Biogeography of Holocene coral species in the western Indian

Ocean

Running title: Biogeography of Holocene coral species

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30 Abstract

31 Understanding the relationship between coral biogeography and reef development is a
32 key topic in sedimentology and paleoecology. Although the knowledge of coral reef
33 growth and internal facies patterns during the Holocene has increased since the 1970s,
34 the biogeography of Holocene coral species in the Indo-Pacific regions remains poorly
35 constrained. In this study, we examined quantitative records of coral species based on
36 data from five cores retrieved from two Holocene reefs in the western Indian Ocean: La
37 Pointe-au-Sable reef on Mauritius Island and Toliara reef on Madagascar. Our results
38 indicate that the dominant reef-building corals on both reefs were *Isopora palifera*,
39 *Acropora robusta/abrotanoides* complex. Some corals (e.g., the *A.*
40 *robusta/abrotanoides* complex and *Acropora digitifera*) from 6 ka were found in
41 Mauritius, whereas these were not identified in the cores from Madagascar before 1.5–1
42 ka. This delay may have been controlled by ocean currents and/or the competency
43 period of the coral larvae. A comparison of these coral assemblages with those in other
44 regions (Seychelles, Mayotte, Ryukyu Islands, Palau Islands, Papua New Guinea, the
45 Great Barrier Reef, New Caledonia, and Vanuatu) showed that *I. palifera* was common
46 in all of the studied regions, whereas *Goniastrea retiformis* probably migrated recently
47 to Mauritius and Madagascar in response to prevailing surface ocean currents,

48 including the South Equatorial Current and the Agulhas Current. One explanation for
49 the late arrival of *G. retiformis* to the study sites could be that the competency period of
50 *G. retiformis* larvae is shorter than that of *I. palifera*. Moreover, our quantitative
51 analysis suggests that a given population size during the Holocene may have
52 contributed to the abundance of species in modern reefs. This study emphasizes the
53 need for further quantitative research on Holocene coral species in other regions to
54 better understand the temporal and spatial patterns of coral biogeography.

55

56 **Keywords** Coral, Paleoecology, Biogeography, Indo-Pacific, Holocene

57 1. Introduction

58 The origin, distribution, and diversity of reef-building coral species are
59 controlled by physical factors (e.g., sea surface temperature (SST), salinity, light
60 intensity, hydrodynamic factors, ocean circulation, and sediment input), biological
61 factors (e.g., spawning mode and competency period), and geological factors (plate
62 tectonics, substrate availability, closure and opening of seaways, global cooling and
63 warming events, and sea-level fluctuations) (Grigg and Hey, 1992; Pandolfi, 1992;
64 Veron, 1995). At present, the numbers and abundances of coral species recorded in
65 Indo-Pacific provinces are spatially variable. For example, over 200 coral species have
66 been recorded in the Indian Ocean (Veron, 1995), whereas up to 350 species have been
67 recorded around Australia (Spalding et al., 2001). The dominant species also vary
68 among the regions (e.g., the western Indian Ocean, the northwest Pacific, and the
69 southwest Pacific), although the major reefal environmental conditions are reasonably
70 similar throughout the tropical zone. At present in the western Indian Ocean, *A.*
71 *digitifera*, *Acropora humilis*, and *Acropora abrotanoides*, all with wave-resistant growth
72 forms, dominate the coral assemblages in the reef crest zone of Mauritius (Montaggioni
73 and Faure, 1997). In the northwest Pacific, *A. digitifera*, *A. hyacinthus*, and *G. retiformis*
74 are currently the dominant forms in the same zone in Ishigaki Island in the Ryukyu

75 Islands (Hongo and Kayanne, 2010), whereas *A. humilis*, *A. digitifera*, and *A.*
76 *hyacinthus* are prominent taxa on the Ngemelis barrier reef in the Palau Islands
77 (Kayanne et al., 2002). In the southwest Pacific, *A. humilis* and *I. palifera* are prominent
78 taxa in the reef-crest zone in the central Great Barrier Reef (Done, 1982). On Huon
79 Peninsula, Papua New Guinea, *A. hyacinthus*, *A. humilis*, *Acropora monticulosa*, and *A.*
80 *robusta* are dominant species (Nakamori et al., 1995a). In New Caledonia, *A. digitifera*,
81 *A. humilis*, *A. abrotanoides*, *A. robusta*, *Acropora milleopora*, *Acropora valida*, and
82 *Pocillopora verrucosa* are dominant species on the Ricaudy Reef (Cabioch et al., 1999).
83 One explanation for the local differences in the composition of coral species is the
84 pattern of gene flow, demonstrated with molecular data (e.g., allozymes and
85 mitochondrial DNA). These show that the distribution of coral reef species across the
86 Indo-Pacific regions does not reflect the modern ocean circulation regimes (Benzie,
87 1999). Therefore, the present patterns of genetic variation in the Indo-Pacific may have
88 resulted from highly pulsed dispersal events associated with coral range expansions
89 during interglacial periods. Moreover, during the last glacial maximum (LGM), coral
90 reefs in the Indo-Pacific region were isolated by barriers that emerged during low sea-
91 level stands, such that corals in the Red Sea, Madagascar, Maldives, and southwest
92 Asia–Australia regions were isolated from one another (Benzie, 1999; Pelissier et al.,

2014). Thus, most coral species survived the last glacial period in isolated refuges (Veron, 1995), and the pool of modern coral species in a given region would have been repopulated from these pre-existing refuges during deglacial sea-level rise (Veron, 1995). However, stages of reef-building and the temporal and spatial patterns of coral species in Indo-Pacific regions during the last deglaciation are still largely unknown.

Quantitative data on the temporal and spatial patterns of fossil coral species in Indo-Pacific regions are probably essential if we are to identify the factors that control the abundance of corals on modern reefs. These data relate to the percentage abundances of the corals, derived with paleontological and/or ecological methods (e.g., quadrat and/or belt transects, binary presence/absence data). A small coral population probably means that the population has been isolated. Such isolation may cause a reduction in genetic diversity from genetic drift. This implies that the relevant coral species are likely to have a limited capacity to respond to environmental change (Ayre and Hughes, 2004). It also implies that the long-term dominant species at a given reef site probably contribute to the dominant species on the modern reef, although a variety of environmental factors can change, affecting the composition of the coral population.

Although coral samples extracted with reef coring have been identified at the species level, most previous studies have been limited to qualitative analyses of coral

111 assemblage compositions, with the aim of reconstructing the history of Holocene reef
 112 development in relation to environmental changes (e.g., Montaggioni, 2005; Bard et al.,
 113 2010; Roff et al., 2013). The most detailed descriptions of reef development come from
 114 regions with low species diversity, such as the Caribbean, or from exposed but well-
 115 preserved reefal outcrops in tectonically active areas, such as in Papua New Guinea and
 116 the Ryukyu Islands (Table 1). For example, Nakamori et al. (1995b) reported that the
 117 Holocene reef terraces at Kanzaura and Kwambu in Papua New Guinea are dominated
 118 by *A. humilis*, *I. palifera*, *A. hyacinthus*, and *A. monticulosa*. At Kikai Island in the
 119 Ryukyu Islands, Holocene reefs are predominantly composed of tabular and massive
 120 corals (*A. humilis*, *A. hyacinthus*, *A. monticulosa*, *I. palifera*, *Leptoria phrygia*, *Porites*
 121 *australiensis*, *Porites lutea*, *Porites lobata*, and *P. verrucosa*) (Webster et al., 1998;
 122 Sugihara et al, 2003). Only a few studies have focused on the time spanning the last
 123 deglaciation (for instance, Tahiti: Montaggioni et al., 1997; Abbey et al., 2011; the Great
 124 Barrier Reef: Webster and Davies, 2003; Papua New Guinea: Nakamori et al., 1995b,
 125 Pandolfi et al., 2006; Palau Islands: Hongo and Kayanne, 2011; New Caledonia: Hongo
 126 and Wirrmann, 2015; Mayotte: Camoin et al., 1997, 2004; Seychelles: Camoin et al.,
 127 2004; Mauritius: Montaggioni and Faure, 1997). At Ribbon Reef 5 and Boulder Reef on
 128 the Great Barrier Reef, the *A. robusta/abrotanoides* complex, *A. humilis/monticulosa*

129 complex, *I. palifera*, *Stylophora pistillata*, and *P. verrucosa* are the main contributors to
 130 Holocene reef formation (Webster and Davies, 2003). In the Ryukyu Islands, *Astrea*
 131 *curta*, *A. digitifera*, *A. hyacinthus*, and *Dipsastraea stelligera*, have been the dominant
 132 species in reef-crest formation on Ishigaki Island since 7.8 ka (1 ka = 1000 years ago)
 133 (Hongo and Kayanne, 2009). *Acropora digitifera*, the *A. robusta/abrotanoides* complex,
 134 and the *Acropora muricata/intermedia* complex have been the dominant reef-crest
 135 builders on the Palau Islands since 8.3 ka (Hongo and Kayanne, 2011). At Mayotte, the
 136 *A. robusta/abrotanoides* complex and *G. retiformis* have been the dominant reef
 137 builders since 9.6 ka (Camoin et al., 1997, 2004). In the Seychelles, the *A.*
 138 *robusta/abrotanoides* complex, *G. retiformis*, *P. verrucosa*, *Galaxea fascicularis*, *L.*
 139 *phrygia*, and *S. pistillata* have been the main contributors to reef formation since 7.9 ka
 140 (Camoin et al., 2004). In New Caledonia, the *A. hyacinthus/cytherea* complex,
 141 *Montipora digitata*, *I. palifera*, and the *A. robusta/abrotanoides* complex have been
 142 among the main reef builders in the fringing reefs (Cabioch et al., 1995). At Papeete in
 143 Tahiti, the *A. robusta/abrotanoides* complex and *P. verrucosa* have actively participated
 144 in reef building since 14 ka (Montaggioni et al., 1997).

145 Few studies have been conducted using quantitative assessments of coral
 146 populations from Holocene reefs (Table 1). One example of such a quantitative

147 estimates is provided by Aronson and Precht (1997), who measured the vertical
148 thicknesses of coral layers from core samples, revealing that *Acopora cervicornis* and
149 *Agaricia* sp. were the most volumetrically abundant. Hongo and Wirrmann (2015)
150 showed that *I. palifera* represents about 20% of the relative abundance in the corymbose
151 and tabular *Acropora* facies within the Holocene sections of the New Caledonian barrier
152 reef. Sugihara et al. (2003) demonstrated from quadrat records that *P. verrucosa*, *A.*
153 *hyacinthus*, *A. digitifera*, *A. curta*, *D. stelligera*, and *G. retiformis* were the dominant
154 species on the Holocene reef terraces in the Kikai Islands in the Ryukyus. Pandolfi et al.
155 (2006) showed that there was a change in community from *I. palifera* to *A. hyacinthus*
156 and *A. humilis* after a disturbance event at 9.1–9.4 ka in Papua New Guinea.

157 Mauritius and Madagascar, in the western Indian Ocean, are key sites for
158 assessing biogeographic patterns of coral species in the Indo-Pacific realm, as this
159 province is located in its westernmost region. Today, water masses coming from the
160 Pacific access the Indian Ocean through the Indonesian Gateway, transported by the
161 Indonesian Throughflow (IT) (Open University, 2001). The intensity of the IT is
162 controlled by four critical passages, the Makassar, Lombok, Ombai, and Timor Straits
163 (Kuhnt et al., 2004). Glacial/deglacial sea-level changes have strongly influenced the
164 throughflow volume in shallow sections of many passages at the Gateway (Kuhnt et al.,

2004), so the dispersal of coral larvae from the Pacific to the Indian Ocean was probably limited during low sea-level stands until the early Holocene. The dispersal of coral larvae is also promoted by the North Equatorial Current (NEC), the South Equatorial Current (SEC), the Equatorial Counter Current (ECC), the Somali Current (SC), and the Agulhas Current (AC) in the Indian Ocean. In addition to the influence of the prevailing currents, the ocean current increases from west to east at the Indian Ocean Dipole (Saji et al., 1999; Murtugudde et al., 2000). Before the present study, qualitative analyses of coral species abundance have been performed on a number of cores extracted from Holocene reefs, in Mauritius Island, at La Pointe-au-Sable reef (Montaggioni and Faure, 1997) and in Madagascar, at Toliara reef (Camoin et al., 1997, 2004).

The goal of the present study was three-fold: (1) to obtain quantitative records of coral species from Mauritius and Madagascar reefs, based on a re-examination of the existing cores; (2) to reconstruct the history of reef development based on coral ecological succession over time, in relation to changes in environmental factors, including sea level (Gischler et al., 2008; Kench et al., 2009), SST, insolation, ocean circulation regimes, and biological factors (e.g., competency period of coral larvae); and (3) to reconstruct the biogeographic distribution of the coral species involved in the development of Indo-Pacific reefs, by comparing the compositional patterns of coral

183 assemblages from different regional reef sites: the Seychelles, Mayotte, Ryukyu Islands,
184 Palau Islands, Papua New Guinea, Great Barrier Reef, New Caledonia, and Vanuatu.

185

186 **2. Material and methods**

187 **2.1 Study sites**

188 **2.1.1 Mauritius**

189 Mauritius Island is located in the western Indian Ocean (20.0°S, 57.8°E to
190 20.5°S, 57.3°E) (Fig. 1A); the island is almost completely encircled by fringing reefs,
191 with a substantial lagoon and barrier reef system developed on the east and southwest
192 coasts (Montaggioni and Faure, 1980; Spalding et al., 2001). Mauritius is subsiding at a
193 rate of 0.03 m/kyr (Montaggioni, 1978). Average SSTs range from 23°C in winter to
194 27°C in summer (Turner et al., 2000), and southeast trade winds blow most of the year,
195 especially during the cooler season of May–November; the region is affected annually
196 by cyclones. More than 290 coral species have been identified on the reefs (Faure, 1982;
197 Spalding et al. 2001).

198 La Pointe-au-Sable reef (20.164°S, 57.455°E), located on the relatively
199 sheltered west coast of Mauritius (Fig. 1B), is a fringing reef facing the open ocean and
200 is therefore subjected to moderate wave energy according to the season (Montaggioni

201 and Faure, 1997). The reef consists of three morphological zones comprising, from the
202 sea to shore, the reef slope, reef crest, and backreef (water depth < 2 m) (Montaggioni
203 and Faure, 1997). The reef crest forms a topographic high along the outer reef margin,
204 ~100 m wide and is emergent at low tide. The reef slope consists of gently sloping spur
205 and groove systems that extend seaward to water depths of 20 m (Montaggioni and
206 Faure, 1997). Tides in the area are semidiurnal, with a range of 0.9 m at spring tide and
207 a mean low-water spring tide of 0.45 m below mean sea level (MSL) (Montaggioni and
208 Faure, 1997).

209 Three cores (Pas1–3; 15.2–22.3 m in length; 85 mm in diameter) were
210 extracted from La Pointe-au-Sable reef: one from the reef crest, one from the outer
211 backreef zone, and one from the inner backreef zone (Fig. 2A). The cores were
212 recovered in 1979 using a portable hydraulic drilling rig with double-tube core barrels
213 (Montaggioni and Faure, 1997). Percent recovery varied from 35% to 90%, depending
214 on the presence of internal cavities, beds of sand, and other unconsolidated materials.
215 The core bit was advanced successively at intervals of 1.5 m during coring; the core
216 depth accuracy was estimated at ± 0.1 –0.5 m (Montaggioni and Faure, 1997).

217

218 **2.1.2 Madagascar**

219 Madagascar, the world's fourth largest island and situated in the westernmost
220 Indian Ocean (12°S, 50°E to 25°S, 44°E), is ~1600 km long and ~580 km wide. Reefs
221 are extensively developed on the north and west coasts (Spalding et al., 2001) and
222 poorly developed on the east coast, which is bounded by a steep continental shelf.
223 Madagascar is subsiding at a rate of 0.16 m/kyr (Camoin et al., 2004). Average SSTs are
224 22°C in winter and 28°C in summer (Cooke et al., 2000). The island is exposed to two
225 principle wind systems, the southeast trade winds and the monsoon (Webster and
226 McMahon, 2002). The northwest and west coasts as far as 17°S are directly affected by
227 the monsoon (Cooke et al., 2000). Sea conditions along the east and south coasts are
228 rough. The island is affected by cyclones in the warm season (December to March, on
229 average, 1.3/year) (Webster and McMahon, 2002). More than 310 coral species have
230 been identified on Madagascar (Spalding et al. 2001).

231 Toliara reef, situated on the southwest coast of Madagascar (23.385°S,
232 46.631°E) (Fig. 1C), is a barrier reef parallel to the shoreline and separated from the
233 shore by a major embayment (Camoin et al., 2004); a backreef lagoon (boat channel) is
234 shallow or absent (Camoin et al., 2004). The reef is not directly affected by constant
235 winds and is therefore subject to low–moderate wave energy conditions. Tides are

236 semidiurnal, with a range of 3.0 m at spring tide and a mean low-water spring tide of
 237 1.5 m below MSL.

238 Two cores were recovered from the reef flat of Toliara reef in 1997 (Camoin et
 239 al., 2004; Fig. 2B): cores To1 and To2; 21.1 and 25.2 m in length, respectively; 50 mm
 240 in diameter.

241

242 **2.2 Previous research on the study cores**

243 **2.2.1 Mauritius Island**

244 Montaggioni and Faure (1997) reconstructed the growth history of La Pointe-
 245 au-Sable reef during the past 7.5 kyr and delineated four major coral facies: (1) robust
 246 branching coral facies, (2) tabular–branching coral facies, (3) robust branching–domal
 247 coral facies, and (4) foliaceous coral facies (Table 2). The reef crest is interpreted as
 248 having caught up with sea level at 2.5 ka. The growth history of the reef was
 249 reconstructed only in relation to sea level and changes in water energy, as inferred from
 250 the type and depth ranges of identified coral assemblages. Recently, additional
 251 reconstructed sea-level curves for the Indian Ocean were proposed by Gischler et al.
 252 (2008) and Kench et al. (2009), and Holocene SST records from the studied areas were
 253 reported by Sonzogni et al. (1998) and Abram et al. (2009).

254

255 2.2.2 Madagascar

256 Camoin et al. (2004) presented a reconstructed sea-level curve for Madagascar
257 for the past 7.6 kyr based on analyses of the cores reexamined in this study. The study
258 reported only a single coral facies (branching *Acropora* facies) (Table 2).

259

260 2.3 Identification and quantitative analyses of coral species

261 The coral surface is usually obscured by encrusters (such as coralline algae and
262 foraminifera) or lithified sediment crusts or by its poor state of preservation due to
263 abrasion or bioeroders (such as sponges, bivalves, and serpulid worms) (Bromley, 1978;
264 Scoffin, 1992). Therefore, it is important to observe the relationships between the
265 internal structures of samples and their surface morphologies (Humblet et al., 2015).
266 The nature and reliability of criteria used to identify coral colonies *in situ* vary
267 according to growth orientation and state of preservation. In principle, the criteria are
268 similar to those established by Montaggioni and Faure (1997), Webster and Davies
269 (2003), and Blanchon and Perry (2004). Multiple criteria were used to distinguish
270 colonies *in situ* from coral rubble larger than the core diameter. These include: (1) a lack
271 of severe abrasional surfaces and of rounding; (2) the upward orientation of well-

272 preserved collumella and/or corallites; (3) the upward orientation of branching corals;
273 and (4) the top of the coral rubble covered by algae. For example, the concave surfaces
274 of corymbose and tabular *Acropora* are usually orientated upwards during growth, so
275 the growth orientation is unambiguous. In contrast, massive corals may re-acquire a
276 normal growth orientation after displacement. Abrasional surfaces and rounding are
277 important indicators of transport. Corals that did not meet the criteria for an *in situ*
278 growth habit were classified as reworked. In the present study, *in situ* and reworked
279 fossil corals were identified at the lowest taxonomic level possible (species or generic
280 level), following the coral taxonomy established by Veron (2000), Budd et al. (2012),
281 and Huang et al. (2014a, b). However, the accuracy of the identification of some fossil
282 corals at the species level was low because their colony surfaces were poorly preserved.
283 Some species with similar skeletal characteristics were assigned to species groups (e.g.,
284 *A. robusta/abrotanoides* complex and *Pavona duerdeni/clavus* complex). The
285 designation “sp.” is generally assumed to indicate a taxonomically unknown or
286 unidentified species. However, in this study, it was difficult to distinguish among corals
287 labeled “sp.”. The morphology of corymbose *Acropora* colonies is similar to that of
288 tabular *Acropora*; therefore, both are combined under the label of corymbose *Acropora*.

289 During the quantitative analyses, the *in situ* and reworked coral fragments were
 290 counted separately, and the relevant data were converted to binary presence/absence
 291 data (assigned as “1”/“0”, respectively). The numbers of reworked fragments were
 292 totaled for each biolithological unit. The biolithological units in the cores were also
 293 delineated based on both biological (corals and other calcareous components) and
 294 textural (rubble and sand) patterns. The abundance of dominant corals and the
 295 presence/absence of unconformities were especially key criteria for the delineation of
 296 units. We used a facies classification based on multiple criteria: previous descriptions by
 297 Montaggioni and Faure (1997) and Camoin et al. (2004); occurrences and types of
 298 corals; presence or absence of calcareous algae (e.g., *Halimeda*), gastropods, bivalves,
 299 or sea urchins; color of gravels; and diagenetic marks. The facies previously identified
 300 were re-defined as follows: (1) corymbose *Acropora* and robust-branching *Isopora*
 301 facies, (2) massive *Porites* facies, (3) arborescent *Acropora* facies, (4) foliaceous coral
 302 facies, and (5) detritus facies.

303

304 **2.4 New and previously reported ages**

305 Camoin et al. (1997, 2004) and Montaggioni and Faure (1997) reported 27
 306 radiocarbon ages and 24 uranium-series ages of corals from La Pointe-au-Sable reef,

307 Mauritius (cores Pas1–3) (see Tables 3 and 4), and Camoin et al. (2004) reported 14
308 uranium-series ages for corals from Toliara reef, Madagascar (cores To1 and 2) (Table
309 4). All radiocarbon ages were calibrated to calendar years using the program CALIB 6.0
310 (Stuiver and Reimer, 1993) and the marine calibration dataset Marine09 (Reimer et al.,
311 2009). The marine reservoir correction (ΔR) value for the tropical southwest Indian
312 Ocean was assumed to be 140 ± 25 (Southon et al., 2002). However, age reversals were
313 recognized; thus, one additional coral sample from core Pas1 and two from core Pas3
314 were selected for radiocarbon dating (Table 3). Any visible evidence of sample
315 contamination was mechanically removed. The samples were analyzed by X-ray
316 diffraction (XRD) to confirm that the aragonite content was >99%. The radiocarbon
317 ages of the samples were determined by Beta Analytic (Miami, USA) using an
318 accelerator mass spectrometer (AMS).

319 **3. Results**

320 **3.1 Identification of sedimentary units and coral species**

321 A total of 23 units, each defined by distinct sedimentological and biological
 322 characteristics, were identified in the core set; detailed descriptions of the sedimentary
 323 and biological features of each unit are shown in Figure 3A (for Mauritius) and 3B (for
 324 Madagascar). A total of 22 genera and 64 species of corals (17 genera and 43 species of
 325 *in situ* corals; 18 genera and 43 species of reworked corals) were recognized in the
 326 sequences (Tables 5 and Supplement Table 1). The biosedimentological characteristics
 327 of each unit are summarized below. The relative abundance (%) of the corals in each
 328 unit is bracketed (Supplement Table 2).

329

330 ***Core Pas1* (0–22.3 m)**

331 Seven units were identified in core Pas1 (Units 1–7). Two major
 332 unconformities are present, at depths of 19.8 and 20.1 m. Unit 1 consists of volcanic
 333 rocks and Unit 2 is a pre-Holocene reef. Unit 3 is composed of *in situ* corymbose
 334 *Acropora* sp. (25.0%) and branching *Acropora* sp. (50.0%). Unit 4 consists of *in situ*
 335 branching *Acropora* sp. (100%) and calcareous rubble and sand (foraminifera tests,
 336 gastropods, sea-urchin tests, and calcareous algae), and Unit 5 contains *in situ* massive

337 *Porites* sp. (66.7%) and branching *Acropora* sp. (33.3%). Unit 6 is composed of *in situ*
 338 *Platygyra sinensis* (100%) and calcareous rubble and Unit 7 is characterized by *in situ* *A.*
 339 *digitifera* (8.8%), *A. robusta/abrotanoides* complex (5.9%), branching *Acropora* sp.
 340 (32.4%), branching *Porites* sp. (20.6%), and reworked *Galaxea astreata*. A new ^{14}C age
 341 of 5060 cal. years BP was obtained at a core depth of 3.2 m.

342

343 ***Core Pas2 (0–20.0 m)***

344 Seven units were identified in core Pas2 (Units 8–14), along with two
 345 unconformities, at depths of 16.4 and 19.2 m. Unit 8 consists of volcanic rocks and Unit
 346 9 is a pre-Holocene reef. Unit 10 is composed of *in situ* massive *Porites* sp. (58.3 %),
 347 *Echinopora hirsutissima* (8.3%), and *Cyphastrea* sp. (8.3%). Unit 11 contains *in situ*
 348 massive *Porites* sp. (21.4%), *Cyphastrea* sp. (28.6%), *D. stelligera* (14.3%), *Echinopora*
 349 *gemmacea* (7.1%), *P. duerdeni/clavus* complex (7.1%), and *Turbinaria peltata* (7.1%).
 350 Unit 12 consists of *in situ* *I. palifera* (16.7%), *D. stelligera* (16.7%), *Platygyra*
 351 *ryukyuensis* (8.3%), corymbose *Acropora* sp. (16.7%), and Unit 13 contains *in situ*
 352 branching *Acropora* sp. (100%). Unit 14 is composed of *in situ* *Platygyra daedalea*
 353 (10.3%), *E. gemmacea* (3.4%), branching *Acropora* sp. (82.8%), and the *A.*
 354 *robusta/abrotanoides* complex (5.9%).

355

356 **Core Pas3 (0–15.2 m)**

357 Five units were identified in core Pas3 (Units 15–19), along with a major
 358 unconformity at a depth of 13.6 m. Unit 15 consists of volcanic rocks. Unit 16 is
 359 composed of *in situ* massive *Porites* sp. (42.3%), *in situ* *E. hirsutissima* (3.8%),
 360 branching *Acropora* (11.5%), *D. stelligera* (7.7%), *P. clavus* (3.8%), and reworked *I.*
 361 *palifera*. Unit 17 consists of *in situ* *I. palifera* (8.3%), *P. clavus* (16.7%), *A. digitifera*
 362 (2.8%), *D. stelligera* (2.8%), branching *Acropora* sp. (11.1%), and massive *Porites* sp.
 363 (30.6%). Unit 18 contains reworked *Pavona frondifera*, *Pavona decussata*, and *Pavona*
 364 *cactus*, and Unit 19 is composed of reworked *P. frondifera*. Two new ¹⁴C ages were
 365 obtained from this core at core depths of 7.2 and 10.4 m, of 6340 and 7050 cal. years BP,
 366 respectively.

367

368 **Core To1 (0–25.2 m)**

369 Only one unit was identified in core To1 (Unit 20). Unit 20 comprises two
 370 distinct sections: the lower unit dominantly contains rubble and sand derived from
 371 corals, gastropods, bivalves, sea urchins, and calcareous algae, and the upper section is
 372 composed of *in situ* *A. digitifera* (3.0%), *I. palifera* (24.2%), *P. verrucosa* (3.0%),

373 *Pocillopora eydouxi* (3.0%), *D. stelligera* (3.0%), *Favites pentagona* (9.1%),
 374 corymbose *Acropora* sp. (18.2%), *Astreopora listeri* (9.1%), and *Dipsastraea laxa*
 375 (3.0%). Eight uranium series ages were obtained at core depths between 1.5 m and 20.2
 376 m, giving ages of 990–7270 years BP.

377

378 ***Core To2 (0–21.1 m)***

379 Three units were identified in core To2 (Units 21–23). A major unconformity
 380 was recognized at a core depth of 13.8 m. Unit 21 consists of a Pleistocene reef deposit
 381 (Camoin et al., 2004). Unit 22 is composed of *in situ* *I. palifera* (16.7%), *Acropora* sp.
 382 cf. *A. humilis* (16.7%), *Favites* sp. cf. *Favites chinensis* (33.3%) and Unit 23 is
 383 characterized by *I. palifera* (24.2%), *P. eydouxi* (14.5%), *Acropora retusa/gemmifera*
 384 complex (6.5%), *A. robusta/abrotanoides* complex (4.8%), and corymbose *Acropora* sp.
 385 (30.6%).

386 3.2 Temporal and spatial changes in coral species

387 Some species have experienced changes in space and time.

388 *I. palifera*

389 In Mauritius, the species appears within Units 12 and 17 at 6–5 ka (Fig. 3A). In

390 Madagascar, the species is present in the upper part of Unit 20 at around 6 ka, in Unit 22

391 before 7.6 ka, and in Unit 23 between 7.6 and 1.5 ka (Fig. 3B).

392

393 *A. digitifera*

394 In Mauritius, the species is present in Units 7 and 12 at around 6 ka (Fig. 3A). In

395 Madagascar, the species first appeared in the upper part of Unit 20 at around 1 ka (Fig.

396 3B).

397

398 *A. robusta/abrotanoides* complex

399 In Mauritius, the species first occurred in Unit 7 at around 6 ka (Fig. 3A). In

400 Madagascar, the species appeared in the upper part of Unit 23 after 1.5 ka (Fig. 3B).

401

402 *D. stelligera*

403 In Mauritius, the earliest appearance of this species occurred in Units 11 and 16 at 7–6
 404 ka (Fig. 3A). Similarly, in Madagascar this species is not present in the upper part of
 405 Unit 20 before 6 ka (Fig. 3B).

406

407 *P. clavus*

408 In Mauritius, the species is present in Unit 16 at around 7 ka (Fig. 3A). In Madagascar,
 409 the species was not observed in any study core.

410

411 *P. eydouxi*

412 In Madagascar, the species appeared in Unit 23 at around 5 ka (Fig. 3A). In Mauritius,
 413 the species is not observed *in situ*, but occurs as transported fragments in Unit 12.

414

415 **3.3 Correlations between sedimentary units and coral facies**

416 Five main facies were identified. The relative abundances of the *in situ* coral
 417 species were estimated for each facies (Fig. 4).

418

419 *Corymbose Acropora and robust-branching Isopora facies*

420 The corymbose *Acropora* and robust-branching *Isopora* facies is represented in
 421 Units 6 and 7 (core Pas1), Unit 12 (core Pas2), Unit 17 (Pas3), the upper part of Unit 20
 422 (core To1), and Units 22 and 23 (core To2). The facies is characterized by *A.*
 423 *robusta/abrotanoides* complex, corymbose *Acropora*, branching *Acropora*, *A. digitifera*,
 424 *I. palifera*, *D. stelligera*, *Favites* sp. cf. *F. chinensis*, *P. eydouxi*, *P. clavus*, branching
 425 *Porites*, *A. listeri*, massive *Porites*, *A. retusa/gemmifera* complex, *Acropora* sp. cf. *A.*
 426 *humilis*, and *F. pentagona*. In modern reef settings, these species occupy water depths of
 427 less than 10 m on the reef crest and upper outer reef slope zone (i.e., moderate–high
 428 wave energy) on Mauritius and on other Indo-Pacific reefs (Montaggioni and Faure,
 429 1997; Cabioch et al., 1999; Camoin et al., 2004; Montaggioni, 2005; Hongo and
 430 Kayanne, 2011).

431

432 ***Massive Porites facies***

433 The massive *Porites* facies is represented in Unit 5 (core Pas1), Units 10 and
 434 11 (core Pas2), and Unit 16 (core Pas 3). The facies consists of massive *Porites* and
 435 *Cyphastrea* sp., and associated branching *Acropora* and *D. stelligera*. Based on direct
 436 comparisons with modern reefs on Mauritius and other Indo-Pacific reefs, the presence
 437 of these species is interpreted to represent low–moderate wave energy settings at water

438 depths of less than 15 m in upper reef and lower slope zones (Montaggioni and Faure,
439 1997; Cabioch et al., 1999; Montaggioni, 2005).

440

441 ***Arborescent Acropora facies***

442 The arborescent *Acropora* facies is represented in Units 3 and 4 (core Pas1)
443 and Units 13 and 14 (core Pas2). The facies is typified by branching *Acropora* and
444 associated other corals (*P. daedalea*, corymbose *Acropora*, *Cyphastrea* sp., *E.*
445 *gemmacea*, *Porites*, and *A. robusta/abrotanoides* complex). The facies is thought to
446 represent sheltered areas subjected to low–moderate wave energy conditions at water
447 depths of less than 15 m, such as on lower reef slopes to outermost backreef zones on
448 Mauritius and other Indo-Pacific reefs (Montaggioni and Faure, 1997; Montaggioni,
449 2005; Hongo, 2012).

450

451 ***Foliaceous coral facies***

452 The foliaceous coral facies, which is limited to Units 18 and 19 (core Pas3), is
453 characterized by the occurrence of a foliaceous *Pavona* community. The species in this
454 community occupy low wave energy conditions at various water depths less than 10 m

455 in shallow backreef zones on modern Mauritius and other Indo-Pacific reefs
456 (Montaggioni and Faure, 1997; Montaggioni, 2005).

457

458 *Detritus facies*

459 The detritus facies, which is restricted to lower Unit 20 (core To1), is
460 characterized by common reworked coral fragments and skeletal sand. The depositional
461 environment for this facies is interpreted to correspond to moderate wave energy
462 conditions along an outer reef slope or a backreef zone (Montaggioni, 2005).

4. Discussion

4.1 Growth of corals and reefs in response to Holocene climate change

On Mauritius, the history of Holocene reefs has been previously reconstructed on the basis of sea-level change and/or wave energy alone (Montaggioni and Faure, 1997). However, Holocene reef growth is known to be influenced by other factors, including SST and insolation (for a review, see Montaggioni and Braithwaite, 2009). The distribution of tropical reef-building corals is roughly limited to temperatures below the 18°C isotherm (Veron, 1995). Alkenone-based SSTs recorded in the vicinity of Madagascar have revealed that the differences in SST between the Holocene and the modern do not exceed 2°C (Sonzogni et al., 1998). These results indicate that SSTs near the study sites were, on average, 23°C ± 2°C in winter during the Holocene. In an analysis of the Sr/Ca values of fossil corals, Abram et al. (2009) also pointed out that the SST fluctuations in the tropical Indian Ocean during the past 7 kyr have been ≤ 2°C. These findings suggest that changes in SSTs in the study areas have not played a significant role in the evolution of coral reefs during the Holocene.

The average annual mid-month insolation at 20°S during the past 10 kyr has varied by only 4 W/m² (390–394 W/m²) (Fig. 5) (Berger and Loutre, 1991). Similarly, the average summer insolation at 20°S from 10 cal. kyr BP to the present has increased

481 by only 29 W/m^2 (from 457 to 486 W/m^2) (Fig. 5). As levels of solar radiation are
482 known to decrease exponentially with depth in the water column (Bosscher and
483 Schlager, 1992), a difference in insolation of 29 W/m^2 represents a difference in the
484 depth of penetration of solar radiation of less than 2–3 m. This observation strongly
485 suggests that at the study sites insolation variations were not an important control on the
486 composition of coral assemblages or on reef growth during the Holocene.

487 The above observations suggest that the formation of Holocene reefs on
488 Mauritius and Madagascar was driven predominantly by changes in sea level, and by
489 corresponding changes in wave energy. These findings are consistent with those of
490 Montaggioni and Faure (1997). New curves of Holocene sea-level changes in the Indian
491 Ocean have recently been provided by Camoin et al. (1997), Gischler et al. (2008), and
492 Kench et al. (2009). These show that the sea level rose rapidly between 10 and 7 ka,
493 slowed down between 7 and 4–3 ka, and then stabilized at its present position by ca. 3
494 ka (Fig. 6). Upward reef growth began after the inundation of Pleistocene precursor
495 reefs at 7.6–8.4 ka (Pas1–14 and Pas2–26) on Mauritius and at 7.3–7.6 ka (To1–8 and
496 To2–6) on Madagascar (Fig. 6). Reef growth patterns at the study sites indicate that
497 Holocene reef development on Mauritius started by upward accumulation of arborescent
498 *Acropora* facies on the reef crest and massive *Porites* facies on the backreef, while on

499 Madagascar, reef development occurred by vertical accretion of detritus facies and
500 corymbose *Acropora* and robust-branching *Isopora* facies on reef flats. On Mauritius,
501 the arborescent coral facies was replaced by the corymbose *Acropora* and robust-
502 branching *Isopora* facies (cores Pas1–3) between 7 and 6 ka, reflecting an increase in
503 wave energy. After the reef crest rose to sea level at 4–3 ka (core Pas1), arborescent
504 *Acropora* and foliaceous coral assemblages developed in the backreef zone in response
505 to a decrease in wave energy. In Madagascar, the reef-flat zone was composed of
506 corymbose *Acropora* and robust-branching *Isopora* facies throughout the Holocene.
507 This implies that the wave energy conditions were relatively stable during the reef
508 growth at the site considered, thus maintaining the long-term dominance of the
509 *Acropora–Isopora* facies. The coral assemblages have grown at a rate close to that of
510 the rising sea level. Similarly, a number of Indo-Pacific reef sequences display single
511 facies that have developed beneath exposed to sheltered reef-crest or reef-flat zones
512 throughout the Holocene (for reviews, see Montaggioni, 2005; Montaggioni and
513 Braithwaite, 2009).

514 There was a time lag in the initiation of the Mauritian and Madagascan reefs,
515 which was probably controlled by a number of factors (e.g., non-conductive climatic or
516 oceanographic factors, lack of suitable substrate, terrestrial influences, and absence of

larval replenishment) (Davies et al., 1985). The later initiation of the reef in Madagascar was probably driven by the later arrival of coral larvae because the Toliara site is located at the end of the paths of the SEC and AC (Fig. 7).

There also appears to have been a time lag between the Mauritian and Madagascan reefs in their compensation for the increase in sea level. The Pointe-au-Sable reef crest in Mauritius caught up with sea level 2.5 ka after sea-level stabilization (Montaggioni and Faure, 1997) and its growth mode is of the “catch-up 2” type (Davies and Montaggioni, 1985; Davies et al., 1985; Neumann and Macintyre, 1985). Although the reef flat at Madagascar is also characterized by the “catch-up 2” type growth mode (Fig. 6), its sea-level catch-up was delayed for about 1000–1500 years. This time lag could be explained by differences in the timing of larval arrival. An alternative explanation could be local differences in wave energy. The test reef at Mauritius is subject to moderate wave energy, whereas the test reef at Madagascar experiences lower wave energy. An increase in wave energy causes an increase in the magnitude of wave set-up on reef crests (Gourlay, 2011) and thus promotes an increase in the accommodation space in the reef crest setting and faster upward reef accumulation, as observed at Mauritius.

534 There were temporal differences in the arrival of a number of coral species to
535 Mauritius and Madagascar, and these events were probably governed by oceanographic
536 and/or biological factors. For example, the *A. robusta/abrotanoides* complex and *A.*
537 *digitifera* settled on the western Mauritius coast at 6 ka, but along the western coast of
538 Madagascar, these corals seem to have arrived later, at 1.5–1 ka, presumably because
539 the Toliara site is located at the end of the SEC and AC paths (Fig. 7). Moreover, the
540 average survival time of most *Acropora* corals is approximately 10–20 days (Graham et
541 al., 2008). More specifically, the survival time of *A. digitifera* larvae does not exceed 11
542 days (Nishikawa and Sakai, 2005). Therefore, the successful dispersal of *Acropora*
543 larvae requires the maintenance of favorable oceanographic parameters for a long time.
544 In contrast, *I. palifera* and *D. stelligera* appeared coevally at Mauritius and Madagascar
545 at 7–6 ka. This implies that the larvae of these species migrated broadly and quickly via
546 the ocean circulation after the initiation of the Holocene reef. It is noteworthy that *I.*
547 *palifera* is characterized by brooding larvae (Baird et al., 2009). The planulae of *I.*
548 *palifera* do not have zooxanthellae (Kojis, 1986), similar to those of *Heliopora coerulea*,
549 which have a competency period of about 30 days (Hariri et al., 2002). *Isopora palifera*
550 may have a similar competency period, promoting a rapid dispersal.

551 Notably, the diversity of modern coral populations is different from that of
552 Holocene coral assemblages at the study sites. There was a significant change in the
553 composition of the dominant coral assemblages between the Holocene and the present.
554 For example, whereas *I. palifera* was one of the main reef builders at Mauritius during
555 the Holocene (this study), it is not a dominant species on the modern reef (Montaggioni
556 and Faure, 1997) (Table 6). These patterns indicate that environmental conditions have
557 changed in response to Holocene sea-level change and subsequent sea-level stabilization,
558 affecting the distributions and abundances of coral species. *Isopora palifera* is
559 characterized by a rapid growth rate and a wave-resistant morphology. Its ecological
560 strategies are thought to be adapted to the rapid Holocene sea-level rise, but poorly
561 adapted to a stable sea level. The present study also shows that 20 genera contributed to
562 the Holocene reef accretion in Mauritius, whereas 25 genera have been described in the
563 modern reef zones (Montaggioni and Faure, 1997) (Table 6). Two explanations may
564 account for this discrepancy. First, the larger number of modern coral forms could be a
565 response to the stable sea level, which has promoted an increase in the heterogeneity of
566 the reef environments from the outer-reef to the inner-back-reef zones. Second, a
567 prolonged period of consistent seaways and currents since the late Holocene could be
568 responsible for maintaining a stable supply of new coral larvae. However, the fewer

coral species determined with coring studies could also be a sampling artefact because vertical coring is a highly selective and restricted method of sampling.

4.2 Biogeography of Holocene coral species

Previous studies have indicated that within the Indo-Pacific realm, patterns of Holocene reef growth in different areas are very similar, whereas marked differences occur in the composition and successions of coral assemblages from region to region (Montaggioni, 2005). Our analysis of the coral assemblages in Holocene cores from Mauritius and Madagascar suggests that some corals expanded their habitats throughout the Indo-Pacific in response to environmental changes in the Holocene. For example, *I. palifera* was a common species on Holocene reefs in a number of areas, including Mauritius, Madagascar, the Ryukyu Islands, Papua New Guinea, the Great Barrier Reef, and New Caledonia (Fig. 7). At the same time, *G. retiformis* was also widely distributed from the Seychelles, Mayotte, and Ryukyu Islands to New Caledonia. However, although this species currently contributes to the modern coral populations in Mauritius and Madagascar, it was absent from both islands for the most of the Holocene. *Goniastrea retiformis* was found at Mauritius and Madagascar within the uppermost sections of the study cores, suggesting that this species settled during the last 2 kyr

587 interval (Montaggioni and Faure, 1997; Veron, 2000) and Madagascar (Pichon, 1978).
588 From these data, it seems that *I. palifera* larvae dispersed widely over the Indo-Pacific
589 regions on ocean currents after the initiation of the Holocene reef because this species
590 reproduces by brooding (Baird et al., 2009) and/or survived during low sea-level stands
591 within each region. In contrast, *G. retiformis*, which is typified by a spawning
592 reproductive mode (Richmond and Hunter, 1990), may have reached Mauritius and
593 Madagascar relatively recently because the competency of *G. retiformis* is weak (less
594 than 10 days) (Connolly and Baird, 2010), Consequently, the late arrival of *G. retiformis*
595 to Mauritius and Madagascar, compared with their arrival in surrounding areas (e.g.,
596 Mayotte and Seychelles), could have been driven by the regional circulation regime,
597 especially by prevailing SEC and/or AC currents, which may have favored the
598 displacement of *G. retiformis* larvae to the northern areas of the Western Indian Ocean.

599 The amounts of coral larvae that moved from the Pacific to the Indian Ocean
600 may have been controlled by Holocene sea-level changes. The IT was disrupted by land
601 barriers arising at the Indonesian Gateway during periods of low sea levels, from the
602 LGM to the early Holocene (Lambeck et al., 2014). Simulation results showed a net
603 reduction in throughflow within the Makassar Strait when the sea level fell (Khunt et al.,
604 2004). A significant effect of such a drop in sea level occurred in the Lombok Strait,

605 where the total volume transported was reduced by approximately 50% (Khunt et al.,
606 2004). Ocean currents may also have been weakened during the times of lower sea
607 levels, which could have had the same impact as blocked currents (i.e., reduced or
608 abolished larval supply). These data indicate that changes in the major surface ocean
609 currents, including the IT, NEC, SEC, ECC, and AC, govern the transportation and
610 settlement of coral larvae.

611 It is clear that *A. digitifera* was present in Mauritius, the Ryukyus, and Palau
612 Islands during Holocene reef building (Fig. 7), but it was not dominant in New
613 Caledonia, Vanuatu, or the Great Barrier Reef at this time. *Acropora digitifera* occurs at
614 present on the modern reefs in all of these regions (Veron, 2000), suggesting that this
615 species was isolated between the northwest Pacific and the southwest Pacific during the
616 Holocene by the presence of a land barrier around Papua New Guinea and the Solomon
617 Islands, and/or weak ocean currents during low sea-level stands. Because the average
618 survival of *A. digitifera* larvae is 11 days (Nishikawa and Sakai, 2005), this species may
619 not have the capacity to reach the southwest Pacific regions. After the Holocene sea-
620 level rise, these coral larvae may have been transported by normal ocean currents and/or
621 episodic currents during El Niño events. Extreme El Niño events result in sudden and
622 marked changes in the circulation routes. Therefore, ocean currents can greatly

623 influence the west-to-east dispersal pathway, because high atmospheric pressure,
624 typically located in the west Pacific, shifts to the central Pacific (Feingold, 2011). This
625 explanation is partly speculative because only a limited core dataset is available, so
626 additional core records are required to confirm the dispersal patterns of coral larvae
627 through the Indo-Pacific.

628 The long-term persistence of coral species may increase the abundance of the
629 species in modern reefs. For example, as shown by our quantitative analysis (Fig. 4), the
630 *A. robusta/abrotanoides* complex was dominant at Mauritius during both the Holocene
631 (this study) and in the present-day coral populations (Montaggioni and Faure, 1997).
632 This suggests that a number of colonies of a given coral species may have contributed to
633 an increase in the genetic diversity of that species. Increased genetic diversity may
634 increase the adaptive potential of a specific coral population to rapid environmental
635 changes (Arye and Hughes, 2004). Similarly, *A. digitifera* was one of the dominant
636 species in the Ryukyu Islands both throughout the Holocene (Fig. 7) and today (Hongo
637 and Kayanne, 2010). Although the average survival time of *A. digitifera* larvae is only
638 11 days (Nishikawa and Sakai, 2005), a high level of gene flow and high genetic
639 diversity are maintained in *A. digitifera* populations throughout the Ryukyu Islands
640 because of the strong Kuroshio Current (Nakajima et al. 2010).

641

642 **5. Conclusions**

643 This study presents the biogeographical patterns of some Holocene coral species
644 in the western Indian Ocean and the northwest to southwest Pacific. Our investigation
645 of the spatial and temporal coral distributions revealed that: (1) *I. palifera* was a
646 common species during the Holocene at all the reef sites studied; and (2) *G. retiformis*
647 appears to have arrived recently in Mauritius and Madagascar, and *A. digitifera* in New
648 Caledonia, Vanuatu, and the Great Barrier Reef. This study also suggests that given
649 population sizes occurring during the Holocene may have contributed to the populations
650 of the corresponding modern reefs. From these data, it appears that the selection of key
651 coral species identified from the Holocene record is an important factor in genetic
652 research and in planning long-term reef restoration and conservation.

653 In the future, global environmental factors (e.g., changes in sea level and ocean
654 circulation, the appearance and disappearance of land barriers) will probably cause
655 further changes in the biogeographic patterns of corals. Changes in the paths and
656 intensities of ocean currents (e.g., IT and NEC) will particularly affect these patterns.
657 Other global factors (e.g., elevated SST, ocean acidification, and super cyclones) and

658 local factors (e.g., increased sediment runoff and nutrients) will also affect the
659 biological characters of corals (e.g., competency periods and settlement timing).

660 The present study emphasizes that further quantitative research is required
661 regarding the composition of coral species in Holocene reef sequences in the central
662 (e.g., Maldives) and eastern Indian Ocean (e.g., Cocos Islands, Indonesia, and Western
663 Australia), the northwest Pacific (e.g., Mariana Islands), the southwest Pacific (e.g.,
664 Solomon Islands). Examining Pleistocene reefs in these areas is also important to
665 determine the timing of the earlier or later settlement of coral species on these reefs. For
666 example, *G. retiformis* has been recorded in the Seychelles from the last interglacial
667 (Dutton et al., 2015). Such investigations will allow us to better understand the temporal
668 and spatial patterns of coral biogeography in the Indo-Pacific realm from the late
669 Pleistocene to the present. Finally, the present results are based on a limited dataset from
670 cores. A more robust analysis of the spatial–temporal distribution of coral communities
671 from taphonomically biased cores would require both an increased number of cored
672 sites and the use of larger-diameter core barrels (Blanchon and Perry, 2004).

673

674 **Acknowledgments**

675 The authors are grateful to Evan Edinger for logistical support for the analysis of
676 drilled cores at Aix-Marseille University. We thank Jody Webster, Gilbert Camoin, and
677 three anonymous reviewers for their comments, which significantly improved the clarity
678 of an earlier version of the manuscript. We thank Editor-in-Chief Thierry Corrège and
679 two anonymous reviewers for their constructive comments. This research was supported
680 by the Japan Society for the Promotion of Science (JSPS) Institutional Program for
681 Young Researcher Overseas Visits; the Ministry of Education, Culture, Sports, Science
682 and Technology (MEXT) of Japan (Grant-in-Aid for Scientific Research on Innovative
683 Areas: “Coral Reef Science for Symbiosis and Coexistence of Humans and Ecosystems
684 under Combined Stresses”; No. 20121006); JSPS KAKENHI Grant Number 24-4044;
685 JSPS Research Fellowships for Young Scientists Grant Number 24-4044, and JST/JICA,
686 SATREPS.

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Figure 1

(B) Pointe-au-Sable reef, Mauritius

(C) Toliara reef, Madagascar

Fig. 1 Hongo and Montaggioni

Figure 2

(A) Pointe-au-Sable reef, Mauritius

(B) Toliara reef, Madagascar

Fig. 2 Hongo and Montaggioni

Figure 3A

Fig. 3A Hongo and Montaggioni

Figure 3B

(B) Madagascar

Fig. 3B Hongo and Montaggioni

Figure 4

Fig. 4 Hongo and Montaggioni

Figure 5

Fig. 5 Hongo and Montaggioni

Figure 6

(A) Mauritius

(B) Madagascar

Fig. 6 Hongo and Montaggioni

Figure 7

Fig. 7 Hongo and Montaggioni

1 **Figure captions**

2 **Fig. 1. (A)** Location map of the study area. The arrows indicate the positions of the
 3 schematic paths corresponding to the North Equatorial Current (NEC), the South
 4 Equatorial Current (SEC), the Indonesian Throughflow (IT), the Equatorial Counter
 5 Current (ECC), the Somali Current (SC), the Agulhas Current (AC), the Kuroshio
 6 Current (KC), the East Australian Current (EAC), and the West Australian Current
 7 (WAC). (B) Location of La Pointe-au-Sable reef on Mauritius Island, and (C) the
 8 Toliara reef on Madagascar. The solid lines indicate the location of transects along
 9 which water depths were surveyed. The black circles show the locations of drilling sites.
 10 The dashed lines show the locations of modern reef crests.

11

12 **Fig. 2.** Topographic profiles and location of the drilling sites at La Pointe-au-Sable reef,
 13 Mauritius (A) and Toliara reef, Madagascar (B). MSL refers to mean sea level.

14

15 **Fig. 3.** Sedimentary characteristics of La Pointe-au-Sable reef, Mauritius (A) and
 16 Toliara reef, Madagascar (B). Twenty-three sedimentary units (Units 1–23) and 5 major
 17 biofacies (corymbose *Acropora* and robust-branching *Isopora* facies, massive *Porites*
 18 facies, arborescent *Acropora* facies, foliaceous coral facies, and detritus facies) are

delineated at the study sites. Calibrated radiocarbon ages and uranium series ages are given in Tables 3 and 4.

Fig. 4. Distribution and abundance of *in situ* coral species observed in each coral facies (corymbose *Acropora* and robust-branching *Isopora* facies, massive *Porites* facies, and arborescent *Acropora* facies).

Fig. 5. Mid-month insolation at 20°S during the past 10 kyr. The upper and lower horizontal bars refer to maximum and minimum values, respectively. The solid circles represent average annual values.

The data are from Berger and Loutre (1991) and are archived at the NOAA National Climatic Data Center (for orbital variations, see <http://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/climate-forcing>).

Fig. 6. Reef growth and sea-level curves relative to present-day mean sea level (MSL) at La Pointe-au-Sable reef on Mauritius (A) and Toliara reef on Madagascar (B). Radiometric counter errors are given in terms of two standard deviations (2σ) at the study sites. Vertical distribution errors are ± 0.5 m (Montaggioni and Faure, 1997). The

vertical bars above each plot represent paleowater depth ranges based on environmental conditions. Sea-level curves for the western Indian Ocean are from Camoin et al. (1997) and those for the central Indian Ocean are from Gischler et al. (2008) and Kench et al. (2009).

Fig. 7. Biogeographic distributions of Holocene coral species identified from the study sites in the western Indian Ocean and from other reef sites in the Indo-Pacific region. The species *I. palifera* (solid circle) was common to the Holocene reefs at Mauritius and Madagascar, the Ryukyu Islands, Papua New Guinea, Great Barrier Reef, and New Caledonia. The species *G. retiformis* (solid triangle) was distributed in the Holocene reefs at Mayotte and Mahé Island (Seychelles) in the western Indian Ocean and in the Ryukyu Islands, New Caledonia, and in the northwest and southwest Pacific, but was absent from the Holocene reefal sequences in Mauritius and Madagascar. The species *A. digitifera* was present in the Holocene reefs in Mauritius and Madagascar (not dominant), the Ryukyus, and Palau Islands, whereas it was absent from the Holocene reefs in the southwest Pacific (i.e., Great Barrier Reef, New Caledonia, and Vanuatu). The *A. robusta/abrotanoides* species complex (open circles) was common in the western Indian Ocean and the southwest Pacific during the Holocene, but was not common in

the Ryukyu Islands at that time. Coral species records: Mauritius and Madagascar (this study), Seychelles (Camoin et al., 2004), Mayotte (Camoin et al., 1997, 2004), Ryukyu Islands (Hongo and Kayanne, 2011; Hongo, 2012), Palau Islands (Hongo and Kayanne, 2011), Papua New Guinea (Nakamori et al., 1995), Great Barrier Reef (Webster and Davies, 2003), New Caledonia (Cabioch et al., 1995; Montaggioni et al., 2011; Hongo and Wirrmann, 2015), and Vanuatu (Cabioch et al., 1998). Some forms were not identified at the species level (e.g., corymbose *Acropora* spp. and massive *Porites* spp.) and are not shown in the figure. Locality symbols: MAU, Mauritius; MAD, Madagascar; SE, Seychelles; MY, Mayotte; RY, Ryukyu Islands; PL, Palau Islands; PNG, Papua New Guinea; GBR, Great Barrier Reef; NC, New Caledonia; and VA, Vanuatu. Meanings of arrows are as shown in Fig. 1.

Table 1

Table 1 Survey of quantitative and qualitative assessments of Holocene coral species conducted in different studies.

Reef location	Area	Region	Sampling method	Sampling quality	Cited reference
Galeta reef	Panama	Caribbean	Drilled core	qualitative	Macintyre and Glynn (1976)
Channel Cay	Belieze	Caribbean	Submarine trench and drilled core	quantitative [†]	Aronson and Precht (1997)
Channel Cay and other cays	Belieze	Caribbean	Drilled core	quantitative [†]	Aronson et al. (2002)
Pamandzi reef	Mayotte	Western Indian Ocean	Drilled core	qualitative	Camoin et al. (1997; 2004)
Anse aux Pins reef	Seychelles	Western Indian Ocean	Drilled core	qualitative	Camoin et al. (2004)
La Pointe-au-Sable reef	Mauritius	Western Indian Ocean	Drilled core	qualitative	Montaggioni and Faure (1997)
Reefs at Pacific coast	Panama	NE Pacific	Drilled core	qualitative	Glynn and Macintyre (1977)
Punta Isloles reef	Golfo Dulce, Costa Rica	NE Pacific	Drilled core	qualitative	Cortés et al. (1994)
Kaneohe Bay and Hilo Bay	Oahu Island, Hawaii Islands	NE Pacific	Drilled core	qualitative	Grigg (1998)
Kailua Bay	Ohau Island, Hawaii Islands	NE Pacific	Drilled core	qualitative	Grossman and Fletcher (2004)
Ibaruma reef	Ishigaki Island, Ryukyu Islands	NW Pacific	Drilled core	qualitative	Hongo and Kayanne (2009)
Kurohana reef	Yoron Island, Ryukyu Islands	NW Pacific	Drilled core	qualitative	Hongo and Kayanne (2011)
Shitooke reef	Kikai Island, Ryukyu Islands	NW Pacific	Raised reef	quantitative [‡]	Sugihara et al. (2003)
Nakaguma reef	Kikai Island, Ryukyu Islands	NW Pacific	Raised reef	quantitative[‡]	Webster et al. (1998)
Reef crest and shallow lagoon sites	Okinotori Island, Japan	NW Pacific	Drilled core	qualitative	Kayanne et al. (2012)
Ngemelis reef	Babeldaob Island, Palau Islands	NW Pacific	Drilled core	qualitative	Hongo and Kayanne (2011)
Huon Peninsula	Papua New Guinea	SW Pacific	Raised reef	qualitative	Nakamori et al. (1995b)
Huon Peninsula	Papua New Guinea	SW Pacific	Raised reef	quantitative[‡]	Pandolfi et al. (2006)
Paluma Shoals	Great Barrier Reef	SW Pacific	Drilled core	quantitative [§]	Perry et al. (2008)
Ribbon Reef 5 and Boulder Reef	Great Barrier Reef	SW Pacific	Drilled core	qualitative	Webster and Davies (2003)
Islets Kendec, Bayes, and Amédée	New Caledonia	SW Pacific	Drilled core	quantitative [§]	Hongo and Wirrmann (2015)
Tasmaloum	Vanuatu	SW Pacific	Drilled core	qualitative	Cabioch et al. (1998)
Papeete	Tahiti Island, Society Islands	SE Pacific	Drilled core	qualitative	Montaggioni et al. (1997)

[†] measured thickness of coral layer.
[‡] measured projected area of corals.
[§] counts of coral pieces (based on presence/absence data).

Table 2

Table 2 Summary of the main characteristics and distribution of sedimentary facies in the cores from Mauritius and Madagascar, based on data from the present and previous studies.

Montaggioni and Faure (1997)				
Facies	(A) Robust branching coral facies	(B) Tabular-branching coral facies	(C) Robust branching-domal coral facies	(D) Foliaceous coral facies
Characteristics of sediment	Robust branching corals (<i>Acropora robusta</i> , <i>Acropora abrotanoides</i> , <i>Acropora digitifera</i> , and <i>Acropora humilis</i>), associated with branching and massive corals (<i>Pocillopora verrucosa</i> , <i>Pocillopora eydouxi</i> , <i>Porites</i> sp. cf. <i>P. lutea</i> , <i>Leptoria phrygia</i> , <i>Platygyra daedalea</i> , <i>Goniastrea retiformis</i> , and <i>Dipsastraea stelligera</i>). Other calcareous organisms (coral fragments, shells, and echinoids) and sand.	Tabular and/or branching corals (<i>Acropora hyacinthus</i> , <i>Acropora cytherea</i> , <i>P. verrucosa</i> , <i>Pocillopora damicornis</i> , and <i>Porites nigrescens</i>), associated with other corals (A. <i>abrotanoides</i> , <i>Echinophyllia aspera</i> , <i>Porites</i> sp. cf. <i>P. lutea</i> , <i>Echinopora gemmacea</i> , <i>Leptastrea</i> sp., <i>Alveopora</i> sp., <i>Platygyra pini</i> , and <i>Montipora</i> sp.). Other calcareous organisms (coral fragments, gastropods, echinoids, and benthic foraminifera) and sand.	Robust branching-domal corals (<i>P. daedalea</i> , <i>Porites</i> sp. cf. <i>P. lutea</i> , <i>Galaxea fascicularis</i> , and <i>P. damicornis</i>) and fragments of corals (A. <i>abrotanoides</i> , A. <i>digitifera</i> , <i>D. stelligera</i> , and <i>E. gemmacea</i>). Other calcareous organisms (molluscs, sponges, and coralline algae), sand, and silt.	Foliaceous corals (<i>Pavona cactus</i> , <i>Pavona divaricata</i> , <i>Pavona decussata</i> , <i>Montipora foliosa</i> , <i>Seriatopora hystrix</i> , and <i>P. nigrescens</i>), associated with other corals (<i>G. fascicularis</i> , <i>P. damicornis</i> , and <i>Echinopora</i> sp.). Other calcareous organisms (coral fragments, seagrass-dwelling molluscs and urchins, and coralline algae), sand, and silt.
Environmental condition	Moderate–high wave energy, from reef crest to upper reef slope, and water depth of 0–6 m.	Low–moderate wave energy, from upper reef slope to middle reef slope, and water depth of 6–15 m.	Moderate wave energy, from reef crest to the outermost of back reef, and water depth of 0–6 m.	Low wave energy, middle part of back reef, and water depth of 0–10 m.
Camoin et al. (2004)				
Facies	(E) Branching <i>Acropora</i> facies			
Characteristics of sediment	Branching <i>Acropora</i> corals (<i>Acropora</i> gr. <i>robusta</i>), associasted with other corals (<i>Acropora</i> sp. cf. A. <i>humilis</i> , <i>Pocillopora</i> sp. cf. <i>P. verrucosa</i> , <i>P. eydouxi</i> , <i>Dipsastraea</i> sp. cf. <i>D. stelligera</i> , <i>Diploastrea heliopora</i> , and <i>Heliopora coerulea</i>). Other calcareous organisms (thick crust of red coralline algae, foraminifera <i>Homotrema</i> , and serpulids) and sand.			
Environmental condition	Moderate-high wave energy, from upper reef slope to reef flat, and water depth of 0–10 m.			

Table 2. (continued)

This study					
Facies	(F) Corymbose <i>Acropora</i> and robust-branching <i>Isopora</i> facies	(G) Massive <i>Porites</i> facies	(H) Arborescent <i>Acropora</i> facies	(I) Foliaceous coral facies	(J) Detritus facies
Characteristics of sediment	Corymbose <i>Acropora</i> and robust-branching <i>Isopora</i> corals (<i>A. digitifera</i> , corymbose <i>Acropora</i> , <i>A. robusta</i> / <i>abrotanoides</i> complex, <i>Isopora palifera</i> , <i>Favites</i> sp. cf. <i>F. chinensis</i> , <i>P. eydouxi</i> , <i>Pavona clavus</i> , branching <i>Porites</i> , and massive <i>Porites</i>), associated with other corals (<i>Acropora retusa</i> / <i>gemmifera</i> complex, <i>Acropora</i> sp. cf. <i>A. humilis</i> , and <i>D. stelligera</i>). Other calcareous organisms (coral fragments, shells, and echinoids) and sand.	Massive corals (massive <i>Porites</i> and <i>Cyphastrea</i> sp.), associated with other corals (branching <i>Acropora</i> and <i>D. stelligera</i>). Other calcareous organisms (coral fragments, shells, and echinoids) and sand.	Arborescent <i>Acropora</i> and associated with other coral (<i>P. daedalea</i> , corymbose <i>Acropora</i> , <i>Cyphastrea</i> sp., <i>E. gemmacea</i> , <i>Porites</i> , and <i>A. robusta</i> / <i>abrotanoides</i> complex). Other calcareous organisms (coral fragments, benthic foraminifera, calcareous algae, shells, and echinoids) and sand.	Reworked foliaceous corals (<i>P. cactus</i> , <i>P. decussata</i> , and <i>Pavona frondifera</i>). Other calcareous organisms (coral fragments, shells, and echinoids) and sand.	Reworked coral fragments and skeletal sand (gastropod, bivalve, echinoids, and calcareous algae).
Environmental condition	Moderate–high wave energy, from reef crest to upper reef slope, and water depth of 0–10 m.	Low–moderate wave energy, from upper reef slope to lower reef slope, and water depth of 0–15 m.	Low–moderate wave energy, from lower reef slope to the outermost of back reef, and water depth of 0–15 m.	Low wave energy, middle part of back reef, and water depth of 0–10 m.	Low wave energy, outer reef slope and/or within back reef.
Integration of previous studies	This facies is combined (A) robust branching coral facies with part of (E) branching <i>Acropora</i> facies.	This facies is combined (B) tabular-branching coral facies with part of (E) branching <i>Acropora</i> facies.	This facies is combined part of (B) tabular-branching coral facies, part of (C) robust branching-domal coral facies with part of (E) branching <i>Acropora</i> facies.	This facies is followed by (D) foliaceous coral facies.	This facies is new one.

Table 3

Table 3 Radiocarbon ages of fossil corals from Mauritius.

Sample ID	Laboratory code and number	Depth from core top (m)	Depth from MSL (m) [†]	Sample	Mineralogy (A: aragonite and A-C: aragonite with calcite)	Conventional ¹⁴ C age (years BP)	Calibrated ¹⁴ C age (cal. years BP ± 2σ)	Cited reference
Mauritius								
Pas1-1	Gif-4974	-0.5	-0.9	<i>Acropora</i> sp.	A-C [‡]	2500 ± 70	1990 ± 200	1
Pas1-2	Gif-4975	-1.5	-1.9	<i>Acropora</i> sp.	A	2780 ± 70	2350 ± 230	1
Pas1-3	Beta-323828	-3.2	-3.5	<i>Acropora digitifera</i>	A	4920 ± 30	5060 ± 170	This study
Pas1-4	Gif-4976	-5.1	-5.5	<i>Acropora</i> sp.	A	2800 ± 70	2380 ± 230	1
Pas1-5	Gif-5199	-6.5	-6.9	<i>Dipsastraea</i> sp.	A	3150 ± 100	2780 ± 280	1
Pas1-6	Gif-4977	-7.6	-7.9	<i>Goniastrea</i> sp.	A-C [‡]	6170 ± 90	6460 ± 200	1
Pas1-7	Gif-4978	-9.1	-9.3	<i>Porites</i> sp.	A	4950 ± 100	5080 ± 260	1
Pas1-8	Gif-4979	-12.0	-12.3	<i>Porites</i> sp.	A	5300 ± 80	5500 ± 190	1
Pas1-9	Gif-4980	-16.2	-16.4	<i>Acropora</i> sp.	A-C [‡]	6600 ± 90	6950 ± 230	1
Pas1-10	Gif-4907	-19.2	-19.4	<i>Porites</i> sp.	A	6790 ± 120	7150 ± 260	1
Pas2-1	Gak-9130	-0.5	-1.4	<i>Acropora</i> sp.	A-C [‡]	2680 ± 130	2230 ± 350	1
Pas2-2	Gak-9131	-3.0	-3.9	<i>Acropora</i> sp.	A	3070 ± 130	2670 ± 330	1
Pas2-3	Gak-9132	-6.5	-7.4	<i>Dipsastraea</i> sp.	A	3580 ± 110	3290 ± 270	1
Pas2-4	Gak-9133	-8.0	-8.8	<i>Acropora</i> sp.	A-C [‡]	5430 ± 130	5650 ± 270	1
Pas2-5	Gak-9134	-9.6	-10.4	<i>Porites</i> sp.	A	5260 ± 180	5440 ± 440	1
Pas2-6	Gak-9135	-12.4	-13.3	<i>Acropora</i> sp.	A	3540 ± 150	3240 ± 380	1
Pas2-7	Gak-9136	-14.9	-15.6	<i>Acropora</i> sp.	A-C [‡]	6590 ± 130	6940 ± 300	1
Pas2-8	Gak-9137	-16.3	-17.0	<i>Leptastrea</i> sp.	A-C [‡]	6850 ± 160	7200 ± 340	1
Pas3-1	Gak-9138	-1.5	-3.1	<i>Acropora</i> sp.	A-C [‡]	2080 ± 110	1520 ± 240	1
Pas3-2	Gak-9139	-4.6	-6.1	<i>Pavona</i> sp.	A-C [‡]	4380 ± 130	4340 ± 370	1
Pas3-3	Gak-9140	-6.2	-7.7	<i>Acropora</i> sp.	A	5650 ± 140	5900 ± 310	1
Pas3-4	Beta-323829	-7.2	-8.7	<i>Porites</i> sp.	A	6060 ± 30	6340 ± 80	This study
Pas3-5	Gak-9141	-8.1	-9.6	<i>Dipsastraea</i> sp.	A-C [‡]	5280 ± 130	5520 ± 330	1
Pas3-6	Gak-9142	-10.0	-11.5	<i>Porites</i> sp.	A	4280 ± 160	4200 ± 450	1
Pas3-7	Beta323830	-10.4	-11.8	<i>Porites</i> sp.	A	6680 ± 40	7050 ± 130	This study
Pas3-8	Gak-9143	-12.0	-13.5	<i>Porites</i> sp.	A	3740 ± 120	3520 ± 300	1
Pas3-9	Gak-9144	-13.5	-15.0	<i>Porites</i> sp.	A	5380 ± 130	5600 ± 290	1

[†] Values are corrected for a subsidence variation of 0.03 m/kyr. MSL, mean sea level.

[‡] The sample has more than 95 % of aragonite content. They were adequate for dating.

Cited reference: (1) Montaggioni and Faure (1997).

Table 4

Table 4 Uranium series ages of fossil corals from Mauritius and Madagascar.

Sample ID	Laboratory [†]	Depth from core top (m)	Depth from MSL (m) [‡]	Sample	Aragonite content (%)	Age (years BP ± 2σ)	Cited reference
Mauritius							
Pas1-11	B	-8.8	-9.1	<i>Porites</i> sp.	98	5000 ± 70	2
Pas1-12	B	-9.7	-10.0	<i>Porites</i> sp.	98	6170 ± 100	2
Pas1-13	B	-9.9	-10.1	<i>Porites</i> sp.	99	7400 ± 70	2
Pas1-14	C	-17.4	-17.6	<i>Porites</i> sp.	97	7590 ± 90	2
Pas2-9	A	-0.8	-1.7	<i>Acropora abrotanoides</i>	99	1600 ± 300	1
Pas2-10	A	-2.2	-3.0	<i>Acropora abrotanoides</i>	98	3400 ± 200	1
Pas2-11	A	-3.9	-4.7	<i>Porites</i> sp.	99	3700 ± 200	1
Pas2-12	A	-5.0	-5.8	<i>Porites</i> sp.	95	4200 ± 200	1
Pas2-13	A	-7.5	-8.3	<i>Acropora abrotanoides</i>	99	4900 ± 200	1
Pas2-14	A	-7.7	-8.5	<i>Porites</i> sp.	98	5500 ± 200	1
Pas2-15	A	-8.2	-9.0	<i>Acropora abrotanoides</i>	94 [§]	6100 ± 200	1
Pas2-16	A	-9.2	-10.0	<i>Galaxea fascicularis</i>	96	5800 ± 300	1
Pas2-17	C	-10.1	-10.9	<i>Acropora abrotanoides</i>	99	5910 ± 100	2
Pas2-18	A	-10.7	-11.5	<i>Galaxea fascicularis</i>	97	6200 ± 300	1
Pas2-19	C	-11.0	-11.8	<i>Porites</i> sp.	98	6480 ± 50	2
Pas2-20	A	-11.2	-11.9	<i>Acropora hyacinthus</i>	98	6800 ± 200	1
Pas2-21	A	-12.8	-13.6	<i>Porites</i> sp.	97	6600 ± 200	1
Pas2-22	A	-13.8	-14.5	<i>Porites</i> sp.	98	7400 ± 200	1
Pas2-23	A	-14.8	-15.5	<i>Galaxea fascicularis</i>	99	7000 ± 300	1
Pas2-24	A	-15.5	-16.2	<i>Porites</i> sp.	100	7300 ± 200	1
Pas2-25	A	-16.0	-16.7	<i>Porites</i> sp.	99	8200 ± 300	1
Pas2-26	C	-16.2	-16.9	<i>Porites</i> sp.	98	8440 ± 180	2
Pas3-10	C	-10.6	-12.0	<i>Acropora abrotanoides</i>	99	7190 ± 50	2
Pas3-11	C	-13.2	-14.6	<i>Acropora hyacinthus</i>	97	7340 ± 60	2
Madagascar							
To1-1	C	-1.5	-2.8	<i>Acropora abrotanoides</i>	100	990 ± 20	2
To1-2	C	-3.6	-4.9	<i>Acropora abrotanoides</i>	99	1530 ± 10	2
To1-3	B	-3.8	-4.5	<i>Acropora abrotanoides</i>	100	5250 ± 60	2
To1-4	C	-8.1	-8.7	<i>Acropora abrotanoides</i>	99	5710 ± 50	2
To1-5	C	-14.1	-14.5	<i>Pocillopora</i> sp.	98	6630 ± 100	2
To1-6	C	-17.0	-17.4	<i>Acropora</i> sp.	97	6600 ± 60	2
To1-7	C	-18.5	-18.9	<i>Acropora</i> sp.	96	7090 ± 130	2
To1-8	C	-20.2	-20.5	<i>Acropora</i> sp.	97	7270 ± 140	2
To2-1	B	-3.0	-4.3	<i>Acropora abrotanoides</i>	99	1530 ± 100	2
To2-2	C	-3.0	-4.2	<i>Pocillopora eydouxi</i>	99	1710 ± 50	2
To2-3	C	-4.0	-5.2	<i>Acropora abrotanoides</i>	98	1900 ± 80	2
To2-4	C	-7.0	-8.2	<i>Acropora abrotanoides</i>	98	2130 ± 40	2
To2-5	C	-9.5	-10.2	<i>Acropora</i> sp. cf. <i>A. humilis</i>	98	5110 ± 50	2
To2-6	C	-12.0	-12.3	<i>Diploastrea heliopora</i>	99	7580 ± 100	2

[†] (A): BRGM-Orléans, France, (B): GEOTOP-Montreal, Canada and BRGM-Orléans, France, and (C):Univ Heidelberg, Germany.

[‡] Values are corrected for a subsidence variation of 0.03 m/kyr at Mauritius and 0.16 m/kyr at Madagascar. MSL, mean sea level.

[§] The sample is inadequate for this study.

Cited reference: (1) Camoin et al. (1997) and (2) Camoin et al. (2004).

Table 5

Table 5 The number of pieces of *in situ* coral species in the studied cores

Unit, Facies, and coral species

[illegible]

Co-Ac-Iso facies, corymbose *Acropora* and robust-branching *Isopora* facies; Ma-Po facies, massive *Porites* facies; Ar-Ac facies, arborescent *Acropora* facies; Fo-coral facies, foliaceous coral facies; and Det facies, detritus facies.

Table 6

Table 6 Dominant coral species on modern reefs in Mauritius.

	Lower reef slope, water depth of more than 25–30 m	Lower to middle reef slope, water depth of 6–20 m	Upper reef slope, water depth of 0–6 m	Reef crest	Back reef zone
<i>Acropora abrotanoides</i>			○	○	
<i>Acropora cytherea</i>		○			
<i>Acropora digitifera</i>				○	
<i>Acropora granulosa</i>	○				
<i>Acropora humilis</i>				○	
<i>Acropora hyacinthus</i>		○	▲		
<i>Acropora robusta</i>			○		
<i>Acropora tenuis</i>		○			
<i>Astreopora ocellata</i>		○			
<i>Cyphastrea microphthalma</i>		○			
<i>Dipsastraea pallida</i>	○				
<i>Dipsastraea</i> sp.		▲			
<i>Dipsastraea speciosa</i>		○			
<i>Dipsastraea stelligera</i>			▲		
<i>Echinophyllia aspera</i>	○	▲			
<i>Echinopora gemmacea</i>		▲			
<i>Favites flexuosa</i>		○			
<i>Favites</i> sp.		▲			
<i>Fungia fungites</i>	○				
<i>Galaxea fascicularis</i>		○		○	
<i>Goniastrea pectinata</i>		○	▲		
<i>Goniastrea retiformis</i>		○	▲		
<i>Goniopora</i> sp.		○			
<i>Herpolitha limax</i>	○				
<i>Hydnophora microconos</i>	○	○			
<i>Leptoria phrygia</i>				○	
<i>Lobophyllia hemprichii</i>	○	▲			
<i>Millepora platyphylla</i>			▲		
<i>Montipora</i> sp.		▲			
<i>Montipora</i> sp. cf. <i>M. tuberculosa</i>				○	
<i>Oulophyllia crispa</i>	○	○			
<i>Pachyseris speciosa</i>	○				
<i>Pavona cactus</i>					○
<i>Pavona decussata</i>					○
<i>Pavona divaricata</i>					○
<i>Platygyra daedalea</i>		○			
<i>Pocillopora damicornis</i>	○			○	
<i>Pocillopora eydouxi</i>		▲			
<i>Pocillopora verrucosa</i>		▲	▲		
<i>Porites lobata</i>	○				
<i>Porites lutea</i>	○	○		○	○
<i>Porites nigrescens</i>					○
<i>Porites rus</i>					○
<i>Porites solida</i>		○			
<i>Seriatopora hystrix</i>					○
<i>Stylophora pistillata</i>				○	

Data from Montaggioni and Faure (1997).

Circles and triangles indicate dominant and associated species, respectively.

1 **Table captions**

2 **Table 1.** Survey of quantitative and qualitative assessments of Holocene coral species
3 conducted in different studies.

4

5 **Table 2.** Summary of the main characteristics and distribution of sedimentary facies in
6 the cores from Mauritius and Madagascar, based on data from the present and previous
7 studies.

8

9 **Table 3.** Radiocarbon ages of fossil corals from Mauritius.

10

11 **Table 4.** Uranium series ages of fossil corals from Mauritius and Madagascar.

12

13 **Table 5.** Numbers of pieces of *in situ* coral species in the studied cores.

14

15 **Table 6.** Coral species on modern reefs in Mauritius.

16

17