

1 Basalt Mounds and Adjacent Depressions Attract Contrasting  
2 Biofacies on a Volcanically Active Middle Miocene Coastline  
3 (Porto Santo, Madeira Archipelago, Portugal)

4 Ana Santos<sup>1\*</sup>, Eduardo Mayoral<sup>1</sup>, Markes E. Johnson<sup>2</sup>, B. Gudveig Baarli<sup>2</sup>, Carlos M. da  
5 Silva<sup>3</sup>, Mário Cachão<sup>3</sup>, Jorge Ledesma-Vázquez<sup>4</sup>

6

7 <sup>1</sup>Departamento de Geodinámica y Paleontología, Facultad de Ciencias Experimentales, Campus  
8 de El Carmen, Universidad de Huelva, Avda. 3 de Marzo, s/n, 21071 Huelva, Spain

9 <sup>2</sup>Department of Geosciences, Williams College, Williamstown, MA 01267 USA

10 <sup>3</sup>Departamento de Geologia and Centro de Geologia, Faculdade de Ciências, Universidade de  
11 Lisboa, Campo Grande, 1749-016 Lisbon, Portugal

12 <sup>4</sup>Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Ensenada, BC 22800,  
13 Mexico

14 \* Corresponding author. (AS) asantos@dgyu.uhu.es

15

16 **Abstract**

17 Small basalt mounds with encrusting corals and inter-mound carbonate sandy zones with  
18 abundant rhodoliths corresponding to an ancient intertidal to shallow-water sea floor are  
19 exhumed from overlying volcanoclastic deposits and basalt lava flows at Pedra de Água  
20 on Ilhéu de Cima off Porto Santo, one of the islands of the northeastern Atlantic Madeira  
21 Archipelago (Portugal). The mounds rise above the surrounding surface to attain a height  
22 of about half a meter. The mounds exhibit an *in situ* assemblage of hermatypic corals,  
23 dominated by *Tarbellastrae* and *Solenastrea*. They formed as massive (4.2 × 1.9 m

24 average length), isolated patches in a protected bay close to shore eroded from an uneven  
25 basalt substrate dated to the Middle Miocene (14 to 15 Ma). The slightly deeper zones  
26 between basalt mounds, which alternate with them over a distance of more than 20 m, are  
27 covered mainly by coarse carbonate sand on which rhodoliths up to 14.8 cm in diameter  
28 are preserved *in situ*. Many rhodoliths have grown around a basalt core, which indicates a  
29 local, nearshore source for development. Complete burial of the elevated coral  
30 settlements and intervening low zones populated by rhodoliths occurred when volcanic  
31 lapilli and other tephra catastrophically buried this part of the rocky shore. The rhodoliths  
32 and coral assemblages exposed in an area of 12 m<sup>2</sup> were canvassed systematically using  
33 census quadrats to quantify community relationships.

34

35 **Key words** rocky shores, Miocene, shallow-subtidal zonation, corals, rhodoliths,

36 Ostrution deposits, Volcanic island

37

38

### 39 **Introduction**

40 Rocky shores constitute a special environment with an evolutionary history of a dynamic  
41 ecosystem since the Precambrian (Johnson and Baarli 2012). Geographically they ranged  
42 across tropical to boreal latitudes, just as today (Johnson 2006). In this context, hard  
43 stable substrates exposed to intertidal and shallow-subtidal waters provide exceptional  
44 conditions for colonization by boring and encrusting organisms. The *in situ* fossils of  
45 these organisms, mostly algae and invertebrates, represent potential tools in  
46 paleoenvironmental analysis of shoreline settings. Not all unconformities, however, are

47 equally significant as ancient coastlines (Johnson 1988). Typically, those rocks most  
48 resistant to coastal erosion, such as basalt or quartzite, tend to form unconformity  
49 surfaces with appreciable topographic relief under transgressive conditions that promote  
50 the development of intertidal boulder beds and cliffs.

51 Nearly all studied former islands are situated on epicontinental platforms or  
52 continental shelf margins (e.g., Lescinsky et al. 1991; Doyle et al. 1997; Johnson et al.  
53 1988, 1995, 2010; Johnson and Ledesma-Vázquez 1999; Betzler et al. 2000; Wilson and  
54 Taylor 2001; Surlyk and Sørensen 2010). Despite widespread availability for study short-  
55 term biological colonization on rockgrounds (see Taylor and Wilson 2003), the paleo  
56 coasts of oceanic islands are surprisingly under-represented. In fact, few observations are  
57 recorded on the dynamics between coastal sedimentation and settlement patterns in the  
58 intertidal to shallow subtidal zone with respect to intermittent volcanism and related  
59 tectonics (Meco et al. 2007; Johnson et al. 2010).

60 The present contribution is the fourth in a series of studies on the paleoecology of  
61 Miocene shallow-water marine benthic communities on basaltic rocky shores of Ilhéu de  
62 Cima (Madeira Archipelago, Portugal). Santos et al. (2011) focused on a Miocene rocky-  
63 shore biota from Ilhéu de Cima, providing a clear example of fossil marine invertebrates  
64 preserved on a wave-cut platform and related cliff face of solid basalt. Johnson et al.  
65 (2011) described an extraordinary deposit of fossil rhodoliths washed against a Miocene  
66 rocky shore as a result of storms of near-hurricane strength, and Santos et al. (2012a) re-  
67 evaluated the extent of organic boring on basalt surfaces on the same islet.

68 This paper describes two adjoining Miocene biofacies reflecting a definite pattern  
69 of intertidal to shallow-water zonation preserved on a low-relief rocky shore at a place

70 named Pedra de Água (Fig.1). At this locality, encrusting corals were briefly established  
71 on low basalt mounds and surrounded by a coarse carbonate sandy gravel substrate that  
72 supported many rhodoliths prior to sudden burial by volcanic lapilli and other tephra,  
73 thereafter succeeded by massive basaltic flows. Ostrution deposits similar to this are  
74 otherwise well known in the paleoecological literature (Brett et al. 1997), but rare in  
75 terms of sudden burial by volcanoclastic material. Experience with Holocene and modern  
76 settings where local extermination of coral communities took place should, however,  
77 facilitate our search for comparable patterns in the geologic record (Heikoop et al. 1996;  
78 Pandolfi et al. 2006). Here, we investigate the dynamics between environmental  
79 conditions and biotic colonization from a Miocene sheltered cove on Pedra de Água that  
80 became catastrophically entombed by volcanoclastic material.

81

## 82 **Location and geological setting**

83 Portugal's Madeira Archipelago sits 650 km off the shores of Moroccan Africa in the  
84 North Atlantic Ocean. Porto Santo is an outlying island located 50 km northeast of the  
85 principal island of Madeira (Fig. 1). Ferreira (1997) produced a geological map of Porto  
86 Santo, including its various satellite islets. The second largest is Ilhéu de Cima with a  
87 perimeter of approximately 3 km and maximum elevation of 115 m. Fossiliferous  
88 sedimentary successions occur in several places on the main island of Porto Santo in  
89 relation to the transition between two major volcanic units: a lower trachytic to basaltic  
90 submarine basal volcanic complex with ages ranging from 18.8 to 13.5 Ma; and an upper  
91 subaerial alkali basaltic to hawaiitic complex dated between 14 and 10.2 Ma (Ferreira  
92 1985). Based on calcareous nannofossil assemblages at Lombinhos on the east side of

93 Porto Santo, Cachão et al. (1998) correlated sedimentary units to the Middle Miocene,  
94 lower Serravalian (Calcareous Nanofossil biozone CN4 of Okada and Bukry 1980). A  
95 comparable age of about 14 to 15 Ma is extrapolated for sedimentary intercalations  
96 between volcanic rocks on Ilhéu de Cima.

97 The study site described in this paper is located approximately 225 m northwest of  
98 the only landing place on Ilhéu de Cima, at an elevation of 7 m above mean sea level  
99 (Fig. 1).

100

## 101 **Methods**

102 Two methods were used to test the visual impression at the outcrop scale of physical and  
103 biological zonation preserved intact on the rocky paleo-shore at Pedra de Água. The first,  
104 was the establishment of transect lines with grids, for methodical sampling of the Middle  
105 Miocene encrusting corals and associated rhodolith beds (Fig. 2). Four transects 0.5 m  
106 apart (labeled A-D) were laid out parallel to the base of the present-day cliff line across  
107 the fossil deposit located approximately 30 m inland from the present shore. A grid  
108 (0.5×0.5 m in size and divided into twenty-five units of 10 × 10 cm each) was deployed  
109 and moved along each transect line to collect data on fossil content and to map settlement  
110 patterns. The same operation was applied to low-lying areas between the basalt mounds,  
111 where rhodoliths are commonly found on a thin bed of coarse bioclastic debris. The  
112 number of grid samples recorded for each transect line was 24. The completed survey  
113 entailed full coverage of an area 12 by 2 m (24 m<sup>2</sup>). All fossil biogenic components  
114 within this area were identified to species level where possible and tabulated to  
115 graphically show how populations in each category change grid-by-grid along each of the

116 transects (A to D). Bioerosional structures were also identified when present. Criteria  
117 used to distinguish *in situ* material from reworked material included: (1) orientation of  
118 corallites, (2) whether or not fossil bivalves are articulated, and (3) presence or absence  
119 of encrusting coralline algae. Coral identification conforms to the taxonomy followed by  
120 Best and Boekschoten (1982) in their revision of Chevalier (1972).

121 In order to facilitate the sample analyses and map transitional boundaries between  
122 the two biofacies, three blocks (16 grids to one block, equal to 4 m<sup>2</sup>) were chosen for  
123 illustration from the full array (Fig. 2). The blocks are labeled 1 (outside of the cliff line  
124 to the NW), 2 (middle block) and 3 (outside of the cliff line to the SE). Every fossil and  
125 every area with bare substrate was plotted precisely in place.

126 A second supplementary method of data collection was applied randomly on the  
127 outcrop surface with the purpose of collecting data on size variation in rhodoliths and the  
128 extent to which rhodoliths formed around basalt cores. The study on size variation and  
129 nucleation of 100 rhodoliths was simplified by determining only the two major visible  
130 axes of their shape and rock core. In addition, 39 isolated rhodoliths were measured along  
131 the three axes – long (L), intermediate (I), and short (S) – in order to plot them on the  
132 Sneed and Folk (1958) pebble-shape diagram to generate the sphericity index for  
133 rhodoliths after Bosence (1976, 1983a). Thin-sections were made of selected rhodoliths  
134 so that their inner arrangements could be described and the constituent coralline algae  
135 identified.

136

137 **Stratigraphic sucession**

138 An irregular subaerial basaltic flow (with large columnar disjunctions) provided  
139 the substrate for the fossiliferous horizon at Pedra de Água, which accumulated as a  
140 rhodolith biocalcarenite over the lowermost depressions (near the current seashore),  
141 changing eastward to fossiliferous limestone with rhodoliths on a more level surface (Fig.  
142 3). Here, near the present day cliff line about 30 m inland, the uppermost sediment-free  
143 basaltic substrate is almost completely covered by *in situ* encrusting corals. In turn, these  
144 fossiliferous deposits are covered by approximately 1.5 m of yellow-orange volcanic tuff  
145 with an irregular thickness, followed immediately above by a 1 m thick volcanic breccia.  
146 The succession continues with a 13 m thick basaltic lava flow. Above this volcanic unit is  
147 another whitish fossiliferous horizon, mainly composed of corals. The succession is  
148 completed by two to three subaerial basalt flows separated by a single marker bed of red  
149 tuff (Fig. 3).

150 The lowermost volcanic unit irregularly thickens towards the northwest, forming a  
151 rocky ramp at Furninha, against which the lower fossiliferous unit ends (Fig. 1). The lava  
152 flow above the fossiliferous unit also thickens northward, while the subsequent subaerial  
153 basaltic surfaces have an overall sigmoid shape with maximum thickness attained  
154 towards the southeastern end of the island. The upper units formed under subaerial  
155 conditions may be slightly younger in age relative to the fossiliferous units interbedded  
156 with submarine hyaloclastites dated at 15-14 Ma (Cachão et al. 1998) located some 5 km  
157 northeast, at Lombinhos (on the adjacent main island of Porto Santo).

158

## 159 **Paleontological analysis**

### 160 ***Census Data***

161 The transects from A to D (Fig. 2) show no significant changes from the present cliff line  
162 in the present-day seaward direction. However, the frequency data on a grid-by-grid basis  
163 for each fossil entity revealed two distinct biofacies along the paleoshore (Fig. 4a-b).

164 There is a distinct spatial affinity between the locations of the corals and  
165 *Gastrochaenolites* borings, while the rhodoliths cluster separately (Figs. 4a, 5a-b).

166 The results of the systematic survey across the surface of the paleoshore are  
167 plotted as "ecologic zonation" maps representing half of the total surface area studied  
168 (blocks 1, 2 and 3; Fig. 6a-c). As summarized in Table 1, 50% of the mapped area (12  
169 m<sup>2</sup>) was occupied by bioclastic coarse and unsorted sandy gravel and in 7% the gravel  
170 was mixed with rhodoliths. The rest of the exposed surface was bare basalt (27%) and  
171 corals attached directly on it (16%). An unknown proportion of bare basalt in the census  
172 area may have been stripped of its carbonate crust and/or other distinguishable  
173 macrofossils as a result of Recent erosion, but the spatial distribution of the remaining  
174 fossils still reveals a distinct pattern. A thick white carbonate rind is recognized in some  
175 places on top of the basalt.

176 If we focus on the distribution of substrate nature and *in situ* fossils by individual  
177 blocks (Table 1), block 1 and 2 are those with the highest percentage of coarse and  
178 unsorted sandy gravel mixed with rhodoliths (63% and 61%, respectively). Block 3  
179 exhibits only 46% of coarse and unsorted sandy gravel mixed with rhodoliths. The  
180 number of rhodoliths counted is 47 both for blocks 1 and 2, but rhodoliths are more  
181 abundant in block 3 with 74 individuals (Table 1). The number of rhodoliths per square-  
182 meter of sand is 18.7 for block A, 19.3 for block B and 40.2 for block C. In contrast, the  
183 percentage of bare basalt surface is greater (39%) for block 3, but only 28% and 15% for

184 blocks 2 and 1, respectively. Regarding corals, block 1 presents the highest percentage of  
185 surface occupied by encrusting corals (22%), followed by block 3 with 15% and block 2  
186 with only 11%. Block 2 contains the largest number of *Spondylus* sp. (six individuals).  
187 Both of the other two blocks contain only two individuals each.

188 Although abundance is high, fossil diversity on the Pedra da Água rocky shore is  
189 quite low. Only two coeval benthic communities are represented: a mound community  
190 (zone of coral encrustation) and an inter-mound community (zone of rhodolith  
191 pavement).

192

193 ***Mound community (zone of coral encrustation)***

194 An assemblage of encrusting colonial corals dominates the tops of the basalt mounds,  
195 corresponding to the higher local topography and the more exposed rocky intertidal to  
196 shallow-subtidal environment. The mounds are circular in shape (maximum length:  $8.5 \times$   
197  $3$  m; minimum length:  $2 \times 1$  m), and rise above the surrounding soft bottom for about half  
198 a meter.

199 At least two species of scleractinian corals (*Tarbellastrea reussiana* Milne-  
200 Edwards and Haime, 1850 and *Solenastrea* sp.) are present in the mound community.  
201 Figure 7 a illustrates the closely packed coral colonies attached directly to the basalt  
202 surface and preserved in growth position. Lesser elements such as the epifaunal bivalve  
203 *Spondylus* sp., the encrusting bryozoan *Conopeum* sp., and the coral-inhabiting barnacle  
204 *Ceratoconcha costata* Kramberger-Gorjanović (1889) are also present. Representative  
205 trace fossils present in the corals include borings produced by demosponges (*Entobia*  
206 isp.), coral-inhabiting barnacles (*Imbutichnus costatum* Santos et al., 2012) and borings of

207 bivalves (*Gastrochaenolites torpedo* Kelly and Bromley, 1984) (Fig. 7 b). *Imbutichnus*  
208 *costatum* structures are found exclusively on *Tarbellastrea* sp. indicating a clear host  
209 preference by the producer *Ceratoconcha costata* (Santos et al. 2012b). The post-mortem  
210 bivalve borings are arranged perpendicularly to the coral surface and most of them are  
211 truncated, presenting an average diameter of 1.5 cm. Counts from the sampling grid  
212 yielded an average of ten *T. reussiana/Solenastrea* sp. colonies/m<sup>2</sup>. The average number  
213 of *G. torpedo* /block was 201/m<sup>2</sup> for block 1, 57/m<sup>2</sup> for block 2, and 65/m<sup>2</sup> for block 3  
214 (Table 1).

215 *Spondylus* sp. with articulated valves occurs preserved in life position among the  
216 corals. Some of the shells are partially covered with crustose coralline algae and  
217 encrusting bryozoans. As noted previously, it is possible to recognize in some places on  
218 top of the basalt a thick conspicuous white carbonate rind. Such crusts are devoid of  
219 fossils. Both rhodoliths and bioturbation structures are absent. For a more generalized  
220 paleoecologic setting of the described biofacies see Table 2.

221

### 222 ***Inter-mound community (zone of rhodolith pavement)***

223 The inter-mound community consists entirely of rhodoliths often encrusted by serpulids  
224 and showing *Gastrochaenolites* isp. bioerosion. Lumpy in morphology, clustered  
225 rhodoliths are restricted to a separate zone occupying a lower topographic position  
226 between the raised patches of basalt. Composed of crustose coralline red algae, these  
227 rhodoliths are mainly multispecific. *Lithophyllum* and *Sporolithon* most commonly occur  
228 together (Fig.8a), although monospecific rhodoliths of *Sporolithon* sp. have also been  
229 identified, as well as a less common combination of *Lithophyllum* and *Hydrolithon* (Fig.

230 8b). The matrix in which the rhodoliths occur contains very coarse and unsorted sandy  
231 gravel (average diameter 2 mm) with clasts up to 10 mm in diameter, as well as some  
232 shell fragments derived from *Spondylus* sp. (Fig. 9a). The packing density of rhodoliths  
233 varies from 18.7/m<sup>2</sup> and 19.3/m<sup>2</sup> for block 1 and 2, respectively, to 40.2/m<sup>2</sup> for block 3.

234 The shape of these rhodoliths is spheroidal to ellipsoidal (according to Bosence's  
235 (1983b) growth terminology (Fig. 10). The diameter of the rhodoliths varies from a  
236 minimum of 1.9 cm to a maximum of 14.8 cm. Most of the rhodoliths include a nucleus  
237 composed of rock (Fig. 9b). The high correlation coefficient ( $R^2 = 0.82$ ) between data for  
238 maximum diameters of rhodoliths and cores indicates a positive, linear relationship (Fig.  
239 11) showing that the rock nucleus influenced the general shape of the rhodolith. The size  
240 of rock cores tends to very large (4.7 cm on average) compared to the total size of the  
241 rhodoliths with an average size of 6.4 cm (Fig. 9b). The average thickness of the coralline  
242 red algae crust is thus less than 1.7 cm with little difference between small and large  
243 rhodoliths.

244 In thin-section, rhodoliths reveal a massive inner arrangement with no  
245 macroscopic cavities. The inner arrangement is laminar-concentric around the nucleus to  
246 slightly columnar towards the surface according to Bosence's (1983b) nomenclature.  
247 Thin-sections show some degree of reworking and erosion, although many rhodoliths are  
248 unabraded. Rare instances of two basalt cores or cores consisting of corals also are found.  
249 Cross-sections through rhodoliths do not show a faunal succession nor overgrowth  
250 patterns.

251 No bioturbation structures are recognized in the matrix in which the rhodoliths  
252 occur. For a more generalized paleoecologic setting of the biofacies see Table 2.

253

254 **Discussion**

255 ***Water depth***

256 As evaluated by some authors (James and MacIntyre 1985; Bourillot et al. 2009),  
257 paleotopography is the essential controlling factor for coral-reef location because reefs  
258 flourish in elevated zones exposed to good marine circulation. Also, light conditions as  
259 well as the ambient water energy influence the growth form of individuals that compose  
260 the coral assemblages (Mankiewicz 1995).

261 According to Bourillot et al. (2009), coral communities that are dominated by  
262 domal forms, such as *Tarbellastrea*, indicate shallow, high-energy waters. Another  
263 argument in support for this interpretation derives from the presence of abundant bivalve  
264 borings on the coral colonies of Pedra de Água, generally suggesting a very shallow  
265 marine environment (waters only a few meters deep) with a low or zero sedimentation  
266 rate (Bromley and Asgaard 1993; Bromley 1994). The size of pebbles and cobbles which  
267 the rhodoliths encrusted suggests a source area close to the paleoshore at Pedra de Água,  
268 as does the immediately overlying tuff layer. Thus, the water depth in this area was  
269 shallow and well above the fair-weather wave-base.

270 Coralline red algal taxa forming rhodoliths have often been used to infer  
271 paleodepth. However, Rasser and Piller (1997) showed that depth analysis based on  
272 genera was problematic. Such analyses are best done at species level. The genus  
273 *Sporolithon* is generally most abundant below 20 m in the northern hemisphere and in  
274 tropical areas (Adey et al. 1982; Perrin et al. 1995; Aguirre et al. 2000; Braga and Bassi  
275 2007; Basso et al. 2009). However, there are exceptions to this. Basso et al. (2009)

276 described Recent rhodoliths formed by *Sporolithon* from intertidal pools and tidal  
277 channels on wave-cut platforms from New Zealand, while Baarli et al. (2012) recorded  
278 rhodoliths formed by the same algae in Quaternary calcareous sands deposited in water  
279 depths of less than 6.5 m in Baja California (Mexico).

280

### 281 ***Substrate***

282 The studied corals at Pedra de Água are directly cemented to mounds of basalt, which is  
283 in accordance with their environmental preferences because these encrusting coral  
284 colonies developed preferentially on hard rather than soft substrates (Cabioch et al.  
285 1995). According to Johnson and McKerrow (1995), very few examples are known of  
286 fossil corals attached directly to inorganic surfaces. They documented encrustation of the  
287 Early Jurassic coral *Heterastrea* sp. on Carboniferous limestone at Southerndown (South  
288 Wales). Johnson and Baarli (1987) recorded *Favosites* sp. from the Upper Ordovician of  
289 Hudson Bay encrusting quartzite boulders in a rocky-shore setting. An unidentified  
290 scleractinian coral has been shown by Lescinsky et al. (1991) to encrust andesite boulders  
291 in a rocky-shore setting of Late Cretaceous age in Baja California (Mexico). The colonial  
292 corals *Tarbellastraea reussiana* (Milne-Edwards and Haime, 1850) and *Isophyllastrea*  
293 *orbignyana* (Mayer, 1864) were reported encrusting basaltic substrate in a rocky-shore  
294 setting of Middle Miocene age in Ilhéu de Cima (Madeira Archipelago; Santos et al.  
295 2011).

296

### 297 ***Water energy***

298 The fossil encrusting corals occurring on the top of the basalt mounds at Pedra de Água  
299 were not originally covered by the sediment that presently fills the surfaces around them  
300 prior to burial by tuff. It is clearly seen in the base of the cliff that the overlying volcanic  
301 tuff bed (Figs. 3, 12) formed directly on the top of the corals and the rhodoliths alike,  
302 extending across both ecological zones, that was responsible for their demise. Therefore,  
303 the wave energy at Pedra de Água locality was sufficient to prevent sediment grains from  
304 settling to suffocate corals and also to carry smaller eroded basalt clasts seaward, but  
305 insufficient to do much damage to the coral colonies because they were firmly attached in  
306 a higher topographic position. The eroded basalt clasts filled the lower areas of  
307 paleorelief around the coral mounds on the basalt substrate and were readily adopted as  
308 nuclei by the coralline red algae living there. The presence of rhodoliths also implies a  
309 low sedimentation rate and unlithified substrate (Bosence 1991) subjected to turbulent  
310 waters (Adey and Burke 1976; Johnson et al. 2009).

311 Rhodoliths have an unattached mode of life. Marrak (1999) suggested that high  
312 disturbance by infaunal organisms could be an important agent to stimulate overturning.  
313 However, considering the lack of bioturbation, the large, heavy rhodoliths, and the  
314 associated thin, coarse sediment layer at Pedra de Água, wave energy was the more likely  
315 responsible for rhodolith overturning.

316 The external morphology and internal structure of rhodoliths may be useful  
317 indicators of hydraulic energy. Spheroidal to ellipsoidal shape, massive inner  
318 arrangement with a uniform lumpy surface growth-form and the occurrence of a lithic  
319 nucleus are consistent with a frequent and regular overturning of the rhodoliths by wave  
320 action (e.g., Bosellini and Ginsburg 1971; Bosence 1983a, b; Scoffin et al. 1985; Johnson

321 and Hayes 1993; Steller and Foster 1995; Foster et al. 1997; Gischler and Pisera 1999;  
322 Bassi et al. 2009). Thin-sections also show a symmetrical accretion around the core and  
323 few empty voids, both of which indicate high water energy and frequent overturning  
324 (Bassi et al. 2009). Likewise, the low presence of sediment in the interior of the  
325 rhodoliths is often considered to be evidence of a low sedimentation rate or of a regular  
326 overturning of the rhodoliths on the sea floor (Basso 1998).

327         There is some evidence of abrasion of the Pedra de Água rhodoliths, as is often  
328 the case for rhodoliths in fairly shallow waters on a coarse bioclastic substrate (Bassi et  
329 al. 2009). Dead rhodoliths may be exploited as substrate for new colonization leading to  
330 polyspecific rhodoliths (Basso et al. 2009), which are commonly encountered in this  
331 study.

332         Basso (1998) demonstrated that the packing is crucial in explaining the hydraulic  
333 behavior of rhodoliths. With a higher density, stronger wave action is needed to move the  
334 rhodoliths. Comparing rhodoliths at Pedra de Água on the southwest side of Ilhéu de  
335 Cima with rhodoliths at Cabeço das Laranjas on the northeast side of the islet (Johnson et  
336 al. 2011), some 300 m away, they are of comparable sizes, but the thickness of the  
337 deposits and their packing density differs profoundly. The former site displays less than  
338 40 rhodoliths per square meter while the latter shows more than 200 /m<sup>2</sup>. The rhodolith  
339 assemblage at Cabeço das Laranjas was identified as transported into the site from deeper  
340 off-shore banks by hurricanes or strong storms. In contrast, the rhodoliths at Pedra de  
341 Água formed a living community with a density level and bed thickness sufficiently  
342 limited to promote rotation leading to even growth around a rock core.

343

344 *Rhodolith nucleus*

345 The shape of pebbles and cobbles present in the sediment matrix was responsible for the  
346 ultimate shape of the rhodoliths (Lund et al. 2000). This is in accordance with the data  
347 obtained by Scoffin et al. (1985) from Recent shallow reef rhodoliths at Cook Islands  
348 (central Pacific). These authors analyzed and compared different rhodolith nuclei (basalt  
349 pebbles, stick corals, mussel valves, and gastropods) with the final shape of the algae and  
350 concluded that most of these rhodoliths, at least initially, are greatly influenced by the  
351 shape of its nucleus. As a general rule, the more spherical the nuclei (e.g., basalt pebbles)  
352 the more regular the concentric encrustations, while on tabular or bowl-shaped nuclei  
353 (e.g., mussel shells) the encrustations are of uneven thickness (Scoffin et al. 1985).

354 Another good example is the Pliocene rhodolith deposits at Punta San  
355 Francisquito in the Gulf of California studied by Johnson et al. (2009), because there  
356 relatively large rhodoliths have a solid granodiorite core. At present, this Pliocene site is  
357 the only known locality in the Gulf of California where this peculiarity is known to occur.  
358 However, some differences exist between the two places in terms of overall rhodolith  
359 size. The rhodoliths from Punta San Francisquito measure 5 cm across on average with  
360 calcareous rinds that completely enclose granodiorite pebbles up to 3 cm in diameter  
361 (Johnson et al. 2009). This is in contrast to the much larger Miocene rhodoliths at Pedra  
362 de Água. Johnson and Hayes (1993) studied small andesite pebbles from the Late  
363 Cretaceous at Las Minas (Pacific coast of northern Baja California), with rinds 5 mm to 8  
364 mm in thickness. This effectively doubled the diameter of the pebbles as a consequence  
365 of algal encrustation. In this particular case, the relative proportion of the crust was larger  
366 than at Pedra de Água, but the size and shape of the nuclei still primarily influenced the

367 shapes of nucleated rhodoliths as found in many other studies (Basso and Tomaselli  
368 1994; Ballantine et al. 2000; Bassi et al. 2009).

369         Generally, the Pedra de Água rhodoliths have a uniform size and shape and a  
370 basalt core with a thin crust of algae of about the same thickness regardless of size. This  
371 suggests there was just one population with the same, relatively short history of  
372 development, which could only be achieved by fairly frequent movement.

373

#### 374 *Paleoenvironmental interpretation*

375 According to the surrounding topography at Pedra de Água (Fig. 1), the study area  
376 features encrusting corals on basalt mounds that grew within a small protected  
377 embayment at the paleo-island at Ilhéu de Cima. Wave action within the bay was still  
378 sufficient to promote the growth of small patches of corals and to keep the rhodoliths in  
379 between the basalt mounds in motion. The fact that some rhodoliths display signs of  
380 erosion and the coarse bioclastic matrix suggest some degree of bottom reworking by  
381 currents as shown by Bassi (1998). In this context, the topographic configuration may  
382 have controlled local current patterns. The patches of corals on low mounds of basalt are  
383 surrounded by sandy gravel and rhodolith beds. Wave action from the south or southwest  
384 was the only possible source for wind-driven waves to reach the shelf at this locality.  
385 This is confirmed by Santos et al. (2011), who show that the Miocene coastline ran  
386 parallel to the present one southeast of Pedra de Água. This is in marked contrast to  
387 Cabeço das Laranjas on the opposite side of the islet, where much sediment was  
388 transported from offshore banks by strong storms or hurricanes from the southeast or east  
389 and piled up against paleocliffs and boulders (Johnson et al. 2011).

390 The *in situ* preservation of corals and rhodoliths is a result of the rapid,  
391 catastrophic burial of the small embayment at Pedra de Água by a layer consisting of  
392 volcanic lapilli and finer tephra (Fig. 12). As such, the Miocene fossil assemblages  
393 representing two different biofacies at this locality are interpreted as obrution deposits  
394 according to the criteria set out by Brett et al. (1997). The rapid burial of coral beds at  
395 present and in the geologic past is a well-documented phenomenon (e.g., Heikoop et al.  
396 1996; Pandolfi et al. 2006; Multer 2006; Reuter and Piller 2011). This is the first well  
397 documented example of obrution deposits due to volcanic ejecta from the Miocene.  
398 Essentially, the biofacies preserved intact at Pedra de Água constitute a kind of  
399 paleontological Pompeii for Miocene coastal habitats.

400 The Middle Miocene fossil assemblages at the Pedra de Água site do not signify a  
401 genuine rocky shore, but may be seen as a *in situ* preserved rocky shore communities  
402 because, in agreement with Lescinsky et al. (1991), they represent a near-shore, hard-  
403 substrate community influenced by wave energy.

404

## 405 **Conclusions**

406 (1) Two zones with distinctly different biotic communities developed in adjacent,  
407 shallow subtidal areas: (a) a zone of coral encrustation and (b) a zone of  
408 rhodolith pavement. The first zone is characterized by encrusting colonial dome-  
409 shaped scleractinian corals accompanied by subordinate components such as the  
410 cemented bivalve *Spondylus*, boring bivalves producing *Gastrochaenolites*  
411 bioerosional structures, and bryozoans. The second zone is characterized by the

412 presence of rhodoliths with a lumpy morphology that accrued as free rolling  
413 algal nodules.

414 (2) These zones occupied two distinct but interpenetrating high energy shallow  
415 subtidal areas corresponding to the same surface of that former stretch of the  
416 coast: (a) basalt mounds forming hard substrates occupying topographic highs  
417 and (b) about a half meter deeper, a soft sandy gravel bottom occupying  
418 topographic lows between the basalt mounds.

419 (3) Based in part on the depositional style of the rhodolith beds the southwestern  
420 side of Miocene Ilhéu de Cima represents a comparatively sheltered setting in  
421 contrast to the storm-impacted northeastern side of the islet.

422 (4) The Pedra de Água outcrop features the first well documented example of  
423 obrution deposits affecting two coeval *in-situ* preserved Miocene  
424 paleocommunities, a coral-dominated and a rhodolith-dominated  
425 paleocommunity, which were catastrophically buried by volcanic lapilli and fine  
426 tephra.

427

428

#### 429 **Acknowledgments**

430 A. Santos received financial support from the Ministry of Science and Technology of

431 Spain in the form of a Juan de la Cierva contract (Ref<sup>a</sup> JCI-2008-2431). Johnson's

432 participation was supported by a travel grant from the Class of 1945 Faculty World

433 Fellowship during sabbatical leave from Williams College in 2009–2010. Participation

434 by Ledesma-Vázquez was supported by travel grants from the Universidad Autónoma de

435 Baja California under the 14<sup>th</sup> Research Program, and from the Cuerpo Académico de  
436 Geología Costera/Programa Integral de Fortalecimiento Institucional. Financial support  
437 was also given by the Junta de Andalucía (Spanish government) to the Research Group  
438 RNM316 (Tectonics and Palaeontology) and by the Spanish DGI Project CGL 2010-  
439 15372/BTE. The Portuguese Navy and Porto Santo Municipality (Porto Santo Verde)  
440 provided transportation to and from Ilhéu de Cima. Rafael Riosmena-Rodríguez  
441 (Universidad Autónoma de Baja California Sur, La Paz, Mexico) kindly provided the  
442 generic identifications for the Pedra de Água rhodoliths. Finally, the authors are grateful  
443 to Franz Fürsich (Facies Editor-in-Chief), Davide Bassi (University of Ferrara, Italy), and  
444 Eberhard Gischler (University of Frankfurt, Germany) for helpful and constructive  
445 comments, which significantly improved the manuscript.

446

447 **References**

- 448 Adey WH, Burke R (1976) Holocene bioherms (algal ridges and bank-barrier reefs) of  
449 the eastern Caribbean. *Geol Soc America Bull* 87:95–109
- 450 Adey WH, Townsend RA, Boykins WT (1982) The crustose coralline algae  
451 (Rhodophyta: Corallinacea) of the Hawaiian Islands. *Smithson Contrib Mar Sci*  
452 15:1–74
- 453 Aguirre J, Riding R, Braga JC (2000) Late Cretaceous incident light reduction evidence  
454 from benthic algae. *Lethaia* 33:205–213
- 455 Baarli BG, Santos A, Silva CM da, Ledesma-Vázquez J, Moyoral E, Cachão M, Johnson  
456 ME (2012) Diverse macroids and rhodoliths from the Upper Pleistocene of Baja  
457 California Sur, México. *J Coast Res* 28:296–305
- 458 Ballantine DL, Bowden-Kerby A, Aponte NE (2000). *Cruoriella* rhodoliths from  
459 shallow-water back reef environments in La Parguera, Puerto Rico (Caribbean  
460 sea). *Coral Reefs* 19:75–81

- 461 Bassi D (1998) Coralline algal facies and their palaeoenvironments in the Late Eocene of  
462 Northern Italy (Calcare di Nago, Trento). *Facies* 39:179–202
- 463 Bassi D, Nebelsick JH, Checconi A, Hohenegger J, Iryu Y (2009) Present-day and fossil  
464 rhodolith pavements compared: their potential for analysing shallow-water  
465 carbonate deposits. *Sediment Geol* 214:74–84
- 466 Basso D (1998) Deep rhodolith distribution in the Pontian Islands, Italy: A model for the  
467 paleoecology of a temperate sea. *Palaeogeogr Palaeoclimatol Palaeoecol*  
468 137:173–187
- 469 Basso D, Nalin R, Nelson CS (2009) Shallow-water *Sporolithon* rhodoliths from North  
470 Island (New Zealand). *Palaios* 24:92–103
- 471 Basso D, Tomaselli V (1994) Palaeoecological potentiality of rhodoliths: a Mediterranean  
472 case history. In: Matteucci R, Carboni MG, Pignatti JS (eds) *Studies on ecology*  
473 *and paleoecology of benthic communities*. *Boll Soc Paleont Ital Spec Vol* 2:17–27
- 474 Best MW, Boekschoten GJ (1982) On the coral fauna in the Miocene reef at Baixo, Porto  
475 Santo (Eastern Atlantic). *Netherlands J Zool* 32:412–418
- 476 Betzler C, Martin JM, Braga JC (2000) Non-tropical carbonates related to rocky  
477 submarine cliffs (Miocene, Almeria, southern Spain). *Sediment Geol* 131:51–65
- 478 Bosence DWJ (1976) Ecologic studies on two unattached coralline algae from western  
479 Ireland. *Palaeontology* 19:71–88
- 480 Bosence DWJ (1983a) The occurrence and ecology of Recent rhodoliths – A review. In:  
481 Peryt TM (ed) *Coated grains*. Springer-Verlag, Berlin, pp 225–242
- 482 Bosence DWJ (1983b) Description and classification of rhodoliths (rhodoids, rhodolites).  
483 In: Peryt TM (ed) *Coated grains*. Springer-Verlag, Berlin, pp 217–224

- 484 Bosence DWJ (1991) Coralline algae: mineralization, taxonomy and palaeoecology. In:  
485 Riding R (ed) *Calcareous algae and stromatolites*. Springer-Verlag, Berlin, pp  
486 98–113
- 487 Bosellini A, Ginsburg RN (1971) Form and internal structure of Recent algal nodules  
488 (rhodolites) from Bermuda. *J Geol* 79:669–682
- 489 Bourillot R, Vennin E, Kolodka C, Rouchy J-M, Caruso A, Durllet C, Chaix C,  
490 Rommevaux V (2009) The role of topography and erosion in the development and  
491 architecture of shallow-water coral bioherms (Tortonian-Messinian, Cabo de  
492 Gata, SE Spain). *Palaeogeogr Palaeoclimatol Palaeoecol* 281:92–114
- 493 Braga JC, Bassi D (2007) Neogene history of *Sporolithon* Heydrich (Corallines,  
494 Rhodophyta) in the Mediterranean region. *Palaeogeogr Palaeoclimatol Palaeoecol*  
495 243:189–203
- 496 Brett CE, Baird GC, Speyer SE (1997) Fossil lagerstätten: Stratigraphic record of  
497 paleontological and taphonomic events. In: Brett CE, Baird C (eds) *Paleontological*  
498 *events – Stratigraphic, ecological, and evolutionary implications*. Columbia  
499 University Press, New York, pp 3–40
- 500 Bromley RG (1994) The palaeoecology of bioerosion. In: Donovan SK (ed) *The*  
501 *palaeobiology of trace fossils*. Wiley, New York, pp 134–154
- 502 Bromley RG, Asgaard U (1993) Endolithic community replacement on a Pliocene rocky  
503 coast. *Ichnos* 2:93–116
- 504 Cabioch G, Montaggioni LF, Faure G (1995) Holocene initiation and development of  
505 New Caledonian fringing reefs, SW Pacific. *Coral Reefs* 14:131–140

- 506 Cachão M, Rodrigues D, Silva CM da, Mata J (1998) Biostratigrafia (nanofósseis  
507 calcários) e interpretação paleoambiental do Neogénico de Porto Santo (Madeira),  
508 (dados preliminares). Com Inst Geol Min 84:A185–A188
- 509 Chevalier J-P (1972) Les Scléactiniaires du Miocène de Porto Santo (Archipel de  
510 Madère. *Annls Paléont Invert* 58:141–164
- 511 Doyle P, Mather AE, Bennet MR, Bussel MA (1997) Miocene barnacle assemblages  
512 from southern Spain and their palaeoenvironmental significance. *Lethaia*  
513 29:267–274
- 514 Ferreira MP (1985) Evolução geocronológica e paleomagnética das ilhas do arquipélago  
515 da Madeira - uma síntese. *Mem Not Mus Lab Miner Geol Univ Coimbra*  
516 99:213–218
- 517 Ferreira MP (1997) Carta Geológica de Portugal, Folha da Ilha de Porto Santo. Ministério  
518 da Economia, Escala 1:25,000. Instituto Geológico e Mineiro, Portugal.
- 519 Foster MS, Riosmena-Rodríguez R, Steller DL, Woelkerling WJ (1997) Living rhodolith  
520 beds in the Gulf of California and their implications for paleoenvironmental  
521 interpretation. In: Johnson ME, Ledesma-Vázquez J (eds) *Pliocene carbonates and*  
522 *related facies flanking the Gulf of California, Baja Califórnia, México. Geol Soc*  
523 *Am, Speci Pap* 318:127–139
- 524 Gischler E, Pisera A (1999) Shallow water rhodoliths from Belize reefs. *N Jb Geol*  
525 *Paläont Abh* 214:71–93
- 526 Heikoop JM, Tsuijita CJ, Heikoop CE, Risk MJ, Dickin AP (1996) Effects of volcanic

527 ashfall recorded in ancient marine benthic communities: comparison of a nearshore  
528 and an offshore environment. *Lethaia* 29:125–140

23

529 James NP, MacIntyre IG (1985) Carbonate depositional environments. Part 1: Reefs.  
530 *Colorado School Mines Quart* 80:1–70

531 Johnson ME (1988) Why are ancient rocky shores so uncommon?. *J Geol* 96:469–480

532 Johnson ME (2006) Uniformitarianism as a guide to rocky-shore ecosystems in the  
533 geological record. *Can J Earth Sci* 43:1119–1147

534 Johnson ME, Baarli BG (1987) Encrusting corals on a latest Ordovician to earliest  
535 Silurian rocky shore, southwest Hudson Bay, Manitoba, Canada. *Geobios*  
536 15:15–17

537 Johnson ME, Baarli BG (2012) Development of intertidal biotas through Phanerozoic  
538 time. In: Talent JA (ed) *Earth and life: Global biodiversity, Extinction intervals*  
539 *and biogeographic perturbations through time. International Year of Planet Earth.*  
540 Springer-Verlag, Dordrecht, The Netherlands. DOI: 10.1007/978-481-3428-1\_5

541 Johnson ME, Baarli BG, Scott JH Jr (1995) Colonization and reef growth on a Late  
542 Pleistocene rocky shore and abrasion platform in western Australia. *Lethaia*  
543 28:85–98

544 Johnson ME, Backus DH, Riosmena-Rodríguez R (2009) Contribution of rhodoliths to  
545 the generation of Pliocene-Pleistocene limestone in the Gulf of California. In:  
546 Johnson ME, Ledesma-Vázquez J (eds) *Atlas of coastal ecosystems in the western*  
547 *Gulf of California: tracking limestone deposits on the margin of a young sea. The*  
548 *University of Arizona Press, Tucson, pp 83–94*

- 549 Johnson ME, Hayes ML (1993) Dichotomous facies on a Late Cretaceous rocky island as  
550 related to wind and wave patterns (Baja California, Mexico). *Palaios* 8:385–395
- 551 Johnson ME, Karabinos PM, Mendia V (2010) Quaternary intertidal deposits intercalated  
552 with volcanic rocks on Isla Sombrero Chino in the Galápagos Islands (Ecuador). *J*  
553 *Coast Res* 26:762–768
- 554 Johnson ME, Ledesma-Vázquez J (1999) Biological zonation on a rocky shore boulder  
555 deposit: Upper Pleistocene Bahía San Antonio (Baja California Sur, Mexico).  
556 *Palaios* 14:569–584
- 557 Johnson ME, McKerrow WS (1995) The Sutton Stone: an early Jurassic rocky shore  
558 deposit in South Wales. *Palaeontology* 38:529–541
- 559 Johnson ME, Silva CM da, Santos A, Baarli BG, Cachão M, Mayoral E, Rebelo AC,  
560 Ledesma-Vázquez J (2011) Rhodolith transport and immobilization on a  
561 volcanically active rocky shore: Middle Miocene at Cabeço das Laranjas on Ilhéu  
562 de Cima (Madeira Archipelago, Portugal). *Palaeogeogr Palaeoclimatol Palaeoecol*  
563 300:113–127
- 564 Johnson ME, Skinner DF, Macleod KG (1988) Ecological zonation during the carbonate  
565 transgression of a Late Ordovician rocky shore (Northeastern Manitoba, Hudson  
566 Bay, Canada). *Palaeogeogr Palaeoclimatol Palaeoecol* 65:93–114
- 567 Kelly SRA, Bromley RG (1984) Ichnological nomenclature of clavate borings.  
568 *Palaeontology* 27:793–807
- 569 Kramberger-Gorjanović D (1889) Berichtigung bezüglich *Ceratoconcha costata* aus dem

- 570 Miozän von Podsused. Verh Kais-königl Geol Reichsanst 6:142
- 571 Lescinsky HL, Ledesma-Vázquez J, Johnson ME (1991) Dynamics of Late Cretaceous  
572 rocky shores (Rosario Formation) from Baja California, Mexico. *Palaios*  
573 6:126–141
- 574 Lund M, Davies PJ, Braga JC (2000) Coralline algal nodules off Fraser Island, eastern  
575 Australia. *Facies* 42:25–34
- 576 Mankiewicz C (1995) Response of reef growth to sea-level changes (Late Miocene,  
577 Fortuna Basin, Southeastern Spain). *Palaios* 10:322–336
- 578 Marrack E (1999) The relationship between water motion and living rhodolith beds in the  
579 southwestern Gulf of California, Mexico. *Palaios* 14:159–171
- 580 Mayer K (1864) Systematisches Verzeichniss der fossilen Reste von Madeira, Porto Santo  
581 und Santa Maria nebst Beschreibung der neuen Arten. Author's edition, Zürich,  
582 p107
- 583 Meco J, Scaillet S, Guillou H, Lomoschitz A, Carracedo C, Ballester J, Betancort JF,  
584 Cilleros A (2007) Evidence for long-term uplift on the Canary Islands from  
585 emergent Mio-Pliocene littoral deposits. *Global and Planet Change* 57:222–234
- 586 Milne-Edwards H, Haime J (1850) A monograph of the British fossil corals. Part 1:  
587 Introduction: Corals of the Tertiary and Cretaceous formations. *Monogr*  
588 *Palaeontogr Soc*, 1–171
- 589 Multer HG (2006) A site of both sudden and slow death coral framework, together with  
590 survival attempts by corals. *Coral Reefs* 25:567
- 591 Okada H, Bukry D (1980) Supplementary modification and introduction of code numbers  
592

593 to the low-latitude coccolith biostratigraphic zonation. *Mar Micropaleont*  
594 5:321–325

594 Pandolfi JM, Tudhope AW, Burr G, Chappell J, Edinger E, Frey M, Steneck R, Sharma  
595 C, Yeates A, Jennoins M, Lescinsky H, Newton A (2006) Mass mortality  
596 following disturbance in Holocene coral reefs from Papua New Guinea. *Geology*  
597 34:949–952

598 Perrin C, Bosence D, Rosen B (1995) Quantitative approaches to palaeozonations and  
599 palaeobathymetry of corals and coralline algae in Cenozoic reefs. In: Bosence  
600 DWJ, Allison PA (eds) *Marine palaeoenvironmental analysis from fossils*. *Geol*  
601 *Soc Lond Spec Publ* 83:181–229

602 Rasser M, Piller WE (1997) Depth distribution of calcareous encrusting associations in  
603 the northern Red Sea (Safaga, Egypt) and their geological implications. In:  
604 Lessios HA, Macintyre IG (eds) *Proceedings 8<sup>th</sup> International Coral Reef*  
605 *Symposium*, Smithsonian Tropical Research Institute, Panama 1:743-748

606 Reuter M, Piller WE (2011) Volcaniclastic events in coral reef and seagrass  
607 environments: evidence for disturbance and recovery (Middle Miocene, Styrian  
608 Basin, Austria). *Coral Reefs* 30:889–899

609 Santos A, Mayoral E, Silva CM da, Cachão M, Johnson ME, Baarli BG (2011) Miocene  
610 intertidal zonation on a volcanically active shoreline: Porto Santo in the Madeira  
611 Archipelago Portugal. *Lethaia* 44:26–32

612 Santos A, Mayoral E, Johnson ME, Baarli BG, Cachão M, Silva CM da, Ledesma-

613 Vázquez J (2012a) Extreme habitat adaptation by boring bivalves on volcanically  
614 active paleoshores from North Atlantic Macaronesia. *Facies* DOI  
615 10.1007/s10347-011-0283-z

616 Santos A, Mayoral E, Baarli BG, Silva CM da, Cachão M, Johnson ME (2012b)  
617 Symbiotic association of a pyrgomatid barnacle and a coral from a volcanic  
Middle Miocene shoreline (Porto Santo, Madeira Archipelago, Portugal).  
618  
619 *Palaeontology* 55:173–182

620 Scoffin TP, Stoddart DR, Tudhope AW, Woodroffe C (1985) Rhodoliths and coralliths of  
621 Muri Lagoon, Rarotonga, Cook Islands. *Coral Reefs* 4:71–80

622 Sneed ED, Folk RL (1958) Pebbles in the lower Colorado River, Texas, a study in  
623 particle morphogenesis. *J Geol* 66:114–150

624 Steller DL, Foster MS (1995) Environmental factors influencing distribution and  
625 morphology of rhodoliths in Bahía Concepción, B.C.S., México. *J Exp Mar Biol*  
626 *Ecol* 194:201–212

627 Surlyk F, Sørensen AM (2010) An early Campanian rocky shore at Ivö Klack, southern  
628 Sweden. *Cret Res* 31:567–576

629 Taylor PD, Wilson MA (2003) Palaeoecology and evolution of marine hard substrate  
630 communities. *Earth-Sci Rev* 62:1–103

631 Wilson MA, Taylor PD (2001) Palaeoecology of hard substrate faunas from the  
632 Cretaceous Qahlah Formation of the Oman Mountains. *Palaeontology* 44:21-41  
633

634 **Figure captions**

635

636 **Fig. 1** Geographic location of the study site at Pedra de Água on Ilhéu de Cima (Porto  
637 Santo, Portugal). Star showing position of the study site

638

639 **Fig. 2** Sample plan showing the layout of the census on the outcrop at Pedra de Água.  
640 The four transects are labeled A, B, C, and D. Blocks 1, 2, and 3 are the three  
641 square blocks chosen for illustration from the full layout. (16 grids to one block  
642 equal to 4 m<sup>2</sup>)

643

644 **Fig. 3** Cross-section along the exposed side of Pedra de Água outcrop, showing the  
645 position of cemented corals on top of basalt mounds and very coarse and unsorted  
646 sandy gravel with rhodoliths in the adjacent depressions

647

648 **Fig. 4** Frequency data depicting the lateral zonation at Pedra de Água along the transects

649

650

A B, C, and D. **a** Spatial distribution of corals. **b** Spatial distribution of bare  
, basalt. **c** Spatial distribution of coarse bioclastic sand

651

652 **Fig. 5** Frequency data depicting the lateral zonation at Pedra de Água along the transects

653 A, B, C, and D. **a** Spatial distribution of *Gastrochaenolites* borings. **b** Spatial  
654 distribution of rhodoliths

655

29

656 **Fig. 6** Ecologic zones mapped on the rocky paleoshore at Pedra de Água. Each block  
657 represents four square meters. **a** Block 1. **b** Block 2. **c** Block 3

658

659 **Fig. 7** General view of the rocky paleoshore at Pedra de Água. **a** Closely packed coral  
660 colonies attached directly to the basalt. Scale bar: 20 cm. **b** Bivalve borings  
661 *Gastrochaenolites torpedo* in corals. Scale bar: 10 cm

662

663 **Fig. 8** Generic affinities of rhodoliths from Pedra de Água. **a** *Lithophyllum* with  
664 sporangia (*black arrow*) and *Sporolithon* (*red arrow*) most commonly can occur.  
665 Scale bar: 200 µm. **b** Less common combination of *Lithophyllum* and *Hydrolithon*.  
666 Scale bar: 200 µm

667

668 **Fig. 9 a** Matrix of very coarse and unsorted sandy gravel on which the rhodoliths rest. **b**  
669 Natural cross-section through a lumpy rhodolith with a rock core 3.5 cm in  
670 diameter. Scale bar: 2 cm

671

672 **Fig. 10** Shape classification of rhodoliths from Pedra de Água based on the triangular plot  
673 formulated by Sneed and Folk (1958)

674

675 **Fig. 11** Linear relationship between maximum diameter of rhodoliths (DR) and rock core  
676 (RC), with  $R^2=0.82$

677

30

678 **Fig. 12** Volcanic tuff directly overlying the coral biofacies (under the present sea cliff) on  
679 the rocky paleoshore at Pedra de Água. Scale bar: 15 cm

680

681 **Table captions**

682

683 **Table 1** Percentages based on census data collected for blocks A, B, and C from the  
684 mound and inter-mound communities at Pedra de Água. Each block represents 4 m<sup>2</sup>

685

686 **Table 2** Generalized paleoenvironmental interpretation from the basalt mound and inter-  
687 mound communities at Pedra de Água

Accepted manuscript

Figure 1

[Click here to download high resolution image](#)

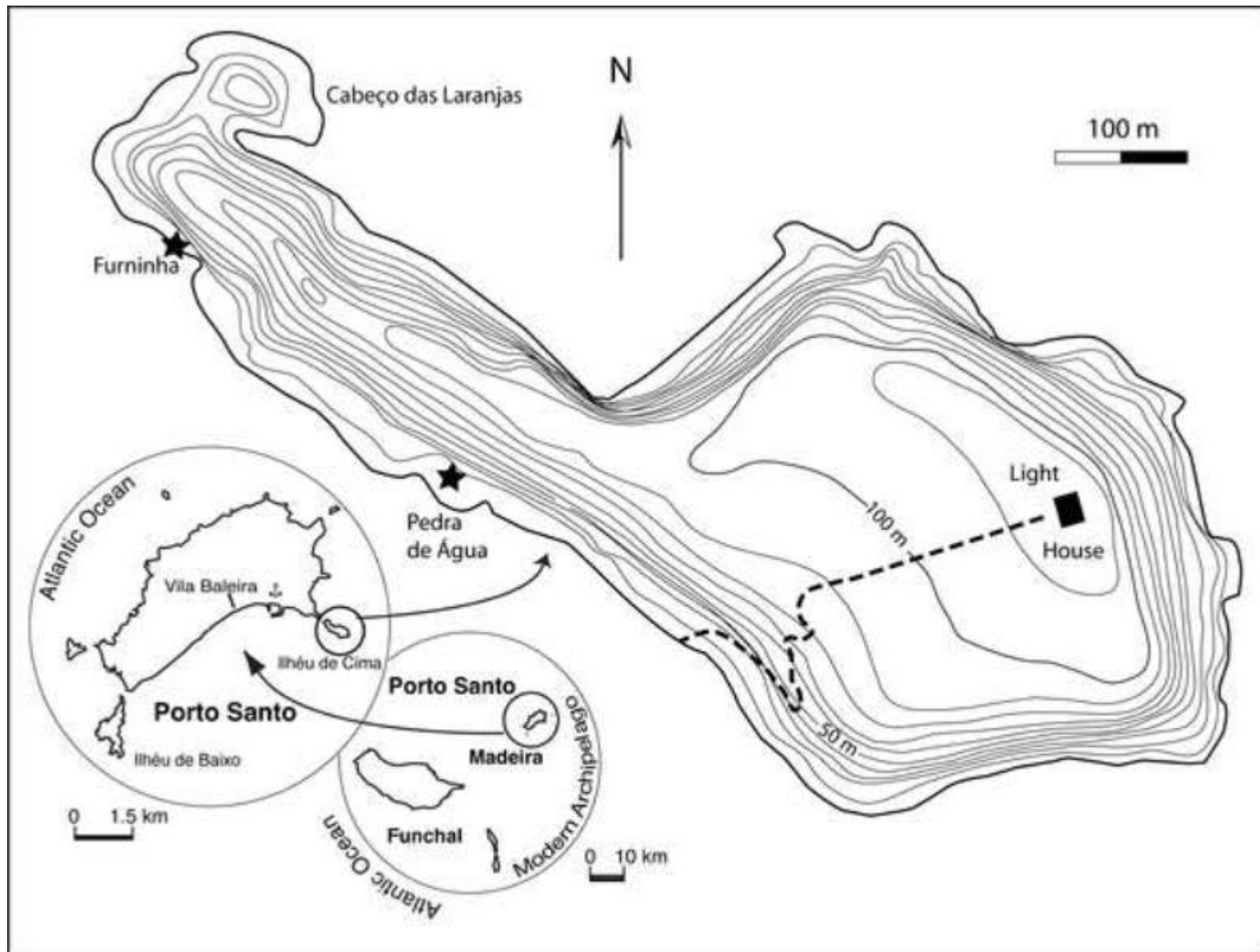
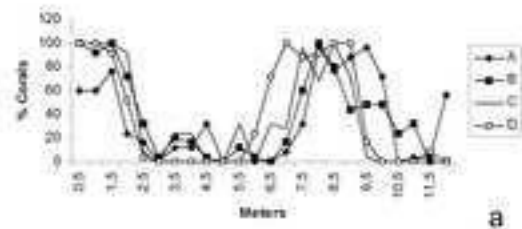
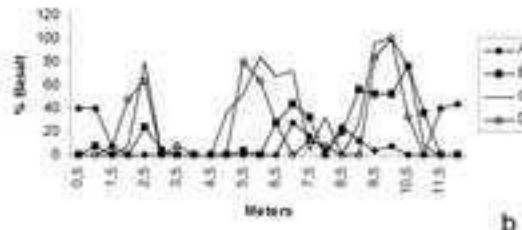


Figure 4

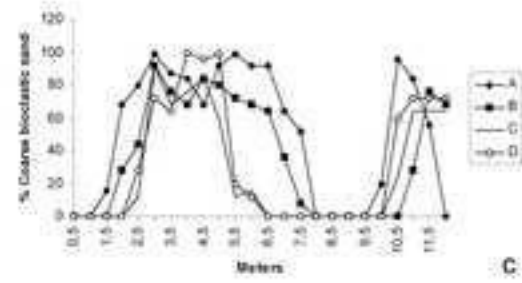
[Click here to download high resolution image](#)



a



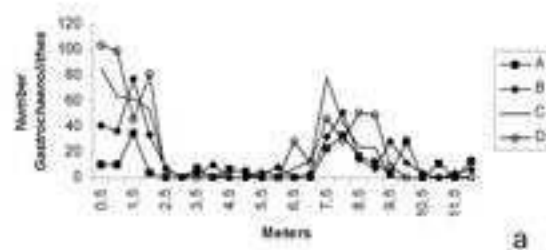
b



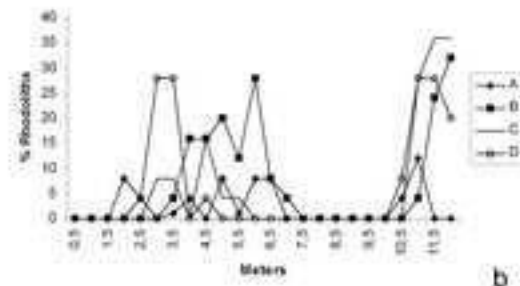
c

Figure 5

[Click here to download high resolution image](#)



a



b

Figure 6

[Click here to download high resolution image](#)

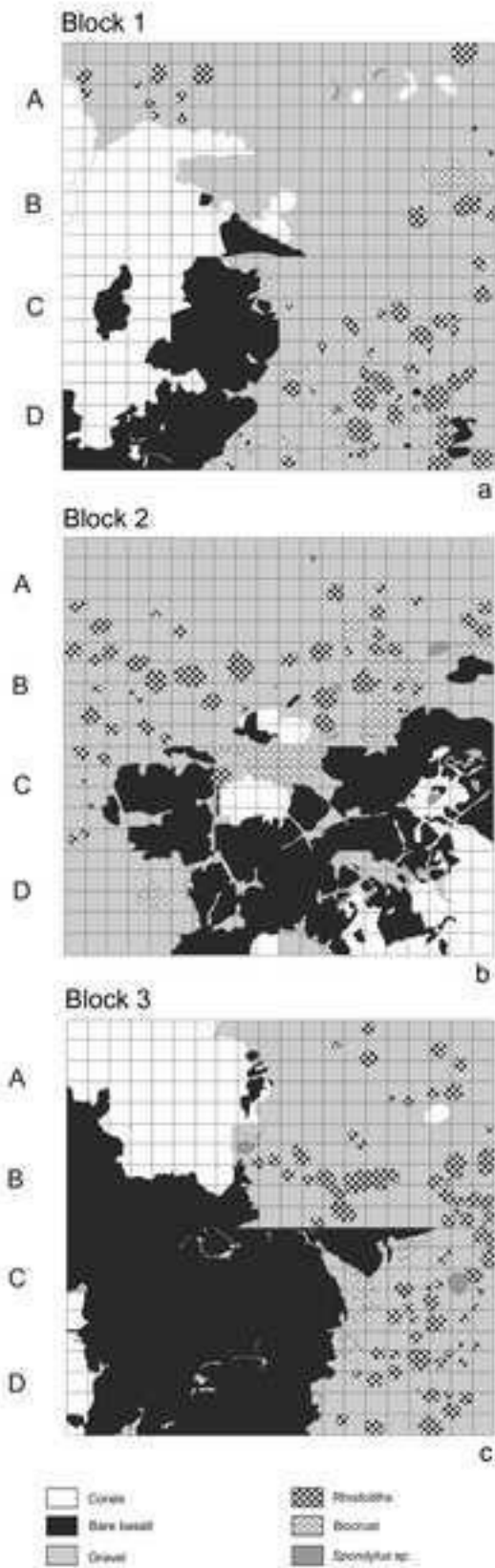


Figure 2  
[Click here to download high resolution image](#)

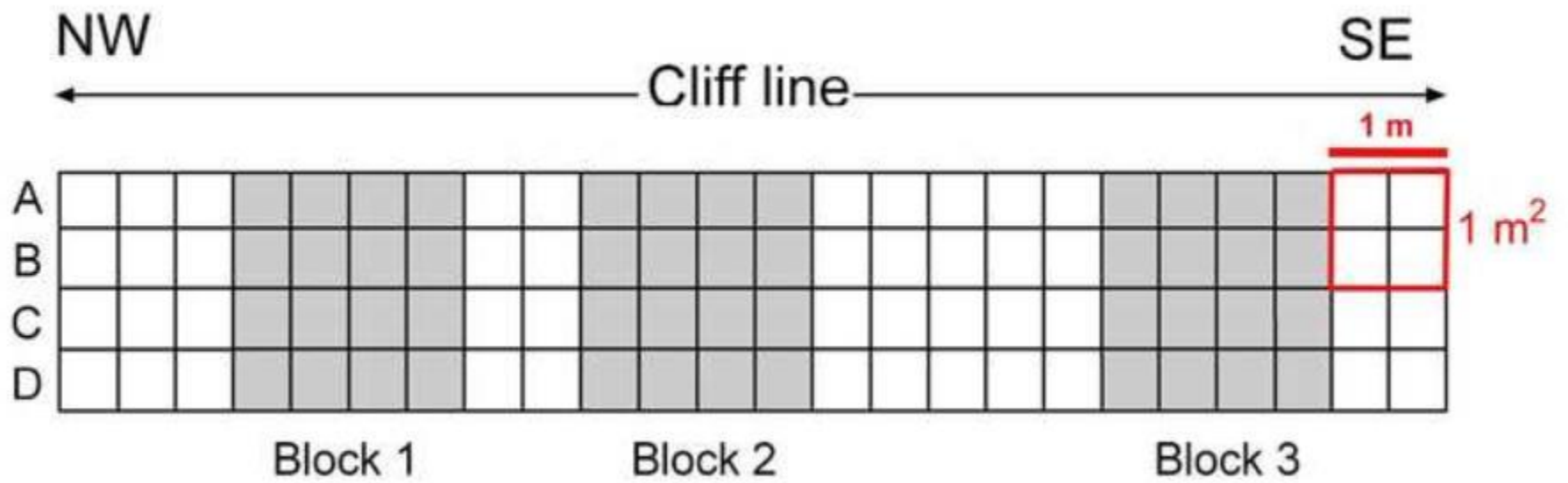


Figure 3

[Click here to download high resolution image](#)

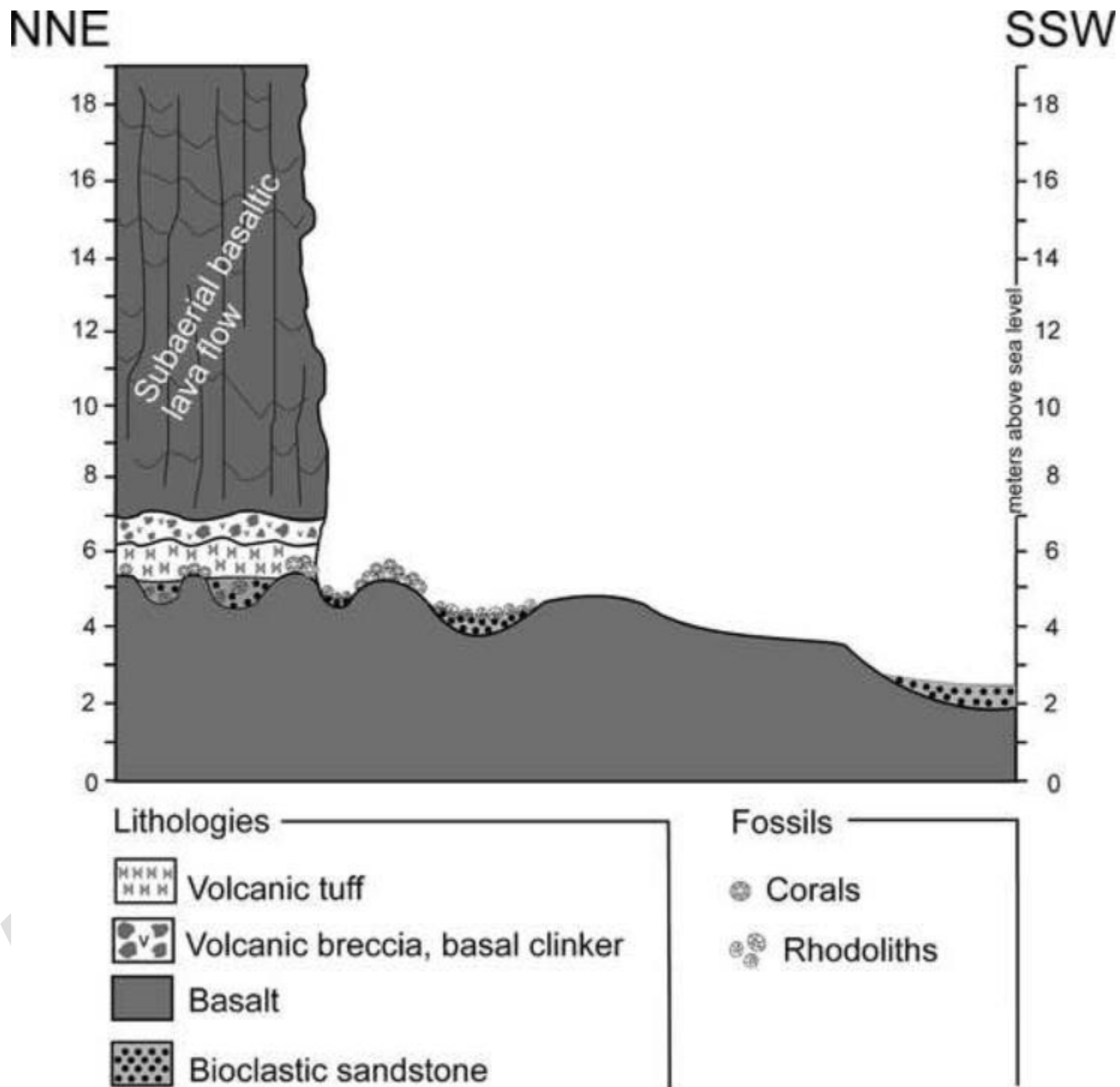


Figure 7

[Click here to download high resolution image](#)



Figure 8  
[Click here to download high resolution image](#)

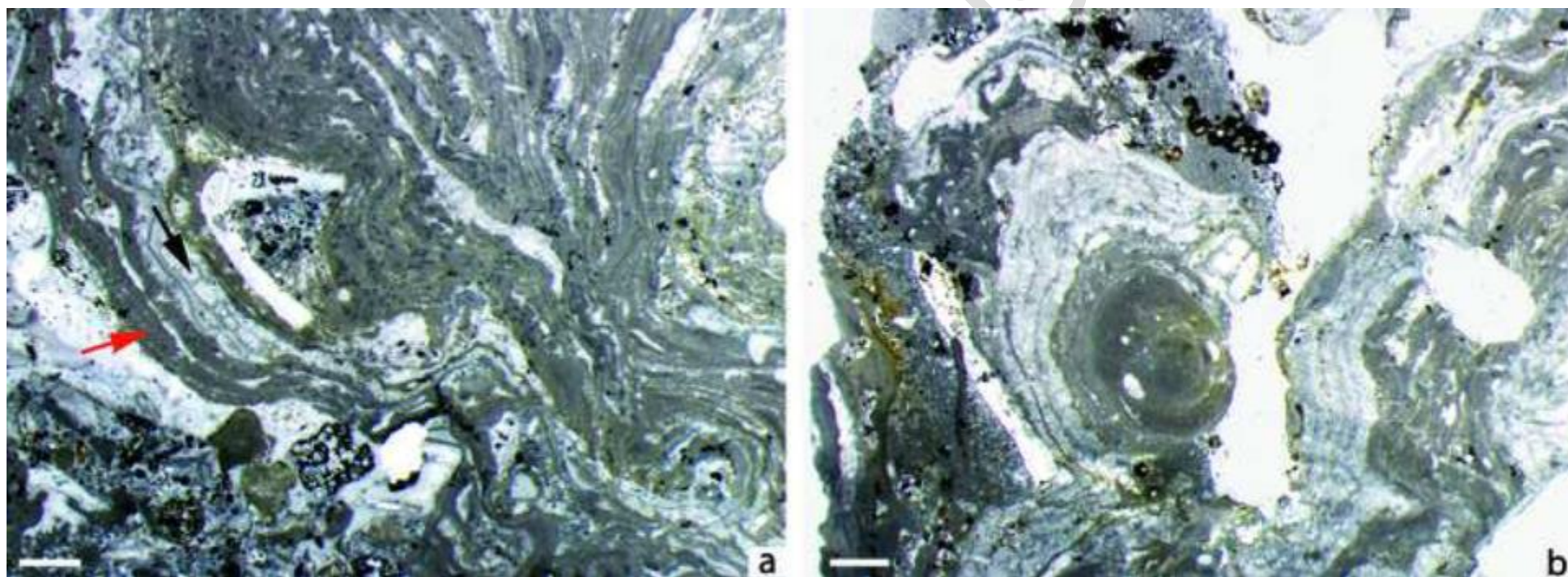


Figure 9

[Click here to download high resolution image](#)

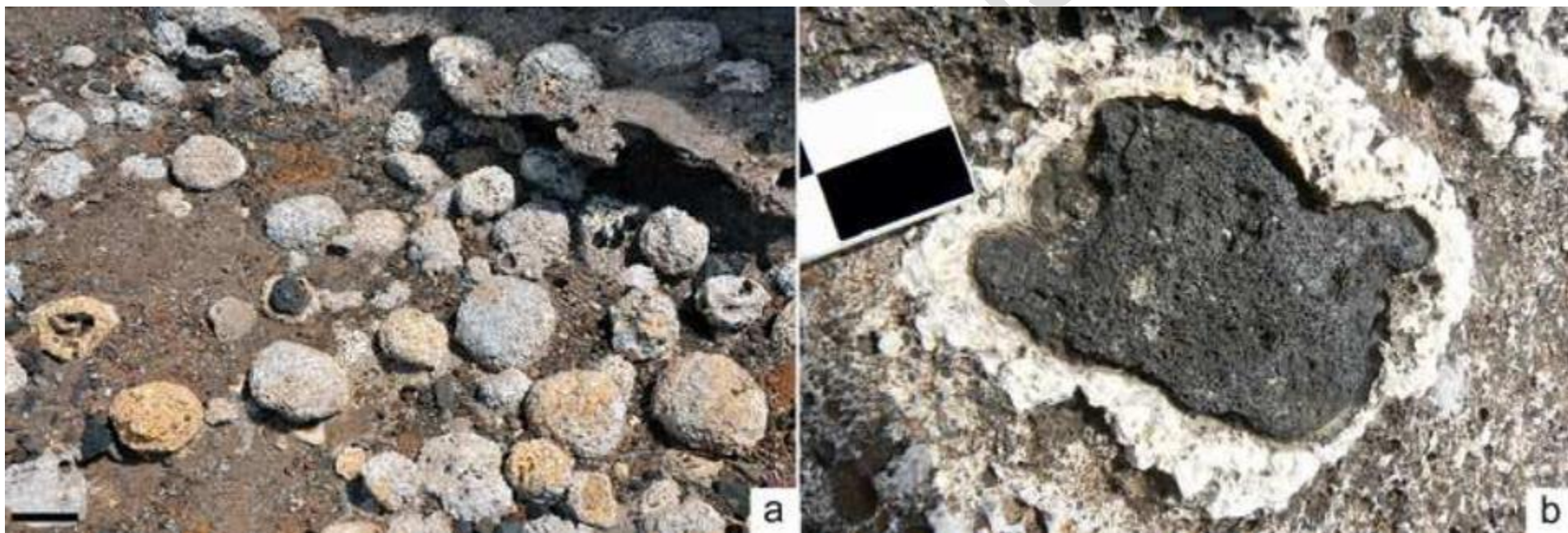


Figure 10

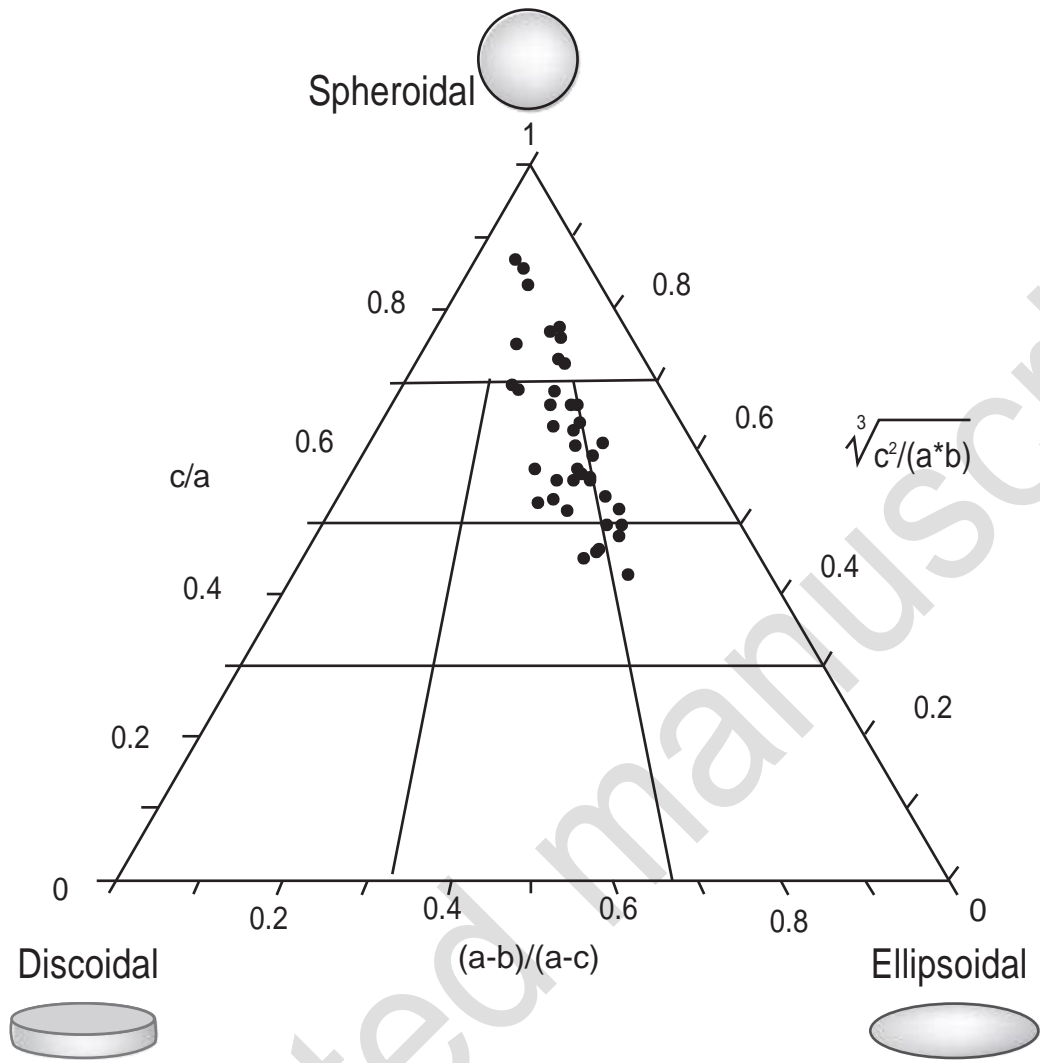


Figure 11

[Click here to download high resolution image](#)

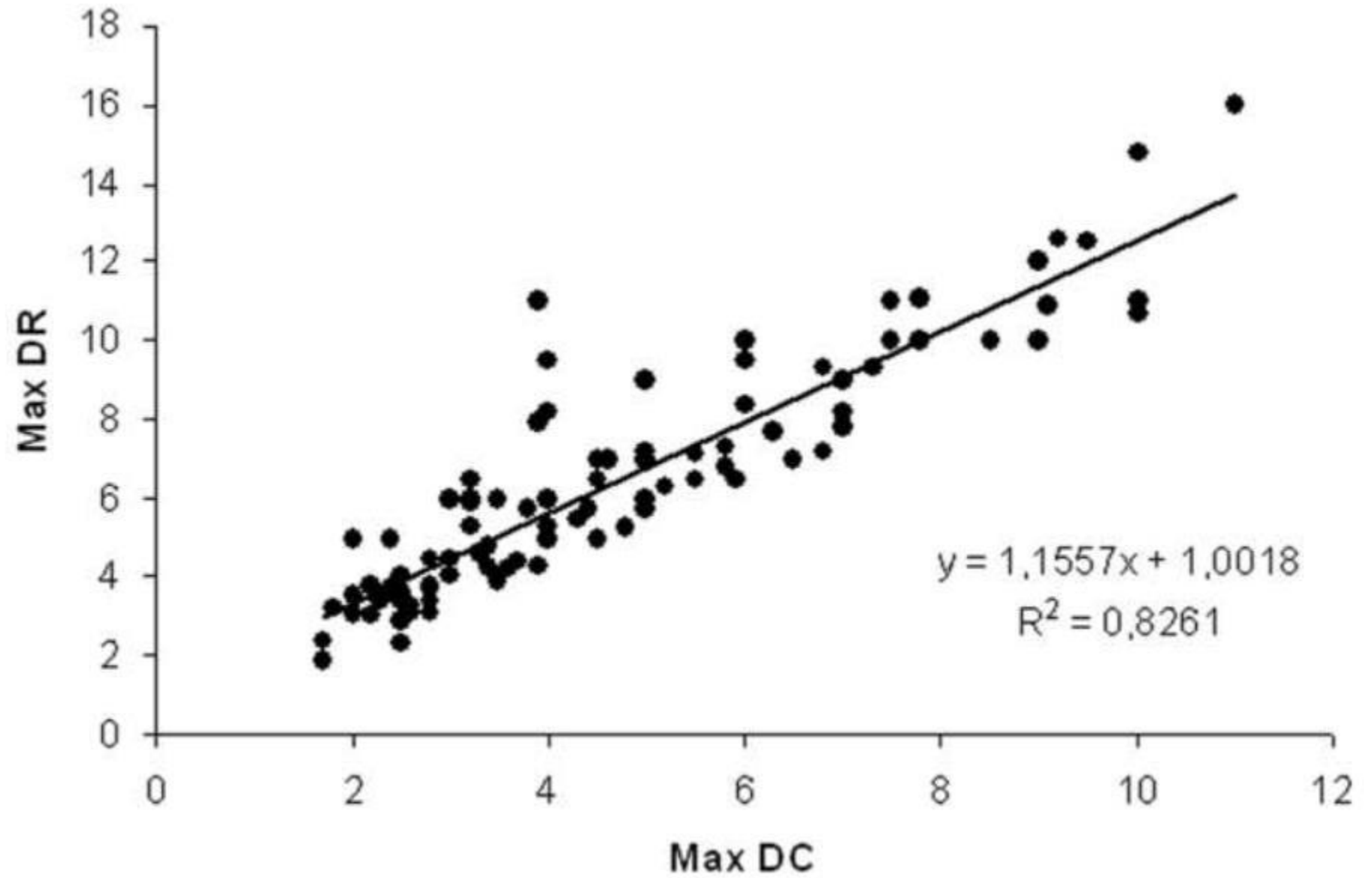


Figure 12

[Click here to download high resolution image](#)



Table 1

Block 1	Block 2	Block 3	Average (Blocks 1 + 2 + 3)
			50
			56
			108
			16
			7
			27

Accepted manuscript

Table 2

Table 2

	Hard substrate	Soft substrate
	Zone of coral encrustation	Zone of rhodolith pavement
Type of sediment	basalt	coarse and unsorted sandy gravel
Bioerosion	medium	low
Bioturbation	absent	absent
Rhodoliths	absent	large
Predominant algal taxa	/	polyspecific ( <i>Lithophyllum</i> and <i>Sporolithon</i> )
Algal growth-forms	crusts	crusts
Paleodepth	shallow (above fair-weather wave-base)	shallow (above fair-weather wave-base)