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MIOCENE RHODOLITHS OF THE ATLANTIC ARCHIPELAGOS (AZORES, MADEIRA, CANARIES AND CAPE VERDE): SYSTEMATICS, PALAEOECOLOGY AND PALAEOBIOGEOGRAPHY

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TABLE OF CONTENTS

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ABSTRACT

Rhodoliths are free-living nodules composed mostly (>50%) of nongeniculate encrusting coralline red algae. These nodules were described for the first time during the 18th century and are the response of coralline algae to unstable substrates where, due to their calcified cell walls, they are able to live, withstanding abrasion.

Rhodolith beds are aggregations of rhodoliths, and such beds are found in many parts of the world. The calcified frameworks preserve well and may, after death, be incorporated into sediments. Depending on conditions during and after preservation, fossil assemblages of calcareous organisms can provide insights into geological processes and, combined with information on species composition and morphological attributes of the frameworks, may be used as indicators of palaeoenvironmental conditions. Despite being widely distributed in all seas, studies of the distribution and ecology of both past and living beds are few and generalizations concerning environmental interpretations are still debated. Its ecological and economic importance are still poorly understood in the world. Taxonomic difficulties have also hampered these interpretations. Though some authors mention that the rhodalgal lithofacies are of Paleogene age, these mainly developed during the Neogene. There are known thick rhodolith-dominated accumulations from the Miocene of the Tethys and Paratethys regions, as well as from a variety of localities in the tropical Pacific, Southeast Asia, and the Caribbean. In the Circum-Mediterranean region, Burdigalian to Serravalian (late-early to late-middle Miocene) rhodalgal carbonates are volumetrically more important than coral-reef facies. Some of these depositional carbonate sequences are completely dominated by rhodoliths. Rhodalgal deposits typified by dense concentrations of rhodoliths are globally distributed as the dominant carbonate facies from the Burdigalian to the lower Tortonian crossing the middle Miocene and exhibiting their greatest species richness during the early and middle Miocene. As palaeoclimatology has become a central topic of carbonate sedimentology, palaeoecology is particularly significant for climate research because the carbonate secreting biotas are very sensitive archives of climate.

ABSTRACT

In this PhD thesis, the study of Miocene rhodolith deposits from the Atlantic archipelagos of Azores, Madeira, Canary Islands and Cape Verde was conducted in order to understand the species composition, the ecology, the (palaeo)biogeographical relationships, and to test if local factors were more important in deciding the relative scarcity or surplus of rhodoliths in this region than some of the possible global influences that also impacted the Miocene world.

The present work displays a range of taphofacies and sedimentary dynamics on ancient and modern rhodolith deposits from the Macaronesian realm. Special focus was given to the Archipelago of the Azores, where studies on the size and shape analysis and taxonomical studies were produced, again both for fossil and extant rhodoliths. These kind of data help to better understand the environmental constraints on the size and shape distributions of rhodolith assemblages found as fossils elsewhere on volcanic islands in the northeast Atlantic Ocean. Also palaeoenvironmental reconstructions of selected outcrops were created in order to gain further insight on the life cycle (and death) of rhodoliths living within a mid-ocean active volcanic setting. Finaly, cathodoluminescence techniques were applied to Pliocene rhodoliths from Santa Maria Island (Azores) in order to gain additional insight regarding the trace element content distribution throughout the algae thalli. This allowed to understanding the influence of volcanic activity due to the extrusion of lavas and associated products and/or the presence of active shallow-water hydrothermal vents, reflected in the sea water chemistry, which mirrored on the rhodolith Mn^{2+} high concentration.

RESUMO

Os rodólitos são nódulos de vida livre compostos maioritariamente (>50%) por algas vermelhas coralinas encrustantes, não geniculadas. Este tipo de nódulos foi descrito pela primeira vez no séc. XVIII e é o resultado do crescimento de algas coralinas em substratos móveis, possível graças às suas paredes celulares calcificadas, que lhes permitem resistir à abrasão marinha.

Os bancos de rodólitos são acumulações de rodólitos que podem ser encontradas em muitas partes do mundo. As estruturas calcificadas preservam bem e podem, depois de mortas, ser incorporados nos sedimentos. Dependendo das condições durante e após a preservação, as acumulações de organismos calcários fósseis podem providenciar informação preciosa sobre os processos geológicos. Apesar de se encontrarem em todos os mares, os rodólitos são pouco conhecidos no mundo e são ainda poucos os estudos da distribuição e ecologia de bancos fósseis e recentes. A importância ecológica e económica destas formações algais e as interpretações ambientais que lhes estão associadas são ainda objecto de discussão. Dificuldades na identificação taxonómica também dificultam estas interpretações. Apesar de alguns autores mencionarem que as litofácies rodoalgais são de idade Paleogénica, estes desenvolveram-se maioritariamente durante o Neogénico. São conhecidas grandes acumulações de rodólitos do Miocénico das regiões de Tétis e Paratétis, bem como de uma variedade de locais no Pacífico tropical, Sudeste Asiático e nas Caraíbas. Na região circum-Mediterrânica, do Burdigaliano ao Serravaliano (Miocénico superior-inferior ao superior-médio) os carbonatos rodoalgais são volumetricamente mais importantes do que as fácies de recifes de corais. Algumas sequências destes depósitos de carbonato estão completamente dominadas por rodólitos. Os depósitos rodoalgais tipificados por densas concentrações de rodólitos estão globalmente distribuídos como sendo as fácies de carbonato dominantes desde o Burdigaliano ao Tortoniano inferior, atravessando o Miocénico médio e exibindo uma maior riqueza de espécies durante o Miocénico inferior e médio. Assim como a paleoclimatologia tornou-se um tema central da sedimentologia de carbonatos e a paleoecologia é particularmente importante para a investigação sobre o clima porque os biotas que segregam carbonatos são "arquivos" muito sensíveis do clima.

RESUMO

Este projeto de doutoramento tem como objetivo estudar os depósitos de rodólitos Miocénicos dos arquipélagos Atlânticos dos Açores, Madeira, Canárias e Cabo Verde a fim de compreender a sua composição específica, a sua ecologia e as relações (paleo)biogeográficas, bem como testar se os fatores locais foram mais importantes para a escassez relativa ou excedente de rodólitos do que algumas das possíveis influências globais que também tiveram impacto no mundo Miocénico.

O presente trabalho expõe uma gama de tafofácies e dinâmica sedimentar em depósitos de rodólitos fósseis e recentes do domínio Macaronésico. Foi dada especial atenção ao Arquipélago dos Açores, onde foram feitos estudos acerca do tamanho e forma, bem como estudos taxonómicos, quer para os rodólitos fósseis, quer para os recentes. Estes dados ajudam a compreender melhor as limitações ambientais na distribuição do tamanho e forma das acumulações de rodólitos fósseis encontradas noutros locais em ilhas volcânicas no Oceano Atlântico nordeste. Também foram criadas reconstruções paleoambientais de jazidas fósseis seleccionadas, de modo a obter informação detalhada sobre o ciclo de vida (e morte) dos rodólitos que vivem num cenário de vulcanismo activo no meio do oceano. Por fim, técnicas de catodoluminescência foram aplicadas a rodólitos Pliocénicos da ilha de Santa Maria (Açores) no intuito de perceber a distribuição dos elementos-traço no talo das algas. Isto permite comprender a influência da actividade vulcânica devido à extrusão de lavas e produtos associados e/ou a presença de fontes hidrotermais activas de pouca profundidade, a qual se reflete na química da água do mar que, por seu turno, fica mimetizada na elevada concentração de Mn^{2+} que os rodólitos analisados através desta metodologia patenteiam.

AUTHOR'S DECLARATION

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the result of the candidate's own independent research performed at the University of the Azores, Department of Oceanography and Fisheries, between January 2012 and December, 2015.

Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author and not necessarily those of the University.

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CHAPTER 1

GENERAL INTRODUCTION

Introduction

An island is a solitary mountain in the sea and is the result of lava erupting from the sea floor reaching the ocean's surface.

Ocean island volcanoes constitute some of the most prominent and rapidly-formed features on the Earth's surface (Ramalho, 2011). Oceanic islands have been associated with the study of evolution since Darwin (1859) (Johnson *et al.*, 2012; Ávila, 2013).

Islands harbour numerous discrete ecosystems and represent geographical entities isolated by oceanic barriers that reduce genetic interchanges with continental areas (Ávila, 2013) which makes them prime localities to look at present and past coastal biotopes and sedimentary processes in an ocean setting, as well as places to gain insights on ancient patterns of wind and ocean current (Johnson *et al.*, 2014). The rapid and dramatic ecological changes resulting from geological dynamics, associated with historical and contemporary volcanic and erosional activity promote fast rates of endemic speciation, making islands ideal natural laboratories for the study of evolution (Ávila, 2013).

Island groups from the North Atlantic realm of Macaronesia, which include the Azores, Madeira, Selvagens, Canary and Cape Verde Archipelagos, have a volcanic history tracking back to the Oligocene or older (Johnson *et al.*, 2014). Additionally, many of the Macaronesian islands were subjected to uplift, making them particularly rich in exposed marine sedimentary and volcanic sequences (Johnson *et al.*, 2014 and references therein).

The relatively isolated oceanic islands that form the Azores archipelago first appeared in the middle of the northern Atlantic in the Late Miocene at around 6 Ma (Ramalho *et al.*, 2014). As volcanic islands, these once empty habitats suffered colonization from elsewhere. The nearest colonizing source is the Madeira archipelago, presently about 900 km southeast, but other plausible sources are the Iberian and West European Atlantic shores, the Mediterranean, the western African shores, the Canary Islands and also the Caribbean region (Ávila, 2013).

The Azorean islands provide a diverse range of habitats for algal colonisation at intertidal and subtidal levels down to 100 m depth (Tittley and Neto, 2006). With a warm temperate climate, the Azores have a moderately rich benthic marine algal flora with 377 species (Tittley *et al.*, 2009; Rosas-Alquicira *et al.*, 2009; Léon-Cisneros *et al.*, 2009).

The first studies of (non-fossil) coralline geniculate red algae (Corallinales, Rhodophyta) in this region go back to the beginning of the XIX century with the paper from Lamarck (1815: 233, 237) for the Canary Islands. An important contribution to the knowledge of Macaronesian Corallinales, with an extensive collection for the region, was done by the Dutch oceanographic expeditions CANCAP, in the 1970s and 1980s, with material collected in the Azores, Madeira, Selvagens, the Canaries and Cape Verde Islands (Rosas-Alquicira *et al.*, 2011).

Fossil coralline algae from Santa Maria Island (Azores) have been described as "fragments de Lithothamnium" (Berthois, 1950) or as "fragments d'algues calcaires" (Zbyszewski and Ferreira, 1962), and the rhodoliths have been referred to as rolled debris ("Les lithothamnium s'observent aussi en debris roules" - Berthois, 1950). The first phycological study for the same island was done by Amen *et al.* (2005) on a Quaternary deposit.

Rhodoliths

Rhodoliths are nodules composed of coralline red algae (Rhodophyta). The coralline algae are the most consistently and heavily calcified group of red algae. The calcification involves high magnesium calcite (and occasionally brucite) precipitation within most cell walls (Miyata *et al.*, 1980; Bosence, 1991). Rhodoliths are unattached and roll freely on the sea floor. Circumrotary movement pushed by wave action and bottom currents allows for organic growth in a concentric pattern due to photosynthesis on all surfaces with equitable access to sunlight in shallow subtidal waters (Johnson *et al.*, 2011). An individual rhodolith may be composed of one or several coralline species and may also include other encrusting organisms such as bryozoans, foraminifers and gastropods. Rhodoliths can also be formed by some geniculate corallines and other red algae, such as members of the Peyssonneliaceae (Harvey and Woelkerling, 2007). Rhodoliths can form around a rock core or other organic fragment and develop by concentric growth - nucleated rhodoliths - indicating that they can grow from fragments or from spore settlement on a hard substrate. Fragments and hard substrate may originate in the bed or be broken from nearby reefs and be transported to the site of growth. Rhodolith beds are aggregations of rhodoliths, and such beds are found in many parts of the world. Maërl may also refer to environments composed principally of such corallines, whether living or dead, or a mixture of the two (Foster, 2001).

The rhodoliths in rhodolith beds can have large effects on associated organisms, causing an increase in diversity over that of purely soft benthic habitats at similar depths (Steller and Foster, 1995; Foster, 2001). In ecological terms they are "habitat modifiers" or "bioengineers" that, by virtue of their rigid structural complexity, provide relatively stable microhabitats for other organisms. These habitats include the natural spaces within branched forms, spaces between individuals, and hard (albeit mobile) calcareous surfaces for sessile organisms and borers (Foster, 2001). Rhodoliths may be described in terms of their morphology (size, shape and structure) and their taxonomic composition (monospecific or multispecific) (Bosence, 1983b).

Size

Size is usually applicable to both recent and fossil material and independent of the internal structure of the rhodolith. For this reason weight and volume (by displacement) are not recommended (Bosence, 1983b).

Shape

Shape has been of particular interest because many observations show it can be affected by water motion, particularly spherical shapes that occur where water motion, and thus turning, is high (Foster, 2001).

A size measurement based on the long (L), intermediate (I) and short (S) axes, using the formula $\sqrt[3]{S^2/LI}$ allow to determine among spherical, ellipsoidal and discoidal shapes, based on the triangular plot applied to rhodolith by Bosence (1976, 1983b) modified from Sneed and Folk (1958). This scheme is used to classify both recent and ancient rhodoliths and in both cases rhodolith shapes have shown to be congruent and characteristic of different sedimentary environments (Bosence, 1983b).

Structure

The structure of many rhodoliths is complex and may reflect the changing conditions during their history. Three basic coralline morphologies have been found to be present in rhodoliths: laminar, branching and columnar growths (Bosence, 1983b).

Taxonomic composition

Species that form rhodoliths usually cannot be identified with certainty using only growth form or other external morphological features. Accurate and reliable identification usually requires sectioning for examination of pertinent vegetative and reproductive characters. Identification is a two-tiered process involving identification of specimens to genus followed by identification of specimens to species (Irvine and Chamberlain, 1994; Harvey and Woelkerling, 2007).

The unification of taxonomy of recent and fossil corallines is crucial to the understanding of their phylogeny, palaeoecology and palaeobiogeography (Rasser and Piller, 1999). Diagnostic anatomical features used for the taxonomical identification of both recent and fossil corallines are: (1) thallus organization, (2) cell connections, (3) shape and arrangement of epithallial cells and subepithallial initials, (4) reproductive organs and (5) measurements of thalli cells and reproductive organs conceptacles (Braga *et al.*, 1993; Rasser and Piller, 1999).

Fossil rhodoliths from dozens of genera are attributed to seven subfamilies (Sporolithoideae, Melobesioideae, Choreonematoideae, Lithophylloideae, Mastophoroideae, Amphiroideae, and Metagoniolithoideae) with a geological record tracing back to the Lower Cretaceous System (Aguire *et al.*, 2000, 2010).

In their classification, rhodoliths are also separated into monospecific comprising all those composed by one single species and multispecific for those containing more than one species of coralline algae).

Habitat

According to Foster (2001), the living algae that build rhodoliths are known to occur in all present-day seas over a wide spectrum of latitudes from tropical to polar settings.

Geological significance

The longevity of coralline genera, together with their ecological restrictions and plasticity of growth forms in relation to environmental parameters, makes the corallines a good group for palaeoenvironmental analyses (Bosence, 1991). Because coralline algae are heavily calcified, they occur extensively as fossils (Irvine and Chamberlain, 1994). Adey (1979) suggested that they evolved in high latitudes during the Mesozoic, moved into cryptic situations in low latitudes during the early Tertiary, evolving later as "sun forms" tolerant of bright light conditions. The rhodalgal habitat is considered to have achieved maximum global domination as a carbonate facies during the Middle Miocene at about 15 Ma, before undergoing a decline concomitant with resurgence of the hermatypic-coral habitat during the later Neogene (Halfar and Mutti, 2005).

Rhodoliths also represent an important carbonate source even in siliclastic-dominated environments under intertidal conditions (Perry, 2005).

The status of these coralline red algae as contributors to the rock record is being reassessed and they are recognized as playing a significant role in the bulk production of limestone (Johnson *et al.*, 2011).

Few studies consider fossil rhodoliths from the many islands of Macaronesia scattered through the Atlantic Ocean off the northwest coast of Africa (Johnson *et al.*, 2011). According to Foster (2001 and references therein), geologists are interested in rhodoliths because of their representation in calcareous sediments and fossil deposits. The latter have been of particular interest as rhodoliths were perhaps even more abundant at times in the geological past than they are today (e.g. Cambrian–Late Devonian) and can register palaeoenvironmental conditions. At coarse scales, the presence of fossil rhodoliths may indicate that a deposit was formed in the photic zone. At finer scales, they may indicate depth, sea level, and hydrodynamic conditions. These indications often require assuming the deposit represents the original site of growth (i.e. rhodoliths were not transported from elsewhere), that rhodolith shape indicates water motion (and water motion is higher in shallow water), and that species and their living depth distributions are accurately known.

This thesis reports on research undertaken to study species composition, ecology and (palaeo)biogeographical relationships of both fossil and extant rhodoliths from Azores Archipelago. It also compares the Azorean rhodoliths with the ones from other Macaronesian archipelagos (Madeira, Canary Islands and Cape Verde).

Thesis Outline

The proposed goals for this thesis aimed the following:

- To produce taxonomical studies of the Neogene rhodolith forming coralline algae from selected outcrops in Santa Maria Island (Azores Archipelago).
- To compile the available information on the coralline algal species forming rhodoliths, using both historical and the most recent literature.
- To do the geological description of selected outcrops for rhodolith colleting (all rhodoliths will be referred to their stratigraphic position).
- To determine the extent of the found living beds and try to understand the environmental conditions that may affect their geographical distribution.
- To do a comparative study of the existing beds and fossil deposits in order to determine when and how the current can be used in interpreting the fossil.
- To establish a palaeoenvironmental relation for the fossil rhodolith assemblages found and the existing living rhodolith beds.

The research developed in order to achieve the proposed goals of this project resulted in the following thesis structure:

Chapter 1 introduces the theme of this PhD thesis and outlines the structure of the work.

Chapter 2 assesses living and fossil rhodolith beds from the Macaronesian realm approaching a range of taphofacies and sedimentary dynamics. This contribution is organized into two main subdivisions: 1) a description of modern coastal deposits with substantial rhodolith debris as related to shelf development, based on an island example drawn from each of the archipelagos in the Macaronesian realm (sensu lato), and 2) a review and comparison of fossil rhodolith beds representing a wide range of taphofacies reported in the literature, together with new material previously unreported.

Chapter 3 surveys rhodoliths dredged from the insular shelf of Pico Island (Azores), which are studied in relation to their size and shape, in order to obtain reliable data derived from localities with a known depth and distance from the shore. This kind of data helps to better understand the environmental constraints on the size and shape distributions of rhodolith assemblages found as fossils elsewhere on volcanic islands in the northeast Atlantic Ocean.

Chapter 4 focuses on fossil rhodoliths from a Neogene sequence at Santa Maria Island (Azores), in order to gain further insight on the life cycle (and death) of rhodoliths living within a mid-ocean active volcanic setting.

Chapter 5 presents a taxonomic study of the rhodolith forming coralline algae species during the Neogene of Santa Maria Island, mentioned in Chapter 4.

Chapter 6 introduces cathodoluminescence techniques applied to Pliocene rhodoliths from Santa Maria Island in order to gain additional insight regarding the trace element content distribution throughout the algae thalli, and to ascertain palaeoenvironmental interpretations. Two types of luminescence were obtained: (1) high and (2) low luminescence. Rhodoliths with high luminescence are related with high concentrations of Mn^{2+} in seawater, whereas low luminescence rhodoliths are related with low concentrations of Mn^{2+} in seawater. The influence of volcanic activity due to the extrusion of lavas and associated products and/or the presence of active shallow-water hydrothermal vents, was reflected in the sea water chemistry, with penecontemporaneous palaeoshores of the island featuring a high sea water concentration of Mn^{2+}, which mirrored on the rhodolith Mn^{2+} high concentration.

Chapter 7 presents the final considerations.

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