

# 1 Coral community changes in the Great Barrier Reef in 2 response to major environmental changes over glacial- 3 interglacial timescales

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## 16 17 18 19 20 **Abstract**

21  
22 The Ribbon Reef 5 borehole offers a unique record of reef growth spanning the entire history  
23 of the northern Great Barrier Reef (GBR). Previous studies have reported the main  
24 stratigraphical, lithological and chronological patterns, as well as basic descriptions of the  
25 coralgall assemblages, but no detailed coral community analysis was undertaken. We present  
26 a quantitative analysis of the nature and distribution of Pleistocene coral communities and  
27 apply several statistical tools to define recurrent coral associations and compare the eight  
28 reef-building cycles recognized throughout the evolution of the GBR. The start of significant  
29 reef building occurs at 137 m based on a major change in coral community structure and the  
30 inception of the reef cycles (Cy1-8). This revision, along with available stratigraphical and  
31 chronological data, suggests that barrier reef initiation may have occurred prior to MIS 11,  
32 earlier than previous reports. The coral assemblages at 137 m reflect the transition from lower  
33 mesophotic (60-100 m) to upper mesophotic (30-60 m) settings, while the eight reef cycles  
34 above are characterized by three recurrent shallow-water reef-coral associations: *Porites-*  
35 *Montipora-faviids* (Po-Mo-Fa), pocilloporids (Poc), and *Acropora-Isopora* (Acro-Iso). Typically,

36 these cycles begin with the Po-Mo-Fa association and end with the Acro-Iso association,  
37 reflecting shallowing and a catch-up growth mode. However, the first two cycles are  
38 characterized by a transitional phase dominated by the Poc association. The dominance of  
39 pocilloporids during the early stages of the GBR's history and the long-term shift to an  
40 *Acropora-Isopora*-dominated community may reflect an increase in competitive pressure of  
41 acroporids over pocilloporids. Our findings are consistent with the view that reef coral  
42 community structure is predictable over 100-kyr time scale. However, variations within reef  
43 cycles highlight the importance of environmental changes operating at millennial time scales.  
44 Further studies are needed to better refine the reef chronology and clarify the influence of  
45 environmental variables (i.e. sea surface temperature, turbidity) on reef coral community  
46 structure.

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## 58 **1. Introduction**

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Coral reef ecosystems are in decline worldwide (Bruno and Selig, 2007; Chin et al., 2011; De'ath et al., 2012; Jackson et al., 2014). The impact of local factors such as overfishing and pollution are compounded by the global influence of ocean warming and acidification on coral health and calcification potential (Hoegh-Guldberg, 2011). However, the decline of coral reef ecosystems is not uniform (Cinner et al., 2016) and future trends in reef community structure will depend on multiple factors, such as the intra- and interspecific adaptation potential of reef organisms, range shifts in coral species, and local anthropogenic factors like overfishing and coastal development (Pandolfi et al., 2011). Information on the responses of reef-corals exposed to environmental stressors such as elevated sea surface temperature (SST), reduced pH or high sedimentation rate can be obtained from in vivo experiments involving single coral colonies (e.g. Hoadley et al., 2015; Ganase et al., 2016) or, less commonly, a portion of a reef (Dove et al., 2013; Albright et al., 2016). Large-scale reef monitoring informs us on the current impact of global climate change and other factors as well as on the recent (few decades) history of coral reef ecosystems (e.g. Connell et al., 1997; Bak

74 et al., 2005; De'ath et al., 2012). These approaches are essential to our understanding of the  
75 susceptibility of reefs and reef communities to ongoing environmental perturbations. However,  
76 coral reef ecosystems are long-lived and crucial information about their long-term history and  
77 responses under various natural perturbations and environmental boundary conditions may  
78 be derived from the fossil record. Valuable information on the responses of coral communities  
79 to rapid environmental changes has been obtained from the study of Quaternary coral reef  
80 systems (Pandolfi and Greenstein, 2007; Camoin and Webster, 2015; Braithwaite, 2016). Of  
81 particular interest are the periods of rapid warming and sea level rise leading to interglacial  
82 highstands because these conditions may mimic those which coral reef ecosystems are  
83 experiencing today. Studies of fossil reefs provide important insights into the responses of  
84 coral reef ecosystems to sea level and climate changes (Woodroffe and Webster, 2014;  
85 Kiessling and Pandolfi, 2014). The Holocene and Last Interglacial records are the best  
86 documented and most extensively studied of Quaternary reef-building episodes, and  
87 improving our knowledge of older reef sequences stands as one of the major challenges of  
88 fossil reef studies (Camoin and Webster, 2015).

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90 The Great Barrier Reef (GBR) is a passive margin and pre-Holocene reef limestones  
91 are not normally exposed at the surface (Hopley et al., 2007). Drilling is therefore necessary  
92 to study the history of reef growth and reef communities. Accumulation of reef limestones on  
93 the continental shelf occurred during interglacial periods when sea level was high enough to  
94 flood the shelf (Hopley et al., 2007; Davies, 2011). Reef growth there was consequently  
95 interrupted by sea level falls during glacial periods and became restricted to a narrow band  
96 along the shelf edge during sea level lowstands (Hopley et al., 2007; Davies, 2011). IODP  
97 Expedition 325 drilling into the submerged terraces and ridges off the modern GBR (Fig 1),  
98 combined with site survey data (Hinestrosa et al., 2016), uncovered multigenerational reef  
99 sequences developed during glacial sea level lowstands and subsequent deglacial sea level  
100 rises (Webster et al., 2011).

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102 Few boreholes have penetrated the entire section of reef limestones deposited on  
103 the continental shelf during previous sea level highstands. The earliest, deep drilling  
104 operations were undertaken by the Great Barrier Reef Committee in 1926 at Michaelmas Cay  
105 (183 m) in the northern GBR and in 1937 at Heron Island (223 m) in the southern GBR. A  
106 petroleum exploration well was drilled at Wreck Island in 1958 (575 m) in the southern GBR  
107 (Davies, 2011). The thickness of the entire reef section in these boreholes is interpreted to be  
108 < 150 m but core recovery was poor. Two additional long, high quality boreholes were drilled  
109 in 1995, one at Ribbon Reef 5 (210 m) and the other at Boulder Reef (86 m), in the northern  
110 GBR (Alexander et al., 2001). Ribbon Reef 5 lies near the shelf edge facing the open ocean  
111 (outer-shelf reef) whereas Boulder Reef is close to the land and influenced by terrigenous

112 sedimentation (inner-shelf reef). These reefs lie, respectively, at opposite ends of the cross-  
113 shelf gradient in wave energy and turbidity, and are characterized by distinct coral  
114 communities (Done, 1982) (Fig. 1).

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116 The relationship between the rate of vertical seafloor displacement (uplift vs.  
117 subsidence) and eustatic sea level change controls the relative position of successive reef  
118 sequences (Woodroffe and Webster, 2014). In relatively stable depositional settings such as  
119 the GBR, the resulting geometry of multigenerational reef sequences is a vertical succession  
120 of stacked reefs, each formed during a sea level highstand, bounded by low sea level erosion  
121 surfaces (Davies et al., 1988, 1989). The erosion of the windward margin during sea level  
122 lowstands may result in the retrogradation of successive highstand reef sequences (Davies et  
123 al., 1988, 1989; Webster, 1999). The highstand stack model of reef development explains the  
124 recurrence of shallow coralgall assemblages in the Ribbon Reef 5 cores (Webster and Davies,  
125 2003). Similar successions of stacked Pleistocene reef units have been described in various  
126 other locations, for example, at Eniwetok Atoll (Szabo et al., 1985), Mururoa Atoll (Camoïn et  
127 al., 2001), the Ryukyu Islands (Sagawa et al., 2001), New Caledonia (Cabioch et al., 2008),  
128 the Florida Keys (Multer et al., 2002) and Belize (Gischler, 2007).

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130 Previously, only two basic coral assemblages were described in the Ribbon Reef 5  
131 borehole (Webster, 1999; Webster and Davies, 2003). One characterized by *Isopora* and  
132 robust branching *Acropora* spp. (*humilis* gr. and *robusta* gr.), the other composed of massive  
133 *Porites* and faviids associated with encrusting *Porites* and *Montipora*. Webster and Davies  
134 (2003) interpreted these coral assemblages as representative of higher- and lower-energy  
135 reef settings, respectively. The recurrence of apparently similar coral assemblages in the  
136 Ribbon Reef borehole over at least 400 ka is consistent with detailed paleoecological studies  
137 of uplifted Pleistocene reef terraces at Barbados (Jackson, 1992; Pandolfi and Jackson, 2006),  
138 Huon Peninsula (Pandolfi, 1996, 1999), and, more recently, Egypt and Vanuatu (Mewis, 2016)  
139 reporting the repetition of similar coral assemblages over multiple sea level highstands. These  
140 observations suggest a remarkable persistence in coral community structure over geological  
141 timescales of 10s to 100s kyr despite repeated sea level falls and major changes in SST  
142 (Pandolfi, 1996; Pandolfi, 2002). The predictable nature of reef coral assemblages may result  
143 from the high degree of ecological dependence of reef organisms due to their complex  
144 interactions (e.g. competition, predation, and symbiosis), use of available resources, and  
145 occupation (and re-occupation) of distinct habitats (Pandolfi, 1996; Bode et al., 2012).  
146 However, variability in coral species composition and diversity over glacial-interglacial  
147 timescales may arise from species migration related to elevated SST. Several studies have  
148 presented evidence for latitudinal variations in coral species distribution related to elevated  
149 SST occurring during the last interglacial (western Australia, Greenstein and Pandolfi, 2008;

150 at a global scale, Kiessling et al., 2012), the mid-Holocene (Florida, Precht and Aronson, 2004),  
151 and in recent times (Japan, Yamano et al., 2011; Florida, Vargas-Angel et al., 2003; and  
152 eastern Australia, Baird et al., 2012). Variability in reef-coral community structure also occurred  
153 at a broader timescale during the Quaternary, with the abundance of *Acropora* increasing  
154 markedly after the Pliocene to become the dominant reef-building coral worldwide during the  
155 Middle Pleistocene (Renema et al., 2016). Fast growth rates and asexual reproduction via  
156 fragmentation are attributes of the genus *Acropora* which make this coral particularly suitable  
157 to track rapid Quaternary sea level changes (Renema et al., 2016). In addition, changes in  
158 ocean surface circulation affecting larval dispersion and genetic connectivity of coral  
159 populations during the Quaternary have been proposed as a key factor controlling the  
160 distribution of reef-coral species (Veron, 1995).

161

162 The Ribbon Reef 5 borehole represents a rare archive of the long-term evolution of  
163 coral assemblages in the GBR during successive sea level highstands since the inception of  
164 reef growth in the Middle Pleistocene (for a recent review, see Davies, 2011). Until now the  
165 published taxonomic information was largely qualitative and intended only to highlight basic  
166 trends in taxonomic composition (Webster and Davies, 2003). A more quantitative analysis is  
167 needed to assess the taxonomic similarity of successive coral assemblages and verify the  
168 hypothesis that coral communities have highly predictable taxonomic compositions during  
169 successive interglacial cycles. In this study we present a detailed analysis of the nature and  
170 distribution of coral taxa in the Ribbon Reef 5 borehole based on a new and more  
171 comprehensive taxonomic census. Several statistical approaches are used to identify  
172 objectively the nature of recurrent coral assemblages with similar taxonomic compositions and  
173 reconstruct the history of coral community changes at Ribbon Reef 5 since the inception of  
174 the reef system. We discuss our new results within the context of previously published trends  
175 in taxonomic composition and depositional units described in Webster and Davies (2003) and  
176 the depositional units described in Braithwaite et al. (2004) and Braithwaite and Montaggioni  
177 (2009). Finally, we discuss the implications of our results for understanding the response of  
178 coral communities to individual glacio-eustatic cycles, from the colonization of bare substrate  
179 during shelf inundation to reef demise caused by sea level fall, and coral assembly rules at  
180 the scale of the whole history of the GBR during multiple glacio-eustatic cycles.

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## 182 **2. Material and methods**

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184 Ribbon Reef 5 is about 6.5 km long and 0.7–1 km wide (Fig. 1). It is one of many  
185 ribbon reefs in the northern Great Barrier Reef that form a 700 km long ridge interrupted only  
186 by narrow channels and forming an impressive shelf-edge barrier reef directly exposed to the  
187 swells of the Pacific Ocean (Hopley et al., 2007).

188

189           The Ribbon Reef 5 borehole (15° 22.40' S, 145° 47.149' E) is 210 m long and the  
190 recovery is 76% on average, although recoveries of 95% were common in the lower part of  
191 the main reef section (Webster, 1999; Webster and Davies, 2003). The maximum length of a  
192 core section recovered during one drill is 3 m. A total of 125 core sections (B1-B125) were  
193 drilled with an average length of 1.68 m (Fig. 2A, B).

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195           Three main sections have been recognized in previous publications (Fig. 2C): a basal  
196 lower section composed of grainstones and packstones (210–158 m), a middle section rich in  
197 rhodoliths (158–96 m), and an upper section composed of in situ reef framework (96–0 m)  
198 (Alexander et al., 2001; boundaries revised by Webster and Davies, 2003). Webster and  
199 Davies (2003) defined 6 reef units in the upper section (R1-R6) based on variations in coralgal  
200 assemblages, the occurrence of soil horizons and stable isotope (O, C) data (Fig. 2D-F).  
201 Two additional reef units (R7-R8) were identified within the middle section. Braithwaite et al.  
202 (2004) divided the same borehole into 9 depositional units based on changes in lithology,  
203 diagenetic features, and stable isotope data (Fig. 2G-J); evidence of emergence (erosional  
204 surface, paleosoil) was reported between unit 6, 7, 8 and 9 in the upper section of the borehole.  
205 The unit boundaries defined by Braithwaite et al. (2004) do not match those of Webster and  
206 Davies (2003) except for the base of the uppermost Holocene unit at 16 m (R1 in Webster and  
207 Davies, 2003; unit 9 in Braithwaite et al., 2004). The criteria used to define stratigraphic units  
208 in each publication are detailed in Table 1. The diagenetic history of the borehole was  
209 reconstructed by Braithwaite and Montaggioni (2009). Their study confirmed the correlation  
210 between the nature and diversity of diagenetic features and the unit boundaries defined by  
211 Braithwaite et al. (2004). Moreover, they found evidence for an additional erosional surface  
212 within unit 6 (after Braithwaite et al. (2004)) and therefore defined two new units, i.e. 6a and  
213 6b. Despite considerable age uncertainties, radiometric dating suggests that the main reef  
214 section was probably accreted during the Middle Pleistocene <500 ka (MIS 13) and the lower  
215 section could be as old as 700 ka (MIS 17) (Webster and Davies, 2003; Braithwaite et al.,  
216 2004; Braithwaite and Montaggioni, 2009; Fig. 2K). Paleomagnetic data constrain the age of  
217 the entire borehole to within the Bruhnes chron (<780 ka, Braithwaite et al., 2004).

218

219           In the present study we reexamined the distribution, taxonomy and morphology of  
220 reef corals (Scleractinia) in the borehole. A total of 1332 corals were recorded. Each was  
221 categorized as either in situ (IS), probably in situ (IS?), not in situ (ISX), or context unknown  
222 (ISN) (Webster et al., 2011). A combination of criteria was used to determine the context of fossil  
223 corals: (1) the overall orientation of the corallum (orientation of surface projections, branches),  
224 (2) the orientation of corallites, (3) the presence of thicker algal crusts on the upper surface of  
225 the corallum, (4) the absence of evidence of transport (abraded or broken surfaces), (5) the

226 orientation of geopetal surfaces, and (6) the depositional setting (slumps, rubble) (Webster et  
227 al., 2011). Of all the corals examined, about 60% were tagged as ISX. The taxonomy of corals  
228 follows Veron (2000) except for *Isopora* which is treated as a genus (Wallace et al., 2007).  
229 Corals were identified at the species level whenever possible, but the identification was more  
230 often achieved at the genus level due to the obscuring of surface features by sediments or  
231 encrusters, or the lack of preservation. Species groups were defined for corals belonging to  
232 different species within the same genus that cannot be differentiated because they display  
233 close morphological affinities (e.g. *Favia* gr. *pallida* includes *F. pallida*, *F. speciosa*, and *F.*  
234 *matthaii*). For 17% of the corals examined, no taxonomic identification was possible; 84% of  
235 these unidentified corals are ISX corals. The following morphological traits were quantified:  
236 colony thickness, corallite width and branch width. Colonies attached to the substrate less  
237 than 5 cm in thickness are categorized as encrusting; the others are described as massive.  
238 Branch width is used to classify branching corals into the following three categories: fine-  
239 branching (BF, <1 cm), medium-branching (BM, 1-1.5 cm), and robust-branching (BR, >1.5  
240 cm). Additionally the maximum thickness of coralline algal crusts was also measured.

241

242 In order to investigate the variations of coral taxonomic composition in the borehole  
243 and identify recurrent coral associations, we compared the taxonomic composition of the core  
244 sections using cluster analysis of the Bray-Curtis similarity (BC) coefficient calculated for each  
245 pair of core sections. The analysis was performed on presence-absence data and on  
246 abundance data for both the in situ (corals tagged IS and IS?) and non in situ (corals tagged  
247 ISX) fraction. The few corals for which the context was described as uncertain (ISN) were  
248 considered likely to be not in situ and were added into the list of non in situ corals (ISX). For  
249 the analysis involving abundance data, the BC coefficient was calculated using the square  
250 root of abundance values in order to mitigate the influence of taxa with high count numbers  
251 (Perry et al., 2008; Roche et al., 2011). The analysis performed on in situ corals involved the  
252 comparison of the distribution of 37 taxa across 75 core sections. For the analysis of ISX  
253 corals, the data matrix is composed of 21 taxa and 114 core sections. The lower number of  
254 taxa in the analysis of the ISX fraction results from the overall lower resolution of the taxonomic  
255 identification of allochthonous corals due to their poorer state of preservation. The results of  
256 these analyses enable us to identify any regularity in the sequence of corals observed in the  
257 borehole and highlight stratigraphic intervals displaying recurrent coral associations. 2-D MDS  
258 ordination of BC coefficients and analyses of similarities (ANOSIM test) are used to assess  
259 differences in taxonomic composition between these stratigraphic intervals. A similarity  
260 percentage analysis (SIMPER) is conducted to constrain the identity of taxa that are  
261 characteristic of the recurrent coral associations. Statistical analyses were performed using  
262 the computer software PRIMER v6 (Clarke and Gorley, 2006).

263

264 **3. Results**

265

266 The reexamination of the Ribbon Reef 5 borehole led to the identification of 58  
267 species or species groups of scleractinian corals under 34 genera (Table 2, S1). Three  
268 additional genera of non-scleractinian corals have also been identified (*Tubipora*, *Millepora*  
269 and *Sinularia?*). The majority of in situ corals identified belong to *Acropora*, *Isopora*, *Montipora*,  
270 *Porites*, faviids and pocilloporids. There is a clear inflection point in the cumulative number of  
271 in situ corals identified in the borehole as a function of depth at around 120-125 m (Fig. 3).  
272 The thickness of in situ coral colonies and coralline algal crusts increases steadily in the lower  
273 half of the borehole, reaching a first maximum around 117 m and 132 m, respectively, and  
274 then shows large fluctuations (Fig. 4A,C). Upcore trends in colony thickness vary among coral  
275 genera. Faviids display a broadly decreasing trend in colony thickness at the scale of the  
276 borehole (Fig. 4A). The thickness of *Porites* and *Montipora* colonies is highly variable unlike  
277 that of *Acropora* and *Isopora* colonies (Fig. 4A). In addition, acroporids with robust-size  
278 branches become common above 130 m and increase in frequency toward the borehole top  
279 (Fig. 4B).

280

281 3.1. Analysis of in situ (IS, IS?) corals

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283 3.1.1 Comparison of core sections

284

285 Cluster analysis of the BC coefficient calculated between each pair of core sections  
286 using presence-absence data produces 15 clusters (G1-G15) and two isolated core sections  
287 (54, 106) (Fig. 5A). These groups can be characterized by the systematic occurrence of one  
288 or a combination of the following taxa: *Acropora*, *Isopora*, encrusting and massive *Porites*,  
289 encrusting and massive *Montipora*, pocilloporids, and faviids (Fig. 5B). A large cluster defined  
290 by the association of encrusting *Porites* and *Montipora* (G12) can be further subdivided into 5  
291 groups of core sections (a-e) and 1 isolated core section (41). Similar results are obtained  
292 using the same analysis based on abundance data (Figs S2 and S3).

293

294 There is a dramatic change in coral assemblage composition at around 137 m (Fig.  
295 6A). Below that limit, the proportion of in situ corals is low and the coral assemblages are  
296 characterized by *Galaxea* (106), *Goniastrea* (G9), foliaceous pectiniids (most likely  
297 *Echinophyllia*, G2), encrusting *Porites* and/or *Montipora* (G11, G14, G7). Above that limit, the  
298 number of in situ corals increases sharply, and so does the diversity of coral assemblages.  
299 The sequence of coral assemblages above 137 m is complex and characterized by a high  
300 variability in composition at the scale of the core section. However, there is a cyclic pattern  
301 that is overprinted on this apparent complexity (Fig. 6B). This cycle is defined by repeated



302 intervals devoid of *Acropora* and characterized by encrusting and massive *Porites*, encrusting  
303 *Montipora*, and diverse faviids (mainly G12e). These intervals are systematically followed by  
304 intervals enriched in *Acropora* and/or *Isopora* (G5, G3, G12b, G12c and G12d). The transition  
305 is in places marked by the occurrence of a pocilloporid-rich interval (mainly G4). We therefore  
306 conclude that one complete cycle is defined by the following succession of coral associations:  
307 a *Porites-Montipora-faviids* association (Po-Mo-Fa), a pocilloporid association (Poc), and an  
308 *Acropora-Isopora* association (Acro-Iso) (Fig. 6A, B). We identify 8 cycles in total based on  
309 these recurrent shifts in composition (Cy1-Cy8) overlying the lower unit (Lw) (Fig. 6B). Two of  
310 these cycles (Cy8 and Cy7) are composed of all three coral associations. The Poc association  
311 is missing in 4 cycles (Cy6, Cy5, Cy4 and Cy1) and its presence at the base of Cy2 is uncertain  
312 due to the sparse occurrences of pocilloporids in this interval. The Po-Mo-Fa association is  
313 only absent in Cy3 (and perhaps Cy2), and is poorly developed in Cy8. Interestingly, the Po-  
314 Mo-Fa interval is thickest in Cy7 and becomes progressively thinner in subsequent cycles.  
315 *Leptoseris* occurs at the base of the Po-Mo-Fa interval in Cy7 and Cy6 and coexists with  
316 *Pachyseris speciosa* in Cy7. The Po-Mo-Fa interval in Cy6 also contains several colonies of  
317 *Galaxea astreata*. Massive *Isopora* occurs in the Po-Mo-Fa interval in Cy4 only. The Poc  
318 intervals in Cy7 and Cy6 are well developed and characterized mostly by *Stylophora*, in  
319 association with *Seriatopora* and an *Echinopora*-rich assemblage (G13) in Cy6. The Poc  
320 association at the base of Cy3 is also composed of *Stylophora*. The species composition of  
321 *Acropora* in the Acro-Iso association is variable from one cycle to another and includes the  
322 following major taxonomic groups: *A. gr. humilis*, *A. gr. robusta?*, *A. gr. formosa* and various  
323 fine-branching morphological groups (corymbose, digitate, arborescent and platy). *Isopora*  
324 colonies display encrusting, massive or robust-branching growth forms. *Acropora* and *Isopora*  
325 may coexist or else may appear in sequence. In two cycles, Cy4 and Cy6, the shift from  
326 *Isopora*- to *Acropora*-dominated assemblages is particularly clear. The Acro-Iso association  
327 includes *Porites* and *Montipora* as well as diverse faviids in Cy6, Cy4 and Cy1.

328

329 In summary, comparison of the taxonomic compositions of core sections shows (1)  
330 high variability in taxonomic composition from one core to the next, (2) a regular pattern of  
331 taxonomic composition at the scale of several core sections characterized by the repetition of  
332 three main coral associations (Po-Mo-Fa, Poc and Acro-Iso), and (3) two main units at the  
333 scale of the whole borehole – a non-reefal unit with low density, mostly encrusting or  
334 foliaceous coral assemblages changing at around 137 m to a reefal unit with high-density,  
335 high-diversity coral assemblages displaying cyclicities in taxonomic composition.

336

### 337 3.1.2. Comparison of reef cycles (Cy1-Cy8) and the lower unit (Lw)

338

339 Cluster analysis of the BC coefficient calculated between each pair of cycles using

340 presence-absence data reveals two clusters: cluster 1 composed of cycles Cy8, Cy3 and Cy2,  
341 and cluster 2 composed of cycles Cy4, Cy5, Cy6 and Cy7 (Fig. 7A). The 2D MDS plot clearly  
342 shows the two groups of data points occupying distinct regions of space (Fig. 7B). The  
343 difference in taxonomic composition between clusters 1 and 2 is confirmed by the ANOSIM  
344 test which gives an  $R$  value of +0.80 ( $p=2.9\%$ ). The average BC similarities of the cycles in  
345 clusters 1 and 2 are 61.9% and 66.5%, respectively (Fig. 7C). The taxonomic diversity of the  
346 cycles in cluster 1 is lower than that of those in cluster 2. The SIMPER analysis shows that  
347 cluster 1 is characterized by robust-branching *Acropora*, encrusting and massive *Porites*, and  
348 *Stylophora*, whereas cluster 2 is defined by medium-branching *Acropora*, encrusting to  
349 massive *Isopora*, encrusting to massive *Porites* and *Montipora*, *Stylophora*, *Favia*, and  
350 pectiniids (mainly *Echinophyllia*) (Table 3A). Cy1 is more closely related to cluster 2 than  
351 cluster 1 and the lower unit of the borehole (Lw) is clearly distinct from the reef cycles based  
352 on presence-absence data.

353

354 Cluster analysis based on the square root of abundance data provides a slightly  
355 different result. The same cluster 2 is produced but Cy2 is grouped with Cy1 instead of with  
356 Cy3 and Cy8. Cycles Cy1 and Cy2 have in common the following taxa: fine-branching  
357 *Acropora*, encrusting to massive *Porites* and *Montipora*, and *Favites*. The lower unit (Lw) is  
358 grouped with Cy1 and Cy2 due to similarities in abundances of encrusting *Montipora*, and  
359 encrusting and massive *Porites*.

360

### 361 3.1.3. Comparison of coral associations (Po-Mo-Fa, Poc and Acro-Iso)

362

363 Cluster analysis and 2D MDS ordination of BC similarities were also used to compare  
364 the taxonomic compositions of the three coral associations (Po-Mo-Fa, Poc and Acro-Iso)  
365 among reef cycles and with the lower unit (Lw). The clustering reflects the separation between  
366 the three previously identified coral associations (Fig. 8A). Cluster 1 is composed of two of the  
367 four Poc intervals, and clusters 2 and 3 mostly include Po-Mo-Fa and Acro-Iso intervals,  
368 respectively. However, there is some overlap as the clustering is not entirely determined by  
369 the type of association to which each interval is assigned. The 2D MDS plot also shows that  
370 the three associations define three overlapping domains (Fig. 8B). The ANOSIM test suggests  
371 there is a significant difference in taxonomic composition between the three coral associations  
372 ( $R = +0.34$ ). The SIMPER analysis highlights the corals that are the most representative of  
373 each association and the results are entirely consistent with the description presented above  
374 (Table 3B). Massive to encrusting *Porites* and encrusting *Montipora* are characteristic of both  
375 associations Po-Mo-Fa and Acro-Iso but the latter is distinguished primarily by the presence  
376 of diverse *Acropora* species. *Stylophora* is indicative of the Poc association. The average BC  
377 similarities of the intervals within each association are widely different, i.e. 50.3%, 37.7% and

378 23.2% for associations Acro-Iso, Po-Mo-Fa and Poc, respectively (Fig. 8C). This variability is  
379 illustrated by the spread of the data points associated with each domain in the 2D MDS plot.  
380 The association Acro-Iso displays the compositions that are the most consistent among  
381 different stratigraphic intervals. The composition of the lower unit (Lw) is most similar to that  
382 of the Po-Mo-Fa association of Cy6.

383

384 The separation between the three coral associations is less clear when the square  
385 root of abundance data is used for cluster analysis. This is mostly due to the influence of  
386 encrusting *Porites* and *Montipora* which can be equally abundant in intervals assigned to  
387 different coral associations so that these intervals are more closely related in the cluster  
388 diagram when abundance data are used.

389

### 390 3.2. Analysis of non-in situ (ISX) corals

391

392 The number and proportion of non-in situ corals is largest in the lower unit of the borehole  
393 below 137 m. The proportion of non-in situ corals that could be identified is lower than in the  
394 in situ fraction because non-in situ corals have commonly undergone some degree of physical  
395 alteration that tends to reduce the size of individual specimens and erase morphological  
396 details. The taxonomic composition of the non-in situ fraction is clearly dominated by *Acropora*  
397 and pocilloporids. Together these taxa represent 37-84% of the number of ISX corals identified  
398 in each cycle.

399

400 Cluster analysis of the BC coefficient calculated between each pair of core sections  
401 using presence-absence data for the ISX fraction leads to the segregation of 12 groups (Fig.  
402 9). The occurrence of *Acropora* or pocilloporids together or separately clearly determines the  
403 clustering of most of the core sections. For example the large cluster G7 is defined primarily  
404 by the association of *Acropora* and pocilloporids whereas G11 is defined on the basis of the  
405 absence of all taxa but *Acropora*. Like the in situ corals, the composition of the lower detrital  
406 unit is distinct from that of the overlying reefal unit. The ISX coral fraction in the lower unit is  
407 characterized by pocilloporids, encrusting *Porites* and *Montipora*, and lesser agariciids (mostly  
408 *Leptoseris*) and pectiniids (mostly *Echinophyllia*) (Fig. 10). The main difference with the in situ  
409 fraction is the abundance of pocilloporids and agariciids. Interestingly, there is a difference in  
410 the generic composition of pocilloporids in the ISX fraction between the lower and upper unit:  
411 *Seriatopora* occurs more consistently in core sections of the lower unit whereas *Stylophora*  
412 and *Pocillopora* are generally dominant in the overlying reefal unit (with the notable exception  
413 of Cy7) (Fig. 10). There is also a significant increase in the frequency of occurrence and  
414 relative abundance of *Acropora* and pocilloporids in the reefal unit and most of the ISX coral  
415 assemblages defined by cluster analysis occurring in the main reefal unit are characterized by

416 a combination of pocilloporids and *Acropora* (Figs. 9, 10).

417

418 The cyclic pattern observed in the reefal unit above 137 m is not clearly reflected in  
419 the ISX fraction. However, there are variations in the ISX fraction that coincide with changes  
420 in the compositions of in situ corals. The transition between the Po-Mo-Fa and Poc  
421 associations in Cy8 and Cy7 coincides with an increase in the abundance of pocilloporids in  
422 the ISX fraction (Fig. 10). In addition, the Po-Mo-Fa intervals in Cy7 and Cy6 correlate with a  
423 marked increase in the abundance of non-in situ *Porites* and/or *Montipora* (Fig. 10).

424

#### 425 **4. Discussion**

426

##### 427 4.1. Long-term trends in coral community structure

428

429 Variations in the abundance, taxonomy and morphology of in situ corals in the Ribbon  
430 Reef 5 borehole indicate a general shallowing upward trend and a transition from a relatively  
431 deep, non-reefal setting to cycles of reef growth and demise, in agreement with previously  
432 published works (Alexander et al., 2001; Webster and Davies, 2003; Braithwaite et al., 2004;  
433 Braga and Aguirre, 2004). We identify the start of the major reef-building processes at 137 m  
434 based on: (1) a significant change in coral community structure and, (2) the inception of a  
435 cyclic pattern in coral succession which characterizes the upper part of the borehole. This  
436 boundary corresponds with the base of the first reef unit (i.e. R8) originally described in  
437 Webster and Davies (2003).

438

439 The in situ coral assemblage below 162 m is dominated by thin laminar *Porites*,  
440 *Montipora* and *Echinophyllia*, also occurring in the non in situ fraction with *Leptoseris*. The  
441 taxonomy and morphology of these corals and their association with Melobesoid algae (Braga  
442 and Aguirre, 2004) suggest a depositional setting deeper than 60 m (Abbey et al., 2013). Fine  
443 branching *Seriatopora* is common among coral clasts and could be derived from the upper  
444 mesophotic zone (30-60 m). *Seriatopora* is currently found down to 55 m in the GBR (Bridge  
445 et al., 2012) and forms dense populations in the upper mesophotic zone in the Ryukyu Islands  
446 (Sinniger et al., 2013; Sinniger, 2016). The transition at 162 m to recurrent Lithophylloid-rich  
447 intervals coincides with a marked increase in coral colony thickness (Fig. 4). Abbey et al.  
448 (2013) reported a similar shift in coral thickness at 60 m in the GBR with modern and  
449 postglacial mesophotic corals primarily thin platy to encrusting (less than 2 cm in thickness)  
450 below 60 m and more massive above 60 m. In addition, faviids, particularly *Echinopora*,  
451 become more common in the ISX fraction above 162 m in the Ribbon Reef 5 borehole. Faviids,  
452 in particular *Echinopora*, were reported in the mesophotic zone from depths <60 m by Abbey  
453 et al. (2013). In conclusion, the coralgal assemblages in the lower section of the Ribbon Reef

454 5 borehole are similar to the mesophotic coralgall communities of the modern GBR and the  
455 evolution in taxonomic and morphological composition indicates the transition from a lower  
456 mesophotic (60-100 m) to an upper mesophotic (30-60 m) coralgall assemblage.

457

458 Above 137 m the thicknesses of corals and algae and the numbers and diversity of  
459 corals increase sharply. The 137 m boundary also marks a sharp increase in the abundance  
460 of branching *Isopora* and *Acropora* species (Figs. 4, 11), two major components of modern  
461 shallow exposed reef crest communities of outer shelf reefs in the GBR (Done, 1982). The  
462 evolution of coralgall assemblages in the Ribbon Reef 5 borehole clearly indicates a general  
463 shallowing trend initiated in the lower section (Webster and Davies, 2003; Braga and Aguirre,  
464 2004). The Ribbon Reef 5 record suggests that *Isopora* and *Acropora* were important  
465 contributors to the reef-building process from the beginning of the reef growth history since  
466 the Acro-Iso association is present in the initial cycle (Cy8) and was reestablished during each  
467 subsequent cycle. This observation is in line with a recent compilation showing that *Acropora*  
468 became a dominant reef builder during the Middle Pleistocene, and this success has been  
469 attributed to the ability of *Acropora* to cope with rapid sea level rise (Renema et al., 2016). In  
470 the modern GBR *Isopora* is closely associated with *Acropora* in wave-exposed habitats (Done,  
471 1982) and our record shows that this was also the case during the past 3-5 interglacial  
472 highstands (Webster, 1999; Braithwaite and Montaggioni, 2009), indicating that these two taxa  
473 have played a key role in not only the initiation but also the long-term maintenance of the  
474 barrier reef ecosystem during successive rapid post-glacial sea level rises.

475

#### 476 4.2. Barrier reef initiation

477

478 Drilling into submerged fossil reefs along the shelf edge of the modern GBR has  
479 demonstrated that lowstand and early deglacial reef communities may have been important  
480 sources of coral propagules to support the early colonization of the newly inundated shelf  
481 (Webster et al., 2011). In the absence of a precursor lowstand reef ecosystem coral  
482 propagules may have been initially supplied by nearby non-reefal shallow communities. The  
483 morphology and taxonomy of the ISX corals in the lower section of the Ribbon Reef 5 borehole,  
484 mostly laminar *Porites*, *Montipora*, agariciids and fine-branching *Seriatopora*, suggests that  
485 the majority of coral clasts were derived from nearby deep mesophotic communities and no  
486 clear signature of shallow water coral reef communities is recognized. Another possibility  
487 involves a more distant source of propagules, either from locations farther north, i.e. the Torres  
488 Shelf or the Gulf of Papua, where reefs may have already been established (Davies et al.,  
489 1991), or from the Queensland Plateau (McKenzie et al., 1993). The latter seems more likely  
490 given the present-day configuration of ocean currents with the westward-flowing South  
491 Equatorial Current dividing around Cairns into the northward-flowing North Queensland

492 Current and the southward-flowing East Australian Current (Choukroun et al., 2010). However,  
493 simulations of larval dispersal trajectories show that the connectivity between Papua New  
494 Guinea and the GBR may be enhanced during La Niña events (Trembl et al., 2008).

495

496 The timing of barrier reef initiation is still poorly constrained. The warm SST's and  
497 high-amplitude sea level during the MIS 11 interglacial have been proposed as triggers for the  
498 initiation of extensive barrier reef growth worldwide, including the GBR (Droxler et al., 2003;  
499 Montaggioni et al., 2011; Droxler and Jory, 2013). This view has been challenged by  
500 sedimentological studies of distal boreholes from the upper slope of the Marion Plateau  
501 placing the onset of the southern central GBR earlier, during MIS 15 (Dubois et al., 2008) or  
502 MIS 17 (Obrochta, MS 2004). Given that alkenone SST reconstructions in the region indicate  
503 MIS 11 was not particularly warm (Lawrence and Herbert, 2005), the claim that barrier reef  
504 initiation on the Eastern Australian Shelf occurred at MIS 11 needs to be reassessed. A similar  
505 pre-MIS 11 age (MIS 15 or MIS 13) has been suggested for reef initiation on the Western  
506 Australian Shelf and linked to the strengthening of the Leeuwin Current as well as increased  
507 aridity and alkalinity (Gallagher et al., 2014). Higher-amplitude sea level oscillations after the  
508 Mid-Pleistocene Transition (Elderfield et al., 2012) have also been proposed as a possible  
509 trigger for extensive barrier reef growth on the Eastern Australian Shelf through prolonged  
510 shelf flooding (Dubois et al., 2008) and the creation of a cyclone corridor reducing terrigenous  
511 sediment input on the outer shelf (Larcombe and Carter, 2004). Our analysis of the coral  
512 succession in the Ribbon Reef 5 borehole, combined with previously published data on  
513 coralline algae (Braga and Aguirre, 2004) and the currently available age data, suggest the  
514 emergence of a cyclic pattern of reef growth and demise took place prior to MIS 11. Based on  
515 the chronology of the Ribbon Reef 5 borehole presented in Montaggioni et al. (2011), reef  
516 initiation would therefore have occurred during MIS 15, in agreement with Dubois et al. (2008).

517

#### 518 4.3. Environmental interpretation of the coral associations

519

520 The Ribbon Reef 5 borehole above 137 m is characterized by a cyclic pattern in the  
521 coral community structure. Each cycle is composed of up to three coral associations (Po-Mo-  
522 Fa, Poc and Acro-Iso). The Po-Mo-Fa association, dominated by encrusting to massive  
523 *Porites* and encrusting *Montipora* associated with faviids and agariciids, indicates a relatively  
524 deep, mid to lower reef slope habitat or a turbid environment (Done, 1982; Veron, 2000).  
525 *Porites* and *Montipora* are typical of highly turbid carbonate environments (Sanders and  
526 Baron-Szabo, 2005). The occurrence of Lithophylloid and Melobesiod algae in Cy7, with this  
527 coral association may indicate more temperate climatic conditions (Braga and Aguirre, 2004).  
528 The pioneer Po-Mo-Fa association is replaced by the Poc association in Cy8 and Cy7 which  
529 consists primarily of *Stylophora pistillata*, associated with *Seriatopora hystrix* and faviids

530 (mostly branching *Echinopora*) only in Cy7. *Stylophora pistillata* and *Seriatopora hystrix* have  
531 a broad range of distribution, from shallow to deep (>30 m) reef habitats with *Stylophora*  
532 *pistillata* locally dominant on exposed reef fronts and *Seriatopora hystrix* typical of reef flats  
533 (Done, 1982; Veron, 2000; Bridge et al., 2012; Abbey et al., 2013). Dense communities of  
534 *Seriatopora hystrix* have been reported from the upper mesophotic zone in the Ryukyu Islands  
535 (Sinniger et al., 2013; Sinniger, 2016). The association of *Echinopora* (probably *E.*  
536 *mammiformis*) and *Seriatopora hystrix* in Cy7 indicates a low-energy upper reef slope or  
537 lagoonal setting (Done, 1982; Veron, 2000). The lithology in this interval is best described as  
538 a floatstone with bioclasts heavily encrusted by Lithophylloid algae (Rhodolith unit 1 of  
539 Webster and Davies, 2003), in concordance with a hydrodynamic regime characterized with  
540 low-wave exposure. The Acro-Iso association, composed of *Isopora* and medium-size to  
541 robust branching *Acropora* gr. *humilis* and *Acropora* gr. *robusta*, indicates a shallow exposed  
542 (<10 m) reef setting in the GBR (Done, 1982) and other Indo-Pacific reefs (Cabioch et al.,  
543 1999; Hongo and Kayanne, 2010; Hongo, 2012). In contrast, the assemblage characterized  
544 by arborescent *Acropora* gr. *formosa* between 90-95 m in Cy7 is typically found in the modern  
545 GBR in lower-energy habitats on reef slopes or in lagoons (Done, 1982; Oliver et al., 1983;  
546 Wallace, 1999).

547

548 Notable shifts in taxonomic composition occur within the Acro-Iso association and  
549 consist of transitions between *Isopora*-dominated and *Acropora*-dominated intervals. In Cy7,  
550 the transition from arborescent *Acropora* gr. *formosa* to *Isopora* was discussed above and  
551 interpreted as a shallowing-upward trend. In Cy6 and Cy4, the transition from *Isopora*-  
552 dominated to *Acropora*-dominated intervals does not seem to reflect any major change in  
553 paleowater depth as both assemblages are associated with shallow Mastophoroid algae.  
554 Interestingly, the shift in these two cycles coincides with unit boundaries defined in Braithwaite  
555 et al. (2004). Transitions between *Acropora*-dominated and *Isopora* dominated intervals are  
556 observed in Holocene core sections from the southern GBR (Dechnik et al., 2015). In particular,  
557 the replacement of an *Acropora* assemblage by an *Isopora* assemblage on the windward  
558 margin of the Fitzroy reef was interpreted as reflecting a minor shallowing within the 0-10 m  
559 depth range. There is however no clear evidence, based on associated species and algal crust  
560 thicknesses, that the two assemblages in the Ribbon Reef 5 borehole occupied distinct reef  
561 zones.

562

#### 563 4.4 Interpretation of reef cycles

564

565 The repeating cycles observed in the Ribbon Reef 5 borehole begins with the Po-Mo-  
566 Fa association and terminates with the Acro-Iso association with or without a transitional  
567 phase characterized by the Poc association. The repeated cycles of coral succession

568 observed in Ribbon Reef 5 are broadly similar to Holocene sequences described in the GBR,  
569 characterized by a pioneer assemblage of massive *Porites* and faviids replaced by a high-  
570 energy *Acropora-Isopora* assemblage (Montaggioni, 2005; Dechnik et al., 2015). This type of  
571 coral succession is common in the Holocene and interpreted as a shallowing-upward  
572 sequence reflecting a catch-up mode of reef growth (Montaggioni and Braithwaite, 2009). In  
573 a similar fashion, the Po-Mo-Fa association in the successive reef-building episodes observed  
574 at Ribbon Reef 5 likely represents the first stage of colonization of the shelf after inundation  
575 during each post-glacial sea level rise, perhaps also influenced by lower SSTs based on the  
576 occurrence of Lithophylloid and Melobesoid algae (Braga and Aguirre, 2004). The first of  
577 these pioneer corals in the Ribbon Reef 5 are colonies of *Goniastrea* (probably *G. edwardsi*)  
578 at the base of Cy8. Several species of *Goniastrea*, including *G. edwardsi*, are stress-tolerant,  
579 particularly to sedimentation and turbidity (Perry and Smithers, 2009; Darling et al., 2012), and  
580 therefore may be particularly tolerant to sediments resuspended during shelf inundation.  
581 Subsequent Po-Mo-Fa intervals are stratigraphically thicker and more diverse, characteristics  
582 which may reflect the increase in diversity of the regional species pool and/or higher  
583 amplitudes of sea level rise. Greater accommodation space created by higher-amplitude sea  
584 level rise could have led to thicker vertical accumulations of the initial Po-Mo-Fa assemblage  
585 but this remains to be explored.

586

587         The Poc association precedes the Acro-Iso association in three reef cycles, i.e. Cy8,  
588 Cy7 and Cy3. In Cy8, a *Stylophora*-Mastophoroid assemblage is overlain by an *Acropora* gr.  
589 *humilis*-Mastophoroid assemblage. Both indicate a shallow exposed (<10 m) reef setting. A  
590 similar interpretation can be proposed for the coral succession in Cy3. In Cy7, a *Stylophora*-  
591 *Seriatopora* and Lithophylloid assemblage is replaced by an *Acropora* gr. *formosa* and  
592 Lithophylloid assemblage, which is in turn replaced by an *Isopora* and Mastophoroid  
593 assemblage. The coralgal succession in Cy7 suggests a general shallowing-upward sequence.  
594 The transition to Mastophoroid algae could also reflect higher SST's (Braga and Aguirre, 2004).  
595 However, it is not clear whether the transition between the first two assemblages results from  
596 decreasing paleowater depths as their distribution range overlaps. In conclusion, the transition  
597 from the Poc association to the Acro-Iso association in Cy8, Cy7 and Cy3 does not necessarily  
598 reflect any major change in depositional setting or environmental conditions and may result  
599 from variations in community structure within the same habitat caused by lateral reef accretion  
600 (Dechnik et al., 2016; Webb et al., 2016; Webster and Davies, 2003). However, this hypothesis  
601 does not explain the dominance of the Poc association in the first two reef cycles and the  
602 subsequent long-term shift to acroporid-dominated branching coral assemblages. An  
603 alternative explanation is that this transition reflects an ecological succession driven by  
604 intrinsic ecological factors. Two reasons may explain the success of *Stylophora* and  
605 *Seriatopora* during the early phase of the GBR evolution. First, the pool of *Acropora* and



606 *Isopora* colonies may have been less extensive during the early phase of the GBR history.  
607 The newly formed barrier reef may not have been as extensive as it is today due to the  
608 absence of an antecedent barrier reef to support further reef growth (Larcombe and Carter,  
609 2004). The presence of well-developed Rhodolith facies (Rd1 and Rd2; Webster and Davies,  
610 2003) in Cy7 supports this interpretation. Furthermore, the less abundant and patchier  
611 populations of fast-growing acroporids may have given an opportunity to pocilloporids to  
612 colonize the substrate first. This hypothesis is supported by the general upward increase in  
613 *Acropora* abundance at Ribbon Reef 5 (Fig. 11). Both *Stylophora pistillata* and *Seriatopora*  
614 *hystrix* are fast-growing corals (Pratchett et al., 2015), release fertilized larvae (Hugues et al.,  
615 1999), and have a broad depth distribution range in the GBR (Done, 1982, Bridge et al., 2012).  
616 They are successful early colonizers of denuded substrates after disturbance (Loya, 1976;  
617 Fan and Dai, 1996) and have been described as “weedy” species (Darling et al., 2012).  
618 *Stylophora pistillata* and *Seriatopora hystrix* are therefore ideal candidates to rapidly colonize  
619 available substrates during rapid environmental and sea level changes, in exposed and  
620 protected settings, respectively. The second reason is that environmental conditions early in  
621 the GBR history may have favored opportunistic species like *S. pistillata* and *S. hystrix*. The  
622 lack of a fully developed barrier reef system may have exposed the outer shelf reefs to more  
623 storm-induced disturbances and terrigenous influence (Larcombe and Carter, 2004), favoring  
624 opportunistic species like *S. pistillata* and *S. hystrix*. This would also explain the paucity of reef  
625 framework below 85 m despite the inception of the reef cycles much earlier (Webster et al.,  
626 2003; Braithwaite et al., 2004).

627

#### 628 4.5. Comparison of reef cycles

629

630 The remarkable cycles of coral community structure observed in the Ribbon Reef 5  
631 borehole and the repetition of similar types of coral associations in successive generations of  
632 reefs is consistent with records of high persistence in coral community structure during  
633 successive highstands reported elsewhere (Jackson, 1992; Pandolfi, 1996; Pandolfi and  
634 Jackson, 2006). Our analysis shows high similarity in taxonomic compositions between  
635 successive cycles, particularly between Cy4, Cy5, Cy6 and Cy7 that are also the cycles with  
636 the highest taxonomic diversity. However, the Ribbon Reef 5 record also shows that the  
637 competition between pocilloporids and acroporids may have caused variations in the relative  
638 abundance of these taxa during the history of the GBR. In addition, some of the cycles  
639 identified, specifically Cy4, Cy5 and Cy6, may represent more than one highstand episode  
640 based on the previous interpretation of the reef units in the same borehole (Webster, 1999).  
641 Braithwaite and Montaggioni (2009) also identified two subaerial erosion surfaces at 36 m and  
642 57 m, respectively. We do not see any persistent change in reef setting associated with these  
643 events. However, it is possible that the initial coral association after the reflooding of the shelf

644 was an Acro-Iso association indicating a shallow exposed reef setting similar to that of the  
645 Acro-Iso association terminating the preceding cycle.

646

647 The similarities among intervals characterized by the same types of coral association  
648 (Po-Mo-Fa, Poc or Acro-Iso) are variable. Intervals displaying the highest similarities are  
649 characterized by the Acro-Iso association. Except for the interval in Cy7, the Acro-Iso  
650 association probably represents an aggrading phase of reef growth in a shallow exposed  
651 environment under relatively stable hydrodynamic conditions that may have promoted higher  
652 similarities in taxonomic composition. Conversely, the Po-Mo-Fa association represents the  
653 initial phase of reef development during sea level rise and initial conditions on the submerged  
654 shelf may have been more unpredictable (Dechnik et al., 2015). Furthermore the composition  
655 of the initial coral association depends on the pool of coral species available to recolonize the  
656 shelf that is, in turn, controlled by environmental conditions during the preceding lowstand and  
657 subsequent sea level rise. The higher variability in taxonomic composition among the Poc  
658 intervals may reflect the contrasting paleoenvironmental interpretations assigned to the Poc  
659 interval in Cy7 (low-energy) and those of Cy8 and Cy3 (high-energy).

660

661 Trends in colony thickness across reef cycles also vary from one taxon to another.  
662 Some trends underline similarities in community structure between intervals from different reef  
663 cycles. For example, in most cycles thicker *Porites* colonies are systematically associated with  
664 the first phase of reef growth, i.e. the Po-Mo-Fa intervals (Fig. 4A). Massive *Porites* associated  
665 with faviids typically occurs in a semi-exposed or sheltered environment in Indo-Pacific reefs  
666 consistent with our interpretation of the Po-Mo-Fa association (Montaggioni, 2005). In addition,  
667 peaks in *Montipora* colony thickness coincide with Acro-Iso intervals (Fig 4A). Massive  
668 *Montipora* is a major component of some shallow (<10 m) reef facies and agrees well with our  
669 interpretation of the Acro-Iso association (Camoin et al., 2012). Conversely, the colony  
670 thickness of faviids does not seem to be determined by the coral association, but rather shows  
671 a long-term decline across multiple reef cycles (Fig. 4A). This is correlated with a notable  
672 increase in the frequency of acroporids with robust branches toward the top of the borehole  
673 (Fig. 4B). One possible explanation for this would be an incremental increase in wave  
674 exposure due to the progressive retrogradation of reef sequences over multiple sea level  
675 highstands (Davies et al., 1988, 1989; Webster, 1999). In addition, the fast-growing acroporids  
676 may have had a long-term competitive advantage over slow-growing faviids (Renema et al.,  
677 2016).

678

679 Based on our analysis of the nature and distribution of coral taxa in the Ribbon Reef  
680 5 borehole, we have identified patterns of coral community changes at varied time scales (Fig.  
681 12). Superimposed on the long-term cycles of reef initiation and demise are variations in

682 community structure within each cycle, represented by successive stratigraphic intervals with  
683 distinct coral associations as well as short-term variations in community structure within these  
684 intervals. Coral succession in each cycle is clearly influenced by glacial-interglacial sea level  
685 changes that ultimately control accommodation space and reef growth. In addition, millennial-  
686 scale environmental changes, such as variations in SST and turbidity, associated with  
687 deglacial conditions and shelf inundation are likely to influence coral community structure.  
688 However, the importance of these factors is still poorly constrained. A key objective of future  
689 studies will therefore be to quantify these environmental variables and analyze their  
690 relationship with the observed patterns of coral community changes. Promising techniques  
691 include laser abrasion ICP-MS U/Th measurements to improve reef chronologies and novel  
692 geochemical proxies (REE, lithium isotopes) to reconstruct terrigenous sediment influx.

693

## 694 **5. Conclusions**

695

696 Our detailed study of the taxonomy and distribution of coral taxa in the Ribbon Reef 5  
697 borehole, combined with previously published records, leads to the following conclusions:

- 698 1. The pattern of repeated reef growth and demise starts at 137 m. Available  
699 stratigraphical and chronological data suggest that barrier reef initiation may have  
700 occurred prior to MIS 11. The non-reefal section, below 137 m, shows a transition from  
701 a lower to an upper mesophotic coral assemblage, replaced in turn by the initial coral  
702 association of the first reef cycle at 137 m, indicating a shallowing-upward trend.
- 703 2. Three coral associations are identified in the reefal section: (1) encrusting to massive  
704 *Porites*, encrusting *Montipora* and faviids (Po-Mo-Fa) – mid to lower reef slope habitat  
705 or turbid environment, (2) pocilloporids (Poc) – shallow exposed reef fronts (*Stylophora*  
706 *pistillata*) and protected settings (*Seriatopora hystrix*), and (3) massive or branching  
707 *Isopora* and medium to robust-branching *Acropora* (Acro-Iso) – shallow exposed (<10  
708 m) reef settings (*Isopora-Acropora* gr. *humilis-Acropora* gr. *robusta*) and lower-energy  
709 reef-slope or lagoonal settings (*Acropora* gr. *formosa*).
- 710 3. Eight reef cycles are identified. Each typically starts with the Po-Mo-Fa association  
711 (pioneer) and ends with the Acro-Iso association. We interpret this as a shallowing-  
712 upward sequence following shelf inundation during each successive post-glacial sea  
713 level rise and highstand. Poor water quality due to sediment resuspension and/or lower  
714 SST's may also have influenced the pioneer association.
- 715 4. The Poc association is prominent in the first two reef cycles (Cy8, Cy7) and represents  
716 a transitional phase between the Po-Mo-Fa and Acro-Iso associations. The singular  
717 predominance of pocilloporids during the early stages (Cy8, Cy7) of reef history and  
718 the long-term shift to an *Acropora-Isopora*-dominated shallow reef community may be  
719 attributed to an increase in competitive pressure of acroporids over pocilloporids within

720 the same reef habitat.

721 5. The recurrence of broadly similar coral associations throughout multiple interglacial  
722 highstands is consistent with the view that reef coral community structure is predictable  
723 over 100-kyr time scales. However, variations within reef units indicate that other  
724 important processes are also operating on millennial scales, particularly during initial  
725 stages of shelf reflooding, causing differences in water clarity, SST, or the pool of coral  
726 species available to reseed the newly inundated substrate.

727

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729

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733

## 734 **References**

735

736 Abbey, E., Webster, J. M., Braga, J. C., Jacobsen, G. E., Thorogood, G., Thomas, A. L.,  
737 Camoin, G., Reimer, P. J., and Potts, D. C., 2013. Deglacial mesophotic reef demise on  
738 the Great Barrier Reef. *Palaeogeography, Palaeoclimatology, Palaeoecology* 392, 473–  
739 494.

740 Albright, R., Caldeira, L., Hoffelt, J., Kwiatkowski, L., Maclaren, J. K., Mason, B. M.,  
741 Nebuchina, Y., Ninokawa, A., Pongratz, J., Ricke, K. L., Rivlin, T., Schneider, K., Sesboüé,  
742 M., Shamberger, K., Silverman, J., Wolfe, K., Zhu, K., and Caldeira, K., 2016. Reversal of  
743 ocean acidification enhances net coral reef calcification. *Nature* 531, 362–365.

744 Alexander, I., Andres, M. S., Braithwaite, C. J. R., Braga, J. C., Cooper, M. J., Davies, M. J.,  
745 Elderfield, P. J., Gilmour, M. A., Kay, R. L. F., Kroon, D., McKenzie, J. A., Montaggioni, L.  
746 F., Skinner, A., Thompson, R., Vasconcelos, C., Webster, J. M., and Wilson, P. A., 2001.  
747 New constraints on the origin of the Australian Great Barrier Reef: Results from an  
748 international project of deep coring. *Geology* 29 (6), 483–486.

749 Baird A. H., Sommer, B., and Madin, J. S., 2012. Pole-ward range expansion of *Acropora* spp.  
750 along the east coast of Australia. *Coral Reefs* 31, 1063.

751 Bak, R. P., Nieuwland, G., and Meesters, E. H., 2005. Coral reef crisis in deep and shallow  
752 reefs: 30 years of constancy and change in reefs of Curacao and Bonaire. *Coral Reefs*  
753 24, 475–479.

754 Beaman, R. J., Webster, J. M., and Wust, R. A. J., 2008. New evidence for drowned shelf edge  
755 reefs in the Great Barrier Reef, Australia. *Marine Geology* 247, 17–34.

756 Bode, M., Connolly, S. R., and Pandolfi, J. M., 2012. Species differences drive nonneutral  
757 structure in Pleistocene coral communities. *The American Naturalist* 180 (5), 577–588.

- 758 Braga, J. C. and Aguirre, J., 2004. Coralline algae indicate Pleistocene evolution from deep,  
759 open platform to outer barrier reef environments in the northern Great Barrier Reef margin.  
760 *Coral Reefs* 23, 547–558.
- 761 Braithwaite, C. J. R., Dalmaso, H., Gilmour, M. A., Harkness, D. D., Henderson, G. M., Kay,  
762 R. L. F., Kroon, D., Montaggioni, L. F. and Wilson, P. A., 2004. The Great Barrier Reef: the  
763 chronological record from a new borehole. *Journal of Sedimentary Research* 74, 298–  
764 310.
- 765 Braithwaite, C. J. R. and Montaggioni, L. F., 2009. The Great Barrier Reef: a 700,000 year  
766 diagenetic history. *Sedimentology* 56, 1591–1622.
- 767 Braithwaite, C. J. R., 2016. Coral-reef records of Quaternary changes in climate and sea-level.  
768 *Earth-Science Reviews* 156, 137–154.
- 769 Bridge, T. C. L., Fabricius, K. E., Bongaerts, P., Wallace, C. C., Muir, P. R., Done, T. J., and  
770 Webster, J. M., 2012. Diversity of Scleractinia and Octocorallia in the mesophotic zone of  
771 the Great Barrier Reef, Australia. *Coral Reefs* 31, 179–189.
- 772 Bruno, J. F. and Selig, E. R., 2007. Regional decline of coral cover in the Indo-Pacific: timing,  
773 extent, and subregional comparisons. *PloS ONE* 2 (8), e711, DOI:  
774 10.1371/journal.pone.0000711.
- 775 Cabioch, G., Montaggioni, L. F., Faure, G., and Ribaud-Laurenti, A., 1999. Reef coralgal  
776 assemblages as recorders of paleobathymetry and sea level changes in the Indo-Pacific  
777 province. *Quaternary Science Reviews* 18, 1681–1695.
- 778 Cabioch, G., Montaggioni, L., Thouveny, N., Frank, N., Sato, T., Chazottes, V., Dalmaso, H.,  
779 Payri, C., Pichon, M., and Sémah, A-M., 2008. The chronology and structure of the  
780 western New Caledonian barrier reef tracts. *Palaeogeography, Palaeoclimatology,*  
781 *Palaeoecology* 268, 91–105.
- 782 Camoin, G. F., Ebren, P., Eisenhauer, A., Bard, E., and Faure, G., 2001. A 300,000-yr coral  
783 reef record of sea level changes, Mururoa atoll (Tuamotu archipelago, French Polynesia).  
784 *Palaeogeography, Palaeoclimatology, Palaeoecology* 175, 325–341.
- 785 Camoin, G. F., Seard, C., Deschamps, P., Webster, J. M., Abbey, E., Braga, J. C., Iryu, Y.,  
786 Durand, N., Bard, E., Hamelin, B., Yokoyama, Y., Thomas, A. L., Henderson, G. M., and  
787 Dussouillez, P., 2012. Reef response to sea-level and environmental changes during the  
788 last deglaciation: Integrated Ocean Drilling Program Expedition 310, Tahiti Sea Level.  
789 *Geology* 40, 643–646.
- 790 Camoin, G. and Webster, J. M., 2015. Coral Reef response to Quaternary sea-level and  
791 environmental changes: state of the science. *Sedimentology* 62, 401–428.
- 792 Chin, A., Lison De Loma, T., Reyta, K., Planes, S., Gerhardt, K., Clua, E., Burke, L., and  
793 Wilkinson, C., 2011. Status of coral reefs of the Pacific and outlook: 2011. Publishers  
794 Global Coral Reef Monitoring Network, 260 pages.
- 795 Choukroun, S., Ridd, P. V., Brinkman, R., and McKinna, L. I. W., 2010. On the surface

- 796 circulation in the western Coral Sea and residence times in the Great Barrier Reef. *Journal*  
797 *of Geophysical Research* 115, C06013, DOI: 10.1029/2009JC005761.
- 798 Cinner, J. E., Huchery, C., MacNeil, M. A., Graham, N. A. J., McClanahan, T. R., Maina, J.,  
799 Maire, E., Kittinger, J. N., Hicks, C. C., Mora, C., Allison, E. H., D'Agata, S., Hoey, A.,  
800 Feary, D. A., Crowder, L., Williams, I. D., Kulbicki, M., Vigliola, L., Wantiez, L., Edgar, G.,  
801 Stuart-Smith, R. D., Sandin, S. A., Green, A. L., Hardt, M. J., Beger, M., Friedlander, A.,  
802 Campbell, S. J., Holmes, K. E., Wilson, S. K., Brokovich, E., Brooks, A. J., Cruz-Motta, J.  
803 J., Booth, D. J., Chabanet, P., Gough, C., Tupper, M., Ferse, S. C. A., Sumaila, U.R.,  
804 and Mouillot, D., 2016. Bright spots among the world's coral reefs. *Nature* 535, 416–419.
- 805 Clarke, K. R. and Gorley, R. N., 2006: *Primer v6: User Manual/Tutorial*, PRIMER-E Ltd, 190  
806 pages.
- 807 Connell, J. H., Hughes, T. P., and Wallace, C. C., 1997. A 30-year study of coral abundance at  
808 several scales in space and time. *Ecological Monographs* 67 (4), 461–488.
- 809 Darling, E. S., Alvarez-Filip, L., Oliver, T. A., McClanahan, T. R., and Côté, I., 2012. Evaluating  
810 life-history strategies of reef corals from species traits. *Ecology Letters* 15, 1378–1386.
- 811 Davies, P. J., Symonds, P. A., Feary, D. A., and Pigram, C. J., 1988, Facies models in  
812 exploration - the carbonate platforms of north-east Australia: *The APEA Journal*, v. 28, no.  
813 1, p. 123-143.
- 814 Davies, P. J., Symonds, P. A., Feary, D. A., and Pigram, C. J., 1989. The evolution of the  
815 carbonate platforms of northeast Australia. In: Crevello, P. D., Wilson, J. L., Sarg, J. F.,  
816 and Read, J. F. (Eds.), *Controls on carbonate platforms and basin development*. Society  
817 of Economic Paleontologists and Mineralogists Special Publication 44, 233–258.
- 818 Davies, P. J., McKenzie, J. A., Palmer-Julson, A. A., Betzler, C., Brachert, T. C., Chen, M-P. P.,  
819 Crumière, J-P., Dix, G. R., Droxler, A. W., Feary, D. A., Gartner, S., Glenn, C. R., Isern, A.,  
820 Jackson, P. D., Jarrard, R. D., Katz, M. E., Konishi, K., Kroon, D., Ladd, J. W., Martin, J.  
821 M., McNeill, D. F., Montaggioni, L. F., Muller, D. W., Omarzai, S. K., Pigram, C. J., Swart,  
822 P. K., Symonds, P. A., Watts, K. F., Wei, W., 1991. *Proceedings of the Ocean Drilling*  
823 *Program, Initial Reports, Vol. 133*, College Station, TX (Ocean Drilling Program).
- 824 Davies, P. J., 2011. Great Barrier Reef: Origin, evolution, and modern development. In: Hopley,  
825 D. (Ed), *Encyclopedia of modern coral reefs: structure, form and process*, *Encyclopedia*  
826 *of earth science series*, 504–534.
- 827 De'ath, G., Fabricius, K. E., Sweatman, H., and Puotinen, M., 2012. The 27-year decline of  
828 coral cover on the Great Barrier Reef and its causes. *Proceedings of the National*  
829 *Academy of Sciences* 109 (44), 17995–17999.
- 830 Dechnik, B., Webster, J. M., Davies, P. J., Braga, J. C., and Reimer, P. J., 2015. Holocene  
831 “turn-on” and evolution of the Southern Great Barrier Reef: revisiting reef cores from the  
832 Capricorn Bunker Group. *Marine Geology* 363, 174–190.
- 833 Done, T. J., 1982. Patterns in the distribution of coral communities across the central Great

- 834 Barrier Reef. *Coral Reefs* 1, 95–107.
- 835 Dove, S. G., Kline, D. I., Pantos, O., Angly, F. E., Tyson, G. W., and Hoegh-Guldberg, O.,  
836 2013, Future reef decalcification under a business-as-usual CO2 emission scenario: *Proc*  
837 *Natl Acad Sci U S A*, v. 110, no. 38, p. 15342-15347.
- 838 Droxler, A., Alley, R. B., Howard, W. R., Poore, R. Z., and Burckle, L. H., 2003. Unique and  
839 exceptionally long interglacial Marine Isotope Stage 11: window into Earth warm future  
840 climate. In: Droxler, A. W., Poore, R. Z., and Burckle, L. H. (Eds.), *Earth's Climate and*  
841 *Orbital Eccentricity: The Marine Isotope Stage 11 Question*. *Geophysical Monograph* 137,  
842 1–14.
- 843 Droxler, A. W. and Jory, S. J., 2013. Deglacial origin of barrier reefs along low-latitude mixed  
844 siliciclastic and carbonate continental shelf edges. *Annual Review of Marine Science* 5,  
845 165–190.
- 846 Dubois, N., Kindler, P., Spezzaferri, S., and Coric, S., 2008. The initiation of the southern  
847 central Great Barrier Reef: new multiproxy data from Pleistocene distal sediments from  
848 the Marion Plateau (NE Australia). *Marine Geology* 250, 223–233.
- 849 Fan, T-Y. and Dai, C-F., 1996. Reproductive ecology of the pocilloporid corals in Taiwan. I.  
850 *Seriatopora hystrix*. *Acta Oceanographica Taiwanica* 35 (3), 311–321.
- 851 Gallagher, S. J., Wallace, M. W., Hoiles, P. W., and Southwood, J. M., 2014. Marine and  
852 Petroleum Geology 57, 470–481.
- 853 Ganase, A., Bongaerts, P., Visser, P. M., and Dove, S. G., 2016. The effect of seasonal  
854 temperature extremes on sediment rejection in three scleractinian coral species. *Coral*  
855 *Reefs* 35, 187–191.
- 856 Gischler, E., 2007. Pleistocene facies of Belize barrier and atoll reefs. *Facies* 53, 27–41.
- 857 Greenstein, B. J. and Pandolfi, J. M., 2008. Escaping the heat: range shifts of reef coral taxa  
858 in coastal Western Australia. *Global Change Biology* 14, 1–16.
- 859 Hinestrosa, G., Webster, J. M., and Beaman, R. J., 2016, Postglacial sediment deposition  
860 along a mixed carbonate-siliciclastic margin: New constraints from the drowned shelf-  
861 edge reefs of the Great Barrier Reef, Australia: *Palaeogeography, Palaeoclimatology,*  
862 *Palaeoecology*, v. 446, p. 168-185.
- 863 Hoadley, K. D., Pettay, D. T., Grottoli, A. G., Cai, W-J., Melman, T. F., Schoepf, V., Hu, X., Li,  
864 Q., Xu, H., Wang, Y., Matsui, Y., Baumann, J. H., and Warner, .E., 2015. Physiological  
865 response to elevated temperature and pCO2 varies across four Pacific coral species:  
866 understanding the unique host+symbiont response. *Scientific Reports* 5, 18371, DOI:  
867 10.1038/srep18371
- 868 Hoegh-Guldberg, O., 2011. Coral reef ecosystems and anthropogenic climate change.  
869 *Regional Environmental Change* 11 (Supplement 1), 215–227.
- 870 Hongo, C., 2012. Holocene key coral species in the Northwest Pacific: indicators of reef  
871 formation and reef ecosystem responses to global climate change and anthropogenic

- 872 stresses in the near future. *Quaternary Science Reviews* 35, 82–99.
- 873 Hongo, C. and Kayanne, H., 2010. Holocene sea-level record from corals: reliability of  
874 paleodepth indicators at Ishigaki Island, Ryukyu Islands, Japan. *Palaeogeography,*  
875 *Palaeoclimatology, Palaeoecology* 287, 143–151.
- 876 Hopley, D., Smithers, S. G., Parnell, K. E., 2007. The geomorphology of the Great Barrier  
877 Reef: development, diversity and change. Cambridge University Press, USA, 532 pages.
- 878 Hugues, T. P., Baird, A. H., Dinsdale, E. A., Moltschanivskyj, N. A., Pratchett, M. S., Tanner,  
879 J. E., and Willis, B. L., 1999. Patterns of recruitment and abundance of corals along the  
880 Great Barrier Reef. *Nature* 397, 59–63.
- 881 Jackson, J. B. C., 1992. Pleistocene perspectives on coral reef community structure. *American*  
882 *Zoologist* 32, 719–731.
- 883 Jackson, J. B. C., Donovan, M. K., Cramer, K. L., and Lam, W., 2014. Status and trends of  
884 Caribbean coral reefs: 1970–2012. Global Coral Reef Monitoring Network, IUCN, Gland,  
885 Switzerland.
- 886 Kiessling, W., Simpson, C., Beck, B., Mewis, H., and Pandolfi, J. M., 2012. Equatorial decline  
887 of reef corals during the last Pleistocene interglacial. *Proceedings of the National*  
888 *Academy of Sciences* 109 (52), 21378–21383.
- 889 Kiessling, W. and Pandolfi, J. M., 2014. Gaining insights from past reefs to inform  
890 understanding of coral reef response to global climate change. *Current Opinion in*  
891 *Environmental Sustainability* 7, 52–58.
- 892 Larcombe, P. and Carter, R.M., 2004. Cyclone pumping, sediment partitioning and the  
893 development of the Great Barrier Reef shelf system: a review. *Quaternary Science*  
894 *Reviews* 23, 107–135.
- 895 Lawrence, K. T., and Herbert, T. D., 2005, Late Quaternary sea-surface temperatures in the  
896 western Coral Sea: Implications for the growth of the Australian Great Barrier Reef:  
897 *Geology*, v. 33, no. 8, p. 677-680.
- 898 Loya, Y., 1976. The Red Sea coral *Stylophora pistillata* is an *r* strategist. *Nature* 259, 478–  
899 480.
- 900 McKenzie, J. A., Davies, P. J., Palmer-Julson, A. A., Betzler, C., Brachert, T. C., Chen, M-P. P.,  
901 Crumière, J-P., Dix, G. R., Droxler, A. W., Feary, D. A., Gartner, S., Glenn, C. R., Isern, A.,  
902 Jackson, P. D., Jarrard, R. D., Katz, M. E., Konishi, K., Kroon, D., Ladd, J. W., Martin, J.  
903 M., McNeill, D. F., Montaggioni, L. F., Muller, D. W., Omarzai, S. K., Pigram, C. J., Swart,  
904 P. K., Symonds, P. A., Watts, K. F., Wei, W., 1993. *Proceedings of the Ocean Drilling*  
905 *Program, Initial Reports, Vol. 133, College Station, TX (Ocean Drilling Program).*
- 906 Mewis, H., 2016. Ecological stability of Indo-Pacific coral reefs during Quaternary climatic  
907 fluctuations: Case studies from Vanuatu and Egypt. Doctoral Thesis, Faculty of Life  
908 Sciences, Humboldt-Universität zu Berlin, 328 pages.
- 909 Montaggioni, L. F., 2005. History of Indo-Pacific coral reef systems since the last glaciation:



- 910 development patterns and controlling factors. *Earth-Science Reviews* 71, 1–75.
- 911 Montaggioni, L. F., Cabioch, G., Thouveny, N., Frank, N., Sato, T., Sémah, A.-M., 2011.
- 912 Revisiting the Quaternary development history of the western New Caledonian shelf
- 913 system: from ramp to barrier reef. *Marine Geology* 280, 57–75.
- 914 Multer, H. G., Gischler, E., Lundberg, J., Simmons, K. R., and Shinn, E. A., 2002. Key Largo
- 915 Limestone revisited: Pleistocene shelf-edge facies, Florida Keys, USA. *Facies* 46, 229–
- 916 272.
- 917 Obrochta, S. P., 2004. Australian Great Barrier Reef initiation timing constrained by seaward
- 918 shallow-water sediment drift architecture (ODP Leg 194, Marion Plateau). Master Thesis,
- 919 College of Marine Science, University of South Florida, 56 pages.
- 920 Oliver, J. K., Chalker, B. E., and Dunlap, W. C., 1983. Bathymetric adaptations of reef-building
- 921 corals at Davies Reef, Great Barrier Reef, Australia. I. Long-term growth responses of
- 922 *Acropora formosa* (Dana 1846). *Journal of Experimental Marine Biology and Ecology* 73,
- 923 11–35.
- 924 Pandolfi, J. M., 1996. Limited membership in Pleistocene reef coral assemblages from the
- 925 Huon peninsula, Papua New Guinea: constancy during global change. *Paleobiology* 22,
- 926 152–176.
- 927 Pandolfi, J. M., 1999. Response of Pleistocene coral reefs to environmental change over long
- 928 temporal scales. *American Zoologist* 39, 113–130.
- 929 Pandolfi, J. M., 2002. Coral community dynamics at multiple scales. *Coral Reefs* 21, 13–23.
- 930 Pandolfi, J. M. and Jackson, J.B.C., 2006. Ecological persistence interrupted in Caribbean
- 931 coral reefs. *Ecology Letters* 9, 818–826.
- 932 Pandolfi, J. M. and Greenstein, B.J., 2007. Using the past to understand the future:
- 933 palaeoecology of coral reefs. In: Johnson, J. E. and Marshall, P. A. (Eds.), *Climate change*
- 934 *and the Great Barrier Reef: a vulnerability assessment*, Great Barrier Reef Marine Park
- 935 Authority and Australian Greenhouse Office, Australia, Chapter 22, 717–744.
- 936 Pandolfi, J. M., Connolly, S. R., Marshall, D. J., and Cohen, A. L., 2011. Projecting coral reef
- 937 futures under global warming and ocean acidification. *Science* 333, 418–422.
- 938 Perry, C. T., Smithers, S. G., Palmer, S. E., Larcombe, P., and Johnson, K. G., 2008. 1200
- 939 years paleoecological record of coral community development from the terrigenous inner
- 940 shelf of the Great Barrier Reef. *Geology* 36 (9), 691–694.
- 941 Perry, C. T., Smithers, S.G., 2009. Stabilization of intertidal cobbles and gravels by *Goniastrea*
- 942 *aspera*: an analogue for substrate colonization during marine transgressions? *Coral*
- 943 *Reefs* 28, 805–806.
- 944 Pratchett, M. S., Anderson, K. D., Hoogenboom, M. O., Widman, E., Baird, A. H., Pandolfi, J.
- 945 M., Edmunds, P. J., and Lough J. M., 2015. Spatial, temporal and taxonomic variation in
- 946 coral growth – implications for the structure and function of coral reef ecosystems.
- 947 *Oceanography and Marine Biology: An Annual Review* 53, 215–295.

- 948 Precht, W. F. and Aronson, R. B., 2004. Climate flickers and range shifts of reef corals.  
949 *Frontiers in Ecology and the Environment* 2 (6), 307–314.
- 950 Renema, W., Pandolfi, J. M., Kiessling, W., Bosellini, F. R., Klaus, J. S., Korpany, C., Rosen,  
951 B. R., Santodomingo, N., Wallace, C. C., Webster, J. M., and Johnson, K. G., 2016. Are  
952 coral reefs victims of their own past success? *Science Advances* 2 (4), e1500850, DOI:  
953 10.1126/sciadv.1500850.
- 954 Roche, R. C., Perry, C. T., Johnson, K. G., Sultana, K., Smithers, S. G., and Thompson, A. A.,  
955 2011. Mid-Holocene coral community data as baselines for understanding contemporary  
956 reef ecological states. *Palaeogeography, Palaeoclimatology, Palaeoecology* 299, 159–  
957 167.
- 958 Sagawa, N., Nakamori, T., and Iryu, Y., 2001. Pleistocene reef development in the southwest  
959 Ryukyu Islands, Japan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 175, 303–  
960 323.
- 961 Sanders, D. and Baron-Szabo, R. C., 2005. Scleractinian assemblages under sediment input:  
962 their characteristics and relation to the nutrient input concept. *Palaeogeography,*  
963 *Palaeoclimatology, Palaeoecology* 216, 139–181.
- 964 Sinniger, F., Morita, M., and Harii, S., 2013. “Locally extinct” coral species *Seriatopora hystrix*  
965 found at upper mesophotic depths in Okinawa. *Coral Reefs* 32, 153.
- 966 Sinniger, F., 2016. Mesophotic coral ecosystems examined: Ryukyu archipelago, Japan. In:  
967 Baker, E.K., Puglise, K.A., and Harris, P.T. (Eds.), *Mesophotic coral ecosystems: a lifeboat*  
968 *for coral reefs? The United Nations Environment Programme and GRID-Arendal, Nairobi*  
969 *and Arendal*, 43–44.
- 970 Szabo, B. J., Tracey, J. I., and Goter, E. R., 1985. Ages of subsurface stratigraphic intervals in  
971 the Quaternary of Enewetak Atoll, Marshall Islands. *Quaternary Research* 23, 54–61.
- 972 Treml, E. A., Halpin, P. N., Urban, D. L., and Pratson, L. F., 2008. Modeling population  
973 connectivity by ocean currents, a graph-theoretic approach for marine conservation.  
974 *Landscape Ecology* 23, 19–36.
- 975 Vargas-Ángel, B., Thomas, J. D., and Hoke, S. M., 2003. High-latitude *Acropora cervicornis*  
976 thickets off Fort Lauderdale, Florida, USA. *Coral Reefs* 22, 465–473.
- 977 Veron, J.E.N., 1995. *Corals in space and time: the biogeography and evolution of the*  
978 *Scleractinia*. UNSW Press, Sydney.
- 979 Veron, J. E. N., 2000. *Corals of the World*, 3 vols, Australian Institute of Marine Science,  
980 Townsville.
- 981 Wallace, C. C., 1999. *Staghorn Corals of the World: a revision of the coral genus Acropora*  
982 *(Scleractinia; Astrocoeniina; Acroporidae) worldwide, with emphasis on morphology,*  
983 *phylogeny and biogeography*. CSIRO Publishing, Melbourne, 421 pages.
- 984 Wallace, C. C., Chen, C. A., Fukami, H., and Muir, P. R., 2007. Recognition of separate genera  
985 within *Acropora* based on new morphological, reproductive and genetic evidence from

986 *Acropora togianensis*, and elevation of the subgenus *Isopora* Studer, 1878 to genus  
987 (Scleractinia: Astrocoeniidae; Acroporidae). *Coral Reefs* 26, 231–239.

988 Webb, G. E., Nothdurft, L. D., Zhao, J.-X., Opdyke, B., Price, G., and Eberli, G., 2016,  
989 Significance of shallow core transects for reef models and sea-level curves, Heron  
990 Reef, Great Barrier Reef. *Sedimentology*, DOI: 10.1111/sed.12266.

991 Webster, J. M., 1999. The response of coral reefs to sea level change: evidence from the  
992 Ryukyu Islands and the Great Barrier Reef. Doctoral Thesis, School of Geosciences,  
993 University of Sydney, 478 pages.

994 Webster, J. M. and Davies, P. J., 2003. Coral variation in two deep drill cores: significance for  
995 the Pleistocene development of the Great Barrier Reef. *Sedimentary Geology* 159 (1–2),  
996 61–80.

997 Webster, J. M., Yokoyama, Y., Cotterill, C., and the Expedition 310 Scientists, 2011.  
998 Proceedings of the IODP, 325, Integrated Ocean Drilling Program Management  
999 International, Inc, Tokyo.

1000 Woodroffe, C. D. and Webster, J.M., 2014. Coral reefs and sea-level change. *Marine Geology*  
1001 352, 248–267.

1002 Yamano, H., Sugihara, K., and Nomura, K., 2011. Rapid poleward range expansion of tropical  
1003 reef corals in response to rising sea surface temperatures. *Geophysical Research Letters*  
1004 38, L04601, DOI: 10.1029/2010GL046474.

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## 1007 **Figure and Table captions**

1008

1009 **Figure 1:** (A) Map showing the location of Ribbon Reef 5 and Boulder Reef in the northern  
1010 Great Barrier Reef and (B) detailed bathymetric map of Ribbon Reef 5 based on Laser  
1011 Airborne Depth Sounder (LADS) (0-40 m) and multibeam echo sounder (40-250 m) data  
1012 (Beaman et al., 2008). The yellow and white sticks show the approximate location of the deep  
1013 Ribbon Reef 5 bore hole and the shorter (<20 m) Holocene cores (Davies and Montaggioni,  
1014 1985). (C) Schematic profile of the continental shelf showing the broad geologic setting of the  
1015 onshore boreholes Ribbon Reef 5 and Boulder Reef and the offshore IODP 325 boreholes  
1016 (Webster et al., 2011).

1017

1018 **Figure 2:** (A) Representation of the core sections (1-125) of the Ribbon Reef 5 borehole with  
1019 (B) core recovery. The basic subdivisions of the borehole defined in previous publications are  
1020 presented in the other columns. (C) The three main sections of the borehole with boundaries  
1021 from Webster and Davies (2003). (D-F) Depositional reef units (R1-R8) and corresponding  
1022 variations in lithology and coralgall assemblages as described in Webster and Davies (2003).  
1023 (G) Depositional units (U1-U9) and lithological variations (H), reported in Braithwaite et al.

1024 (2004) (with U6 divided into U6a and U6b in Braithwaite and Montaggioni, 2009),  $\delta^{18}\text{O}$  and  
1025  $\delta^{13}\text{C}$  profiles (I, J) and age data (K) published in Braithwaite et al. (2004).

1026

1027 **Figure 3:** Cumulative numbers of corals as a function of depth (time). Note that the cumulative  
1028 number of non in situ corals (ISX) is an underestimation.

1029

1030 **Figure 4:** Bar charts showing the variations in some key morphological characteristics of  
1031 corals and coralline algae with depth: (A) thickness of coral colonies, (B) branch width of  
1032 *Acropora* and *Isopora* and (C) thickness of coralline algal crusts.

1033

1034 **Figure 5:** (A) Group-averaged hierarchical clustering of the BC coefficient calculated between  
1035 core sections based on taxonomic presence-absence data for in situ corals; (B) two-way table  
1036 showing the taxa indicative of each cluster (coral assemblage).

1037

1038 **Figure 6:** (A) Column showing the succession of in situ (IS, IS?) coral assemblages defined  
1039 by cluster analysis (using the same colour code as in Figure 5) and distribution of major  
1040 taxonomic groups in the borehole; (B) succession of coral associations (Po-Mo-Fa, Poc and  
1041 Acro-Iso) and reef cycles (Cy1-Cy8) defined on the basis of the sequence of coral taxa  
1042 presented in this study; (C) comparison of the depositional units of Webster and Davies (2003)  
1043 and of Braithwaite et al. (2004) (D) (modified by Braithwaite and Montaggioni, 2009).

1044

1045 **Figure 7:** (A) Group-averaged hierarchical clustering of the Bray-Curtis similarity coefficient  
1046 calculated between each reef cycles (Cy1-Cy8) and the lower unit (Lw); (B) the same analysis  
1047 but represented as a 2D MDS plot of the BC coefficient with the two clusters identified in (A)  
1048 circled in black; (C) the average similarity between reef cycles in each cluster and the results  
1049 of the ANOSIM test.

1050

1051 **Figure 8:** (A) Group-averaged hierarchical clustering of the Bray-Curtis similarity coefficient  
1052 calculated between borehole intervals assigned to one of the three coral associations (Po-Mo-  
1053 Fa, Poc and Acro-Iso) and the lower unit (Lw); (B) the same analysis but represented as a 2D  
1054 MDS plot of the BC coefficient with colours identifying each interval as belonging to the  
1055 association Po-Mo-Fa (black), Poc (orange), Acro-Iso (blue) and the lower unit (purple); (C)  
1056 the average similarity within each group of intervals assigned to a coral association and the  
1057 results of the ANOSIM test.

1058

1059 **Figure 9:** (A) Group-averaged hierarchical clustering of the BC coefficient calculated between  
1060 core sections based on taxonomic presence-absence data for non-in situ (ISX) corals; (B) two-  
1061 way table showing the taxa indicative of each cluster (coral assemblage).

1062

1063 **Figure 10:** Columns showing (A) the succession of non in situ (ISX) coral assemblages  
1064 defined by cluster analysis (using the same colour code as in Figure 8), (B) the distribution of  
1065 coral associations described in this paper and (C) the succession of reef cycles against  
1066 stacked area charts showing the variations in the number of non-in situ corals identified in  
1067 each core section for various major coral taxa.

1068

1069 **Figure 11:** Bar chart of the number of *Acropora* recorded in each core section for in situ (IS)  
1070 and non in situ (ISX) specimens. The asterisks indicate core sections in which the number of  
1071 non-in situ *Acropora* was likely underestimated. (A) Above the bar chart are displayed the  
1072 available chronologic data for the Ribbon Reef 5 borehole, (B) the reef cycles and coral  
1073 associations defined in this paper, (C) the depositional units published in Braithwaite and  
1074 Montaggioni (2009), and (D) those defined by Webster and Davies (2003).

1075

1076 **Figure 12:** Schematic representation of the coral associations and their successions in the  
1077 reef cycles identified in the Ribbon Reef 5 borehole, and selected images of coral colonies  
1078 typical of each association. Corals displayed are considered in situ unless stated otherwise in  
1079 this caption. Acro-Iso association, 1. *Acropora* gr. *humilis* (core 70-1), 2. *Acropora* gr. *formosa*  
1080 (core 46-3), 3. *Acropora* gr. *robusta* (cores 9-1, 9-3), 4. massive *Isopora* (core 63-3), 5.  
1081 branching *Isopora* (core 38-2). Po-Mo-Fa association, 6. *Platygyra* gr. *sinensis*, 7-8.  
1082 unidentified corals, 9. *Montipora* (core 29-7), 10. *Porites* (core 20-1), 11. *Montipora* (core 41-  
1083 3), 12. *Goniastrea edwardsi* (core 80-1). Poc association, 13. *Seriatopora hystrix* (core 55-5),  
1084 14-15. *Stylophora pistillata* (cores 56-19, 76-7). Mesophotic association, 16. *Echinophyllia*  
1085 (core 117-5), 17. *Porites* (core 117-2), 18-19. *Seriatopora hystrix* (not in situ), 20. *Porites* (core  
1086 125-5). The scale bar is 5 cm.

1087

1088 **Table 1:** Comparison of criteria used to define depositional unit boundaries.

1089

1090 **Table 2:** List of coral taxa identified in the Ribbon Reef 5 borehole.

1091

1092 **Table 3:** Results of the similarity percentage analysis (SIMPER).

1093

1094 **Supplementary figure S1:** Distribution of in situ (IS, IS?) and non in situ (ISX) coral taxa in  
1095 the Ribbon Reef 5 borehole identified in this study. Each coral is represented by a horizontal  
1096 bar (solid fill: IS, IS? no fill: ISX). Corals displayed in the column Po/Mo are those for which  
1097 the distinction between *Porites* and *Montipora* could not be made and include mainly thin  
1098 encrusting colonies. Bar charts showing the variations in the thickness of in situ corals and  
1099 algal crusts in the borehole are also shown.

1100

1101 **Supplementary figure S2:** (A) Group-averaged hierarchical clustering of the BC coefficient  
1102 calculated between core sections based on the square root of abundance data for in situ  
1103 corals; (B) two-way table showing the taxa indicative of each cluster (coral assemblage).

1104

1105 **Supplementary figure S3:** Columns showing the succession of in situ (IS, IS?) coral  
1106 assemblages defined by cluster analyses: (A) analysis of presence-absence data and (B)  
1107 analysis of the square root of abundance data.

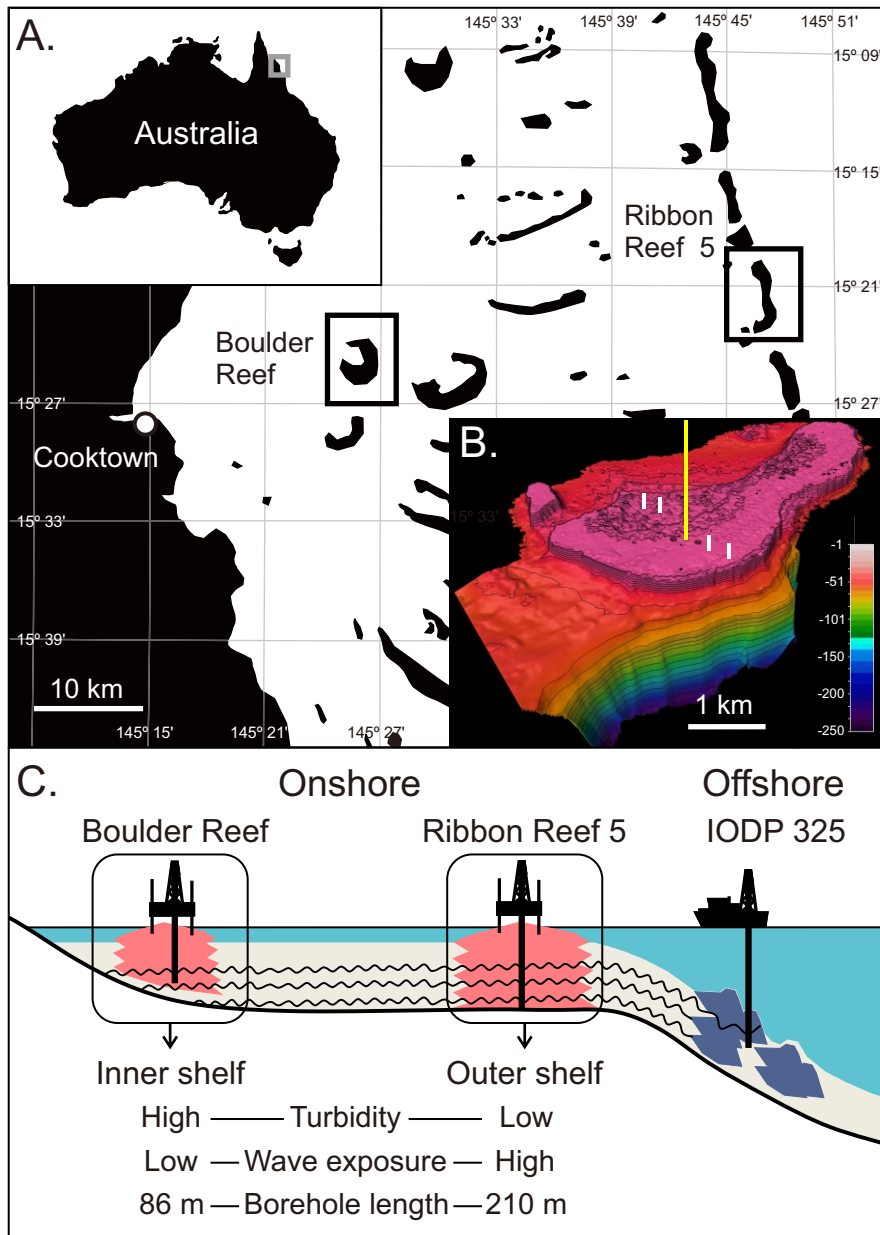


Figure 1

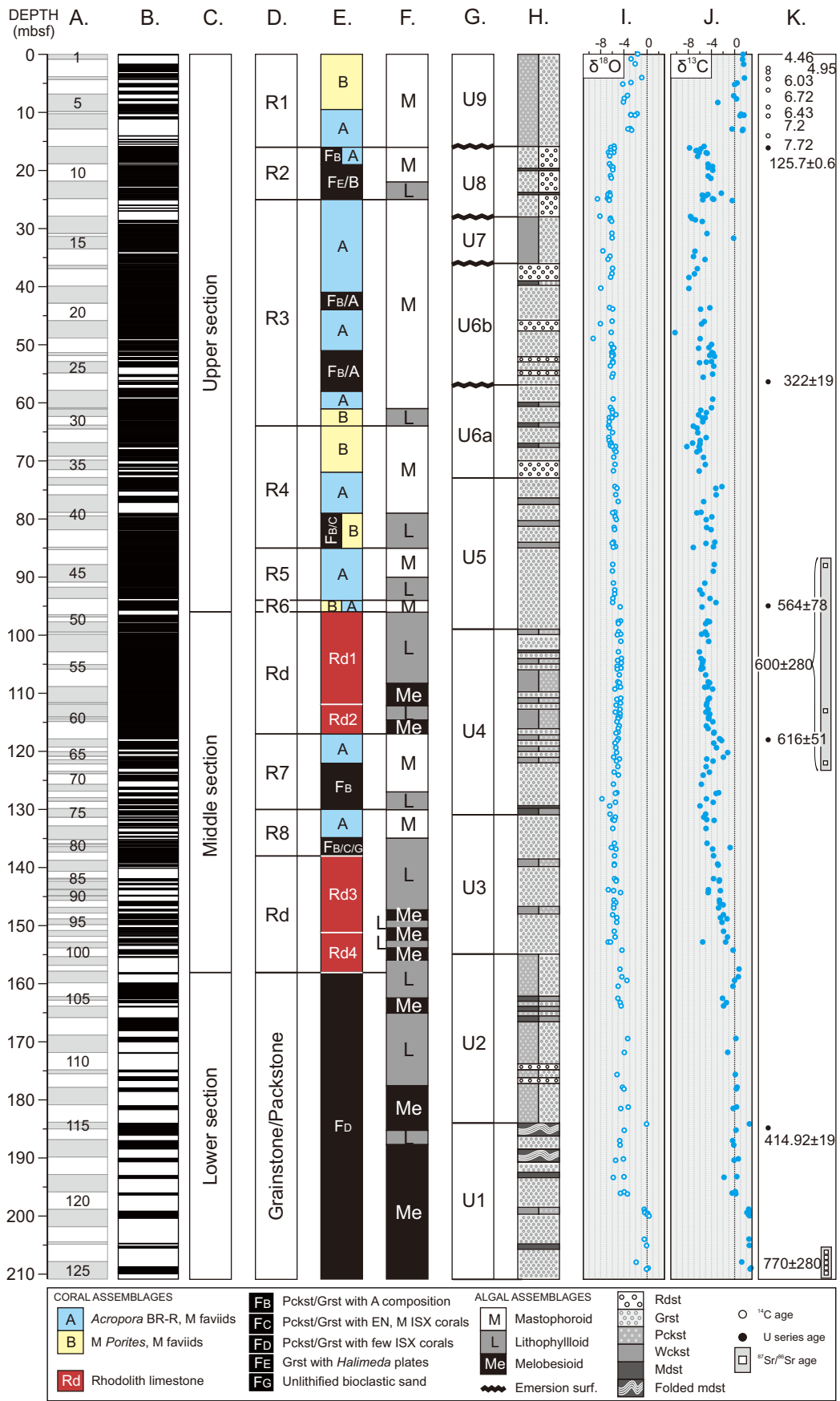


Figure 2



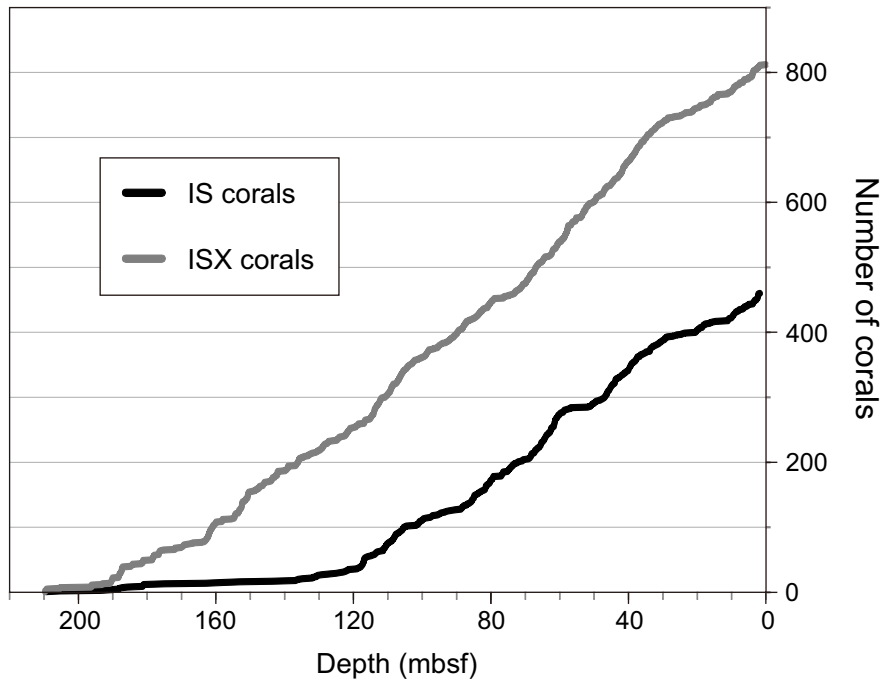


Figure 3

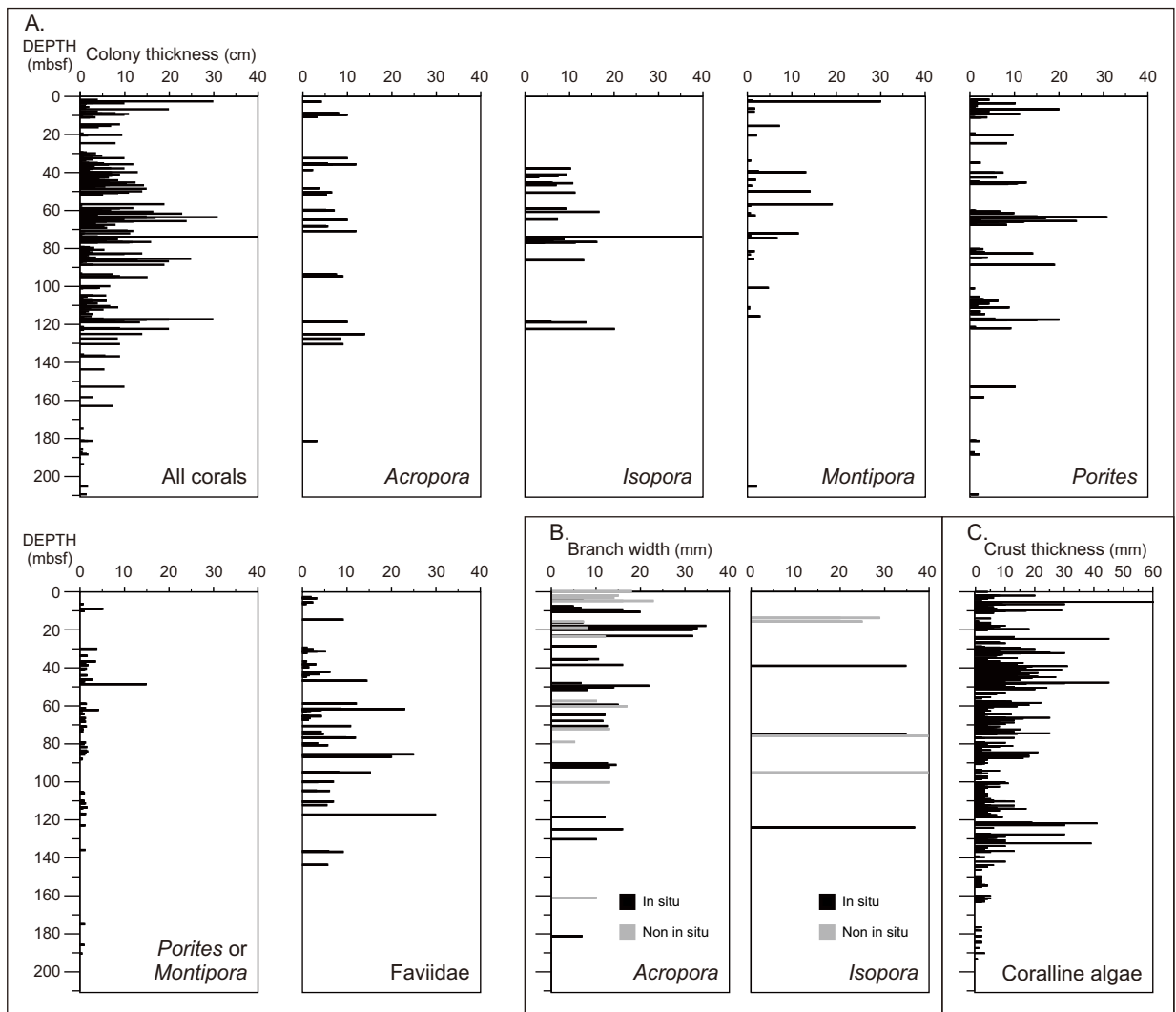


Figure 4

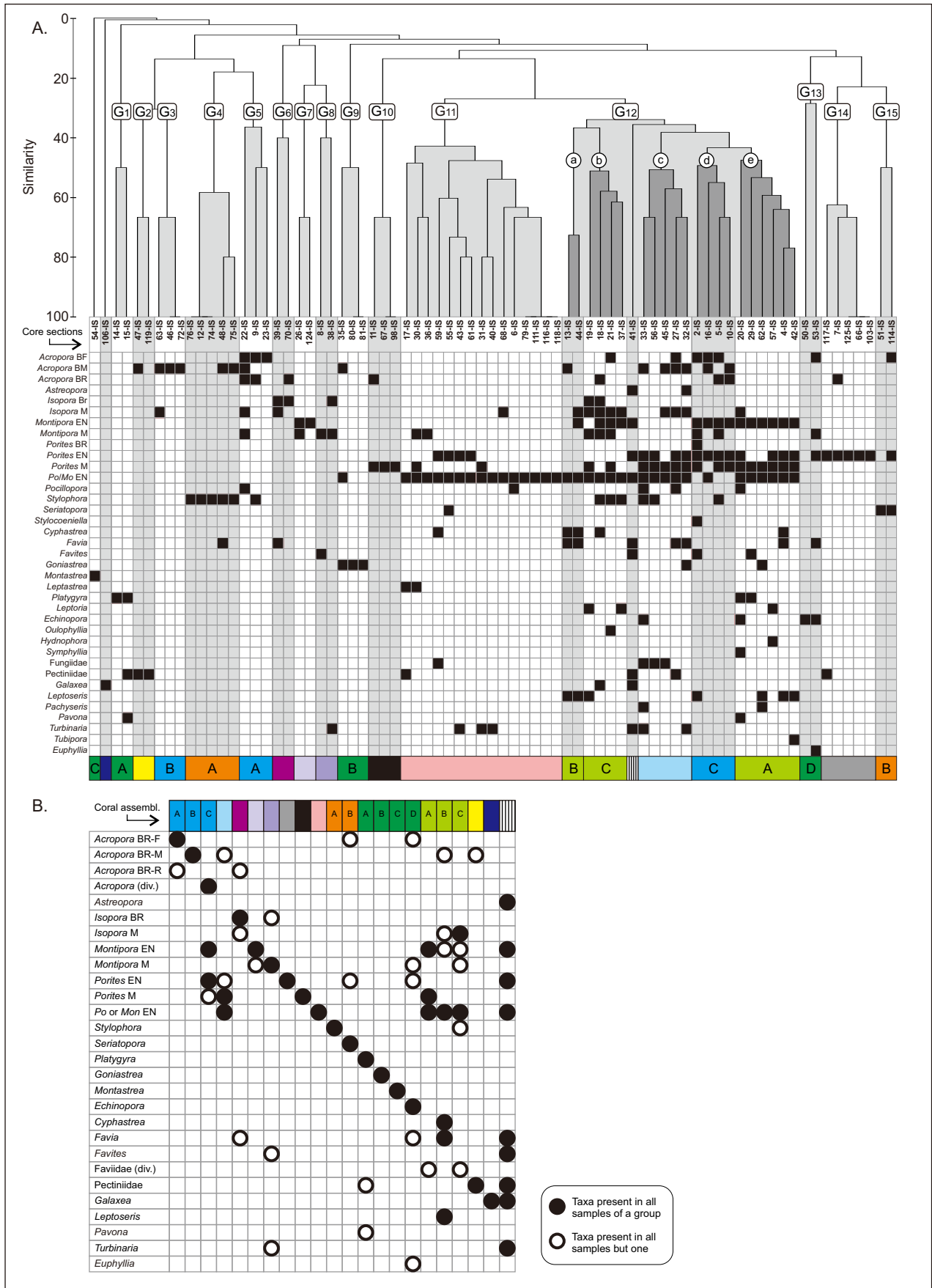


Figure 5

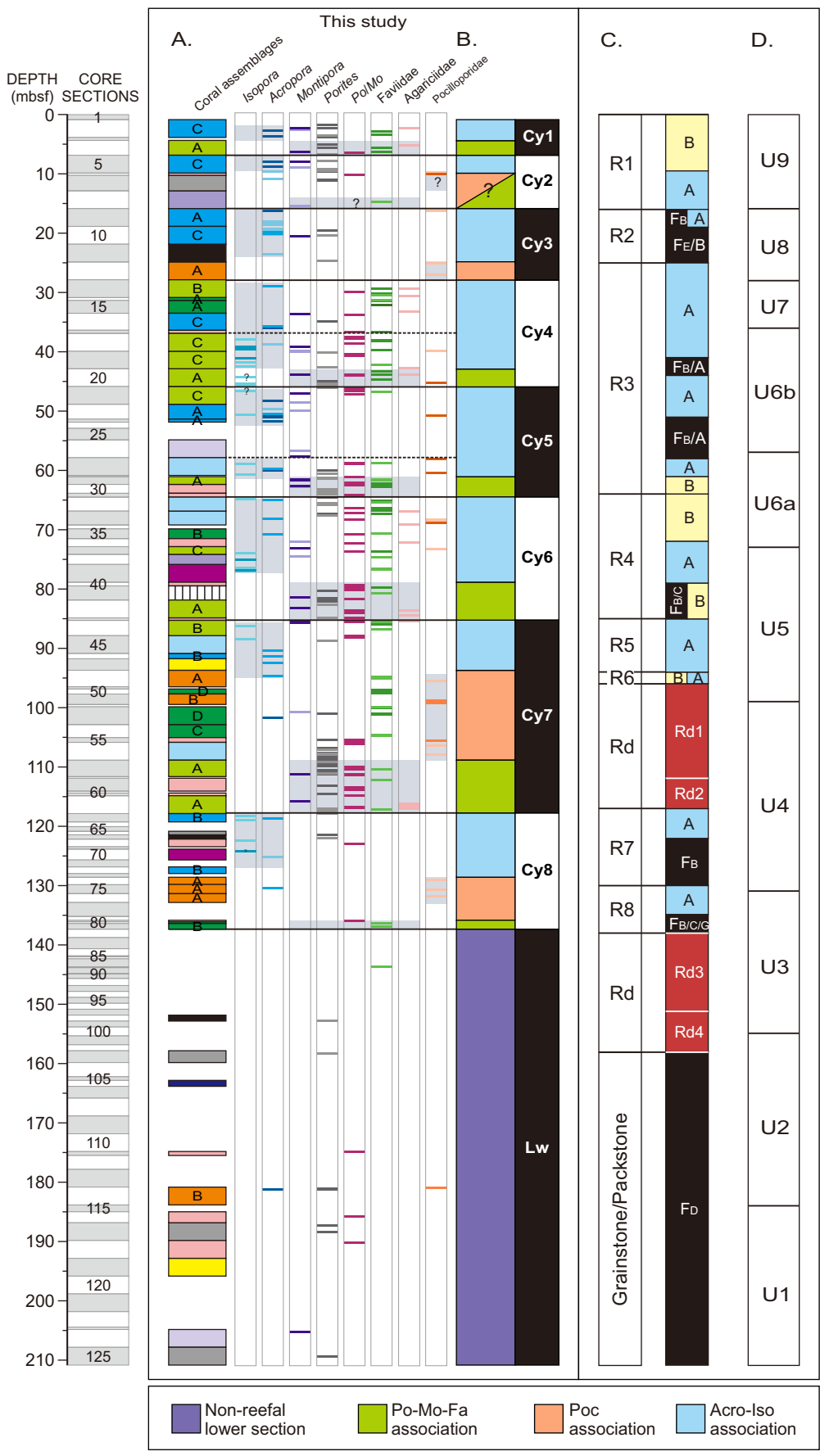


Figure 6

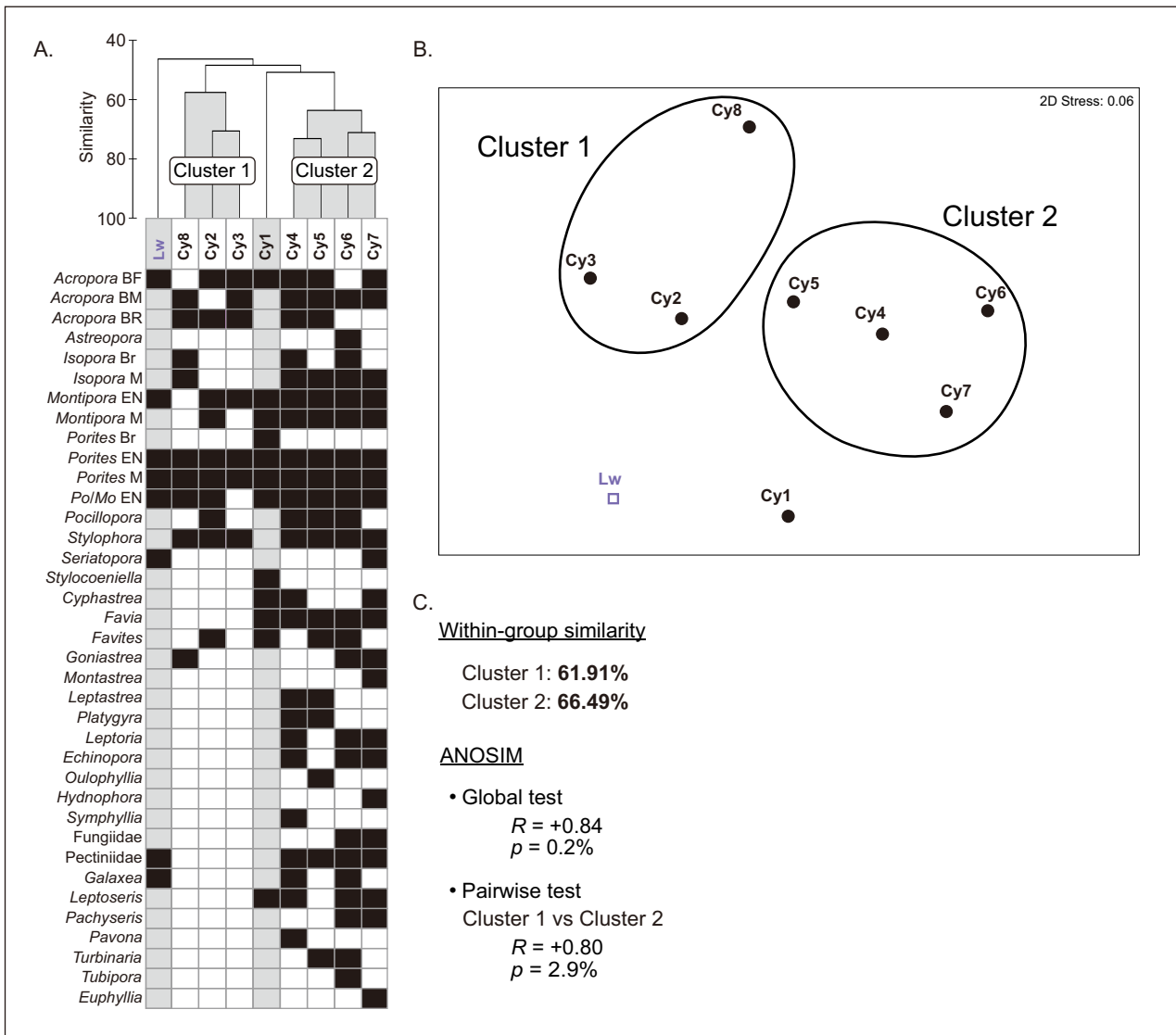


Figure 7

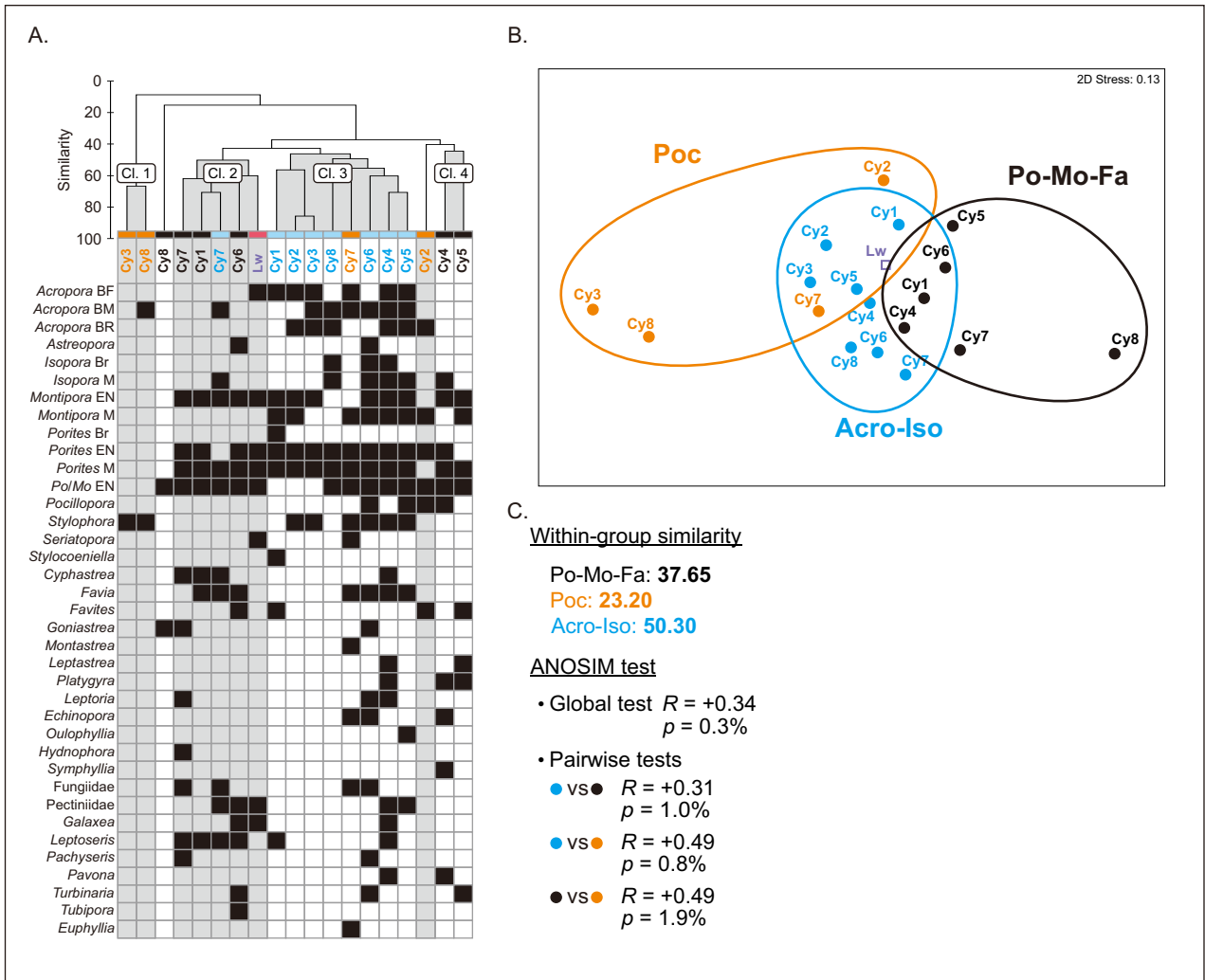


Figure 8

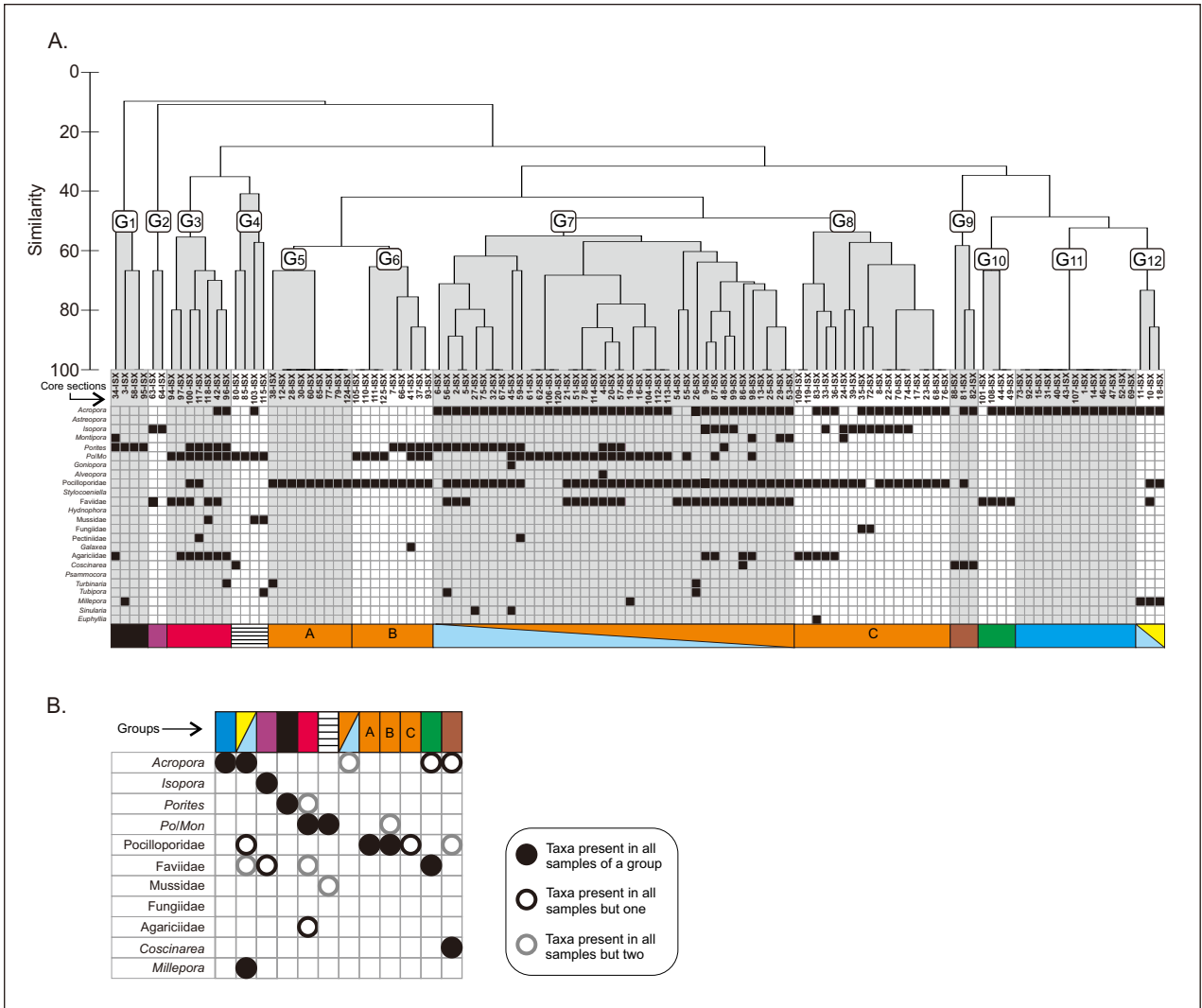


Figure 9

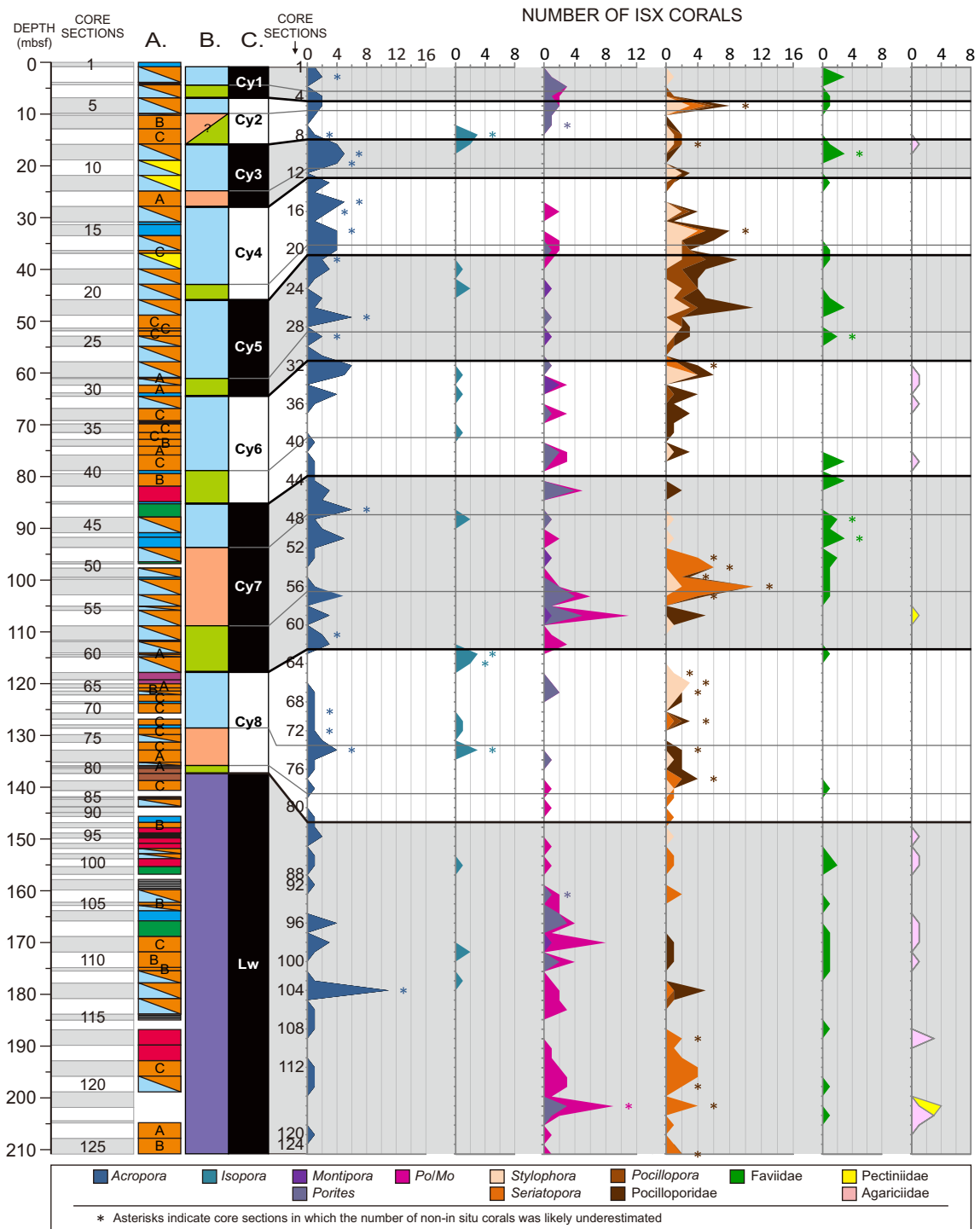


Figure 10



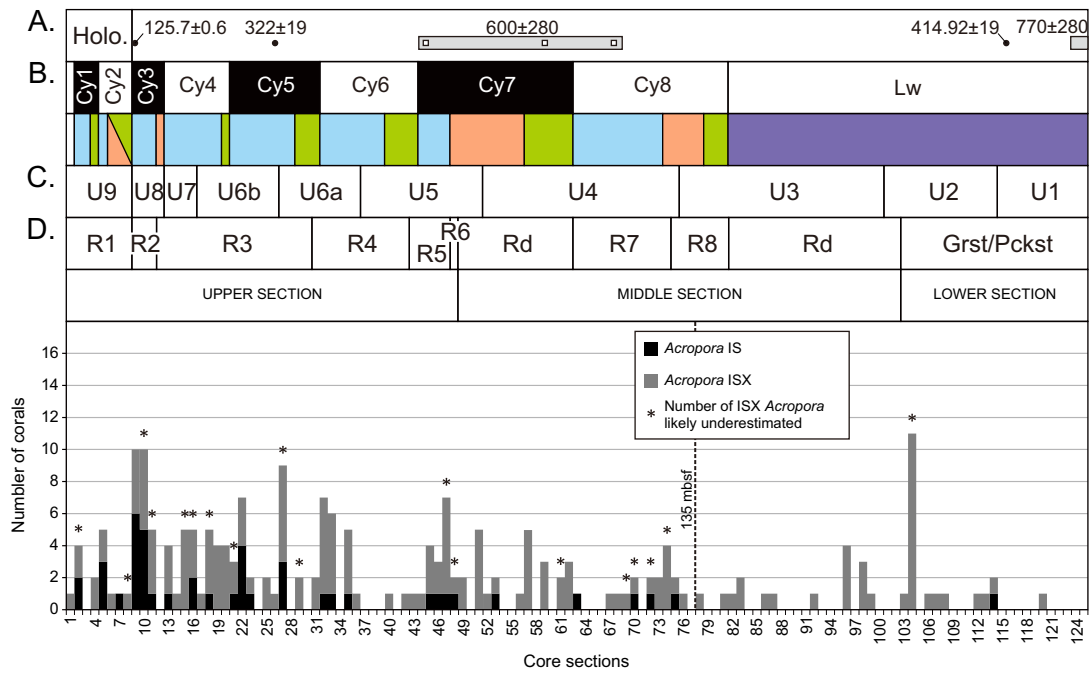


Figure 11

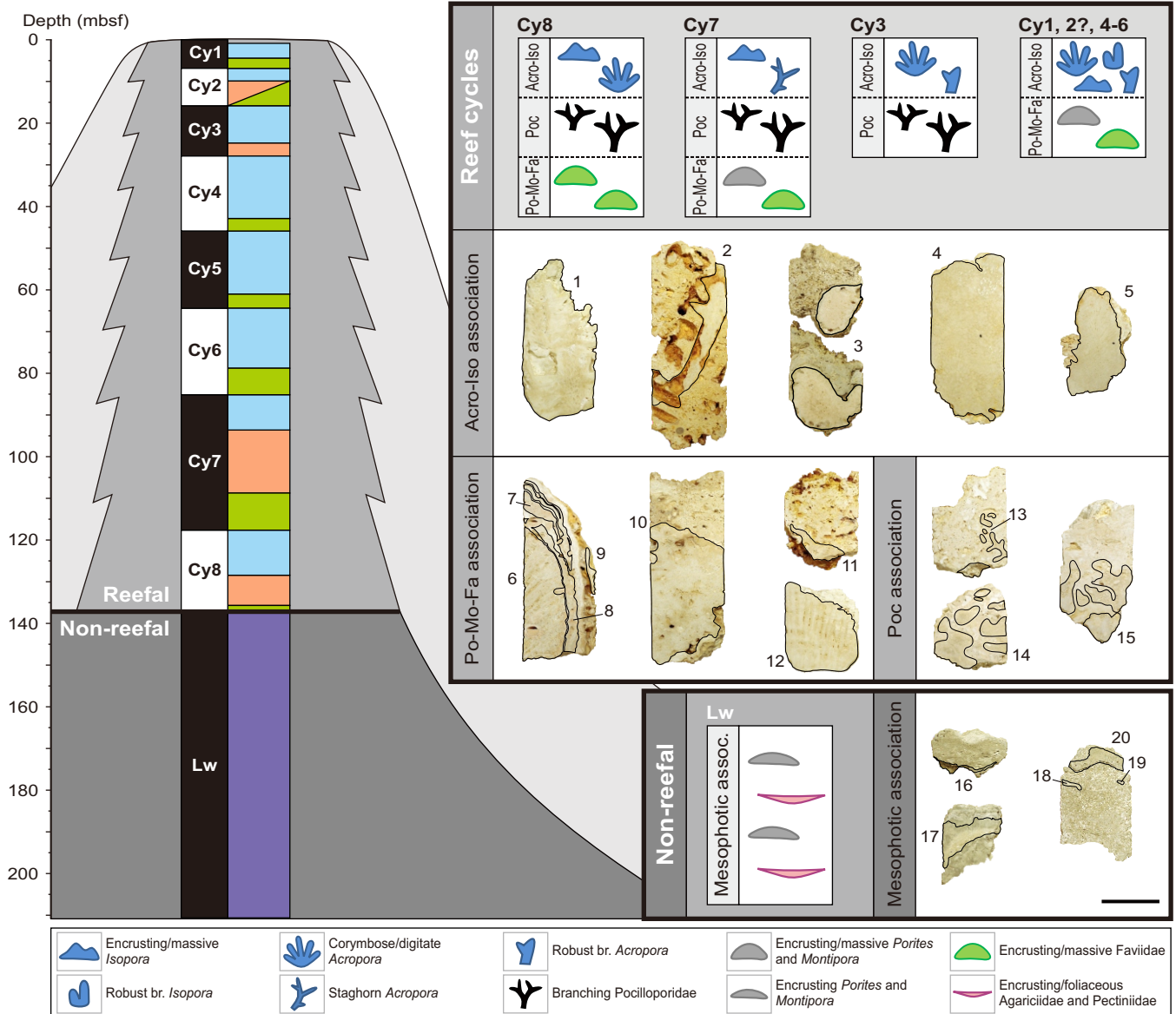


Figure 12



Table 2.

List of coral taxa identified in the Ribbon Reef 5 borehole.

SCLERACTINIAN CORALS		NON-SCLERACTINIAN CORALS	
1. Acroporidae	10. Stylophora	6. Mussidae	15. Tubiporidae
1. <i>Acropora</i>	23. <i>S. pistillata</i>	23. <i>Symphyllia</i>	35. <i>Tubipora</i>
1. <i>A. sp. 1</i> (BRF ARB)	11. Pocillopora	44. <i>S. sp.</i>	59. <i>T. musica</i>
2. <i>A. sp. 2</i> (BRF COR)	24. <i>P. verrucosa</i>	7. Euphyllidae?	16. Milleporidae
3. <i>A. sp. 3</i> (BRF DIG)	5. Faviidae	24. <i>Euphyllia?</i>	36. <i>Millepora</i>
4. <i>A. sp. 4</i> (BRF TUB) <sup>ISX</sup>	12. <i>Caulastrea</i>	45. <i>E. sp.?</i>	60. <i>M. sp.</i>
5. <i>A. sp. 5</i> (BRM ARB)	25. <i>C. furcata</i> <sup>ISX</sup>	8. Oculinidae	17. Alcyonidae
6. <i>A. gr. hyacinthus</i> (PLATY)	13. <i>Favia</i>	25. <i>Galaxea</i>	37. <i>Sinularia</i>
7. <i>A. gr. formosa</i> (STAG)	26. <i>F. ? sp. 1*</i>	46. <i>G. astreata</i>	61. <i>S. sp.</i>
8. <i>A. gr. humilis</i> (DIG, COR)	27. <i>F. stelligera</i>	47. <i>G. fascicularis</i> <sup>ISX</sup>	
9. <i>A. gr. robusta?</i>	28. <i>F. laxa</i>	9. Siderastreidae	
2. <i>Isopora</i>	29. <i>F. gr. pallida</i>	26. <i>Coscinarea</i>	
10. <i>I. sp. 1</i> (BR)	14. <i>Favites</i>	48. <i>C. gr. columna</i>	
11. <i>I. sp. 2</i> (EN-M)	30. <i>F. pentagona</i> <sup>ISX</sup>	10. Agarciidae	
3. <i>Astreopora</i>	31. <i>F. gr. abdita</i>	27. <i>Pavona</i>	
12. <i>A. sp.</i>	15. <i>Goniastrea</i>	49. <i>P. clavus</i> <sup>ISX</sup>	
4. <i>Montipora</i>	32. <i>G. retiformis</i>	28. <i>Leptoseris</i>	
13. <i>M. sp. 1</i> (EN)	33. <i>G. edwardsii</i>	50. <i>L. foliosa?</i> <sup>ISX</sup>	
14. <i>M. sp. 2</i> (M)	16. <i>Platygyra</i>	51. <i>L. gardineri?</i> <sup>ISX</sup>	
2. Poritidae	34. <i>P. pini</i>	29. <i>Pachyseris</i>	
5. <i>Porites</i>	35. <i>P. gr. sinensis</i>	52. <i>P. rugosa</i>	
15. <i>P. sp. 1</i> (BR)	17. <i>Leptoria</i>	53. <i>P. speciosa</i>	
16. <i>P. sp. 2</i> (KN)	36. <i>L. phrygia</i>	11. Fungiidae	
17. <i>P. sp. 3</i> (EN)	18. <i>Oulophyllia</i>	30. <i>Fungia</i>	
18. <i>P. sp. 4</i> (M)	37. <i>O. sp.</i>	54. <i>F. sp.</i>	
6. <i>Goniopora</i>	19. <i>Montastrea</i>	31. <i>Cycloseris</i>	
19. <i>G. sp.</i> <sup>ISX</sup>	38. <i>M. curta</i>	55. <i>C. sp.</i>	
7. <i>Alveopora</i>	20. <i>Leptastrea</i>	12. Pectiniidae	
20. <i>A. sp.</i> <sup>ISX</sup>	39. <i>L. pruinosa</i>	32. <i>Echinophyllia</i>	
3. Astrocoeniidae?	21. <i>Echinopora</i>	56. <i>E. echinata?</i> <sup>ISX</sup>	
8. <i>Stylocoeniella?</i>	40. <i>E. lamellosa</i>	13. Merulinidae	
21. <i>S. sp.</i>	41. <i>E. mammiformis</i>	33. <i>Hydnophora</i>	
4. Pocilloporidae	42. <i>E. gemmacea</i> <sup>ISX</sup>	57. <i>H. sp.</i>	
9. <i>Seriatopora</i>	22. <i>Cyphastrea</i>	14. Dendrophylliidae	
22. <i>S. hystrix</i>	43. <i>C. serailia</i>	34. <i>Turbinaria</i>	
		58. <i>T. sp.</i>	

ISX The superscript ISX indicates taxa recorded only in the non-in situ fraction.

Table 2

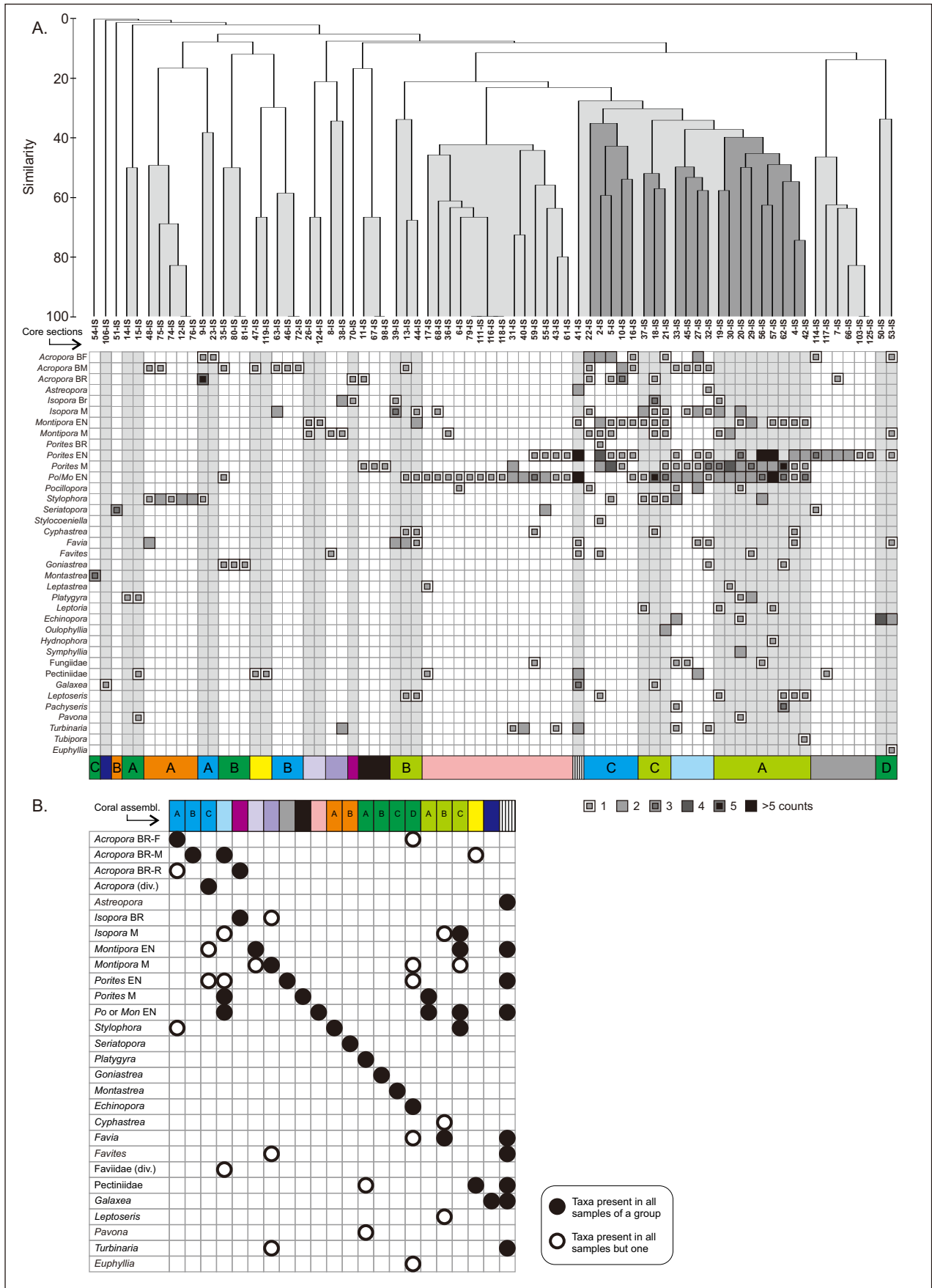
Table 3.  
Results of the similarity percentage analysis (SIMPER).

A. Comparison of reef cycles <sup>a</sup>						B. Comparison of coral associations <sup>b</sup>					
	Av.Abund <sup>c</sup>	Av.Sim	Sim/SD <sup>d</sup>	Contrib%	Cum.% <sup>e</sup>		Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<u>Cluster 1</u>						<u>Po-Mo-Fa assoc.</u>					
<i>Acropora</i> BR	1.00	11.60	11.63	18.73	18.73	<i>Po/Mo</i>	1.00	12.95	3.19	34.39	34.39
<i>Porites</i> EN	1.00	11.60	11.63	18.73	37.47	<i>Montipora</i> EN	0.83	7.05	1.34	18.71	53.10
<i>Porites</i> M	1.00	11.60	11.63	18.73	56.20	<i>Porites</i> M	0.83	7.05	1.34	18.71	71.82
<i>Stylophora</i>	1.00	11.60	11.63	18.73	74.93	<i>Porites</i> EN	0.67	4.05	0.78	10.75	82.57
<i>Acropora</i> BM	0.67	4.17	0.58	6.73	81.66						
<u>Cluster 2</u>						<u>Poc assoc.</u>					
<i>Acropora</i> BM	1.00	4.67	16.48	7.02	7.02	<i>Stylophora</i>	0.75	15.71	0.61	67.73	67.73
<i>Isopora</i> M	1.00	4.67	16.48	7.02	14.03	<i>Acropora</i> BM	0.50	2.22	0.41	9.58	77.31
<i>Montipora</i> EN	1.00	4.67	16.48	7.02	21.05	<i>Montipora</i> M	0.50	1.75	0.41	7.56	84.88
<i>Montipora</i> M	1.00	4.67	16.48	7.02	28.07						
<i>Porites</i> EN	1.00	4.67	16.48	7.02	35.09	<u>Acro-Iso assoc.</u>					
<i>Porites</i> M	1.00	4.67	16.48	7.02	42.10	<i>Porites</i> M	1.00	9.41	3.46	18.71	18.71
<i>Po/Mo</i>	1.00	4.67	16.48	7.02	49.12	<i>Porites</i> EN	0.88	6.98	1.45	13.88	32.59
<i>Stylophora</i>	1.00	4.67	16.48	7.02	56.14	<i>Montipora</i> EN	0.88	6.63	1.49	13.19	45.78
<i>Favia</i>	1.00	4.67	16.48	7.02	63.15	<i>Acropora</i> BM	0.75	4.54	0.97	9.03	54.81
Pectiniidae	1.00	4.67	16.48	7.02	70.17	<i>Acropora</i> BR	0.63	3.55	0.68	7.07	61.88
<i>Acropora</i> BF	0.75	2.39	0.91	3.59	73.76	<i>Acropora</i> BF	0.63	3.38	0.69	6.72	68.60
<i>Pocillopora</i>	0.75	2.35	0.91	3.54	77.30	<i>Stylophora</i>	0.63	2.91	0.69	5.79	74.38
<i>Leptoria</i>	0.75	2.21	0.91	3.32	80.61	<i>Montipora</i> M	0.63	2.78	0.70	5.53	79.91
						<i>Isopora</i> M	0.63	2.72	0.70	5.41	85.32

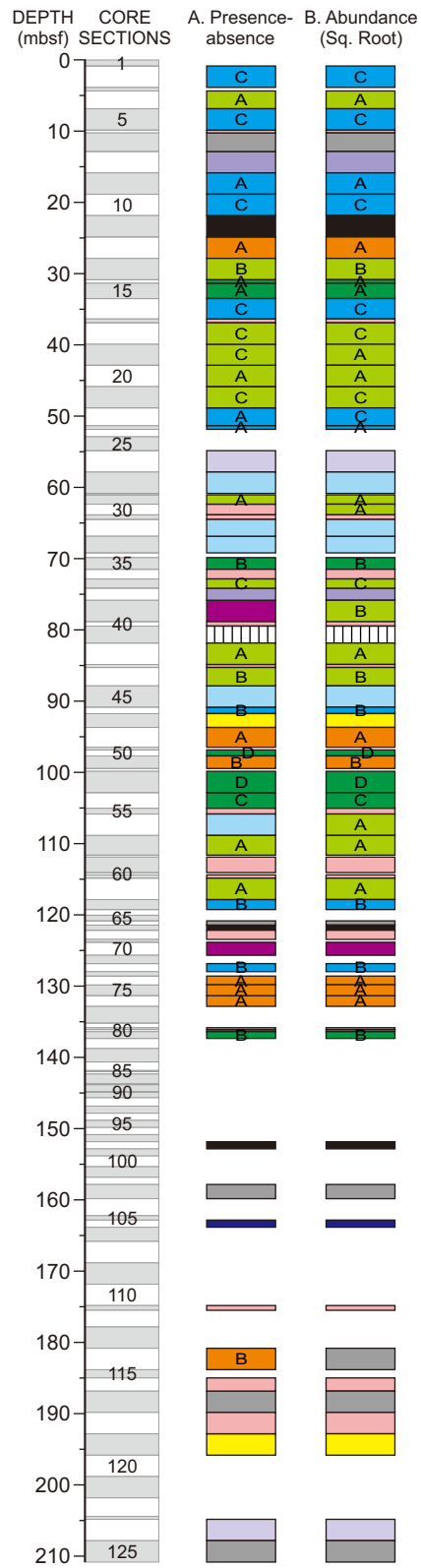
- a Results of the similarity percentage analysis for the two clusters identified in figure 6.  
b Results of the similarity percentage analysis for the three coral associations (Po-Mo-Fa, Poc and Acro-Iso).  
c Frequency of occurrence (1.00 meaning the coral occurs in 100% of the samples).  
d Ratio of the contribution of a taxon to the average similarity of a group (SIM) to the standard deviation of their contribution (SD). Taxa with the highest Sim/SD are present most consistently among the samples of a group.  
e The listed corals are those which account for 80-85% of the within-group similarity.

Table 3





Supplementary figure S2



Supplementary figure S3