ORIGINAL ARTICLE

Mass extinctions in the Azores during the last glaciation: fact or myth?

Sérgio P. Ávila[1,2,3]*, Patrícia Madeira[3], Nuno Mendes[3], Ana Rebelo[3], André Medeiros[3], Cidalina Gomes[3], Francisco García-Talavera[4], Carlos Marques da Silva[5], Mário Cachão[5], Claude Hillaire-Marcel[6] and António M. de Frias Martins[1,3,7]

[1]*Departamento de Biologia, Universidade dos Açores, Azores, Portugal,* [2]*Centro do IMAR da Universidade dos Açores, Azores, Portugal,* [3]*MPB – Marine Palaeobiogeography Working Group of the University of the Azores, Azores, Portugal,* [4]*Museo de la Naturaleza y el Hombre (Ciencias Naturales), Canary Islands, Spain,* [5]*Departamento e Centro de Geologia, Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal,* [6]*GEOTOP – Université du Québec à Montréal (UQAM), Montréal, QC, Canada and* [7]*CIBIO Centro de Investigação em Recursos Genéticos - Pólo Açores, Departmento de Biologia, Universidade dos Açores, Azores, Portugal*

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

ABSTRACT

Aim The influence of the last glaciation on the shallow-water marine malacofauna of the Azores Islands is reviewed. We test, for this fauna, the 'Pleistocene temperature theory' of J.C. Briggs, which hypothesizes that a (supposed) lack of endemics in the older (Azorean endemic) fauna resulted from extinctions caused by a severe drop in sea surface temperatures during the Pleistocene.

Location Santa Maria Island, Azores, Portugal.

Methods We compare the fossil mollusc fauna of Prainha, Praia do Calhau and Lagoinhas Pleistocene outcrops with the recent mollusc fauna of the Azores Islands. We dated the fossil fauna, using shells of *Patella aspera* Röding, 1798, by standard U/Th methodology at the GEOTOP laboratory (Université du Québec à Montreal, Canada).

Results Dating of the shells of *P. aspera* indicates that the deposition of the lower unit of the Prainha outcrop corresponded to Marine Oxygen Isotope Substage 5e (MISS 5e). Not a single endemic Azorean species of mollusc that is present in the Pleistocene fossil record has since become extinct, and we found no signs of 'mass extinctions' in the littoral marine molluscs of the Azores. The only species that were extirpated from these islands were thermophilic molluscs and littoral bivalves living in fine sand.

Main conclusions Our results do not support Briggs' 'Pleistocene temperature theory'. Nor did we find evidence supporting the hypothesis that most of the marine organisms now present in the Azores recolonized the islands after the last glacial maximum.

Keywords
Azores, last glaciation, marine malacofauna, mass extinctions, Mollusca, oceanic islands, Pleistocene.

INTRODUCTION

The Azorean archipelago is located in the middle of the northern Atlantic Ocean (36°55′ to 39°45′ N, 24°45′ to 31°17′ W) (Fig. 1). It comprises nine islands, about 1500 km west of Portugal. Owing to their isolation, these oceanic islands are considered a natural laboratory, where patterns and processes of dispersal, colonization and speciation can be studied, and ecological, evolutionary and biogeographical theories tested.

Despite the archipelago's volcanic origins, there are fossiliferous sites in Santa Maria Island and the Formigas' islets. Most of the literature on Azorean fossils, published since the middle of the 19th century, deals with Upper Miocene to Lower Pliocene marine molluscs from Santa Maria. However, in Santa Maria, there are also several fossiliferous beds of Pleistocene age at scattered locations (Prainha, Praia do Calhau and Lagoinhas) (Ávila *et al.*, 2002). The fossiliferous beds of Santa Maria have been studied by the authors since 1998. Three international workshops entitled *Palaeontology in Atlantic Islands*, were held on Santa Maria Island in 2002, 2005 and 2006, and more than 20 fieldtrips were organized to Santa Maria. Three papers devoted entirely to these Pleistocene

doi:10.1111/j.1365-2699.2008.01881.x

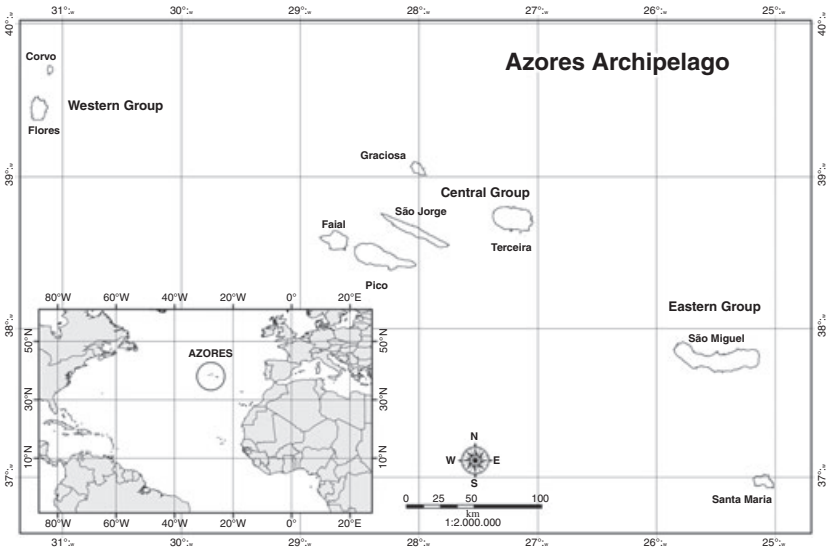

Figure 1 Geographical location of the Azores archipelago in the northern Atlantic Ocean. Western, Central and Eastern Groups of islands (Azores archipelago).

sites have recently been published (García-Talavera, 1990; Callapez & Soares, 2000; Ávila *et al.*, 2002).

Detailed data about the Pleistocene fossil molluscs from Santa Maria Island were not available when Briggs (1966) hypothesized that there was a relationship between oceanic islands, endemism, extinction and marine palaeotemperatures [sea surface temperatures (SSTs)]. He attributed the (supposed) lack of Azorean endemic to mass extinctions caused by the Pleistocene glaciations. In this paper, we provide new data and arguments with the intention of evaluating Briggs' (mass) extinction scenario for the Azorean shallow marine faunas.

METHODS

During the third *Palaeontology in Atlantic Islands* workshop held on Santa Maria Island, from 15 to 25 June 2006, the Prainha, Praia do Calhau and Lagoinhas Pleistocene outcrops were sampled for mollusc fossils. For more details, general stratigraphical setting, graphic columnar section, and additional references see Ávila *et al.* (2002) and Ávila (2005). All samples were deposited at the Department of Biology of the University of the Azores (Ponta Delgada, São Miguel Island) (listed at http://www.uac.pt/~fosseis/DBUA-F.pdf) (Table S1).

We constructed a table with all bivalve and gastropod species present in the Pleistocene of the Azores but which are no longer present in the archipelago, including notes on the type of habitat and bathymetric range of these species, reported from the Pleistocene fossil record of Santa Maria Island, using data adapted from Ávila *et al.* (2002, 2008a) (Table 1). We consider these as extirpated species, that is, species that locally disappeared from the archipelago as a result of the last glaciation. Data modified from Ávila (2005) and Ávila *et al.* (2002, 2008a,b) were also used to compare the Pleistocene fossil record from Prainha and Lagoinhas (Santa Maria Island, Azores), with the Recent molluscan fauna of the Azores (Ávila, 2000, 2005) (Table 2).

Shells of *Patella aspera* Röding, 1798, collected from cleaned vertical exposure faces at the basal conglomerate of the Prainha outcrop (36º 57′ 06,50″ N, 25°06′ 13,95″ W) (Santa Maria Island) (unit A_1 of Ávila *et al.*, 2002), or by excavating intact sediment blocks, were dated by standard U/Th methodology at the GEOTOP laboratory (Université du Québec à Montreal, Canada).

Abbreviations used in text

DBUA-F – fossil reference collection of the Department of Biology of the University of the Azores (Ponta Delgada, São Miguel Island, Azores).

RESULTS

Biogeographical analysis

Fossils of 20 species (16 gastropods and 4 bivalves) that are reported from the Pleistocene fossil record of Santa Maria Island (Azores) (Ávila *et al.*, 2002, 2008a) are no longer present anywhere on the archipelago (Table 1). Notwithstanding this local disappearance of some mollusc species, the biogeographical relationships of the Pleistocene molluscs known from the Azores are very similar to those of Recent taxa, with the Eastern Atlantic being the region that shares the most species with the Azores in both Pleistocene and Recent faunas (71.6% and 76.6%, respectively). Only about 10–12% of species are related to Western Atlantic taxa (Table 2).

Age model (geochronology)

Dating of Patella aspera *samples*

The mean uranium isotopic ages of the shells of *Patella aspera* range between 64.713 ka +0.987/−0.975 (*Patella* #3) and 77.140 ka +1.183/−1.167 (*Patella* #2) (Table 3). The Pleistocene deposits of Santa Maria Island are poorly consolidated and highly porous. This porosity, plus the wet climatic

Table 1 Bivalve and gastropod species that locally disappeared from the Archipelago during the last glaciation and probable recent (re)colonizers of the Azores archipelago (adapted from Ávila *et al.*, 2002, 2008a)

Species	Class	Family	Habitat	Pleistocene fossil record	Bathymetric range (m)	Local disappearence during the last glaciation	Recent (re)colonizer
Laevicardium crassum (Gmelin, 1791)	Bivalvia	Cardiidae	Gravel, Sand, Mud	Yes	0–2195	Yes (?)	No
Lucinella divaricata (Linnaeus, 1758)	Bivalvia	Lucinidae	Sand, Mud	Yes	?–60	Yes	No
Myoforceps aristatus (Dillwyn, 1817).	Bivalvia	Mytilidae	Soft substrate	Yes	0–100	Yes	No
Ensis minor (Chenu, 1843)	Bivalvia	Pharidae	Sand	Yes	0–10	Yes	No
Solemya togata (Poli, 1795)	Bivalvia	Solemyidae	Sand, Mud	No	0–30	?	Probable
Basterotia clancula Cosel, 1995	Bivalvia	Sportellidae	Sand, Gravel (?)	No	1–20	?	Probable
Tellina pygmaea Lóven, 1846	Bivalvia	Tellinidae	Sand	No	0–150	?	Probable
Callista chione (Linnaeus, 1758)	Bivalvia	Veneridae	Sand	No	?5–200	?	Probable
Bulla amygdala	Gastropoda	Bullidae		Yes		Yes	No
Cantharus variegatus (Gray, 1839)	Gastropoda	Buccinidae		Yes		Yes	No
Conus ambiguus Reeve, 1844	Gastropoda	Conidae		Yes		Yes	No
Conus cf. *ermineus* Börn, 1778	Gastropoda	Conidae		Yes		Yes	No
Conus cf. *miruchae* Röckel, Rolán & Monteiro, 1980	Gastropoda	Conidae		Yes		Yes	No
Conus cf. *roeckeli* Rolán, 1980	Gastropoda	Conidae		Yes		Yes	No
Conus ventricosus Gmelin, 1791	Gastropoda	Conidae		Yes		Yes	No
Conus venulatus Hwass *in* Bruguière, 1792	Gastropoda	Conidae		Yes		Yes	No
Trachyppolia nodulosa (C.B.Adams, 1845)	Gastropoda	Muricidae		Yes		Yes	No
Seila trilineata (Philippi, 1836)	Gastropoda	Cerithiopsidae		Yes		Yes	No
Epitonium sp.	Gastropoda	Epitoniidae		Yes		Yes	No
Zebina vitrea A. Adams, 1854	Gastropoda	Rissoidae		Yes		Yes	No
Zonaria pyrum Gmelin, 1791	Gastropoda	Cypraeidae		Yes		Yes	No
Zonaria picta (Gray, 1824)	Gastropoda	Cypraeidae		Yes		Yes	No
Polynices lacteus (Guilding, 1834)	Gastropoda	Naticidae		Yes		Yes	No
Gibbula umbilicalis (da Costa, 1778)	Gastropoda	Trochidae		Yes		Yes	No

Table 2 Total number of Pleistocene and recent mollusc species from Prainha and Lagoinhas (Santa Maria, Azores) (data modified from Ávila, 2000, 2005 and Ávila *et al.*, 2002, 2008a,b)

	Pleistocene (Ávila *et al.*, 2002, 2008a,b)	%	Recent (Ávila, 2000, 2005).	%
Western Atlantic	11	10.8	39	12.2
Macaronesia endemics	7	6.9	16	5.0
Eastern Atlantic	73	71.6	245	76.6
Azorean endemics	17	16.7	35	10.9
Pelagic species	0	0.0	24	7.5
Amphi-Atlantic species	6	5.9	36	11.2
Total number of species	102	–	320	–

conditions prevailing on the island, means that continuous U-fluxes may be expected in such deposits. Furthermore, as mollusc shells are deprived of syngenetic uranium, the U-series measurements from their fossilized remains can only help constrain the age of the uranium uptaken diagenetically (Kaufman *et al.*, 1996; Labonne & Hillaire-Marcel, 2000). When the fossilization process produces rapid chemical closure for uranium (e.g. early cemented beach-rocks and arid environments), U-series ages may provide reasonable indications of the age of the embedding units (e.g. Zazo *et al.*, 2002). Unfortunately, as expected in the present setting, U-series data from Prainha indicate an open system, providing mean ^{230}Th-ages that are much younger than the true age of the unit, which we assume to belong to the Marine Oxygen Isotope Substage 5e (MISS 5e) high sea level interval. They suggest relatively steady, more or less continuous, diagenetic U-uptake by the fossils since their deposition in the Pleistocene. Thus, if we accept an age of 130–120 ka for the deposits, we estimated that within the embedded biogenic carbonates U-uptake rates varied from *c.* 2.5 to 5 μg $gCaCO_3^{-1}$ kyr^{-1}. This was based on

Table 3 U-series from samples of *Patella aspera* Röding, 1798 collected from the basal conglomerate of the Prainha outcrop (Santa Maria Island) (unit A_1 of Ávila *et al.*, 2002)

Sample	^{238}U ppb	±	^{232}Th ppb	±	^{234}U/^{238}U	±	^{230}Th/^{234}U	±	^{230}Th/^{232}Th	±	Mean uranium age (ka)	±
Patella #1	677.275	4.445	6.527	0.063	1.0979	0.0113	0.4633	0.0065	161.294	2.452	66.925	+1.381/−1.357
Patella #2	314.685	1.58	5.924	0.041	1.1271	0.0056	0.5139	0.0052	94.04	1.163	77.140	+1.183/−1.167
Patella #3	343.951	1.825	3.751	0.025	1.0815	0.0078	0.4514	0.0048	136.826	1.586	64.713	+0.987/−0.975

^{230}Th-ages in the 60–70 ka range (Table 3), for shells that would have started accumulating diagenetic U some 130–120 ka ago (i.e. during the MISS 5e).

DISCUSSION

During the Pleistocene, the shallow-marine faunas of the higher latitude Atlantic Islands were repeatedly affected by glacial interglacial cycles. Although many Pleistocene outcrops that reflect shallow marine depositional environments have been described from both the Western and Eastern Atlantic coasts, only a few scattered outcrops can be studied in the archipelagos located between these two opposite sides of the North Atlantic Ocean. Among them, the Upper Pleistocene outcrops of Santa Maria Island (Azores) are notable for their abundant and well-preserved fossil assemblages (especially of molluscs, but also of sponges, bryozoans and echinoderms). Their study, in close association with studies of the Recent faunas of the Azores (Ávila, 2000, 2005; Ávila & Albergaria, 2002), provided useful insights into the influence of the last glaciation on the shallow water marine communities. Although thermophilic species and sandy-shallow bivalves did locally disappear from the Azores during the last glaciation, most other species reported from these Pleistocene beds still occur in the Azores today (Ávila, 2005; Ávila *et al.*, 2008a).

Mass extinctions in the Azores during the last glaciation?

Forty years ago, Briggs (1966) formulated the 'Pleistocene temperature theory', which hypothesized a relationship between oceanic islands, endemism, extinction and 'marine paleotemperatures'. He attributed a lack of endemism in the shallow marine faunas of several Atlantic oceanic islands to extinctions caused by reduced temperatures associated with the Pleistocene glaciations (Briggs, 1966, 1969). In a series of papers, McDowall (1968, 1971) questioned the relationships between Pleistocene glaciations and patterns of endemism on oceanic islands and explicitly said that a '…more realistic attempt to establish causes of endemism in these island faunas should have been made before it was assumed that low endemism signifies extinction' (McDowall, 1971, pp. 110–111). However, Briggs (1974) persisted in claiming that the lack of endemism in the shallow Azorean marine biota was due to '…severe drops in Pleistocene sea surface temperature that may have wiped out the older fauna'. He considered that if the Azores had been repopulated within the past 12,000 years, very little evolutionary change could be expected. Consistent with this idea, Santos *et al.* (1995, p. 323) suggested that the Pleistocene temperature drop, although not very sharp (2–3°C) (Crowley, 1981), 'probably resulted in mass extinctions' from the littoral fish fauna of the Azores. This view was shared by other recent authors, who also postulated mass extinction of warm-water littoral fish in the Azores during the last glaciation. Based on molecular data, Domingues *et al.* (2006, p. 145) claimed that 'most of the organisms now present [in the Azores] would have recolonized the islands after the last glaciating event from some southern, less affected regions like the northwestern coast of Africa south of Cape Blanco, the westernmost Canary Islands and Madeira'.

This may be true for some organisms, such as littoral mollusc species living in fine sand (Ávila *et al.*, 2008a), which may have locally disappeared during the last glaciation and subsequently recolonized the Azores Islands very recently (Table 1) [e.g. *Solemya togata* (Poli, 1795), *Basterotia clancula* Cosel, 1995, *Tellina pygmaea* Lóven, 1846 and *Callista chione* (Linnaeus, 1758)]. However, our data suggest that only 20 of the 102 marine species living on Santa Maria Island during the Pleistocene (19.6%) did locally disappear during the last glaciation (Tables 1 and 2). Of these 20 species, two are shallow water bivalves associated with sandy substrate [*Ensis minor* (Chenu, 1843) and *Lucinella divaricata* (Linnaeus, 1758)]; another is a bivalve with a wide bathymetric range, occupying different habitats (sand, gravel and mud) [*Laevicardium crassum* (Gmelin, 1791)]; one is a lithophagous bivalve [*Myoforceps aristatus* (Dillwyn, 1817)]; and 16 are warm-water gastropods, most of which presently occur on the Eastern Atlantic shores of Europe, Africa, or are restricted to the Cape Verde Islands. Only two of those warm-water gastropods currently occur in the Western Atlantic: *Zebina vitrea* A. Adams, 1854, and *Polynices lacteus* (Guilding, 1834).

Table 2 clearly shows that the mollusc fossil record of Santa Maria Island (Azores) does not support Briggs' postulated 'extinction' scenario. When the Recent and the Pleistocene Azorean shallow-water marine malacofaunas are compared, a different scenario emerges. At present there are 409 species of shallow-water marine molluscs in the Azores (S.P. Ávila, unpublished data). Of these, 15 taxa are not yet identified to the species level, 44 are considered as dubious

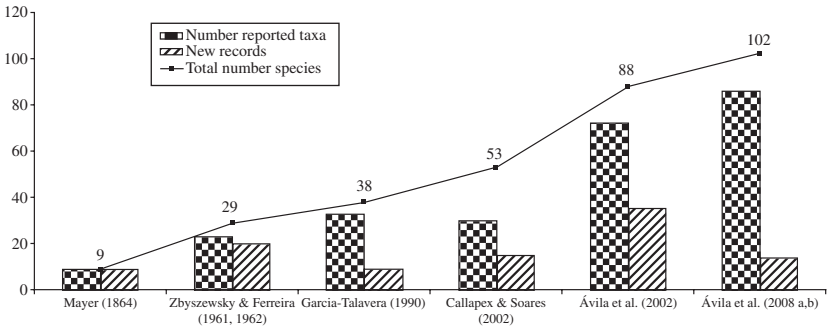

Figure 2 Number of reported Mollusc species, new records, and total number of Pleistocene species reported for Santa Maria Island (Azores).

records (most are old references; see Ávila (2005) and references therein for a review), 24 are pelagic species, and six species were recently introduced into the archipelago, and are considered by Cardigos *et al.* (2006) as non-indigenous: the gastropods *Hexaplex trunculus* (Linnaeus, 1758), *Pollia dorbignyi* (Payraudeau, 1826) and *Truncatella subcylindrica* (Linnaeus, 1767), and the bivalves *Hiatella arctica* (Linnaeus, 1758), *Pinctada radiata* (Leach, 1814) and *Ruditapes decussatus* (Linnaeus, 1758). We consider that in a biogeographic context, none of the above-mentioned species should be taken into account, and therefore, the total number of shallow-water marine molluscs presently reported for the Azores Islands is 320 species, of which 35 (10.9%) are endemic to this archipelago. Considering the great isolation of the Azores Islands and their geological ages (the oldest island, Santa Maria, is about 8 Myr old) (Abdel-Monem *et al.*, 1975), this rate of endemism is substantial, and such endemism is contrary to Briggs' (1974) hypothesis of a 'tabula rasa' in the Azores, as a consequence of the last glaciation – clearly, many endemic Azorean species survived. Moreover, analysis of the Pleistocene fossil record of the Azores, shows that 17 out of the 102 species (16.7%) of the fossil molluscs reported from the Lagoinhas and Prainha outcrops are Azorean endemics (Ávila *et al.*, 2002, 2008a; see also Fig. 2), and all of them still occur in shallow marine environments of the archipelago.

Geological age of the Prainha Pleistocene outcrop

Based on the fossil molluscan assemblage found at Prainha and on its faunal, and stratigraphical similarities with dated outcrops from the Canary Islands, García-Talavera (1990) ascribed the Prainha outcrop to Tyrrhenian age (a stage about 115–90 kyr BP, related to shallow-marine sequences of Italy). Callapez & Soares (2000) reached a similar conclusion, based on fossil molluscs collected at Prainha and Lagoinhas (Santa Maria Island, Azores). However, these deposits were never dated isotopically, and our analysis shows that they are unsuitable for U-series dating. For the shells of *Patella aspera*, and the deposition of unit A_1 (Ávila *et al.*, 2002), we suggest an age of 130–120 kyr BP, which corresponds to the Marine Oxygen Isotope Substage 5e (MISS 5e). To obtain independent age confirmation, we will undertake amino acid racemization measurements in the near future.

CONCLUSIONS

Both the Lagoinhas and Prainha outcrops at the Azores are older than the last glaciation. Based on the fossils found there, and on the extant molluscan fauna of the Azores, we conclude that: (1) no endemic Azorean species of mollusc present in the Pleistocene fossil record became extinct as a result of the last glaciation; (2) most of the species present in the Azores prior to the last glaciation have persisted through to the present day; and (3) no signs of 'mass extinctions' were found in the littoral marine molluscs of the Azores. In fact, the only species that disappeared from these islands were: (1) thermophilic molluscs (the West African and Caribbean 'warm guests') such as *Cantharus variegatus*, *Zebina vitrea*, several *Conus* spp. (*C. ermineus*, *C. miruchae*, *C.* cf. *roeckeli*, *C. ventricosus* and *C. venulatus*), *Polynices lacteus*, *Trachypollia nodulosa* and *Zonaria picta* (Gray, 1824); and (2) littoral bivalves living in fine sand (e.g. *Ensis minor*, *Lucinella divaricata* and *Laevicardium crassum*) (Ávila *et al.*, 2008a).

Thus, our results do not support Briggs' 'Pleistocene temperature theory', which argued that a (supposed) lack of endemism indicates that the older (Azorean endemic) fauna was wiped out by a severe drop in sea surface temperatures during the Pleistocene. Nearly all of the molluscs now present in the Azores were there prior to the last glaciation (Ávila, 2005).

We also suggest that caution should be exercised when using the term 'mass extinction', since the word 'extinction' means the definitive, global disappearance of a given species, from all the sites where it occurred. On the other hand, local disappearance (or extirpation) may be temporary, as it may be followed by recolonization from regions where the species did not disappear. Moreover, by definition, marine mass extinctions should be understood as affecting different phyla with different ecological pre-requisites (meiofauna, macrofauna, benthos, plankton, etc.).

It is probable that Azorean warm-water fishes, such as *Chromis limbata*, *Tripterygion delaisi*, *Ophioblennius atlanticus* and *Abudebduf* spp., were adversely affected by low Pleistocene temperatures, and they probably disappeared from the islands but then recolonized them after the last glaciation (Domingues *et al.*, 2006, 2007). Other species, such as *Lipophrys pholis*, which are more tolerant of low temperatures, probably were not significantly affected (V. Almada, personal communica-

tion.). However, the shallow-water marine molluscs of the Azores do not provide evidence supporting the hypothesis that 'most of the marine organisms now present in the Azores recolonized the islands after the last glaciating event', as was stated by Domingues *et al.* (2006, p.145; 2007) for the marine fishes.

Increasing data on the Pleistocene faunas of the Azores will provide an opportunity to better understand the evolution of the littoral faunas on oceanic islands. This work should be expanded to include other invertebrate phyla (e.g. Bryozoa, Echinodermata and Crustacea). Comparisons of palaeobiogeographic relationships with the Recent ones will be the basis of further studies of the processes and patterns that govern the dispersion, colonization and speciation of organisms on oceanic islands, an issue of global biogeographical interest.

ACKNOWLEDGEMENTS

We are grateful for financial support from the organizers of the third *Palaeontology in Atlantic Islands* workshop. We thank FCT (Fundação para a Ciência e Tecnologia) of the Portuguese Government, Direcção Regional da Ciência e da Tecnologia/ (Regional Government of the Azores), Direcção Regional do Ambiente e do Mar (Regional Government of the Azores), CCPA/UA (Centro de Conservação e Protecção do Ambiente/ Universidade dos Açores), Clube Naval de Santa Maria, Câmara Municipal de Vila do Porto, 'Geo-Fun' and 'Nerus'. We are indebted to our colleagues Ricardo Serrão Santos, Vera Domingues and Vítor Almada, who critically commented on the manuscript. We also thank Bassam Ghaleb (GEOTOP, Canada) for dating of the *Patella aspera* shells from Santa Maria. We are also grateful to two anonymous referees and to Robert McDowall, whose comments greatly improved this manuscript. S.P.A. was supported by grant SFRH/BPD/22913/ 2005 (FCT – Fundação para a Ciência e Tecnologia) from the Portuguese government.

REFERENCES

Abdel-Monem, A.A., Fernandez, L.A. & Boone, G.M. (1975) K-Ar ages from the eastern Azores group (Santa Maria, São Miguel and the Formigas Islands). *Lithos*, **8,** 247–254.

Ávila, S.P. (2000) Shallow-water marine molluscs of the Azores: biogeographical relationships. Arquipélago. *Life and Marine Sciences*, **(Supplement 2, Part A),** 99–131.

Ávila, S.P. (2005) *Processos e padrões de dispersão e colonização nos Rissoidae (Mollusca: Gastropoda) dos Açores*. x + 329 pp. PhD Thesis, Universidade dos Açores, Ponta Delgada, Azores, Portugal, x + 329 pp.

Ávila, S.P. & Albergaria, A. (2002) The shallow-water Polyplacophora of the Azores and some comments on the biogeographical relationships of the Azorean malacofauna. *Bollettino Malacologico*, **38,** 41–44.

Ávila, S.P., Amen, R., Azevedo, J.M.N., Cachão, M. & Garcia-Talavera, F. (2002) Checklist of the Pleistocene marine molluscs of Praínha and Lagoínhas (Santa Maria Island, Azores). *Açoreana*, **9,** 343–370.

Ávila, S.P., Madeira, P., da Silva, C.M., Cachão, M., Quartau, R. & de Frias Martins, A.M. (2008a) Local disappearance of bivalves in the Azores during the last glaciation. *Journal of Quaternary Science* (in press).

Ávila, S.P., Madeira, P., Garcia-Talavera, F., da Silva, C.M., Cachão, M. & de Frias Martins, A.M. (2008b) *Luria lurida* (Mollusca: Gastropoda), a new record for the Pleistocene of Santa Maria (Azores, Portugal). *Arquipélago*, in press.

Briggs, J.C. (1966) Oceanic islands, endemism and marine paleotemperatures. *Systematic Zoology*, **15,** 153–163.

Briggs, J.C. (1969) Oceanic islands and endemism: a reply. *Systematic Zoology*, **18,** 145–148.

Briggs, J.C. (1974) *Marine zoogeography*. McGraw-Hill Book Co., New York.

Callapez, P. & Soares, A.F. (2000) Late Quaternary marine mollusks from Santa Maria (Azores); paleoecologic and paleobiogeographic considerations. *Ciências da Terra (UNL)*, **14,** 313–322.

Cardigos, F., Tempera, F., Ávila, S.P., Gonçalves, J., Colaço, A. & Santos, R.S. (2006) Non-indigenous marine species of the Azores. *Helgoland Marine Research*, **60,** 1–10.

Crowley, T.J. (1981) Temperature and circulation changes in the eastern North Atlantic during the last 150,000 years: evidence from the planktonic foraminiferal record. *Marine Micropaleontology*, **6,** 97–129.

Domingues, V.S., Santos, R.S., Brito, A. & Almada, V.C. (2006) Historical population dynamics and demography of the eastern Atlantic pomacentrid *Chromis limbata* (Valenciennes, 1833). *Molecular Phylogenetics and Evolution*, **40,** 139–147.

Domingues, V.S., Almada, V.C., Santos, R.S., Brito, A. & Bernardi, G. (2007) Phylogeography and evolution of the triplefin *Tripterygion delaisi* (Pisces, Blennioidei). *Marine Biology*, **150,** 509–519.

García-Talavera, F. (1990) Fauna tropical en el Neotirreniense de Santa Maria (I. Azores). *Lavori Societá Italiana di Malacologia*, **23,** 439–443.

Kaufman, A., Ghaleb, B., Wehmiller, J.F. & Hillaire-Marcel, C. (1996) Uranium concentration and isotope ratio profiles within *Mercenaria* shells. *Geochimica et Cosmochimica Acta*, **19,** 3735–3746.

Labonne, M. & Hillaire-Marcel, C. (2000) Geochemical gradients within modern and fossil shells of *Concholepas concholepas* from Northern Chile: an insight into U-Th systematics and diagenetic/authigenic isotopic imprints in mollusk shells. *Geochimica et Cosmochimica Acta*, **64,** 1523–1534.

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.

McDowall, R.M. (1968) Oceanic islands and endemism. *Systematic Zoology*, **17,** 346–350.

McDowall, R.M. (1971) Oceanic islands and endemism: further comment. *Systematic Zoology*, **20,** 109–111.

Santos, R.S., Hawkins, S., Monteiro, L.R., Alves, M. & Isidro, E.J. (1995) Case studies and reviews. Marine research, resources and conservation in the Azores. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **5,** 311–354.

Zazo, C., Goy, J.-L., Hillaire-Marcel, C., Gillot, P.Y., Soler, V., González, J.A., Dabrio, C.J. & Ghaleb, B. (2002) Raised marine sequences of Lanzarote and Fuerteventura revisited—a reappraisal of relative sea-level changes and vertical movements in the eastern Canary Islands during the Quaternary. *Quaternary Science Reviews*, **21,** 2019–2046.

Zbyszewsky, G. & O. Ferreira, da V. (1961) La faune marine des basses plages quaternaires de Praia et Prainha dans l'ile de Santa Maria (Açores). *Comunicações dos Serviços Geológicos de Portugal*, **45,** 467–478.

Zbyszewsky, G. & O. Ferreira, da V. (1962) Étude géologique de l'île de Santa Maria (Açores). *Comunicações dos Serviços Geológicos de Portugal*, **46,** 209–245.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Table S1 Fossil collection of the Department of Biology of the University of the Azores (DBUA-F). Date of collection of the samples, name of the collector, island and site, time period and stratigraphic sequence.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2008.01881.x (This link will take you to the article abstract).

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BIOSKETCH

Sérgio Ávila received his PhD from University of the Azores on the patterns and processes of dispersal and colonization of the Rissoidae (Mollusca, Gastropoda) in the Azores Islands. He is now a postdoctoral research fellow at Centro do IMAR da Universidade dos Açores and at the Department of Biology (University of the Azores). His research to date has focused on the biogeographical relationships of the Recent littoral molluscs of the Azores, as well as of the Pleistocene and Miocene molluscs of the Azores. He also investigates seamounts and their role in the processes of dispersion.

Editor: Robert McDowall