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Late Quaternary warm marine mollusks from Santa Maria (Azores) paleoecologic and paleobiogeographic considerations

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RESUMO

Palavras-chave: Plistocénico; invertebrados marinhos; Macaronésia; paleoecologia; paleobiogeografia.

A fauna marinha sub-fóssil dos depósitos quaternários de Santa Maria é composta por mais de 50 espécies de gastrópodes e de bivalves, 19 das quais foram recolhidas recentemente e pela primeira vez na costa Norte da ilha (Baía de Lagoinhas). As conchas sub-fósseis encontram-se em depósitos com areias de praia, situados 2 a 3 metros acima do nível de preia-mar actual. Nos níveis basais, bastante cimentados, identificou-se uma associação autóctone com foládios, dominada pelo bivalve *Myoforceps aristata* (Dillwin, 1817). As areias marinhas incluem concentrações de *beach drift*, compreendendo conchas bem preservadas de gastrópodes supra-litorais e litorais, entre os quais numerosos rissoídeos. Nos bivalves predominam concentrações de valvas desarticuladas de *Ervilia castanea* (Montagu, 1803), uma pequena espécie infaunal colonizadora de substratos arenosos móveis. Na composição total da fauna intervêm essencialmente espécies do litoral da Europa Ocidental, muitas delas existentes na costa portuguesa. Todavia, estão também presentes algumas espécies exóticas, "quentes", características das faunas de moluscos da costa ocidental de África ou das Caraíbas. Este elenco apresenta semelhanças significativas com diversas associações sub-fósseis encontradas em depósitos plistocénicos do Mediterrâneo Ocidental, considerados como "tirrenianos".

ABSTRACT

Key-words: Pleistocene; marine invertebrates; Macaronesia; paleoecology; paleobiogeography.

The sub-fossil fauna from the Late Quaternary marine deposits of Santa Maria is made of more than 50 species of gastropods and bivalves, 19 of them collected recently and for the first time in the northern coast of the island (Lagoinhas Bay). The sub-fossil shells are found in deposits of beach sands, situated 2-3 meters above the present low tide. The carbonated sands from the basal part of the succession yield an autochthonous association of borers dominated by the bivalve *Myoforceps aristata* (Dillwin, 1817). Upwards, the marine sands contain concentrations of beach drift shells, including well-preserved supratidal and intertidal gastropods, among them a large number of Rissoidae. The bivalve fauna is dominated by disarticulated valves of *Ervilia castanea* (Montagu, 1803), a small infaunal coloniser of mobile sandy substrates. The composition of the fauna is made essentially of West European species, many of them common to the West Coast of Portugal. However, a few "warm guests" with West African or Caribbean affinities were also found, suggesting a close relation with some of the "Tyrrhenian" warm associations found in the Western Mediterranean.

INTRODUCTION

The Pleistocene marine deposits from Santa Maria are known for a long time, after the works of Mayer (1864) and Berthois (1951, 1953), revised by Zbyszewski & Ferreira (1961) and Zbyszewski *et al.* (1961). Some of these deposits proved to be exceptional sites to collect sub-fossil shells, with special emphasis to those described near the Bay of Prainha, a few kilometers eastward Vila do Porto, on the southern coast of the island (fig. 1). After Zbyszewski & Ferreira (*op. cit.*), the succession observed near Prainha is situated about 2-3 meters above the present low tide, and built of a basal conglomerate with algal-limestone concretions followed by 0.80 to 1.50 m of fossiliferous beach sands.

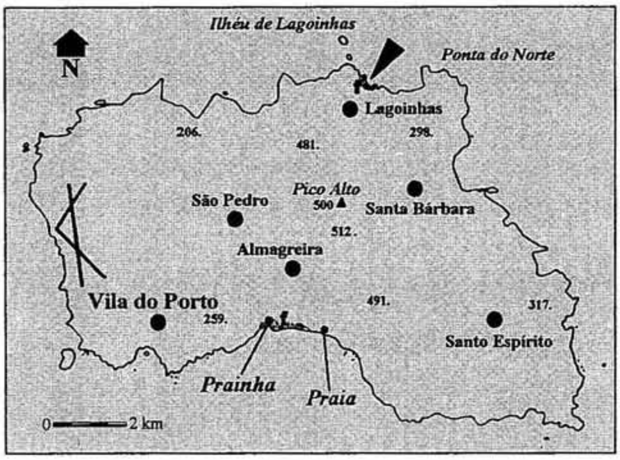

Fig. 1 - Simplified map of Santa Maria, showing the location of the upper Pleistocene sites of Praia, Prainha and Lagoinhas.

In the northern coast of Santa Maria, a new deposit correlative with Prainha has been identified and sampled, supplying several hundreds of sub-fossil shells, mostly micro-gastropods. This deposit is best exposed near the cliffs of Lagoinhas, between Ponta do Norte and the islet of Lagoinhas. Near this point, the succession begins with cemented and bored carbonated sands, overlaid by 0.50m of beach sands with concentrations of shell debris, and a cover of torrential sediments (pl. I).

As in Prainha Bay, the fossiliferous beds yield an abundant and diversified fauna of sub-fossil gastropods and bivalves, most of them belonging to small-sized species. Besides its systematic and ecological relevance, this fauna is of special interest for biogeographic purposes due to the particular location of the Azores in the central Atlantic. The bulk of the Quaternary marine mollusks from this archipelago of Macaronesia show strong West European affinities (Morton, *et al.*, 1998), with many species being common to the West Coast of Portugal (Nobre, 1930, 1940). However, some West African and Caribbean influences can be noted by the introduction of *warm-guests* in the sub-fossil faunas, suggesting the occurrence of positive fluctuations in the mean temperatures of the Atlantic surface waters, during late Pleistocene interglacial events.

This account pretends to summarise the paleontologic data carried out after Mayer (1864) and Zbyszewski & Ferreira (1961), together with a comparison with a new collection of specimens recently collected in Santa Maria and housed in the Earth Sciences Department of the University of Coimbra (DCTUC). The same faunas are analysed in the point of view of their paleoecologic, paleobiogeographic and climatic significance.

FAUNAL COMPOSITION

The systematic analysis of the newbulk sample was concluded with the identification of 26 species of marine gastropods and 5 bivalves. Mixed with the shell debris were also found a few fragments of indeterminable erect bryozoans, decapods, *Balanus* sp. and the sea urchin *Sphaerechinus granularis* (Lamarck, 1822). The collected species are (pl. II):

Classe Gastropoda

Fam. Haliotidae
Haliotis tuberculata Linné, 1758

Fam. Patellidae
Patella ulyssiponensis Gmelin, 1791

Fam. Trochidae
Calliostoma zizyphinum (Linné, 1758)
Jujubinus exasperatus (Pennant, 1777)
Jujubinus striatus (Linné, 1758)

Fam. Littorinidae
Melarhaphe neritoides (Linné, 1758)

Fam. Rissoidae
Alvania cancellata (da Costa, 1778)
Alvania cimicoides (Forbes, 1844)
Cingula cingillus (Montagu, 1803)
Manzonia unifasciata Dautzemberg, 1889
Rissoa similis Scacchi, 1836

Fam. Rissoinidae
Zebina vitrea A. Adams, 1854

Fam. Vermetidae
Vermetus sp.

Fam. Cerithiidae
Bittium reticulatum (da Costa, 1778)

Fam. Fossaridae
Fossarus ambiguus (Linné, 1758)

Fam. Thaididae
Thais haemastoma (Linné, 1767)

Fam Coralliophilidae
Coralliophila meyendorffi (Calcara, 1845)

Fam. Buccinidae
Cantharus variegatus (Gray, 1839)

Fam. Columbellidae
Mitrella broderipii (Sowerby, 1844)

Fam. Cymatiidae
Charonia lampas (Linné, 1758)

Fam. Marginellidae
Gibberula sp.

Fam Turridae
Mangelia costata (Donovan, 1803)
Mangelia sp.

Fam. Conidae
Conus ermineus Börn, 1778

Fam. Triphoridae
Monophorus perversus (Linné, 1758)

Fam. Ellobiidae
Ovatella (Mysotella) myosotis (Draparnaud, 1805)

Classe Bivalvia

Fam Arcidae
Arca tetragona Poli, 1795

Fam. Mytilidae
Myoforceps aristata (Dillwin, 1817)

Fam. Pectinidae
Chlamys distorta (da Costa, 1778)

Fam. Carditidae
Cardita calyculata (Linné, 1758)

Fam. Mesodesmatidae
Ervilia castanea (Montagu, 1803)

A comparison with the systematic lists already known from the researches of Mayer (1864) and Zbyszewski & Ferreira (1961) shows that 19 of the *taxa* are, for the first time, referred to the Pleistocene deposits of Santa Maria. These *taxa* are: *Calliostoma zizyphinum* (Linné, 1758), *Jujubinus exasperatus* (Pennant, 1777), *Jujubinus striatus* (Linné, 1758), *Melarhaphe neritoides* (Linné, 1758), *Alvania cancellata* (da Costa, 1778), *Cingula cingillus* (Montagu, 1803), *Manzonia unifasciata* Dautzemberg, 1889, *Zebina vitrea* A. Adams, 1854, *Vermetus* sp., *Mitrella broderipii* (Sowerby, 1844), *Charonia lampas* (Linné, 1758), *Gibberula* sp. *Mangelia costata* (Donovan, 1803), *Mangelia* sp., *Conus ermineus* Börn, 1778, *Ovatella (Mysotella) myosotis* (Draparnaud, 1805), *Arca tetragona* Poli, 1795, *Myoforceps aristata* (Dillwin, 1817) and *Chlamys distorta* (da Costa, 1778).

The *taxa* previously mentioned by the same workers but not collected this time are:

Classe Gastropoda

Patella caerulea Linné, 1758 [*Patella candei* d'Orbigny, 1840]
Patella vulgata Linné, 1758 [probably a *Patella candei* d'Orbigny, 1840]
Gibbula cineraria (Linné, 1758) [referred as *"Trochus"strigosus* Gmelin, 1791]
Tricolia pullus (Linné, 1758)
Manzonia crassa (Kanmacher, 1798) [referred as *costata* Adams, 1796]
Alvania pagodula (Bucquoy, Dautzenberg & Dollfus, 1884)
Rissoa variabilis (Muhlfeldt, 1824)
Rissoa dolium Nyst, 1845
Rissoina bruguierei (Pyraudeau, 1826) [referred as *canariensis* d'Orbigny, 1839]
Polinices lacteus (Guilding, 1834)
Zonaria pyrum (Gmelin, 1791)
Phalium undulatum (Gemlin, 1791)
Cabestana cutacea (Linné, 1767)
Mitra cornicula Linné, 1758
Mangelia nebula (Montagu, 1803)
Cerithiopsis nana Jeffreys, 1867
Seila trilineata (Philippi, 1836)

Classe Bivalvia

Lithophaga lithophaga (Linné, 1758) [probably a *Myoforceps aristata* (Dillwin, 1817)]
Neopycnodonte cfr. *cochlear* (Poli, 1795)
Lyropecten cfr. *nodosus* (Linné, 1758)
Laevicardium norvegicum (Spengler, 1797)
Solen cfr. *marginatus* (Pennant, 1777)

With the contribution of these 22 *taxa* the diversity of the invertebrate fauna from the Pleistocene of Santa Maria reaches 57 species, most of them gastropods (43) and bivalves (11). However, this systematic list should be reviewed in some aspects, with special attention to the micro-shells (Rissoidae and others), because there are several species mentioned by Mayer (1864) and never collected again. The Rissoidae and Rissoinidae, they were object of detailed reviews in the last decades, and some of the *taxa* listed by this worker are Mediterranean species without distribution in the adjacent Atlantic areas.

The borer bivalve *Lithophaga lithophaga* (Linné, 1758) described by Zbyszewski & Ferreira (1961) as one of the dominant elements from the fauna of Prainha is also a typical Mediterranean species. The specimens of borers from the recent collection of the DCTUC belong to *Myoforceps aristata* (Dillwin, 1817), which is a close species from the West European and East American coasts. It can be differentiated by its small size, together with two pointed and curved tips in the posterior ends of the valves. These tips are difficult to observe in the sub-fossil shells, since most of them are strongly incrusted in the carbonate concretions.

The limpet *Patella caerulea* Linné, 1758 listed by Zbyszewski & Ferreira (1961) is surely the macaronesian *Patella candei* d'Orbigny, 1840, an endemic species from Azores, Madeira and Canaries. On the contrary, the recent distribution of *Patella caerulea* is restricted to the Mediterranean (Poppe & Goto, 1991). The occurrence of *Patella vulgata* Linné, 1758 also needs confirmation, since the sub-fossil shells of this Northwest European limpet can be confused with young specimens of the highly variable *Patella candei.*

The Conidae from the fauna of Prainha were compared by M. Brebion (*in* Zbyszewski & Ferreira, 1961) with the West African *Conus ambiguus* Reeve, 1844 and *Conus testudinarius* Hwass, *in* Bruguière, 1792. However, "*testudinarius*" is a synonymous frequently used to designate the Eastern Atlantic populations of *Conus ermineus* Börn, 1778 (Korn, 1987). The morphology of these shells, including the specimen recently housed in the collection of the DCTUC, is closer to weakly developed forms of the amphiatlantic *Conus ermineus*. After Burnay & Monteiro (1977) and Walls (1979) these diagnostic features include a shoulder roundly angled, a low to moderate spire with 2-3 spiral ridges and very week and few axial threads, and a body whorl with 6-10 low spiral ridges restricted to the area above the base. *Conus ambiguus* can be easily distinguished because of the pattern of the spire, which has sometimes a cancellate appearance. Usually the shoulder is more roundly and the body whorl is irregularly spirally sculptured.

BIOSTRATINOMIC AND PALEOECOLOGIC FEATURES

The sub-fossil malacofaunas from Prainha Bay and Lagoinhas are the result of an heterogeneous mixing of shells with distinct grades of abrasion, fragmentation and disarticulation, belonging to species typical of rocky, sandy or algal substrates from the supralittoral to upper sublittoral marine environments. Two different types of concentrations can be defined:

(1) Autochthonous concentrations of borer and cryptic bivalves found articulated in sandy carbonated substrates, strongly cemented and partly of algal origin.

(2) Parautochthonous concentrations of gastropods and bivalves, including some mixed allochthonous elements represented by abraded and fragmented shells of sublittoral species. These concentrations can be interpreted as the result of beach drift accumulated during high tides, especially during storm events or equinoctial tides.

The upper intertidal biota of exposed rocky substrates is represented by *Melarhaphe neritoides* (Linné, 1758) and *Ovatella (Mysotella) myosotis* (Draparnaud, 1805).

Many other species from this fauna are typical elements of middle or lower intertidal shores. The gastropods *Patella ulyssiponensis* Gmelin, 1791, *Calliostoma zizyphinum* (Linné, 1758), *Vermetus* sp., *Bittium reticulatum* (da Costa, 1778), and the bivalves *Myoforceps aristata* (Dillwin, 1817) and *Cardita calyculata* (Linné, 1758) inhabit some of these hard intertidal substrates colonised with algae and sponges. Many of the small Rissoidae listed above are herbivorous feeders that can be found in lower intertidal or upper sublittoral algal prairies and mats.

The algal and rocky bottoms from the upper part of the sublittoral stage are represented by the gastropods *Haliotis tuberculata* Linné, 1758, *Jujubinus exasperatus* (Pennant, 1777), *J. striatus* (Linné, 1758), *Coralliophila meyendorffi* (Calcara, 1845), *Cantharus variegatus* (Gray, 1839), *Mitrella broderipii* (Sowerby, 1844), *Charonia lampas* (Linné, 1758), *Gibberula* sp., *Mangelia costata* (Donovan, 1803), and *Conus ermineus* Börn, 1778. Occasionally, the same species can be found in intertidal rocks.

The small but very abundant infaunal bivalve *Ervilia castanea* (Montagu, 1803) is a very successful coloniser of mobile sandy substrates, through the growth of dense populations in the shallow sandy bars that surround coastal cliffs (Morton, *et al.*, 1998). The shell debris from this species contribute with a significant volume to the neighbourhood beach sands, being one of the most common elements of the fossil associations found on the Pleistocene deposits.

Figure 2 summarises an ecological section representing the sub-fossil marine molluscs from Santa Maria.

PALEOBIOGEOGRAPHIC AND CLIMATIC SIGNIFICANCE

Just as the recent marine fauna of molluscs from the Azores, most species from the sub-fossil fauna of Santa Maria are common to the Atlantic coasts of Western Europe, from the Channel to Portugal. Some of the known ranges of these species also reach the Western Mediterranean, the coastline of Morocco, and the Madeira and Selvagens islands. Nevertheless, the particular interest of Pleistocene malacofauna from Santa Maria arises from the existence of West African and Caribbean *warm-guests*, today unknown from the Azores waters.

Cantharus variegatus (Gray, 1839) is a tropical West African species, reaching today the Canaries islands. During the Pleistocene its northern range area was prolonged to North, into the littoral of Morocco (*Harounian* and *Ouljian* of Lecointre, 1963, and Brebion, 1979) and the Mediterranean (Tyrrhenian II and III of Charrier, 1961 and Dieny & Massari, 1966).

Conus ermineus Börn, 1778 is a widespread tropical amphiatlantic species, common on the West African coasts from the Sahara to Angola (Walls, 1979), but also on the Brazilian coast, Antilles, Central America, Gulf of Mexico and Bahamas. As in the previous species, several occurrences are known from the Tyrrhenian of the Western and Central Mediterranean, together with the classical "*Strombus bubonius*" and *Mytilus senegalensis* warm faunas (Charrier, 1961; Vazzana, 1988).

Polinices lacteus (Guilding, 1834) is one of the best examples of tropical amphiatlantic gastropods, ranging from Mauritania, Madeira and Canaries to Angola and Santa Helena, and from the Brazilian coast to the Caribbean (Abbott, 1968; Dixon & Ryall, 1986; Gofas *et al.*, 1987; Poppe & Goto, 1991). This naticid is occasionally found in the Azores (Morton, *et al.*, 1998). It is also cited in the Mediterranean Pleistocene, together with the previous species and *Strombus* faunas.

The small *Zebina vitrea* A. Adams, 1854 is a warm temperate North-Atlantic gastropod, known from the Antilles and also found in the Canaries and Selvagens (Poppe & Goto, 1991).

Lyropecten nodosus (Linné, 1758) is a West Atlantic pectinid that range from the Brazilian coasts to the Caribbean and the Southeast littoral of USA (Abbott, 1968).

This association of warm-temperate species suggests that the 2-3 meters marine deposits of Santa Maria can be

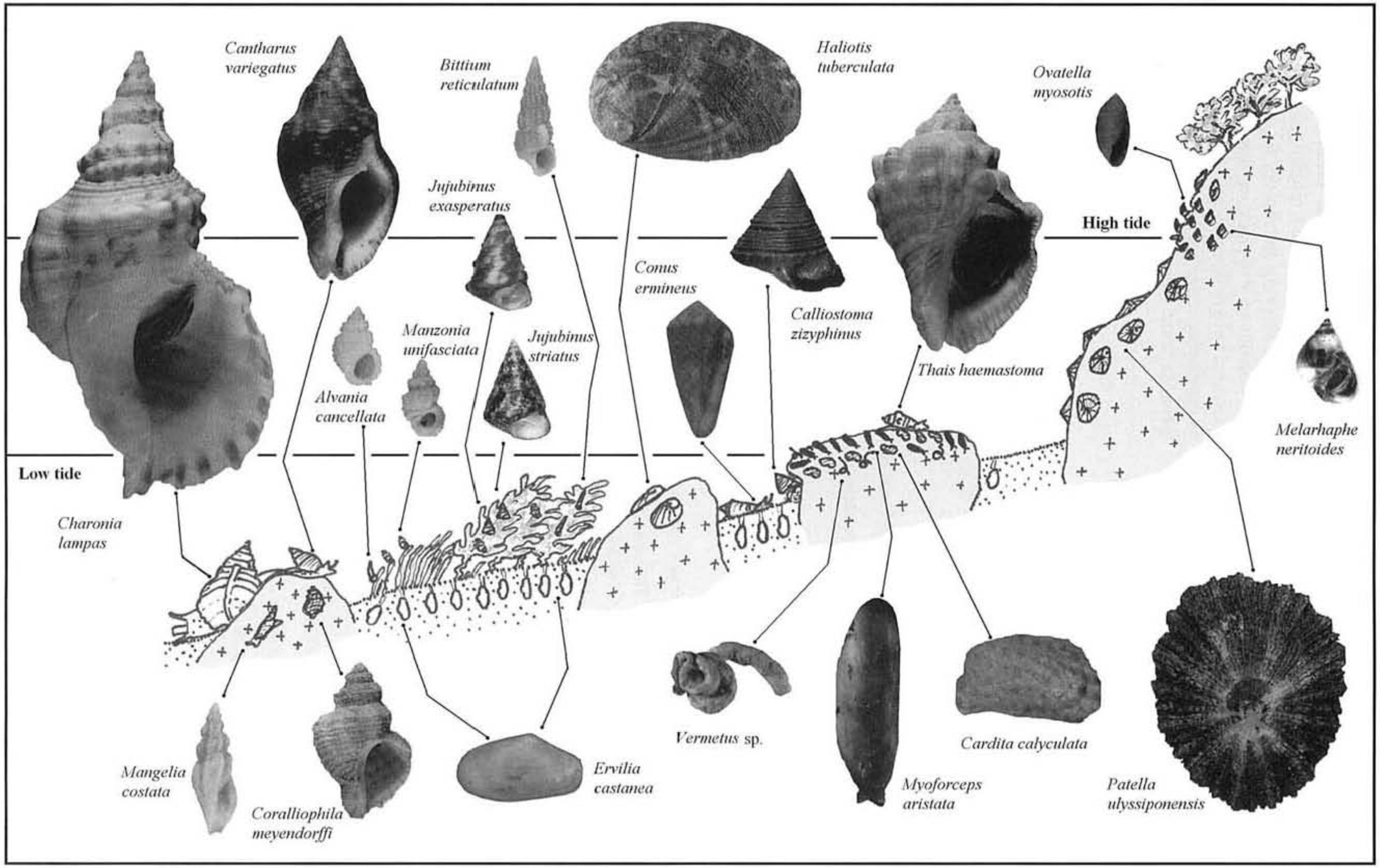

Figure 2 - Ecological section with a representation of the sub-fossil marine molluscs from Santa Maria in their original marine environments.

related with a Pleistocene warm period, marked by the migration northwards of species traditionally found in lower latitudes. A comparison with the Mediterranean classical faunas, containing "*Strombus bubonius*" and other sub-tropical components, seems evident. Both faunal associations from Santa Maria and from the Mediterranean yield *Cantharus variegatus*, *Conus ermineus* and *Polinices lacteus*. In the "Tyrrhenian" deposits of Italy, Southeast Spain and Canaries (Brebion, 1979), these species can be collected together with "*Strombus bubonius*", *Mytilus senegalensis*, *Cardita senegalensis*, and other molluscs of warm-temperate waters.

The geographic range of the species from the Pleistocene of Santa Maria also emphasises the particular importance of the Azores archipelago, as a crossing and mixing area between the Western and Eastern Atlantic molluscan faunas. During warmer interglacial events, the positive oscillations in the mean temperatures of the surface waters promoted migrations of warm species northward, reaching the Azores for some times. From the Caribbean Province, a few other species with prolonged veliger development were also able to extend its geographic range eastwards, colonising the littoral of Santa Maria and other of the Central Atlantic shallow areas.

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Plate I

Fig. 1 - The northern coast of Santa Maria, near the bay and islet of Lagoinhas, with the 2-3 meters platform exposed at low tide.

Fig. 2 - Detailed view of the Upper Pleistocene fossiliferous sands.

Plate II

1, 2 – *Thais haemastoma* (Linné, 1767), back and aperture views. (x1,5)

3 - *Melarhaphe neritoides* (Linné, 1758), aperture view. (x2)

4 - *Calliostoma zizyphinum* (Linné, 1758), aperture view of incomplete specimen. (x1,5)

5a-b - *Mangelia costata* (Donovan, 1803), back and aperture views. (x5)

6 - *Bittium reticulatum* (da Costa, 1778), back view. (x5)

7 - *Myoforceps aristata* (Dillwin, 1817), bored algal limestone with articulated shell. (x1,5)

8, 9 - *Ervilia castanea* (Montagu, 1803), left and right valves. (x5)

10, 11 - *Cardita calyculata* (Linné, 1758), left and right valves. (x5)

12a-b – *Mangelia* sp., back and aperture views. (x5)

13a-b - *Fossarus ambiguus* (Linné, 1758), back and aperture views. (x5)

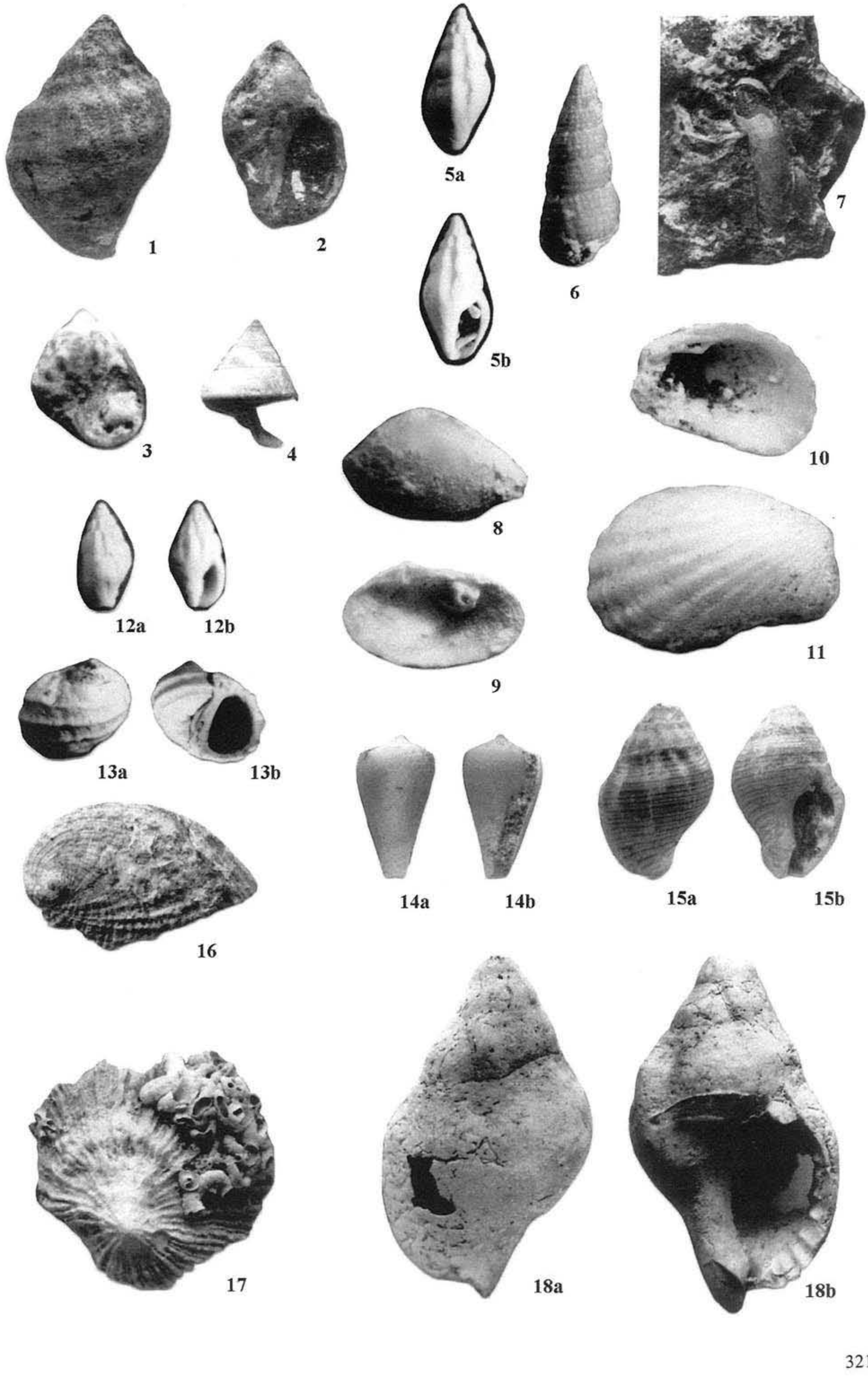
14a-b - *Conus ermineus* Börn, 1778, back and aperture views. (x 1,5)

15a-b - *Cantharus variegatus* (Gray, 1839), back and aperture views. (x1,5)

16 - *Haliotis tuberculata* Linné, 1758, external view. (x 1,5)

17 - *Patella ulyssiponensis* Gmelin, 1791, fragment of a large shell with a colony of *Vermetus* sp. (x1,5)

18a-b - *Charonia lampas* (Linné, 1758), back and aperture views of young specimen. (x 1)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