

# Diverse staghorn corals (*Acropora*) in high-latitude Eocene assemblages: implications for the evolution of modern diversity patterns of reef corals

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*Acropora* is the most diverse genus of reef-building corals in the world today. It occurs in all three major oceans; it is restricted to latitudes 31° N–31° S, where most coral reefs occur, and reaches greatest diversity in the central Indo-Pacific. As an exemplar genus, the long-term history of *Acropora* has implications for the evolution and origins of present day biodiversity patterns of reef corals and for predicting their response to future climate change. Diversification of *Acropora* was thought to have occurred in the central Indo-Pacific within the previous two million years. We examined Eocene fossils from southern England and northern France and found evidence that precursors of up to nine of 20 currently recognized *Acropora* species groups existed 49–34 Myr, at palaeolatitudes far higher than current limits, to 51° N. We propose that pre-existing diversity contributed to later rapid speciation in this important functional group of corals.

**Keywords:** Eocene; coral reefs; biogeography; climate change; molecular clock

## 1. INTRODUCTION

The purpose of this paper is to draw attention to the currently overlooked deep fossil record of *Acropora* (Oken 1815), and its implications for the evolution of modern diversity patterns of reef corals. *Acropora* is the most diverse modern coral genus (more than 120 extant species; Wallace 1999; Veron 2000) and provides a major element of modern reef coral diversity and coral reef frameworks throughout the world, reaching its greatest diversity in the central Indo-Pacific (Veron 1995; Wilson & Rosen 1998; Wallace 1999). Owing to this diversity and abundance, *Acropora* has been the subject of a number of evolutionary studies (e.g. Fukami *et al.* 2000; van Oppen *et al.* 2001; Volmer & Palumbi 2002; Wolstenholme 2003). The genus also has an extensive fossil history, which is becoming more accessible as new studies provide more data and finer resolution (e.g. Carbone *et al.* 1994; McCall *et al.* 1994; Wilson & Rosen 1998; Budd 2000; Schuster 2002). It is thus an ideal exemplar for studying the origins of modern diversity and distribution patterns for reef corals.

Although Southeast Asia is the current locality of the greatest diversity of *Acropora* and other modern Indo-Pacific reef coral genera, this region was lacking in most zooxanthellate coral genera ('z-corals') and z-coral-dominated carbonates up until the latest Oligocene to earliest Miocene (around 26 Myr), a phenomenon dubbed the 'Paleogene gap' by Wilson & Rosen (1998). While future discoveries could conceivably show that the Paleogene gap is an observational artefact,

Wilson & Rosen (1998) pointed out that this pattern is founded on numerous preceding studies over 80 years, and that it also applies to other tropical shallow water marine organisms. Moreover, this biotic and palaeoenvironmental gap corresponds to a real oceanic gap. Wilson & Rosen (see also Wilson 2002) reviewed the carbonate record of the entire region in the context of plate movements and palaeogeographical changes through the Cenozoic. Significantly, a 3000 km wide oceanic void, with few shallow water areas and land-masses, existed in the earlier Paleogene between Australasia and the Southeast Asia mainland. This gap gradually narrowed through the Paleogene, and shallow water areas increasingly emerged as the Australasian craton moved northwards, colliding with the Southeast Asian craton during the Paleogene–Neogene transition time.

The distribution pattern of *Acropora* in particular, also shows a Paleogene gap, since there are no records of it to date in the Indo-West Pacific or Pacific regions until the Paleogene–Neogene transition. In contrast, in addition to the English and French Eocene material examined in this paper, *Acropora* species occurred in Eocene shallow water carbonates in Mediterranean France, Spain, Italy and the former Yugoslavia (see Wallace 1999, p. 20). The earliest known record of the genus occurs in the Late Paleocene (65–54 Myr) from Somalia (Carbone *et al.* 1994). The first record of *Acropora* dominating a reef structure comes from the Late Oligocene (28–23 Myr) in Greece (Schuster 2002), but by the Mid-Miocene (16–12 Myr) the genus is no longer represented in the Mediterranean region, having disappeared during the progressive Miocene extinction of all reefal biotas throughout this region (Rosen 1999).

It is commonly assumed that the species composition of extant reef corals, including *Acropora*, has been most

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The electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2005.3307> or via <http://www.journals.royalsoc.ac.uk>.

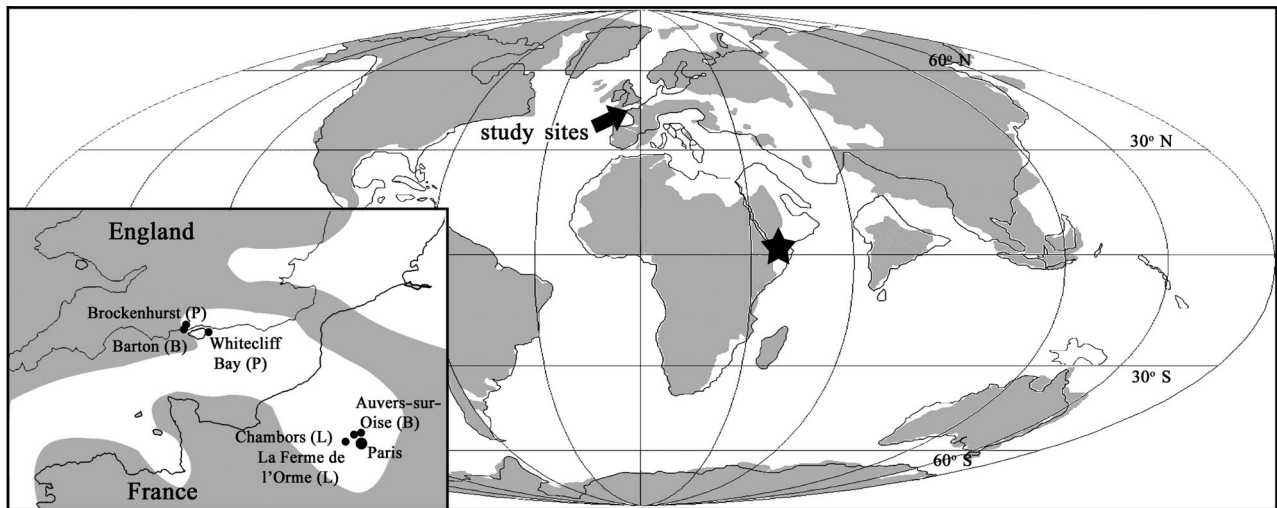


Figure 1. Reconstructed Lutetian–Bartonian world landforms (solid) after Golonka (2000) with permission, indicating locality of Eocene fossil localities (arrow) and locality of earliest recorded *Acropora* fossil (star). Inset: area covering fossil localities from this study. Deposit age indicated as L (Lutetian), B (Bartonian) and P (Priabonian).

strongly influenced by Neogene evolutionary events, particularly the Panama closure and Plio-Pleistocene sea level fluctuations of the last two million years (Stehli & Wells 1971; Potts 1985; Veron 1995; Fukami *et al.* 2000). An Eocene appearance date (54 Myr) for *Acropora* has been used as a molecular clock calibration (Fukami *et al.* 2000), but potentially the fossil record could provide much further information about the relationship between past and present taxonomic composition. For an indication of Eocene coral diversity, we examined Eocene *Acropora* fossils from England and France in the collections of the Natural History Museum, London (NHM). These fossils occurred in assemblages 49–34.2 Myr old, during the Lutetian, Bartonian and Priabonian (figure 1, Berggren *et al.* 1995), i.e. after Early Eocene extreme global warmth but before dramatic cooling in the Oligocene (Huber & Caballero 2003).

The current distribution of *Acropora* is almost exclusively between latitudes 31°N and S of the Equator (figure 2), within the temperature and calcium carbonate saturation limits suitable for modern reef development (Opdyke & Wilkinson 1993; Kleypas *et al.* 2001); however, the Eocene fossils of *Acropora* studied here, as well as other *z*-corals and tropical organisms, occurred at palaeolatitudes 49–51°N. Although such records have existed for some time (Duncan 1866), their implications for modern reefs and *z*-corals in the context of global warming and diversity patterns have not been previously realized, and much relevant material in museum collections has not been studied or identified. The high-latitude fossils have unusually good preservation, because they are preserved in muds or silty and marly sands (table 1). They, therefore, give an insight into Eocene coral diversity, which is not readily available from indurated carbonates typical of many other coral-bearing deposits.

Modern coral species are defined primarily by morphological discontinuities in skeletal structures; although molecular techniques are increasingly used to explore species boundaries (Wallace & Willis 1994; Volmer & Palumbi 2002; Wolstenholme *et al.* 2003), clearly these cannot be applied to fossils. On the other hand, fossil material is variously subject to taphonomic and diagenetic processes, and this often obscures some of the taxonomic

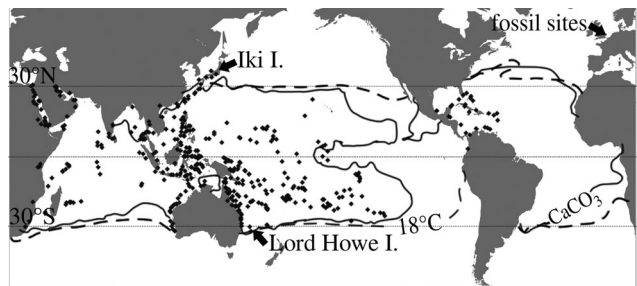


Figure 2. Present distribution of *Acropora*, from Worldwide *Acropora* Collection database. Lines indicate critical boundaries of SST (18 °C) and aragonite saturation for coral reef accretion (CaCO<sub>3</sub>) as given by Kleypas *et al.* (1999). Highest north and south latitude reefs (Iki I., Lord Howe I.) and Eocene fossil localities in this paper are indicated.

characters that are available to those studying modern counterparts of fossil taxa. This can also lead to different methodologies (e.g. studies of skeletal sections are more widely used for fossil than modern corals). While successful integrated studies of corals at species level are possible (e.g. Budd 1991), these can be labour-intensive. Forey *et al.* (2004) recommend that, in general, for studies based on compilations of fossil taxa, generic level is a more pragmatic approach. However, to identify the present Eocene *Acropora* fossils, we adopted a level of classification not previously used for fossil corals, but in common use for living *Acropora* (Wallace 1999). The genus has two subgenera, only one of which is represented in the Eocene: the larger subgenus *Acropora* (*Acropora*) (hereafter shortened to *Acropora*). This has been subdivided into 20 'species groups', based on shared skeletal character states (Veron & Wallace 1984) and on clades in a morphological phylogeny (Wallace 1999). We employed this species group level to make direct comparisons between modern and Eocene faunas.

## 2. MATERIAL AND METHODS

### (a) Localities

Material examined came from six main localities (table 1 and figure 1 inset), two Late Priabonian localities: Whitecliff Bay (Isle of Wight) and Brockenhurst in England, two Bartonian:

Table 1. Characteristics of localities from which the Eocene *Acropora* fossils in this study had been collected. (Quotation marks indicate poor precision of locality or age. NP refers to nannoplankton zone and P to planktonic foraminiferal zone after Berggren *et al.* (1995). Palaeolatitudes, ages and facies have been inferred from locality information in column 1 using sources including: 1, Davis (1952); 2, Insole & Daley (1985); 3, Melville & Daley (1982); 4, Gale *et al.* (1999); 5, Cavelier *et al.* (1980); 6, Mégnien (1980); 7, Harris & Burrows (1891); 8, Pomerol (1982); 9, Debrand-Passard (1980); 10, Mégnien & Mégnien (1980).)

locality	palaeolatitude	estimated age (Myr)	relative (biostratigraphical) age	facies	sources
Brockenhurst, Hampshire, England	51° N	36.0–34.2	Late Eocene (Late Priabonian, NP19–20)	mainly composed of muds, sandy muds and muddy sands	1, 2, 3
Whitecliff Bay, Isle of Wight, England	51° N	36.0–34.2	Late Eocene (Late Priabonian, NP19–20)	mainly composed of muds, sandy muds and muddy sands	2, 5
Auvers-sur-Oise, France	49° N	41.4–37.0	Late Mid-Eocene (Bartonian, NP 16–18, P12–15)	sands of variable character, horizontal or false-bedded, buff, grey or ferruginous	5, 6, 7, 8
Barton, England	51° N	41.4–37.2	Late Mid-Eocene (Bartonian, NP 16–18, P12–15)	fine sands and muds	2, 3, 4
Chambors, France	49° N	47.3–45.5	Early Mid-Eocene (Lutetian, NP15)	fine sands and muds	7, 8, 9, 10
La Ferme de l'Orme, France	49° N	49.0–41.3	Lutetian	fine sands and muds	6, 7
'Paris Basin', France	'45° N'	49.0–37.0	Mid-Eocene	not available	
Paris, France	'45° N'	55.0–33.7	'Eocene'	not available	

Table 2. Skeletal characters for *Acropora* which were discernible in fossils, with their character states. (Scheme 1, character numbering used by Wallace (1999), scheme 2 that used by Wolstenholme *et al.* (2003)). States include all known to be possible for extant material; no new states seen in the fossil specimens examined.)

character	states	scheme	
		1	2
branch formation	around a single axial corallite/more than one axial corallite	1	—
branching orders	tertiary or later orders: present/not present	2	1
predominant outline	cuneiform/arborescent/hispidose/encrusting/elkhorn/corymbose/tabular <sup>a</sup>	3	2
coenosteum	same on and between radial corallites/different on and between radial corallites	6	4
coenosteum on radial corallites	costate or reticulo-costate <sup>a</sup> /open spinules	7	5
coenosteum between radial corallites	reticulo-costate/reticulate <sup>a</sup> /open spinules	8	6
radial corallite sizes	one size or graded/two distinct sizes <sup>a</sup>	10	8
radial corallite inner wall	developed/not developed/neither inner or outer wall developed	11	9
radial corallite shape	nariform/dimidiate/lipped/tubular/appressed tubular <sup>a</sup> /conical/rounded appressed/round tubular/immersed	12	10
radial corallites relative size	very large/large/medium/small	16	13
maximum branch thickness	> 20 mm /20–25 mm/10–19.9 mm/< 5–9.9 mm /2.5–4.9 mm/< 2.5 mm	17	14
radial crowding	radials do not touch/some radials touch/radials crowded, touching	20	17

<sup>a</sup> Character states illustrated in figure 3.



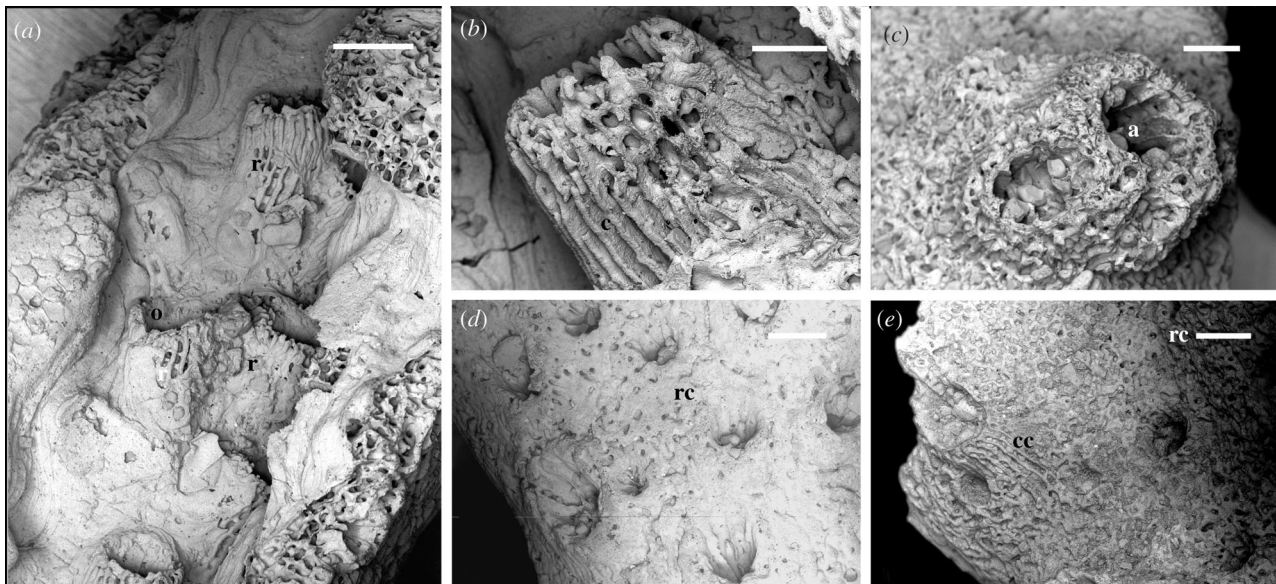


Figure 3. Scanning electron micrographs of NHM fossils showing diagnostic characters. (a, b) R54844, France, Mid-Eocene, 'latistella group' slender branch with appressed tubular radial corallites (r) with costate coenosteum (c) and rounded openings (o) scales 1 mm and 500  $\mu$ m, respectively. (c) R18265 Auvers, France, lower Bartonian, 'hyacinthus group' one of five vertical short branchlets with axial corallite indicating tabular colony (a) and radial corallites, scale 500  $\mu$ m. (d) R54837 Paris, Eocene, 'muricata group' evenly sized and shaped radial corallites with costate walls and reticulate coenosteum (rc), scale 1 mm. (e) R54847 'aspera group' with two distinct sizes of radial corallites, costate walls (cc) and reticulate coenosteum (rc), scale 1 mm.

Auvers-sur-Oise in France and Barton in England and two Lutetian: Chambors and La Ferme de l'Orme in France. Data on the most recent interpretations of stratigraphy and facies of these localities were reviewed and compiled from sources given in table 1.

#### (b) Material examined

We examined 56 fossil fragments of *Acropora* from the NHM, collected at the localities from mid-nineteenth to late-twentieth centuries. Specimen details are given in the electronic supplementary material, table 1. Most of these were identified on the museum labels as the fossil species *Acropora solanderi* (DeFrance) and the remainder as two other fossil species, non-specific *Acropora* or another genus (electronic supplementary material, table 1).

#### (c) Methods

Each fossil was examined in detail, using a Wild binocular microscope with eyepiece graticule, for the presence of features used for recognition of branching type, radial corallite structure and coenosteal structure (see Wallace 1999; Wolstenholme *et al.* 2003). Examples of morphological characters were examined and photographed using the JEOL JSM-5410LV Scanning Electron Microscope at James Cook University, Townsville. To establish the species group of each fossil, we compared the characters visible on the fossil against those on modern specimens in the Worldwide *Acropora* Collection (with over 20 000 specimens, located in the Museum of Tropical Queensland (MTQ), Australia: this includes types and mentioned specimens of Veron & Wallace (1984), Wallace (1999), Wolstenholme *et al.* (2003), Veron (2000), (2003) and others). We assigned the fossil to the species group meeting the diagnostic character combinations (Wallace 1999). We also nominated a 'most similar extant species' for each fossil, based on comparisons with the collections.

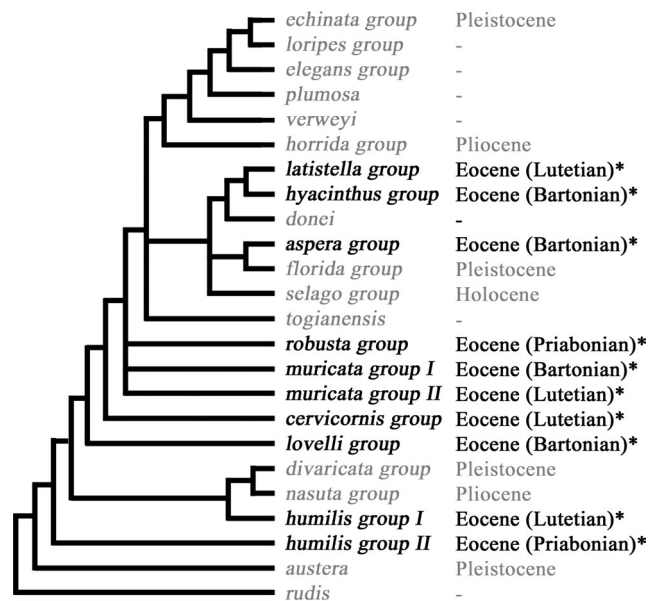


Figure 4. Morphology-based cladogram of species group relationships within genus *Acropora* updated from Wallace (1999), indicating earliest fossil occurrences: those from the present study indicated with an asterisk.

### 3. RESULTS

Of 22 skeletal characters already established for interpretation and analysis of extant *Acropora*, we found that 12 could be determined in the fossils (table 2). Most individual fossils had at least five of the 12 characters visible (see figure 3 for examples). No character states additional to those of present day *Acropora* were seen, although several modern states were missing. Seventeen specimens were either too small or too degraded to provide sufficient characters. We were able to assign the remaining 39 of the 56 available *Acropora* fossils to nine currently existing

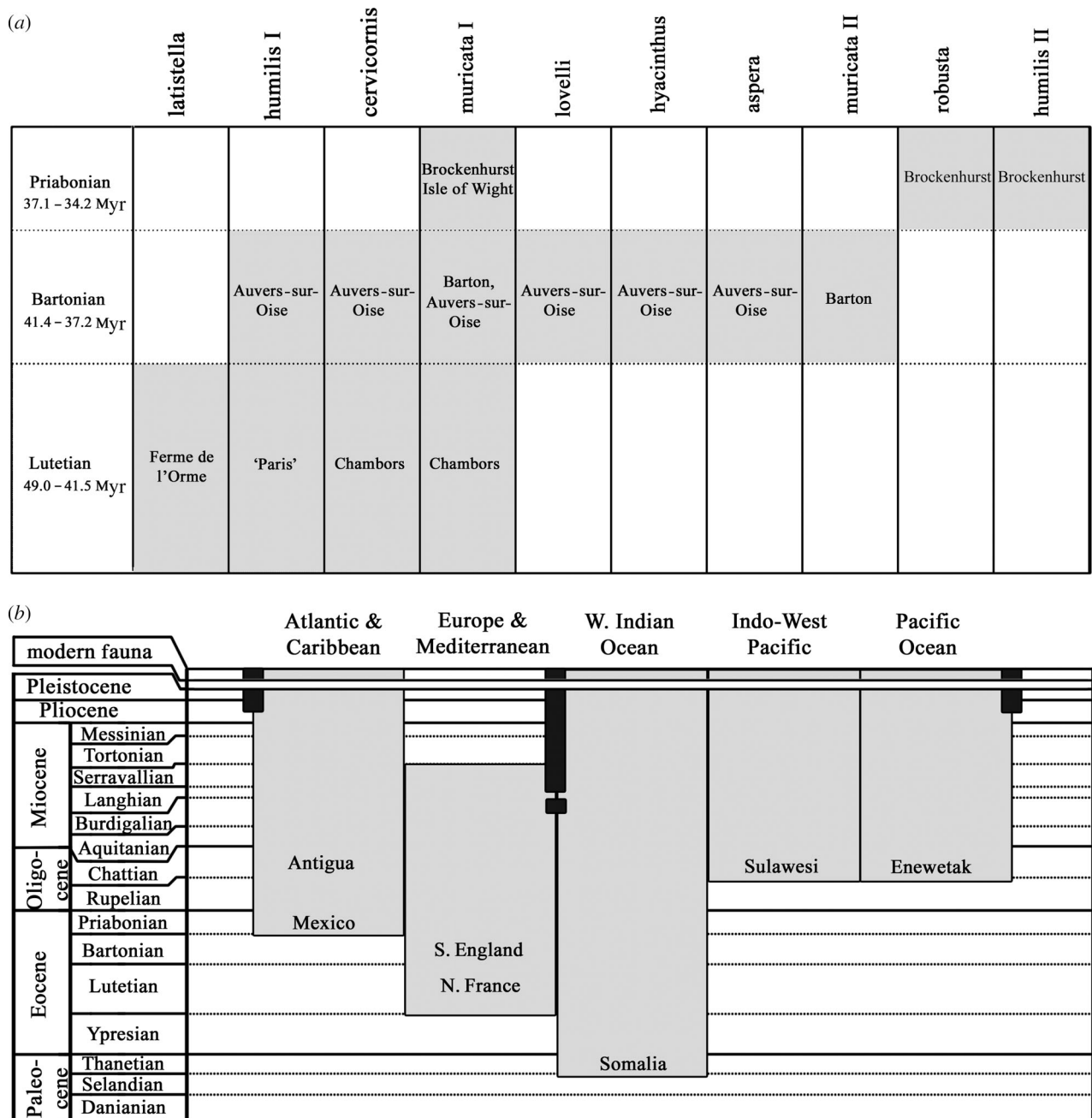


Figure 5. The fossil record of *Acropora*. (a) Occurrence of identified *Acropora* species groups in Eocene strata studied. Quotation marks denote poor precision of locality or age. (b) Occurrence of *Acropora* in major world regions over time. Dark bars indicate land barriers; earliest known fossil localities after Wilson & Rosen (1998), with subsequent time ranges interpolated from records in Rosen (1999), Wallace (1999), and our unpublished compilations.

species groups, as well as to nominate a most similar extant species for each of these 39 fossils (electronic supplementary material, table 2). Two species groups, *humilis* and *muricata*, were represented by two morphologies presumed to be separate species (figure 4).

We found that morphologies identifiable to more than one-third of the currently recognized species groups of *Acropora* were present before the end of the Eocene epoch (figure 4). The greatest number of fossil forms (seven from six species groups) was recognized from the Bartonian samples (41.4–37.0 Myr) from Barton in England and Auvers-sur-Oise in France, with four forms from four species groups found before this in the Lutetian of France (49.0–41.3 Myr) and three forms (three groups) later in the Priabonian of England (36.0–34.2 Myr) (figure 5a).

#### 4. DISCUSSION

Our results, together with the existing knowledge of fossil *Acropora* summarized in Wallace (1999, p. 20), show that the genus was diverse (figure 5a), distributed in the Tethys seaway across three major world regions (figure 5b), and beginning to contribute to reef frameworks (Schuster 2002) ahead of the isolation of the Indo-Pacific from Europe. The earliest record, from Late Paleocene deposits in Berbera, Somalia (figure 1; Carbone *et al.* 1994), can be reasonably extrapolated to the western Indian Ocean, possibly to the then still open Tethyan seaway between Southwest Asia and Arabia.

*Acropora* had disappeared from the European record by the Mid-Miocene (Rosen 1999), by which time it was established throughout much of its Indo-Pacific range (figure 5b; Wallace 2002). While the genus is known from

the Indo-Australian Arc in the Late Oligocene (Wilson & Rosen 1998), no *Acropora* material of Eocene or Early Oligocene age has been reported from the Pacific or central Indo-Pacific (figure 5b). This suggests that the varied and widespread Indo-Pacific *Acropora* of Late Oligocene to Miocene age were derived from a European–western Indian Ocean origin.

It has been argued that all extant Indo-Pacific *Acropora* species diversified from a single Pliocene ancestor, any other fossil lines having become extinct by the Mid-Miocene (Veron 1995; Fukami *et al.* 2000). The morphological similarity of the present collection of Eocene fossils to modern representatives of such a large number of groups (a finding noted by Duncan (1866), but disregarded since) supports an alternative proposal: that several species group lineages already present in the Europe–western Indian Ocean region during the Eocene survived to contribute to Indo-Pacific diversification. Evolutionary persistence of several groups, rather than origin from a single species ancestor, would be more compatible with widespread Indo-Pacific distribution of *Acropora*, including at least three modern species by the Miocene and continuation of *Acropora* as a reef dominant with many modern species widely distributed throughout the Plio–Pleistocene, in some cases more so than today (Wallace 2001; Wallace 2002).

There is insufficient stratigraphic or sedimentological documentation from which to infer the original autochthonous coral facies to which the fossils belonged and, thus, the actual conditions in which they lived. The specimens, being fragmentary, suggest a taphonomic history of colony break-up, followed by at least some transportation with subsequent detrital deposition and possibly re-working. The geology of the sedimentary basins which yielded our present samples has been intensively studied in an extensive literature going back over two centuries (see references table 1), but so far we have been unable to find any work showing that our samples could have been derived from reefal formations. However, *Acropora* today is not restricted to reefal biotopes (Wallace 1999; Veron 2000).

Typical colony shapes of the most similar modern species in the identified species groups include digitate, tabular, corymbose and arborescent forms (Wallace 1999). Missing are flat-branched and hispidose ('bottle brush') forms, found in the *echinata*, *loripes*, *elegans* and *horrida* species groups. The colony shapes present give useful clues to habitat type: in modern coral assemblages, they occur mostly on shallow parts of reefs, including intertidal reef flats, reef and rock edges, upper slopes and shallow shoals (usually less than 12 m depth, Wallace 1999). We interpret the fossil assemblages as occurring in shallow patches in embayments, similar to those presently found in Moreton Bay, Australia (27° S), which has seven *Acropora* species groups represented, including five of those identified from the European Eocene localities (C. C. Wallace, I. Fellegara & P. L. Harrison, unpublished data). Although high latitude daylight levels are sub-optimal for coral growth (Guinotte *et al.* 2003), this could be mitigated where the corals occur at very shallow depths (Harriott & Banks 2002) as in Moreton Bay (Johnson & Neil 1998) and in the Eocene localities discussed here.

Episodes of elevated sea surface temperatures (SSTs) have recently placed severe stress on modern tropical reefs

(Lough 2000), and, in combination with increased atmospheric CO<sub>2</sub>, these may reduce the capacity of many tropical reefs to sustain carbonate accretion in the event of persistent global warming (Guinotte *et al.* 2003). Models of the interaction of aragonite saturation, SSTs and atmospheric CO<sub>2</sub> indicate that it is unlikely that this will be compensated by new reef development in higher latitudes. Nevertheless, our demonstration of a diversity of *Acropora* existing in Northern Hemisphere Eocene assemblages provides a precedent for the survival of coral species at high latitude in warmer global temperatures, possibly contributing to preservation of genetic diversity in the event of depletion of species from lower latitudes.

Our findings support the proposal (Wilson & Rosen 1998) that the central Indo-Pacific, rather than being the locality of a global centre of origin for numerous coral genera and all Indo-Pacific species groups of *Acropora* as previously interpreted (Stehli & Wells 1971), was the locality of only a regional subset of speciation events. Pending future discovery of pre-Chatian *Acropora* in Southeast Asia, the Paleogene gap (Wilson & Rosen 1998) indicates that within this region, new species of *Acropora* could only have appeared from the Chatian (28–23 Myr) onwards. We propose that the existence of several species group lines, originating in the Eocene outside the central Indo-Pacific, subsequently allowed both speciation events within existing species groups and evolution of new groups, and therefore facilitated rapid speciation in the Indo-Pacific. This would be consistent with the observed non-concentric distribution of modern *Acropora* species ranges around the Southeast Asian centre of diversity (Wallace 2001; Wallace 2002), and with cladistic biogeographical interpretations made by Wallace *et al.* (1991) and Pandolfi (1992).

Fossil evidence of species group lines in *Acropora* offers the potential of further data points for calibration of a molecular clock for this exemplar coral group. Presently, calibration points for species evolution in corals are based only on time of first occurrence of the genus or higher level taxon, and this may have contributed to various dilemmas in accounting for apparent rapid sympatric speciation and widespread species distributions (Fukami *et al.* 2000; van Oppen *et al.* 2001). We can now offer minimum dates for the first appearances of nine species groups. This demonstrates the potential value of the fossil record in understanding evolutionary origins of modern biodiversity patterns.

The authors thank: P. Muir for assistance with all aspects of manuscript preparation; A. Jorre, Z. Richards and B. Chick for further assistance; P. Wilson, P. L. Harrison, R. P. M. Bak, J. Wolstenholme, A. Beltran-Torres, K. Johnson and Z. Dinesen for manuscript advice; M. Huber, J. Golonka, and F. Rögl for access to maps and simulations; A. Gale and C. Perrin for geological advice; C. Daniels for surveying the NHM Cenozoic collections; J. Darrell (NHM) for specimen loans, and NHM, MTQ and ARC Discovery grant to T.P. Hughes for funding support.

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