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Pleistocene coralline algal buildups on a mid-ocean rocky shore – Insights into the MIS 5e record of the Azores

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ABSTRACT

Located on the northern coast of Santa Maria Island (Azores Archipelago, central North Atlantic), the Lagoinhas section preserves a carbonate buildup correlated with Marine Isotope Substage (MIS) 5e, the warmest interval of the Last Interglacial. The buildup is formed mainly by crustose coralline algae (CCA) identified as *Spongites* sp., and some subordinate crusts of *Lithophyllum* sp. and *Neogoniolithon* sp., as well as cf. *Titanoderma* sp. Extant CCA buildups are not recorded in the archipelago. Herein, we describe in detail the morphological and taphonomical features of the Lagoinhas CCA buildup and interpret the environment in which it grew. Additionally, this buildup is compared with another of similar age, exposed in the Prainha-Praia do Calhau section on the island's opposite southern coast. The hydrodynamic regime appears to play a crucial role in the development of Azorean CCA buildups during the MIS 5e.

1. Introduction

Crustose coralline algae (CCA) are non-geniculate red algae (Rhodophyta) that produce Mg-calcite thalli, growing either as stable buildups, known as algal ridges, algal reefs or Coralligène (Steneck et al., 1997; Ballesteros, 2006; Bracchi et al., 2015, 2016, 2017; Marchese et al., 2020), or growing around a nucleus to form free-living nodules known as rhodoliths (Bosellini and Ginsburg, 1971; Adey, 1978, 1986; Bosence, 1983; McCoy and Kamenos, 2015; Aguirre et al., 2017). CCA buildups may occur from the polar regions (Freiwald and

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Henrich, 1994; Adey et al., 2015) to the tropics where they constitute an important element of coral reefs, acting as frame-builders and contributing significantly to reef calcification and cementation (Fabricius and De'ath, 2001; Caragnano et al., 2009). This role is particularly important in high-wave energy environments where wave-resistivity is crucial for reef growth (Littler and Littler, 2013; Weiss and Martindale, 2017). In reefal and other settings, CCA are also key habitat providers to many benthic species, including several species with economic interest (Bak, 1976; Basso, 2012; Littler and Littler, 2013). Moreover, CCA are one of the world's most important calcium carbonate producers (second only to coral reefs, to which they also contribute) and in the Atlantic Ocean, in the near-absence of coral reefs, they even constitute the most important reef builders (Adey, 1975; Steneck and Adey, 1976; Gherardi and Bosence, 2001; Tâmega et al., 2014; Spotorno-Oliveira et al., 2015), either on their own or together with other encrusting organisms such as corals, bryozoans, serpulids and molluscs (Bosence, 1983; Di Geronimo et al., 2002; Basso et al., 2007; Aguirre et al., 2014).

Buildups are particularly important in marine geomorphology, given that calcareous algae are capable of forming extensive solid substrates on an originally unconsolidated sea floor (Basso et al., 2007; Aguirre et al., 2012; Bracchi et al., 2017; Lo Iacono et al., 2018), or building algal crests on reef edges and thus serving a key reef-binding role, and consequently becoming important sediment contributors (Adey, 1986). Common features of these buildups include decimetre to metre-sized three-dimensional erosional cavities, depressions filled with sediment, and the occurrence of columns and protruding ledges departing from the main mass (Basso et al., 2007). Their architecture and morphology are controlled mainly by taxonomic composition (Ingrosso et al., 2018) as well as by biological carbonate productivity that responds to climate, oceanography, physiography, changes in accommodation space, substrate stability and sediment input (Rasser and Piller, 2004; Bracchi et al., 2015 and references therein).

Several types of modern CCA frameworks have been described based on the climate, type of substrate and water depth (Table 1).

Whereas buildups constituted by CCA are well known from present oceanic settings, descriptions of fossil representatives are still uncommon (Rasser and Piller, 2004; Nalin et al., 2006; Titschack et al., 2008; Bracchi et al., 2016, 2019; Weiss and Martindale, 2017). The aims of the present study are thus to: 1) provide identification and description of an in situ CCA buildup from the Pleistocene fossil record of the central North Atlantic Azores Archipelago, located at the Lagoinhas section on the high-energy northern coast of Santa Maria Island; 2) compare the buildup on the windward northern coast with a coeval buildup on the leeward, more sheltered southern coast of the same island; and 3) contribute to our scientific understanding of MIS 5e and its fossil record, given the importance this interglacial holds as case study (or proxy) to the ongoing global warming and associated future climate changes.

Table 1
Types of modern CCA frameworks according to climate, substrate type and water depth (after Ginsburg and Schroeder, 1973; Bosence, 1985; Adey, 1986; Steneck et al., 1997; Di Geronimo et al., 2002; Bracchi et al., 2015).

Framework type	Climate	Substrate type	Water depth
Algal ridges	Tropical	Rocky	Intertidal to shallowest subtidal
Algal cup reefs	Tropical	Rocky	Intertidal to shallowest subtidal
Trottoirs	Temperate	Rocky	Intertidal to shallowest subtidal
Coralligène	Temperate	Rocky	Shallow subtidal down to −160 m
Coralligène de Plateau	Temperate	Sedimentary	Shallow subtidal down to −160 m

2. Geological setting

2.1. Santa Maria Island

Santa Maria Island in the Azores (central North Atlantic), the oldest in the archipelago, is remarkably rich in exposed marine fossiliferous sediments (Ferreira, 1955; Zbyszewski and Ferreira, 1962; Madeira et al., 2011; Ávila et al., 2012, 2015a, 2015b, 2015c, 2016, 2020; Meireles et al., 2012; Rebelo et al., 2014, 2016a, 2016b; Santos et al., 2015; Uchman et al., 2016, 2017, 2018; Hyžný et al., 2021) and submarine volcanic successions (Serralheiro and Madeira, 1990; Serralheiro, 2003; Johnson et al., 2017; Ramalho et al., 2017; Uchman et al., 2020). This richness, explained by its distinct geological history, was characterised by an initial period (from 6 to 3.5 Ma) during which volcanism, erosion, sedimentation and fast subsidence contributed to the formation of submarine sequences. Later, in the last 3.5 it reversed to a striking uplift trend Myr (see Figs. 6 and 7 of Ramalho et al., 2017), thus contributing to the exposure of these sequences, which otherwise would be inaccessible. This trend in uplift, in conjunction with marine erosion and glacio-eustatic oscillations, was also responsible for the formation of a staircase of raised and submerged marine terraces that extend from the present-day shelf-edge at −140 m to up to +200 m (or possibly +230 m) in elevation (Ramalho et al., 2017, 2020; Ricchi et al., 2018, 2020). It is in this context that well-preserved fossiliferous sections attributed to the last interglacial (e.g. see Callapez and Soares, 2000; Ávila et al., 2002; Ávila et al., 2010; Ávila et al., 2015a; Amen et al., 2005; Meireles et al., 2013) are found on both the southern and northern coasts of the island, perched atop former rocky shore platforms which are now between 2 and 11 m in elevation (the actual terrace shore angle is at 7–11 m in elevation – see Fig. 1B) (Ávila et al., 2015a; Ramalho et al., 2017; Ricchi et al., 2018). The Lagoinhas section, the object of this study, is one of such outcrops, being located on the island's north coast (Fig. 1).

The Lagoinhas section displays a fossiliferous marine sequence, including a well-developed CCA buildup, perched atop a former shore platform eroded on the volcanic succession of the Anjos Volcanic Complex (dated 5.8–5.3 Ma; (Sibrant et al., 2015)Ramalho et al., 2017). The fossiliferous marine sediments are, in turn, covered by Pleistocene-Holocene slope deposits and colluvium, which offered some protection to the buildup, ensuring its preservation.

2.2. Present-day local hydrodynamics

The remote Azores Archipelago is impacted by northwesterly trade winds, and frequently subjected to high wave energy (Quartau et al., 2010, 2012; Rusu and Soares, 2012). Extreme storms brought by the North Atlantic Oscillation and Eastern Atlantic atmospheric circulation affect the Azores at least once every seven years (Borges, 2003; Andrade et al., 2008; Zhao et al., 2019; Ricchi et al., 2020). Rare hurricanes can affect the islands with storm surges from the south and southeast (Elsner et al., 2000; Andrade et al., 2008; Johnson et al., 2017). A recent study by Ricchi et al. (2020) for the island of Santa Maria showed that the prevailing swells approach the island from the northwest (35%) and west (22%), with average significant wave heights (Hs) of 2.14 m and 2.44 m, respectively (Fig. 2). Waves from north and northeast are also frequent (respectively 19% and 12%) but of lower Hs (respectively 1.92 m and 1.83 m). Although the remaining directions are less significant (< 5% each), waves from the southwest can still reach 2.45 m, during 5% of the year, normally occurring during the arrival of tropical depressions from the Caribbean, during the North Atlantic hurricane season.

Finally, in terms of tides, the mid-oceanic Azores are subjected to a micro-tidal regime, with a mean annual tidal amplitude of approximately 0.9 m. It is presumed that this regime did not vary significantly during the last interglacial.

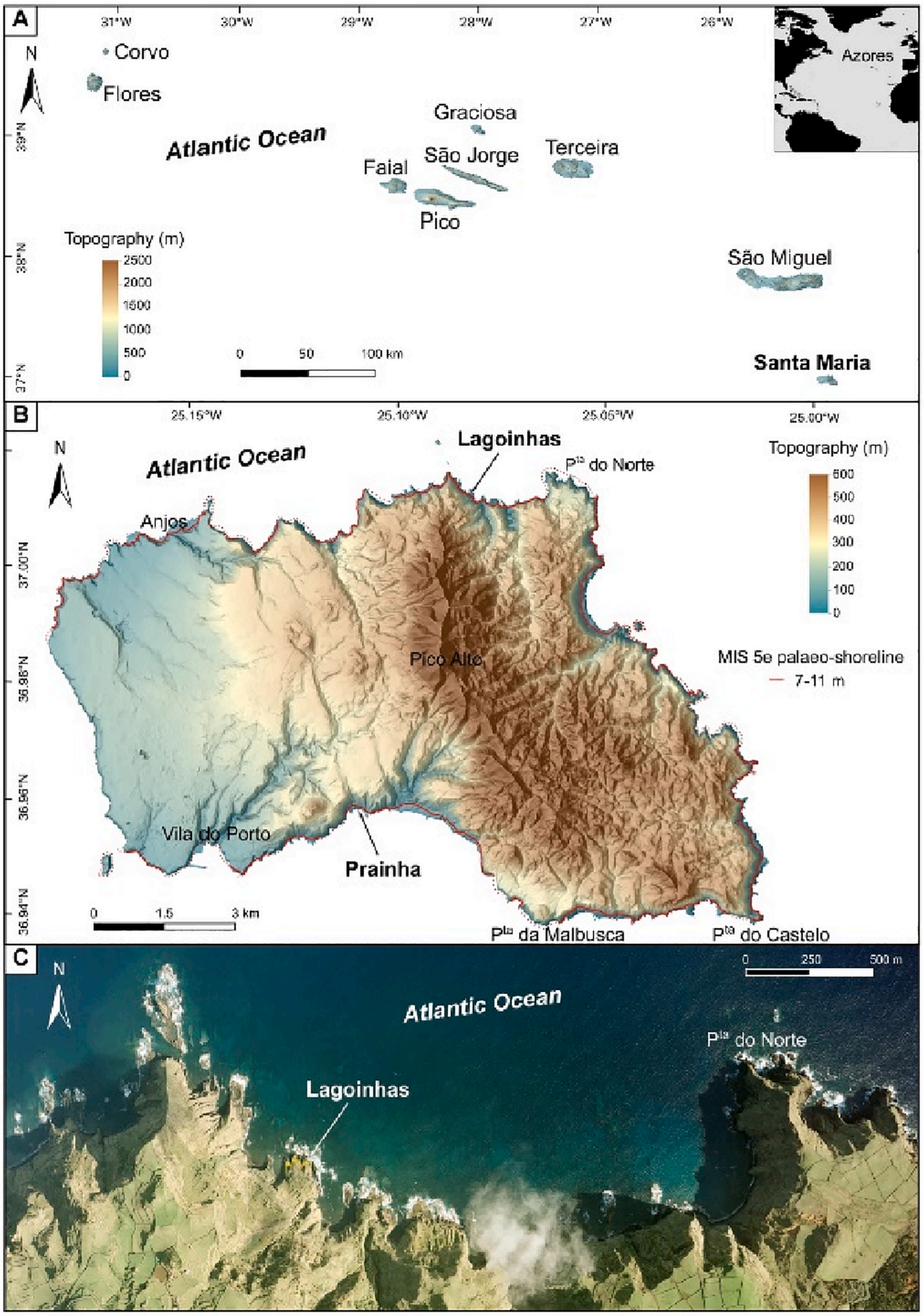

Fig. 1. Geographical location of the Lagoinhas outcrop and study area in the wider context of the Atlantic Ocean. (A) Location of Santa Maria Island within the Azores Archipelago (inset shows the location of the Azores in the central North Atlantic); subaerial topography was generated from a 1:25,000 scale digital altimetric database from Instituto Geográfico do Exército; (B) Digital elevation model (~2 m in resolution) of Santa Maria Island showing the location of Lagoinhas and Prainha sequences within the MIS 5e palaeo-shoreline reconstruction of Ramalho et al. (2017); subaerial topography was generated from a 1:5000 scale digital altimetric database; (C) Vertical aerial photo of the study area, showing the location and extent of Lagoinhas sequence; vertical aerial photo number 6177, row 2, at an approximate scale of 1:18,000, dated of September 2005, and provided by Secretaria Regional do Turismo e Transportes.

2.3. CCA buildups and previous studies

Pleistocene buildups formed by crustose coralline algae (CCA) developed both on the north and south coasts of the island, and were hitherto uplifted to the present positions that range between 2 and 7.4 m above present mean sea-level (Callapez and Soares, 2000; Ávila et al., 2002; Ávila et al., 2010; Amen et al., 2005).

The first study of the Lagoinhas outcrop, on the north coast, was compiled by Callapez and Soares (2000), who focused on the composition of mollusc species and their palaeoecological interpretation. Later, Ávila et al. (2002, 2007, 2009, 2015a) re-described the stratigraphic succession, and revised the checklist for molluscs, as well as the palaeoecological reconstruction for both outcrops Lagoinhas and Prainha, on the north and south coasts, respectively.

Previous research (Callapez and Soares, 2000; Ávila et al., 2002, 2007, 2009, 2015a) paid little attention to the fossil CCA buildups on the north coast at Lagoinhas. The framework supports a varied epifauna of molluscs, echinoderms and bryozoans. Macrobioerosion structures in the biostrome are assigned to the ichnogenus *Gastrochaenolites* Leymerie, 1842 (Ávila et al., 2009, 2015a). The sequence continues with a 70–cm thick layer of poorly consolidated dominantly bioclastic white-yellowish marine sands, which in turn are capped by fine terrigenous sediments (poorly consolidated colluvial sandstones and breccias) (Ávila et al., 2002). The overlying white-yellowish unconsolidated sands (facies 4, Fig. 4 in Ávila et al., 2015a) exhibit thicknesses as much as ~0.7 m and are rich in very-well preserved fossil assemblages dominated by molluscs. In total, for the CCA buildup and the fossiliferous sands, 57 specific taxa were reported (46 gastropods, 5 bryozoan, 3 bivalve and 3 echinoderm species), testifying a warm temperate rocky shore palaeoenvironment with biogeographical relationships with the

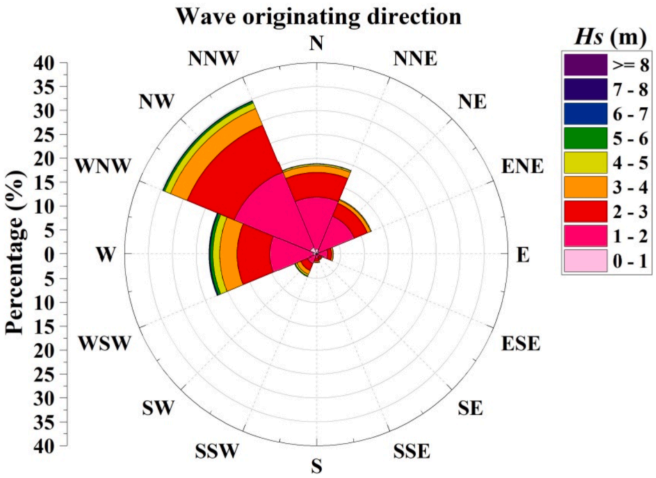

Fig. 2. Offshore significant wave heights around Santa Maria Island (modified after Ricchi et al., 2020).

northeastern Atlantic and the Mediterranean (Madeira et al., 2011; Ávila et al., 2015a).

3. Methods

A stratigraphic cross section was constructed, of the exposed sequence at Lagoinhas (37°00′47.5” N, 25°04′58.1” W). The stratigraphy of the Prainha section is described in detail in Amen et al. (2005). Seven rock samples of the CCA buildup were randomly collected at within the succession for preparation of thin sections. Thirty thin sections (4.8 × 4.8 cm) representative of the CCA framework and sediment composition were studied under a compound polarizing microscope (Leica DM750P) equipped with a digital camera (Leica ICC50W). Anatomical and taxonomical terminologies on corallines conform to the works by Braga et al. (1993), Irvine and Chamberlain (1994), Rasser and Piller (1999) and Hrabovský et al. (2016); growth form terminology follows Woelkerling et al. (1993). Cell and conceptacle dimensions were measured according to Rasser and Piller (1999) using ImageJ. Mean (M) and standard deviation (SD) were calculated for both cells and conceptacles, whenever the number of measurements allowed ($n = 5$). All material is stored in the fossil collection (DBUA–F) of the Department of Biology of the University of the Azores (Faculty of Science and Technology), Ponta Delgada, São Miguel Island.

4. Results

4.1. Description of the CCA buildups

The Lagoinhas and Prainha CCA buildups developed in some spots directly over the basalt surface, whereas in other places they grew on top of bioclastic sediments (Figs. 3 and 4).

4.1.1. Prainha section

On the southern coast, the Prainha outcrop (36°57′06.8” N, 25°06′47.1” W) is exposed at an elevation of 3 to 4 m above present mean sea level (Serralheiro et al., 1987; Serralheiro, 2003), exhibiting a lateral extension of ~800 m (Fig. 3A) (Ávila et al., 2002). The outcrop consists of poorly consolidated shallow-water marine deposits (conglomerates, limestones and sandstones/calcarenites) overlying an irregular shore platform carved in the subaerial basaltic sequence of the Anjos Volcanic Complex. Along the outcrop, many parts of the original buildup have been eroded. The visible CCA buildup with warty to lumpy morphologies growing one over the other and with a maximum thickness of ~50 cm, covers a coeval beach conglomerate or, locally, developed directly on the basaltic substrate (Figs. 3 C, E, Fig. 4). Fragments of mollusc shells, bryozoans, and echinoderms, are accessory components (Ávila et al., 2009). Amen et al. (2005) described four species of Corallinaceae: *Spongites fruticulosus* Kützing, 1841 being the main builder of the framework, followed by *Lithophyllum incrustans* Philippi, 1837, *Neogoniolithon brassica-florida* (Harvey) Setchell and Mason, 1943, and *Titanoderma pustulatum* (Lamouroux) Nägeli, 1858. The buildup shows abundant macro-bioerosion structures, mostly clavate borings, assigned to the ichnogenus *Gastrochaenolites*. Remains of the endolithic bivalve *Leiosolenus aristatus* (Dillwyn, 1817) (= *Myoforceps aristatus*) can still be found in situ inside most of the borings. The boring clionid sponge *Entobia* Bronn, 1838 is present as well. The upper surface and complete vertical section of the CCA buildup exhibit fractures that resulted from local extension (Ávila et al., 2009, 2015a). The buildup is overlain by 1.3–2.5 m thick, yellowish, partly cross-laminated, dominantly bioclastic, uncemented sands that also fill most of these fractures. The grain-size distribution is dominated by the 125–250 μm fractions. The bioclasts consist almost exclusively of small mollusc fragments. Lenses with ripple marks, trace-fossils and/or root casts are preserved locally (Ávila et al., 2002, 2015a). The deposits correspond to a beach foreshore (intertidal) facies and show cross-lamination. A thin carbonate crust of pedogenic origin occurs at the top of the bioclastic sandy sediments. The crust consists mostly of micrite that precipitated together with clay and other silt-sized impurities and exhibits a clotted texture. Sediment below the carbonate crust includes bioclasts (molluscs, echinoid spines, and geniculate coralline algae), poorly-sorted volcanic grains and very poorly-sorted rock fragments. Aeolian dunes and colluvial-alluvial deposits cover the carbonate crust (Ávila et al., 2009, 2015a) (Fig. 4).

4.1.2. Lagoinhas section

The Lagoinhas buildup is today expressed as an erosional relict therefore the original lateral and vertical extent is unknown. The buildup exhibits a variable height from 6 to 30 cm and covers an area up to 1110 m^2, exposed along a ~ 80 m section (Fig. 3). Initial growth of the buildup starts directly on the basalt or the bioclastic sediments with an encrusting form that transitions into warty, lumpy and branching forms, typically infilled with sediment (Fig. 5A–C). Abundant borings *Gastrochaenolites* cf. *torpedo* Kelly and Bromley, 1984 produced by the endolithic bivalve *Leisolenus aristatus* are in the CCA buildup (Figs. 5D, 6A–D). These occur in patches on the seaward side of the buildup. Moulds of shells are preserved in some borings, but most of them are empty and partly or completely filled with sands different from the overlying bioclastic sand. In some places the CCA framework is bored with *Entobia* isp. pProduced mostly by clionid sponges (Fig. 6B, D). Several specimens of the infralittoral hard bottom trochid gastropod (*Calliostoma lividum* Dautzenberg, 1927) and disarticulated valves of the Semelidae bivalve *Ervilia castanea* (Montagu, 1803), a common dweller of subtidal, were also incorporated in the buildup (for details on mollusc species see Ávila et al., 2002). Some small volcanoclastic pebbles are also encrusted within the buildup (Fig. 5C).

Visibly, the shore platform on which the Lagoinhas deposits sit is irregular with a relief up to 30 cm above the general surface. Moreover, it exhibits large intertidal potholes (1–3 m in diameter, ~80 cm deep; Fig. 5E) on its seaward edge, eroded into the rocky substrate by the gyratory grinding action of pebbles, cobbles and boulders stirred by wave motion. These fossil potholes are filled by the same well-consolidated beach conglomerates that rest on the shore platform, and which exhibit a fossiliferous calcarenitic matrix enveloping well-rounded basaltic boulders, cobbles, and pebbles (Fig. 5F). Among them are pebbles encrusted by coralline algae. The thickness of the algal encrustation around the volcanic nucleus is generally thin, therefore these elements, with a maximum diameter of 5 cm, would be more properly defined as coated grains (Steneck, 1986). Inside the potholes, the cobbles and boulders are usually larger than the ones resting on the rocky shore platform, and so are the rhodoliths, which are rare outside the potholes. Fragments of geniculate corallines often are present in the framework cavities and in the sediments (Fig. 7).

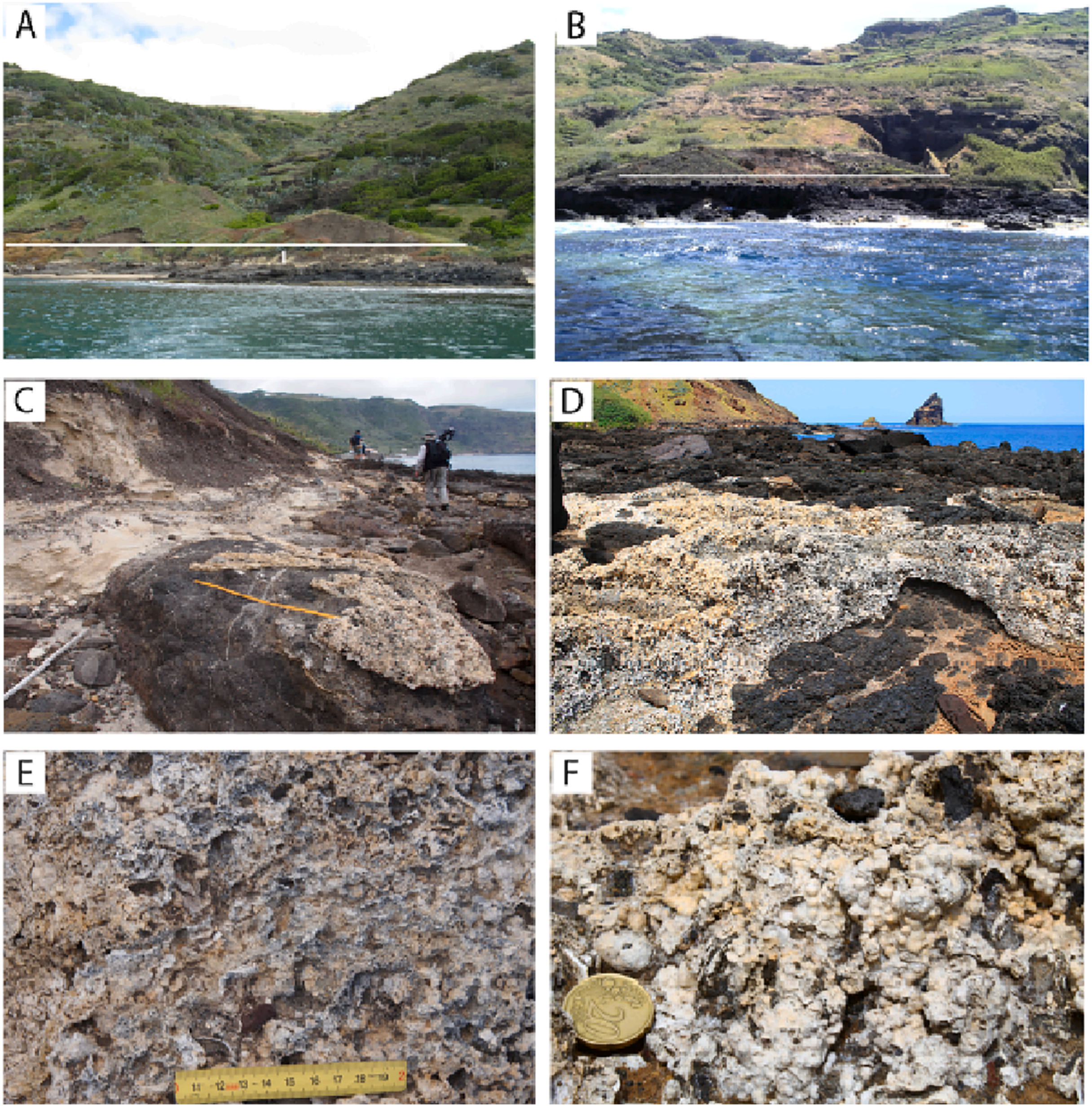

Fig. 3. General views of the A) Prainha outcrop on the southern coast (white horizontal line marks the lateral extent of the outcrop ~800 m and vertial white line the height of the CCA buildup ~50 cm) and B) the Lagoinhas outcrop on the northern coast (white line marks the lateral extent of the outcrop ~100 m); Aspect of the CCA buildups of C) Prainha and D) Lagoinhas; Details of the CCA buildups of E) Prainha and F) Lagoinhas.

Poorly consolidated bioclastic sands (white/yellow in coloration) rest on top of the CCA buildup (or directly above the substrate when the CCA buildup is absent). These sediments are mostly composed of shell debris mixed with subordinate amounts of volcanic lithoclasts/mineroclasts, in varying proportions. These sands exhibit a variable thickness, up to 50 cm; the top is deeply eroded with a very irregular relief, suggesting the presence of erosional gullies. Unconformably above these sands, a package of dark brown terrigenous sands can be found, completely filling the underlying erosive topography on the bioclastic sands. This package attains a maximum thickness of up to 1.5 m and exhibits rare sub-rounded to sub-angular pebbles "floating" in the terrigenous matrix, as well as some incipient calcrete crusts (and possibly rhyzoconcretions) towards the top. The sequence is capped by an unstratified and unconsolidated colluvium-alluvial slope deposit, which abuts against the back beach cliff/slope; the top of the colluvial fan rises several tens of meters in continuity with the present-day topography of the slope behind.

4.2. *Coralline taxonomy*

Two components of CCA are identified as being the main framework builders of the Lagoinhas buildup. *Spongites* sp. is present in 92% of the studied thin sections, and *Lithophyllum* sp. in 34%. Few thalli of *Neogoniolithon* sp. and *Titanoderma* sp. also were found within the framework. The subfamily for *Spongites* is still under revision (Rösler et al., 2016; Caragnano et al., 2018), and therefore a subfamily assignment for this genus is not given here (Fig. 8).

Order **Corallinales** Silva and Johansen, 1986.
Family **Spongitaceae** Kützing, 1843.
Genus ***Spongites*** Kützing, 1841.
***Spongites* sp.**

(Fig. 8A)
Description: Growth form encrusting to lumpy. Thallus thickness

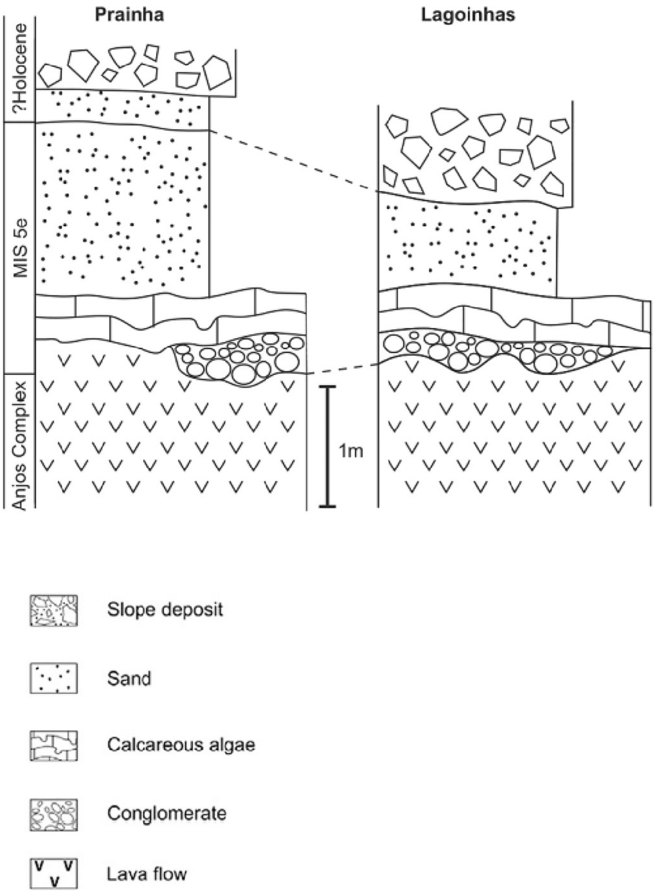

Fig. 4. Simplified strip logs of the Prainha and Lagoinhas sections, representing main lithologies, and contacts (modified after Ávila et al., 2015a).

varies from 674 μm in encrusting portions to 7.04 mm in the lumpy portions. The thallus organisation is monomerous and non-coaxial. The core filaments, 116–434 μm in thickness, curve upwards to become perpendicular to the dorsal surface in the peripheral region. Core cells are 13–27 μm (M = 20, SD = 4) in length, and 8–18 μm (M = 11, SD = 2) in diameter. Cells of peripheral filaments are 13–22 μm (M = 17, SD = 2) in length, and 7–14 μm (M = 10, SD = 2) in diameter. Some cells of contiguous filaments are joined by cell fusions. Epithallial cells flat and round, but not flared, 7–11 μm (M = 8, SD = 1) in diameter and 5–7 μm (M = 6, SD = 0.7) long.

Sporangial uniporate conceptacles, usually completely raised above thallus surface, older conceptacles can become buried in the thallus. Conceptacles are rounded in shape, 316–482 μm (M = 395, SD = 38) in diameter and 137–205 μm (M = 177, SD = 17) in length. Pore canals in section vary from triangular to cylindrical shapes, 69–192 μm (M = 110, SD = 23) in diameter and 10–164 μm (M = 108, SD = 26) in height. The pore canals are lined by cells arranged subparallel to the conceptacle roof. In some conceptacles, remnants of a columella are present.

Remarks: The genus *Spongites* comprises those corallines with non-geniculate, monomerous, or thin dimerous thalli, non-coaxial primigenous filaments without palisade cells, and trichocytes that can be absent, single or in vertical row. The cells of adjacent filaments are joined by cell fusions, and the conceptacles are uniporate. The pore canals of tetrasporangial conceptacles are bordered by cells that arise from peripheral roof filaments, protruding into the canal, and are oriented more or less parallel to the roof surface (Penrose and Woelkerling, 1992; Braga et al., 1993; Hrabovský et al., 2016). The monomerous non-coaxial thallus, the presence of cell fusions, the uniporate conceptacles and the cell filaments surrounding the conceptacle pore canals subparallel to the roof surface of the studied specimens indicate the genus *Spongites*.

Studied thin sections: DBUA–F 1107(1.1); 1107(1.2); 1107(1.3); 1107(1.4); 1108(2.1); 1108(2.2); 1108(2.2.1); 110(3.1); 1109(3.1.1); 1109(3.2); 1109(3.3); 1109(3.4); 1110(4.1); 1110(4.3); 1112(6.1); 1112(6.2); 1112(6.2.1); 1112(6.3); 1113(7.1); 1113(7.2); 1113(7.3); 1113(7.4); 1113(7.5); 1113(7.6).

***Neogoniolithon* sp.**

(Fig. 8B)

Description: The thallus organisation is monomerous and coaxial. The core region is 241–252 μm in thickness and the peripheral region is 1070–1951 μm. Cell fusions absent. Of the three conceptacles present, only two were measurable, 282–320 μm in diameter and 169–214 μm in height, but the pore canals were not measurable.

Remarks: Only one fragment of this type of thallus and a coaxial core were found. The uniporate conceptacles, the coaxial core and the cell fusions (Braga et al., 1993; Hrabovský et al., 2016) indicate that the specimen belongs to the genus *Neogoniolithon*.

Studied thin section: DBUA–F 1109(3.1); 1112(6.1).

Family **Lithophyllaceae** Athanasiadis, 2016.
Subfamily **Lithophylloideae** Setchell, 1943.
Genus ***Lithophyllum*** Philippi, 1837.

***Lithophyllum* sp.**
(Fig. 8C)

Description: The thallus organisation is dorsiventral with a dimerous construction and no palisade cells on the primigenous filaments. The thallus thickness varies from 817 to 2304 μm. Cell filaments are quite distinct and the lack of cell fusions indicate that only secondary pit connections are present. Cells are rectangular in section, and their size ranges from 6 to11 μm in diameter and from 9 to 13 μm in length. The conceptacles are uniporate, with a pronounced central columella, and some are buried in the thallus. Conceptacles measure 175–235 μm in diameter and 73–131 μm in height. The pore canal is conical in shape and varies from 19 to 66 μm in diameter and from 32 to 82 μm in height.

Remarks: The uniporate conceptacles and the absence of cell fusions place this alga in the Lithophylloideae subfamily (Irvine and Chamberlain, 1994; Hrabovský et al., 2016). The vegetative and reproductive morphologies allow *Lithophyllum* to be identified.

Studied thin sections: DBUA–F 1109(3.1.1); 1109(3.2); 1109(3.3); 1109(3.4); 1110(4.2); 1110(4.3); 1112(6.2.1); 1113(7.5); 1113(7.6).

Genus ***Titanoderma*** Nägeli, 1858.
?*Titanoderma* sp.

(Fig. 8D)

Description: A few poorly preserved thalli appear interspersed in the algal framework. Thallus organisation is dorsiventral with a single layer of palisade cells. No evidence for cell fusions. No conceptacles were observed.

Remarks: *Titanoderma pustulatum* (J.V. Lamouroux) Nägeli, 1858 is present in the algal framework from Prainha, on the south coast of the island (Amen et al., 2005). The dimerous construction of the thalli with palisade cells and the apparent lack of cell fusions may suggest that the specimens from Lagoinhas belong to *Titanoderma*.

Studied thin sections: DBUA–F 1108(2.2.1); 1110(4.3); 1113(7.2); 1113(7.3).

5. Discussion

5.1. Local sequence interpretation

The Lagoinhas sedimentary sequence is perched atop a rocky shore platform, and both are attributed to development during the last

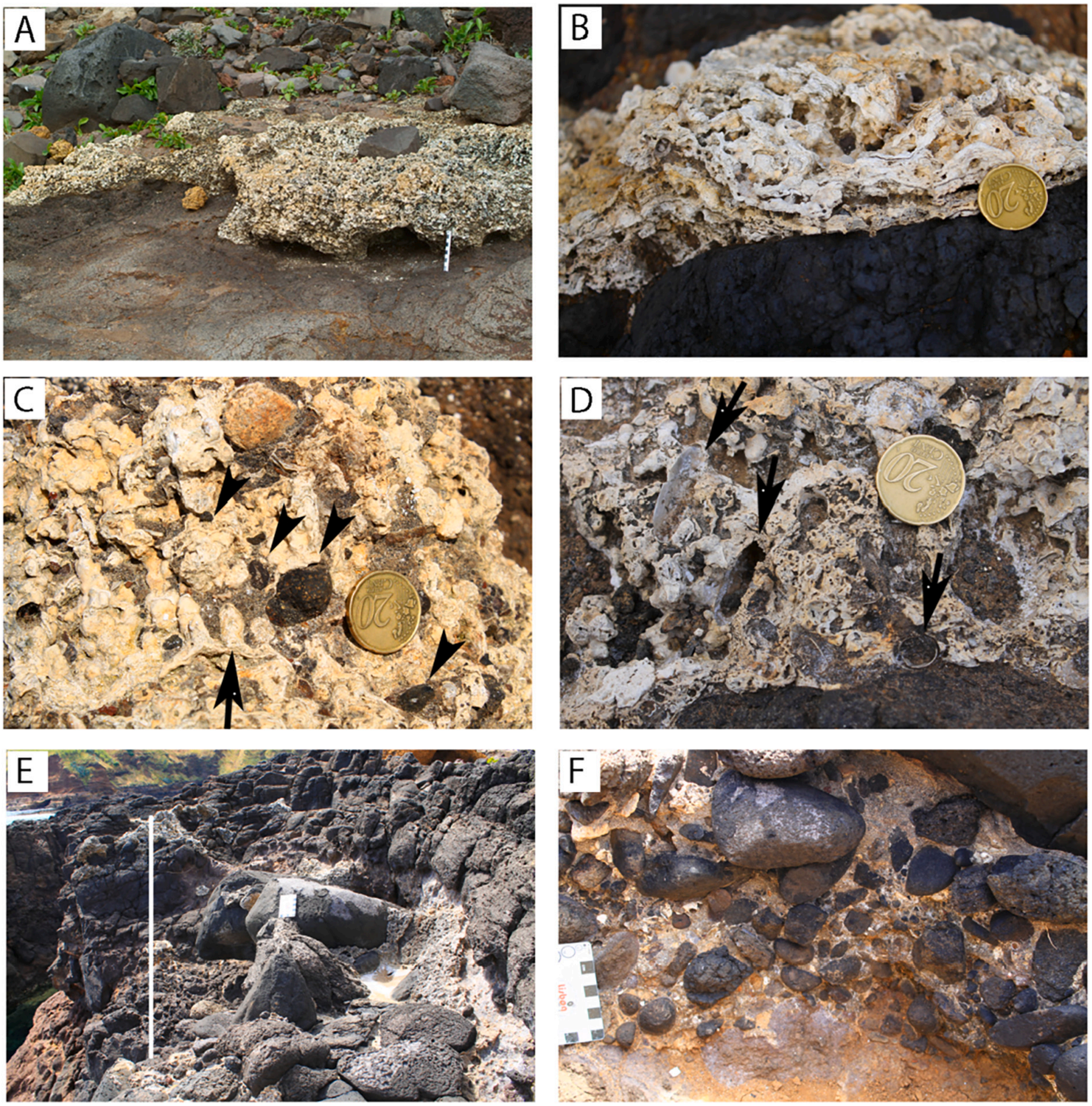

Fig. 5. Details of the Lagoinhas CCA buildup. A) General aspect of the CCA buildup; B) Detail of the CCA framework growing directly on the basalt; C) CCA with long protuberances (arrow) filled with sediment in between, and volcaniclasts incorporated (arrow heads); D) Shells of the bivalve *Leiosolenus aristatus* incorporated in the framework (arrows); E) Pool at the lower level of the relief. Vertical white line = 80 cm; F) Detail of the conglomerate formed in the depression.

interglacial. The CCA buildup was constructed directly above the basaltic substrate or above consolidated beach sediments (conglomerates and calcarenites), which partially infill the topography of the shore platform. Critically, bivalve borings at the top of buildups suggest that there was a long enough exposition of the buildup's hard surface for bioerosion to take place, immediately after their formation (or penecontemporaneous of their formation). As proven by experiments, production of bivalve borings requires at least years of exposition of the substrate (Bromley et al., 1990; Bromley and Asgaard, 1993). Moreover, the borings are not truncated by erosion. This implies that the buildups were very rapidly buried by the overlying bioclastic sands, possibly as a result of a rapid environmental change, which led to deposition of the sands on top of the buildups. The very irregular erosive contact between the bioclastic and the terrigenous sands, in turn, denotes rapid subaerial erosion prior to the deposition of the latter, possibly by torrential rain leading to the formation of gullies. The resulting erosive topography was subsequently infilled by the terrigenous sands and later covered by colluvium.

The succession of events described above is compatible with a scenario in which relative sea level peaked during the construction of the CCA buildups and their rapid burial by the bioclastic sands, followed by a regressive trend represented by the erosion of the bioclastic sands and subsequent deposition of the terrigenous sands, and later by the deposition of the colluvium as the result of subaerial slope evolution. This suggests that the buildups and bioclastic sands were deposited during the peak of MIS 5e, and therefore represent environmental conditions that characterised this last interglacial along the northern shore of Santa Maria.

5.2. *Framework nomenclature*

Rasser and Piller (2004) reviewed several descriptive classification schemes for autochthonous, organically bound carbonate structures and their applicability to CCA frameworks. Following their summary, the

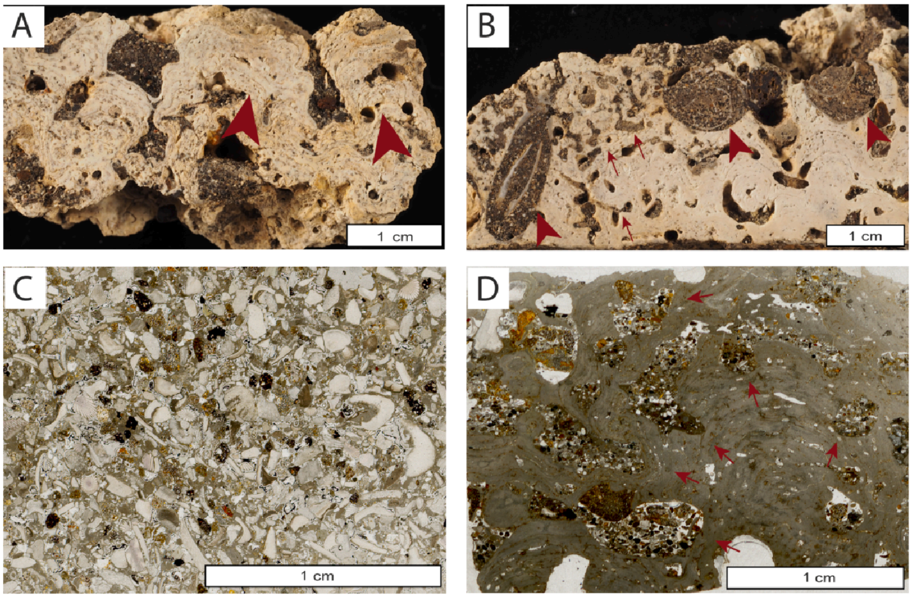

Fig. 6. Section of the Lagoinhas CCA framework illustrating the taphonomic signatures. A) CCA columnar structure (arrow heads), B) Borings of bivalves, i.e. *Gastrochaenolites* cf. *torpedo* (arrow heads) and sponge boring *Entobia* isp. (small arrows), C) thin section photo of the calcarenitic sands that cover the CCA buildup; D) The boring *Entobia* isp. in thin section (arrows) crossing CCA columnar structure.

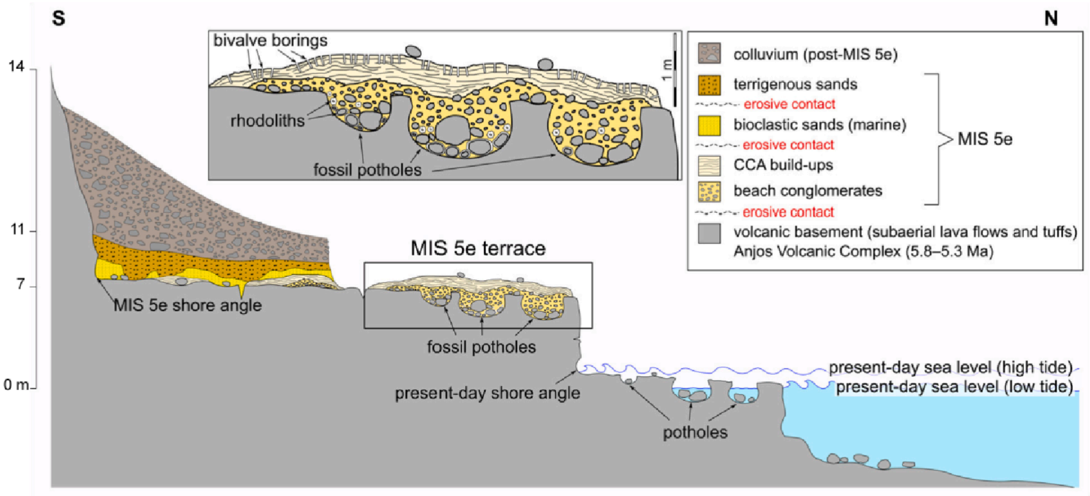

Fig. 7. Schematic cross section of the outcrop illustrating the different facies and its relationship with modern sea level (features not to scale).

framework described herein can be considered a bindstone, a term used to describe boundstones (i.e. organically bound autochthonous limestones) in the classical carbonate nomenclature of Dunham (1962) and expanded by Embry and Klovan (1971), where organisms encrust and bind. In the nomenclature of Cuffey (1985), the Lagoinhas framework can be identified as cruststone, formed by different encrusting layers, forming a frame of their own skeletons. Based on the nomenclature for the matrix-skeletons-cavity/cement by Riding (2002), the Lagoinhas framework fits in the skeleton-supported reefs-frame reefs, in which in situ skeletons are in direct contact.

Evidence for fast growth can be seen by the encrusting to lumpy growth forms filled with sediment in between, and the incorporated volcaniclasts (Fig. 5B and C).

5.3. Factors leading to the formation of CCA buildups

The occurrence of CCA buildups associated with MIS 5e deposits on Santa Maria Island, with some noticeable differences (see Table 2) between sequences located in the north and south coasts, raises questions as to which factors controlled the growth of those framework structures.

The distribution of CCA buildups depends on the availability of substrate type (e.g. basement rock, coarse detrital material) and on adequate irradiance, under low to moderate sedimentation rate (Ballesteros, 2006; Nalin et al., 2006; Titschack et al., 2008; Bracchi et al., 2016; Tosi et al., 2017). Generally, hard substrates are suitable for the formation of the crustose frameworks. Growth forms of coralline algae are genetically controlled, although they frequently show high phenotypic plasticity, regulated by ecological conditions such as hydrodynamic energy and sedimentation rate (Basso, 1998; Rasser and Piller, 2004; de Queiroz et al., 2016). Many corallines compete for space by growing faster than their neighbours (Bosence, 1983 and references therein; Benzoni et al., 2011). The dense, closely superposed crusts of the CCA, the abundance of boring bivalves and the coarse grained nature of sediment trapped in the structural cavities are indicative of high-energy hydrodynamic conditions (Bosence, 1983, 1985; Di Geronimo

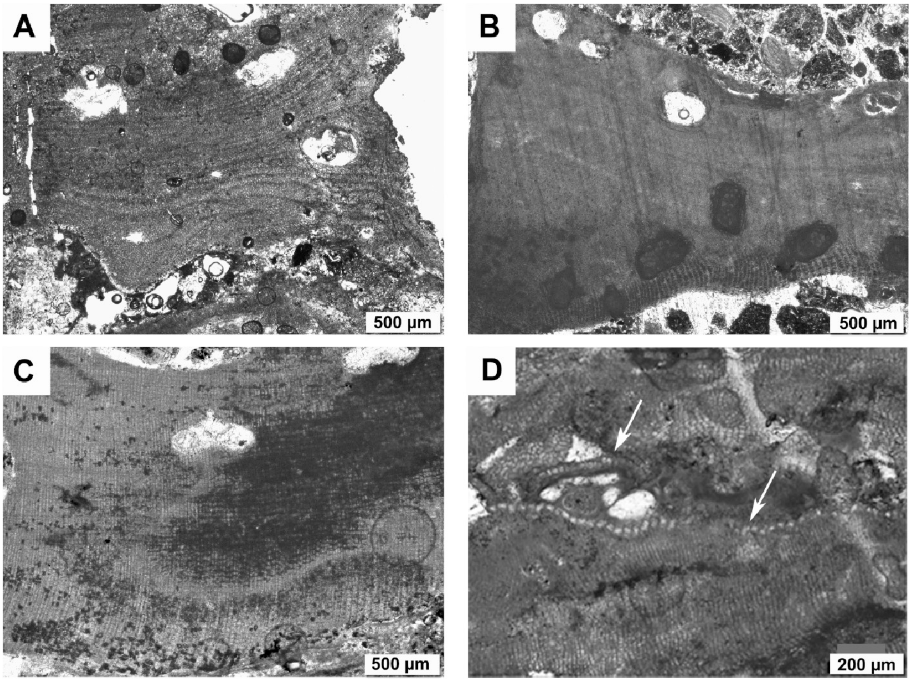

Fig. 8. Representative CCA of the Lagoinhas buildup. A) *Spongites* sp., uniporate conceptacles irregularly distributed throughout the thallus; B) *Neogoniolithon* sp., monomerous thallus with a coaxial core; C) *Lithophyllum* sp., uniporate conceptacle with visible columella and dimerous thallus without palisade cells; D)?*Titanoderma* sp., two single layer thalli of palisade cells (arrows) interspersed other coralline thalli.

Table 2

Comparison of the features from the CCA species of the Pleistocene of Santa Maria Island. Taxonomy is based on conceptacle type, structure and size, thallus organisation and anatomy.

	S. fruticulosus	*Spongites* sp.	*N. brassica-florida*	*Neogoniolithon* sp.	*L. incrustans*	*Lithophyllum* sp.	*T. pustulatum*
Outcrop	Prainha	Lagoinhas	Prainha	Lagoinhas	Prainha	Lagoinhas	Prainha
Thallus thickness	2–3 mm	0.7–7 mm	2.4 mm	1.2–2.4 mm	1–3 mm	0.8–2.3 μm	0.3 mm
Thallus organisation	Monomerous non-coaxial	Monomerous non-coaxial	Monomerous coaxial	Monomerous coaxial	Dimerous	Dimerous	Dimerous with a single layer of palisade cells
Cell fusions joining contiguous filaments	Yes	Yes	Yes		No	No	No
Epithallial cells shape Diameter x Height (μm)	Non-flared 15–20 × 10–13	Rounded non-flared 7–11 × 5–7	–	–	–	–	–
Cells of peripheral/ postigenous filaments Diameter x Length (μm)	15–18 × 23–25	7–14 × 13–22	13–15 × 20–23		10–13 × 18–23	6–11 × 9–14	23–25 × 15–18
Cells of core/ primigenous filaments Diameter x Length (μm)	–	8–18 × 13–27	–	–	8–10 × 13–15	–	18–20 × 24–25
Conceptacle type Diameter x Height (μm)	Uniporate sporangial 515–750 × 316–450	Uniporate 316–482 × 137–205	Uniporate sporangial 724 × 332	Uniporate 282–320 × 169–214	Uniporate sporangial 214–230 × 112 × 117	Uniporate 175–235 × 73–131	Uniporate sporangial 321 × 122
Conceptacle shape	–	–	–	–	Bean- shaped	–	Hemispherical
Central columella	ND	Present	Absent	Present	Present	Present	Absent
Roof thickness	9–30 cells above the sporangial chamber	–	Over 20 cells above sporangial chamber	–	13–21 cells above sporangial chamber	–	4–6 cells above sporangial chamber
Source	Amen et al., 2005	This study	Amen et al., 2005	This study	Amen et al., 2005	This study	Amen et al., 2005

et al., 2002), suggesting that the Lagoinhas framework developed in an exposed setting, an observation that is compatible with both its geographical position and its general characteristics. According to Bosence's seminal work (1985), high-energy hydrodynamic conditions are also suggested by the coralline species forming the buildups at Lagoinhas, given that corallines involved in shallow, high-energy reef construction are reported to be chiefly *Lithophyllum* and *Porolithon* (Adey, 1979; Bosence, 1983). The two sequences of Lagoinhas and

Prainha, however, are very similar at the CCA composition, and so are in terms of their overall stratigraphy and general characteristics. A slightly higher hydrodynamic palaeoenvironment at Lagoinhas, is also supported by the mollusc faunal composition reported by Callapez and Soares (2000) as revised by Ávila et al. (2002, 2015a), which is indicative of a rocky, algal-covered, shallow-water and wave-impacted biota. Moreover, the inferred high-energy hydrodynamic conditions at this site is also suggested by the fact that the carbonate buildups are thinner and generally occur directly over a rocky surface, abraded by wave action, and occur side by side, and even partially cover the walls, of the large potholes, which require a high wave hydrodynamics to form. These potholes nowadays exhibit the described infill of consolidated conglomerates and calcarenites.

As such and given that the Lagoinhas sequence is located at the base of an exposed bluff on the prevailing windward side of Santa Maria, it is reasonable to argue that the same hydrodynamic conditions existed during the Last Interglacial. Notwithstanding the fact that the overall sequence of Lagoinhas is very similar to the one exposed at Prainha from a sedimentological and stratigraphic point of view, the absence of potholes and the presence of smaller basaltic pebbles and cobbles in the conglomerates at Prainha, the finer sand grain size at Prainha, and the higher diversity and density of sand-associated bivalves [e.g., *Ensis minor* (Chenu, 1843), *Lucinella divaricata* (Linnaeus, 1758), *Laevicardium crassum* (Gmelin, 1791), *Ervilia castanea* (Montagu, 1803; Ávila et al., 2015a] also suggest that the southern coast developed under slightly calmer hydrodynamic conditions than the more exposed windward northern coast, as it happens today. Likewise, *Spongites* and *Lithophyllum* are the two main framework builders on both the northern and southern coasts. Therefore, the two sequences possibly represent very similar environments, both energetic in terms of hydrodynamics, but with the Lagoinhas sequence representing a slightly more exposed, wave-beaten setting than the more protected leeward sequence of Prainha. This difference in hydrodynamics is visible on the shelf, with the inner northern shelf almost deprived of sediments and a thick inner shelf deposit near Prainha (Ricchi et al., 2020). Windward coasts lack significant nearshore deposits due to offshore transport of sediments during storms (Quartau et al., 2012; Meireles et al., 2013; Ricchi et al., 2020).

5.4. *Influence of hydrodynamics in species association*

Given the aforementioned considerations, the likely difference in species composition between the sections at Lagoinhas and Prainha (Tables 2 and 3), which are coeval and are very similar from the sedimentological and stratigraphic point of view, may thus be explained by differing ecological factors, with local hydrodynamics being the most obvious. We therefore postulate that the small differences observed between the Lagoinhas and Prainha sequences, in terms of the characteristics of the CCA buildups but also in terms of fauna and sedimentology, are probably due to slightly more energetic hydrodynamics at the former. Consequently, Lagoinhas possibly represents an ecological niche more robust and tolerant to higher wave hydrodynamics, whilst the niche represented at Prainha conversely is more sensitive to this factor, preferring the calmer and more sheltered waters of the leeward shores. This study, therefore, provides unique insights on how small changes in ecological factors influence the characteristics of CCA buildups at a local scale. More importantly, these two reference sequences provide excellent case studies to gain insights on the warm-temperate coralline algae (on other taxa) assemblages (Meneses, 1993; Steneck et al., 1997; Braga and Aguirre, 2001; Bracchi et al., 2014) that existed at the latitude and mid-ocean setting of the Azores during the warmest period of the last interglacial, currently absent, but which may reappear as a result of global warming.

Table 3
Number of species/taxa reported from the Last Interglacial (MIS 5e) of Santa Maria Island, and from Prainha and Lagoinhas fossiliferous outcrops. The last column displays the number of species that occur in both outcrops (Prainha and Lagoinhas).

	Total MIS 5e	Prainha	Lagoinhas	Number of species in common
Algae	4	4	4	0
Cetacea	1	1	0	0
Crustacea Decapoda	7	4	0	0
Echinodermata	3	3	3	3
Bryozoa	11	8	5	2
Bivalvia	24	19	3	3
Gastropoda	112	100	43	40

Hydrodynamics also seem to play a crucial role on the formation of insular CCA buildups. Vinha Velha, another MIS 5e outcrop located on the southeastern tip of Santa Maria Island, about 7.5 km from Prainha, lacks any CCA buildup or encrustation. We believe the reason for this is that both Lagoinhas and Prainha are located in the centre of wide bays, whereas Vinha Velha is situated on a promontory. Considering that the coastline during MIS 5e was very similar to the one today in all these locations (cf. Fig. 1B), wave rays diverged in the bays reducing the wave energy and converged in the promontories, increasing wave energy. Although Lagoínhas is exposed to the north, it is protected from the NW and W waves (see Fig. 3), which account for 57% of the highest waves (average annual Hs of 2.14 m and 2.44 m respectively, in Ricchi et al., 2020). Therefore it is hit only by N and NE waves which account for 31% of total waves and are also the smallest. In contrast, Vinha Velha, which is protected from most waves, is still hit by W waves, SW waves, S waves SE waves and E waves, which account in total to 34%. The W (22%) and SW (5%) waves are also the highest (average annual Hs of 2.44 m and 2.45 m) in Santa Maria Island.

5.5. *Comparison with other settings*

The mediolittoral trottoirs and algal ridges (Adey, 1986) as well as the sublittoral temperate algal reefs of the Mediterranean (coralligenous, see next paragraph) offer the best Recent analogues for the Pleistocene coralline algal buildups from Santa Maria Island. Trottoirs are known from the Mediterranean and northern Atlantic (Adey, 1986; Rasser, 2000 and references therein). They are intertidal frameworks, usually growing on steep rocky shores, but can also form algal "microridges" (Thornton et al., 1978; Rasser, 2000 and references therein). The genus *Lithophyllum* is common in shallow environments and few distinctive lithophylloid species characterise the high-energy intertidal zone, where the full force of the breaking waves ensures an almost constant wetting. The trottoirs are formed mainly by lithophylloid corallines, such as *Tenarea tortuosa* (Esper) Lemoine in the eastern Mediterranean, and *Lithophyllum byssoides* (Lamarck) Foslie in the western Mediterranean and eastern Atlantic (Adey, 1986; Rindi et al., 2019).

A possible coeval analogue for the Lagoinhas algal buildups is the *Lithophyllum byssoides* buildup from the MIS 5e on Porto Alabe coast, NW Sardinia, Italy. This coast is highly exposed to the northwesterly wind and storms, and the Pleistocene buildup occurs over a large wavecut platform dominated by potholes (Sechi et al., 2020), as it happened at Lagoinhas. However, the occurrence of *Lithophyllum byssoides*, the major trottoir builder, could not be confirmed.

The algal ridges are built by *Lithophyllum congestum* (taxonomically revised by Hernandez-Kantun et al., 2016) and *Porolithon* spp. in the tropical western Atlantic and in the Pacific (Bosence, 1983; Taberner and Bosence, 1985; Adey, 1986). Species of *Lithophyllum* and *Porolithon* have been involved in reef construction since the Cenozoic and have been found useful as palaeoecological indicators (Taberner and Bosence, 1985 and references therein). The genus *Titanoderma* is known to occur as a pioneer colonizer of new substrates, like bare rocks (Basso, 1998; Walker and del Moral, 2003; Basso et al., 2007).

Spongites appears to be the ecological equivalent of *Porolithon* in the tropical Pacific and Indian Oceans (Maneveldt and Keats, 2014;

Gabrielson et al., 2018), however in the present-day Azores, no record of *Spongites* as intertidal dweller is known so far.

In summary, in what concerns the species involved and their ecological context, the CCA buildups from the Azores cannot be compared with any other buildups described so far, attesting to its importance as a case study at the global stage.

5.6. Tropical vs non-tropical reefs

The CCA taxonomic composition of the Lagoinhas framework differs from the Prainha framework only on the species level, as they are represented by the same families of Spongitaceae and Lithophyllaceae. Coralline algae from the subfamily Lithophylloideae are commonly recorded or even predominate in shallow-water carbonate deposits, typically formed in warm-temperate to warm-tropical seas (among other: Meneses, 1993, Sartoretto et al., 1996, Steneck et al., 1997; Braga and Aguirre, 2001; Bracchi et al., 2014; Robinson et al., 2017). Species of *Lithophyllum* and *Titanoderma* are known to form frameworks since at least 243 kyrs in the Mediterranean Pleistocene, with no major change across climate fluctuations (MIS7 – Basso et al., 2007; Nalin et al., 2007; MIS6 – Bracchi et al., 2019; Holocene – Sartoretto et al., 1996). *Spongites*, which is the main reef builder both in Lagoinhas and Prainha, is well known to form CCA buildups and also is typically present in coral reefs, being characteristic of shallow-water environments in clear and well-oxygenated tropical waters down to 30–40 m (Rösler et al., 2015 and references therein). Given the algal association found at Lagoinhas – and the considerations expressed above – the CCA buildups at this site thus reflect the warmer waters in which they grew during the Last Interglacial. This is in agreement with the mollusc species composition found at the outcrop, but also with a number of other thermophilic species that have been reported for the MIS 5e fossil record of Santa Maria, including at Vinha Velha, one of the few MIS 5e outcrops in the island that does not feature fossil algal buildups (Ávila et al., 2015).

5.7. Where are the buildups today?

A main question is, why are CCA buildups absent throughout today's Azores Archipelago, since suitable shelf areas are present, and coralline algae fairly common?

One aspect might be the taxonomic inventory, because the main framework builder of the studied buildups, *Spongites*, seems to be absent today (for an updated checklist of present-day corallines of Santa Maria Island see Neto et al. (2021)). The reason for this could be the changing climate, because during MIS 5e the water temperature was higher than today, and as discussed above, *Spongites* is well-represented in warmer Atlantic habitats. Another hypothesis concerns the contrasting levels of storminess in the Azores between the last interglacial and the present day. It is inferred that with a warmer climate, wave conditions in the Azores throughout most of the year would have been calmer, notwithstanding the impact of occasional, possibly more intense hurricanes. Today, however, the Azores are exposed to the brunt of the particularly energetic North Atlantic swell, which only eases considerably during the summer months. This more energetic regime of today, when compared to the last interglacial, may thus be responsible for inhibiting the growth of *Spongites* (and other reef-building coralline algae), preventing the development of CCA buildups in today's Azores waters.

At any rate, the knowledge of coralline algal-diversity of the Azores is incomplete, and therefore these conclusions need to be tested in future studies.

This incompleteness of the record leads to another potential explanation: so far, no researcher has extensively and systematically looked for CCA buildups in Azores waters, and it is possible that comparable subtidal buildups do occur, but they have not yet been discovered.

6. Conclusions

Lagoinhas is one of two fossiliferous geosites in Santa Maria Island with well-developed crustose coralline algae (CCA) buildups. Located in the northern (windward) shore of the island, this site is subjected today (and was also during the Last Interglacial) to a higher hydrodynamic regime than its counterpart geosite, Prainha, located in the southern, more protected (leeward) shores of Santa Maria. The small but noticeable differences in facies and fossil assemblages between the windward/leeward sides of the island is thus interpreted as direct result of varying hydrodynamics, with the sections of Lagoinhas and Prainha providing the type-example of CCA buildups for, respectively, the windward and leeward ecological conditions. Furthermore, given the rarity of this kind of environments on island settings, these two sites fulfil all the criteria to be regarded as key outcrops relevant to the study of coralline algal buildups at mid-latitudes and mid-ocean settings during the warmer climate of the Last Interglacial, providing additional information on the conditions that were prevalent during this climatic stage. The Lagoinhas buildup is unique and cannot be compared to any other related buildup published hitherto, further highlighting its importance at global scale. The question, why such buildups are absent on the Azores shelves today, cannot yet be satisfactorily answered and requires further research.

Declaration of Competing Interest

None.

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