

Local disappearance of bivalves in the Azores during the last glaciation

SÉRGIO P. ÁVILA,^{1,2,3*} PATRÍCIA MADEIRA,^{1,3} C. MARQUES DA SILVA,⁴ MÁRIO CACHÃO,⁴ BERNARD LANDAU,⁴ RUI QUARTAU⁵ and A. M. DE FRIAS MARTINS^{1,2,6}

¹ Departamento de Biologia, Universidade dos Açores, Ponta Delgada, Azores, Portugal

² Centro do IMAR da Universidade dos Açores, Horta, Azores, Portugal

³ MPB – Marine Palaeobiogeography Working Group of the University of the Azores, Rua da Mãe de Deus, Ponta Delgada, Azores, Portugal

⁴ Departamento e Centro de Geologia, Faculdade de Ciências, Universidade de Lisboa, Lisbon, Portugal

⁵ Departamento de Geologia Marinha, INETI, Estrada da Portela, Zambujal, Alfragide, Portugal

⁶ CIBIO Centro de Investigação em Recursos Genéticos – Pólo Açores, Departamento de Biologia, Universidade dos Açores, Ponta Delgada, Azores, Portugal

Ávila, S. P., Madeira, P., Marques da Silva, C., Cachão, M., Landau, B., Quartau, R., and de Frias Martins, A. M. Local disappearance of bivalves in the Azores during the last glaciation. *J. Quaternary Sci.*, (2008). ISSN 0267-8179.

Received 7 August 2007; Accepted 6 December 2007

ABSTRACT: The Pleistocene (Eemian) outcrops of Lagoinhas and Prainha, located at Santa Maria Island (Azores), were investigated and their fossil mollusc content reported. These studies revealed that the last glaciation affected two groups of molluscs: the ‘warm-guest’ gastropods with West African or Caribbean affinities (e.g. *Conus* spp., *Cantharus variegatus*, *Bulla amygdala*, *Trachypollia nodulosa*) and shallow bivalve species mainly associated with sandy habitats (*Ensis minor*, *Lucinella divaricata*, and probably *Laevicardium crassum*). In this paper we focus on this group of bivalves, which has since locally disappeared from the Azores. We relate the local disappearance of these bivalves in the Azores with the lack of sand in the shelf. The specific characteristics of the Santa Maria shelf combined with the sea-level drop during the Weichselian prevented deposition of the lowstand deposits and permitted erosion of the previous ones, leaving the shelf without a sediment cover. Copyright © 2008 John Wiley & Sons, Ltd.

KEYWORDS: Azores; Pleistocene (Eemian); bivalves; sea level; local disappearance.



Introduction

The volcanic mid-Atlantic islands of the Azores originated from a hot-spot associated with the seafloor spreading of the Mid-Atlantic ridge (Mitchell-Thomé, 1976). Santa Maria Island, located in the eastern group of islands of the Azores archipelago (São Miguel, Santa Maria and the Formigas Islets), is the oldest, upper Miocene in age (about 8 M a) (Abdel-Monem *et al.*, 1975; Feraud *et al.*, 1980) (Fig. 1A). Further details on the stratigraphy and geochronology of the island are provided by Serralheiro and Madeira (1990), Salgueiro (1991) and Serralheiro (2003).

Eustatic sea-level oscillations associated with the Pleistocene glacial–interglacial climatic cycles gave rise to extensive wave-cut platforms at 5–10, 15–40, 50–70, 80–120 and 140–160 m (Zbyszewsky and Ferreira, 1962; Madeira, 1981; Serralheiro and Madeira, 1990). No ages are known for the majority of these platforms.

Marine fossils are rare in the Azores, being known only from Santa Maria and Formigas Islands. Most previous studies have dealt with the rich fossiliferous beds of upper Miocene to Pliocene age (Mayer, 1864; Cotter, 1888–1892; Zbyszewsky and Ferreira, 1962). In Santa Maria, however, there are several scattered fossiliferous outcrops of Pleistocene (Eemian) age. The outcrops of Lagoinhas (northern shore) and Prainha (southern shore of Santa Maria) (Fig. 1B) are the best representatives of such deposits (García-Talavera, 1990; Callapez and Soares, 2000). Ávila *et al.* (2002) established the stratigraphy of these deposits and Ávila *et al.* (2007, submitted) revised the marine fossil malacofauna, with a total of 102 species/taxa reported, mostly still found in nearby present-day shores (Ávila, 2000a, 2003, 2005; Ávila *et al.*, 1998, 2000a,b). Those not found nowadays, however, were shown to be more interesting in terms of biogeography, since they represent direct evidence that Pleistocene environmental changes affected the Azores marine molluscan faunas. Ávila *et al.* (2008) recently dated the lower unit of the Prainha outcrop (correlative of the Lagoinhas outcrop) and the ages of fossils correspond to the Eemian Interglacial (roughly equivalent to Marine Isotope Substage 5e), a period that is observed

*Correspondence to: S. P. Ávila, Departamento de Biologia, Universidade dos Açores, 9501-801 Ponta Delgada, Azores, Portugal.
E-mail: avila@notes.uac.pt

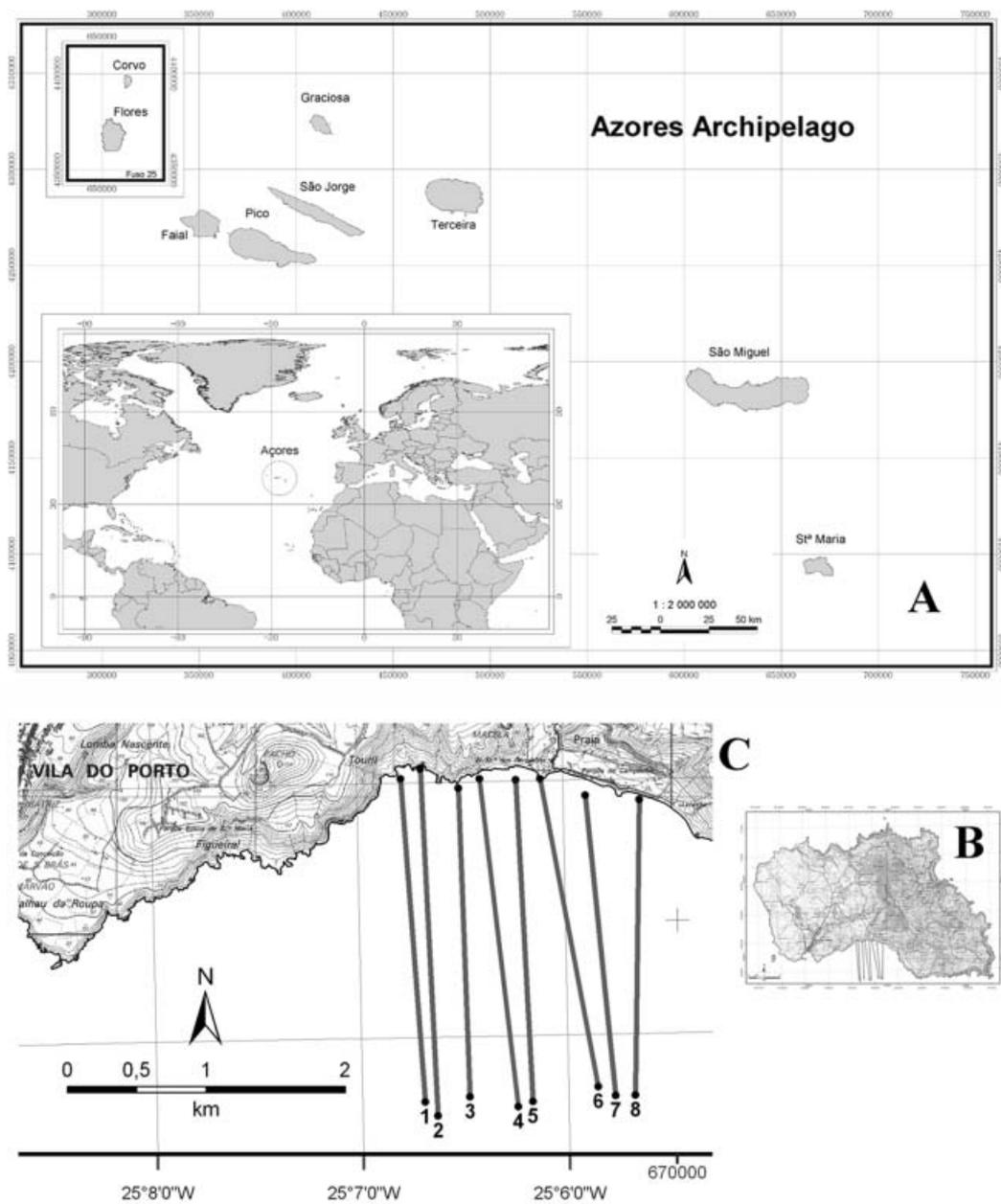


Figure 1 Geographical location of Santa Maria Island in the Azores archipelago (A), location of the sampling sites, Prainha and Lagoinhas (B), and location of the transects performed at Prainha (C). © Secção de Geografia, Universidade dos Açores. Reproduced with permission

to have experienced a milder climate of at least 2°C higher sea surface temperatures (SST) in the North Atlantic during the climatic optimum, around 125 k a (Cortijo *et al.*, 1999; Muhs *et al.*, 2002; Rasmussen *et al.*, 2003). This caused a northward shift of the eastern Atlantic marine faunal provinces. Obviously the warmest taxa present in the Eemian deposits of Prainha and Lagoinhas such as the ‘warm-guest’ gastropods with West African or Caribbean affinities (e.g. *Conus* spp., *Cantharus variegatus*, *Bulla amygdala*, *Trachypollia nodulosa*) (Ávila *et al.*, 2002), should have experienced local disappearance during the Weichselian and none of these species has returned in the Holocene, probably because of the (until now) low temperatures.

Given the age and the isolation of the Azores archipelago, its degree of marine endemism is surprisingly low, with the sole exception of the molluscs, with about 10% of endemic species (Ávila, 2000a,b, 2005). Briggs (1966) hypothesised that ‘the recent effects of sea-level and climatic changes associated with

ice ages probably account for the lower level of endemism [of the Azores marine fauna] than the rest of Macaronesia’. He also claimed that the probable cause of the lack of endemism was the ‘severe drops in Pleistocene sea surface temperature that may have wiped out the older fauna. If the Azores have been repopulated within the past 12 000 years, very little evolutionary change could be expected’ (Briggs, 1974: 208). This view is still held by most of the few authors that have approached the subject (e.g. Santos *et al.*, 1997, for the marine fish, and Prud’homme van Reine, 1988, for seaweeds).

According to García-Talavera (1990) and Callapez and Soares (2000), the species of molluscs most affected by the last glaciation were ‘warm-guest’ gastropods with West African or Caribbean affinities such as *Conus* spp., *Cantharus variegatus* (Gray, 1839), *Bulla amygdala* (= *B. mabilleyi* Locard, 1896), *Trachypollia nodulosa* (C. B. Adams, 1845) that locally disappeared in the Azores. However, Ávila *et al.* (2002) and Ávila (2005) found further evidence for a second group of

disappeared species. This group includes several bivalves usually living at shallow depths and restricted to fine sand or muddy habitats such as *Ensis minor* (Chenu, 1843) and *Lucinella divaricata* (Linnaeus, 1758).

This paper aims to suggest an explanation for the local disappearance of these bivalves in the Azores.

Materials and methods

Ávila (2005) and co-workers (Ávila *et al.*, 2002, 2007, submitted) produced a checklist of the mollusc taxa found at Lagoinhas and Prainha Eemian outcrops (Ávila *et al.*, 2008c) (Santa Maria Island) with their status in Azores. The bivalve information was selected and merged with data obtained from checklists of living shallow-water marine molluscs of the Azores (Ávila, 1997, 2005; Ávila and Azevedo, 1997; Ávila *et al.*, 1998, 2000a,b, 2004) and the type of substrate and bathymetric zonation where the bivalve species usually live was acquired from Tebble (1966), von Cosel (1995), Morton (1995), Rodríguez and Sánchez (1997), Macedo *et al.* (1999), Salas and Gofas (1998) and Krylova (2006), and is presented on Table 1.

As no recent detailed charts of the bottoms of Prainha were available, we have made eight vertical profiles of the present-day shores of Prainha (Fig. 1C). These transects, with a direction N–S, ranged between 2.3 and 2.6 km long, and were made to depths of over 200 m. Depths were measured by boat, with an automatic sounding, every 100 m. The average slope was measured between selected range depths, related to the bottom topography of the island: between 0–40 m and 40–300 m (transects 1–4), and between 0–80 m and 80–300 m (transects 5–8) (Fig. 2).

Results

Bivalve molluscs show a strong bathymetric ecological dependence. To obtain insight into the possibilities of surviving a drastic drop in sea level, the topography of the coastal slopes near the Eemian outcrop of Prainha was investigated. The eight offshore transects (Fig. 2) show that the coastal slope can be roughly subdivided into two parts, each with a different gradient. In the near offshore area between 0 and –40 m (transects 1–4), the average slope is 2.1–2.8%; between 0 and 80 m (transects 5–8), the average slope is 3.8–4.3%. The average gradient between –40 and –300 m is 36–44.2% (transects 1–4), and between –80 and –300 m it is 36.2–47.6% (transects 5–8). Other transects performed in different places along the shores of Santa Maria Island (not shown) revealed similar results.

Discussion

The susceptibility of species to extinction or local disappearance is dependent on a series of factors such as competition, density, resistance to temperature variations, larval development and dispersal ability (for a review, see references in Ávila, 2005). For the dispersal ability of marine molluscs, the duration of the free-swimming larval stage is also a significant factor

(Scheltema, 1986). There is no information on the larval biology of *Ensis minor* in particular, but it is known that the duration of the free-swimming larval phase of other *Ensis* species is about 2 weeks, and this is probably the case also for *Ensis minor* (von Cosel, pers. comm.). *Ensis minor* is a conspicuous species in the sandy beds of the Prainha outcrops (unit B₁ of Ávila *et al.*, 2002) but it is less common in Lagoinhas deposits (Fig. 3). Today, this species has a wide geographical distribution along the Atlantic European shores: the British North Sea coast from the east coast of Scotland (Firth of Tay mouth) to north Yorkshire, southern England, the Netherlands and the Channel; the northwestern part of Wales to northern Morocco and throughout the Mediterranean. It is not present in Scandinavia or the eastern and southeastern North Sea (von Cosel, pers. comm.), nor in Belgium (Backeljau, 1986).

During the Weichselian, between 60 000 and 14 000 a BP, sea surface temperatures in the region of the Azores ranged from 15 to 8°C (values derived from stable isotope measurements on foraminiferal tests in core SU90-08, 40° N, 30° W, 3080 m depth) (Cortijo *et al.*, 1997, 1999; Vidal *et al.*, 1997). These temperatures are similar to those recorded today at British North Sea coast latitudes, where *Ensis minor* presently occurs (von Cosel, pers. comm.). Thus the temperature interval that these bivalves tolerate nowadays suggests that *Ensis minor* was able to survive the last glaciation in the Azores. However, that was not the case, and *Ensis minor* (along with other bivalves like *Lucinella divaricata* and probably *Laevicardium crassum*) disappeared from the Azores. Why?

The present-day offshore of Prainha has an average slope of 2–4% in the shallower areas (0–80 m) and 36–48% (–80 to –300 m) and is mainly covered by sand, with some boulders interspersed. Basaltic dykes are common down to depths of 5–10 m. Relative to present sea level, below 40–80 m depths (depending on the bottom topography of the island), near-shore slope during the last glacial episode was much steeper than for the upper 40–80 m nowadays. During the last glaciation, with sea level progressively lowering, the shallow-marine bivalves living in fine sand or mud could perfectly cope with an average slope of 2–4%. They basically retreated along the coastal slope, following the progressive sea-level lowering, until the critical depth of 40–80 m was reached. Below these depths, a major problem arises.

Volcanic islands are unique among the offshore islands because their shelves are wave-cut features superimposed on the volcanic slopes (Menard, 1983). Around continental margins, stratigraphy develops from a complex interplay of sediment supplied from the continent, transport by currents, shoreline processes and erosion during lowered sea level (Galloway and Hodbay, 1996; Johnson and Baldwin, 1986; Southard and Stanley, 1976; Thorne and Swift, 1991). Despite the knowledge acquired from continental shelves, the sediment stratigraphy of volcanic island shelves is yet poorly known. There are, however, a number of reasons to expect island stratigraphy to be different. For example, the shelf is narrower and steeper than continental shelves, so accommodation space for deposition and residence time is likely to be quite different. In the case of volcanic islands like the Azores, sediment supply to the shelf is mostly from marine erosion during sea-level highstands and volcanic-related processes. Since Santa Maria has been geologically inactive in the last 2 M a (Serralheiro, 2003), marine erosion is the only process we can account for. At the same time, a low rate of subsidence or most likely uplift and a narrow and steep shelf creates little space for accommodation of sediments. When the sea drops below the level of the present highstand, sediment supply becomes sparse due to lack of major river systems, reduced precipitation in glacial periods and low subaerial erosion of the palaeomarine

Table 1 Bivalve species alphabetically ordered according to family, presently reported living in the Azores by Ávila (2005) as well as having locally disappeared from the archipelago (Ávila *et al.*, submitted). Habitat and bathymetric range taken from Tebble (1966), von Cosel (1995), Morton (1995), Macedo *et al.* (1999), Rodríguez and Sánchez, (1997), Salas and Gofas (1998) and Krylova (2006). Fossil record data (Eemian) according to Ávila *et al.* (2002, submitted) and Ávila (2005)

Species	Family	Habitat	Fossil record	Bathymetric range (m)	Local disappearance
<i>Anomia ephippium</i> Linnaeus, 1758	Anomiidae	Rocky substrate		0–150	
<i>Pododesmus patelliformis</i> (Linnaeus, 1761)	Anomiidae	Rocky substrate		0–1400	
<i>Arca noae</i> Linnaeus, 1758	Arcidae	Rocky substrate		0–200	
<i>Arca tetragona</i> Poli, 1795	Arcidae	Rocky substrate	Yes	0–2700	No
<i>Astarte cf. sulcata</i> (da Costa, 1778)	Astartidae	Sand, mud		4–2525	
<i>Acanthocardia aculeata</i> (Linnaeus, 1758)	Cardiidae	Mud, sand		?5–125	
<i>Laevicardium crassum</i> (Gmelin, 1791)	Cardiidae	Gravel, sand, mud	Yes	0–2195	Yes (?)
<i>Papillicardium papillosum</i> (Poli, 1795)	Cardiidae	Gravel	Yes	0–60(0–1494)	No
<i>Parvicardium exiguum</i> (Gmelin, 1791)	Cardiidae	Gravel, sand, mud		0–55	
<i>Parvicardium cf. minimum</i> (Philippi, 1836)	Cardiidae	?		4–2700	
<i>Parvicardium vroomi</i> van Aartsen, Moolenbeek and Gittenberger, 1984	Cardiidae	Rocky substrate	Yes	Littoral	No
<i>Cardita calyculata</i> (Linnaeus, 1758)	Carditidae	Rocky substrate	Yes	0–200	No
<i>Pseudochama gryphina</i> (Lamarck, 1819)	Chamidae	Rocky substrate		0–60	
<i>Chama gryphoides</i> Linnaeus, 1758	Chamidae	Rocky substrate		40–1250	
<i>Cardiomya costellata</i> (Deshayes, 1835)	Cuspidariidae	Sand, mud		5–2000	
<i>Neopycnodonte cochlear</i> (Poli, 1795)	Gryphaeidae	Rocky substrate	Yes	24–1262	No
<i>Hiattella arctica</i> (Linnaeus, 1767)	Hiattellidae	Rocky substrate		0–2190?	
<i>Kellia suborbicularis</i> (Montagu, 1803)	Kelliidae	Rocky substrate, sand, mud		0–120	
<i>Lasaea adansonii</i> (Gmelin, 1791)	Limidae	Rocky substrate, algae		0–1360	
<i>Lima lima</i> (Linnaeus, 1758)	Limidae	Rocky substrate	Yes	?5–1171	No
<i>Limaria hians</i> (Gmelin, 1791)	Limidae	Rocky substrate, sand, detritic bottoms	0–450		
<i>Limatula subauriculata</i> (Montagu, 1808).	Limidae	Detritic bottoms, sand, mud		4–3191	
<i>Limea loscombii</i> (G. W. Sowerby I, 1824)	Limidae	Detritic bottoms, sand, mud		10–2704	
<i>Loripes lacteus</i> Linnaeus, 1758	Lucinidae	Sand, mud		0–150	
<i>Lucinella divaricata</i> (Linnaeus, 1758)	Lucinidae	Sand, mud	Yes	?–60	Yes
<i>Lucinoma borealis</i> (Linnaeus, 1767)	Lucinidae	Gravel, sand, mud		0–1500	
<i>Montacuta ferruginosa</i> (Montagu, 1803)	Montacutidae	Commensal of <i>Echinocardium cordatum</i>	?5–2489		
<i>Mysella bidentata</i> (Montagu, 1803)	Montacutidae	Rocky substrate		0–2500	
<i>Planctomya nilae</i> Van Aartsen and Engl, 2001	Mytilidae	?		?	
<i>Crenella arenaria</i> Monterosato, 1875	Mytilidae	?		?	
<i>Dacrydium hyalinum</i> Monterosato, 1875	Mytilidae	?		High depths	
<i>Gregariella semigranata</i> (Reeve, 1858)	Mytilidae	Rocky substrate, coralline algae		Intertidal–30	
<i>Modiolus adriaticus</i> (Lamarck, 1819)	Mytilidae	Mud		0–75	
<i>Myioforceps aristatus</i> (Dillwyn, 1817)	Mytilidae	Soft substrate		0–100	Yes
<i>Rhomboidella prideauxi</i> (Leach, 1815)	Mytilidae	Sand	Yes	0–high depths	
<i>Neolepton cancellatum</i> Salas and Gofas, 1998	Noeptoionidae	Rocky substrate		0–20	
<i>Striarca lactea</i> (Linnaeus, 1758)	Noeptoionidae	Rocky substrate	Yes	0–130	No
<i>Aequipecten commutatus</i> (Monterosato, 1875)	Pectinidae	Rocky substrate, sand, mud, coralligenous bottoms	30–2700		
<i>Aequipecten opercularis</i> (Linnaeus, 1758)	Pectinidae	Sand, mud, detritic bottoms		4–2660	
<i>Chlamys bruei</i> (Payraudeau, 1826)	Pectinidae	Sand, mud		30–2500	
<i>Chlamys flexuosa</i> (Poli, 1795)	Pectinidae	Sand, mud, detritic bottoms		1–2000	
<i>Chlamys varia</i> (Linnaeus, 1758)	Pectinidae	Rocky substrate, sand, mud		?3–1400	
<i>Crassadoma multisriata</i> (Poli, 1795)	Pectinidae	Gravel, sand		?–150	
<i>Crassadoma pusio</i> (Linnaeus, 1758)	Pectinidae	Rocky substrate	Yes	?–2300	No

<i>Cyclopecten</i> cf. <i>hoskynsi</i> (Forbes, 1844)	Pectinidae	Sand	Yes	73–2064	No
<i>Nodipecten corallinoides</i> (d'Orbigny, 1840)	Pectinidae	Rocky substrate, sand, mud	Yes	6–1250	No
<i>Palliolium incomparabile</i> (Risso, 1826)	Pectinidae	Sand, mud	Yes	?10–2000	Yes
<i>Ensis minor</i> (Chenu, 1843)	Pharidae	Sand	Yes	0–10	No
<i>Pinna rudis</i> Linnaeus, 1758	Pinnidae	Gravel, sand, mud	Yes	0–40	No
<i>Gari costulata</i> (Turton, 1822)	Psammobiidae	Sand, mud		?–55	
<i>Pinctada radiata</i> (Leach, 1814)	Pteriidae	Rocky substrate		1–190	
<i>Pteria hirundo</i> (Linnaeus, 1758)	Pteriidae	Mud, sand, hard substrate		15–1500	
<i>Abra alba</i> (W. Wood, 1802)	Semelidae	Sand, mud, gravel		?5–65	
<i>Ervilia castanea</i> (Montagu, 1803)	Semelidae	Sand	Yes	10–1800	No
<i>Solemya togata</i> (Poli, 1795)	Solemyidae	Sand, mud		0–30	
<i>Spondylus senegalensis</i> Schreibers, 1793	Spondyliidae	Rocky substrate		5–30	
<i>Basterotia clancula</i> von Cosel, 1995	Sportellidae	Sand, gravel (?)		1–20	
<i>Arcopagia balaustina</i> (Linnaeus, 1758)	Tellinidae	Sand, mud, gravel		0–750	
<i>Gastrana</i> cf. <i>fragilis</i> (Linnaeus, 1758)	Tellinidae	Mud		Intertidal	
<i>Tellina donacina</i> Linnaeus, 1758	Tellinidae	Sand, mud		0–800	
<i>Tellina incarnata</i> Linnaeus, 1758	Tellinidae	Gravel, mud, sand	Yes	0–85	No
<i>Tellina pygmaea</i> Löven, 1846	Tellinidae	Sand		0–150	
<i>Nototeredo norvegica</i> (Spengler, 1792)	Teredinidae	Timber		0–700	
<i>Psiloteredo megotara</i> (Hanley in Forbes and Hanley, 1848)	Teredinidae	Floating timber		Sea surface	
<i>Thracia corbuloides</i> Deshayes, 1830	Thraciidae	Sand, gravel		?–high depths	
<i>Thracia papyracea</i> (Poli, 1791)	Thraciidae	Sand, mud, gravel		0–50	
<i>Thracia</i> cf. <i>villosuscula</i> (Macgillivray, 1827)	Thraciidae	Sand, mud, gravel		0–50	
<i>Diplodonta apicalis</i> Philippi, 1836	Ungulinidae	Sand, mud, gravel		15–500	
<i>Callista chione</i> (Linnaeus, 1758)	Veneridae	Sand, mud		?5–200	
<i>Globivenus effossa</i> (Philippi, 1836)	Veneridae	Sand		9–1139	
<i>Gouldia minima</i> (Montagu, 1803)	Veneridae	Gravel		0–200	
<i>Irus irus</i> (Linnaeus, 1758)	Veneridae	Sand, mud		0–100	
<i>Paphia aurea</i> (Gmelin, 1791)	Veneridae	Rocky substrate		0–100	
<i>Pitar rudis</i> (Poli, 1795)	Veneridae	Sand, mud, gravel		0–36	
<i>Timoclea ovata</i> (Pennant, 1777)	Veneridae	Gravel, sand		0–80	
<i>Venerupis pullastra</i> (Montagu, 1803)	Veneridae	Gravel, sand, mud		4–2489	
<i>Venus casina</i> Linnaeus, 1758	Veneridae	Sand, mud, gravel		0–40	
<i>Venus nux</i> Gmelin, 1791	Veneridae	Gravel, sand, mud		5–200	
<i>Xylophaga dorsalis</i> (Turton, 1819)	Xylophagidae	Sand, mud		?5–700	
		Timber		0–2700	

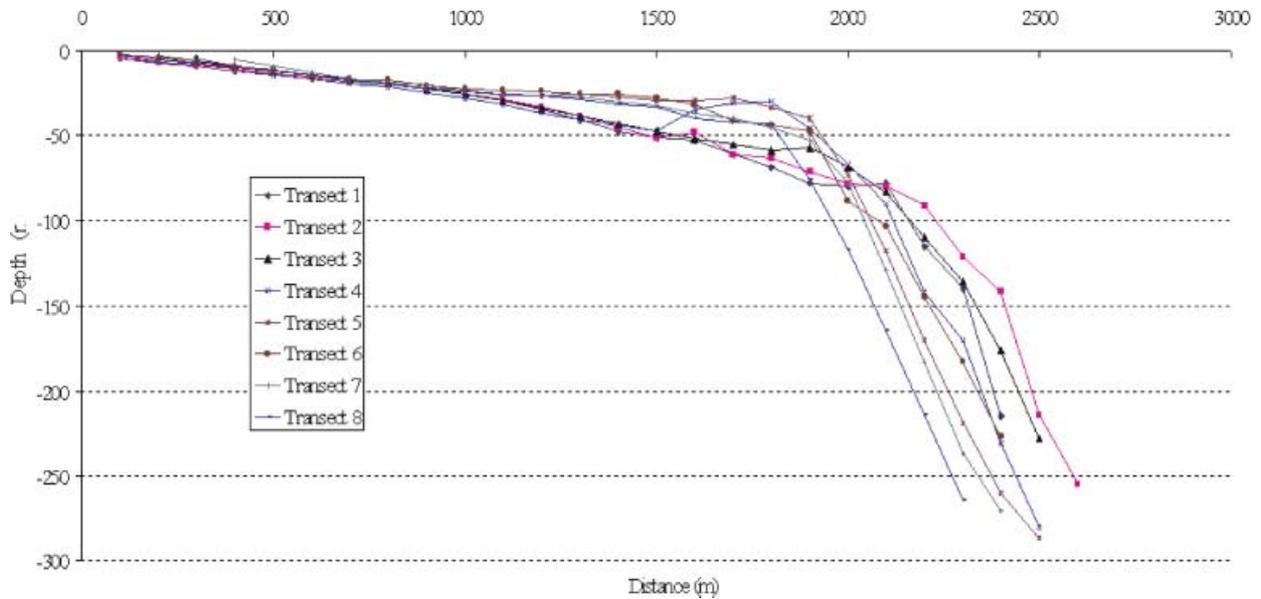


Figure 2 Vertical profile of the eight transects done on the shores of Prainha (Santa Maria Island, Azores). This figure is available in colour online at www.interscience.wiley.com/journal/jqs

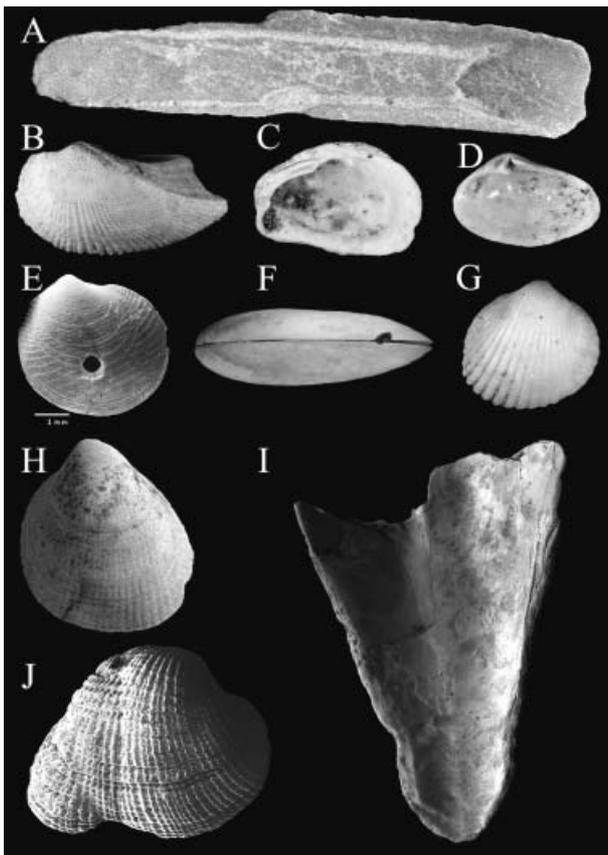


Figure 3 Species of bivalves collected in the Pleistocene outcrops of Prainha and Lagoinhas (Santa Maria Island, Azores). (A) *Ensis minor* DBUA-F/42-2 (9.78 × 1.92 cm); (B) *Arca tetragona* DBUA-F 81/44-13 (1.39 × 0.78 cm); (C) *Cardita calyculata* DBUA-F 80/44-19 (1.09 × 0.75 cm); (D) *Ervilia castanea* DBUA-F 61/44-8; (E) *Lucinella divaricata* DBUA-F 2/140-2-21; (F) *Myoforceps aristatus* DBUA-F 127/41-20 (1.78 cm long); (G) *Papillicardium papillosum* DBUA-F 61 (0.82 × 0.90 cm); (H) *Laevicardium crassum* DBUA-F/42-16 (5.49 × 4.86 cm); (I) *Pinna rudis* DBUA-F 147 (9.60 × 6.60 cm); (J) (?) *Striarca lactea* DBUA-F 137/160-1/63 (teratological specimen)

cliffs left behind. Consequently, during sea-level falls, the lack of sediment supply prevents the formation of large lowstand deposits. On the other hand, when the base level falls below the shelf break (which has always been the case) the preservation potential of the falling stage strata that accumulates on the shelf is very slow, making the Low Stand System Tract very reduced or non-existent (Catuneanu, 2002). Furthermore, the presence of a narrow and steeper insular margin may enable faster transport of sediment offshore, with regressive ravinements sweeping away the highstand sediments from the shelf, leaving the shelf devoid of sediments.

The published biological information on the sand environments of the Azores is very scarce (Morton, 1990; Morton *et al.*, 1998) and the geological information on this subject is restricted to Borges (2003). As in other places, in the Azores and in the present times, winter storms usually remove the sand from the littoral strip of Santa Maria, leaving sand-stripped beaches (Komar, 1998; Short, 1999). These beaches are again refurbished with sand during the next summer (Borges, 2003). When sea level drops and reaches the shelf break below 40–80 m (36–48%; Fig. 2) it probably became physically impossible to keep the sand in the littoral of Prainha. While winter storms continued to remove sand, a fair-weather regime could no longer restore it because it had been lost to the island slopes (Shepard, 1973). As a result of this tendency, sand beaches became progressively poorer and depleted of sand.

The sea-level oscillation from Thompson and Goldstein (2006) is the more recent curve for the last 240 k based on corals (Fig. 4). It also uses a new approach to correct many of the problems associated with imprecise conventional U–Th ages, producing sea-level reconstructions with improved accuracy and resolution (millennium step) that confidently correlates with SPECMAP, the benchmark of $\delta^{18}\text{O}$ records (Thompson and Goldstein, 2006). Assuming a maximum lowering of the sea level between 120 and 130 m in relation to the present sea level, according to the latest estimates (Wilson *et al.*, 2000; Thompson and Goldstein, 2006) for this global event, those species living in the first 30 m of water and associated with a sandy or muddy habitat must have been severely affected by this sea-level change. Species with a wider bathymetric zonation or associated with a different habitat (e.g. gravel or rocky bottoms) were not affected by the lack of sand or

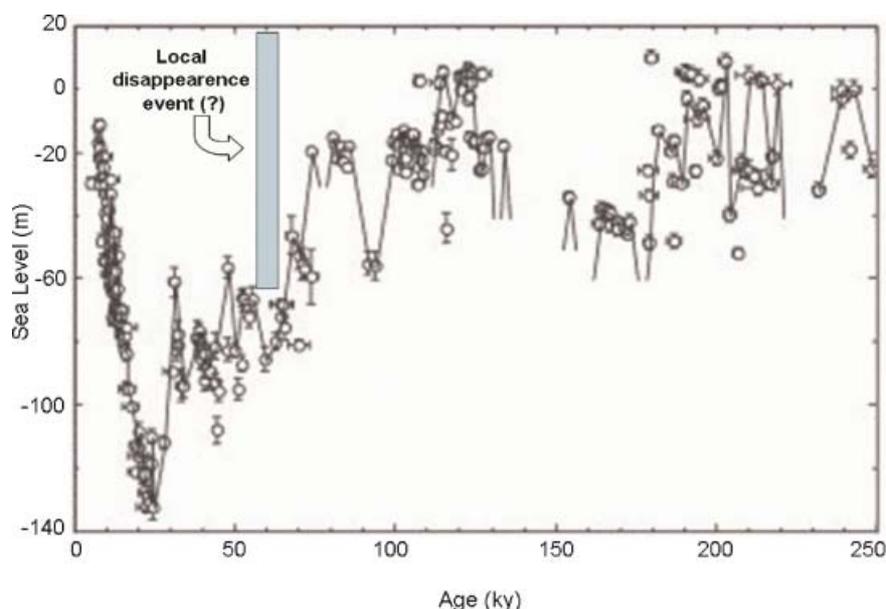


Figure 4 Global sea-level curve reconstruction (adapted from Thompson and Goldstein, 2006). Superimposed is the probable local disappearance event (around 60 k a, MIS 4). This figure is available in colour online at www.interscience.wiley.com/journal/jqs

muddy habitats. In the case of Santa Maria Island, the cross-shore profiles revealed a shelf-break between 40 and 80 m water depth (Fig. 3). Therefore, the sea-level drop at approximately 85 m revealed by the curve of Thompson and Goldstein (2006) around 60 k a (Fig. 4) can explain the drain of sand across the shelf-break, leaving the shelf uncovered, and this reasoning has two logical corollaries:

1. The species most affected by the lowering of the sea level were those bivalves living in the first 30–50 m depth and solely associated with fine sand or muddy habitats. They locally disappeared.
2. Besides bivalves living in littoral sandy/muddy environments, other species with similar environmental requirements, namely some echinoderms and amphipods, should have suffered severely from the lack of sand. For instance, species such as the irregular sea urchin *Brissus unicolor* (Leske, 1778) or the heart-urchin *Echinocardium cordatum* (Pennant, 1777), presently living in the Azores in fine sandy beaches between 10 and 30 m depth, must have either locally disappeared from these islands or, at least, became very rare, passing through a drastic reduction of the population size (bottleneck effect). It is predicted that the genetic variability of the Azorean populations of these species should be lower than continental European ones, either due to the bottlenecking process or to a recent colonisation event, and we will test this hypothesis in the near future.

Table 1 shows the 82 bivalve species that are presently recorded from the Azores. It also contains information on the substrate and bathymetric zonation of these species. Two

species were removed from the following analysis: the recently introduced species *Ruditapes decussatus* (Linnaeus, 1758), and *Mytilus edulis* Linnaeus, 1758, a species recorded several times, mainly in drifting objects, but without resident or viable populations in the Azores (for further information on these species see Ávila *et al.*, 2000a, and Cardigos *et al.*, 2006). Of the remaining 80 species, three are timber-borer bivalves – *Psiloterredo megotara* (Hanley in Forbes and Hanley, 1848), *Nototerredo norvegica* (Spengler, 1792) and *Xylophaga dorsalis* (Turton, 1819) – and were also removed. Of the 77 species left, only 13 are restricted to the first 50 m of water and, of these, only *Ensis minor* is solely associated with fine sand habitats (see Table 1).

Comparing the species presently occurring in the Azores with those that locally disappeared from this area, probably around 60 k a, during MIS 4 (see Fig. 4), in respect to habitat type, we see that of the four species recorded as fossils at Prainha and now presumably not present in the Azores (there is some doubt concerning the local disappearance of *Laevicardium crassum*; Ávila *et al.*, 2002) three species live in sandy habitats, two may live in muddy habitats and one can live also in gravel bottoms (Tables 1 and 2).

From the 16 Eemian bivalves recorded from Santa Maria Island by Ávila (2005) and co-workers (Ávila *et al.*, 2002, submitted), six species are associated with sandy bottoms. Of these, two locally disappeared (*Ensis minor* and *Lucinella divaricata*) and the same probably happened with *Laevicardium crassum* (Table 2).

A given species may live in more than one habitat, and this may have been responsible for the differential local disappearance that has occurred at Prainha. Several of the species

Table 2 Habitat preference of bivalve species occurring in the present and in the Pleistocene (Eemian) of the Azores as well as those that locally disappeared during the last glaciation (data from Ávila *et al.*, 2002, submitted; Ávila, 2005)

	Total	Fine Sand	Rocky shores	Gravel	Mud	Soft substrates (calcareous algae; biostromic crust)	Detritic bottoms	Timber
Present	78	45	26	19	36	0	5	3
Fossil record	16	7	7	4	5	1	0	0
Locally disappeared	3–4(?)	2–3	0	1	2	1	0	0

may have survived the drop in sea level below the 80 m depth threshold, by living in sand or mud pockets, or, most probably, in gravel bottoms. A detailed analysis of Table 1 shows that other bivalve species, not yet found in the fossil record at Prainha or at Lagoinhas, but living today in the Azores, may have locally disappeared (and have recently recolonised the Azores) or passed by a bottlenecking process. Examples are *Solemya togata* (Poli, 1795), *Modiolus adriaticus* (Lamarck, 1819), *Gastrana cf. fragilis* (Linnaeus, 1758) and *Gari costulata* (Turton, 1822), all inhabiting sandy or muddy bottoms from the intertidal down to 55 m depth (Table 1). With the present data we cannot discard the alternative hypothesis, that these species could be new arrivals, first appearing during the Holocene or shortly before, during Termination 1.

Other bivalves, like *Abra alba* (W. Wood, 1802), *Basterotia clancula* von Cosel, 1995, *Paphia aurea* (Gmelin, 1791), *Venerupis pullastra* (Montagu, 1803), *Thracia papyracea* (Poli, 1791) and *Thracia cf. villosiuscula* (Macgillivray, 1827), inhabiting depths (1–65 m; see Table 1) that were certainly affected by the drop in sea level, benefited from living also in gravel bottoms, and therefore with less susceptibility of local disappearance than those living solely in fine sand or mud.

Conclusions

The fauna and flora that inhabit the intertidal zone of sandy beaches are usually impoverished in relation to those of rocky shores. Morton *et al.* (1998) explored in detail the intertidal zone of the few sandy beaches that, nowadays in the Azores, have some expression (e.g. Praia Formosa and Praia de São Lourenço, Santa Maria Island; Praia das Milícias and Praia Pequena do Pópulo, São Miguel Island; Praia da Vitória, Terceira Island; Praia de Porto Pim and Praia do Almoxarife, Faial Island) and concluded that they are almost devoid of animal life in the intertidal zone, with the exception of the sandhopper amphipod *Talitrus saltator* (Montagu, 1808) and the beachflea amphipod *Orchestia gammarellus* (Pallas, 1766). The authors postulated that this pattern was probably due to the isolation of the Azores archipelago or to the oligotrophic nature of the islands, as most of the species living in beaches are dependent on the allochthonous supply of nutrients from the sea (Morton *et al.*, 1998).

In this paper, we provide an explanation why shallow endobenthonic bivalves associated with sand and present in the Azores during the Eemian have locally disappeared from these islands during the last glaciation, which simultaneously explains the very low biodiversity of the present sandy beaches of the Azores. The main reason for the local disappearance of the shallow bivalves predominantly living in fine sand was the lack of suitable habitat (sand) related to the sea-level drop during the last glaciation. This sea-level drop, coupled with the specific characteristics of the Santa Maria shelf, enhanced the erosion of the previous System Tracts and non-deposition of lowstand deposits. Consequently, other species also living in the Eemian beaches of Santa Maria Island (a warmer interglacial than the present one) must also have been affected. Moreover, this process must have been very widespread and it probably occurred in previous glacial/interglacial cycles (e.g. MIS 7, 9 and 11).

It may be expected that species that locally disappeared did not all reappear in the cooler Holocene, as recolonisation in oceanic islands is partly a matter of chance. The very short interval since the end of Termination 1 and the beginning of the

Holocene may be the most plausible explanation for the almost life-devoid sandy beaches in the Azores in present times.

References

- Abdel-Monem AA, Fernandez LA, Boone GM. 1975. K–Ar ages from the eastern Azores group (Santa Maria, São Miguel and the Formigas Islands). *Lithos* **8**: 247–254.
- Ávila SP. 1997. Moluscos marinhos recolhidos no Banco 'D. João de Castro'. *Açoreana* **8**: 331–332.
- Ávila SP. 2000a. Shallow-water marine molluscs of the Azores: biogeographical relationships. *Arquipélago, Life and Marine Sciences* Suppl 2 (Part A): 99–131.
- Ávila SP. 2000b. The shallow-water Rissoidae (Mollusca, Gastropoda) of the Azores and some aspects of their ecology. *Iberus* **18**(2): 51–76.
- Ávila SP. 2003. The littoral molluscs (Gastropoda, Bivalvia and Polyplacophora) of São Vicente, Capelas (São Miguel Island, Azores): ecology and biological associations to algae. *Iberus* **21**: 11–33.
- Ávila SP. 2005. *Processos e Padrões de Dispersão e Colonização nos Rissoidae (Mollusca: Gastropoda) dos Açores*. PhD thesis, Universidade dos Açores, Ponta Delgada.
- Ávila SP, Azevedo JMN. 1997. Shallow-water molluscs from the Formigas islets, Azores, collected during the 'Santa Maria e Formigas 1990' scientific expedition. *Açoreana* **8**: 323–330.
- Ávila SP, Azevedo JMN, Gonçalves JM, Fontes J, Cardigos F. 1998. Checklist of the shallow-water marine molluscs of the Azores. 1. Pico, Faial, Flores and Corvo islands. *Açoreana* **8**: 487–523.
- Ávila SP, Azevedo JMN, Gonçalves JM, Fontes J, Cardigos F. 2000a. Checklist of the shallow-water marine molluscs of the Azores. 2. São Miguel island. *Açoreana* **9**: 139–173.
- Ávila SP, Fontes J, Tempera F, Cardigos F. 2000b. Additions to the marine molluscs of the Formigas islets, Azores. *Açoreana* **9**: 175–178.
- Ávila SP, Amen R, Azevedo JMN, Cachão M, García-Talavera F. 2002. Checklist of the Pleistocene marine molluscs of Prainha and Lagoinhas (Santa Maria Island, Azores). *Açoreana* **9**: 343–370.
- Ávila SP, Cardigos F, Santos RS. 2004. D. João de Castro bank, a shallow-water hydrothermal-vent in the Azores: checklist of the marine mollusks. *Arquipélago* **21A**: 75–80.
- Ávila SP, Madeira P, Mendes N, Rebelo A, Medeiros A, Gomes C, García-Talavera F, Marques da Silva C, Cachão M, de Frias Martins AM. 2007. *Luria lurida* (Mollusca: Gastropoda), a new record for the Pleistocene of Santa Maria (Azores, Portugal). *Arquipélago* (in press).
- Ávila SP, Marques da Silva C, Schiebel R, Cecca F, Backeljau T, de Frias Martins AM. How did they get here? Palaeobiogeography of the Pleistocene marine molluscs of the Azores. (submitted).
- Ávila SP, Madeira P, Mendes N, Rebelo A, Medeiros A, Gomes C, García-Talavera F, Marques da Silva C, Cachão M, Hillaire-Marcel C, de Frias Martins AM. 2008. Mass extinctions in the Azores during the last glaciation: fact or myth? (in press).
- Backeljau T. 1986. *Lijst van de recente mariene Mollusken van België*, Studiedocumenten, Vol. 29. Institut Royal des Sciences Naturelles de Belgique: Brussels; 1–126.
- Borges PJS deA. 2003. *Ambientes litorais nos Grupos Central e Oriental do Arquipélago dos Açores. Conteúdos e Dinâmica de Microescala*. PhD thesis, Universidade dos Açores, Ponta Delgada.
- Briggs JC. 1966. Oceanic islands, endemism and marine paleotemperatures. *Systematic Zoology* **15**: 153–163.
- Briggs JC. 1974. *Marine Zoogeography*. McGraw-Hill: New York.
- Callapez P, Soares AF. 2000. Late Quaternary marine mollusks from Santa Maria (Azores); paleoecologic and paleobiogeographic considerations. *Ciências da Terra* **14**: 313–322.
- Cardigos F, Tempera F, Ávila SP, Gonçalves J, Colaço A, Santos RS. 2006. Non-indigenous marine species of the Azores. *Helgoland Marine Research* **60**: 1–10.
- Catuneanu O. 2002. Sequence stratigraphy of clastic systems: concepts, merits, and pitfalls. *Journal of African Earth Sciences* **35**: 1–43.

- Cortijo E, Labeyrie L, Vidal L, Vautravers M, Chapman M, Duplessy JC, Elliot M, Arnold M, Turon JL, Auffret G. 1997. Changes in sea surface hydrology associated with Heinrich event 4 in the North Atlantic Ocean between 40° N and 60° N. *Earth and Planetary Science Letters* **146**: 29–45.
- Cortijo E, Balbon E, Elliot M, Labeyrie L, Turon J-L. 1999. Glacial and interglacial hydrological changes in the North Atlantic Ocean. In *Reconstructing Ocean History: A Window into the Future*, Abrantes F, Mix A (eds). Kluwer Academic/Plenum: New York; 83–101.
- Cotter JCB. 1888–1892. Notícia de alguns fósseis terciários da ilha de Santa Maria no Arquipélago dos Açores. *Comunicações da Comissão de Trabalhos Geológicos de Portugal* **2**: 255–287.
- Feraud G, Schincke H-U, Lietz J, Gostaud J, Pritchard G, Bleil U. 1980. New K-Ar ages, chemical analyses and magnetic data of rocks from the islands of Santa Maria (Azores), Porto Santo and Madeira (Madeira archipelago) and Gran Canaria (Canary Islands). *Arquipélago* **5**: 213–240.
- Galloway WE, Hodbay DK. 1996. Terrigenous shelf systems. In *Terrigenous Clastic Depositional Systems: Applications to Fossil Fuel and Groundwater Resources*, (2nd edn), Galloway WE, Hodbay DK (eds). Springer: Berlin; 159–185.
- García-Talavera F. 1990. Fauna tropical en el Neotirreniense de Santa Maria (I. Azores). *Lavori SIM* **23**: 439–443.
- Johnson HD, Baldwin CT. 1986. Shallow siliclastic seas. In *Sedimentary Environments and Facies*, (2nd edn), Reading HG (ed.). Blackwell Scientific: Oxford; 229–282.
- Komar PD. 1998. *Beach Processes and Sedimentation* (2nd edn). Prentice-Hall: Englewood Cliffs, NJ.
- Krylova EM. 2006. Bivalves of seamounts of the north-eastern Atlantic. Part I. In *Biogeography of the North Atlantic Seamounts*, Mironov AN, Gebruk AV, Southward AJ (eds). KMK Scientific Press, Russian Academy of Sciences, P.P. Shirov Institute of Oceanology: Moscow; 76–95.
- Macedo MCC, Macedo MIC, Borges JP. 1999. *Conchas Marinhas de Portugal*. Editorial Verbo: Lisbon.
- Madeira MAV. 1981. *Esboço pedológico da ilha de Santa Maria (Açores)*. Instituto Nacional de Investigação Científica, Centro de Pedologia da Universidade Técnica de Lisboa: Lisbon.
- Mayer K. 1864. *Die Tertiär-Fauna der Azoren und Madeiren. Systematisches Verzeichniss der fossilen Reste von Madeira, Porto Santo und Santa Maria nebst Beschreibung der neuen Arten*. Zürich.
- Menard HW. 1983. Insular erosion, isostasy, and subsidence. *Science* **220**: 913–918.
- Mitchell-Thomé RC. 1976. *Geology of the Middle Atlantic Islands*. Gebrüder Borntraeger: Berlin.
- Morton B. 1990. The biology and functional morphology of *Ervilia castanea* (Bivalvia: Tellinacea) from the Azores. In *The Marine Fauna and Flora of the Azores: Proceedings of the First International Workshop of Malacology*, São Miguel, Azores. *Açoreana* Suppl 2: 75–96.
- Morton B. 1995. The biology and functional morphology of *Trichomusculus semigranatus* (Bivalvia: Mytiloidea) from the Azores. In *The Marine Fauna and Flora of the Azores: Proceedings of the Second International Workshop of Malacology and Marine Biology*, de F Martins AM, (ed.). *Açoreana* Suppl 4: 279–295.
- Morton B, Britton JC, de Frias Martins AM. 1998. *Ecologia Costeira dos Açores*. Sociedade Afonso Chaves: Ponta Delgada.
- Muhs DR, Simmons KR, Steinke B. 2002. Timing and warmth of the Last Interglacial period: new U-series evidence from Hawaii and Bermuda and a new fossil compilation from North America. *Quaternary Science Reviews* **21**: 1355–1383.
- Prud'homme van Reine WF. 1988. Phytogeography of seaweeds of the Azores. *Helgoländer Meeresuntersuchungen* **42**: 165–185.
- Rasmussen TL, Thomsen E, Kuijpers A, Wastegard S. 2003. Late warming and early cooling of the sea surface in the Nordic seas during MIS 5e (Eemian Interglacial). *Quaternary Science Reviews* **22**: 809–821.
- Rodríguez RG, Sánchez JMP. 1997. *Moluscos Bivalvos de Canarias*. Ediciones del Cabildo Insular de Gran Canaria: Las Palmas de Gran Canaria.
- Salas C, Gofas S. 1998. Description of four new species of *Neolepton* Monterosato, 1875 (Mollusca: Bivalvia: Neoleptonidae), with comments on the genus and on its affinity with the Veneracea. *Ophelia* **48**: 35–70.
- Salgueiro MAO. 1991. Estudo paleomagnético e cronologia estratigráfica de formações vulcânicas da ilha de Santa Maria, Açores. *Arquipélago, Life and Earth Sciences* **9**: 83–99.
- Santos RS, Porteiro FM, Barreiros JP. 1997. Marine fishes of the Azores: an annotated checklist and bibliography. *Arquipélago, Life and Marine Sciences* Suppl 1.
- Scheltema RS. 1986. On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. *Bulletin of Marine Science* **39**: 290–322.
- Serralheiro A. 2003. A geologia da ilha de Santa Maria, Açores. *Açoreana* **10**: 141–192.
- Serralheiro A, Madeira J. 1990. *Stratigraphy and Geochronology of Santa Maria Island (Azores)*, Livro de Homenagem ao Prof. Carlos Romariz. Departamento de Geologia da Faculdade de Ciências da Universidade de Lisboa; 357–376.
- Shepard F. 1973. *Submarine Geology* (3rd edn). Harper & Row: New York.
- Short AD. 1999. *Handbook of Beach and Shoreface Morphodynamics*. Wiley: Chichester.
- Southard JB, Stanley DJ. 1976. Shelf-break processes and sedimentation. In *Marine Sediment Transport and Environmental Management*, Stanley DJ, Swift DJP (eds). Wiley: New York; 351–377.
- Tebble N. 1966. *British Bivalve Seashells: A Handbook for Identification*. Trustees of the British Museum (Natural History): London.
- Thompson WG, Goldstein SL. 2006. A radiometric calibration of the SPECMAP timescale. *Quaternary Science Reviews* **25**: 3207–3215.
- Thorne JA, Swift DJP. 1991. Sedimentation on continental margins. VI. A regime model for depositional sequences, their components system tracts, and bounding surfaces. In *Shelf Sand and Sandstone Bodies: Geometry, Facies and Sequence Stratigraphy*. Special publication of International Association of Sedimentologists, Vol. 14. Blackwell Scientific: Oxford; 189–255.
- Vidal L, Labeyrie L, Cortijo E, Arnold M, Duplessy JC, Michel E, Becqué S, van Weering TCE. 1997. Evidence for changes in the North Atlantic Deep Water linked to meltwater surges during the Heinrich events. *Earth and Planetary Science Letters* **146**: 13–26.
- von Cosel R von. 1995. Fifty-one new species of marine bivalves from tropical West Africa. *Iberus* **13**: 1–115.
- Wilson RCL, Dury SA, Chapman JL. 2000. *The Great Ice Age: Climate Change and Life*. Routledge: London.
- Zbyszewsky G, Ferreira O da V. 1962. Étude géologique de l'île de Santa Maria (Açores). *Comunicações dos Serviços Geológicos de Portugal* **46**: 209–245.