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

3
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44 **ABSTRACT**

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

56

57 **Keywords:** Rhodophyta, bio-construction, Last Interglacial, volcanic oceanic islands,
58 North Atlantic

59

60 **1. Introduction**

61 Crustose coralline algae (CCA) are non-geniculate red algae (Rhodophyta) that
62 produce Mg-calcite thalli, growing either as stable buildups, known as algal ridges,
63 algal reefs or Coralligène (Steneck et al., 1997; Ballesteros, 2006; Bracchi et al., 2015,
64 2016, 2017; Marchese et al., 2020), or growing around a nucleus to form free-living
65 nodules known as rhodoliths (Bosellini and Ginsburg, 1971; Adey, 1978, 1986;
66 Bosence, 1983; McCoy and Kamenos, 2015; Aguirre et al., 2017). CCA buildups may
67 occur from the polar regions (Freiwald and Henrich, 194; Adey et al., 2015) to the
68 tropics where they constitute an important element of coral reefs, acting as frame-

69 builders and contributing significantly to reef calcification and cementation (Fabricius
70 and De'ath, 2001; Caragnano et al., 2009). This role is particularly important in high-
71 wave energy environments where wave-resistivity is crucial for reef growth (Littler and
72 Littler, 2013; Weiss and Martindale, 2017). In reefal and other settings, CCA are also
73 key habitat providers to many benthic species, including several species with economic
74 interest (Bak, 1976; Basso, 2012; Littler and Littler, 2013). Moreover, CCA are one of
75 the world's most important calcium carbonate producers (second only to coral reefs, to
76 which they also contribute) and in the Atlantic Ocean, in the near-absence of coral reefs,
77 they even constitute the most important reef builders (Adey, 1975; Steneck and Adey,
78 1976; Gherardi and Bosence, 2001; Tâmega et al., 2014; Spotorno-Oliveira et al.,
79 2015), either on their own or together with other encrusting organisms such as corals,
80 bryozoans, serpulids and molluscs (Bosence, 1983; Di Geronimo et al., 2002; Basso et
81 al., 2007; Aguirre et al., 2014).

82 Buildups are particularly important in marine geomorphology, given that calcareous
83 algae are capable of forming extensive solid substrates on an originally unconsolidated
84 sea floor (Basso et al., 2007; Aguirre et al., 2012; Bracchi et al., 2017; Lo Iacono et al.,
85 2018), or building algal crests on reef edges and thus serving a key reef-binding role,
86 and consequently becoming important sediment contributors (Adey, 1986). Common
87 features of these buildups include decimetre to metre-sized three-dimensional cavernous
88 erosional cavities, depressions filled with sediment, and the occurrence of columns and
89 protruding ledges departing from the main mass (Basso et al., 2007). Their architecture
90 and morphology are controlled mainly by taxonomic composition (Ingrosso et al. 2018)
91 as well as by biological carbonate productivity that responds to climate, oceanography,
92 physiography, changes in accommodation space, substrate stability and sediment input
93 (Rasser and Piller, 2004; Bracchi et al., 2015 and references therein).

94 Several types of modern CCA frameworks have been described based on the climate,
 95 type of substrate and water depth (Table 1).
 96 Whereas buildups constituted by CCA are well known from present oceanic settings,
 97 descriptions of fossil representatives are still uncommon (Rasser and Piller, 2004; Nalin
 98 et al., 2006; Titschack et al., 2008; Bracchi et al., 2016, 2019; Weiss and Martindale,
 99 2017). The aims of the present study are thus to: 1) provide identification and
 100 description of an *in situ* CCA buildup from the Pleistocene fossil record of the central
 101 North Atlantic Azores Archipelago, located at the Lagoinhas section on the high-energy
 102 northern coast of Santa Maria Island; 2) compare the buildup on the windward northern
 103 coast with a coeval buildup on the leeward, more sheltered southern coast of the same
 104 island; and 3) contribute to our scientific understanding of MIS 5e and its fossil record,
 105 given the importance this interglacial holds as case study (or proxy) to the ongoing
 106 global warming and associated future climate changes.

107 **Table 1.** Types of modern CCA frameworks according to climate, substrate type and water depth (after
 108 Ginsburg and Schroeder, 1973; Bosence, 1985; Adey, 1986; Steneck et al., 1997; Di Geronimo et al.,
 109 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

110

111 **2. Geological setting**

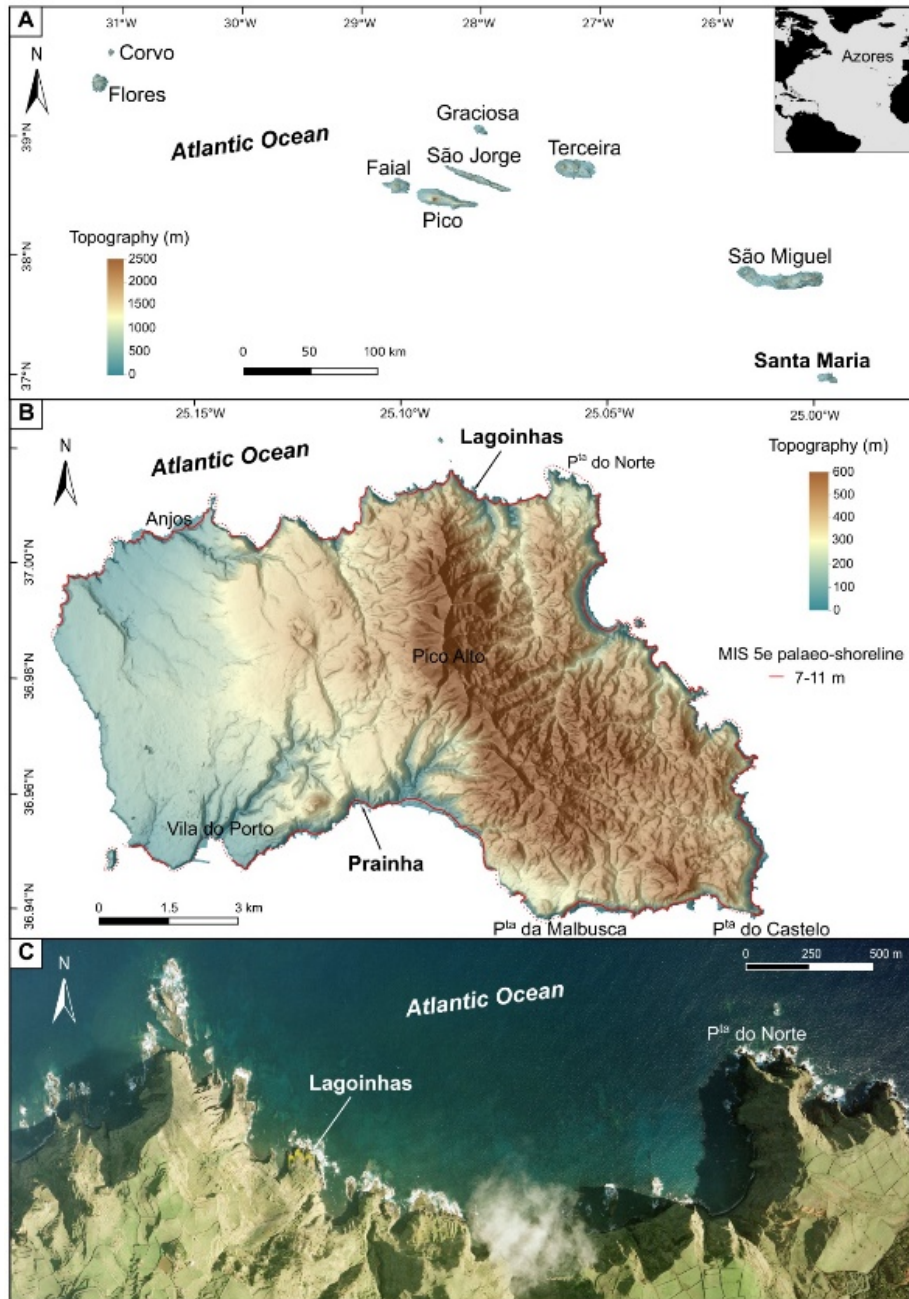
112 **2.1. Santa Maria Island**

113 Santa Maria Island in the Azores (central North Atlantic), the oldest in the archipelago,
 114 is remarkably rich in exposed marine fossiliferous sediments (Ferreira, 1955;
 115 Zbyszewski and Ferreira, 1962; Madeira et al., 2011; Ávila et al., 2012, 2015a, 2015b,
 116 2015c, 2016, 2020; Meireles et al., 2012; Rebelo et al., 2014, 2016a, 2016b; Santos et

117 al., 2015; Uchman et al., 2016, 2017, 2018; Hyžný et al., 2021) and submarine volcanic
118 successions (Serralheiro and Madeira, 1990; Serralheiro, 2003; Johnson et al., 2017;
119 Ramalho et al., 2017; Uchman et al., 2020). This richness, explained by its distinct
120 geological history, was characterised by an initial period (from 6 to 3.5 Ma) during
121 which volcanism, erosion, sedimentation and fast subsidence contributed to the
122 formation of submarine sequences. Later, in the last 3.5 it reversed to a striking uplift
123 trend Myr (see Figs. 6 and 7 of Ramalho et al., 2017), thus contributing to the exposure
124 of these sequences, which otherwise would be inaccessible (~~Ramalho et al., 2017,~~
125 ~~2020~~). This trend in uplift, in conjunction with marine erosion and glacio-eustatic
126 oscillations, was also responsible for the formation of a staircase of raised and
127 submerged marine terraces that extend from the present-day shelf-edge at -140 m to up
128 to +200 m (or possibly +230 m) in elevation (Ramalho et al., 2017, 2020; Ricchi et al.,
129 2018, 2020). It is in this context that well-preserved fossiliferous sections attributed to
130 the last interglacial (e.g. see Callapez and Soares, 2000; Ávila et al., 2002, 2010, 2015a;
131 Amen et al., 2005; Meireles et al., 2013) are found on both the southern and northern
132 coasts of the island, perched atop former rocky shore platforms which are now between
133 2 and 11 m in elevation (the actual terrace shore angle is at 7–11 m in elevation – see
134 [Fig. 1B](#)) (Ávila et al., 2015a; Ramalho et al., 2017; Ricchi et al., 2018). The Lagoinhas
135 section, the object of this study, is one of such outcrops, being located on the island's
136 north coast ([Fig 1](#)).

137 The Lagoinhas section displays a fossiliferous marine sequence, including a well-
138 developed CCA buildup, perched atop a former shore platform eroded on the volcanic
139 succession of the Anjos Volcanic Complex (dated 5.8–5.3 Ma; Ramalho et al., 2017).
140 The fossiliferous marine sediments are, in turn, covered by Pleistocene-Holocene slope

141 deposits and colluvium, which offered some protection to the buildup, ensuring its
142 preservation.
143



144
145 **Figure 1.** Geographical location of the Lagoinhas outcrop and study area in the wider context of the
146 Atlantic Ocean. (A) Location of Santa Maria Island within the Azores Archipelago (inset shows the
147 location of the Azores in the central North Atlantic); subaerial topography was generated from a 1:25,000
148 scale digital altimetric database from Instituto Geográfico do Exército; (B) Digital elevation model (~2 m
149 in resolution) of Santa Maria Island showing the location of Lagoinhas and Prainha sequences within the

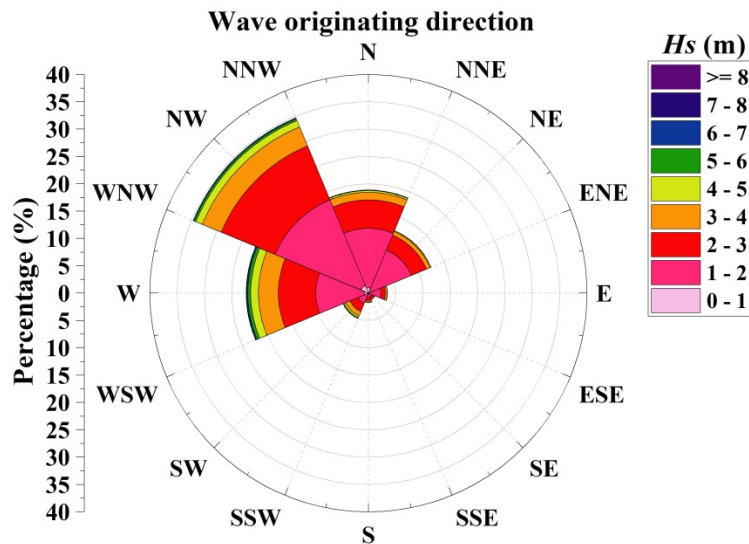
150 MIS 5e palaeo-shoreline reconstruction of Ramalho et al., (2017); subaerial topography was generated
151 from a 1:5,000 scale digital altimetric database; (C) Vertical aerial photo of the study area, showing the
152 location and extent of Lagoinhas sequence; vertical aerial photo number 6177, row 2, at an approximate
153 scale of 1:18,000, dated of September 2005, and provided by Secretaria Regional do Turismo e
154 Transportes.

155

156 **2.2. Present-day local hydrodynamics**

157 The remote Azores Archipelago is impacted by northwesterly trade winds, and
158 frequently subjected to high wave energy (Quartau et al., 2010, 2012; Rusu and Soares,
159 2012). Extreme storms brought by the North Atlantic Oscillation and Eastern Atlantic
160 atmospheric circulation affect the Azores at least once every seven years (Borges, 2003;
161 Andrade et al., 2008; Zhao et al., 2019; Ricchi et al., 2020). Rare hurricanes can affect
162 the islands with storm surges from the south and southeast (Elsner et al., 2000; Andrade
163 et al., 2008; Johnson et al., 2017). A recent study by Ricchi et al. (2020) for the island
164 of Santa Maria showed that the prevailing swells approach the island from the northwest
165 (35%) and west (22%), with average significant wave heights (Hs) of 2.14 m and 2.44
166 m, respectively (Fig. 2). Waves from north and northeast are also frequent (respectively
167 19% and 12%) but of lower Hs (respectively 1.92 m and 1.83 m). Although the
168 remaining directions are less significant (< 5% each), waves from the southwest can still
169 reach 2.45 m, during 5% of the year, normally occurring during the arrival of tropical
170 depressions from the Caribbean, during the North Atlantic hurricane season.

171



172

173 **Figure 2.** Offshore significant wave heights around Santa Maria Island (modified after Ricchi et al.,
 174 2020).

175

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

179

180 **2.3. CCA buildups and previous studies**

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

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

189 the palaeoecological reconstruction for both outcrops Lagoinhas and Prainha, on the
190 north and south coasts, respectively.

191 Previous research (Callapez and Soares, 2000; Ávila et al., 2002, 2007, 2009, 2015a)
192 paid little attention to the fossil CCA buildups on the north coast at Lagoinhas. The
193 framework supports a varied epifauna of molluscs, echinoderms and bryozoans.

194 Macrobioerosion structures in the biostrome are assigned to the ichnogenus
195 *Gastrochaenolites* Leymerie, 1842 (Ávila et al., 2009, 2015a). The sequence continues
196 with a 70–cm thick layer of poorly consolidated dominantly bioclastic white-yellowish
197 marine sands, which in turn are capped by fine terrigenous sediments (poorly
198 consolidated colluvial sandstones and breccias) (Ávila et al., 2002). The overlying
199 white-yellowish unconsolidated sands (facies 4, fig. 4 in Ávila et al., 2015a) exhibit
200 thicknesses as much as ~0.7 m and are rich in very-well preserved fossil assemblages
201 dominated by molluscs. In total, for the CCA buildup and the fossiliferous sands, 57
202 specific taxa were reported (46 gastropods, 5 bryozoan, 3 bivalve and 3 echinoderm
203 species), testifying a warm temperate rocky shore palaeoenvironment with
204 biogeographical relationships with the northeastern Atlantic and the Mediterranean
205 (Madeira et al., 2011, Ávila et al., 2015a).

206

207 **3. Methods**

208 A stratigraphic cross section was constructed, of the exposed sequence at Lagoinhas
209 (37°00'47.5'' N, 25°04'58.1'' W). The stratigraphy of the Prainha section is described
210 in detail in Amen et al. (2005). Seven rock samples of the CCA buildup were randomly
211 collected at within the succession for preparation of thin sections. Thirty thin sections
212 (4.8 x 4.8 cm) representative of the CCA framework and sediment composition were
213 studied under a compound polarizing microscope (Leica DM750P) equipped with a

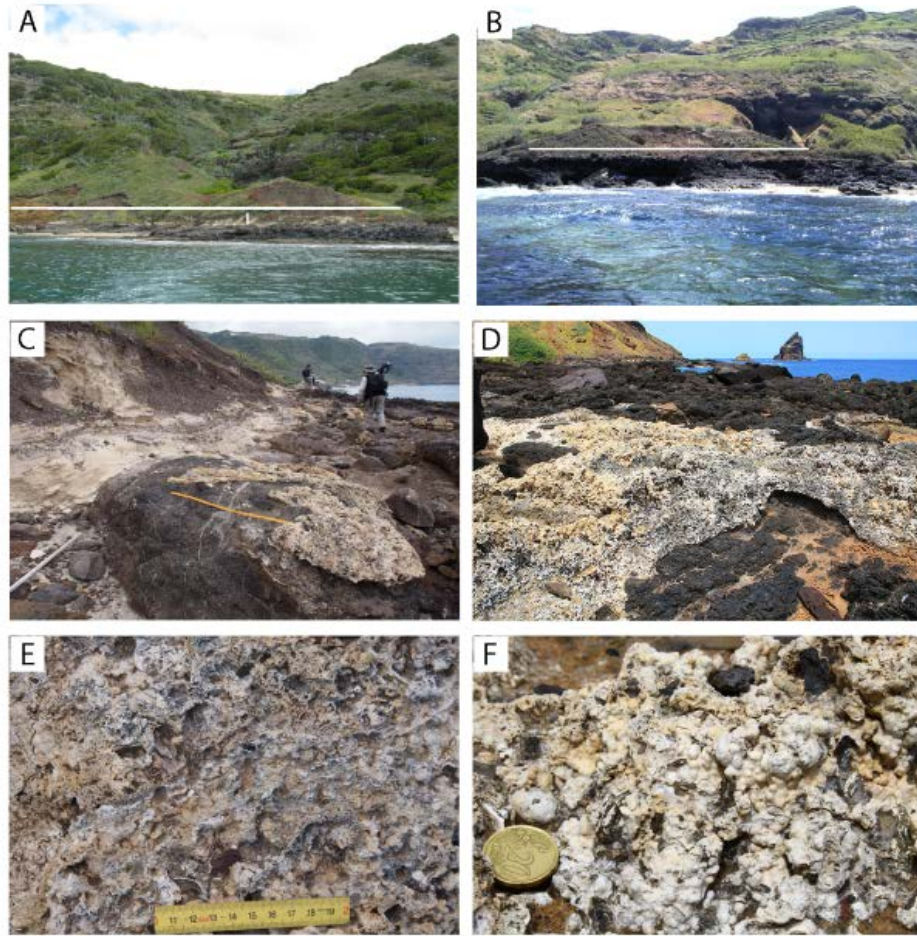
214 digital camera (Leica ICC50W). Anatomical and taxonomical terminologies on
215 corallines conform to the works by Braga et al. (1993), Irvine and Chamberlain (1994),
216 Rasser and Piller (1999) and Hrabovský et al. (2016); growth form terminology follows
217 Woelkerling et al. (1993). Cell and conceptacle dimensions were measured according to
218 Rasser and Piller (1999) using ImageJ. Mean (M) and standard deviation (SD) were
219 calculated for both cells and conceptacles, whenever the number of measurements
220 allowed (n = 5). All material is stored in the fossil collection (DBUA–F) of the
221 Department of Biology of the University of the Azores (Faculty of Science and
222 Technology), Ponta Delgada, São Miguel Island.

223

224 **4. Results**

225 **4.1. Description of the CCA buildups**

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



229

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

235

236 **4.1.1. Prainha section**

237 On the southern coast, the Prainha outcrop (36°57'06.8'' N, 25°06'47.1'' W) is exposed
 238 at an elevation of 3 to 4 m above present mean sea level (Serralheiro et al., 1987;
 239 Serralheiro, 2003), exhibiting a lateral extension of ~800 m (Fig. 3A) (Ávila et al.,
 240 2002). The outcrop consists of poorly consolidated shallow-water marine deposits
 241 (conglomerates, limestones and sandstones/calcarenites) overlying an irregular shore

242 platform carved in the subaerial basaltic sequence of the Anjos Volcanic Complex.
243 Along the outcrop, many parts of the original buildup have been eroded. The visible
244 CCA buildup with warty to lumpy morphologies growing one over the other and with a
245 maximum thickness of ~50 cm, covers a [coeval](#) beach conglomerate or, locally,
246 developed directly on the basaltic substrate (Figs. 3 C, 3E, 4). Fragments of mollusc
247 shells, bryozoans, and echinoderms, are accessory components (Ávila et al., 2009).
248 Amen et al. (2005) described four species of Corallinaceae: *Spongites fruticulosus*
249 Kützing, 1841 being the main builder of the framework, followed by *Lithophyllum*
250 *incrustans* Philippi, 1837, *Neogoniolithon brassica-florida* (Harvey) Setchell and
251 Mason, 1943, and *Titanoderma pustulatum* (Lamouroux) Nägeli, 1858. The buildup
252 shows abundant macro-bioerosion structures, mostly clavate borings, assigned to the
253 ichnogenus *Gastrochaenolites*. Remains of the endolithic bivalve *Leiosolenus aristatus*
254 (Dillwyn, 1817) (= *Myoforceps aristatus*) can still be found *in situ* inside most of the
255 borings. The boring clionid sponge *Entobia* Bronn, 1838 is present as well. The upper
256 surface and complete vertical section of the CCA buildup exhibit fractures that resulted
257 from local extension (Ávila et al., 2009, 2015a). The buildup is overlain by 1.3–2.5 m
258 thick, yellowish, partly cross-laminated, dominantly bioclastic, uncemented sands that
259 also fill most of these fractures. The grain-size distribution is dominated by the 125–250
260 µm fractions. The bioclasts consist almost exclusively of small mollusc fragments.
261 Lenses with ripple marks, trace-fossils and/or root casts are preserved locally (Ávila et
262 al., 2002, 2015a). The deposits correspond to a beach foreshore (intertidal) facies and
263 show cross-lamination. A thin carbonate crust of pedogenic origin occurs at the top of
264 the bioclastic sandy sediments. The crust consists mostly of micrite that precipitated
265 together with clay and other silt-sized impurities and exhibits a clotted texture.
266 Sediment below the carbonate crust includes bioclasts (molluscs, echinoid spines, and

267 geniculate coralline algae), poorly-sorted volcanic grains and very poorly-sorted rock
268 fragments. Aeolian dunes and colluvial-alluvial deposits cover the carbonate crust
269 (Ávila et al., 2009, 2015a) (Fig. 4).

270

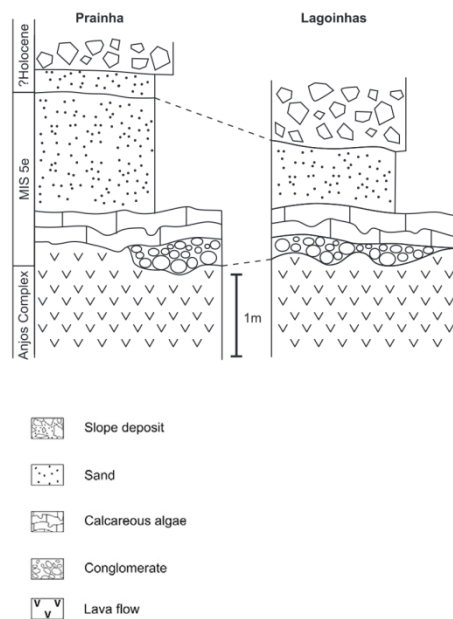
271 **4.1.2. Lagoinhas section**

272 The Lagoinhas buildup is today expressed as an erosional relict therefore the original
273 lateral and vertical extent is unknown. The buildup exhibits a variable height from 6 to
274 30 cm and covers an area up to 1,110 m², exposed along a ~80 m section (Fig.3). Initial
275 growth of the buildup starts directly on the basalt or the bioclastic sediments with an
276 encrusting form that transitions into warty, lumpy and branching forms, typically
277 infilled with sediment (Fig. 5A–C). Abundant borings *Gastrochaenolites* cf. *torpedo*
278 Kelly and Bromley, 1984 produced by the endolithic bivalve *Leisolenus aristatus* are in
279 the CCA buildup (Figs. 5D, 6A–D). These occur in patches on the seaward side of the
280 buildup. Moulds of shells are preserved in some borings, but most of them are empty
281 and partly or completely filled with sands different from the overlying bioclastic sand.
282 In some places the CCA framework is bored with *Entobia* isp. produced mostly by
283 clionid sponges (Figs. 6B, D). Several specimens of the infralittoral hard bottom trochid
284 gastropod (*Calliostoma lividum* Dautzenberg, 1927) and disarticulated valves of the
285 Semelidae bivalve *Ervilia castanea* (Montagu, 1803), a common dweller of subtidal,
286 were also incorporated in the buildup (for details on mollusc species see Ávila et al.,
287 2002). Some small volcanoclastic pebbles are also encrusted within the buildup (Fig.
288 5C).

289 Visibly, the shore platform on which the Lagoinhas deposits sit is irregular with a relief
290 up to 30 cm above the general surface. Moreover, it exhibits large intertidal potholes (1–
291 3 m in diameter, ~80 cm deep; Fig. 5E) on its seaward edge, eroded into the rocky

292 substrate by the gyratory grinding action of pebbles, cobbles and boulders stirred by
 293 wave motion. These fossil potholes are filled by the same well-consolidated beach
 294 conglomerates that rest on the shore platform, and which exhibit a fossiliferous
 295 calcarenitic matrix enveloping well-rounded basaltic boulders, cobbles, and pebbles
 296 (Fig. 5F). Among them are pebbles encrusted by coralline algae. The thickness of the
 297 algal encrustation around the volcanic nucleus is generally thin, therefore these
 298 elements, with a maximum diameter of 5 cm, would be more properly defined as coated
 299 grains (Steneck, 1986). Inside the potholes, the cobbles and boulders are usually larger
 300 than the ones resting on the rocky shore platform, and so are the rhodoliths, which are
 301 rare outside the potholes. Fragments of geniculate corallines often are present in the
 302 framework cavities and in the sediments (Fig. 7).

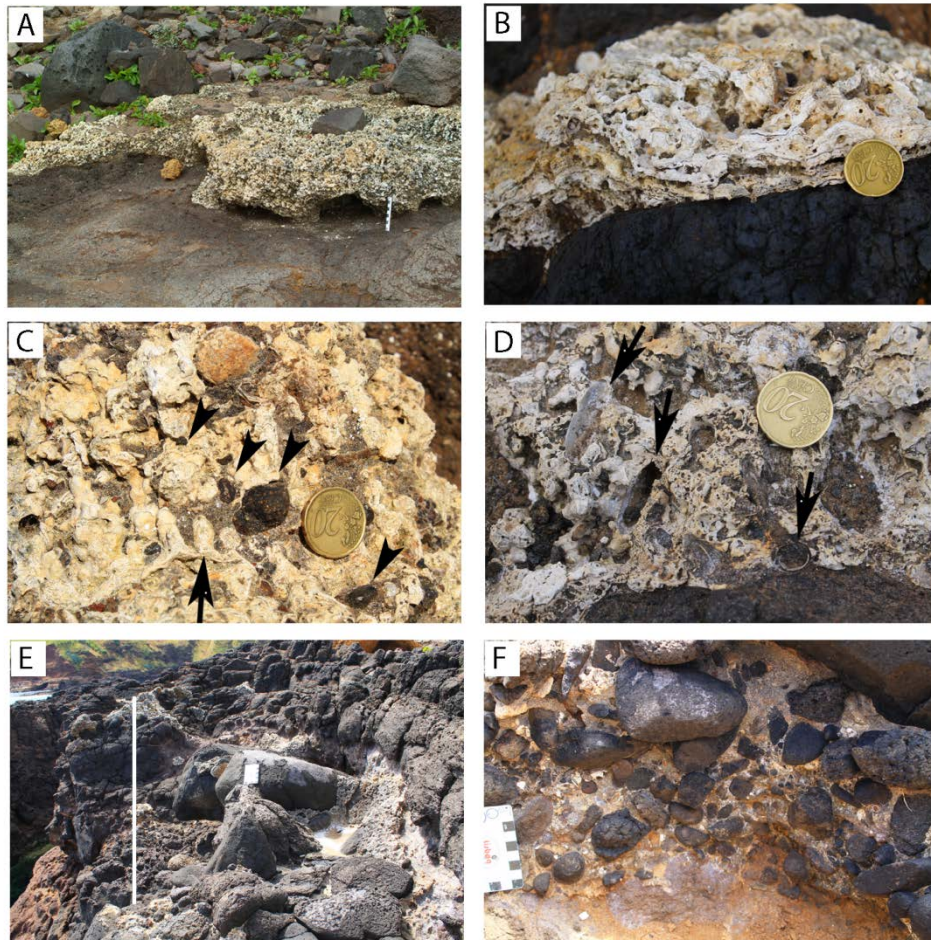
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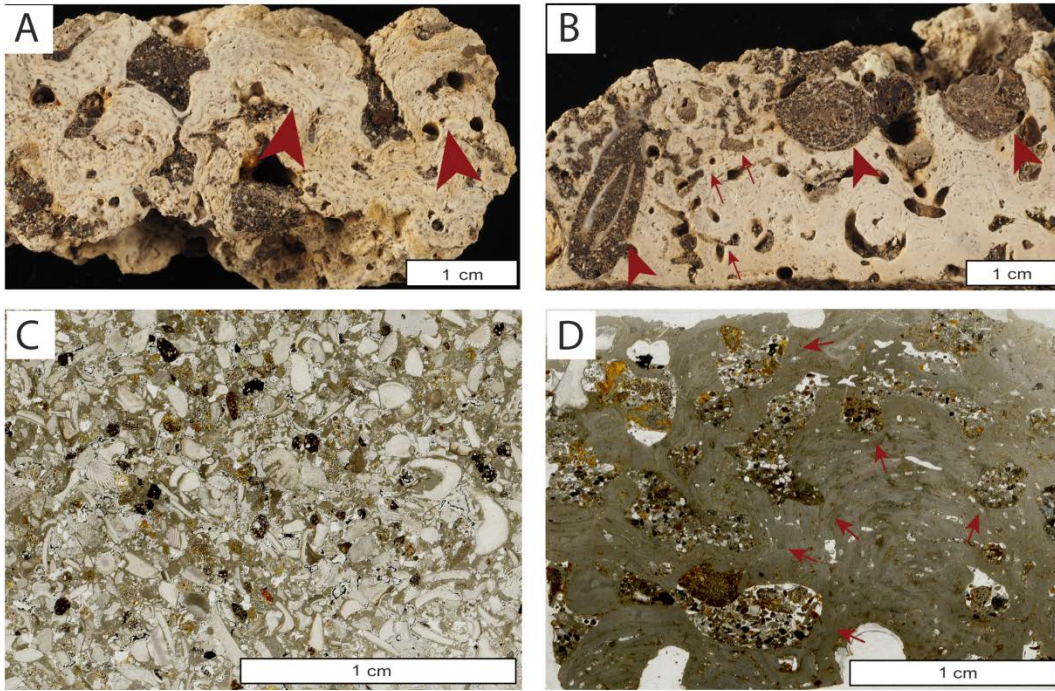
305 **Figure 4.** Simplified strip logs of the Prainha and Lagoinhas sections, representing main lithologies, and
 306 contacts (modified after Ávila et al., 2015a).

307



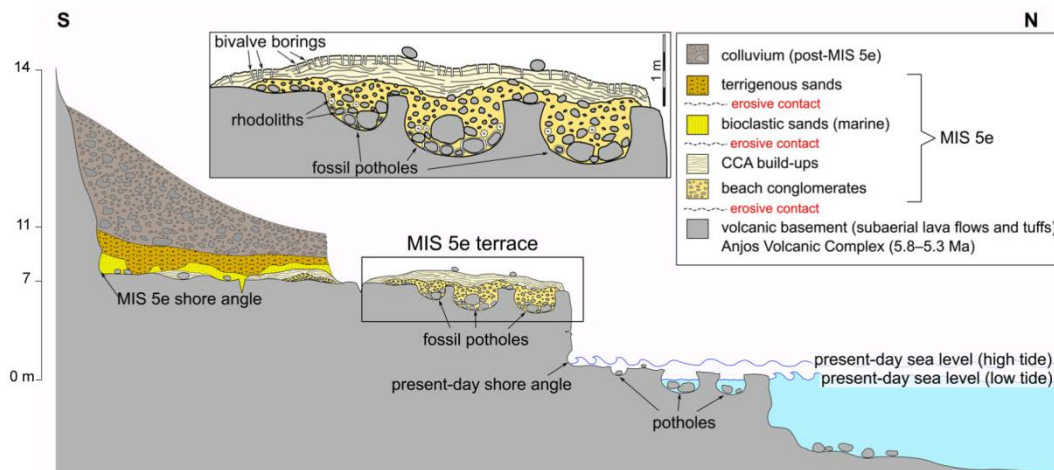
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309 **Figure 5.** Details of the Lagoinhas CCA buildup. A) General aspect of the CCA buildup; B) Detail of the
 310 CCA framework growing directly on the basalt; C) CCA with long protuberances (arrow) filled with
 311 sediment in between, and volcaniclasts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



314
 315 **Figure 6.** Section of the Lagoinhas CCA framework illustrating the taphonomic signatures. A) CCA
 316 columnar structure (arrow heads), B) Borings of bivalves, i.e. *Gastrochaenolites cf. torpedo* (arrow
 317 heads) and sponge boring *Entobia* isp. (small arrows), C) thin section photo of the calcarenitic sands that
 318 cover the CCA buildup; D) The boring *Entobia* isp. in thin section (arrows) crossing CCA columnar
 319 structure.

320



321
 322 **Figure 7.** Schematic cross section of the outcrop illustrating the different facies and its relationship with
 323 modern sea level (features not to scale).

324 Poorly consolidated bioclastic sands (white/yellow in coloration) rest on top of the CCA
325 buildup (or directly above the substrate when the CCA buildup is absent). These
326 sediments are mostly composed of shell debris mixed with subordinate amounts of
327 volcanic lithoclasts/mineroclasts, in varying proportions. These sands exhibit a variable
328 thickness, up to 50 cm; the top is deeply eroded with a very irregular relief, suggesting
329 the presence of erosional gullies. Unconformably above these sands, a package of dark
330 brown terrigenous sands can be found, completely filling the underlying erosive
331 topography on the bioclastic sands. This package attains a maximum thickness of up to
332 1.5 m and exhibits rare sub-rounded to sub-angular pebbles “floating” in the terrigenous
333 matrix, as well as some incipient calcrete crusts (and possibly rhizoconcretions)
334 towards the top. The sequence is capped by an unstratified and unconsolidated
335 colluvium-alluvial slope deposit, which abuts against the back beach cliff/slope; the top
336 of the colluvial fan rises several tens of meters in continuity with the present-day
337 topography of the slope behind.

338

339 **4.2. Coralline taxonomy**

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

346

347 **Order Corallinales** Silva and Johansen, 1986

348 **Family Spongitaceae** Kützing, 1843

349 Genus *Spongites* Kützing, 1841

350 *Spongites* sp.

351 (Fig. 8A)

352 **Description:** Growth form encrusting to lumpy. Thallus thickness varies from 674 μm
353 in encrusting portions to 7.04 mm in the lumpy portions. The thallus organisation is
354 monomerous and non-coaxial. The core filaments, 116–434 μm in thickness, curve
355 upwards to become perpendicular to the dorsal surface in the peripheral region. Core
356 cells are 13–27 μm ($M = 20$, $SD = 4$) in length, and 8–18 μm ($M = 11$, $SD = 2$) in
357 diameter. Cells of peripheral filaments are 13–22 μm ($M = 17$, $SD = 2$) in length, and 7–
358 14 μm ($M = 10$, $SD = 2$) in diameter. Some cells of contiguous filaments are joined by
359 cell fusions. Epithallial cells flat and round, but not flared, 7–11 μm ($M = 8$, $SD = 1$) in
360 diameter and 5–7 μm ($M = 6$, $SD = 0.7$) long.

361 Sporangial uniporate conceptacles, usually completely raised above thallus surface,
362 older conceptacles can become buried in the thallus. Conceptacles are rounded in shape,
363 316–482 μm ($M = 395$, $SD = 38$) in diameter and 137–205 μm ($M = 177$, $SD = 17$) in
364 length. Pore canals in section vary from triangular to cylindrical shapes, 69–192 μm
365 ($M = 110$, $SD = 23$) in diameter and 10–164 μm ($M = 108$, $SD = 26$) in height. The pore
366 canals are lined by cells arranged subparallel to the conceptacle roof. In some
367 conceptacles, remnants of a columella are present.

368 **Remarks:** The genus *Spongites* comprises those corallines with non-geniculate,
369 monomerous, or thin dimerous thalli, non-coaxial primigenous filaments without
370 palisade cells, and trichocytes that can be absent, single or in vertical row. The cells of
371 adjacent filaments are joined by cell fusions, and the conceptacles are uniporate. The
372 pore canals of tetrasporangial conceptacles are bordered by cells that arise from
373 peripheral roof filaments, protruding into the canal, and are oriented more or less

374 parallel to the roof surface (Penrose and Woelkerling, 1992; Braga et al., 1993;
375 Hrabovský et al., 2016). The monomerous non-coaxial thallus, the presence of cell
376 fusions, the uniporate conceptacles and the cell filaments surrounding the conceptacle
377 pore canals subparallel to the roof surface of the studied specimens indicate the genus
378 *Spongites*.

379 **Studied thin sections:** DBUA–F 1107(1.1); 1107(1.2); 1107(1.3); 1107(1.4);
380 1108(2.1); 1108(2.2); 1108(2.2.1); 110(3.1); 1109(3.1.1); 1109(3.2); 1109(3.3);
381 1109(3.4); 1110(4.1); 1110(4.3); 1112(6.1); 1112(6.2); 1112(6.2.1); 1112(6.3);
382 1113(7.1); 1113(7.2); 1113(7.3); 1113(7.4); 1113(7.5); 1113(7.6).

383

384 *Neogoniolithon* sp.

385 (Fig. 8B)

386 **Description:** The thallus organisation is monomerous and coaxial. The core region is
387 241–252 µm in thickness and the peripheral region is 1070–1951 µm. Cell fusions
388 absent. Of the three conceptacles present, only two were measurable, 282–320 µm in
389 diameter and 169–214 µm in height, but the pore canals were not measurable.

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

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

394

395 Family **Lithophyllaceae** Athanasiadis, 2016

396 Subfamily **Lithophylloideae** Setchell, 1943

397 Genus **Lithophyllum** Philippi, 1837

398 *Lithophyllum* sp.

399

(Fig. 8C)

400 **Description:** The thallus organisation is dorsiventral with a dimerous construction and
401 no palisade cells on the primigenous filaments. The thallus thickness varies from 817 to
402 2304 μm . Cell filaments are quite distinct and the lack of cell fusions indicate that only
403 secondary pit connections are present. Cells are rectangular in section, and their size
404 ranges from 6 to 11 μm in diameter and from 9 to 13 μm in length. The conceptacles are
405 uniporate, with a pronounced central columella, and some are buried in the thallus.
406 Conceptacles measure 175–235 μm in diameter and 73–131 μm in height. The pore
407 canal is conical in shape and varies from 19 to 66 μm in diameter and from 32 to 82 μm
408 in height.

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

412 **Studied thin sections:** DBUA–F 1109(3.1.1); 1109(3.2); 1109(3.3); 1109(3.4);
413 1110(4.2); 1110(4.3); 1112(6.2.1); 1113(7.5); 1113(7.6).

414

415 Genus *Titanoderma* Nägeli, 1858

416 *?Titanoderma* sp.

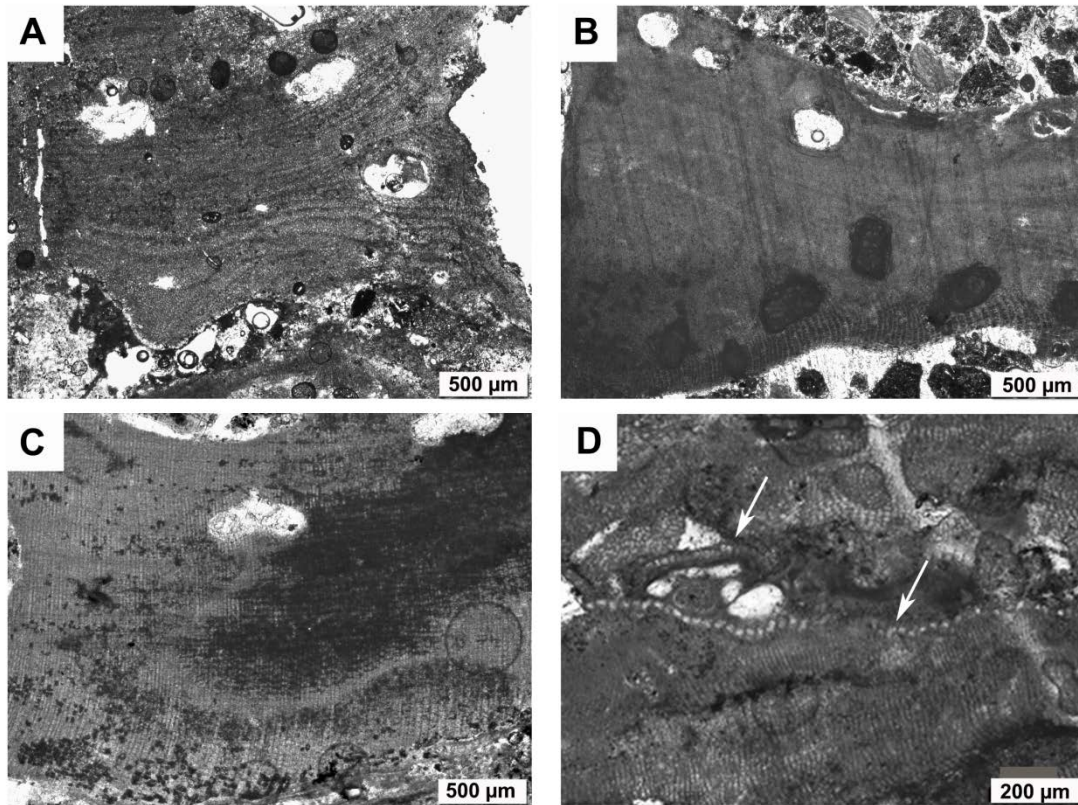
417

(Fig. 8D)

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

421 **Remarks:** *Titanoderma pustulatum* (J.V. Lamouroux) Nägeli, 1858 is present in the
422 algal framework from Prainha, on the south coast of the island (Amen et al., 2005). The

423 dimerous construction of the thalli with palisade cells and the apparent lack of cell
 424 fusions may suggest that the specimens from Lagoinhas belong to *Titanoderma*.
 425 **Studied thin sections:** DBUA–F 1108(2.2.1); 1110(4.3); 1113(7.2); 1113(7.3).



426
 427 **Figure 8.** Representative CCA of the Lagoinhas buildup. A) *Spongites* sp., uniporate conceptacles
 428 irregularly distributed throughout the thallus; B) *Neogoniolithon* sp., monomerous thallus with a coaxial
 429 core; C) *Lithophyllum* sp., uniporate conceptacle with visible columella and dimerous thallus without
 430 palisade cells; D) ?*Titanoderma* sp., two single layer thalli of palisade cells (arrows) interspersed other
 431 coralline thalli.

432

433 5. Discussion

434 5.1. Local sequence interpretation

435 The Lagoinhas sedimentary sequence is perched atop a rocky shore platform, and both
 436 are attributed to development during the last interglacial. The CCA buildup was
 437 constructed directly above the basaltic substrate or above consolidated beach sediments

438 (conglomerates and calcarenites), which partially infill the topography of the shore
439 platform. Critically, bivalve borings at the top of buildups suggest that there was a long
440 enough exposition of the buildup's hard surface for bioerosion to take place,
441 immediately after their formation (or pene-contemporaneous of their formation). As
442 proven by experiments, production of bivalve borings requires at least years of
443 exposition of the substrate (Bromley et al., 1990; Bromley and Aasgard, 1993).
444 Moreover, the borings are not truncated by erosion. This implies that the buildups were
445 very rapidly buried by the overlying bioclastic sands, possibly as a result of a rapid
446 environmental change, which led to deposition of the sands on top of the buildups. The
447 very irregular erosive contact between the bioclastic and the terrigenous sands, in turn,
448 denotes rapid subaerial erosion prior to the deposition of the latter, possibly by torrential
449 rain leading to the formation of gullies. The resulting erosive topography was
450 subsequently infilled by the terrigenous sands and later covered by colluvium.
451 The succession of events described above is compatible with a scenario in which
452 relative sea level peaked during the construction of the CCA buildups and their rapid
453 burial by the bioclastic sands, followed by a regressive trend represented by the erosion
454 of the bioclastic sands and subsequent deposition of the terrigenous sands, and later by
455 the deposition of the colluvium as the result of subaerial slope evolution. This suggests
456 that the buildups and bioclastic sands were deposited during the peak of MIS 5e, and
457 therefore represent environmental conditions that characterised this last interglacial
458 along the northern shore of Santa Maria.

459

460 **5.2. Framework nomenclature**

461 Rasser and Piller (2004) reviewed several descriptive classification schemes for
462 autochthonous, organically bound carbonate structures and their applicability to CCA

463 frameworks. Following their summary, the framework described herein can be
464 considered a bindstone, a term used to describe boundstones (i.e. organically bound
465 autochthonous limestones) in the classical carbonate nomenclature of Dunham (1962)
466 and expanded by Embry and Klovan (1971), where organisms encrust and bind. In the
467 nomenclature of Cuffey (1985), the Lagoinhas framework can be identified as
468 cruststone, formed by different encrusting layers, forming a frame of their own
469 skeletons. Based on the nomenclature for the matrix-skeletons-cavity/cement by Riding
470 (2002), the Lagoinhas framework fits in the skeleton-supported reefs-frame reefs, in
471 which *in situ* skeletons are in direct contact.
472 Evidence for fast growth can be seen by the encrusting to lumpy growth forms filled
473 with sediment in between, and the incorporated volcaniclasts (Fig. 5B and C).

474

475 **5.3. Factors leading to the formation of CCA buildups**

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

480 The distribution of CCA buildups depends on the availability of substrate type (e.g.
481 basement rock, coarse detrital material) and on adequate irradiance, under low to
482 moderate sedimentation rate (Ballesteros, 2006; Nalin et al., 2006; Titschack et al.,
483 2008; Bracchi et al., 2016; Tosi et al., 2017). Generally, hard substrates are suitable for
484 the formation of the crustose frameworks. Growth forms of coralline algae are
485 genetically controlled, although they frequently show high phenotypic plasticity,
486 regulated by ecological conditions such as hydrodynamic energy and sedimentation rate
487 (Basso, 1998; Rasser and Piller, 2004; de Queiroz et al., 2016). Many corallines

488 compete for space by growing faster than their neighbours (Bosence, 1983 and
489 references therein; Benzoni et al., 2011). The dense, closely superposed crusts of the
490 CCA, the abundance of boring bivalves and the coarse grained nature of sediment
491 trapped in the structural cavities are indicative of high-energy hydrodynamic conditions
492 (Bosence, 1983, 1985; Di Geronimo et al., 2002), suggesting that the Lagoinhas
493 framework developed in an exposed setting, an observation that is compatible with both
494 its geographical position and its general characteristics. According to Bosence's seminal
495 work (1985), high-energy hydrodynamic conditions are also suggested by the coralline
496 species forming the buildups at Lagoinhas, given that corallines involved in shallow,
497 high-energy reef construction are reported to be chiefly *Lithophyllum* and *Porolithon*
498 (Adey, 1979; Bosence, 1983). The two sequences of Lagoinhas and Prainha, however,
499 are very similar at the CCA composition, and so are in terms of their overall
500 stratigraphy and general characteristics. A slightly higher hydrodynamic
501 palaeoenvironment at Lagoinhas, is also supported by the mollusc faunal composition
502 reported by Callapez and Soares (2000) as revised by Ávila et al. (2002, 2015a), which
503 is indicative of a rocky, algal-covered, shallow-water and wave-impacted biota.
504 Moreover, the inferred high-energy hydrodynamic conditions at this site is also
505 suggested by the fact that the carbonate buildups are thinner and generally occur
506 directly over a rocky surface, abraded by wave action, and occur side by side, and even
507 partially cover the walls, of the large potholes, which require a high wave
508 hydrodynamics to form. These potholes nowadays exhibit the described infill of
509 consolidated conglomerates and calcarenites.

510 As such and given that the Lagoinhas sequence is located at the base of an exposed bluff
511 on the prevailing windward side of Santa Maria, it is reasonable to argue that the same
512 hydrodynamic conditions existed during the Last Interglacial. Notwithstanding the fact

513 that the overall sequence of Lagoinhas is very similar to the one exposed at Prainha
514 from a sedimentological and stratigraphic point of view, the absence of potholes and the
515 presence of smaller basaltic pebbles and cobbles in the conglomerates at Prainha, the
516 finer sand grain size at Prainha, and the higher diversity and density of sand-associated
517 bivalves [e.g., *Ensis minor* (Chenu, 1843), *Lucinella divaricata* (Linnaeus, 1758),
518 *Laevicardium crassum* (Gmelin, 1791), *Ervilia castanea* (Montagu, 1803; Ávila et al.,
519 2015a)] also suggest that the southern coast developed under slightly calmer
520 hydrodynamic conditions than the more exposed windward northern coast, as it happens
521 today. Likewise, *Spongites* and *Lithophyllum* are the two main framework builders on
522 both the northern and southern coasts. Therefore, the two sequences possibly represent
523 very similar environments, both energetic in terms of hydrodynamics, but with the
524 Lagoinhas sequence representing a slightly more exposed, wave-beaten setting than the
525 more protected leeward sequence of Prainha. This difference in hydrodynamics is
526 visible on the shelf, with the inner northern shelf almost deprived of sediments and a
527 thick inner shelf deposit near Prainha (Ricchi et al., 2020). Windward coasts lack
528 significant nearshore deposits due to offshore transport of sediments during storms
529 (Quartau et al., 2012; Meireles et al., 2013; Ricchi et al., 2020).

530

531 **5.4. Influence of hydrodynamics in species association**

532 Given the aforementioned considerations, the likely difference in species composition
533 between the sections at Lagoinhas and Prainha (Tables 2 and 3) which are coeval and
534 are very similar from the sedimentological and stratigraphic point of view may thus be
535 explained by differing ecological factors, with local hydrodynamics being the most
536 obvious. We therefore postulate that the small differences observed between the
537 Lagoinhas and Prainha sequences, in terms of the characteristics of the CCA buildups

538 but also in terms of fauna and sedimentology, are probably due to slightly more
539 energetic hydrodynamics at the former. Consequently, Lagoinhas possibly represents an
540 ecological niche more robust and tolerant to higher wave hydrodynamics, whilst the
541 niche represented at Prainha conversely is more sensitive to this factor, preferring the
542 calmer and more sheltered waters of the leeward shores. This study, therefore, provides
543 unique insights on how small changes in ecological factors influence the characteristics
544 of CCA buildups at a local scale. More importantly, these two reference sequences
545 provide excellent case studies to gain insights on the warm-temperate coralline algae
546 (on other taxa) assemblages (Meneses, 1993; Steneck et al., 1997; Braga and Aguirre,
547 2001; Bracchi et al., 2014) that existed at the latitude and mid-ocean setting of the
548 Azores during the warmest period of the last interglacial, currently absent, but which
549 may reappear as a result of global warming.

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

563 to 34%. The W (22%) and SW (5%) waves are also the highest (average annual Hs of
564 2.44 m and 2.45 m) in Santa Maria Island.

565

566 **5.5. Comparison with other settings**

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

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

586 The algal ridges are built by *Lithophyllum congestum* (taxonomically revised by
587 Hernandez-Kantun et al., 2016) and *Porolithon* spp. in the tropical western Atlantic and

588 in the Pacific (Bosence, 1983; Taberner and Bosence, 1985; Adey, 1986). Species of
589 *Lithophyllum* and *Porolithon* have been involved in reef construction since the
590 Cenozoic and have been found useful as palaeoecological indicators (Taberner and
591 Bosence, 1985 and references therein). The genus *Titanoderma* is known to occur as a
592 pioneer colonizer of new substrates, like bare rocks (Basso, 1998; Walker and del
593 Moral, 2003; Basso et al., 2007).
594 *Spongites* appears to be the ecological equivalent of *Porolithon* in the tropical Pacific
595 and Indian Oceans (Maneveldt and Keats, 2014; Gabrielson et al., 2018), however in the
596 present-day Azores, no record of *Spongites* as intertidal dweller is known so far.
597 In summary, in what concerns the species involved and their ecological context, the
598 CCA buildups from the Azores cannot be compared with any other buildups described
599 so far, attesting to its importance as a case study at the global stage.

600

601 **5.6. Tropical vs non-tropical reefs**

602 The CCA taxonomic composition of the Lagoinhas framework differs from the Prainha
603 framework only on the species level, as they are represented by the same families of
604 Spongitaceae and Lithophyllaceae. Coralline algae from the subfamily Lithophylloideae
605 are commonly recorded or even predominate in shallow-water carbonate deposits,
606 typically formed in warm-temperate to warm-tropical seas (among other: Meneses,
607 1993, Sartoretto et al., 1996, Steneck et al., 1997; Braga and Aguirre 2001; Bracchi et
608 al., 2014; Robinson et al., 2017). Species of *Lithophyllum* and *Titanoderma* are known
609 to form frameworks since at least 243 kyrs in the Mediterranean Pleistocene, with no
610 major change across climate fluctuations (MIS7 – Basso et al., 2007; Nalin et al., 2007;
611 MIS6 – Bracchi et al., 2019; Holocene – Sartoretto et al., 1996). *Spongites*, which is the
612 main reef builder both in Lagoinhas and Prainha, is well known to form CCA buildups

613 and also is typically present in coral reefs, being characteristic of shallow-water
 614 environments in clear and well-oxygenated tropical waters down to 30–40 m (Rösler et
 615 al., 2015 and references therein). Given the algal association found at Lagoinhas – and
 616 the considerations expressed above – the CCA buildups at this site thus reflect the
 617 warmer waters in which they grew during the Last Interglacial. This is in agreement
 618 with the mollusc species composition found at the outcrop, but also with a number of
 619 other thermophilic species that have been reported for the MIS 5e fossil record of Santa
 620 Maria, including at Vinha Velha, one of the few MIS 5e outcrops in the island that does
 621 not feature fossil algal buildups (Ávila et al., 2015).

622

623 **Table 2.** Comparison of the features from the CCA species of the Pleistocene of Santa Maria Island.

624 Taxonomy is based on conceptacle type, structure and size, thallus organisation and anatomy.

	<i>S. fruticulosus</i>	<i>Spongites</i> sp.	<i>N. brassica-florida</i>	<i>Neogoniolithon</i> sp.	<i>L. incrustans</i>	<i>Lithophyllum</i> sp.	<i>T. pustulatum</i>
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	Non-flared	Rounded non-flared	-	-	-	-	-
Diameter x Height (µm)	15-20 x 10-13	7-11 x 5-7					
Cells of peripheral/posti	15-18 x 23-25	7-14 x 13-22	13-15 x 20-23		10-13 x 18-23	6-11 x 9-14	23-25 x 15-18

genous							
filaments							
Diameter x							
Length (µm)							
Cells of	-	8-18 x 13-27	-	-	8-10 x 13-15	-	18-20 x 24-25
core/primigeno							
us filaments							
Diameter x							
Length (µm)							
Conceptacle	Uniporate	Uniporate	Uniporate	Uniporate	Uniporate	Uniporate	Uniporate
type	sporangial	316-482 x	sporangial	282-320 x 169-214	sporangial		sporangial
Diameter x	515-750 x	137-205	724 x 332		214-230 x	175-235 x 73-131	321 x 122
Height (µm)	316-450				112x117		
Conceptacle	-	-	-	-	Bean- shaped	-	Hemispherical
shape							
Central	ND	Present	Absent	Present	Present	Present	Absent
columella							
Roof thickness	9-30 cells	-	Over 20 cells above	-	13-21 cells	-	4-6 cells above
	above the		sporangial chamber		above		sporangial
	sporangial				sporangial		chamber
	chamber				chamber		
Source	Amen et al., 2005	This study	Amen et al., 2005	This study	Amen et al., 2005	This study	Amen et al., 2005

625

626 **Table 3.** Number of species/taxa reported from the Last Interglacial (MIS 5e) of Santa Maria Island, and
627 from Prainha and Lagoinhas fossiliferous outcrops. The last column displays the number of species that
628 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

629

630 **5.7. Where are the buildups today?**

631 A main question is, why are CCA buildups absent throughout today's Azores
632 Archipelago, since suitable shelf areas are present, and coralline algae fairly common?
633 One aspect might be the taxonomic inventory, because the main framework builder of
634 the studied buildups, *Spongites*, seems to be absent today (for an updated checklist of
635 present-day corallines of Santa Maria Island see Neto et al. (2021)). The reason for this
636 could be the changing climate, because during MIS 5e the water temperature was higher
637 than today, and as discussed above, *Spongites* is well-represented in warmer Atlantic
638 habitats. Another hypothesis concerns the contrasting levels of storminess in the Azores
639 between the last interglacial and the present day. It is inferred that with a warmer
640 climate, wave conditions in the Azores throughout most of the year would have been
641 calmer, notwithstanding the impact of occasional, possibly more intense hurricanes.
642 Today, however, the Azores are exposed to the brunt of the particularly energetic North
643 Atlantic swell, which only eases considerably during the summer months. This more
644 energetic regime of today, when compared to the last interglacial, may thus be
645 responsible for inhibiting the growth of *Spongites* (and other reef-building coralline
646 algae), preventing the development of CCA buildups in today's Azores waters.
647 At any rate, the knowledge of coralline algal-diversity of the Azores is incomplete, and
648 therefore these conclusions need to be tested in future studies.
649 This incompleteness of the record leads to another potential explanation: so far, no
650 researcher has extensively and systematically looked for CCA buildups in Azores

651 waters, and it is possible that comparable subtidal buildups do occur, but they have not
652 yet been discovered.

653

654 **6. Conclusions**

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

672

673 **Sample CRediT author statement**

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678

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701

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