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Angulo, Rodolfo José, Fonseca Giannini, Paulo César, de Souza, Maria Cristina et al. (2026) Ages of different shell species associated to vermetid bioconstructions remains and their implications on Mid-to Late-Holocene Brazilian sea-level curves. *Quaternary Science Reviews*. 109788. ISSN: 0277-3791

<https://doi.org/10.1016/j.quascirev.2025.109788>

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1 Ages of different shell species associated to vermetid bioconstructions remains and  
2 their implications on Mid- to Late-Holocene Brazilian sea-level curves

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23  
24 **Abstract**

25 Vermetid bioconstructions have been widely used as Holocene paleo-sea level  
26 indicators along the Brazilian coast, due to their abundance and accuracy, especially in  
27 the case of *Petalconchus varians* (d'Orbigny 1841). Most age determinations for this  
28 species have been performed using conventional <sup>14</sup>C dating of bulk bioconstruction  
29 samples. However, this type of sample may contain several types of carbonate or  
30 carbonaceous impurities, including remains of other organisms such as mollusks and  
31 barnacles, which can affect the reliability of the age. This work compares previous  
32 conventional <sup>14</sup>C ages of vermetid bioconstruction bulk samples with <sup>14</sup>C AMS ages of  
33 shells from different species dated individually. The objectives are: i. to establish the  
34 relationship among the ages of different species in order to reveal the direction or  
35 tendency of past sea-level changes; ii. to evaluate the error in dating bulk samples; iii.  
36 to analyze the reliability of the ages obtained from each species, based on aspects such  
37 as purity, alteration and neomorphism. The dating results obtained for fossil shells of  
38 different species were in agreement with the relative ages expected based on the

39 observed spatial relationship between them. *Tetraclita stalactifera* parietal plates were  
40 older than overgrowing vermetids shells, and shells of the bivalve *Leiosolenus* af.  
41 *bisulcatus* in life position, which perforate the bioconstruction, were younger. The ages  
42 of individual shells were older than those obtained by dating bulk vermetid  
43 bioconstructions, and this difference increased with the age. Taking the paleolevels  
44 previously determined for the studied samples and using the revised ages reported here,  
45 we infer that relative sea level in southern Brazil was more than 2 m above present  
46 between 6000 and 7000 cal aBP. The differences in ages between bulk and individual  
47 shell samples highlight that paleo-sea levels inferred from bulk vermetid remains and  
48 respective Holocene sea-level curves need revision. More data for separate species are  
49 therefore necessary to improve the accuracy of Holocene sea-level curves from Brazil.  
50 Furthermore, methodological care must be taken to avoid the influence of micritic  
51 envelopes, bioturbation, biofouling, and cement infill on the age.

52

53 **Keywords:** *Petalocochus varians*; *Tetraclita stalactifera*; Mytilida; paleo-sea level;  
54 radiocarbon dating; AMS dating; Holocene highstand.

55

## 56 **1. Introduction**

57 Vermetid gastropod bioconstructions have been used as paleo-sea level indicators along  
58 the Brazilian coast since the seminal work of Van Andel and Laborel (1964). From the  
59 mid 20<sup>th</sup> century onward, hundreds of dated samples have been used to determine  
60 paleo-sea levels and build up Mid- to Late-Holocene relative sea-level curves (e.g. Martin  
61 et al., 2003; Angulo et al., 2006). In particular, bioconstructions of *Petalocochus varians*  
62 (d'Orbigny 1841), the most common species of vermetid in Brazil, have been considered  
63 one of the best Holocene sea-level indicators (e.g. Angulo et al., 2006; Angulo and Souza,  
64 2014; Toniolo et al., 2020). Most of the age determinations from this species have been  
65 performed using conventional <sup>14</sup>C dating, which demands large (25-30 g) samples (e.g.  
66 see compilations by Martin et al. 2003 and Angulo et al. 2006). More recently, smaller  
67 vermetid samples (10-25 mg) have been dated using the Accelerator Mass Spectrometry  
68 (AMS) method (e.g. Toniolo et al. 2020, Angulo et al. 2022a, 2022c). Furthermore,  
69 vermetid bioconstructions may also contain the remains of several other species that  
70 precipitate carbonate shells, including mollusks and barnacles (Angulo, 1992, 1993;  
71 Angulo and Souza, 2014; Angulo et al., 2022a). Therefore, this work explores the  
72 potential for dating shells of different species within vermetid bioconstruction remains  
73 to identify whether they are synchronous or diachronous with *P. varians*. The main  
74 importance of establishing the relationship of ages lies in the fact that it could help to  
75 reveal the direction or tendency of past changes in sea level. For example, if species that  
76 live on a lower or a higher fringe are superposed on the vermetid fringe, this would  
77 indicate that sea level was raising or lowering, respectively. To test this hypothesis, we  
78 chose four vermetid bioconstruction remains previously dated using bulk samples  
79 (Angulo, 1989, 1992; Angulo et al., 2002, 2022a), to have shells of different species dated  
80 individually by <sup>14</sup>C AMS. This hypothesis test assumes that the <sup>14</sup>C dating results obtained  
81 from the different species are reliable indicators of the life span of each building animal.  
82 In view of this, a parallel objective of this work is to analyze the reliability of the ages

83 obtained from each species, based on aspects such as their purity, alteration and  
84 neomorphism.

#### 85 *Vermetid bioconstructions*

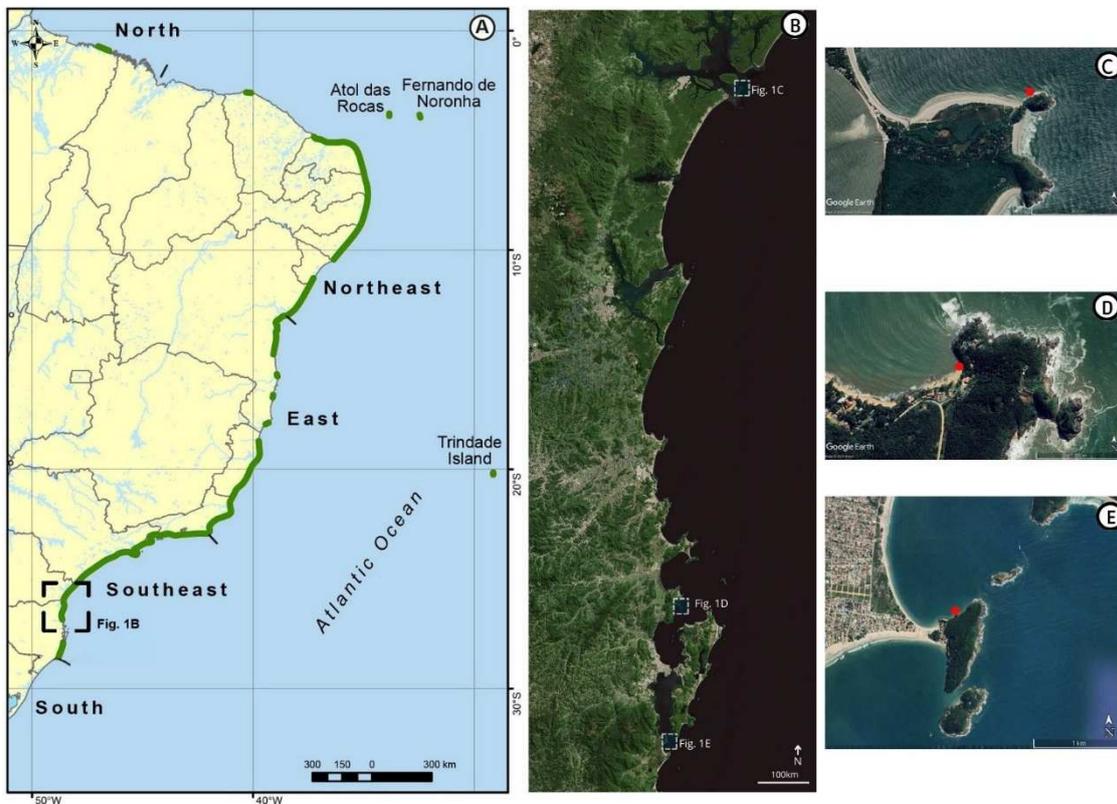
86 Vermetid bioconstruction remains are widely dispersed along the Brazilian coast. They  
87 occur, at least, from Cristovão, Rio Grande do Norte state (4° 55' S, Bezerra et al., 2003)  
88 to Santa Marta Cape, Santa Catarina state (28° 36' S, Angulo et al., 1999). They are found  
89 on the mainland and on several oceanic islands such as São Pedro & São Paulo (0° 55' N,  
90 Angulo et al., 2013a), Rocas Atoll (3° 52' S, Angulo et al., 2022c), Fernando de Noronha  
91 (3° 49-52' S, Angulo et al., 2013b), Abrolhos (17° 58' S, Angulo et al., 2022b) and Trindade  
92 (20° 30' S, Angulo et al., 2013b) (Fig. 1). Therefore, they can provide useful data to  
93 construct or refine Mid- to Late-Holocene sea level curves along the western Atlantic  
94 Ocean coast.

95 Two species are the main vermetid reef builders along Brazilian coasts: *P. varians* and  
96 *Dendropoma irregulare* (d'Orbigny 1842) (Laborel, 1969, 1979, 1986; Spotorno-Oliveira  
97 et al., 2012). Subfossil bioconstructions, as well as bioconstructions with living  
98 vermetids, occur fixed to rock substratum. *P. varians* lives at the upper limit of the infra-  
99 littoral zone (sensu Peres and Picard, 1964) or the lower midlittoral fringe (sensu  
100 Stephenson and Stephenson, 1949) (Laborel and Kempf, 1966; Kempf and Laborel, 1968;  
101 Laborel 1968, 1969, 1977, 1979, 1986). Its biological zone is not strictly horizontal and  
102 the altitude varies according to wave exposure and tidal range (Laborel and Kempf,  
103 1966; Kempf and Laborel, 1968; Laborel 1969, 1979, 1986). In biological zonation, *P.*  
104 *variens* bioconstructions are associated with calcareous algae. According to Laborel  
105 (1979), they are located above the red algae fringe and below the *Tetraclita stalactifera*  
106 (Lamarck, 1818) fringe. The upper part of the *P. varians* biological zone coincides with  
107 the lower part of that of *T. stalactifera* and the two species can coexist in life in the same  
108 bioconstruction (Laborel, 1979; Angulo et al., 2022a). The ecological conditions of these  
109 two species are similar to those observed in the polychaete *Phragmatopoma sp.* and in  
110 the bivalves *Leiosolenus bisulcatus* (A. d'Orbigny, 1853), *Petricola bicolor* G. B. Sowerby  
111 II, 1854, and *Petricola stellae* Narchi, 1975 (Narchi, 1974, 1975; Angulo and Souza, 2014;  
112 Pardal et al., 2023).

113 Colonial vermetids, which built reefs, are widely dispersed in tropical and subtropical  
114 waters along high-energy rocky coasts (Laborel, 1986). Donnarumma et al. (2021),  
115 studying Mediterranean reefs of living *Dendropoma* vermetids, detected a well-defined  
116 zonation pattern, with a gradual decrease in structural complexity (e.g. indentation  
117 degree) from the outer edge, facing the open-sea, to the inner edge. Such structural  
118 complexity zonation reflects underlying environmental gradients and plays a crucial role  
119 in the distribution of associated benthic communities (Picone and Chemello, 2023).

120 On the Brazilian mainland coast, the southern limit of occurrence of living colonies is  
121 between Cabo Frio (22° 54' S, Laborel, 1986) and the south of the Rio de Janeiro state  
122 (23° 05' S, Spotorno-Oliveira et al., 2012, Breves et al., 2017, Toniolo et al., 2020), over  
123 5° north of the southern limit of occurrence of bioconstruction remains, at Santa Marta  
124 Cape (Angulo et al., 1999). The presence of these bioconstruction remains south of the  
125 current range of living vermetids is probably related to the occurrence of warmer waters  
126 during the Holocene climatic optimum (Laborel, 1977, 1979, 1986; Angulo et al., 1999)  
127 or in specific time intervals of the Mid- and Late-Holocene (Toniolo et al., 2020). In the

128 southern Brazilian region, vermetid bioconstruction remains were reported from  
129 Cardoso Island (25° 11' S, Angulo et al., 2006) to Santa Marta Cape (Fig. 1). They occur  
130 attached to igneous and metamorphic rocks exposed to breaking wave action.



131

132 Fig. 1: Distribution of vermetidae bioconstruction remains on the mainland and oceanic  
133 island coasts of Brazil (A, green line), and locations where the vermetid bioconstruction  
134 samples were obtained for this work (B): Ilha do Mel (C), Armação do Itapocoroi (D), and  
135 Ponta do Papagaio (E).

136

## 137 2. Regional setting and study area

138 From a coastal physiography standpoint, the study area can be divided into two sectors  
139 (Giannini et al., 2007, 2009, Hesp et al., 2009), both with inland high relief, supported by  
140 crystalline rocks (Dominguez, 2009). In the northern sector, north of latitude 26° 24' S,  
141 the coastline lies between the Serra do Mar, a mountain range with an altitude of over  
142 1900 m, and the Santos Basin. The Serra do Mar delimits a series of large Quaternary  
143 estuaries (tens to hundreds of km<sup>2</sup>), such as the bays of São Francisco, Laranjeiras,  
144 Paranaguá and Guaratuba (Angulo et al., 2009, 2016, 2018; Giannini et al., 2009; Hesp  
145 et al., 2009). In the southern sector, the coastline lies between the Serra do Taboleiro,  
146 reaching up to 1300 m, and the Florianópolis Paleogene submerged structural high,  
147 which separates the Santos and Pelotas basins. This sector has a narrower and steeper  
148 inner shelf and a more restricted coastal plain (Giannini et al., 2007), and is also more  
149 rugged, with headlands, rocky shores, pocket beaches and small embayments, including  
150 log-spiral ones (Hesp et al., 2009).

151 The coastline is characterized by the alternation between quartzose sandy beaches and  
152 rocky headlands. The headlands are formed of gneisses and migmatites of the Lower  
153 Proterozoic Coastal Complex, which are intruded by a Lower Cretaceous basaltic dike  
154 system related to the opening of the South Atlantic Ocean (Mineropar, 1989; Wildner et  
155 al., 2014).

156 The regional climate is mesothermic wet subtropical, without a dry season and with a  
157 warm summer (Monteiro and Furtado, 1995). Cyclonic winds from E and NE  
158 predominate during spring-summer and winds generated by cold fronts from S and SW  
159 predominate during autumn-winter (Mendes and Giannini, 2015).

160 The tide in the region is microtidal and semi diurnal with diurnal inequalities (DHN,  
161 2023). The mean tidal range is 1.5 m at Ilha do Mel (Marone and Jamiyanaa, 1997) and  
162 decreases to the south, reaching 0.6 m at Imbituba Port, located 35 km south from Ponta  
163 do Papagaio (CHM, 2020, Fig. 1).

164 Offshore, the seasonal mean wave heights range from 1.7-1.9 m with mean periods of  
165 7.7-7.8 s in the spring-summer to 2.0-2.2 m with period of 8.9-8.7 s in the autumn-winter  
166 (Pianca et al., 2010). The main wave directions are from NE and E during spring-summer  
167 and from S and SE during the autumn-winter (Pianca et al., 2010).

#### 168 *Study area*

169 The study sites are Ponta das Conchas, at Ilha do Mel (25° 32' 19" S, 48° 17' 30" W),  
170 Praia da Armação do Itapocoroi, in Penha (26° 46' 53" S, 48° 36' 08" W), and Ponta do  
171 Papagaio, in Palhoça (27° 50' 43" S, 48° 24' 45" W), on the Southern Brazilian coast (Fig.  
172 1). At these sites, bulk samples of vermetid bioconstruction remains were dated in  
173 previous works (Angulo, 1989, 1992; Angulo et al., 2022a). These samples give ages from  
174  $1045 \pm 75$  aBP (Angulo, 1989) to  $3860 \pm 80$  aBP (Angulo et al., 2022a) and indicate sea  
175 levels between  $1.5 \pm 0.3$  m (Angulo et al., 2022a) and  $2.9 \pm 0.5$  m (Angulo, 1992; Angulo  
176 et al., 2022a) above present (Table 1).

177 The vermetid bioconstructions from Ponta das Conchas occur on a rocky coast  
178 moderately exposed to waves, under a boulder approximately 3 m in diameter. In the  
179 1980s, the lower limit of terrestrial plants was near the vermetid bioconstruction  
180 remains, which were penetrated by some roots (Angulo, 1993). In 2025, that limit had  
181 lowered, surrounding the boulder, and vermetid remains were no longer visible. This  
182 change in plant distribution was favored by sand deposition in front of the rocky coast,  
183 which reduced wave action. The sand supply also favored the growth of  
184 *Phragmatopoma caudata* bioconstructions. The top of these bioconstructions was  
185 considered equivalent to the top of the vermetid bioconstructions and used to  
186 determine the paleo-sea level, since bioconstructions with living vermetids are missing  
187 from this region (Angulo, 1993).

188 The vermetid bioconstructions remains at Praia da Armação de Itapocoroi were 40 cm  
189 thick and, in the 1980s, covered by a thin sand cover, being exposed by erosion  
190 generated by a small pedestrian trail (Angulo, 1989). In 2024, the sand was completely  
191 eroded and only gravels constituted by vermetid bioconstructions were found on the  
192 beach.

193 The vermetid bioconstruction remains at Ponta do Papagaio occur under granitic  
194 boulders, where they remained relatively protected from freshwater dissolution and  
195 wave action (Angulo et al. 2022a).

197 Table 1: Paleo-sea levels and conventional radiocarbon and calibrated ages (SHCal20 curve) before present (BP) of bulk vermetid bioconstructions, published  
 198 in former works, and of different species associated to vermetid bioconstructions dated in the present work.

Sample ID	Location	Material	Lab. code	Radiocarbon age (aBP)	Calibrated age (aBP)	Paleo-sea level (m)
PCIM	Ponta das Conchas, Ilha do Mel	Bulk	GSC-5255 <sup>(1)</sup>	3500 ± 60 <sup>(1)</sup>	3897-3499	2.9 ± 0.3 <sup>(1)</sup>
		Pv <sup>(a)</sup>	Beta-618167	5890 ± 30	6781-6556	
		Ts <sup>(a)</sup>	Beta-618168	6020 ± 30	6941-6684	
		My	Beta-618169	4600 ± 30	5441-5051	
		Oy <sup>(b)</sup>	Beta-618170	5960 ± 30	6852-6659	
PA	Praia da Armação do Itapocorói	Bulk	GX-14061 <sup>(2)</sup>	1045 ± 75 <sup>(2)</sup>	1057-741	2.6 ± 0.3 <sup>(3)</sup>
		Pv <sup>(a)</sup>	Beta-618171	1500 ± 30	1405-1302	
		Pv <sup>(c)</sup>	Beta-618172	1460 ± 30	1363-1282	
		Ts <sup>(a)</sup>	Beta-618173	1490 ± 30	1403-1298	
Pnh2	Ponta do Papagaio	Bulk	CEN-1005 <sup>(4)</sup>	2310 ± 70 <sup>(4)</sup>	2489-2063	1.5 ± 0.3 <sup>(4)</sup>
		Pv	Beta-618174	2510 ± 30	2719-2367	
		Ts	Beta-618175	2550 ± 30	2741-2437	
Pnh5	Ponta do Papagaio	Bulk	CEN-1008 <sup>(4)</sup>	3860 ± 80 <sup>(4)</sup>	4501-3936	2.4 ± 0.3 <sup>(4)</sup>
		Pv <sup>(a)</sup>	Beta-618176	5040 ± 30	5894-5604	
		Ts <sup>(a)</sup>	Beta-618177	5340 ± 30	6260-5943	
		My <sup>(d)</sup>	Beta-618178	4740 ± 30	5575-5321	

199 Notes: (aBP) years before present; (GSC) Geological Survey of Canada, (GX) Kruger Enterprises Inc. Geochron Laboratories Division, (CEN) Radiocarbon Laboratory of the  
 200 Center for Nuclear Energy in Agriculture (CENA), (Beta) Beta Analytic.; (Bulk) Bulk vermetid bioconstruction; (Pv) *P. varians*; (Ts) *T. stalactifera*; (My) *Mytilida L. af. bisulcatus*;  
 201 (Oy) Oyster, (a) from the bioconstruction bottom, (b) small shell fixed inside the *T. stalactifera* shell, (c) from the bioconstruction top, (d) for complete the mass, the sample  
 202 was composed by one shell plus shell fragments of three other specimens. References: (1) Angulo, 1992; Angulo et al., 2002, (2) Angulo, 1989, (3) Angulo et al., 2006, (4)  
 203 Angulo et al., 2022a. The error margin of samples PCIM and PA were adjusted according to Angulo et al. (2022a).

204 **3. Methods**

205 Bioconstruction samples ranging in width from cm to dm and thickness in cm were  
206 collected in the field at the four study sites. In the laboratory, taxa were identified and  
207 their associations described across the thickness of the bioconstruction, that is, between  
208 the surface adhered to the rock (here designated as the basal surface) and the opposite  
209 (exposed or apical) surface.

210 Whole shells or pieces of shell from different species of the four previously dated  
211 vermetid bioconstructions were separately extracted (Table 1). Selected aliquots of this  
212 material, showing no evidence of cementation under a 10X hand lens, were dated by <sup>14</sup>C  
213 AMS at Beta Analytic Inc., Miami, USA. Conventional <sup>14</sup>C ages were calibrated using  
214 CALIB version 8.2 (Stuiver and Reimer, 1993) and the and the SHCal20 Southern  
215 Hemisphere calibration curve (Hogg et al., 2020).

216 Aliquots (~2-10 cm<sup>3</sup>) were extracted from the same bioconstructions samples, for thin  
217 section microscopy analysis. They were initially examined using a reflected light  
218 stereoscopic magnifying glass up to 60x (Carl Zeiss, model Stemi SV.11). Digital images  
219 were acquired by a coupled camera (Leica MC170HD) with a multifocal acquisition  
220 device. Each sample was then vacuum-impregnated using a liquid mixture of Epoxy resin  
221 and blue dye. The aim was to allow differentiation between the original (colored) pores  
222 and the artificial (colorless) ones subsequently induced by the thin sections preparation.  
223 These sections, ~30 µm thick, were obtained transversally to the bioconstruction  
224 thickness.

225 The descriptions of the four thin sections were completed with a polarized light  
226 microscope (Carl Zeiss, model Axioplan) with maximum magnification of 1000x, coupled  
227 with Leica Application Suite (LAS) software and a Leica MC170HD photographic camera.

228 The analysis of each thin section under the optical microscope included: 1. recognition  
229 and percentage estimation of six major components: biogenic growth framework,  
230 extraclastic (terrigenous) silty sand fill, intraclastic silty sand fill, syn- or post-  
231 depositional clayey matrix, cement and original pores; 2. identification and percentage  
232 estimation of mineralogical components of the terrigenous fraction; 3. characterization  
233 of the terrigenous fraction in terms of texture (modal grain size, on the Wentworth 1922  
234 scale, and estimation of quartz roundness according to the Powers 1953 graphic scale)  
235 and fabric (e.g., packing, spatial segregation and grading); 4. identification and  
236 percentage estimation of types of intraclast; 5. characterization of the intraclastic  
237 fraction in terms of texture (modal grain size) and fabric; 6. description of the  
238 mineralogy, texture and fabric of the matrix and cement; 7. characterization of the  
239 macro- and meso-pores (larger than clay size, according to Pittman, 1979) regarding  
240 shape and fabric based on Choquette and Pray (1970); and 8. classification of the  
241 depositional fabric of the bioconstruction as a whole.

242 To describe the constituent parts of the main bioconstructor organisms, the  
243 nomenclature used by d'Orbigny (1841), Laborel (1986), Savazzi (1996) and Scuderi  
244 (2012) was adopted, in the case of vermetids, and Tsang et al. (2015), in the case of  
245 barnacles.

246 In the description of the thin section, emphasis was placed on the relationships between  
247 vermetids and barnacles *in situ* and with other components in general. Particular  
248 attention was given to the possible presence of features indicative of neomorphism of  
249 their carbonate, or other post-depositional modifications, such as surface alteration,  
250 encrustation or breakage, that could have influenced in some way the dating results.

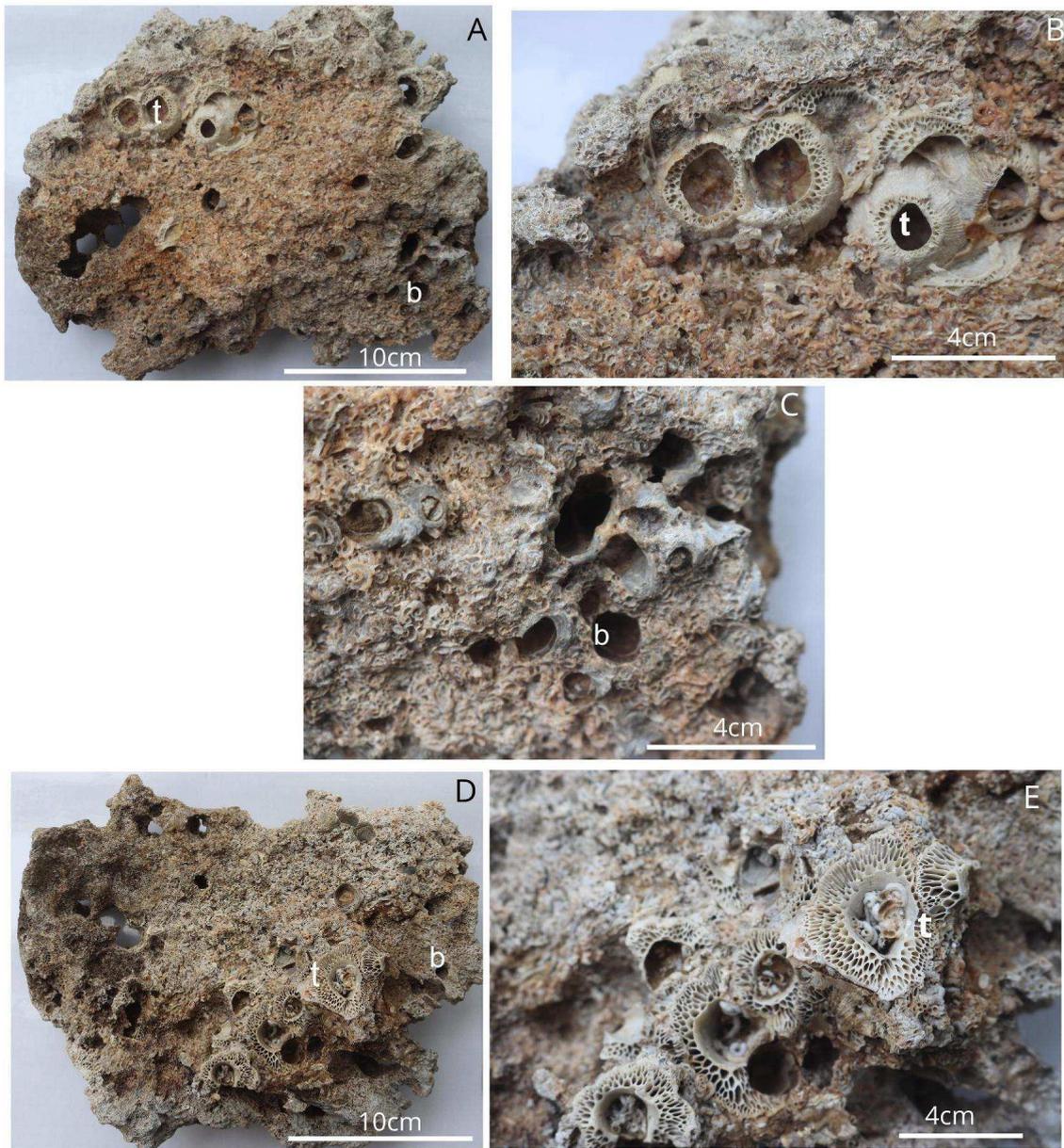
## 251 **4. Results**

### 252 *4.1. Ages and description of samples*

253 The conventional and calibrated <sup>14</sup>C ages of the shell samples of different species from  
254 the studied sites are presented at Table 1. A description of the bioconstruction  
255 components follows, organized by collection site.

#### 256 *Ponta das Conchas, Ilha do Mel*

257 The vermetid bioconstruction remains from Ponta das Conchas, Ilha do Mel, are  
258 approximately 11 cm thick. Barnacles were observed in the apical, middle, and basal  
259 zones, through its thickness. The bioconstruction is constituted by *P. varians* tubes, *T.*  
260 *stalactifera* shells, and borings attributed to Mytilida cf. *Gastrochaenolites* isp.,  
261 sometimes with the *L. af. bisulcatus* shells in life position inside. In addition, a cemented  
262 chela of a crustacean and a *Bostrycapulus aculeatus* (Gmelin, 1791) shell, were identified  
263 at the basal surface; and oysters were found on the exposed surface of vermetid  
264 bioconstruction, thus totaling seven identified taxa (Table 2, Figs. 2A and 2B). The  
265 external surface of the vermetid bioconstruction presented typical signals of carbonate  
266 dissolution similar to lapiés (Fig. 2A). The vermetids were superposed on the *T.*  
267 *stalactifera* shells and, sometimes, the vermetids tubes penetrated the barnacle by the  
268 upper opening, indicating that the *T. stalactifera* specimens were dead when the  
269 vermetids grew (Fig. 2B).



270

271 Fig. 2: Apical (A, B and C) and basal (D and E) surface views of Ponta das Conchas  
 272 bioconstruction of *Petalocochus varians* with: *Tetraclita stalactifera* (t); boreholes of  
 273 Mytilida (b). Notice the vermetid tube growing inside the upper opening of a *T.*  
 274 *stalactifera* shell (arrow).

275

276 The age of different species from the Ponta das Conchas sample ranged from 6,941-  
 277 6,684 cal aBP (*T. stalactifera*) to 5,441-5,051 cal aBP (Mytilida) (Table 1). The age of the  
 278 different species correspond to the expected life sequence inferred from the  
 279 observation of the samples (Fig. 2). First, the *T. stalactifera* fixed on the naked rock at  
 280 6,941-6,684 <sup>14</sup>C cal aBP; subsequently, the *T. stalactifera* died and a small oyster fixed  
 281 inside the barnacle shell at 6,852-6,659 <sup>14</sup>C cal aBP. After that – 6,781-6,556<sup>14</sup>C cal aBP  
 282 – *P. varians* grew over the barnacles and oyster. Finally, the lithophagus Mytilida bored  
 283 the bioconstruction at 5,441-5,051 <sup>14</sup>C cal aBP (Table 1).

284 At Ponta das Conchas, it was observed that the top of the *P. caudata* bioconstruction  
 285 corresponds to the lower limit of the fringe of *T. stalactifera*, which agrees with the  
 286 former paleo-sea level reconstruction (Angulo, 1989 and 1992; Angulo et al., 2002, 2006  
 287 and 2022a).

288 *Praia da Armação de Itapocoroí*

289 The bioconstruction remains from Praia da Armação de Itapocoroí presented the  
 290 vermetid tubes arranged in three overlapping layers approximately 3 cm thick, totaling  
 291 9 cm between basal and apical surfaces (Fig. 3A). At the basal zone, the tubes were spiral  
 292 in shape and, from the middle to the apical zone, they were almost linear and vertical  
 293 (Fig. 3). This bioconstruction is constituted by *P. varians* tubes, *T. stalactifera* parietal  
 294 plates, borings of Mytilida (*Gastrochaenolites* isp.), and shells of venerid bivalves,  
 295 sometimes with articulated shells of the *P. aff. bicolor* inside. Furthermore, oysters occur  
 296 in cavities amid the vermetid bioconstruction. A total of 11 taxa associated with the  
 297 vermetid bioconstructions were identified (Table 2, Figs. 3A and 3B).

298

299 Table 2: Invertebrate diversity associated with vermetid bioconstructions remains.

Taxa	Sample (Zone)*			
	PCIM (IR; CV)	PA (OR)	PNH2 (CV)	PNH5 (IR)
Arthropoda				
Crustacea				
Balanomorpha				
Tetraclitidae				
<i>Tetraclita stalactifera</i> (Lamarck, 1818)	X	X	X	X
Decapoda sp.1 **	X			
Equinodermata				
Echinoidea sp. 1 ***			X	
Mollusca				
Polyplacophora				
sp. 1			X	
<i>Calloplax af. janeirensis</i> (Gray, 1828) ****			X	
Bivalvia				
Ostreida				
Ostreidae	X	X	X	
<i>Crassostrea</i> sp. 1			X	
<i>Ostrea</i> sp.1			X	X
Mytilida				
Mytilidae				
<i>Leiosolenus af. bisulcatus</i> (d'Orbigny, 1853)	X	X	X	X
<i>Mytilaster solisianus</i> (A. d'Orbigny, 1846)		X	X	X
<i>Modiolus</i> sp. 1			X	
sp. 1		X	X	
sp. 2			X	
Venerida				
Veneridae				
<i>Petricola af. bicolor</i> Sowerby II, 1854		X	X	X
Chamidae			X	
<i>Chama af. congregata</i> Conrad, 1833				X
Myida				
Corbulidae				
<i>Corbula</i> sp. 1			X	
Gastropoda				

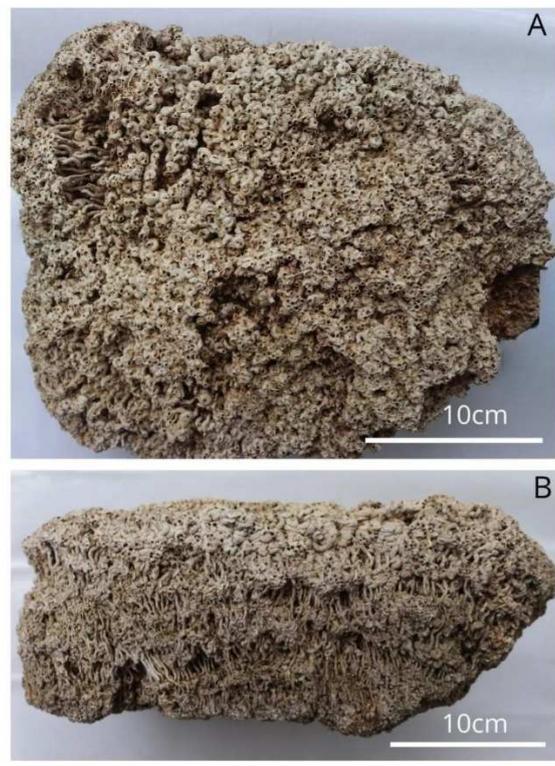
Lottiidae					
<i>Lottia subrugosa</i> (A. d'Orbigny, 1841)		X	X	X	
Littorinimorpha					
sp. 1		X			
sp. 2			X		
Calyptraeidae					
<i>Bostrycapulus aculeatus</i> (Gmelin, 1791)		X		X	
<i>Ergaea walshi</i> (Reeve, 1859)				X	
Vermetidae					
<i>Petalocochus varians</i> (d'Orbigny 1841)		X	X	X	X
Littorinidae					
<i>Littoraria flava</i> (King, 1832)				X	
<i>Fissurella itapema</i> (Ihering, 1927)				X	
<i>Diadora af. meta</i> (Ihering, 1927)			X		
Anellida					
Sabellida					
Serpulidae		X	X	X	X
<b>Total (n)</b>		<b>7</b>	<b>11</b>	<b>23</b>	<b>9</b>

Notes: \* Donnarumma et al. (2021); Picone and Chemello (2023) references; \*\* chela of a crustacean; \*\*\* spine; \*\*\*\* intermediate valve.

300  
301

302

303 The age of different species ranged from 1,405-1,302 cal aBP to 1,363-1,282 cal aBP,  
304 which correspond to the basal and apical generations of *P. varians*, respectively (Fig.3A).  
305 The *T. stalactifera* shell presented an age of 1,403-1,298 <sup>14</sup>C cal aBP, within the age  
306 uncertainty of the basal generation of *P. varians*.



307

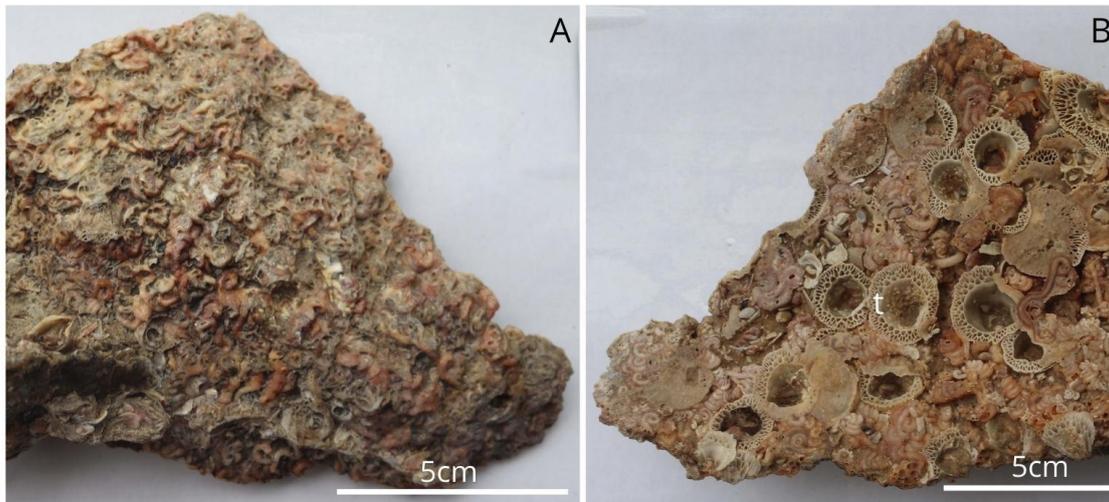
308 Fig. 3: Apical (A) and lateral (B) surface sample views of the Praia da Armação vermetid  
309 bioconstruction remains.

310

311 *Ponta do Papagaio 2 and 5*

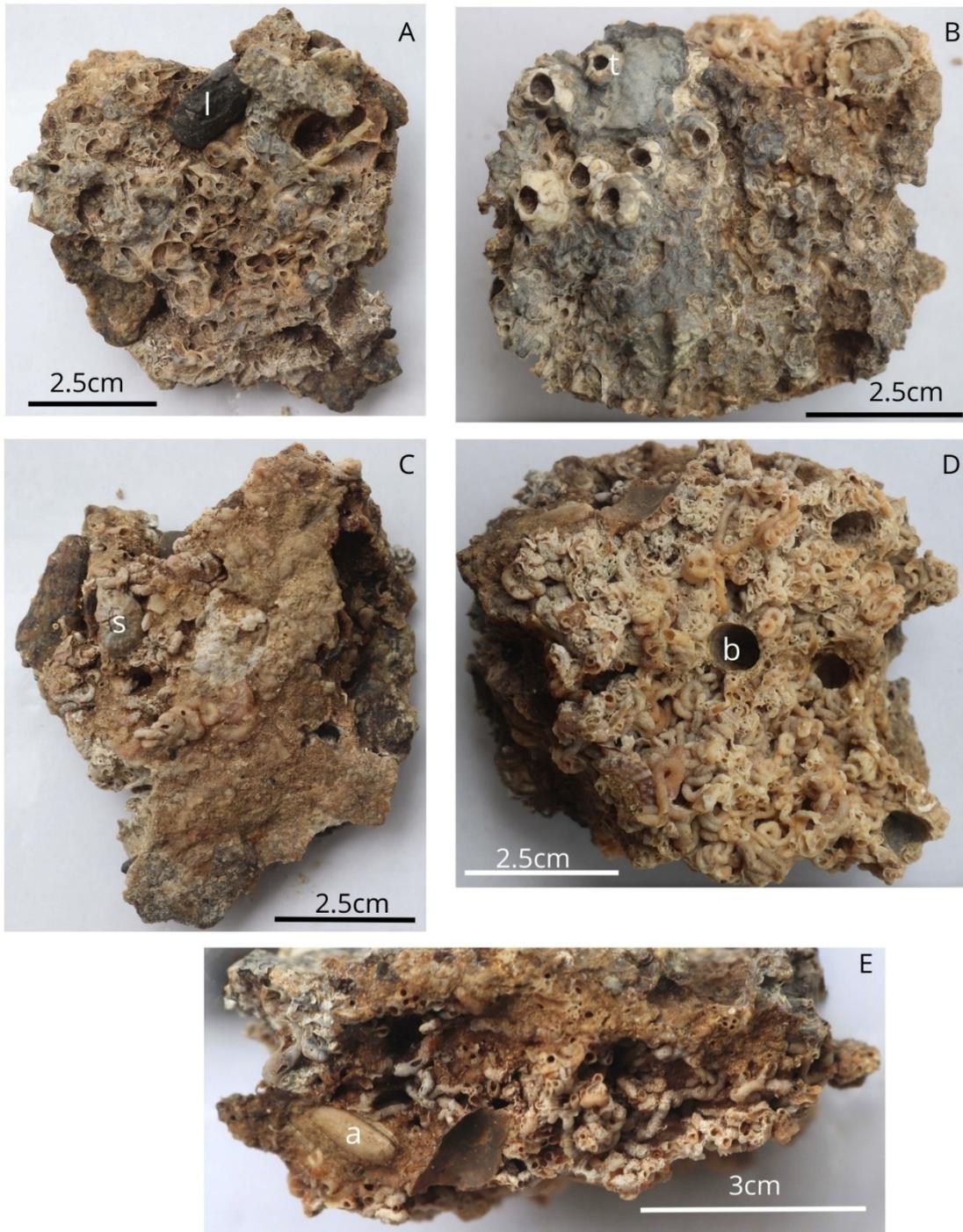
312 The vermetid bioconstructions remains corresponding to samples Pnh2 and Pnh5 from  
313 Ponta do Papagaio consist of *P. varians* tubes approximately 6 cm thick, with *T.*  
314 *stalactifera* and Mytilida borings (*Gastrochaenolites* isp.) and Veneridae, sometimes  
315 with shells of *P. aff. Bicolor*, *L. aff. bisulcatus* (in sample Pnh5), and *M. solisianus* in life  
316 position inside.

317 At sample Pnh2, cemented shells of oysters and three gastropod species (*L. subrugosa*,  
318 *E. walshi*, and *B. aculeatus*) were identified in the middle and apical zones of the  
319 bioconstruction. A greater abundance of barnacles was observed in the middle and basal  
320 zones. Within the barnacle assemblage, serpulid Polychaeta tubes, oyster and *Littoraria*  
321 *flava* shells, and *P. varians* tubes were recognized, primarily distributed in the basal and  
322 middle zones. A total of 23 taxa were identified (Table 2, Figs. 4A and 4B).



323  
324 Fig. 4: Apical (A) and basal (B) surface views of Ponta do Papagaio vermetid  
325 bioconstruction, sample Pnh2, with *Tetraclita stalactifera* (t) shells.

326 At sample Pnh5, the barnacles were observed in the apical and middle zones of the  
327 bioconstruction, inside the borings attributed to Mytilida, and serpulid Polychaeta  
328 tubes. Cemented *L. subrugosa* shells were recognized at the basal surface. A total of  
329 nine taxa were identified (Table 2, Figs. 5A and 5B).



330

331 Fig. 5: Apical (A and B), basal (C and D), and lateral (E) surface views of Ponta do Papagaio  
 332 vermetid bioconstruction, sample Pnh5, with: l. lithic gravels; t. *Tetraclita stalactifera*  
 333 shells on the bioconstruction surface; b. Mytilida boring (*Gastrochaenolites* isp.); a.  
 334 articulated shells of *Leiosolenus* aff. *Bisulcatus*, in living position; s. *Lottia subrugosa*  
 335 shell.

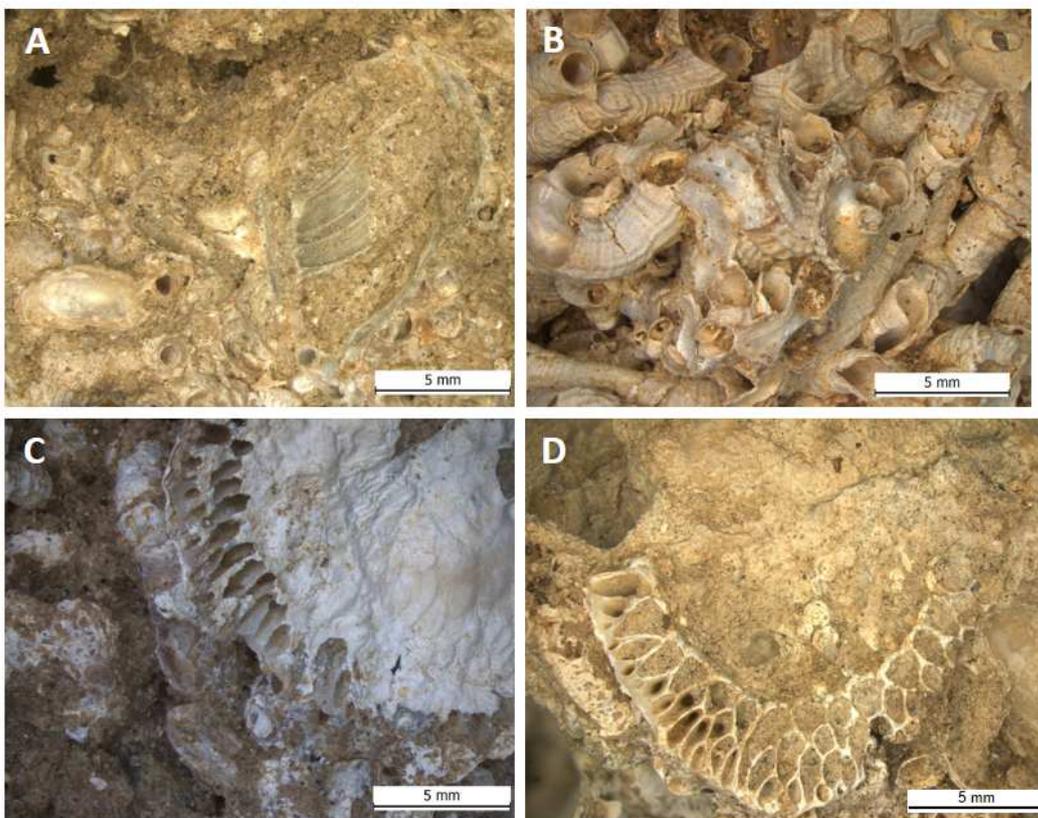
336

337 The ages of *P. varians* and *T. stalactifera* shells from sample Pnh2 were similar – 2,719-  
 338 2,367 <sup>14</sup>C cal aBP and 2,741-2,437 <sup>14</sup>C cal aBP, respectively. In contrast, the ages of

339 different species from the sample Pnh5 ranged from 6,260-5,943 <sup>14</sup>C cal aBP to 5,575-  
340 5,321 <sup>14</sup>C cal aBP.

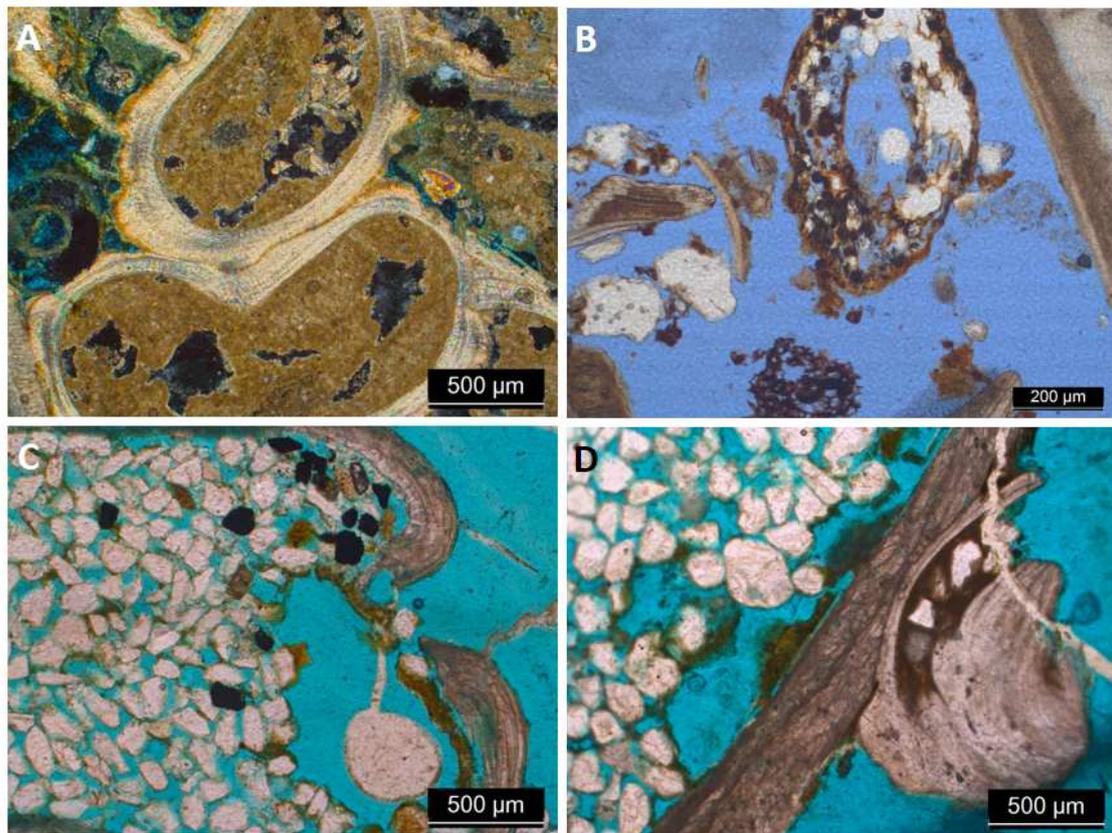
#### 341 4.2. Optical microscopy analysis

342 When observed under the stereoscopic magnifying glass (Fig. 6), *P. varians*, *T.*  
343 *stalactifera* and *L. af. bisulcatus* presented homogeneous color, both internally and  
344 externally. Under the magnifying glass and microscope (Figs. 7 to 10), *P. varians* showed  
345 four main shapes: spiral or concentric; subcircular to oval (Figs 6A and 6B); similar to a  
346 cloverleaf or a pair of symmetrical cloverleaves (Fig. 9A); and similar to a bean or  
347 dumbbell (Fig. 7A). The internal diameter of the tubes varied around 1.2 mm, and the  
348 wall thickness around 0.2 mm (Figs. 6 and 7). External ornamentation was typical of the  
349 gastropod species (Fig. 6B), in the form of either transverse striations, corresponding to  
350 the tube growth lines, or longitudinal ridges. In cross-section of the tube, the  
351 longitudinal lines appeared as subtle (Figs. 9A and 10A) to sharp (Fig. 8D) undulations  
352 on the outer surface of the tube.



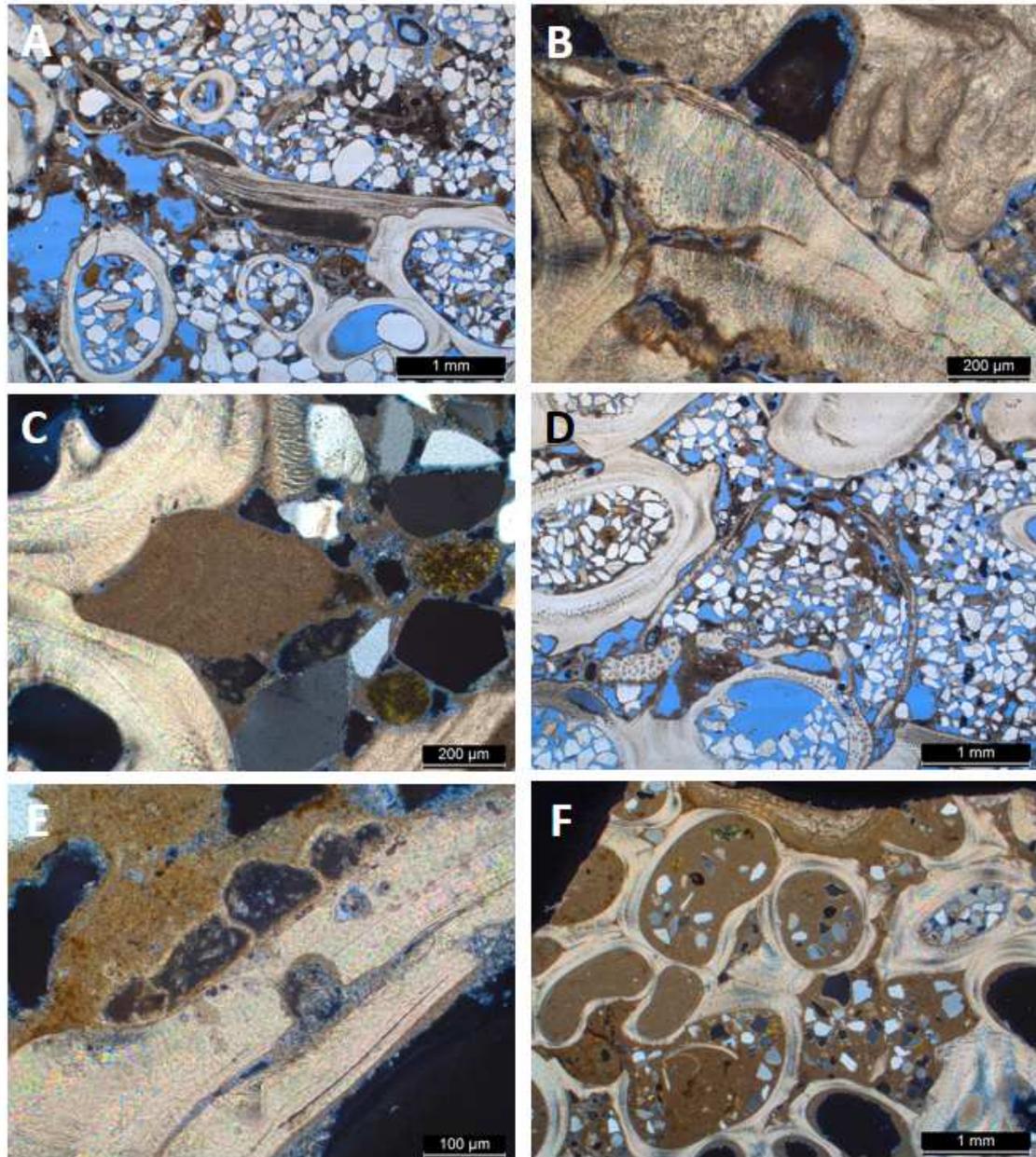
353

354 Fig. 6: General appearance of the studied bioconstruction samples under reflected light  
355 stereomicroscope: A. Vermetids (v) and Mytilida (M) shell filled with micrite and sand  
356 grains (c) in sample PCIM. B. PA sample with vermetids (v), bryozoan encrustation (b)  
357 and clastic filling (c). C. Flat basal surface of sample Pnh2, with barnacle (t) surrounded  
358 by vermetids. D. Sample Pnh5 exhibiting barnacle (t) overgrown by vermetids (v). Note  
359 the barnacle parietal tubes (pt) in C and D.



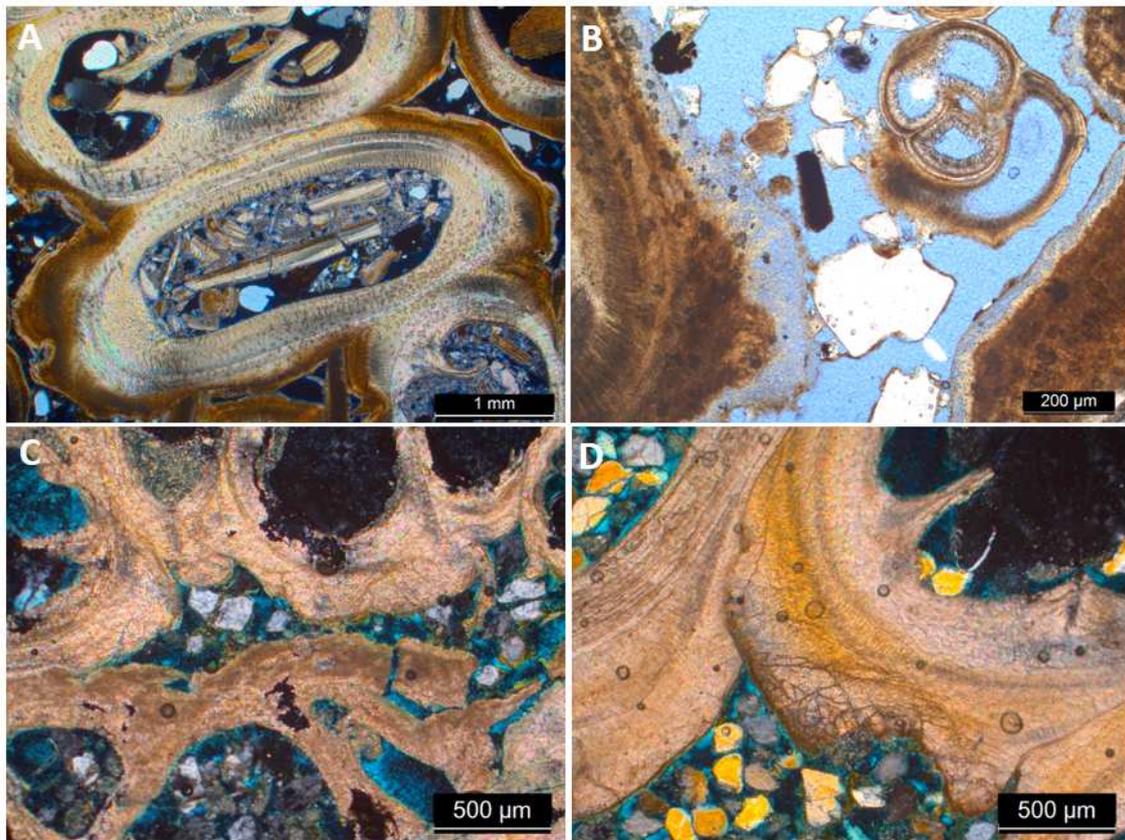
360

361 Fig. 7: Components of the framework under polarized transmitted light microscopy: A.  
 362 Vermetids (v) and smaller gastropod (g) in sample PCIM. Note the vermetid chambers  
 363 with brown outer envelope (e) and filled by micrite (m) containing elongated pores. B.  
 364 Plant remains (p) in sample PA, including probable rootlet. C. *Leiosolenus* af. *bisulcatus*  
 365 valves in sample Pnh2. Note the filling with terrigenous clasts (q), including opaque  
 366 heavy minerals, and clay-ferruginous cement (f). D. Vermetid (v) attached to a barnacle  
 367 (t) in sample Pnh5. Note the filling with terrigenous clasts (q) and micrite (m), including  
 368 inside the vermetid. Crossed polarizers in A and parallel polarizers in B, C and D.



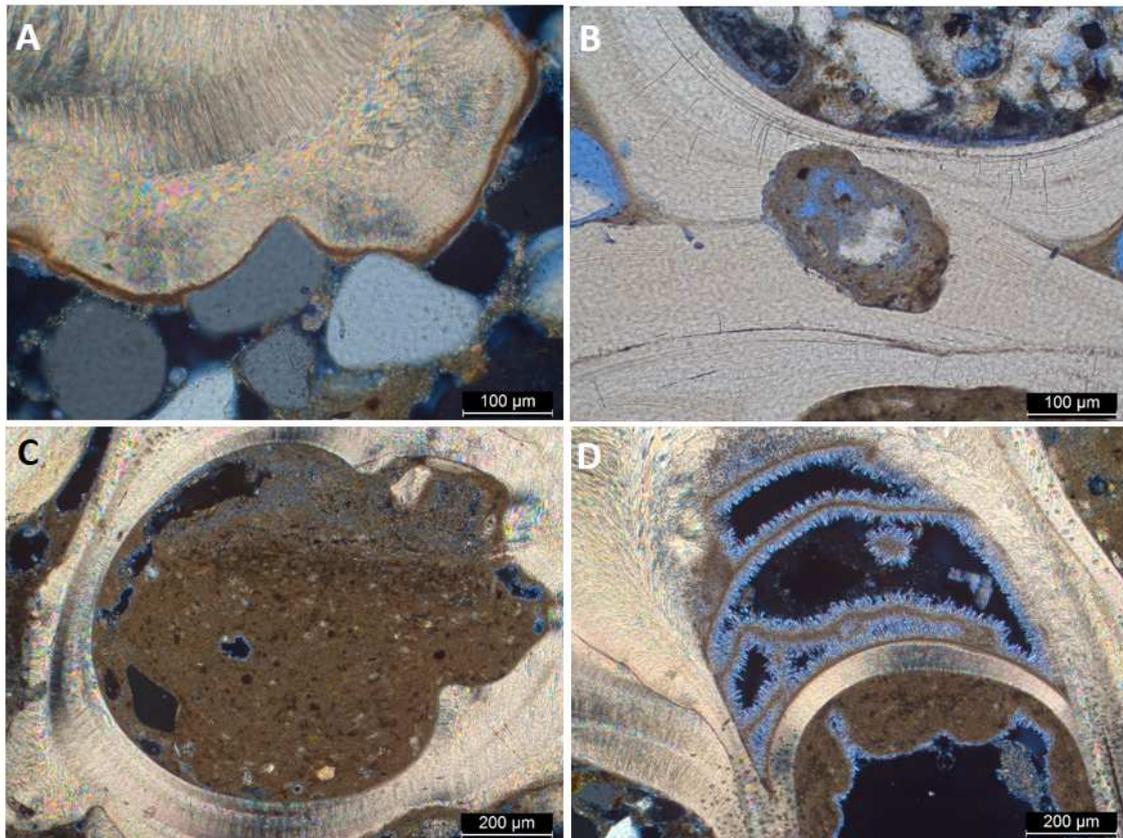
369

370 Fig. 8: Associations between bioconstructor organisms in sample Pnh5, under polarized  
 371 transmitted light microscope: A, B. Vermetid (v) – barnacle (t). C: Vermetid (v) – red  
 372 algae (r) . D. Vermetid (v) – bivalve (supposedly Mytilida, M). E. Vermetid (v) – encrusting  
 373 foraminifera (ef). F. Microbial mat (cb) on top of the vermetid (v) bioconstruction. Note  
 374 the intense filling of the chambers by terrigenous grains (q) and micrite (m). Parallel  
 375 polarizers in A and D, and crossed polarizers in B, C, E and F.



376

377 Fig. 9: Post-depositional modifications in the vermetid bioconstruction framework (v):  
 378 A. Dark brown outer border, with the appearance of a micritic envelope (e) (sample PA).  
 379 B. External anisopaque coating, constituted of thin carbonate, attributed to encrustation  
 380 by a bryozoan (b) (sample PA). C. Chemical alteration and dismantling at the top of the  
 381 bioconstruction, overlapped by a new horizon of unaltered chambers, suggestive of a  
 382 pause in colony growth (sample Pnh2). D. Dark, cracked outer border (e) (sample Pnh2).  
 383 Note the partial filling of the pores by bioclasts (c) and terrigenous material (q). Crossed  
 384 polarizers in A, C and D, and parallel polarizers in B.



385

386 Fig. 10: Post-depositional modifications of the vermetid framework (v) in sample Pnh5:  
 387 A. Dark brown outer border, with the appearance of a micritic envelope (e), showing  
 388 adhered quartz grains (q). B. Bioperforation crossing the contact between two adjacent  
 389 chamber walls, partially filled with micrite. C. Filling of the chamber by two generations  
 390 of micrite, in a geopetal pattern. D. Partial filling of the chambers by anisopachous  
 391 pendulous micrite (m) and isopachous fringe of microspar (ms). Crossed polarizers in A,  
 392 C and D, and parallel polarizers in B.

393

394 In *T. stalactifera*, the parietal tubes exhibited a polygonal shape in cross-section, with a  
 395 major axis of 0.2 to 1.0 mm (Fig. 6D), or an elongated arch, up to approximately 2 mm  
 396 long (Fig. 6C). The wall thickness (septum) was similar to that of the vermetid, but the  
 397 shell edges (inner and outer lamella) could reach several millimeters thick. The  
 398 carbonate coloration is slightly darker than that of the vermetid (Figs. 7D, 8A and 8B)  
 399 and with the occasional presence, inside, of elongated pockets (Fig. 8A) and serrated or  
 400 parabolic shapes (Fig. 8B) that are even darker, almost black.

401 The flat surface by which the shells were attached to the rocky shore appeared better  
 402 developed or evident in the barnacle than in the vermetid (Figs. 6C and 6D). A concentric  
 403 relationship between the two, with *T. stalactifera* serving as the growth nucleus of *P.*  
 404 *varians*, was sometimes noticeable (Figs. 6C and 6D).

405 The summary of the thin section descriptions is given in Table 3. The depositional fabric  
 406 of the four samples was carbonatic growth framework, with partial filling dominated  
 407 either by micrite (PCIM) or by extraclastic (terrigenous) sand-silt (other samples).  
 408 Despite this, the growth framework was only the major textural component of the

409 encrustations in one sample (Pnh5). In the others, the dominant component was either  
410 micrite (PCIM) or pores (PA and Pnh2).

411

412 Table 3: Summary of carbonate bioconstructions petrographic analysis. TR = trace amount (&lt;&lt;1%). HM = heavy mineral.

Component		Sample			
		PCIM	PA	PNH2	PNH5
Growth framework	Proportion (%)	25	25	35	35
	Composition	<i>P. varians</i> (100), Mytilida (TR), other gastropode (TR)	<i>P. varians</i> (96), bryozoan (2), traces of vegetables, including rootlets (2)	<i>P. varians</i> (65), <i>T. stalactifera</i> (30), Mytilida (5)	<i>P. varians</i> (75), <i>T. stalactifera</i> (15), red algae (4), Mytilida (4), other gastropode (1), encrusting foraminifera (1)
Extraclastic (terrigenous) silty-sand fill	Proportion (%)	5	10	10	20
	Composition	Quartz (95), feldspar (5), opaque HM (TR)	Quartz (90), lithic fragment (6), composite grain rich in opaque HM (3), feldspar (1), HM (TR)	Quartz (95), feldspar (3), opaque HM (2), transparent HM (TR)	Quartz (95), feldspar (2), chert (2), opaque HM (1), transparent HM, e.g. tourmaline, zircon (TR)
	Texture	Coarse silt to coarse sand sub-angular to well-rounded grains	Very fine to very coarse sand sub-angular grains	Coarse silt to median sand angular to sub-rounded grains	Well sorted very fine to fine sand angular to sub-rounded grains
	Fabric	Larger loose grains filling the tubes and smaller grains in the middle of the matrix	Preferential occurrence between tubes	As filling, in most bioconstruction pores, locally appearing normal gradation	As intra and inter-tube filling; partial intratube filling occasionally in geopetal pattern
Intraclastic silty-sand fill	Proportion (%)	1	7	2	5
	Composition	Elongated and isolated ellipsoidal (rings) fragments of vermetidae (70), phyllosilicate grains (20), ferruginous grains (10)	Elongated to subequidimensional vermetidae fragments (95), black and yellowish orange pellets (5)	Fragments of barnacles and bivalves (90), echinoid spines (5), ferruginous-phyllosilicate grains (5)	Fragments of vermetidae and other gastropode (70), barnacle (20), foraminifera (2), red algae (2), bivalve (2) and echinoderm (2), and yellowish and black pellets (2)
	Size	Coarse silt to coarse sand	Fine to coarse sand	Very fine sand to granule	Very fine to median sand
	Fabric	Like the terrigenous	Between and inside the tubes	Scattered among the terrigenous	Scattered among the terrigenous
Clayey matrix	Proportion (%)	58	2	3	14
	Description	Micrite in two generations	Micrite	Micrite	Micrite in two generations
	Fabric	Partial filling of inter and intra grain pores, locally forming menisci	Partial filling, sometimes apparently geopetal, of some of the vermetidae chambers	Partial filling of inter and intra grain pores, locally forming menisci	Partial to complete filling of inter and, mainly, intratube pores,

					sometimes forming geopetal, pendular or meniscal fabrics
<b>Cement</b>	<b>Proportion (%)</b>	<b>1</b>	<b>1</b>	<b>2</b>	<b>1</b>
	<b>Description</b>	Phyllosilicate as coatings and menisci in clasts (50), and patches of iron oxyhydroxide amid micrite (50)	Clay-ferruginous coating with a particulate appearance around the clasts	Clay-ferruginous coating and meniscus	Post-micrite anisopaque fringe rimming part of the intratube pores
<b>Porosity</b>	<b>Proportion (%)</b>	<b>10</b>	<b>55</b>	<b>50</b>	<b>25</b>
	<b>Description</b>	Intergrain (60), intramatrix elongated (35) and growth framework (5)	Growth framework (60) and intergrain (40)	Intergrain (80) and growth framework (20)	Intergrain (65), growth framework (15), intragrain (10) and intramatrix elongated (5)
<b>Depositional fabric</b>		Growth framework with intense partial filling by micrite and, subordinately, terrigenous sand	Growth framework with partial filling by terrigenous and bioclastic sand and rare micrite	Growth framework with partial filling by terrigenous sand and rare micrite	Growth framework with intense partial filling by terrigenous sand, micrite and, subordinately, bioclasts

415 The bioconstruction framework was dominated by *P. varians* (65 to almost 100%) in all  
416 samples. Its other components, in order of decreasing mean abundance, were *T.*  
417 *stalactifera* (Pnh2 and Pnh5; Figs. 6C, 6D, 7D, 8A and 8B), *L. af. bisulcatus* (PCIM, Pnh2,  
418 Pnh5; Figs. 6A and 8D), red algae (Pnh5; Fig. 8C), bryozoan (PA; Figs. 6B and 9B), vestiges  
419 of plants (PA; Fig. 7B), encrusting foraminifera (Pnh5; Fig. 8E), other gastropods, with  
420 dimensions approximately three times smaller than *P. varians* (PCIM, Pnh5; Figs. 7A and  
421 9B), and microbial mat (Pnh5; Fig. 8F). Although *T. stalactifera* occupies a limited volume  
422 (<20%) of the bioconstructions studied under the magnifying glass, its carapace is, in the  
423 lamellae, more robust and massive than that of the vermetid, which favored its  
424 representation in area in the two thin sections in which it was found. The low  
425 representation of *L. af. bisulcatus* as a bioconstruction component in the thin sections  
426 (maximum 5%) is due to its dispersed occurrence and thinner shell.

427 The walls of each tube of *P. varians* were generally anisopaque. They are formed by  
428 several concentric layers of prismatic/fibrous aragonite crystals, whose orientation can  
429 vary, in the same tube, between radial, inclined or tangential in relation to the  
430 circumference of the tube (e.g. Fig. 10A). The radial orientation was the dominant one.  
431 Intercalation, in the same tube wall, between orange to light brown colored laminae and  
432 others of white or beige color was frequently observed in the thin sections (Fig. 9D). The  
433 color was more common in the most superficial laminae of the tube. Dark brown colored  
434 laminae were also found, these exclusively on the outer edge (Fig. 7A, 8A, 8D and 9A).  
435 Locally, associated with this darkened surface of the tube, a cracked appearance and  
436 indentations suggestive of corrosion, or more likely, mechanical breakage, were  
437 observed (Fig. 9D). Concave-convex contacts of the dark brown surface with quartz  
438 grains were also observed (Fig. 10A).

439 The clastic components were dominated by terrigenous materials (5 to 20% of the rock),  
440 mainly quartz, with a subordinate presence of intraclasts (1 to 7%), which were formed  
441 by carbonate bioclasts (all samples, e.g. Fig. 9A), black or yellowish-orange pellets (PA,  
442 Pnh5; Fig. 9B) and grains of phyllosilicate and/or ferruginous composition similar to that  
443 of cements (Pnh2, e.g. Fig. 7C). Quartz grains engulfed by vermetid carbonate indicate  
444 contemporaneity between shell growth and terrigenous deposition. Among the  
445 bioclasts, the presence of vermetid fragments (PCIM, PA, Pnh5), and of bivalves,  
446 barnacles and echinoderms (Pnh2, Pnh5) larger than the average clasts in general (fine  
447 to very fine sand) was common. Locally, terrigenous grains filling vermetid tubes showed  
448 normal grading (Pnh2) or geopetal filling pattern (Pnh5).

449 The micritic matrix was found in the form of partial filling of inter and intragrain pores,  
450 in variable proportions (2 to 58%), and may present more than one texture and/or color  
451 (PCIM, Pnh5; Fig. 10C). Among the fabrics found, the menisci between the grains or  
452 between the adjacent walls of the bioconstruction (PCIM, Pnh2, and Pnh5), the pendular  
453 drip (Pnh5; Fig. 10D) and the geopetal filling (PA, Pnh5; Fig. 10C) stand out.

454 The post-micrite cement observed in the four samples is divided into non-carbonate and  
455 carbonate. The non-carbonate cement, with a cryptocrystalline texture, was found in  
456 small quantities (1 to 2%) in three of the analyzed samples (PCIM, PA, Pnh2; Figs. 7B and  
457 7C). It is formed by phyllosilicates, iron oxyhydroxides or by an intimate association  
458 between these two compositions, that is, a clay-ferruginous material. Phyllosilicates

459 and clay-ferruginous material were observed in the form of coatings around the grains  
460 or lining pores (Fig. 7B) or as menisci between grains of fine sand to coarse silt. The  
461 oxyhydroxides appeared forming spots (up to 80  $\mu\text{m}$ ) or filling elongated pores in the  
462 middle of the micrite. The phyllosilicate cement presented an orange first-order  
463 interference color, an optical characteristic more compatible with clay minerals from  
464 the illite or smectite group. The presence of Si, Al, Mg and Fe, detected by SEM-EDS  
465 analysis of this cement (Toniolo, 2017), is indicative of smectite composition.

466 Carbonate cement, in the form of anisopaque microspar fringe, was found in one sample  
467 (Pnh5), lining part of the vermetidae chambers (Fig. 10D) or intergrain porosity. Cement  
468 grains are also embedded in the micrite. The external anisopaque coating of thin  
469 carbonate observed in sample PA (Fig. 9B) showed a microperforated texture, similar to  
470 that of the bryozoan found in this same thin section and detected by magnifying glass  
471 (Fig. 6B). Therefore, it must be a biogenic encrustation and not a cement stricto sensu.

472 Porosity between the clasts filling the bioconstruction (e.g. Figs. 8A and 8D) reach 60 to  
473 80% in area. In the micrite-rich samples, secondary porosity consist of irregular or  
474 elongated and slightly sinuous voids within the micrite itself (Figs. 7A and 10C). To a  
475 lesser extent, subcircular perforations measuring up to 500  $\mu\text{m}$  in the carbonate of  
476 vermetid shells were also observed, both in reflected light stereomicroscopic  
477 examination (Fig. 6B) and in transmitted light thin sections (Figs. 8E and 10B). Some of  
478 these perforations appear partially filled with micrite.

479

## 480 **5. Discussion**

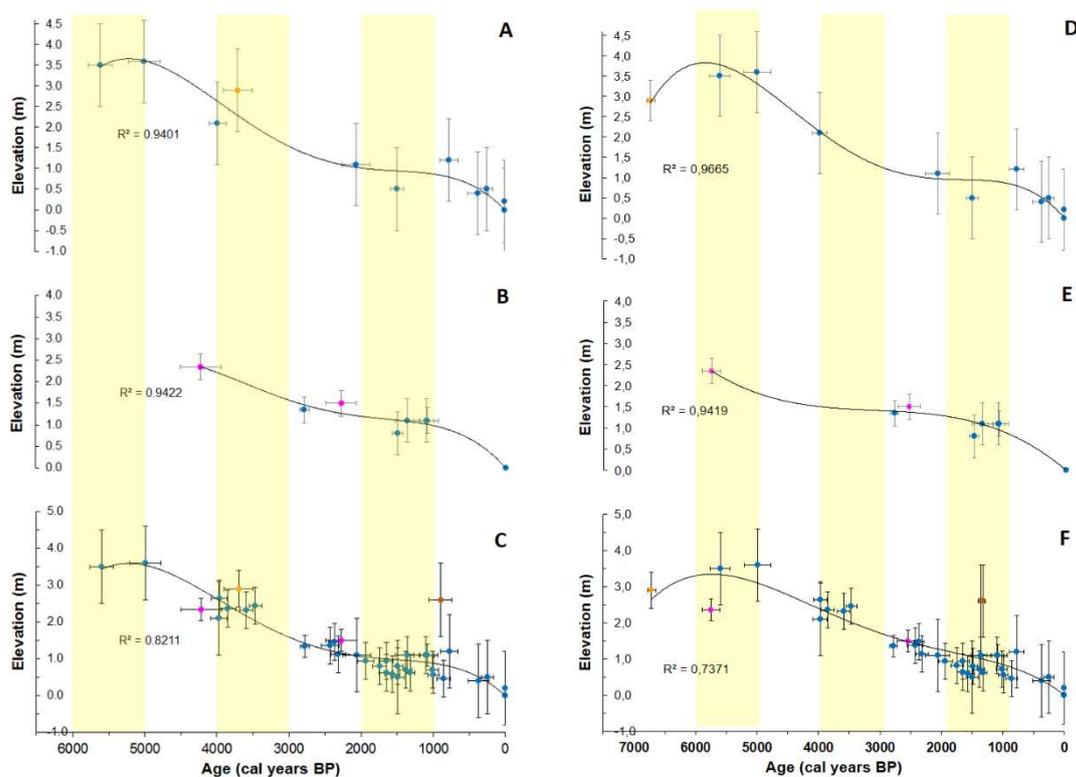
### 481 *5.1. Comparison between ages and implications for sea-level histories*

482 The radiocarbon ages obtained from fossil shells and shell fragments of different species  
483 from the bioconstructions are in agreement with the relative ages expected based on  
484 the spatial relationship observed between them. The *T. stalactifera* shells are older than  
485 the overgrown vermetids shells, and the *L. af. bisulcatus* shells in life position, which  
486 perforate the bioconstruction, are younger (Table 1). At sample Pnh2 the ages also  
487 correspond to the living sequence inferred from the sample observation. First, *T.*  
488 *stalactifera* fixed on the bare rock at 6,260-5,943  $^{14}\text{C}$  cal aBP; thereafter *P. varians* built  
489 the bioconstruction at 5,894-5,604  $^{14}\text{C}$  cal aBP and finally the *L. aff. bisulcatus* bored the  
490 bioconstruction at 5,575-5,321  $^{14}\text{C}$  cal aBP. It stands out that the *P. varians* aliquot was  
491 obtained from the sample basal zone, next to the *T. stalactifera* shells.

492 The ages of individual shells are older than those obtained by dating bulk vermetid  
493 bioconstructions, and this difference increases with the age. The difference between the  
494 bioconstruction and the *P. varians* shell ages is around four centuries for the younger  
495 shells and reaches three thousand years for the older ones (Table 1 and Fig. 11).  
496 Considering the middle ages (e.g. 6,718.5 years for a 6,781-6,556  $^{14}\text{C}$  cal aBP interval),  
497 the two older *P. varians* shells (6,781-6,556  $^{14}\text{C}$  cal aBP and 5,894-5,604  $^{14}\text{C}$  cal aBP), are  
498 82% and 36% older than the bulk bioconstruction age (3,897-3,499  $^{14}\text{C}$  cal aBP and  
499 4,501-3,936  $^{14}\text{C}$  cal aBP, respectively). The two younger *P. varians* shells (1,405-1,302  $^{14}\text{C}$   
500 cal aBP and 2,719-2,367  $^{14}\text{C}$  cal aBP) present ages 51% and 12% older, respectively, than  
501 the age given by the bulk bioconstruction. In the case of Pnh2 sample, the age difference  
502 is within the dating error margin: the *P. varians* shell gives age of 2,719-2,367  $^{14}\text{C}$  cal aBP

503 and the bulk bioconstruction, 2,489-2,063 <sup>14</sup>C cal aBP. These differences imply a great  
504 impact on the reliability of relative sea-level curves built from bulk samples, generally  
505 dated by the conventional radiocarbon method.

506 Considering the paleo-sea levels obtained in previous works for the four samples  
507 (Angulo, 1992; Angulo et al., 2002, 2006, 2022a) and using the revised ages reported  
508 here (Table 1), we infer that a Holocene highstand, more than 2 m above present level,  
509 occurred between 7,000 cal and 5,000 cal BP aBP (Fig. 11). This age is older than  
510 postulated in former works (e.g. Martin et al. 2003; Angulo et al. 2006, 2022a), which  
511 consider that post-glacial relative sea level (RSL) reached a level similar to the present  
512 one around 7,000 cal BP. In addition, as the post-glacial RSL maximum in former works  
513 was inferred from ages obtained from dating bulk samples (e.g. Martin et al. 2003;  
514 Angulo et al. 2006, 2022a), and the bulk samples could give younger ages (Table 1), we  
515 consider that the post-glacial maximum could be older than previously postulated. The  
516 differences in ages between bulk and individual shell samples highlight that paleo-sea  
517 levels inferred from bulk vermetid remains and respective Holocene sea-level curves  
518 need revision. This revision is especially important for the Mid-Holocene ages where the  
519 differences between bulk and individual shell samples are larger. Identification of the  
520 timing of the Mid-Holocene highstand is critical for testing models of glacio-isostatic  
521 adjustment (Woodroffe, 2009; Creel et al., 2024), for the understanding of coastal  
522 evolution, and for determining the role of sea-level in human settlement patterns (e.g.  
523 Giannini et al. 2010, Alessandretti et al. 2023). More data for separate species are  
524 therefore necessary to improve the accuracy of Holocene sea-level curves from Brazil.



525  
526 Fig. 11: Relative sea-level reconstructions from Angulo et al., 2022a (A,B,C) and the data  
527 presented here (D, E, F), with their respective polynomial curves: A and D, Paran; B  
528 and E, Ponta do Papagaio, Santa Catarina; C and F, Southern Brazilian coast north of

529 latitude 28°S. Colored points allow comparison between the previous dates of the bulk  
530 bioconstruction (A,B,C) and the new ones from individual vermetid samples (D,E,F): A,  
531 C, D, F correspond to 4th-order and B, E to 3rd-order polynomial curves. In constructing  
532 the curves, current sea level (0,0) was considered as an additional data point.

533

534 The sequence of the bioconstruction building by the different species – first *T.*  
535 *stalactifera*, subsequently *P. varians* and finally *L. af. bisulcatus* – observed in the  
536 samples and confirmed by the dating (Figs. 2 to 5 and Table 1) could be attributed to  
537 biological competition with stable or rising sea-level.

538 The sequence observed in the older bioconstructions (PCIM and Pnh5, Table 1) may  
539 correspond to a rising sea level, because the species living at lower levels (*P. varians*) is  
540 younger and superimposed on the one living at higher levels (*T. stalactifera*) (Laborel,  
541 1979; Angulo and Souza, 2014; Angulo et al., 2022a; Pardal et al., 2023). This hypothesis  
542 is reinforced by the fact that the ages obtained from both species cover a period when  
543 RSL was supposedly rising (Fig. 11). However, the biological zone vertical extents of  
544 these two species partially coincide. Therefore, the alternative hypothesis that the  
545 recorded succession of building organisms may also result from biological competition  
546 under stable sea levels cannot be entirely ruled out. This hypothesis is best evaluated by  
547 examining the possibilities of differential rejuvenation of the <sup>14</sup>C ages of the two species  
548 by contaminants.

549

## 550 5.2. Characteristics of bioconstruction and its implications for paleo-sea level dating

551 The thin sections studied demonstrated that *P. varians* appears associated with several  
552 other organisms, some of them younger and/or from another biological zone. In view of  
553 that, knowing its typical shapes in flat section is important to allow high-precision  
554 collections of this species aimed at reconstructing the marine paleolevel. The four  
555 different two-dimensional shapes (spiral or concentric, cloverleaf, subcircular to oval,  
556 and dumbbell-like) observed in vermetid chambers result from distinct viewpoints or  
557 thin section orientations. They can be understood based on the description of the three-  
558 dimensional geometry of the shell of *P. varians* (Laborel, 1986) and other species of this  
559 genus (Savazzi, 1996; Scuderi, 2012). The two-dimensional shape depends basically on  
560 the orientation of the section in relation to the tube and whether or not this section cuts  
561 the axis of winding or columella, and in what relative direction. Thus, the spiral or  
562 concentric shape appears when the columella is sectioned transversely, and the tubes,  
563 longitudinally; the cloverleaf shape is due to the presence of a pair of internal laminae  
564 projecting from the columellar wall; therefore, it occurs when the columella is sectioned  
565 longitudinally (Fig. 9A); the subcircular and oval shapes (Figs, 6A and 6B) are found when  
566 the section is transversal or oblique to the tube, respectively, but without sectioning the  
567 columella; finally, the shape similar to a bean or dumbbell (Fig. 7A) also appears in  
568 sections that do not cross the columella, but are longitudinal to the tube.

569 The dark brown outer rim, recorded in part of the vermetid carapaces in all samples  
570 studied (Figs. 7A, 8A, 8B, 8D and 9A), suggests some form of weathering or eodiagenetic  
571 alteration of aragonite in more prolonged contact with the atmosphere, seawater or  
572 microbial communities. It is identical to the micritic envelopes sensu Gvirtzman and

573 Friedman (1977), widely described in carbonate grains of Phanerozoic deposits, and is  
574 therefore interpreted as such here. Micritic envelopes are produced in eodiagenesis by  
575 endolithic microbes deposited in the photic zone (Bathurst, 1966; Calvet, 1982; Perry,  
576 1999) and can be destructive or constructive in origin (Kobluk and Risk, 1977; Calvet,  
577 1982; Reid and Macintyre, 1998, 2000; Perry, 1999; Ge et al., 2020). In the case of  
578 aragonite substrate, as attested in Holocene examples, the alteration implied by micritic  
579 envelope formation may include neomorphism to high Mg calcite (Kendall and Patrick,  
580 1969; Scherer, 1974; Reid et al., 1992; Reid and Macintyre, 1998). This neomorphism  
581 may indicate changes in the chemical composition of the carbonate in terms of Mg and  
582 trace element content (e.g. Sr and Pb), as well as in the ratios between stable isotopes  
583 of O and C; it may also indicate formation of the carbonate after the vermetid's lifetime,  
584 especially if it is a constructive envelope, thus having possible implications for the  
585 interpretation of the dating result.

586 On the other hand, the micritic envelope found in the samples studied is generally not  
587 very expressive in volume, with rare exceptions (Fig. 9A); this means that in most cases  
588 the difference in age of a sample dated from the whole shell, with envelope, in relation  
589 to the original aragonite from the vermetid shell, without the envelope, may be small,  
590 likely within the error margin of the dating method.

591 In the samples studied, both the presence and thickness of the micritic envelope can  
592 vary, even in adjacent chambers of the same thin section (e.g. Figs. 9A and 9D).  
593 Considering that the formation of the envelope presupposes exposure of shell aragonite  
594 to water, this suggests alternation between phases and/or preferential growth sites of  
595 the vermetid carbonate. In some cases, the periphery of the chamber with micritic  
596 envelope is partially surrounded by another layer of aragonite, with little or no micritic  
597 envelope (Fig. 9D). This apparently points to the interruption of growth, marked by the  
598 exposure and alteration of the chamber edge, followed by a new growth phase.

599 Fracturing and indentations at the edge of vermetid chambers with micritic envelope  
600 (Fig. 9D) may result from the creation of planes of weakness in the aragonite crystals  
601 due to the recrystallization force during neomorphism. The close adhesion of rigid  
602 quartz grains, in concave-convex contacts with the surface of the vermetid containing a  
603 micritic envelope (Fig. 10A), indicates that envelope carbonate had ductile or plastic  
604 behavior. This rheology is consistent with the growth of biofilms on the carbonate  
605 surface, a phenomenon described in the formation of constructive micritic envelopes  
606 (Ge et al., 2020).

607 The dominance of quartz and other terrigenous elements among the clastic components  
608 is consistent with the mineralogy of the beaches adjacent to the cliffs where the  
609 bioconstructions were collected. The intraclastic components, on the other hand, reflect  
610 the sessile benthic community existing on the cliff. Two specific types of intraclasts  
611 indicate mechanical reworking of the bioconstructed framework and respective cement.  
612 They are: fragments of gastropods, bivalves and barnacles with a coarser grain size than  
613 the average of the clasts (Figs. 9A and 9B); and grains with phyllosilicate and/or  
614 ferruginous composition similar to that of the cement coating the chambers (Fig. 7C).  
615 These kinds of intraclasts would have been formed by fragmentation during the breaking  
616 of waves against the bioconstruction, with immediate redeposition in its pores.

617 The frequent presence of geopetal patterns in the chambers filled with matrix (Fig. 10C)  
618 or sand clasts (Fig.8D) suggests that the entry of this material occurred under conditions  
619 of non-saturation in water (vadose) (e.g. Tucker and Wright, 1990; Scholle and Ulmer-  
620 Scholle, 2003; Flügel, 2010; Hood and Wallace, 2012), therefore above the mean tide  
621 level. Fabrics of micritic matrix in meniscus and pendular (Fig. 10D) reinforce this  
622 interpretation. Given that *P. varians* lives essentially underwater, it is likely that most of  
623 this vadose filling occurred with RSL lower than that of the animal's lifetime. In this  
624 regard, the large variation in micrite content (2 to 58%) in the studied bioconstructions  
625 may in part be linked to the time of action of vadose processes. In theory, the higher the  
626 paleo-sea level of the bioconstruction, the longer the time of action of these processes  
627 and the greater the probability of filling by micritic matrix. In fact, of the three samples  
628 indicating RSL greater than 2.0 m above present, two (PCIM and Pnh5) presented the  
629 highest micrite contents found (58 and 14%, respectively). There were two phases of  
630 micrite filling, at least in sample Pnh5, where a generation of thinner micrite fills pores  
631 left by the previous generation, including in a geopetal pattern (Fig. 10C). The  
632 interpretation of more than one phase of pore filling by micrite is reinforced by the fact  
633 that the microspar cement fringe which coats the intratube filling of pendulous micrite  
634 (Fig. 10D) also occurs reworked amid this thinner intergrain micrite.

635 Coatings, menisci and pore linings of ferruginous clay material (Fig. 7B) and stains and  
636 elongated pore-filling of iron oxyhydroxides point to prolonged oxidizing conditions,  
637 arising after the significant lowering of the RSL in which the bioconstruction organisms  
638 lived. Those materials are relatively late in the post-depositional history, as suggested  
639 by the fact that they fill narrow, sinuous and elongated pores, attributed to bioturbation  
640 of the intra-tube micrite filling; moreover, they are concentrated on the top of the  
641 bioconstruction. The supposed microbial mat in Pnh5 appears on the top of this iron  
642 oxyhydroxide cement, and is therefore even younger. In view of the flat laminar fabric,  
643 it is assumed to correspond to a smooth microbial mesostructure of tufa microbialite  
644 (e.g. Smith et al., 2011; Edwards et al., 2017; Garner et al., 2024) and to have therefore  
645 developed under inter- to supratidal conditions, with occasional influence from sea  
646 spray.

647 All impurities listed here are more common in vermetids than in barnacles, which may  
648 be related to the aragonitic composition of the former. They are also more difficult to  
649 avoid during sampling in vermetids, due to the small size of their tubules and the larger  
650 specific surface available for filling, cementation or adhesion by contaminants.  
651 Furthermore, as observed in this study, vermetids are more prone than barnacles to the  
652 formation of micritic envelopes, perhaps due to their aragonitic composition and/or  
653 because they compose the part most exposed to light in the bioconstructions studied,  
654 where they appear wrapped around *T. stalactifera*.

655 In view of that, the younger ages given by <sup>14</sup>C conventional dating of large vermetid  
656 bioconstruction samples can be, therefore, attributed to several factors, as  
657 cementation, carbonate neomorphism and late biofouling. Toniolo et al. (2020) alert  
658 that to obtain confident ages from vermetid samples is necessary to avoid  
659 contamination by cements and clay minerals containing organic matter from the  
660 samples. To get around this problem, they recommend, and adopt, the following  
661 succession of treatments: (a) clean the surface sample with a brush under flowing water,  
662 (b) immerse the sample in H<sub>2</sub>O<sub>2</sub>, 30 volumes, for at least 48 h, (c) disaggregate the

663 colonies mechanically, and (d) select fragments of vermetid shells under stereoscopic  
664 microscope.

665 However, even these selected vermetid shell fragments may still contain impurities. This  
666 happens because some of the impurities reported here in vermetid shells may be  
667 imperceptible to the hand lens or magnifying glass, and therefore impossible to avoid  
668 during collection. The micritic envelope is the most difficult to be detected, but micrite  
669 and microspar cement coatings, adhesion of bryozoans and microbial mats, as well as  
670 the presence of rootlets, may also be subtle and go unnoticed. Therefore, the use of  
671 bioconstructions as RSL indicators should ideally be accompanied or even preceded by  
672 analysis of thin sections under an optical microscope. The best solution is collection with  
673 visual control under a microscope in real time, using, for example, high-precision  
674 microdrills or micromills, with diameter of 100  $\mu\text{m}$  or smaller. Once the powder or  
675 particles have been collected by this or another method, the concentration of the  
676 vermetid's original aragonite by density (Araujo et al. 2021) can also be useful. This helps  
677 avoid the inclusion of particles rich in secondary calcite or other light impurities in the  
678 material to be dated.

679

## 680 **6. Conclusion**

681 Vermetid gastropods bioconstructions are a critical paleo-sea level indicator along many  
682 rocky shorelines globally, including the Brazilian coastline. We conclude that there are  
683 significant age discrepancies between radiocarbon ages derived from bulk vermetid  
684 bioconstruction remains and the shells of the different species that constitute the  
685 bioconstruction. The age difference is larger in older bioconstructions and implies a  
686 significant impact on the reliability of RSL curves built from samples dated by bulk  
687 vermetid remains. Consequently, ages of paleo-sea levels inferred from bulk vermetids  
688 remains and respective Holocene sea-level curves need revision. This revision is  
689 especially important for the Mid-Holocene ages, where the differences are larger. For  
690 example, the new species-specific radiocarbon ages presented here indicate that the  
691 the Holocene RSL was > 2m above present level around 7,000 cal aBP, while former  
692 works postulate that, at that time sea level was similar to the present one. More data  
693 are necessary to improve the accuracy of Holocene sea-level curves for the Brazilian  
694 coast, which are heavily based on ages of bulk vermetid bioconstructions.

695 We also conclude that to improve the Holocene paleo-sea levels ages, close inspection  
696 of samples is recommended to avoid carbonate neomorphism and contamination by  
697 other carbonate or carbonaceous materials such as cements, micrite envelope, rootlets  
698 and microbiofoulings.

699

## 700 **Acknowledgments**

701 We are grateful to the Brazilian Research Council (CNPq) for their financial support  
702 though projects numbers 557141/2009-5, 457714/2013-1, 307055/2013-2,  
703 442865/2015-5, 428341-2018-7, 443254/2019-2 and 403552/2024-9, as well as to  
704 Fundação de Amaro à Pesquisa no Estado de São Paulo (FAPESP, process 09/54232-4)  
705 and UK Research and Innovation (UKRI, grant NE/Y003187/1). RJA, PCFG and MCS are  
706 sponsored by CNPq fellowships (311837/2022-0, 304866/2022-9, 314836/2023-3) and

707 JASR by CAPES scholarship (88887.132637/2025-00). TFT was sponsored by CAPES and  
708 FAPESP (13/21941-8).

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## 710 **References**

711 Alessandretti, L., Giannini, P.C.F., Warren, L., Brückmann, M.P., Martini, A. 2023. Earth,  
712 wind and fire: Interactions between Quaternary environmental dynamics and  
713 human occupation on the southern coast of Brazil. *Quaternary Science Reviews*,  
714 301, p. 107950, 2023.

715 Angulo, R.J., 1989. Fossil vermetidae between latitudes 25°34'S and 27°09'S, state of  
716 Paraná and state of Santa Catarina, Brazil. *International Symposium on Global  
717 Changes in South America during Quaternary 1*:263-268. Special Publication.

718 Angulo, R.J., 1992. *Geologia da Planície Costeira do Estado do Paraná*. Ph.D. Thesis,  
719 Instituto de Geociências, Universidade de São Paulo, 332 p. (in Portuguese).

720 Angulo, R.J., 1993. Indicadores biológicos de paleoníveis marinhos quaternários na costa  
721 paranaense. *Boletim Paranaense de Geociências*, 41:1-34. (in Portuguese).

722 Angulo, R.J., Souza, M.C., 2014. Conceptual review of Quaternary coastal paleo-sea level  
723 indicators from Brazilian coast. *Quaternary and Environmental Geosciences*,  
724 5(2):1:32 (in Portuguese).

725 Angulo, R.J., Lessa, G.C., 1997. The Brazilian sea level curves: a critical review with  
726 emphasis on the curves from Paranaguá and Cananéia regions. *Mar. Geol.* 140:  
727 141-166.

728 Angulo, R.J., Giannini, P.C.F., Suguio, K., Pessenda, L.C.R., 1999. Relative sea-level  
729 changes in the last 5.500 years in southern Brazil (Laguna-Imbituba region, Santa  
730 Catarina state) based on vermetid 14C ages. *Marine Geology* 159, 323:339.

731 Angulo, R.J., Borzone, C.A., Noernberg, M.A., Quadros, C.J.L, Souza, M.C., Rosa, L.C.,  
732 2016. The State of Paraná beaches. In: Short A.D., Klein, A.H.F. (eds.) *Brazilian  
733 Beach Systems*. Coastal Research Library 17, Springer, Dordrecht, pp. 419-464.  
734 DOI 10.1007/978-3-319-30394-9\_16.

735 Angulo, R.J., Pessenda, L.C.R., de Souza, M.C., 2002. O significado das datações ao 14C  
736 na reconstrução de paleoníveis marinhos e na evolução das barreiras  
737 quaternárias do litoral paraense. *Rev. Bras. Geociências* 32:95-106 (in  
738 Portuguese).

739 Angulo, R.J., Lessa, G.C., Souza, M.C., 2006. A critical review of mid- to late-Holocene  
740 Sea-level fluctuations on the eastern Brazilian coastline. *Quaternary Science  
741 Reviews* 25:486–506.

742 Angulo, R.J., Lessa, G.C., Souza, M.C., 2009. The Holocene barrier systems of Paranaguá  
743 and northern Santa Catarina coasts, Southern Brazil. In: In: Dillenburg, S.R. &  
744 Hesp, P.A. ed. *Geology and Geomorphology of Holocene Coastal Barriers of  
745 Brazil*. Berlin – Heidelberg, Springer, p. 135-176.

746 Angulo, R.J., Souza, M.C., Campos, T.F.C., Bezerra, F.H.R., Fernandes, L.A., Giannini, P.  
747 C.F., Pitombo, F.B., Veiga, F.A., 2013a. Evidence for Late Quaternary episodic

- 748 uplift of the São Pedro and São Paulo Archipelago, Equatorial Atlantic.  
749 *Quaternary International* 317, 102–111.
- 750 Angulo, R.J., Souza, M.C., Fernandes, L.A., Disaró, S.T., 2013b. Quaternary sea-level  
751 changes and aeolianites in the Fernando de Noronha archipelago, northeastern  
752 Brazil. *Quaternary International* 305, 15–30.
- 753 Angulo, R.J.; Souza, M.C., Müller, M.E.J.; Noernberg M.A.; Oliveira L.H.S.; Soares C.R.;  
754 Borzone C.A.; Marone E.; Quadros C.J.L., 2018. Paraná. In: Muehe, D. (org.).  
755 *Panorama da erosão costeira no Brasil*, Ministério do Meio Ambiente, pp. 586-  
756 640 (in Portuguese).
- 757 Angulo, R.J., Souza, M.C., Giannini, P.C.F., Dillenburg, S.R., Barboza, E.G., Rosa, M.L.C. C.,  
758 Hesp, P.A., Pessenda, L.C.R., 2022a. Late-Holocene sea levels from vermetids and  
759 barnacles at Ponta do Papagaio, 27° 50'S latitude and a comparison with other  
760 sectors of southern Brazil. *Quaternary Science Reviews*, 286(202) 107536.
- 761 Angulo, R.J., Souza, M.C., Rosa, M.L.C.C., Barboza, E.G., Fernandes, L.A., Guedes, C.C.F.,  
762 Oliveira, L.H.S., Manzolli, R.P., Disaró, S.T., Ferreira, A.G., Martin, C.M., 2018b.  
763 Trindade. Quaternary sealevel changes and coastal evolution of the Island of  
764 Trindade, Brazil. *J. S. Am. Earth Sci.* 84, 208–222.
- 765 Angulo, R.J., Souza, M.C., Rosa, M.L.C.C., Barboza, E.G., Lessa, G.C., Pessenda, L.C.R.,  
766 Ferreira Júnior, A.L., 2022b. Late Mid- to Holocene sealevel changes at Abrolhos  
767 Archipelago and Bank, southwestern Atlantic. Brazil. *Marine Geology*, 450 (2022)  
768 106841.
- 769 Angulo, R.J., Souza, M.C., Rosa, M.L.C.C., Caron, F., Barboza, E.G., Costa, M.B., Macedo,  
770 E., Vital, H., Gomes, M.P., Garcia, K.B.L., 2022c. Paleo-sea levels, Late-Holocene  
771 evolution, and a new interpretation of the boulders at the Rocas Atoll,  
772 southeastern Equatorial Atlantic. *Marine Geology*, 447(2022) 106780.
- 773 Araujo, J.C., Macario, K.C.D., Moreira, V.N., dos Santos Passos, A., Jesus, P.B., Seoane,  
774 J.C.S., Dias, F.F. 2021 Bioindicators of sea-level fluctuations in southeastern  
775 Brazil: new data and methodological review. *Radiocarbon*. 63(4): 1149-1163.  
776 doi:10.1017/RDC.2021.50
- 777 Bathurst, R.G.C., 1966. Boring algae, micrite envelopes and lithification of molluscan  
778 biosparites. *Geol. J.* 5, 15–32.
- 779 Breves, A., Széchy, M.T.M., Lavrado, H.P., Junqueira, A.O., 2017. Abundance of the  
780 reefbuilding *Petalocochus varians* (Gastropoda: Vermetidae) on intertidal rocky  
781 shores at Ilha Grande Bay, southeastern Brazil. *An. Acad. Bras. Cienc.* 89 (2), 907–  
782 918.
- 783 Calvet, F., 1982. Constructive micrite envelope developed in vadose continental  
784 environment in Pleistocene eolianites of Mallorca (Spain). *Acta Geológica*  
785 *Hispanica* 17, 169–178.
- 786 Choquette, P.W., Pray, L., 1970. Geologic nomenclature and classification of porosity in  
787 sedimentary carbonates. *AAPG Bull.*, 54: 207-250.

- 788 Creel, R.C., Austermann, J., Kopp, R.E., Khan, N.S., Albrecht, T. and Kingslake, J., 2024.  
789 Global mean sea level likely higher than present during the holocene. *Nature*  
790 *communications*, 15, 10731.
- 791 Dominguez, J.M.L., 2009. The coastal zone of Brazil. In: Dillenburg, S.R. & Hesp, P.A.  
792 (orgs.) *Geology and Geomorphology of Holocene Coastal Barriers of Brazil*.  
793 *Lecture Notes in Earth Sciences*, vol. 107. Springer-Verlag, Berlin, pp. 17-51.
- 794 Donnarumma, L., D'Argenio, A., Sandulli, R., Russo, G.F., Chemello, R., 2021. Unmanned  
795 aerial vehicle technology to assess the state of threatened biogenic formations:  
796 The vermetid reefs of mediterranean intertidal rocky coasts. *Estuarine, Coastal*  
797 *and Shelf Science*, 251, 107228.
- 798 Edwards, M.J.K., Anderson, C.R., Perissinotto, R., Rishworth, G.M., 2017. Macro- and  
799 meso-fabric structures of peritidal tufa stromatolites along the Eastern Cape  
800 coast of South Africa. *Sediment. Geol.*, 359: 62–75,  
801 <https://doi.org/10.1016/j.sedgeo.2017.08.006>, 2017.
- 802 Flügel, E., 2010. *Microfacies of Carbonate Rocks: Analysis, Interpretation and*  
803 *Implications*, vol 2. Springer, Berlin
- 804 Garner, T.W., Andrew, J., Cooper G., Smith, A.M., Rishworth, G.M., Forbes, M., 2024.  
805 Reviews and syntheses: Tufa microbialites on rocky coasts – towards an  
806 integrated terminology. *Biogeosciences*, 21: 4785–4807.  
807 <https://doi.org/10.5194/bg-21-4785-2024>
- 808 Giannini, P.C.F., Sawakuchi, A.O., Martinho, C.T., Tatum, S.H., 2007. Eolian depositional  
809 episodes controlled by Late Quaternary relative sea level changes on the Laguna-  
810 Imbituba coast, South Brazil. *Marine Geology*, 237(2007): 143-168.
- 811 Giannini, P.C.F., Guedes, C.C.F., Nascimento, D.R. Jr., Tanaka, A.P.B., Angulo, R.J., Assine,  
812 M.L., Souza, M.C., 2009. Morphology and sedimentology of Ilha Comprida,  
813 southern São Paulo coast. In: Dillenburg, S.R. & Hesp, P.A. ed. *Geology and*  
814 *Geomorphology of Holocene Coastal Barriers of Brazil*. Berlin – Heidelberg,  
815 Springer, p.177-224.
- 816 Giannini, P.C.F., Villagran, Ximena S., Fornari, M., Nascimento Jr., D.R., Menezes, P.M.L.,  
817 Tanaka, A.P.B., Assunção, D., Deblasis, P., Amaral, P.G.C. 2010. Interações entre  
818 evolução sedimentar e ocupação humana na costa centro-sul de Santa Catarina,  
819 Brasil. *Boletim do Museu Paraense Emílio Goeldi. Ciências Humanas*, 5: 105-128.
- 820 Gvirtzman, G., Friedman, G.M., 1977. Sequence of progressive diagenesis in coral reefs.  
821 In: Frost, H., Weis, M.P., Saunders, J.B. (Eds.), *Reef and Related Carbonates:*  
822 *Ecology and Sedimentology*. *Studies in Geology AAPG*, pp. 357–380 No.4.
- 823 Heaton T.J., Köhler P., Butzin M., Bard E., Reimer R.W., Austin W.E.N., Bronk Ramsey C.,  
824 Hughen K.A., Kromer B., Reimer P.J., Adkins J., Burke A., Cook M.S., Olsen J.,  
825 Skinner L.C., 2020. Marine20-the marine radiocarbon age calibration curve (0-  
826 55,000 cal BP). *Radiocarbon* 62. doi: 10.1017/RDC.2020.68.
- 827 Hesp, P.A., Giannini, P.C.F., Martinho, C.T., Silva, G.M., Asp Neto N.E., 2009. The  
828 Holocene barrier system on the Santa Catarina coast, southern Brazil. In:  
829 Dillenburg, S.R. & Hesp, P.A. (orgs.) *Geology and Geomorphology of Holocene*

- 830 Coastal Barriers of Brazil. Lecture Notes in Earth Sciences, vol. 107. Springer-  
831 Verlag, Berlin, pp. 93-133.
- 832 Hood, A.V.S., Wallace M.W., 2012. Synsedimentary diagenesis in a Cryogenian reef  
833 complex: ubiquitous marine dolomite precipitation. *Sediment Geol.* 324: 12–31
- 834 Kempf M., Laborel J., 1968. Formations de vermetes et d'algues calcaires sur lês côtes  
835 du Brésil. *Recueil des Travaux de la Station Marine d'Endoume*, 59(43)325-435.
- 836 Kendall, C.G.S.C., Patrick, A., 1969. Holocene shallow-water carbonate and evaporate  
837 sediments of Khor al Bazam, Abu Dhabi, southwest Persian Gulf. *AAPG Bulletin*  
838 53, 841–869.
- 839 Kobluk, D.R., Risk, M.J., 1977. Micritization and carbonate-grain binding by endolithic  
840 algae. *AAPG Bull.* 61, 1069–1082.
- 841 Laborel J., 1969. Les pouplements de madréporaires des côtes tropicales du Brésil.  
842 *Annales de l'Universtité D'Abidjan, Serie EII Fascicule 3, Ecologie.* 261p.
- 843 Laborel, J., 1977. Are reef building vermetid disappearing in the South Atlantic? *Proc.*  
844 *Int. Coral Reef Symposium 3*, 233–237.
- 845 Laborel, J., 1979. Fixed marine organisms as biological indicator for the study of recent  
846 sea level and climatic variations along the Brazilian tropical coast. In: *Proceedings*  
847 *International Symposium on: Coastal Evolution in the Quaternary, Sao Paulo,*  
848 *1978. Proceedings, São Paulo, IGCP/Project 61, Instituto de Geociências.*  
849 *Universidade de São Paulo*, pp. 193–211.
- 850 Laborel, J., 1986. Vermetid gastropods as sea-level indicators. In: Van de Plassche, O.  
851 (Ed.), *Sea Level Research, a Manual for the Collection and Evaluation of Data.* 12.  
852 *Geo Books, Norwich*, pp. 281–310.
- 853 Laborel, J., Kempf M., 1966. Formação de vermetos e algas calcárias nas costas do Brasil.  
854 *Trabalhos do Instituto Oceanográfico da Universidade Federal de Pernambuco,*  
855 *7/8:33-50 (in Portuguese).*
- 856 Marone, E., Jamiyanaa, D. 1997. Tidal characteristics and a variable boundary numerical  
857 model for the M2 tide for the estuarine complex of the Bay of Paranaguá, PR,  
858 Brazil. *Nerítica*, 11(1-2):95-107.
- 859 Mineropar – Minerais do Paraná AS, 1989. Mapa geológico do Estado do Paraná.  
860 Departamento Nacional da Produção Mineral (DNPM), Brasília, 1map
- 861 Narchi, W., 1974. Functional morphology of *Petricola (Rupellaria) typica* (Bivalvia:  
862 *Petricolidae*). *Marine Biology*, 27:123-129.
- 863 Narchi, W., 1975. Functional morphology of a new *Petricola* (Mollusca Bivalvia) from the  
864 littoral of São Paulo, Brazil. In: *Proceedings of the Malacological Society of*  
865 *London*, 41(5):451-465.
- 866 Pardal, A., Martinez, A.S., Ciotti, Á.M., Christofolletti, R.A., Cordeiro, C.A., 2023.  
867 Macroecology of rocky intertidal benthic communities along the southwestern  
868 Atlantic: patterns of spatial variation and associations with natural and  
869 anthropogenic variables. *Marine environmental research*, 190, 106099.

- 870 Peres, J.M., Picard, J. 1964. Nouveau Manuel de bionomie benthique em Mer  
871 Méditerranée. Recueil des Travaux de Station Marine d'Endoume, 4, 1.
- 872 Perry, C.T., 1999. Biofilm-related calcification, sediment trapping and constructive  
873 micrite envelopes: a criterion for the recognition of ancient grass-bed  
874 environments? *Sedimentology* 46, 33–45.
- 875 Pianca, C., Mazzini, P.L.F., Siegle, E., 2010. Brazilian offshore wave climate based on  
876 NWW3 reanalysis. *Brazilian Journal of Oceanography* 58(1):53e70.
- 877 Picone, F., Chemello, R., 2023. Seascape characterization of a Mediterranean vermetid  
878 reef: a structural complexity assessment. *Frontiers in Marine Science*, 10,  
879 1134385.
- 880 Pittman, E.D., 1979. Porosity diagenesis and productive capability of sandstone  
881 reservoirs. In: Scholle, P. A. & Schluger, P.R. eds. *Aspects of Diagenesis*. Society  
882 Economic Paleontologists and Mineralogists Special Publication, 26, p. 159-173.
- 883 Powers, M.C., 1953. A new roundness scale for sedimentary particles. *Jour. Sedim.*  
884 *Petrol.*, 23: 117-119.
- 885 Reid, R.P., Macintyre, I.G., 1998. Carbonate neomorphism in shallow marine  
886 environments: a widespread diagenetic process forming micritized grains. *J.*  
887 *Sediment. Res.* 68, 928–946.
- 888 Reid, R.P., Macintyre, I.G., 2000. Microboring versus neomorphism: future insight into  
889 the micritization process. *J. Sediment. Res.* 70, 24–28.
- 890 Reid, R.P., Macintyre, I.G., Post, J.E., 1992. Micritized skeletal grains in northern Belize  
891 Lagoon; a major source of Mg-calcite mud. *J. Sediment. Res.* 62, 145–156.
- 892 Savazzi, E., 1996. Adaptations of vermetid and siliquariid gastropods. *Paleontology*  
893 39:157-177.
- 894 Scherer, M., 1974. Submarine recrystallization of a coral skeleton in a Holocene  
895 Bahamian reef. *Geology* 2, 499–500.
- 896 Scholle, P.A., Ulmer-Scholle, D.S., 2003. *A Color Guide to the Petrography of Carbonate*  
897 *Rocks: Grains, Textures, Porosity, Diagenesis*. Am Assoc Petrol Geol, Tulsa
- 898 Scuderi, D., 2012. A new species of *Petalocochus* Lea, 1843 from the Mediterranean  
899 Sea (Mollusca, Gastropoda, Vermetidae). *Biodiversity Journal*, 3(2): 123-128.  
900 <https://www.molluscabase.org/aphia.php?p=sourcedetails&id=164233>
- 901 Shennan, I., 2015. Handbook of sea-level research: framing research questions. In:  
902 Shennan, I., Long, A.J., Horton, B.P., (Eds.). *Handbook of Sea-level Research*, John  
903 Wiley & Sons, pp. 3-25.
- 904 Smith, A.M., Andrews, J.E., Uken, R., Thackeray, Z., Perissinotto, R., Leuci, R., Marca-Bell,  
905 A., 2011. Rock pool tufa stromatolites on a modern South African wave-cut  
906 platform: partial analogues for Archaean stromatolites? *Terra Nova*: 23, 375–  
907 381, <https://doi.org/10.1111/j.1365-3121.2011.01022.x>, 2011.
- 908 Spotorno-Oliveira, P., Tamega, F.T.S., Bemvenuti, C.E., 2012. An overview of the recent  
909 vermetids (Gastropoda: vermetidae) from Brazil. *Strombus* 19, 1e8.

- 910 Stephenson, T.A., Stephenson, A., 1949. The universal features of zonation between tide  
911 marks on rocky coasts. *Journal of Ecology*, 37(2):289-305.
- 912 Stuiver, M., Reimer, P.J., 1993. Extended 14C Data Base and Revised CALIB 3.0 14C Age  
913 Calibration Program. *Radiocarbon*, 35, 215-230. [https://doi.org/  
914 10.1017/S0033822200013904](https://doi.org/10.1017/S0033822200013904)
- 915 Toniolo, T.F., 2017. Vermetídeos Fósseis como Indicadores da Variação do Nível Relativo  
916 do Mar e de Possíveis Alterações na Circulação Costeira no Holoceno ao Longo  
917 do Litoral Brasileiro. Master Thesis, Instituto de Geociências, Universidade de  
918 São Paulo, 124 p. (in Portuguese).
- 919 Toniolo, T.F., Giannini, P.C.F., Angulo, R.J., Souza, M.C., Pessenda, L.C.R., Spotorno-  
920 Oliveira, P., 2020. Sea-level fall and coastal water cooling during the Late  
921 Holocene in southeastern Brazil based on vermetid bioconstructions. *Marine  
922 Geology*, 428, 106281.
- 923 Tsang, L.M., Chu, K.H., Achituv, Y., Chan, B.K.K., 2015. Molecular phylogeny of the acorn  
924 barnacle family Tetraclitidae (Cirripedia: Balanomorpha: Tetraclitoidea): Validity  
925 of shell morphology and arthropodal characteristics in the systematics of  
926 Tetraclitid barnacles. *Molecular Phylogenetics and Evolution* 82: 324–329.
- 927 Tucker, M.E., Wright, V.P., 1990. *Carbonate Sedimentology*. Blackwell, Oxford
- 928 Van-Andel, T.H., Laborel, J., 1964. Recent high relative sea level stand near Recife, Brazil.  
929 *Science* 145, 580e581.
- 930 Wentworth, C.K., 1922. A scale of grade and class terms for clastic sediments. *Journal of  
931 Geology*, 30: 377-392.
- 932 Wildner, W., Camozzato, E., Toniolo, J.A., Binotto, R.B., Iglesias, C.M.F., Laux, J.H., 2014.  
933 Mapa Geológico do Estado de Santa Catarina, Escala 1:500.000, CPRM, Porto  
934 Alegre, 2014.
- 935 Woodroffe, S.A., 2009. Testing models of mid to late Holocene sea-level change, North  
936 Queensland, Australia. *Quaternary Science Reviews*, 28: 2474-2488.