton* species was recognized along the eastern Atlantic coast and in the Mediterranean Sea. However, based on molecular data, those authors separated the European *Callochiton septemvalvis* specimens into a Mediterranean species (*C. doriae*) with grooves on the valves, and an Atlantic species (*C. septemvalvis*) without grooves. The Vale de Freixo material is imperfectly preserved, but the material considered *C. doriae* herein clearly shows longitudinal grooves (4–8, with short grooves along the diagonal ridge) on the pleural areas of intermediate valves (Fig. 7.13) and on the antemucronal area of the tail valve.

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

Type species.—*Chiton affinis* Issel, 1869, by subsequent designation (International Committee of Zoological Nomenclature, 1971, as proposed by Beu et al., 1969).

Occurrence.—Known from Oligocene to present. Today it is mostly tropical to subtropical, occurring from the eastern Atlantic and South Africa and throughout the Indo-Pacific to the central Pacific, including northern New Zealand to Hawaii (Schwabe et al., 2008).

Rhyssoplax corallina (Risso, 1826)

Figure 8.1–8.9

- 1826 *Lepidopleurus corallinus* Risso, p. 268.
1977 *Lepidopleurus corallinus*; Arnaud, p. 112.
1999 *Chiton (Rhyssoplax) corallinus*; Dell'Angelo and Smriglio, p. 174, pl. 58–59, color figs. 97–107.
2003 *Chiton (Rhyssoplax) corallinus*; Dell'Angelo and Silva, p. 14, fig. 12.
2006 *Chiton (Rhyssoplax) corallinus*; Kaas et al., p. 154, fig. 56.
2016 *Chiton corallinus*; Dell'Angelo et al., p. 78, pl. 2, figs. 1–15.
2018b *Rhyssoplax corallinus*; Dell'Angelo et al., p. 35, fig. 18.

Holotype.—Presumed lost, not present in the Risso collection, MNHN (Arnaud, 1977). Western Mediterranean Sea, France, Nice.

Occurrence.—Upper Oligocene: northeastern Atlantic in France, Aquitaine Basin (Chattian, Dell'Angelo et al., 2018a). Lower Miocene: northeastern Atlantic in France, Aquitaine Basin (Aquitainian–Burdigalian, Dell'Angelo et al., 2018a); Proto-Mediterranean Sea in Italy, Po Basin (Burdigalian, Dell'Angelo et al., 2016). Middle Miocene: northeastern Atlantic in France, Aquitaine Basin (Serravalian, Dell'Angelo et al., 2018a); Proto-Mediterranean in Italy, Po Basin (Langhian, Dell'Angelo et al., 2016); Paratethys, in Slovakia (Ruman and Hudáčková, 2015), Czech Republic (Šulc, 1934), Poland (Bałuk, 1971, 1984; Macioszczyk, 1988; Studencka and Studencki, 1988), Austria (Šulc, 1934; Kroh, 2003), Hungary (Dulai, 2005), Romania (Dell'Angelo et al., 2007), and Ukraine (Studencka and Dulai, 2010). Upper Miocene: northeastern Atlantic in France, Anjou (Tortonian, Dell'Angelo et al., 2018b), Loire Basin (Messinian?, Dell'Angelo et al., 2018a); Proto-Mediterranean in Italy, Po Basin (Tortonian, Laghi, 1977; Dell'Angelo et al., 1999, 2016). Lower Pliocene: central Mediterranean in Italy, Liguria (Chirli, 2004; Dell'Angelo et al., 2013), and Tuscany (Dell'Angelo et al., 2001). Lower to Upper Pliocene: northeastern Atlantic in Portugal, Mondego Basin (MPMU1, Dell'Angelo and Silva, 2003); western Mediterranean, Spain, Estepona Basin (Dell'Angelo et al., 2004); central Mediterranean, Italy (Laghi, 1977). Upper Pliocene to Lower Pleistocene: central Mediterranean in Greece, Rhodes (Koskeridou et al., 2009). Lower Pleistocene: central Mediterranean in Italy (Sabelli and Taviani, 1979; Dell'Angelo et al., 2001). Middle to Upper Pleistocene: central Mediterranean in Greece, Kyllini (Garilli et al., 2005). Upper Pleistocene: central Mediterranean in Italy (Dell'Angelo et al., 2001). Present: Atlantic Ocean, from Spain and Portugal (Macedo et al., 1999; Carmona Zalvide et al., 2000), to

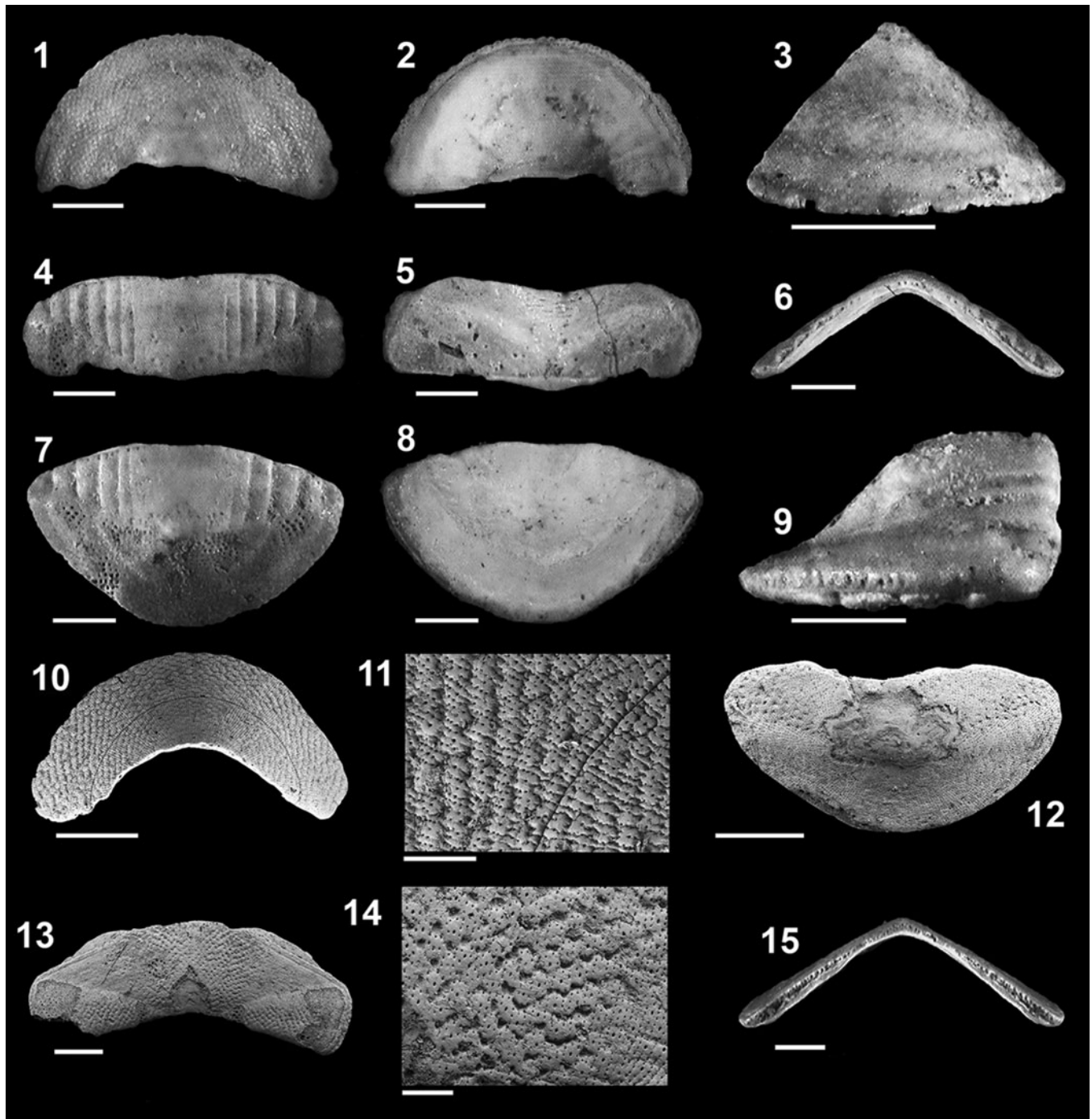


Figure 8. (1–9) *Rhyssoplax corallina* (Risso, 1826) from the Carnide Formation, Pliocene, Portugal: (1–3) RGM.1364014, head valve in (1) dorsal, (2) ventral, and (3) lateral views; width 2.2 mm; (4–6) GeoFCUL VFX.03.342, intermediate valve in (4) dorsal, (5) ventral, and (6) lateral views; width 2.6 mm; (7–9) MNHN.F.A81988, tail valve in (7) dorsal, (8) ventral, and (9) lateral views; width 2.5 mm. (10–15) *Lepidochitona cinerea* (Linnaeus, 1767) from the Carnide Formation, Pliocene, Portugal: (10, 11) head valve (10) in dorsal view and (11) close-up of ornamentation; width 1.9 mm (valve lost, replaced by specimen GeoFCUL VFX.03.358); (12) tail valve in dorsal view; width 1.9 mm (valve lost, replaced by specimen GeoFCUL VFX.03.359); (13–15) intermediate valve (13) in dorsal view, (14) close-up of ornamentation, and (15) frontal view; width 3.3 mm (valve lost, replaced by specimen GeoFCUL VFX.03.360). Scale bars = 0.5 mm (1–10, 12, 13, 15), or 100 μ m (11, 14).

Morocco (Pallary, 1920), and the Ampère and Gettysburg seamounts (Beck et al., 2006); Mediterranean Sea in Spain, Alboran (Salas and Luque, 1986), France (Marion, 1883; Pruvot, 1897), Italy (Dell'Angelo and Smriglio, 1999), Croatia (Leloup and Volz, 1938; Dell'Angelo and Zavodnik, 2004),

Greece and Aegean Sea islands (Strack, 1988, 1990; Koukouras and Karachle, 2005), Turkey (Öztürk et al., 2014), Algeria (Mars, 1957), Tunisia (Kaas, 1989; Cecalupo et al., 2008), Israel (Barash and Danin, 1977), and Lebanon (Crocetta et al., 2014).

Materials.—664 valves (30 head, 416 intermediate and 218 tail valves): RGM.1364014 (Fig. 8.1–8.3), GeoFCUL VFX.03.342 (Fig. 8.4–8.6), MNHN.F.A81988 (Fig. 8.7–8.9), RGM.1364015 (50 valves), GeoFCUL VFX.03.343 (50 valves), MNHN.F.A81989 (50 valves), BD 243 (511 valves). Maximum width: 2.2 | 3.5 | 2.5 mm.

Remarks.—Detailed description and discussion of *R. corallina* were given by Dell’Angelo and Smriglio (1999) and Kaas et al. (2006). The study material is represented by small, incomplete, and abraded valves, in which diagnostic characters are often not clearly distinguishable.

Suborder Acanthochitonina Bergenhayn, 1930
 Superfamily Mopaliaoidea Dall, 1889
 Family Lepidochitonidae Iredale, 1914
 Genus *Lepidochitona* Gray, 1821

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

Occurrence.—Known from Paleocene to present. Today, it occurs in five disjunct areas: (1) Black and Mediterranean seas, and northeastern Atlantic, from northern Norway to Morocco; (2) Red Sea and northern Arabian Sea; (3) off South Africa; (4) Caribbean Sea and adjacent waters of the Atlantic Ocean; and (5) the eastern Pacific Ocean from the Gulf of Alaska to Peru (Kaas and Van Belle, 1985b; Sirenko et al., 2013).

Lepidochitona cinerea (Linnaeus, 1767)
 Figure 8.10–8.15

- 1767 *Chiton cinereus* Linnaeus, p. 1107.
 1952 *Chiton cinereus*; Dodge, p. 23.
 1985b *Lepidochitona (L.) cinerea*; Kaas and Van Belle, p. 84, fig. 39.
 1999 *Lepidochitona (L.) cinerea*; Dell’Angelo and Smriglio, p. 138, pl. 44–45, color figs. 67–72.
 2003 *Lepidochitona (L.) cinerea*; Dell’Angelo and Silva, p. 12, figs. 13, 14.
 2005 *Lepidochitona (L.) cinerea*; Garilli et al., p. 136, pl. 3, figs. 1–3.
 2013 *Lepidochitona cinerea*; Dell’Angelo et al., p. 89, pl. 8, figs. A–E.
 2016 *Lepidochitona cinerea*; Dell’Angelo et al., p. 83, pl. 3, figs. 13–18.

Holotype.—LSL (Dodge, 1952). “In O. Norvegico.” (Linnaeus, 1767).

Occurrence.—Upper Miocene: Proto-Mediterranean Sea in Italy, Po Basin (Tortonian, Sacco, 1897; Dell’Angelo et al., 1999; Dell’Angelo et al., 2016). Lower Pliocene: central Mediterranean in Italy, Liguria (Sosso and Dell’Angelo, 2010; Dell’Angelo et al., 2013), Tuscany (Dell’Angelo et al., 2001). Lower to Upper Pliocene: northeastern Atlantic in Portugal, Mondego Basin (MPMU1, Dell’Angelo and Silva, 2003); central Mediterranean in Italy, Tuscany (Dell’Angelo et al.,

2001; Chirli, 2004). Upper Pliocene to Lower Pleistocene: Mediterranean in Greece, Rhodes (Koskeridou et al., 2009). Pleistocene: Mediterranean in Italy (Dell’Angelo et al., 2001), and Greece (Garilli et al., 2005). Present: Atlantic Ocean, from Iceland and Norway, Tromsø (Sneli and Gudmundsson, 2018), along the European coast (Leloup, 1934; Kaas and Van Belle, 1981; Hansson, 1998) to France, Spain, Portugal (Macedo et al., 1999; Carmona Zalvide and García García, 2000; Urgorri et al., 2017), Morocco, and Senegal (Kaas, 1991); Mediterranean Sea, in Spain and France (Giribet and Penas, 1997), Italy (Dell’Angelo and Smriglio, 1999), Malta (Mifsud et al., 1990), Greece and the Aegean Sea islands (Strack, 1988, 1990; Koukouras and Karachle, 2005), Turkey (Öztürk et al., 2014), Israel (Barash and Danin, 1977, 1992), Algeria (Pallary, 1900), Tunisia (Kaas, 1989; Cecalupo et al., 2008), and in the Black Sea and the Sea of Marmara (Strack, 1988).

Materials.—93 valves (60 head, 26 intermediate, and 7 tail): one head valve, one tail, and one intermediate lost (Fig. 8.10–8.12, 8.13–8.15) and replaced by specimens GeoFCUL VFX.03.358–VFX.03.360, RGM.1364016 (5 valves), GeoFCUL VFX.03.348 (5 valves), MNHN.F.A81990 (5 valves), BD 244 (75 valves). Maximum width: 3 | 3.3 | 2.4 mm.

Remarks.—Detailed descriptions and discussion of specimens of the species were given by Kaas and Van Belle (1985b) and Dell’Angelo and Smriglio (1999).

Lepidochitona canariensis (Thiele, 1909)

- 1909 *Trachydermon canariensis* Thiele, p. 15, pl. 2, figs. 14–25.
 1985b *Lepidochitona (L.) canariensis*; Kaas and Van Belle, p. 95, fig. 44.
 1999 *Lepidochitona (Lepidochitona) canariensis*; Dell’Angelo and Smriglio, p. 154, pl. 51, fig. 78.
 2000 *Lepidochitona canariensis*; Dell’Angelo and Tringali, p. 51, fig. 1.
 2004 *Lepidochitona (L.) canariensis*; Dell’Angelo et al., p. 36, pl. 3, fig. 3.
 2009 *Lepidochitona canariensis*; Anseeuw and Verstraeten, p. 30, pl. 1, figs. 1–3.
 2013 *Lepidochitona canariensis*; Dell’Angelo et al., p. 91, pl. 8, figs. L–Q.
 2020 *Lepidochitona canariensis*; Dell’Angelo et al., p. 29, fig. 19.

Holotype.—ZMHU 101918a (Kilias, 1995, p. 158). Eastern Atlantic, Canary Islands, Tenerife, Puerto.

Occurrence.—Lower Miocene: northeastern Atlantic in France, Aquitaine Basin (Burdigalian, Dell’Angelo et al., 2020). Upper Miocene: northeastern Atlantic in France, Loire Basin (Dell’Angelo et al., 2020). Lower Pliocene: central Mediterranean in Italy, Liguria (Dell’Angelo et al., 2013). Lower to Upper Pliocene: northeastern Atlantic, Portugal, Mondego Basin (MPMU1, this paper); western Mediterranean, Spain, Estepona Basin (Dell’Angelo et al., 2004). Upper

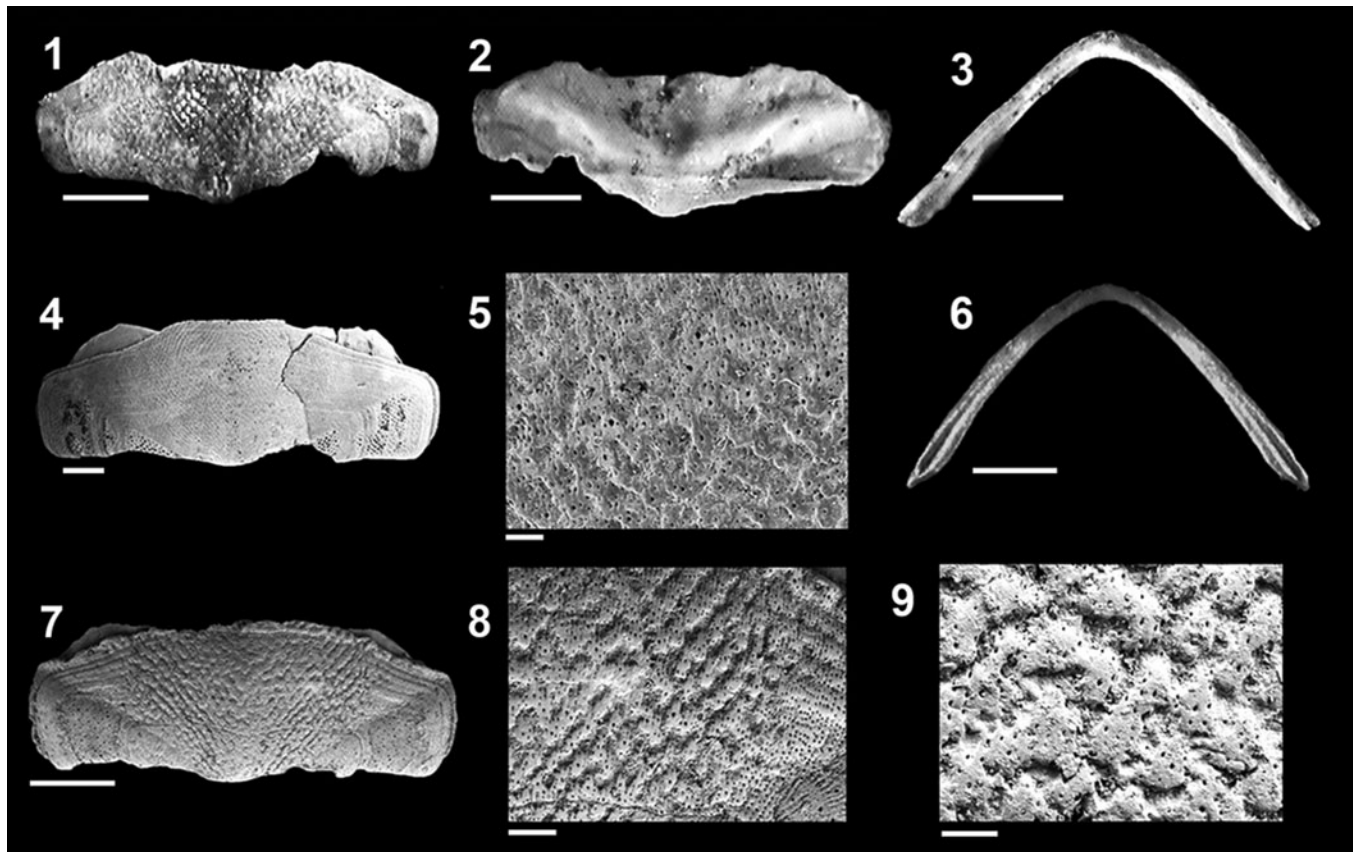


Figure 9. *Lepidochitona rochae* n. sp. from the Carnide Formation, Pliocene, Portugal: (1–3) holotype, RGM.1364017, intermediate valve in (1) dorsal, (2) ventral, and (3) frontal views; width 2.3 mm; (4, 5) paratype, RGM.1364018, intermediate valve in (4) dorsal view and (5) close-up of ornamentation; width 4.8 mm; (6) GeoFCUL VFX.03.344, intermediate valve in frontal view; width 2.4 mm; (7–9) intermediate valve in (7) dorsal view and (8, 9) close-up of ornamentation; width 2.4 mm (valve lost, replaced by specimen GeoFCUL VFX.03.361). Scale bars = 0.5 mm (1–4, 6, 7), or 100 μ m (5, 8, 9).

Pliocene to Lower Pleistocene: central Mediterranean, Greece, Rhodes (Koskeridou et al., 2009). Present: Atlantic Ocean, from southern Portugal and southwestern Spain (Carmona Zalvide and García García, 2000) to Mauritania (Anseeuw and Verstraeten, 2009), Madeira (Van Belle, 1985; Kaas, 1991) and Selvagens islands (Segers et al., 2009), Canaries (Kaas, 1991; Hernández and Rolán, 2011), and Cape Verde islands (Strack, 2005); Mediterranean in the Alboran Sea, and Morocco (Dell'Angelo and Tringali, 2000).

Materials.—Two valves lost during photography. Maximum width: 1.6 mm.

Remarks.—Detailed descriptions and discussion of specimens of this species were given by Kaas and Van Belle (1985b) and Dell'Angelo and Smriglio (1999). The valves are characterized by diamond-shaped granules uniformly covering the tegmentum, with a tendency to form longitudinal striae converging in the pleural areas. The valves are similar to those of *L. cinerea* (see above), from which they differ in being smaller, intermediate valves with a more clearly delimited apex and a coarser granulation of the tegmentum. The material examined exhibits sculpture formed by less-numerous and larger granules than those of *L. cinerea*. Despite the scarcity and the poor preservation of the material, the shape and the

sculpture of the two specimens examined allow attribution to *L. canariensis*.

Lepidochitona rochae new species
Figure 9

Holotype.—Holotype RGM.1364017, intermediate valve (width 2.3 mm, Fig. 9.1–9.3).

Paratype.—Paratype RGM.1364018, intermediate valve (width 4.8 mm, Fig. 9.4, 9.5). Vale de Freixo site, near the village of Carnide, Pombal municipality, central-west Portugal (Fig. 1). Pliocene, upper Zanclean to lower Piacenzian, Carnide Formation, basal fossiliferous gray sands, “Bed 3” in Gili et al. (1995), Dell'Angelo and Silva (2003), and herein (Fig. 2). Equivalent to the Mediterranean MPMU1 of Monegatti and Raffi (2001).

Diagnosis.—Intermediate valves broadly rectangular, elevated, carinate, showing lateral areas sculptured with fine elongate granules, coalescing into continuous, radially oriented lines. Central area covered for ~60% of valve width by roundish irregular granules, the remaining surface, continuing towards side margins, covered by obliquely oriented and widely spaced concentric growth lines.

Occurrence.—Pliocene: northeastern Atlantic, Mondego Basin, Portugal (MPMU1, this paper).

Description.—Intermediate valves broadly rectangular, W/L = 2.70–2.90, elevated (H/W = 0.40–0.50), anterior profile carinate, anterior margin convex with jugal part almost straight, side margins slightly rounded, posterior margin straight or slightly concave on both sides of large and prominent apex, lateral areas slightly raised, sharply delimited, sculptured with fine elongate granules, coalescing into continuous, radially oriented lines; few concentric growth lines more evident towards side margins, central area covered for ~60% of valve width by roundish irregular granules, almost all separated, but some coalescent, with up to eight aesthetes of equal size, 40% continuing towards side margins by obliquely oriented and few concentric growth lines joined with those present on lateral areas. Articulamentum with poorly preserved apophyses, round, apical area triangular, insertion plate short with a single slit, slit ray well visible (a second slit ray lies close to posterior margin on intermediate valves).

Etymology.—Named after Rogério Bordalo da Rocha (1941–2018), Portuguese Jurassic ammonite paleontologist at the Department of Earth Sciences of the Faculty of Sciences and Technology of the Nova University of Lisbon, Portugal, and President of the Portuguese Geological Society from 1987–2006 to 2010–2014. According to the International Phonetic Alphabet (IPA) norm, the word rocha (meaning rock in Portuguese, also a surname) is pronounced /'Rɔ.ʃɐ/.

Other materials.—Fourteen intermediate valves: one valve lost (Fig. 9.7–9.9) and replaced by specimen GeoFCUL VFX.03.361, GeoFCUL VFX.03.344 (one valve) (Fig. 9.6), RGM.1364019 (2 valves), GeoFCUL VFX.03.345 (2 valves), MNHN.F.A81991 (2 valves), BD 245 (6 valves). Maximum width 4.8 mm.

Paleoecology.—Epibenthic vagile mollusks living in coastal infralittoral subtropical marine environments (estimated maximum mean monthly SST, MMSST, of ~23.5°C in September and minimum MMSST of 19°C in January–March; Silva et al., 2010) of normal salinity and sand-pebble shelly substrates.

Remarks.—Only a few incomplete and poorly preserved intermediate valves are present in the study material, nevertheless the unique character of their sculpture warrants description as a new species. The generic attribution, however, is problematic. The granules of the tegmental sculpture of the material at hand are closer to those of *Lepidochitona* than to those of any other genus. Nevertheless, in specimens of *Lepidochitona*, the granules normally cover the entire tegmentum, not only part of it, as seen in the valves of *L. rochae* n. sp. The sculpture of the lateral areas (fine elongate granules coalescing into continuous, radially oriented lines) is similar to that observed in numerous species of *Callochiton* (e.g., *C. septemvalvis* and *C. doriae*, see above). However, *Callochiton* is characterized by unique features

(e.g., apophyses connected across the jugal sinus, and presence of extra-pigmentary eyes) that are not present in *L. rochae* n. sp. specimens. Therefore, the new species is assigned to *Lepidochitona*, mainly on the basis of the similarity of the granules in the central area of the valves with the sculpture typical of this genus.

Lepidochitona is a speciose genus in the Mediterranean Sea (Dell'Angelo and Smriglio, 1999) and five species are known along the Atlantic coasts of the Iberian Peninsula: *L. cinerea*, *L. caprearum* (Scacchi, 1836), *L. simrothi* (Thiele, 1902), *L. canariensis*, and *L. monterosatoi* Kaas and Van Belle, 1981 (Kaas and Van Belle, 1985b; Carmona Zalvide and García García, 2000). All these species show a uniformly granulose sculpture, very different from the sculpture of *L. rochae* n. sp., in which the granules cover only part of the central area.

Superfamily Cryptoplacoidea H. and A. Adams, 1858

Family Acanthochitonidae Pilsbry, 1893

Genus *Acanthochitona* Gray, 1821

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

Occurrence.—Known from the Oligocene of France, Aquitaine Basin (Chattian, Dell'Angelo et al., 2020) to the present. Today, the genus has an almost worldwide distribution, except for polar waters.

Acanthochitona crinita (Pennant, 1777)

Figure 10

1777 *Chiton crinitus* Pennant, p. 71, pl. 36, figs. 1, A1.

1985 *Acanthochitona crinita*; Kaas, p. 588, figs. 7–50.

1999 *Acanthochitona crinita*; Dell'Angelo and Smriglio, p. 198, pl. 66–68, color figs. 124–130.

1999 *Acanthochitona crinita*; Dell'Angelo et al., p. 275, pl. 5, figs. 2, 6.

2001 *Acanthochitona crinita*; Dell'Angelo et al., p. 153, fig. 32.

2004 *Acanthochitona crinita*; Dell'Angelo et al., p. 40, pl. 4, figs. 2, 5.

2009 *Acanthochitona crinita*; Koskeridou et al., p. 322, figs. 11.1, 11.2.

2013 *Acanthochitona crinita*; Dell'Angelo et al., p. 96, pl. 10, figs. H–M.

2016 *Acanthochitona crinita*; Dell'Angelo et al., p. 88, pl. 5, figs. 12–18, pl. 6, figs. 1, 2.

2018b *Acanthochitona crinita*; Dell'Angelo et al., p. 41, table 14.

2020 *Acanthochitona crinita*; Dell'Angelo et al., p. 39, fig. 25.

Holotype.—Neotype RSMNH 1978.052.02601, designated and figured by Kaas (1985, p. 591, fig. 27). Northern Atlantic, Hebrides Islands, Monach Island, North Uist, Great Britain.

Occurrence.—Upper Oligocene: northeastern Atlantic in France, Aquitaine Basin (Chattian, Dell'Angelo et al., 2020). Lower Miocene: northeastern Atlantic in France, Aquitaine Basin (Aquitanian–Burdigalian, Dell'Angelo et al., 2020);

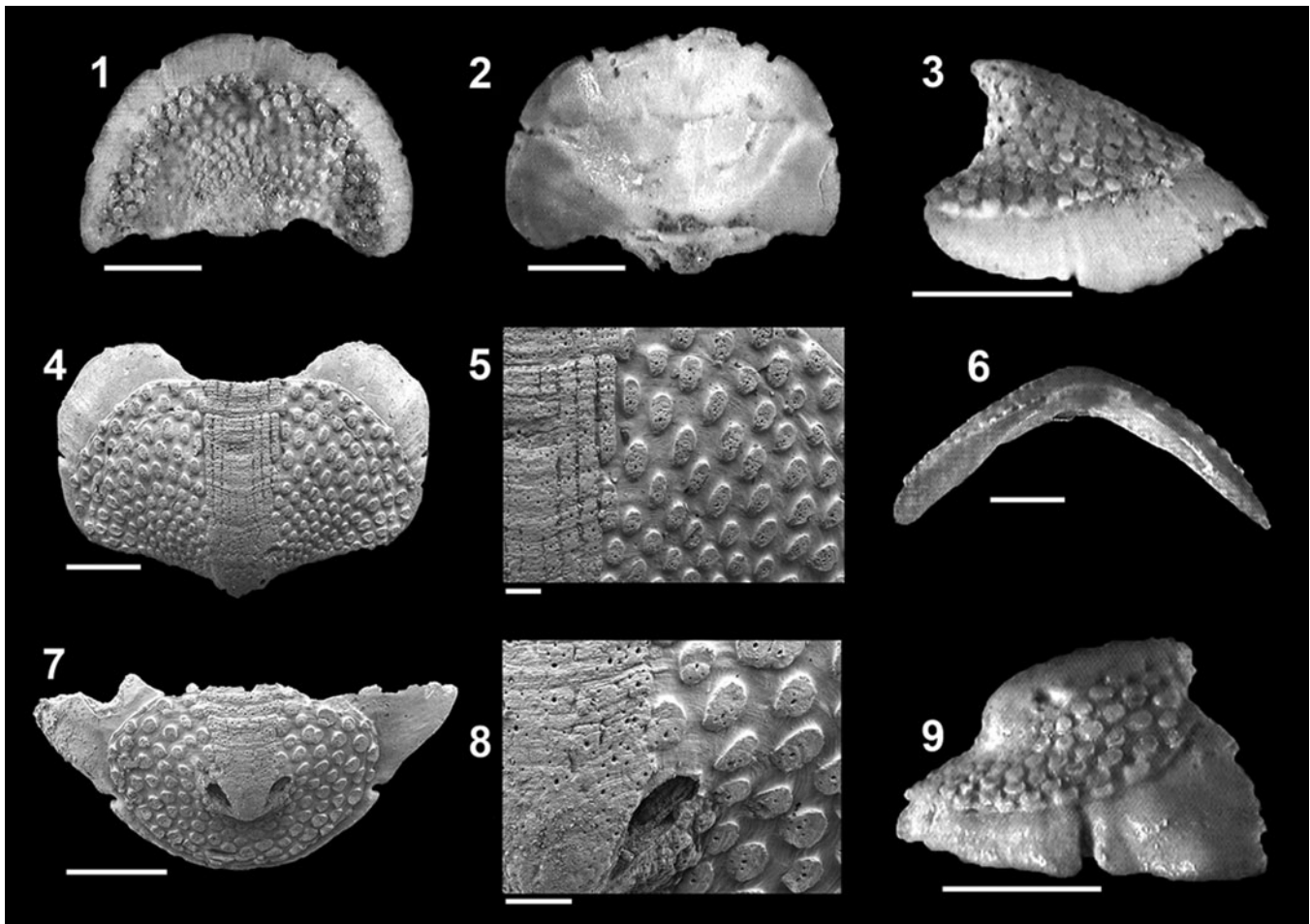


Figure 10. *Acanthochitona crinita* (Pennant, 1777) from the Carnide Formation, Pliocene, Portugal: (1–3) RGM.1364020, head valve in (1) dorsal, (2) ventral, and (3) lateral views, width 1.7 mm; (4–6) intermediate valve in (4) dorsal view, (5) close-up of ornamentation, and (6) frontal view; width 2.5 mm (valve lost, replaced by specimen GeoFCUL VFX.03.362); (7–9) tail valve in (7) dorsal view, (8) close-up of ornamentation, and (9) lateral view; width 2.1 mm (valve lost, replaced by specimen GeoFCUL VFX.03.363). Scale bars = 0.5 mm (1–4, 6, 7, 9), or 100 μ m (5, 8).

Proto-Mediterranean in Italy, Po Basin (Burdigalian, Dell'Angelo et al., 2016). Middle Miocene: northeastern Atlantic in France, Aquitaine Basin (Serravallian, Dell'Angelo et al., 2020); Proto-Mediterranean: Italy, Po Basin (Langhian, Dell'Angelo et al., 2016). Upper Miocene: Proto-Mediterranean in Italy, Po Basin (Tortonian, Dell'Angelo et al., 1999, 2016). Lower Pliocene: Mediterranean in Italy, Liguria (Sosso and Dell'Angelo, 2010; Dell'Angelo et al., 2013), and Tuscany (Dell'Angelo et al., 2001). Lower to Upper Pliocene: northeastern Atlantic, Mondego Basin, Portugal (MPMU1, this paper); western Mediterranean: Spain, Estepona Basin (MPMU1, Dell'Angelo et al., 2004). Upper Pliocene to Lower Pleistocene: central Mediterranean, Greece, Rhodes (Koskeridou et al., 2009). Pleistocene: central Mediterranean, Italy (Dell'Angelo and Forli, 1995; Dell'Angelo et al., 2001). Present: northern Atlantic, from northern Norway south along the European coasts (McKay and Smith, 1979; Hansson, 1998) to the Iberian Peninsula (Rolán Mosquera et al., 1990; Macedo et al., 1999; Urgorri et al., 2017), Madeira, the Canary Islands, and the Cape Verde Archipelago (Kaas, 1991; Strack, 2005; Segers et al., 2009; Hernández and Rolán, 2011); Mediterranean Sea, from Spain (Salas and Luque, 1986) to

France and Italy (Dell'Angelo and Smriglio, 1999), Croatia (Dell'Angelo and Zavodnik, 2004), Greece and the Aegean Sea islands (Kattoulas et al., 1973; Strack, 1988, 1990; Koukouras and Karachle, 2005), Turkey (Öztürk et al., 2014), Israel (Barash and Danin, 1977), Lebanon (Crocetta et al., 2014), and Tunisia (Cecalupo et al., 2008).

Materials.—Forty-two valves (3 head, 35 intermediate, and 4 tail): one intermediate and one tail valve lost (Fig. 10.4–10.6, 10.7–10.9) and replaced by specimens GeoFCUL VFX.03.362, VFX.03.363, RGM.1364020 (one valve) (Fig. 10.1–10.3), RGM.1364021 (7 valves), GeoFCUL VFX.03.347 (7 valves), MNHN.F.A81992 (7 valves), BD 246 (18 valves). Maximum width: 3 | 3.3 | 2.4 mm.

Remarks.—*Acanthochitona crinita* is characterized by having the tegmentum uniformly covered with oval- to drop-shaped, more or less elongated, widely spaced granules. It differs from *A. fascicularis* (Linnaeus, 1767) mainly by the sculpture of tegmentum formed by small roundish, densely packed granules, and from *A. andegavensis* Dell'Angelo et al., 2018 (Dell'Angelo et al., 2018b), from the Miocene (Tortonian) of

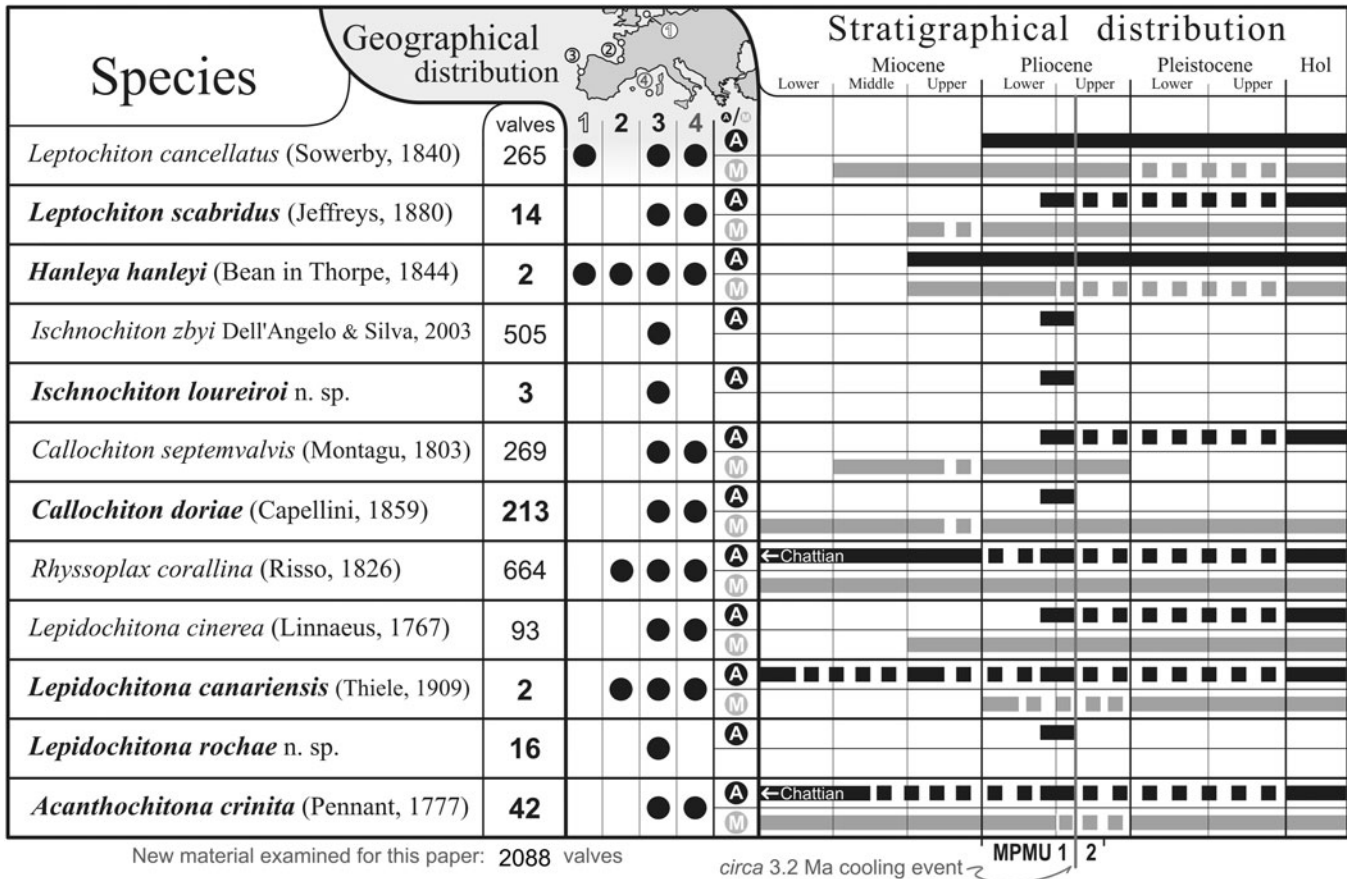


Figure 11. Stratigraphical distribution of the species represented in the Vale de Freixo Pliocene assemblage and available valves for each one of them in this study. New records for the Portuguese Pliocene are marked bold. MPMU = Mediterranean Pliocene Molluscan Units of Monegatti and Raffi (2001). For stratigraphic distribution, black signifies Atlantic distribution (A), gray signifies Mediterranean distribution (M).

the northeastern Atlantic (Anjou, France) by the smooth jugal area and the different shape of intermediate and tail valves. This genus was not reported by Dell'Angelo and Silva (2003), being an addition to the Pliocene chiton biodiversity of western Iberia.

Biogeography of Pliocene Atlanto-Mediterranean polyplacophorans

In the wake of early work of Dell'Angelo and Silva (2003) and based on the experience amassed studying the gastropod biodiversity from the Pliocene French Iberian bioprovince (Silva and Landau, 2007; Silva et al., 2010; Landau et al., 2020), the Pliocene chiton biodiversity of western Iberia is herein reassessed from a biogeographic point of view. In order to obtain new data to properly address the topic, the Vale de Freixo (VFX) fossil record was revisited and extensively sampled. As a result, the assemblage now comprises seven genera and 12 species, two of them described as new: *Ischnochiton loureiroi* n. sp. and *Lepidochitona rochae* n. sp. (Fig. 11). Of these species, seven are new for the Pliocene of Portugal. The occurrence of two genera (*Hanleya*, *Acanthochitona*) that are new for the Pliocene of Portugal is also reported.

Based on the relative abundance of specimens in the extensive study sample at hand, *Rhyssoplax corallina* and

Ischnochiton zbyi are the most represented species, with 31.8% and 24.2% of the total number of valves, respectively. The predominance of *Ischnochiton zbyi* in the VFX chiton assemblage was already noted by Dell'Angelo and Silva (2003).

Other species are also well represented in the assemblage: *Callochiton septemvalvis*, *Leptochiton cancellatus*, and *Callochiton doriae* (12.9%, 12.7%, and 10.2% of the total number of valves, respectively). On the other hand, the presence of *Hanleya hanleyi*, *Ischnochiton loureiroi* n. sp., and *Lepidochitona canariensis* is minimal, represented by 1–3 valves each.

In an early paper, Morais (1941) reported the occurrence of *Chaetopleura fulva* (Wood, 1815), a junior synonym of *Chaetopleura angulata* (Spengler, 1797), from the Pliocene Carnide Formation of Marinha Grande, ~20 km southwest of Carnide (Fig. 1). This report and its possible biogeographic implications were discussed in Dell'Angelo and Silva (2003). Unfortunately, it has not been possible either to confirm or refute the occurrence of *C. angulata* in the Portuguese Pliocene because none of the material from VFX—both in 2003 and now—is attributable to *Chaetopleura fulva*, and it was impossible to track the specimen(s) identified by Cox.

Most of the species and genera discussed herein represent taxa found, almost exclusively, in the Neogene to present-day European record. Only two species have also been reported from the Upper Oligocene (Chattian); *Rhyssoplax corallina*

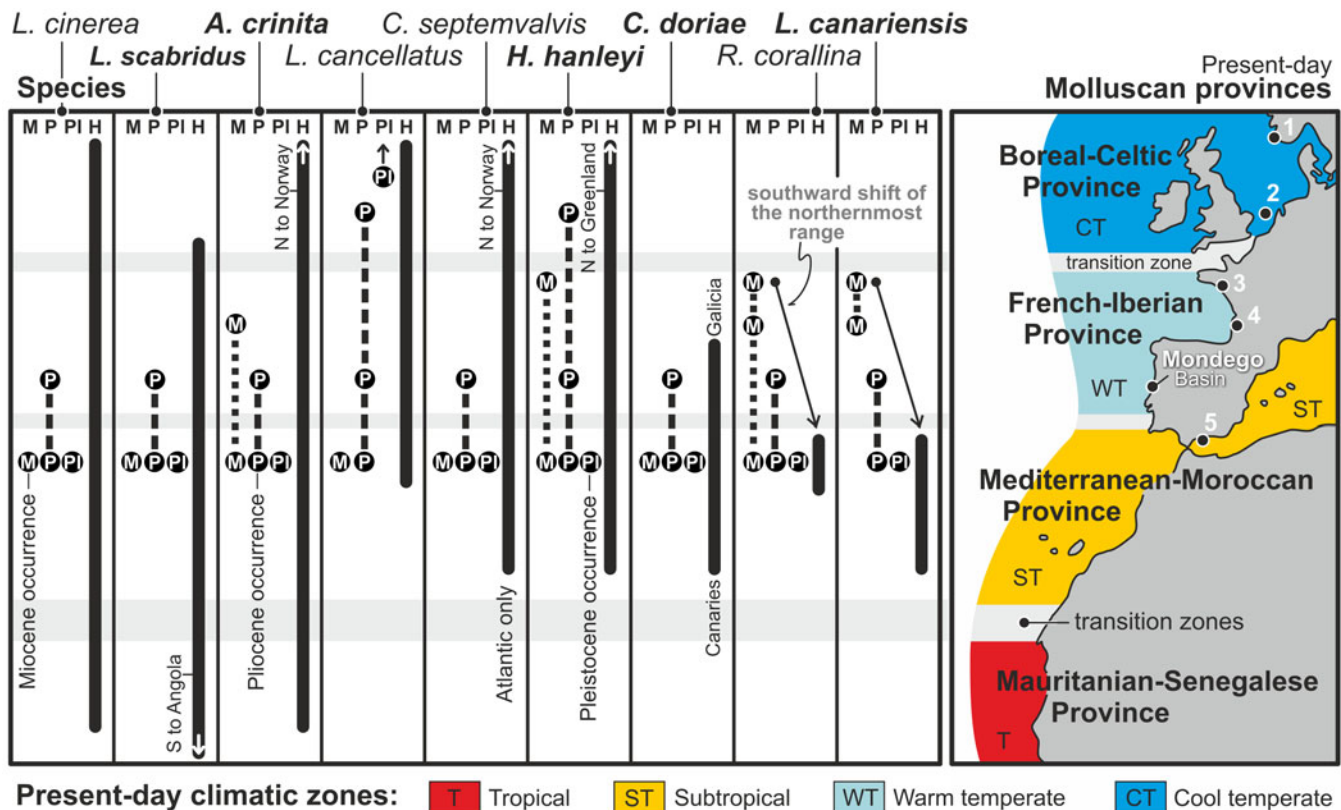


Figure 12. Miocene to present range evolution of the extant chiton species represented in the Pliocene Vale de Freixo assemblage (Mondego Basin). New species for the Portuguese Pliocene are marked bold. M = Miocene, P = Pliocene, Pl = Pleistocene; H = Holocene, present. Dotted vertical line = Miocene latitudinal distribution; dashed line = Pliocene; solid line = present-day latitudinal distribution. Fossil occurrences: 1 = Norway; 2 = North Sea Basin; 3 = Loire Basin; 4 = Aquitanian Basin; 5 = Estepona Basin and Mediterranean. Present-day molluscan provinces after Raffi et al. (1985).

and *Acanthochitona crinita* (Dell'Angelo et al., 2018a, 2020). Three of the 12 specific taxa identified (25%) have no record beyond the Pliocene. It should be noted that these are all endemic taxa that so far have been recorded only from VFX. The remaining nine are extant species, of which seven are present today both in the eastern Atlantic and the Mediterranean: *Leptochiton cancellatus*, *L. scabridus*, *Hanleya hanleyi*, *Rhyssoplax corallina*, *Lepidochitona cinerea*, *L. canariensis*, and *Acanthochitona crinita*, with one limited to the Atlantic (*Callochiton septemvalvis*) and one to the Mediterranean (*C. doriae*) (Fig. 11).

Marquet (2002) reported four species from the Pliocene of Kallo and Doel (Belgium). Among them, only *Leptochiton cancellatus* and *Hanleya hanleyi*—both extant widespread species—also occur in the Portuguese Pliocene. Several chiton species were reported from the Pliocene of England (Wood, 1842, 1848, 1872–1874; Rochebrune, 1882; Reid, 1890), but these occurrences are poorly known and in need of revision, making comparisons futile. However, among the species listed in these early works, four of them, *Leptochiton cancellatus*, *H. hanleyi*, *Lepidochitona cinerea*, and *A. crinita*, also occur in VFX.

Of the extant species represented in the VFX Pliocene, 58% of them (7 of 12)—*L. cinerea*, *L. scabridus*, *A. crinita*, *L. cancellatus*, *C. septemvalvis*, *H. hanleyi*, and *C. doriae*—have widespread present-day distributions (Fig. 12). They span several benthic molluscan biogeographic provinces, from the

northern cool temperate Boreal-Celtic to the subtropical Mediterranean-Moroccan and even the southern tropical Mauritanian-Senegalese Province (present-day bioprovinces sensu Raffi et al., 1985).

The present-day chiton fauna along the Portuguese coasts, including the Berlengas islands, off continental central-west Portugal, and the archipelagos of subtropical Madeira and warm temperate Azores, encompasses 20 species (Macedo et al., 1999; Mendonça, 2012). Of this group of species, seven occur in present-day Azores (Ávila and Sigwart, 2013) and eight were found in the present-day sandy and rocky intertidal environments of Tróia, in the mouth of the River Sado, ~40 km south of Lisbon (Mendonça, 2012). Gomes (2009) reported finding five species in the southern Portuguese continental platform of the Algarve. According to Ávila and Sigwart (2013), no chitons have been reported from the Neogene Azorean fossil record. The same for the Archipelago of Madeira in shallow rocky shore Miocene sequences (e.g., Santos et al., 2012). The subtropical Pliocene chiton assemblage from VFX comprises 12 species, less varied than the overall present-day fauna of the entire Portuguese coast line. However, it does well in terms of diversity when compared to the number of species commonly found in more restricted sectors of the Portuguese coast (e.g., in the Azores or in the Tróia region). To sum up, the Pliocene study assemblage seems representative.

From a biogeographical point of view (Fig. 12), it becomes evident that the northern range of two extant species of the nine

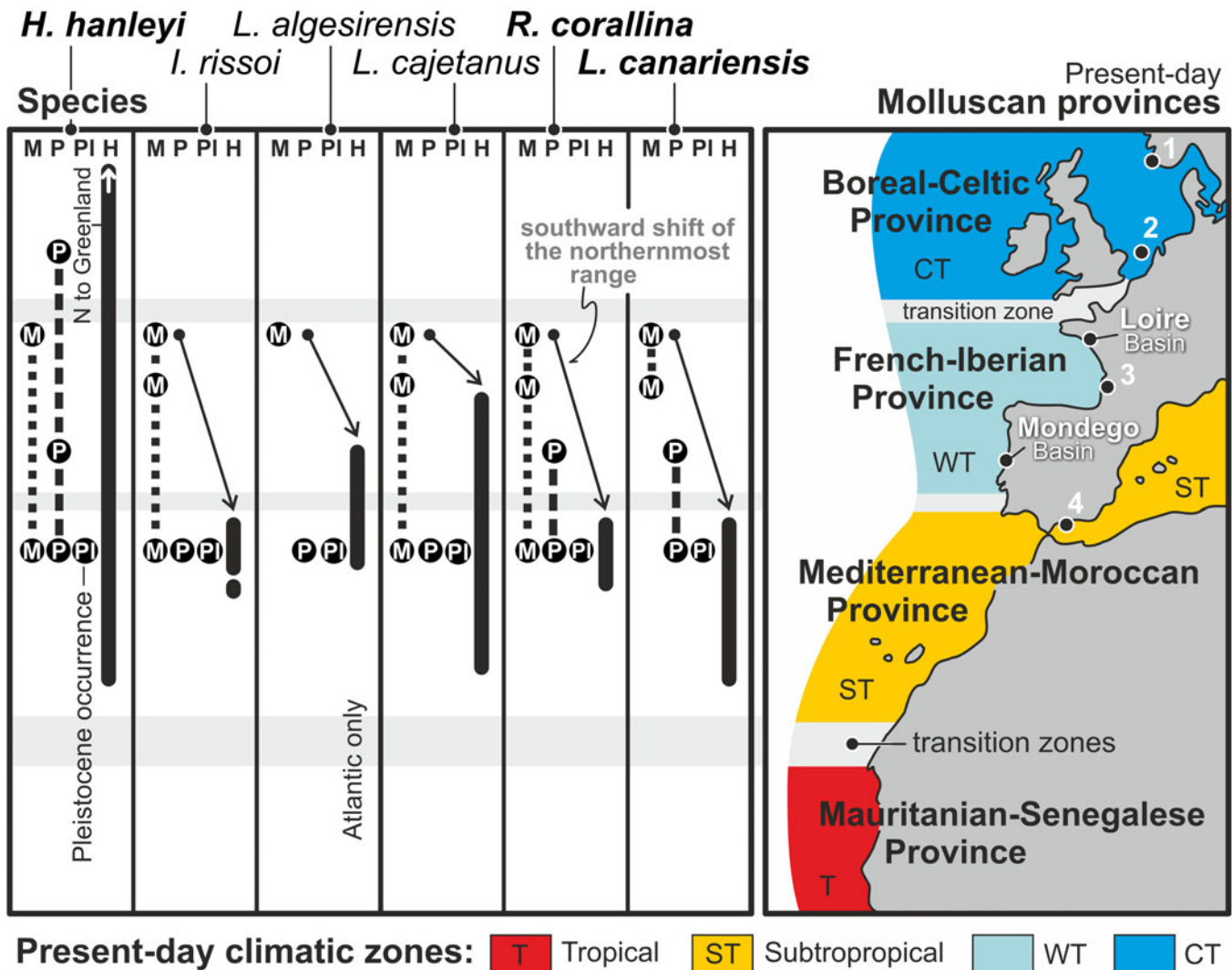


Figure 13. Miocene to present range evolution of the extant chiton species represented in the upper Miocene Assemblage I of northwestern France (Loire Basin). Species in common with the Portuguese Pliocene assemblage are marked bold. M = Miocene, P = Pliocene, PI = Pleistocene, H = Holocene, present. Dotted vertical line = Miocene latitudinal distribution; dashed line = Pliocene; solid line = present day latitudinal distribution. Fossil occurrences: 1 = Norway; 2 = North Sea Basin; 3 = Aquitanian Basin; 4 = Estepona Basin and Mediterranean. Climatic zones: WT = Warm temperate; CT = Cool temperate. Present-day molluscan provinces after Raffi et al. (1985).

(22%, or 15% of the total assemblage, two of 13 species) represented in the Portuguese Pliocene—the warmer-water *L. canariensis* and *R. corallina*—have undergone a marked southward shift since the Miocene and/or the Pliocene, from the French-Iberian Province to the present-day Mediterranean-Moroccan (Neogene benthic molluscan bioprovinces sensu Silva and Landau, 2007). Dell'Angelo and Silva (2003) noticed the Pliocene to present shift southwards of the northern distribution of *Chiton corallinus* (*Rhyssoptax corallina* herein) from VFX. However, Dell'Angelo and Silva (2003) lacked the extensive data available today on Neogene Atlantic and western Mediterranean chiton biodiversity, so were unable to go further into the discussion of the Neogene biogeography of the Atlantic and Mediterranean Polyplacophora.

Among the Assemblage I chitons of the Tortonian Ligerian Gulf of northwestern France, six extant species (27% of the assemblage, six of 22 species) are represented (Dell'Angelo et al., 2018b). Five of these six species (83%) have experienced

a northern range contraction since the Tortonian, with four of them (67%) occurring nowadays only from southern Portugal (from the Algarve) southwards (i.e., present in the Mediterranean-Moroccan Molluscan Province; Fig. 13). This same pattern of equatorward range contraction of warm-water mollusks is well documented among Neogene to present north-eastern Atlantic and Mediterranean gastropods and bivalves since the 3.3 Ma mid-Pliocene major cooling event occurred in Marine Isotope Stage (MIS) M2, during the Mammoth reversed polarity subchron (Monegatti and Raffi, 2007; Silva and Landau, 2007; Silva et al., 2010; Dolan et al., 2015; Landau et al., 2020).

Furthermore, as seen in Figure 12, it also becomes clear that four of the extant taxa represented in the VFX assemblage (*Lepidochitona cinerea*, *Leptochiton scabridus*, *A. crinita*, and *C. septemvalvis*) have wider geographic distributions today than in the Neogene, spanning more biogeographic provinces than in the Miocene and the Pliocene. Moreover, these species

show present-day distributions extending much farther north than their known Neogene ranges. An expansion of their distribution northward since the mid-Pliocene cooling event seems unlikely. Therefore, one plausible explanation for this unexpected “biogeographical pattern” would be the insufficient knowledge of the northernmost distributions of these species during the Neogene, due to fossil record incompleteness and/or deficient sampling of the known northern fossil sites. Either way, to solve this biogeographic conundrum, a more thorough sampling of the northern Pliocene sites, more focused on finding chiton remains, is recommended.

Conclusions

Unlike the records of other benthic mollusks (e.g., gastropods and bivalves), the polyplacophoran European Neogene record was, until recently, too poorly known to be of help in generating a clear picture of the Miocene to present biogeographical evolution of the group in the northeastern Atlantic and the Mediterranean. Extensive new material from the Pliocene of Vale de Freixo (Mondego Basin, Portugal), combined with recent data from the Neogene of the Loire Basin (northeastern France), made it possible to clarify the Late Miocene to Recent biogeography of the Atlanto-Mediterranean Polyplacophora. It is now clear that the northern range of warm-water northeastern Atlantic and Mediterranean Polyplacophora experienced a sharp contraction since, at least, the Late Miocene to Early Pliocene as a result of successive Pliocene and Pleistocene cooling events. Warm-water chiton species represented in the Upper Miocene of the Loire Basin of northwestern France (European-West African Province, *sensu* Silva and Landau, 2007) and the Mondego Basin of central-west Portugal (Pliocene French-Iberian Province) are today confined to the southern Mediterranean-Moroccan Molluscan Province.

This southward range contraction is also well documented among northeastern Atlantic and Mediterranean warm-water benthic gastropods and bivalves. Moreover, this general pattern could also be seen as an inverse analogue for the effects of present-day climate change on molluscan communities. With the rise of North Atlantic sea surface temperatures (SST) as a result of global warming, it is reasonable to expect a northwards range expansion of present-day warm-water benthic molluscan species.

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References

Adams, H., and Adams, A., 1853–1858, The genera of recent Mollusca; arranged according to their organization: London, John van Voorst, v. 1, p. 1–256 (1853), p. 257–484 (1854); v. 2, p. 1–284 (1855), p. 285–412 (1856), p. 413–540 (1857), p. 541–660 (1858).

- Anseeuw, B., and Verstraeten, J., 2009, Range extension for *Lepidochitona canariensis* (Thiele, 1909) (Mollusca: Polyplacophora: Tonicellidae): *Nephtunia*, v. 8, p. 30–32.
- Antevs, E., 1917, Post-glacial marine shell-beds in Bohuslän: *Geologiska Föreningens i Stockholm Förhandlingar*, v. 39, p. 247–425.
- Antevs, E., 1928, Shell Beds on the Skagerack: *Geologiska Föreningens i Stockholm Förhandlingar*, v. 50, p. 479–749.
- Arnaud, P.M., 1977, Revision des taxa malacologiques méditerranéens introduits par Antoine Risso: *Annales du Muséum d'Histoire Naturelle de Nice*, v. 5, p. 101–150.
- Ávila, S.P., and Sigwart, J., 2013, New records for the shallow-water chiton fauna (Mollusca, Polyplacophora) of the Azores (NE Atlantic): *ZooKeys*, v. 312, p. 23–38.
- Ávila, S.P., Melo, C., Bernig, B., Cordeiro, R., Landau, B., and Silva, C.M. da, 2016, *Persististrombus coronatus* (Mollusca: Strombidae) in the lower Pliocene of Santa Maria Island (Azores, NE Atlantic): paleoecology, paleoclimatology and paleobiogeographic implications: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 441, p. 912–923.
- Bałuk, W., 1971, Lower Tortonian chitons from the Korytnica clays, southern slopes of the Holy Cross Mts.: *Acta Geologica Polonica*, v. 21, p. 449–472.
- Bałuk, W., 1984, Additional data on chitons and cuttlefish from the Korytnica clays (Middle Miocene; Holy Cross Mountains, Central Poland): *Acta Geologica Polonica*, v. 34, p. 281–297.
- Barash, A., and Danin, Z., 1977, Polyplacophora (Mollusca) from the eastern Mediterranean: *Journal de Conchyliologie*, v. 114, p. 1–28.
- Barash, A., and Danin, Z., 1992, Fauna Palaestina. Mollusca I. Annotated list of Mediterranean Molluscs of Israel and Sinai: Jerusalem, The Israel Academy of Sciences and Humanities, 405 p.
- Beck, T., Metzger, T., and Freiwald, A., 2006, Biodiversity inventorial atlas (BIAS) of macrofaunal associations from OASIS seamount study sites: Friedrich-Alexander-University of Erlangen-Nürnberg, 127 p.
- Bellomo, E., and Sabelli, B., 1995, A new addition to the Mediterranean Pleistocene “Boreal Guests”: *Hanleya nagelfar* (Lovén, 1864) (Mollusca, Polyplacophora) from Calabria (S. Italy): *Bollettino della Società Paleontologica Italiana*, v. 34, p. 201–204.
- Bergenhayn, J.R.M., 1930, Kurze Bemerkungen zur Kenntnis der Schalenstruktur und Systematik der Loricaten: *Kungliga Svenska vetenskapsakademins handlingar*, v. 9, p. 1–54.
- Bergenhayn, J.R.M., 1955, Die Fossilen Schwedischen Loricaten nebst einer vorläufigen revision des systems der ganzen klasse Loricata: *Acta Universitatis Lundensis*, v. 51, p. 1–44.
- Beu, A.G., Dell, R.K., and Fleming, C.A., 1969, *Rhyssoptax* Thiele, 1893 (Mollusca, Amphineura): request for designation of a type-species under the plenary powers: *Bulletin of Zoological Nomenclature*, v. 25, p. 184–185.
- Brogger, W.C., 1901, Om de sen-glaciale og postglaciale nivåforandringer i Kristiania-feltet (Molluskfaunan): *Norges Geologiske Undersøgelse*, v. 31, p. 1–731.
- Cachão, M., 1990, Posicionamento Biostratigráfico da Jazida Pliocénica de Carnide: *Gaia*, v. 2, p. 11–16.
- Capellini, J., 1859, Catalogue des oscabrions de la Méditerranée suivi de la description de quelques espèces nouvelles: *Journal de Conchyliologie*, v. 7, p. 321–328.
- Carmona Zalvide, P., and García García, F.J., 2000, El género *Lepidochitona* Gray, 1921 (Mollusca, Polyplacophora) en el litoral Atlántico de la Península Ibérica: *Iberus*, v. 18 (2), p. 17–30.
- Carmona Zalvide, P., García, F.J., and Urgorri V., 2000, Nuevos datos anatómicos y taxonómicos del género *Chiton* Linnaeus, 1758 (Mollusca, Polyplacophora) en la Península Ibérica: *Iberus*, v. 18 (2), p. 1–15.
- Carmona Zalvide, P., García, F.J., and Urgorri V., 2002, Consideraciones taxonómicas y zoogeográficas del género *Callochiton* Gray, 1847 en la Península Ibérica: *Archiv für Molluskenkunde*, v. 131, p. 185–199.
- Carvalho, A.M.G., 1961, Note sur les Bryozoaires du Pliocène de Pombal: *Boletim da Sociedade Geológica de Portugal*, v. 14, p. 95–103.
- Cecalupo, A., Buzzurro, G., and Mariani, M., 2008, Contributo alla conoscenza della malacofauna del Golfo di Gabès (Tunisia): *Quaderni della Civica Stazione Idrobiologica di Milano*, v. 31, p. 1–175.
- Cesari, P., 1987, Note sistematiche e geonemiche su alcune specie mediterranee del genere *Leptochiton* Gray, 1847 (Polyplacophora, Leptochitonidae): *Lavori Società Veneziana di Scienze Naturali*, v. 12, p. 3–34.
- Chandan, D., and Peltier, W.R., 2017, Regional and global climate for the mid-Pliocene using the University of Toronto version of CCSM4 and PlioMIP2 boundary conditions: *Climate Past*, v. 13, p. 919–942.
- Cherns, L., and Schwabe, E., 2019, Eocene and Oligocene chitons (Polyplacophora) from the Paris and Hampshire Basins: *Historical Biology*, v. 31, p. 684–695.
- Chirli, C., 2004, Malacofauna Pliocénica Toscana. Vol. 4. Polyplacophora Gray J.E., 1821. Monoplacophora Odhner, 1940. Archaeogastropoda Thiele, 1925: Firenze, Italy, B.B.M., 113 p.

- Costa, O.-G., 1829, Catalogo Sistematico e Ragionato de' Testacei delle Due Sicilie: Napoli, Tipografia Della Minerva, 140 p.
- Crocetta, F., Bitar, G., Zibrowius, H., Capua, C., Dell'Angelo, B., and Oliverio, M., 2014, Biogeographical homogeneity in the eastern Mediterranean Sea—III. New records and a state of the art of Polyplacophora, Scaphopoda and Cephalopoda from Lebanon: *Spixiana*, v. 37, p. 183–206.
- Dall, W.H., 1889, Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U.S. Coast Survey Steamer “Blake”, Lieut.-Commander C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding, 29: report on the Mollusca, 2. Gastropoda and Scaphopoda: Bulletin of the Museum of Comparative Zoology, v. 18, p. 1–492.
- Dell'Angelo, B., and Forli, M., 1995, I Polyplacophora del Pleistocene inferiore di Riparbella (Pisa) con elenco dei molluschi rinvenuti: *Bollettino Malacologico*, v. 30, p. 221–252.
- Dell'Angelo, B., and Giusti, F., 1997, I Polyplacophora di una tafocenosi profonda: *La Conchiglia*, v. 29, p. 51–58.
- Dell'Angelo, B., and Palazzi, S., 1986, Considerazioni sulla famiglia Leptochitonidae Dall, 1889 (Mollusca: Polyplacophora) con descrizione di due nuovi taxa: *Bollettino Malacologico*, v. 22, p. 1–36.
- Dell'Angelo, B., and Palazzi, S., 1989, Considerazioni sulla famiglia Leptochitonidae Dall, 1889 (Mollusca: Polyplacophora). III. Le specie terziarie e quaternarie europee, con note sistematiche e filogenetiche: *Atti Prima Giornata di Studi Malacologici CISMA*, p. 19–140.
- Dell'Angelo, B., and Silva, C.M. da, 2003, Polyplacophora from the Pliocene of Vale de Freixo: central-west Portugal: *Bollettino Malacologico*, v. 39, p. 7–16.
- Dell'Angelo, B., and Smriglio, C., 1999, Chitoni Viventi del Mediterraneo: Roma, Edizioni Evolver, 256 p. [English ed. 2001, Living Chitons of the Mediterranean]
- Dell'Angelo, B., and Tringali, L.P., 2000, Prima segnalazione di *Lepidochitona canariensis* (Thiele, 1909) (Polyplacophora: Ischnochitonidae) per il mar Mediterraneo: *Bollettino Malacologico*, v. 35, p. 51–52.
- Dell'Angelo, B., and Zavodnik, D., 2004, Marine fauna of the Mljet National Park (Adriatic Sea, Croatia). 4. Mollusca: Polyplacophora: *Natura Croatica*, v. 13, p. 319–341.
- Dell'Angelo, B., Lombardi, C., and Taviani, M., 1998, Chitons (Mollusca, Polyplacophora) collected during cruise CS96 in the Strait of Sicily: *Giornale di Geologia*, v. 60, p. 235–252.
- Dell'Angelo, B., Palazzi, S., and Pavia, G., 1999, I molluschi del Messiniano Inferiore di Borelli (Torino). 4. Polyplacophora: *Bollettino del Museo Regionale di Scienze Naturali*, v. 16, p. 257–302.
- Dell'Angelo, B., Forli, M., and Lombardi, C., 2001, I Polyplacophora Pliopleistocenici della Toscana: *Bollettino Malacologico*, v. 36, p. 143–154.
- Dell'Angelo, B., Landau, B., and Marquet, R., 2004, Polyplacophora from the Early Pliocene of Estepona (Málaga, southwest Spain): *Bollettino Malacologico*, suppl. 5, p. 25–44.
- Dell'Angelo, B., Grigis, M., and Bonfitto, A., 2007, Notes on fossil chitons. 2. Polyplacophora from the Middle Miocene of Lăpugiu (Romania): *Bollettino Malacologico*, v. 43, p. 39–50.
- Dell'Angelo, B., Garilli, V., Germanà, A., Reitano, A., Sosso, M., and Bonfitto, A., 2012, Notes on fossil chitons. 4. Polyplacophora from the Pliocene of Altavilla (NW Sicily): *Bollettino Malacologico*, v. 48, p. 51–68.
- Dell'Angelo, B., Sosso, M., Prudenza, M., and Bonfitto, A., 2013, Notes on Fossil Chitons. 5. Polyplacophora from the Pliocene of Western Liguria, northwest Italy: *Rivista Italiana di Paleontologia e Stratigrafia*, v. 119, p. 65–107.
- Dell'Angelo, B., Giuntelli, P., Sosso, M., and Zunino, M., 2015, Polyplacophora from the Miocene of North Italy. Part 1: Leptochitonidae, Hanleyidae, Ischnochitonidae and Callistoplacidae: *Rivista Italiana di Paleontologia e Stratigrafia*, v. 121, p. 217–242.
- Dell'Angelo, B., Giuntelli, P., Sosso, M., and Zunino, M., 2016, Polyplacophora from the Miocene of North Italy. Part 2: Callochitonidae, Chitonidae, Lepidochitonidae, Acanthochitonidae and Cryptoplacidae: *Rivista Italiana di Paleontologia e Stratigrafia*, v. 122, p. 71–102.
- Dell'Angelo, B., Renda, W., Sosso, M., Sigwart, J.D., and Giacobbe, S., 2017, A new species of Callochiton (Mollusca: Polyplacophora) from the Strait of Messina (central Mediterranean): *Archiv für Molluskenkunde*, v. 146, p. 243–250.
- Dell'Angelo, B., Lesport, J.-F., Cluzaud, A., and Sosso, M., 2018a, The Oligocene to Miocene chitons (Mollusca: Polyplacophora) of the Aquitaine Basin, southwestern France, and Ligerian Basin, western France. Part 1: Leptochitonidae, Hanleyidae, Ischnochitonidae, Chitonidae, Spinochitonidae fam. nov. and Schizochitonidae: *Bollettino Malacologico*, v. 54, p. 1–47.
- Dell'Angelo, B., Landau, B., Van Dingenen, F., and Ceulemans, F., 2018b, The upper Miocene chitons of northwest France (Mollusca: Polyplacophora): *Zootaxa*, v. 4447, p. 1–62.
- Dell'Angelo, B., Sosso, M., and Bonfitto, A., 2019, A new species of *Ischnochiton* (Mollusca: Polyplacophora) from the Pleistocene of southern Italy: *Bollettino Malacologico*, v. 55, p. 45–49.
- Dell'Angelo, B., Lesport, J.-F., Cluzaud, A., and Sosso, M., 2020, The Oligocene to Miocene chitons (Mollusca: Polyplacophora) of the Aquitaine Basin, southwestern France, and Ligerian Basin, western France. Part 2: Lepidochitonidae, Tonicellidae, Acanthochitonidae, Cryptoplacidae and Additions to Part 1: *Bollettino Malacologico*, v. 56, p. 1–58.
- Dell'Angelo, B., Renda, W., Sirenko, B.I., Sosso, M., and Giacobbe, S., 2021, The Mediterranean distribution of *Hanleya hanleyi* (Bean in Thorpe, 1844) and *H. mediterranea* Sirenko, 2014 (Polyplacophora): *Bollettino Malacologico*, v. 57, p. 124–135.
- Diniz, F., 1984, Étude palynologique du bassin Pliocène de Rio Maior (Portugal): *Paléobiologie Continentale*, v. 14, p. 259–267.
- Diniz, F., Silva, C.M. da, and Cachão, M., 2016, O Pliocénico de Pombal (Bacia do Mondego, Portugal Oeste): biostratigrafia, paleoecologia e paleobiogeografia: *Estudos do Quaternário*, v. 14, p. 41–59.
- Dodge, H., 1952, A historical review of the mollusks of Linnaeus, Part I. The Classes Loricata and Pelecypoda: *Bulletin of the American Museum of Natural History*, v. 100, p. 1–264.
- Dolan, A.M., Haywood, A.M., Hunter, S.J., Tindall, J.C., Dowsett, H.J., Hill, D.J., and Pickering, S.J., 2015, Modelling the enigmatic Late Pliocene Glacial Event—Marine Isotope Stage M2: *Global and Planetary Change*, v. 128, p. 47–60.
- Dons, C., 1934, Norges strandfauna. V. Chitonidae: *Det Kongelige Norske Videnskabernes Selskab*, v. 7, p. 4–7.
- Dowsett, H.J. and Cronin, T.H., 1990, High eustatic sea level during the middle Pliocene: evidence from the southeastern U.S. Atlantic Coastal Plain: *Geology*, v. 18, p. 435–438.
- Dulai, A., 2005, Badenian (Middle Miocene) Polyplacophora from the central Paratethys (Bánd and Devecser, Bakony Mountains, Hungary): *Fragmenta Palaeontologica Hungarica*, v. 23, p. 29–50.
- Ferreira, A.J., 1979, The family Lepidopleuridae (Mollusca: Polyplacophora) in the eastern Pacific: *The Veliger*, v. 22, p. 145–165.
- Ferreira, F., Pereira, S., and Silva, C.M. da, 2019, Balaníteos do Pliocénico de Vale de Freixo (Pombal, Portugal): dados preliminares: IX CJIG, LEG 2019, Abstracts Volume, Universidade de Évora, Estremoz, Portugal, 23–24 Novembro 2019, Livro de Actas, p. 67–70.
- Garilli, V., Dell'Angelo, B., and Vardala-Theodorou, E., 2005, Polyplacophora from the Pleistocene of Kyllini (NW Peloponnese, Greece): *Bollettino della Società Paleontologica Italiana*, v. 44, p. 117–144.
- Gili, C., Silva, C.M. da, and Martinell, J., 1995, Pliocene nassariids (Mollusca: Neogastropoda) of central-west Portugal: *Tertiary Research*, v. 15, p. 95–110.
- Giribet, G., and Penas, A., 1997, Fauna malacologica del litoral del Garraf (NE de la Peninsula Iberica): *Iberus*, v. 15, p. 41–93.
- Gmelin, J.F., 1791, Vermes testacea, in Gmelin, J.F., ed., *Caroli a Linne systema natura per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis etc.* Editio decima tertia, aucta, reformata: Lipsiae, G.E. Beer, p. 3021–4120.
- Gomes, J.A.J., 2009, Malacofauna da Plataforma Continental Portuguesa [M.Sc. Thesis]: Aveiro, University of Aveiro, 89 p.
- Gray, J.E., 1821, A natural arrangement of Mollusca, according to their internal structure: *London Medical Repository*, v. 15, p. 229–239.
- Gray, J.E., 1828, *Spicilegium Zoologicum; or Original Figures and Short Systematic Descriptions of New and Unfigured Animals. Family Chitonidae*: London, Treuttel, Wurtz and Co., and W. Wood, v. 1, p. 5–6.
- Gray, J.E., 1847, A list of the genera of Recent Mollusca, their synonyms and types: *Proceedings of the Zoological Society of London*, v. 15, p. 129–206.
- Gray, J.E., 1857, *Guide to the systematic distribution of Mollusca in the British Museum*, 1: London, Taylor & Francis, 230 p.
- Hansson, H.G., 1998, NEAT (North East Atlantic Taxa): *Scandinavian marine Mollusca Check-List*: Internet Ed., Aug.1998. <http://www.gu.se/sites/default/files/2020-10/NEAT%2AMollusca.pdf>
- Hernández, J.M., and Rolán, E., 2011, Clase Polyplacophora, in Rolán, E. (Coord.), *Moluscos y Conchas Marinas de Canarias*: Vigo, ConchBooks, p. 46–53, 407–411.
- International Committee on Zoological Nomenclature (ICZN), 1971, Opinion 951. *Rhyssoplax* Thiele, 1893 (Amphineura): designation of a type-species under the Plenary Powers: *Bulletin of Zoological Nomenclature*, v. 28, p. 18–19.
- Iredale, T., 1914, Some more notes on Polyplacophora, part 1: *Proceedings of the Malacological Society of London*, v. 11, p. 123–131.
- Issel, A., 1869, *Malacologia del Mar Rosso. Ricerche Zoologiche e Paleontologiche*: Pisa, Biblioteca Malacologica, 388 p.
- Jeffreys, J.G., 1880, On a new species of chiton lately found on the British coasts: *The Annals and Magazine of Natural History*, v. 6, p. 33–35.
- Kaas P., 1979, On a collection of Polyplacophora (Mollusca, Amphineura) from the Bay of Biscay: *Bulletin du Muséum National d'Histoire Naturelle*, section A, v. 4, ser. 1, p. 13–31.
- Kaas, P., 1981, Scandinavian species of *Leptochiton* Gray, 1847 (Mollusca: Polyplacophora): *Sarsia*, v. 66, p. 217–229.

- Kaas, P., 1985, The genus *Acanthochitona* Gray, 1821 (Mollusca, Polyplacophora) in the north-eastern Atlantic Ocean and in the Mediterranean Sea, with designation of neotypes of *A. fascicularis* (L., 1767) and of *A. crinita* (Pennant, 1777): *Bulletin du Muséum National d'Histoire Naturelle*, section A, v. 4, ser. 7, p. 579–609.
- Kaas P., 1989, Notes on Loricata. 16. Chitons from the Gulf of Gabes, Tunisia: *Basteria*, v. 53, p. 91–92.
- Kaas, P., 1991, Chitons (Mollusca: Polyplacophora) procured by the CANCAP I–VII expeditions, 1976–86: *Zoologische Mededeelingen*, v. 65, p. 89–98.
- Kaas, P., and Van Belle, R.A., 1981, The genus *Lepidochitona* Gray, 1821 (Mollusca: Polyplacophora) in the northeastern Atlantic Ocean, the Mediterranean Sea and the Black Sea: *Zoologische Verhandelingen*, v. 185, p. 1–43.
- Kaas, P., and Van Belle, R.A., 1985a, Monograph of Living Chitons (Mollusca: Polyplacophora). Volume 1. Order Neoloricata: Lepidopleurina: Leiden, E.J. Brill, W. Backhuys, 240 p.
- Kaas, P., and Van Belle, R.A., 1985b, Monograph of Living Chitons (Mollusca: Polyplacophora). Volume 2. Suborder Ischnochitonina, Ischnochitonidae: Schizoplacinae, Callochitoninae & Lepidochitoninae: Leiden, E.J. Brill, W. Backhuys, 198 p.
- Kaas, P., and Van Belle, R.A., 1988, Monograph of Living Chitons (Mollusca: Polyplacophora). Volume 3. Suborder Ischnochitonina: Ischnochitonidae: Chaetopleurinae & Ischnochitoninae (pars). Additions to Vols 1 & 2: Leiden, E.J. Brill, W. Backhuys, 302 p.
- Kaas, P., and Van Belle, R.A., 1990, Monograph of Living Chitons (Mollusca: Polyplacophora). Volume 4. Suborder Ischnochitonina: Ischnochitonidae: Ischnochitoninae (continued). Additions to Volumes 1, 2 and 3: Leiden, E.J. Brill, 298 p.
- Kaas, P., and Van Belle, R.A., 1994, Monograph of Living Chitons (Mollusca: Polyplacophora). Volume 5. Suborder Ischnochitonina: Ischnochitonidae: Ischnochitoninae (concluded), Callistoplacinae; Mopaliidae. Additions to Volumes 1–4: Leiden, E.J. Brill, 402 p.
- Kaas, P., Van Belle, R.A., and Strack, H.L., 2006, Monograph of Living Chitons (Mollusca: Polyplacophora). Volume 6. Suborder Ischnochitonina (concluded): Schizochitonidae; Chitonidae. Additions to Volumes 1–5. Leiden-Boston, E.J. Brill, 463 p.
- Kattoulas, M., Koukouras, A., and Economidis, P., 1973, Benthic fauna of the Evvoia Coast and Evvoia Gulf. 2. Polyplacophora (Mollusca): *Scientific Annals of the Faculty of Physics and Mathematics, University of Thessalonika*, v. 13, p. 2.
- Kiliyas, R., 1995, Polyplacophora-Typen und -Typoide (Mollusca) im Zoologischen Museum in Berlin: *Mitteilungen aus dem Zoologisches Museum in Berlin*, v. 1, p. 155–170.
- Koskeridou, E., Vardala-Theodorou, E., and Moissette, P., 2009, Pliocene and Pleistocene shallow-water chitons (Mollusca) from Rhodes Island, Greece: *Neues Jahrbuch für Geologie und Paläontologie*, v. 251, p. 303–330.
- Koukouras, A., and Karachle, P., 2005, The polyplacophoran (Eumollusca, Mollusca) fauna of the Aegean Sea with the description of a new species, and comparison with those of the neighbouring seas: *Journal of Biological Research*, v. 3, p. 23–38.
- Kroh, A., 2003, The Polyplacophora (Mollusca) of the Langhian (lower Badenian) of the Molasse Zone and the northern Vienna Basin (Austria): *Annalen des Naturhistorischen Museums in Wien*, v. 104A, p. 129–143.
- Laghi, G.F., 1977, Polyplacophora (Mollusca) Neogenici dell'Appennino settentrionale: *Bollettino della Società Paleontologica Italiana*, v. 16, p. 87–115.
- Laghi, G.F., 2005, Upper Triassic chitons from the Italian Dolomites: *Lavori della Società Veneziana di Scienze Naturali*, v. 30, p. 79–84.
- Landau, B.M., Silva, C.M. da, Van Dingenen, F., and Ceulemans, L., 2020, Lower Pliocene gastropod assemblages from northwestern France: palaeoceanographic and palaeobiogeographic implications: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 538, 109387. <https://doi.org/10.1016/j.palaeo.2019.109387>.
- Leloup, E., 1934, Contribution a la connaissance de la faune des chitons de Villafranche-sur-Mer et des environs (France, Méditerranée): *Mededeelingen van het Koninklijk Natuurhistorisch Museum van België*, v. 10 (47), p. 1–20.
- Leloup, E., and Volz, P., 1938, Die Chitonien (Polyplacophoren) der Adria: *Thalassia*, v. 2, p. 1–63.
- Light, J.M., and Baxter, J.M., 1990, *Leptochiton scabridus* (Jeffreys, 1880)—a live record from County Donegal, Ireland: *Journal of Conchology*, v. 33, p. 318.
- Linnaeus, C., 1767, *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Editio duodecima, reformata: Holmiae, Laurentii Salvii, v. 1, p. 1–1327, v. 2, p. 1–37.
- Loureiro, J., 1799, Memoria sobre huma especie de petrificação animal: *Memorias de Mathematica e Phisica da Academia Real das Sciencias de Lisboa*, v. 2, p. 47–48.
- Lovén, S.L., 1846, Index molluscorum litora Scandinaviae Occidentalia habitantium: *Öfversigt Af K. Svenska Vetenskaps-Akademiens Förhandlingar*, v. 3, p. 134–160.
- Lozouet, P., 2014, Temporal and latitudinal trends in the biodiversity of European Atlantic Cenozoic gastropod (Mollusca) faunas. A base for the history of biogeographic provinces: *Carnets Géologie*, v. 14, p. 273–314.
- Macedo, M.C.C., Macedo, M.I.C., and Borges, J.P., 1999, *Conchas Marinhas de Portugal*. Lisboa, Editorial Verbo, 516 p.
- Macioszczyk, W., 1988, Polyplacophora from the Badenian deposits of Weglinnek, Weglin and Lichów (Western Roztocze—Poland): *Prace Museum Ziemi*, v. 40, p. 47–58.
- Malatesta, A., 1962, Mediterranean Polyplacophora Cenozoic and Recent: *Geologica Romana*, v. 1, p. 145–171.
- Marion, M.A.-F., 1883, Esquisse d'une topographie zoologique du golfe de Marseille: *Annales du Musée d'Histoire Naturelle de Marseille, Zoologie*, v. 1, p. 3–108.
- Marquet, R., 1984, A remarkable molluscan fauna from the Kattendijk Formation (Lower Pliocene) at Kallo (Oost-Vlaanderen, Belgium): *Bulletin de la Société Belge de Géologie, Paléontologie et Hydrologie*, v. 93, p. 335–345.
- Marquet, R., 2002, The Neogene Amphineura and Bivalvia (Protobranchia and Periomorpha) from Kallo and Doel (Oost-Vlaanderen, Belgium): *Palaeontos*, v. 2, p. 1–100.
- Mars, P., 1957, Liste des Mollusques testacés marins récoltés en Algérie par le "Dr.Lacaze-Duthiers" Juin–Juillet 1952. Amphineures: *Vie et Milieu*, suppl. 6, p. 121–122.
- McKay, D.W., and Smith, S.M., 1979, *Marine Mollusca of East Scotland*: Edinburgh, Royal Scottish Museum, 185 p.
- Mendonça, V.S.A., 2012, *Padrões de Distribuição Espacial e de Variabilidade Morfológica de Quitones em Zonas entre-marés Rochosas e Arenosas* [M.Sc. Thesis]: Lisbon, University of Lisbon, 140 p.
- Mifsud, C., Cachia, C., and Sammut, P.M., 1990, Note sui Poliplacofori delle isole Maltesi: *La Conchiglia*, v. 22, p. 52–61.
- Monegatti, P., and Raffi, S., 2001, Taxonomic diversity and stratigraphic distribution of Mediterranean Pliocene bivalves: *Palaeogeography, Palaeoclimatology and Palaeoecology*, v. 165, p. 171–193.
- Monegatti, P., and Raffi, S., 2007, Mediterranean-Middle Eastern Atlantic Façade: molluscan biogeography and ecobiostatigraphy throughout the late Neogene: *Açoreana*, suppl. 5, p. 126–139.
- Montagu, G., 1803, *Testacea Britannica, or natural history of British shells, marine, land and the fresh-water, including the most minute: systematically arranged and embellished with figures*: Romsey, London, 606 p.
- Monterosato, M.T.A., 1879, Enumerazione e sinonimia delle conchiglie mediterranee. Parte II. Monografia dei Chitonidi del Mediterraneo: *Giornale Scienze Naturali ed Economiche*, v. 14, p. 1–31.
- Morais, J.C. de, 1941, Mais alguns fósseis da região do Pinhal de Leiria: *Publicações do Museu Mineralógico e Geológico da Universidade de Coimbra, Memórias e Notícias*, v. 10, p. 3–5.
- Moreno, D., and Gofas, S., 2011, Clase Polyplacophora, in Gofas, S., Moreno, D., and Salas, C. (Coords.), *Moluscos Marinos de Andalucía*: Málaga, Universidad de Málaga, v. 1, p. 65–76.
- Nolf, D., and Silva, C.M. da, 1997, Otolithes de Poissons Pliocènes (Plaisancien) de Vale de Freixo, Portugal: *Revue de Micropaléontologie*, v. 40, p. 273–282.
- Okada, H., and Bukry, D., 1980, Supplementary modification and introduction of code numbers to the low-latitude coccolith biostratigraphic zonation: *Marine Micropaleontology*, v. 5, p. 321–325.
- Öztürk, B., Doğan, A., Bitlis-Bakir, B., and Salman, A., 2014, Marine mollusks of the Turkish coasts: an updated checklist: *Turkish Journal of Zoology*, v. 38, p. 1–48.
- Pallary, P., 1900, Coquilles marines du littoral du departement d'Oran: *Journal de Conchyliologie*, v. 48, p. 211–421.
- Pallary, P., 1920, Exploration scientifique du Maroc organisée par la Société de Géographie de Paris et continuée par la Société des Sciences Naturelles du Maroc. Deuxieme fasc. Malacologie (1912): *Empire Chérifien, Archives Scientifiques du Protectorat Français*, p. 1–108.
- Pennant, T., 1777, *The British Zoology*, 4. Crustacea, Mollusca, Testacea: London, Benjamin White, 156 p.
- Pereira, P., 2010, Echinoidea from the Neogene of Portugal mainland: *Palaeontos*, v. 18, p. 1–154.
- Pilsbry, H.A., 1892–1894, Monograph of Polyplacophora, in Tryon, G.W., *Manual of Conchology*: Academy of Natural Sciences, Philadelphia, v. 14, p. 1–128 (1892), p. 129–350 (1893); v. 15, p. 1–64 (1893), p. 65–133 (1894).
- Pimentel, R., 2018, *Bivalvia (Mollusca) do Pliocénico de Vale de Freixo (Pombal)* [M.Sc. Thesis]: Lisbon, Universidade Nova de Lisboa, FCT-UNL, 239 p.
- Plate, L.H., 1898–1901, Die Anatomie und Phylogenie der Chitonien, in *Fauna Chilensis: Zoologische Jahrbücher*, suppl., v. 4, p. 1–243 (1898); v. 5, p. 5–216 (1899); p. 281–600 (1901).
- Pruvot, G., 1897, Essai sur les Fonds et la Faune de la Manche Occidentale (côtes de Bretagne) comparés à ceux du Golfe du Lion: *Archives de Zoologie Expérimentale et Générale*, v. 5, p. 511–664.

- Raffi, S., and Monegatti, P., 1993, Bivalve taxonomic diversity throughout the Italian Pliocene as a tool for climatic-oceanographic and stratigraphic inference: *Ciências da Terra* (UNL), v. 12, p. 45–50.
- Raffi, S., Stanley, S., and Marasti, R., 1985, Biogeographic patterns and Pliocene extinction of Bivalvia in the Mediterranean and southern North Sea: *Paleobiology*, v. 11, p. 368–388.
- Rafinesque, C.S., 1815, *Analyse de la Nature ou tableau de l'univers et des corps organisés*. Palermo, Rafinesque, 223 p.
- Reid, C., 1890, Pliocene deposits of Britain: *Memoirs of the Geological Survey of the UK*, London, Eyre and Spottiswoode, 326 p.
- Risso, A., 1826, *Histoire Naturelle des Principales Productions de l'Europe Méridionale et Principalement de Celles des Environs de Nice et des Alpes-Maritimes*, 4. Mollusques: Paris, Levrault, 439 p.
- Rochebrune, A.T. de, 1882, *Monographie des espèces fossiles appartenant à la classe des Polyplaxiphores*: *Annales des Sciences Géologiques*, v. 14, p. 1–74.
- Rolán Mosquera, E., Otero-Schmitt, J., and Rolán Álvarez, E., 1990, Moluscos de la Ria de Vigo. II. Poliplacoforos, Bivalvos, Escafopodos, Cefalopodos: *Thalassas*, v. 2, 276 p.
- Ruman, A., and Hudácková, N.H., 2015, Middle Miocene chitons (Polyplacophora) from the Slovak part of the Vienna Basin and the Danube Basin (central Paratethys): *Acta Geologica Slovaca*, v. 7, p. 155–173.
- Sabelli, B., and Taviani, M., 1979, I Polyplacophora del Pleistocene inferiore del Torrente Sturone (Preappennino Parmense, Italia): *Bollettino della Società Paleontologica Italiana*, v. 18, p. 157–161.
- Sacco, F., 1897, I Molluschi dei Terreni Terziarii del Piemonte e della Liguria. Parte XXII. Gasteropoda (fine). Pulmonata. Amphineura (Chitonidae). Scaphopoda (Dentaliidae): Torino, Carlo Clausen, 148 p.
- Salas, C., and Luque, A.A., 1986, Contribución al conocimiento de los moluscos marinos de la isla de Alboran: *Iberus*, v. 6, p. 29–37.
- Santos, A., Mayoral, E., Johnson, M.E., Baarli, B.G., Cachão, M., Silva, C.M. da, and Ledesma-Vásquez, J., 2012, Extreme habitat adaptation by boring bivalves on volcanically active paleoshores from North Atlantic Macaronesia: *Facies*, v. 58, p. 325–338.
- Scacchi, A., 1836, *Catalogo Conchyliorum Regni Neapolitani Quae Usque Adhuc Reperit A. Scacchi: Neapoli, Typis Filiatae Sebetii*, 19 p.
- Schumacher, C.F., 1817, *Essai d'un Nouveau Système des Habitations des Vers Testacés*: Copenhagen, Schultz, 287 p.
- Schwabe, E., 2005, A catalogue of recent and fossil chitons (Mollusca: Polyplacophora). *Addenda: Novapex*, v. 6, p. 89–105.
- Schwabe, E., Sirenko, B.I., and Seeto, J., 2008, A checklist of Polyplacophora (Mollusca) from the Fiji islands: *Zootaxa*, v. 1777, p. 1–52.
- Segers, W., Swinnen, F., and De Prins, R., 2009, *Marine mollusks of Madeira. The living marine mollusks of the Province of Madeira (Madeira and Selvagens Archipelago)*: Belgium, Snoeck Publishers, 612 p.
- Sigwart, J.D., and Chen, C., 2018, Life history, patchy distribution, and patchy taxonomy in a shallow-water invertebrate (Mollusca: Polyplacophora: Lepidopleurida): *Marine Biodiversity*, v. 48, p. 1867–1877. <https://doi.org/10.1007/s12526-017-0688-1>.
- Sigwart, J.D., Stoeger, I., Knebelberger, T., and Schwabe, E., 2013, Chiton phylogeny (Mollusca: Polyplacophora) and the placement of the enigmatic species *Choriplax grayi* (H. Adams & Angas): *Invertebrate Systematics*, v. 27, p. 603–621.
- Silva, C.M. da, 2001, *Gastropodes pliocénicos marinhos de Portugal: Sistemática, Paleocologia, Paleobiologia, Paleobiogeografia* [Ph.D. Thesis]: Lisbon, University of Lisbon, 747 p.
- Silva, C.M. da, 2002, *Novos dados sobre os moluscos Pliocénicos marinhos de Portugal: implicações paleoceanográficas e paleobiogeográficas*: *Pliocénica*, v. 2, p. 117–125.
- Silva, C.M. da, and Landau, B.M., 2007, Cenozoic Atlanto-Mediterranean biogeography of *Spiricella* (Gastropoda, Umbraculidae) and climate change: filling the geological gap: *The Veliger*, v. 49, p. 19–26.
- Silva, C.M. da, Landau, B., Domènech, R., and Martinell, J., 2006, Pliocene Atlanto-Mediterranean biogeography of *Patella pellucida* (Gastropoda, Patellidae): palaeoceanographic implications: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 233, p. 225–234.
- Silva, C.M. da, Landau, B.M., Domènech, R., and Martinell, J., 2010, Pliocene Atlantic molluscan assemblages from the Mondego Basin (Portugal): age and palaeoceanographic implications: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 285, p. 248–254.
- Silva, C.M. da, Landau, B.M., and La Perna, R., 2011, Biogeography of Iberian Atlantic Neogene marginelliform gastropods (Marginellidae, Cystiscidae): global change and transatlantic colonization: *Journal of Paleontology*, v. 85, p. 1052–1066.
- Sirenko, B. I., 2006, New outlook on the system of chitons (Mollusca: Polyplacophora): *Venus*, v. 65, p. 27–49.
- Sirenko, B.I., 2014, Composition of the genus *Hanleya* (Mollusca: Polyplacophora: Lepidopleurida), with the description of two new species: *Journal of Natural History*, v. 48, p. 2913–2945.
- Sirenko, B.I., Abramson, N.I., and Yagapov, A.I., 2013, *Schizoplax brandtii* (Middendorff, 1847) (Mollusca: Polyplacophora)—an example of “explosive speciation”? *The Bulletin of the Russian Far East Malacological Society*, v. 17, p. 151–166.
- Sirenko, B.I., Sigwart, J., and Dell'Angelo, B., 2016, *Hanleya hanleyi* (Bean in Thorpe, 1844) (Mollusca, Polyplacophora) and the influence of the Gulf Stream System on its distribution: *Ruthenica*, v. 26, p. 57–70.
- Snelli, J.-A., and Gudmundsson, G., 2018, Polyplacophora (Nökkvar): <http://ni.is/biota/animalia/mollusca/nokkvar-polyplacophora>.
- Sosso, M., and Dell'Angelo, B., 2010, I Fossili del Rio Torsero: Prato, Cartotecnica Beusi, 96 p.
- Sowerby, G.B., II, 1832–1840, *The Conchological Illustrations, or coloured figures of all the hitherto unfigured recent shells*: London, parts 38–45 (1833), 159–177 (1839–1840).
- Spengler, L., 1797, Udførlig beskrivelse over det mangeskallede konkylielægt, af Linnaeus kaldet *Chiton*; met endeel nye Arter og Varieteter: *Skrivter af Naturhistorie Selskabet*, v. 4, p. 62–103.
- Strack, H.L., 1988, The distribution of Chitons (Polyplacophora) in Greece: *Apex*, v. 3, p. 67–80.
- Strack, H.L., 1990, The distribution of Chitons (Polyplacophora) in Greece: *addendum: Apex*, v. 5, p. 13–15.
- Strack, H.L., 2005, Class Polyplacophora, in Rolán, E., *The Malacological Fauna from the Cape Verde Archipelago. Part 1. Polyplacophora and Gastropoda*: Vigo, ConchBooks, p. 27–31, 272–275.
- Studencka, B., and Dulai, A., 2010, Chitons (Mollusca: Polyplacophora) from the Middle Miocene sandy facies of Ukraine, central Paratethys: *Acta Geologica Polonica*, v. 60, p. 257–274.
- Studencka, B., and Studencki, W., 1988, Polyplacophora from the Badenian (Middle Miocene) marine sandy facies of the Holy Cross Mts. (central Poland): *Prace Muzeum Ziemi*, v. 40, p. 37–46.
- Šulc, J., 1934, Studien über die fossilen Chitonen. I. Die fossilen Chitonen im Neogen des Wiener Beckens und der angrenzenden Gebiete: *Annalen des Naturhistorischen Museums in Wien*, v. 47, p. 1–31.
- Sykes, E.R., 1894, Notes on the British chitons: *Proceedings of the Malacological Society of London*, v. 1, p. 35–37.
- Thiele, J., 1893, Das Gebiss der Schrecken zur Begründung einer natürlichen Classification, in Troschel, F.H., *Polyplacophora, Lepidoglossa, Schuppenzüngler*: Berlin, v. 2, p. 353–401.
- Thiele, J., 1902, Die systematische stellung der Solenogastren und die phylogenie der Mollusken: *Zeitschrift für Wissenschaftliche Zoologie*, v. 72, p. 249–466.
- Thiele, J., 1909, Revision des Systems der Chitonen: *Zoologica*, v. 22, p. 1–132.
- Thorpe, C., 1844, *British Marine Conchology*: London, E. Lumley, 267 p.
- Urgorri, V., Díaz-Agras, G., García-Álvarez, O., and Señaris, M.P., 2017, FILO Mollusca, Clase Polyplacophora, in Banón, R. (Ed.), *Inventario de la Biodiversidad Marina de Galicia. Proyecto LEMGAL*: Santiago de Compostela, Consellería do Mar, Xunta de Galicia, p. 269–272.
- Van Belle, R.A., 1972, Over de Polyplacophora van Bretagne: *Gloria Maris*, v. 11, p. 201–204.
- Van Belle, R.A., 1985, De Polyplacophora van Madeira: *Gloria Maris*, v. 24, p. 73–76.
- Vermeij, G.J., 2012, The tropical history and future of the Mediterranean biota and the West African enigma: *Journal of Biogeography*, v. 39, p. 31–41.
- Vieira, M., Castro, L., Pais, J., and Pereira, D., 2006, Estudo palinológico do Pliocénico de Vale do Freixo, in Mirão, J., and Balbino, A. (Coords.), VII Congresso Nacional de Geologia, Portugal, Pólo de Estremoz da Universidade Évora: Abstracts, v. 2, p. 673–675.
- Warén, A., 1980, Marine Mollusca described by John Gwyn Jeffreys, with the location of the type material: *Conchological Society of Great Britain and Ireland, Special Publication 1*, p. 1–60.
- Wood, S.V., 1842, A catalogue of shells from the Crag: *The Annals and Magazine of Natural History*, v. 9, p. 455–462, 527–544.
- Wood, S.V., 1848, A monograph of the Crag Mollusca, or description of shells from the middle and upper Tertiaries of the east of England, 1. Univalves: *Monographs of the Paleontographical Society*, p. 1–208.
- Wood, S.V., 1872–1874, Supplement to the monograph of the Crag Mollusca, with descriptions of shells from the upper Tertiaries of the east of England, 3. Univalves and bivalves, with an introductory outline of the geology of the same district, and map: *Monographs of the Paleontographical Society*, p. 1–99 (1872), 100–231 (1874).
- Wood, W., 1815, *General Conchology; or, a description of shells arranged according to the Linnean system*: London, B. Howlett, p. 1–246.
- Zenetos, A., and Van Aartsen, J.J., 1995, The deep-sea molluscan fauna of the S. Aegean Sea and its relation to the neighbouring faunas: *Bollettino Malacologico*, v. 30, p. 253–268.

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