

## Acroporidae of the Caribbean

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**ABSTRACT.** The scleractinian family Acroporidae reaches its greatest diversity in the Indo-Pacific region, where it has six extant genera and around 250 valid species, and dominates coral species composition on many reefs. Only one genus, *Acropora*, represented by only two species, survives in the Caribbean, although at least four other genera, *Astreopora*, *Alveopora*, *Dendracis* and *Isopora* are present in the Caribbean fossil record. Using fossil specimens from museum collections, this study reviews the Caribbean genera and species of Acroporidae and their relevance to the evolution and biogeography of the family. Two turnover periods (late Oligocene/early Miocene and Plio-Pleistocene) have been recognised as major influences on the post-Tethyan fossil history of Caribbean reef-building Scleractinia. Because of the importance of Acroporidae in the Indo-Pacific today, the successive origination and loss of taxa as well as unique taxon characteristics in the Caribbean setting are of interest in assessing the challenges faced by extant taxa under a regime of global climate change.

**KEYWORDS:** Coral reefs, Oligocene/Miocene turnover, biogeography, evolution, climate change, fossils, Scleractinia.

### 1. Introduction

The history of fossil Caribbean corals and reefs has been documented for at least 150 years (e.g. Duncan, 1863, 1864, 1873; Vaughan, 1919; Vaughan & Hoffmeister, 1926; Weisbord, 1973; Frost & Langenheim, 1974), but with particular vigour in recent decades (e.g. Budd et al., 1994, 1995, 1998; Stemann, 2004; Johnson et al., 2009). These efforts have resulted in collections representing a wide range of taxa, stratum ages and locations. As a result of this body of work, significant events in the history of the Caribbean coral fauna have been identified and quantified in terms of biodiversity (e.g. Edinger & Risk, 1994; Budd, 2000; Johnson & Kirby, 2006). The Caribbean has been home to at least 66 genera of Scleractinia, of which 25 are extant there (Budd, 2000). The consensus is that a cosmopolitan Tethyan fauna existed in the Caribbean from the late Cretaceous to the end of the Eocene (Edinger & Risk, 1994; Budd, 2000). Following this, two intervals of pronounced turnover are documented (a) an Oligocene/early Miocene turnover (OMT), which represented “the early divergence of a distinctive western Atlantic fauna from the previous pan-tropical Tethyan fauna” (Johnston & Kirby, 2006) and (b) a Plio-Pleistocene turnover (PPT), when loss of many genera led to establishment of the modern Caribbean fauna, distinguished by strong representation from certain families, especially Mussidae and Faviidae, and region-wide domination by a few genera and species (Budd, 2000; Johnston & Kirby, 2006).

This paper reports on the Caribbean history of one particular Scleractinian family, the Acroporidae. The family has been placed within the “Complex” clade by molecular phylogenetic analyses (e.g. Romano & Cairns, 2000; Fukami et al., 2008) and is characterised by the entire colony skeleton, including thecae, septa and coenosteum, being an open synaptulate framework (Wells, 1956; Veron & Wallace, 1984). This family of purely reef-building corals reaches its living zenith in the Indo-Pacific, where it has six extant genera and around 250 valid species (Veron & Wallace 1984; Veron, 2000; Dai & Horng, 2009). Frequently, numerous species co-exist, making Acroporidae a dominant contributor to coral biodiversity in shallow-water coral assemblages. One genus, *Acropora*, often

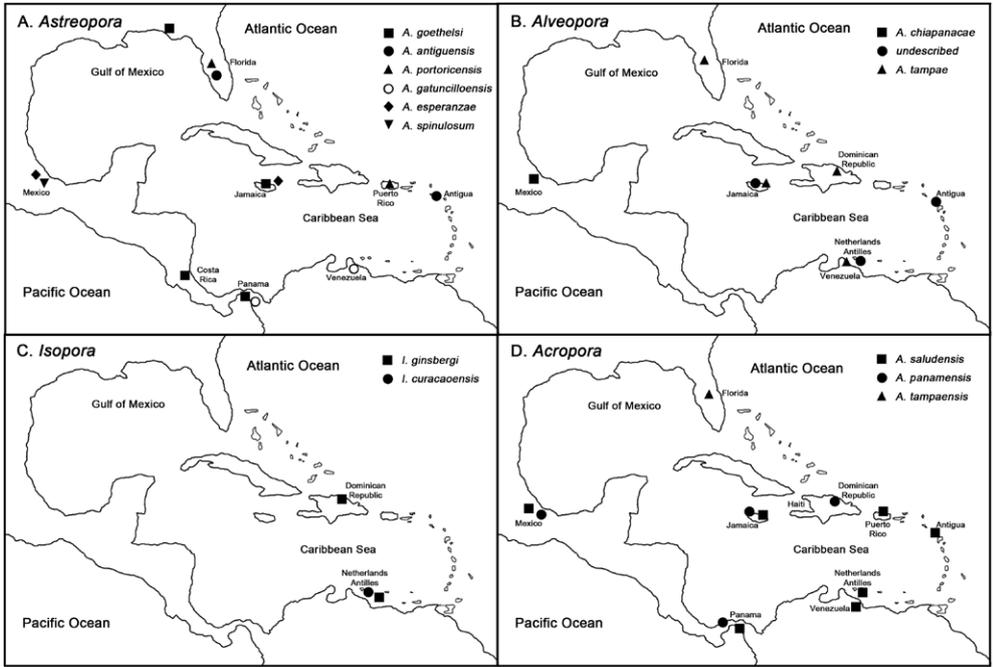
forms the major framework of whole reef zones and has a rapid branching growth mode, allowing many species to be superior competitors for space on the reef (Connell et al., 2004; Wallace, 1999), and it also plays a major role in mass spawning events (Harrison, 2011). Outside the Indo-Pacific today, Acroporidae is represented only in the Caribbean, where just a single species group of *Acropora* with two biological species occurs (along with an F1 hybrid of these: Volmer & Palumbi, 2002; Van Oppen et al., 2000). In contrast to the extant Caribbean fauna, five genera (*Dendracis*, *Astreopora*, *Acropora*, *Isopora* and *Alveopora*) have a fossil history in the region (references above, Budd & Wallace, 2008). All these genera except *Isopora* are also present in the fossil record of Europe, the Mediterranean and the Middle East, making Acroporidae one of the most global families, with a rich evolutionary and biogeographic history (Table 1).

The future of the taxon richness of Acroporidae in the current scenario of rapid global climate change is of great concern, as many species are limited to the upper photic zone, and thus subject to the impact of coral bleaching events resulting, in particular, from elevated sea temperatures (e.g. Hoegh-Guldberg, 1999; Donner et al., 2005) and also to the impacts of human exploitation and disturbance (e.g. Fabricius, 2005; Wilkinson, 2008). While the loss of Acroporidae from the European region is associated with a general loss of all reef-building Scleractinia by the end of the Miocene (Perrin, 2002), the history of the genera in the Caribbean has not been explored. This paper is a first attempt to assess the Caribbean record of Acroporidae for information relevant to the phylogeny and biogeography of the family. The following questions are posed for initial response and future study:

- 1) How do Caribbean occurrences of Acroporidae genera relate to the two major turnover events?
- 2) Was the Caribbean sojourn of these genera a dead-end, or did it contribute to or even benefit from Indo-Pacific lineages?
- 3) Does the Caribbean record include any new first appearance records for the purpose of molecular clock interpretations?
- 4) Are there points of interest, such as characters that might inform interpretations of the evolution and phylogeny of the family?

**Table 1.** Number of documented species for each genus in each geographical area. Numbers for genera still extant within an area are underlined.

Genus	Geological range	Caribbean	Europe & Middle East	Indo-Pacific
<i>Dendracis</i>	upper Cretaceous to Miocene	2	10	2
<i>Astreopora</i>	upper Cretaceous to Recent	3-6	27	<u>17</u>
<i>Acropora</i>	Paleocene to Recent	<u>7</u>	19	<u>~150</u>
<i>Alveopora</i>	Eocene to Recent	2	3	<u>14</u>
<i>Isopora</i>	Miocene to Recent	2	0	<u>6</u>
<i>Montipora</i>	Eocene to Recent	1 record	0	<u>76</u>
<i>Anacropora</i>	Recent	0	0	<u>7</u>



**Figure 1.** Distribution records for extinct Caribbean species of four Acroporidae genera (A) *Astreopora* (B) *Alveopora* (C) *Isopora* (D) *Acropora*.



**Figure 2.** Examples of extinct genera and/or species of Caribbean Acroporidae, represented by NMNH specimens, except where noted. A: *Astreopora antiguensis* Vaughan, 1919 paratype from Antigua NMNH 325609. B: *Isopora ginsbergi* Budd and Wallace, 2008 holotype from Curaçao (University of Iowa Paleontology Repository SUI 102751). C: *Alveopora tampa* Weisbord, 1973 holotype from Tampa, Florida, USA NMNH 66160 lower Miocene. D: *Dendracis cantabrigiensis* Vaughan, 1899 NMNH 44292 from Jamaica. E, I, J: Undescribed *Acropora* species from: (E) Cuba; (I) Antigua and (J) Tampa, Florida. F: *Acropora saludensis* Vaughan, 1919 from Panama NMNH 64046. G: *Acropora tampaensis* Weisbord, 1973 from Tampa, Florida, USA holotype NMNH 68313. H: *Acropora panamensis* Vaughan, 1919 NMNH 325041 from Panama. Scale bar 10 mm.

## 2. Materials and methods

The study is based on examination of fossil specimens at the National Museum of Natural History of the Smithsonian Institution, Washington DC (NMNH). The NMNH collection includes types and published material from Vaughan (1919), Weisbord (1973), Frost and Langenheim (1974) and others including papers of A.F. Budd and colleagues and J.W. Wells, an unpublished manuscript of J.E. Hoffmeister, and specimens collected by numerous authors, researchers and NMNH staff during exploration and/or research on other taxa or geological topics. *Isopora* was studied in Neogene deposits in Curaçao and from specimens from Budd et al. (1998) from the University of Iowa Paleontology Repository. Material was studied using light microscopy, scanning electron microscopy and thin sections. Potential new species mentioned in the text were often represented by only one or a few specimens, and further study is required before these can be published. Literature records for other taxonomic and stratigraphical surveys of Caribbean locations are given in the text.

## 3. Results and discussion

### 3.1. *Astreopora*

*Astreopora* has a distinctive coenosteal structure of sturdy spinules, which makes identification of fossil specimens relatively straightforward. It is recorded from the late Cretaceous in Jamaica (Baron-Szabo, 2006), the middle Eocene of Mexico (*A. esperanzae* and *A. spinulosum*) and Oligocene to early Miocene in Florida, Panama, Antigua and elsewhere (*A. antiguensis*, *A. goethelsi*, *A. portoricensis* and *A. gatuncilloensis*) (Fig. 1A). Some of the latter group of species may be synonyms, as they share a striking general colony form, not seen elsewhere in *Astreopora*. *A. goethelsi* has thick columnar branches, *A. antiguensis* has similar branches that are expanded at the tips (Fig. 2A) and the others have variants of these forms. These sturdy branches are similar in general outline to those of some species of *Isopora* and this is discussed below.

*Astreopora* is rarely dominant or diverse in living assemblages (Lamberts, 1982; Veron, 2000). Despite this, the genus is proving to be more diverse than previously thought, with novel characters recently found in two new species from western Papua (Wallace et al., 2011). *Astreopora* is usually interpreted as basal to the family in molecular phylogenies (Fukami et al. 2000, 2008). Most *Astreopora* are non-branching as are many *Montipora* and *Alveopora*, however the new species are branching. One has a dendritic branching mode, shared with branching *Montipora*,

and another has axial growth, previously found only in the clade containing *Acropora* and *Isopora*. We proposed that these characters might be due to a historical constraint that causes the same condition to originate more than once, but in different character settings, within a lineage (Wallace et al., 2011). The sturdy branching units of the Oligocene-Miocene Caribbean *Astreopora* may offer another example of this phenomenon, being similar to the branching type seen in some *Isopora* (Fig. 3).

*Astreopora* disappears from the Caribbean record in the OMT (Fig. 4A). It is likely that its sojourn in the Caribbean was a dead-end, as there are no indications of the thick-branching lineage elsewhere. Its post-Eocene species, with their large, sturdy skeletons, probably contributed substantially to Caribbean reef development. They also offer an insight into evolutionary novelty and parallelism in the family.

### 3.2. *Alveopora*

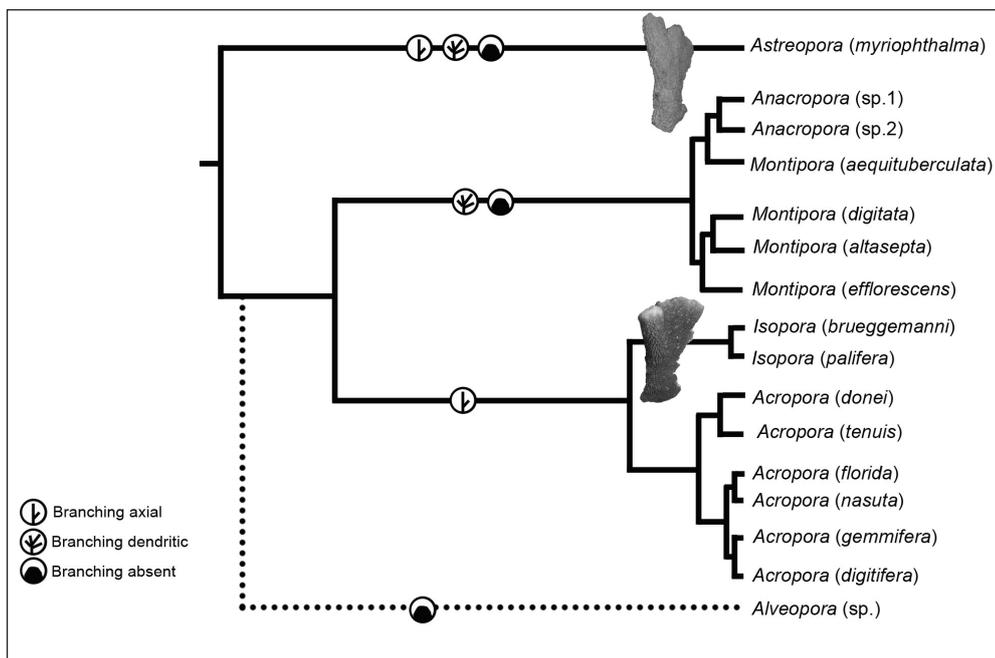
*Alveopora* was transferred from Poritidae to Acroporidae by Dai & Horng (2009) following molecular phylogenies which indicated affinity with the family (e.g. Fukami et al. 2000, 2008). The disparity with other Poritidae genera had previously been noted (e.g. Wells, 1956; Veron & Wallace, 1984). *Alveopora* has the Acroporidae characteristic of synapticulothecate skeleton but does not have coenosteum. Its minimalist skeletal architecture offers few skeletal features for taxonomic comparison or identification, and biologists sometimes seek to use polyp features to distinguish species (Kitano et al., submitted).

*Alveopora* is known from the middle Eocene of Mexico (*Alveopora chiapanecae* Frost & Langenheim 1974) and Oligocene to early Miocene in Florida, Dominican Republic, Venezuela and elsewhere (*Alveopora tampae* Weisbord 1973, see Fig. 2C) as well as an undescribed species. On modern Indo-Pacific reefs, *Alveopora* is usually difficult to find, as species mostly occur deeper than the intertidal, in sheltered habitats. This may also be so for the fossil species, as the genus is infrequent in collections, but it is found frequently enough to indicate a broad distribution (Fig. 1B). From the specimens available to date it is not possible to say whether or not the Caribbean species contributed to Indo-Pacific evolution of this genus.

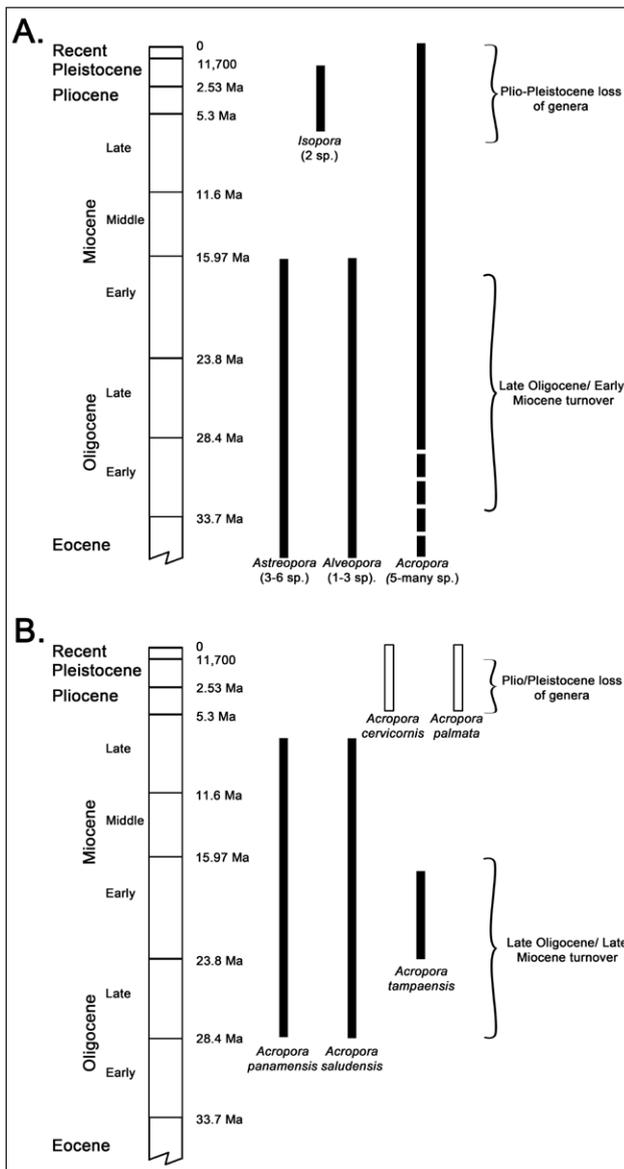
*Alveopora* is found in the fossil history of the Caribbean from the Eocene and disappears in the OMT at around the same time as *Astreopora* (Fig. 4A).

### 3.3. *Isopora*

Previously a subgenus of *Acropora*, *Isopora* was elevated to genus level based on genetic distance as well as differences in axial corallite development, skeletal microstructure and reproductive mode (Wallace et al., 2007). It is a distinctive genus with sturdy



**Figure 3.** Colony form characters shared by the basal Acroporidae genus *Astreopora*, with other genera in the family, indicated on a composite cladogram of Acroporidae phylogeny based on molecular studies of Fukami et al. (2000, 2008). Sturdy branch character from Caribbean *Astreopora* superimposed.



**Figure 4.** Timelines for Acroporidae from the Caribbean and relationship to major turnover events. A: Genera *Astreopora*, *Alveopora*, *Isopora* and *Acropora*. B: Described species of *Acropora*, extinct and extant.

skeleton, whose species can form extensive colonies and play a dominant role in reef-building, especially on reef fronts (Wallace, 1999). It has a characteristic coenosteal microstructure with meandroid spinules, and occurs in two main growth forms: either with thick club-shaped or cuneate branches and numerous axial corallites, or with a single main axial supported by one or more supplementaries (Wallace et al., 2007).

Thought to be absent from the Caribbean, *Isopora* was found from late Miocene to Pliocene reefs of Curaçao by Budd et al. (1998), who initially interpreted it as very thick *Acropora* (Budd & Wallace, 2008). Two species, *Isopora ginsbergi* Budd & Wallace, 2008 (Fig. 2B) and *I. curacaoensis* Budd & Wallace 2008, occurred as an ecological dominant, second only to *Stylophora*, and would have been important in reef-building, as indicated particularly by the abundance of the thick club-shaped branches of *I. ginsbergi* at the type locality (Budd et al., 1998). The second species, *I. curacaoensis* has the growth form based around a main axial corallite (Wallace & Budd, 2009). The NMNH collection also includes two small, *Isopora*-like specimens from the Dominican Republic and these suggest a broader distribution for *Isopora* (Fig. 1C).

*Isopora* is not found in European deposits (Table 1). At the time of discovery, the Curaçao species were the earliest global records for *Isopora*: but the genus was reported subsequently from the middle Miocene of Fiji by Bromfield & Pandolfi (2011).

Curaçao is quite close to the Panama region which would have provided access to and from the Pacific Ocean and it seems a reasonable hypothesis that *Isopora* might have invaded the Caribbean from the Pacific, then become extinct due to events associated with the closure of the isthmus of Panama. Because of its reproductive mode, *Isopora* is quite vulnerable to local extinction (Paulay & Wallace, 2000).

For the present, indications are that *Isopora* had a brief sojourn in the Caribbean, disappearing in the Plio-Pleistocene event, having appeared only 4-5 million years before (Fig. 4A). The location of origination of the genus, whether Atlantic or Indo-Pacific, is as yet unknown, but the Atlantic record has already more than doubled the origination date of two million years ago previously used for *Isopora* in molecular clock calibrations (Fukami et al., 2000).

### 3.4. *Acropora*

This genus is distinguished by its exclusively axial branching mode, and differentiation of two types of corallites: axial and radial, with associated coenosteal differentiation, such that 20 species groups have been recognised using these characters (Wallace, 1999). In the Caribbean today only the *cervicornis* species group is extant (Fig. 2B). This has two widespread species *A. cervicornis* (Lamarck, 1816) and *A. palmata* (Lamarck, 1816), which are considered to be highly endangered, as evidenced by their listing on the US endangered wildlife list (Gardner et al. 2003).

Three species of extinct *Acropora* are described and recorded from the Caribbean: *Acropora saludensis* Vaughan, 1919 and *A. panamensis* Vaughan, 1919 are broadly distributed in Oligocene to late Miocene deposits from Mexico, Panama, and several other locations, while *A. tampaensis* Weisbord, 1973 is recorded only in the early Miocene of Florida (Fig. 1D).

Following a finding of up to 10 of the 20 currently recognized extant species groups of *Acropora* in the Eocene of England and France (Wallace & Rosen, 2006; Wallace, 2008; White et al., 2010), it could be predicted that species groups additional to the *cervicornis* group might also be represented in the fossil history of Caribbean *Acropora*. This does seem to be the case from the characteristics of the species, although further study will be required to place the fossil material in putative species groups. *A. tampaensis* (Fig. 2G) has characters suggestive of the *cervicornis* group. *Acropora saludensis* (Fig. 2F), well represented in the NMNH collections has characteristics of the *muricata* species group. *A. panamensis* (Fig. 2H), does not align with either of these groups, suggesting at least a third species group is represented in the Caribbean.

In addition to these described species of living and fossil *Acropora*, there appear to be at least five undescribed species in the Smithsonian records, three of which from Cuba, Barbados and Florida are shown in Figure 2 (E, I, J). This material, once examined and described, will greatly add to the information about the diversification and history of *Acropora* in the Caribbean.

Even from the currently available information, it can be seen that *Acropora* has been involved in both turnover events (Fig. 4B). *Acropora tampaensis* disappeared in the first event, at least two other species existed up until the Plio-Pleistocene turnover, which was also the time of origination of the modern species. The extant species *Acropora cervicornis* and *A. palmata* are present in the Caribbean record from the early Pliocene (Fig. 4B). The ancestor of these two species, which are extremely similar in skeletal features other than colony form, is unknown at present, but *A. tampaensis* Weisbord, 1973 is suggested as a possibility. The species group is thought to be represented in the Eocene of Europe (Wallace, 2008) and if this is the case it would be expected to be present in the pan-Tethyan fauna, possibly along with other species groups as mentioned above.

### 3.5. *Dendracis*

This globally extinct genus is represented by *Dendracis cantabrigiensis* Vaughan 1899 (type locality Cambridge, Jamaica). *Dendracis* disappeared from the Caribbean at the end of the Eocene (Budd, 2000) and globally in the Miocene (Wells, 1964), so is not included in the timeline considered for this paper.

### 3.6. *Montipora*

One record of *Montipora* has been reported for the Caribbean: Johnson & Kirby (2006) mention "*Montipora* sp. A" from Antigua. At present there do not appear to be other specimens for examination. *Montipora* is not reliably known from the European region (*M. danielli* Reig, 1990 from the Eocene of Spain is *Actinacis cognata* (G. Alvarez-Perez, pers. com.)).

## 4. Conclusions

This preliminary study examines published and museum evidence of Caribbean Acroporidae, in relation to current taxonomic grouping from molecular phylogeny of the extant genera. Some findings are:

1) *Astreopora*, basal genus, distributed through the region possibly from the late Cretaceous, and especially Oligocene to Miocene, demonstrates a unique branching form in some Caribbean members, which finds a possible homologue in a later genus, *Isopora*. *Astreopora* became extinct in the Caribbean in the late Oligocene/early Miocene turnover and probably did not contribute to an Indo-Pacific lineage.

2) *Alveopora* (recently moved to this family from Poritidae), also a basal genus, and present from the Eocene, also became extinct in the Caribbean in the OMT, but little can be said on any lineage in the Pacific, as fossils are infrequent and no unique skeletal features occur in the Caribbean species.

3) *Isopora*, apparently restricted to the Netherlands Antilles but possibly more widely distributed, dominated reef-front assemblages during a period of about 3.9 Ma in the late Miocene to late Pliocene. This genus, now widespread on reefs throughout the Indo-Pacific but never recorded in Europe, probably originated in either the Caribbean or Indo-Pacific. The Curaçao species, when published, were the earliest record for *Isopora*, and made it possible to extend back its date of origination for molecular clock purposes by three million years. A recently published middle Miocene record of *Isopora* in the Pacific Ocean extends this record and raises an obvious hypothesis, that this genus entered the Caribbean from the Pacific and briefly had great ecological success in a localised setting.

4) *Acropora* is now restricted to a single living species group with two main species that are widespread and ecologically abundant from the late Miocene or Plio-Pleistocene to the present. This genus has been represented in the Caribbean by other species and species groups, described and undescribed, up to the late Miocene, indicating a more diverse history for this genus, which will be potentially very informative once studied. Several new species of extinct Caribbean *Acropora* remain to be described, representing additional species groups.

5) The position of *Montipora* as a purely Indo-Pacific genus remains unchallenged by the evidence of this initial study of Caribbean Acroporidae.

These findings indicate that, in particular, detailed study and description of new *Acropora* species and a search for further specimens providing broader distribution of *Isopora*, would enhance understanding of the evolution and biogeography of the family in the region and globally. Extinction of three genera of Acroporidae (*Astreopora*, *Alveopora* and *Isopora*) in the Caribbean appears to have the same root cause as that of other genera lost in the relevant turnover event: OMT in the case of the first two species and PPT in the case of *Isopora*. For *Acropora*, the situation is different, in that it appears that only one of a number of species groups survived through to the present, and the reason for this could be examined in relation to the environmental preferences of the species groups involved.

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