

Response of *Acropora* to warm climates; lessons from the geological past

C.H. White^{1,2}, D.W.J. Bosence¹, B.R. Rosen², C.C. Wallace³

- 1) Royal Holloway University of London, Egham, Surrey TW20 0EX, UK
2) Natural History Museum of London, Cromwell Road, London SW7 5BD, UK
3) Tropical Museum of Queensland, Townsville, Qld 4810, Australia

Abstract. There is currently widespread concern about the deterioration of living reef corals, such as *Acropora*, and tropical reefs. Much of their demise appears to be related to coral bleaching, the underlying cause is probably global climatic warming. Future predictions about the responses of modern coral reefs lacks data from the geological past. The fossil record shows reef coral distributions are highly sensitive to climatic change, modulated by the availability of habitat. Here we follow the history of one individual taxon, *Acropora*, to demonstrate how a particularly important reef coral genus has responded to global change through its geological time-span. *Acropora* is the most diverse, widespread and abundant of today's tropical reef corals, with its centre of diversity in the Indo-West Pacific. Counterintuitively, it was previously absent from this region but was common in the Paleogene to early Neogene in Europe, including high palaeolatitude (48°N) Eocene occurrences of southern England and northern France. We have assessed a unique set of unaltered, but fragmented, specimens of *Acropora* from the Eocene of the Paris and Hampshire basins for their preservational state, diagenesis, and stable isotopic composition ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$). Results suggest post-mortem parautochthonous to autochthonous deposition in low-energy embayments, with rapid burial in silty muds creating a relatively enclosed geochemical system. Taxonomic uniformitarianism and stable isotope data confirm that *Acropora* existed in tropical-like climatic conditions in Northwest Europe during the Eocene.

Key words: *Acropora*, Eocene, Hampshire Basin, Paris Basin, climate change.

Introduction

Global climatic changes, combined with regional anthropogenic processes, are combining to put modern coral diversity and distribution under threat (Hughes et al. 2003). It appears that corals are responding to such changes through acclimatisation and adaptation (Hoegh-Guldberg 1999) to occur in a broader latitudinal occurrence belt. In order to fully understand and predict the type, and magnitude, of future responses of coral reef ecosystems it is necessary to understand these changes from the geological record. Within this record, are data on the effects of both long-term and rapid climatic changes on coral reef distribution and diversity. This therefore provides a baseline, and possible analogues, to aid predictions about the future changes to coral reef ecosystems.

Much of our understanding of coral reef ecosystems from the geological past is based on taxonomic uniformitarianism, but by combining this with independent data it is possible to make higher resolution predictions about future responses. The aim of this paper is to add palaeoenvironmental context to high-latitude Eocene occurrences of the reef-building coral genus *Acropora* in order to test hypotheses on

the effect of an Eocene phase of climatic warming in Northwest Europe. *Acropora* is the most successful of today's tropical reef-building corals and is presently found within the modern coral limits of ~32° north and south of the equator. The genus is found within all three major oceans of the world with a greatest diversity in the Indo-Pacific oceanic realm. Counterintuitively, *Acropora*'s fossil record indicates that it originated and diversified in a North African-Mediterranean region (Wallace & Rosen, 2006, White et al., 2006, Wallace, 2008) with oldest records from the late Paleocene of Italy (Moussavian and Vecsei 1995), Austria (Tragelehn 1996) and Somalia (Carbone et al. 1994).

The localities (Fig. 1) in the Hampshire and Paris basins represent the most northerly latitudinal extent (~48°N) of *Acropora* in its entire history. These high latitudinal occurrences coincide with a period of global warming in the Middle Eocene (Zachos 2001). During the Eocene, the Hampshire and Paris basins formed part of a larger intracratonic basin system which spanned much of southern England, the English Channel and northern France (Curry 1992).

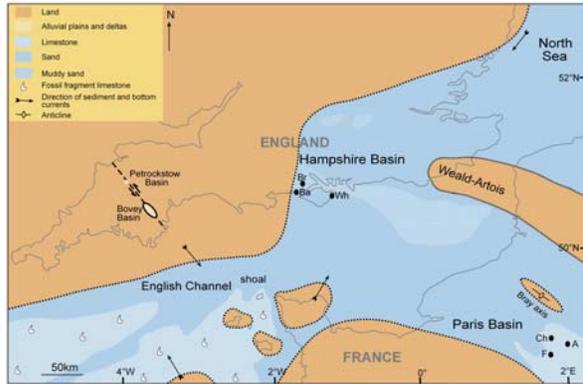


Figure 1: Palaeogeographic setting of the Hampshire and Paris basins in the Middle Eocene (Br: Brockenhurst, Ba: Barton, Wh: Whitecliff Bay, Ch: Chambors, A: Auvers sur Oise, F: La Ferme de L'Orme) (Adapted from Cope et al., 1992, & Gale et al., 2006)

The basins existed as two interconnected, shallow-marine, paralic embayments, connected to the Atlantic and with an intermittent connection to the North Sea. Cenozoic tectonic activity within the two basins included monoclinical and anticlinal folding, resulting from movement on deep-seated faults reactivated during Eocene Pyrenean compression (Lacombe and Obert, 2000). Episodic uplift of these structures led to remobilisation of Mesozoic and Cenozoic clastic sources and the creation of islands within each basin. The formation of structures such as the Weald-Artois anticline, combined with later Eocene global cooling, led to the intermittent isolation of the two basins from the North Sea followed by their Late Eocene restriction and closure. Hence the existence, both temporally and spatially, of *Acropora* in the two basins was limited and modified, not only by global, but regional and local tectonic and climatic factors.

Materials and Methods

Localities

Six localities identified by Wallace and Rosen (2006)

LOCALITY	PALAEOLATITUDE ¹	AGE (MA) ²	STRATIGRAPHIC AGE ²	BIOSTRATIGRAPHIC AGE ²	LITHOSTRATIGRAPHY ³	POSITION WITHIN STRATIGRAPHY ^{3,4}	FACIES ^{4,5}
Brockenhurst, Hampshire, England	48.4°N	36.0-34.2	Priabonian, Late Eocene	NP 19-20	Brockenhurst Bed	Base of Colwell Bay Member (formerly Middle Headon Beds), Headon Hill Formation, Solent Group	Mainly composed of muds, sandy muds and muddy sands
Whitecliff Bay, Isle of Wight, England	48.3°N	36.0-34.2	Priabonian, Late Eocene	NP 19-20	Brockenhurst Bed	Base of Colwell Bay Member (formerly Middle Headon Beds), Headon Hill Formation, Solent Group	Mainly composed of muds, sandy muds and muddy sands
Barton, England	47.5°N	40.4-37.2	Bartonian, Late Eocene	NP 16-17	Barton Group	Above the Bracklesham Group and overlain by the Solent Group	Fine sands and muds
Auvers-sur-Oise, France	46.9°N	43.4-40.4	Bartonian, Late Eocene	NP 16	Sables d'Auvers	Base of the Sables Moyen, Auversian	Sands of variable character
Chambors, France	46.5°N	47.3-43.4	Lutetian, Middle Eocene	NP 15	Calcaire Grossier (Upper)	Upper Middle to Upper Lutetian deposits, Abrard Zone IVa	Fine sands and muds
La Ferme de l'Orme, France	46.1°N	47.3-43.4	Lutetian, Middle Eocene	NP 15	Calcaire Grossier (Middle & Upper)	Middle to Upper Lutetian deposits, Abrard Zone III & IVa	Fine sands and muds

Table 1: Summary of coral-bearing locality information from; 1. Paul Markwick (GETECH, University of Leeds), 2. Gradstein et al., 2004, 3. Various authors, 4. Fieldwork, 5. After Wallace & Rosen, 2006.

were reviewed in this research: two Priabonian sites (Whitecliff Bay and Brockenhurst in England), two Bartonian (Auvers-sur-Oise in France and Barton in England), and two Lutetian (Chambors and La Ferme de l'Orme in France) (Fig. 1). Pristine *Acropora* specimens were available for geochemical analysis from 3 of these localities (Brockenhurst, Auvers-sur-Oise and Chambors) in the Hampshire and Paris Basins. Various sources were used for recent interpretations of the bio-, litho- and magnetostratigraphy for each locality (Aubry 1985, Gely and Lorenz 1991). Stratigraphic and geographic data is summarised in Table 1.

Fieldwork within both basins has shown *Acropora*-bearing lithologies are dominated by fine sands and muds. The associated molluscan fauna in both basins is diverse, abundant and dominantly marine although in some Hampshire Basin lithologies some of the fauna has an estuarine affinity. Other notable fauna includes sharks teeth in the Whitecliff Bay, Brockenhurst Bed and *Nummulites* in the Auvers, Sables d'Auvers Bed. Associated fauna are well preserved and have few limited borings. Reworked pebbles are found within both basin lithologies.

Specimens

71 fossil *Acropora* fragments were studied, with 11 of these used for geochemical analysis with an additional 8 of the genus *Lobosammia* from *Acropora*-bearing lithologies. Five of the *Acropora* specimens were identified as *Madrepora*, the generic synonym extensively used by nineteenth century authors (Dana 1846). Most of the specimens are labelled as the fossil species *Acropora solanderi* (Defrance), with the rest as non-specific *Acropora*. Six of the *Lobosammia* specimens were identified as the fossil species *Lobosammia cariosa* (Goldfuss), with one identified as non-specific *Lobosammia*. All *Acropora* specimens were re-identified on the basis of the taxonomic review of fossil *Acropora* (Wallace and Rosen 2006; Wallace 2008). From the Hampshire

Basin localities 3 species were identified (*Acropora anglica* (Duncan), *A. bartonensis* (Wallace), *A. roemeri* (Duncan)) and from the Paris Basin 6 species were identified (*Acropora alverezi* (Wallace), *A. deformis* (Michelin), *A. ornata* (Defrance), *A. protacea* (Wallace), *A. solanderi* (Defrance), *A. wilsonae* (Wallace)).

Methods

Three approaches were used. Firstly a thorough literature review provided information about the global, regional and local palaeoenvironmental context of *Acropora* in the Eocene Hampshire and Paris basins. Secondly, fieldwork at selected locations provided detailed sedimentological and palaeoenvironmental data. Finally, a variety of quantitative and qualitative techniques (hand & thin section microscopy, x-ray diffraction, cathodoluminescence, scanning electron microscopy and stable C and O isotope analysis), allowed an assessment of preservation and diagenesis, which independently aided the palaeoenvironmental interpretation. Fossil corals often undergo post-depositional diagenesis during which secondary minerals and/or cements are deposited. The inclusion of these in any analysis may significantly affect the bulk coral trace element geochemistry of the sample leading to erroneous estimates of past climate. Petrographic and XRD enabled selection of pristine unaltered skeletal aragonite for stable isotope work.

Stable isotope analysis of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ ratios in carbonates enabled inferences to be made about changes in environmental conditions with oxygen isotope ratios reflecting variables such as temperature and global ice-volumes (e.g. Patterson 1998; Tripathi et al. 2004), while the isotopic signature of carbon may be used as a proxy for metabolism and reproduction (Patterson 1998; Patterson 1999). Powdered carbonate samples were obtained using a computer controlled micromill with samples being taken along linear transects along the axial corallite. Stable isotope mass spectrometry was performed at University College London using a Thermo Delta GASBENCH Mass Spectrometer. Isotope values are reported in per mil V-PDB (‰) with respect to modern ocean water (‰).

Results

Morphology and taphonomy

A comparison between the preserved morphological features of a modern and Eocene *Acropora* specimen confirmed the exceptional preservation of the Eocene specimens. Thin section and scanning electron microscopy of fossil specimens identified intact morphological features including axial corallites,

radial corallites and coenosteum (Fig. 2a & b). All specimens show axial corallite apices with some distinguishable radiating septa. Radial corallites are identifiable with variations in costate or reticulate coenosteum (Fig. 2c & d). Selected specimens show radial corallites abraded flat against the main wall structure (Fig. 2b). In thin section multiple pristine microstructures were identified (Fig. 2a). Primarily, the aragonite composition is shown by the brown colouration of the skeleton with fanning, elongate trabeculae. The coenosteum exhibits a porous nature with large void-rich areas. Axial and radial corallites are recognised by large elongate voids and elongate septal remnants, particularly in the axial corallites.

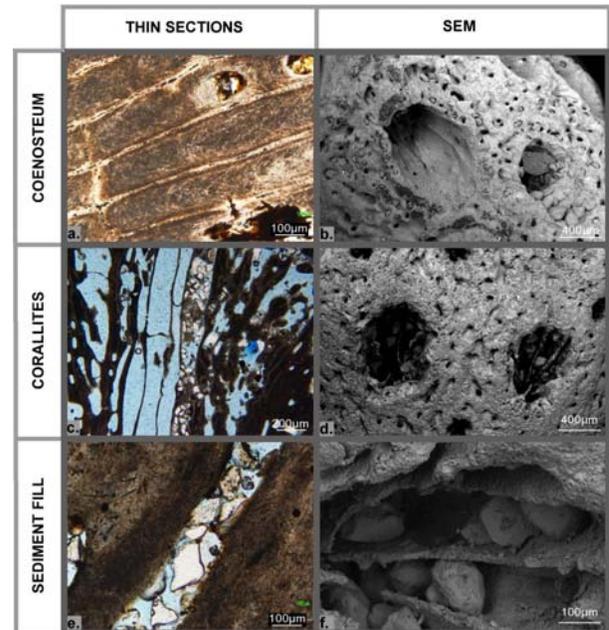


Figure 2: Summary of preservation and diagenetic features identified using thin sections and SEM. a. Characteristic trabeculae structure of skeletal aragonite. b. Highly porous coenosteum with sediment infilling. c. Axial corallite identified by elongate septal remnants and void areas. Fine grained sediment infilling corallite, mostly subangular-angular monocrystalline quartz. d. Radial corallites with remnant septal structure and sediment infilling. e. Fine grained sediment infilling void areas. f. Sediment fill within septal structure of a radial corallite.

Due to the exceptional preservation and limited fragmentation of some of these specimens, evidence of colonial types can also be seen. The Hampshire Basin specimens show variations of the four main colonial growth forms; tabular, arborescent, digitate and hispidose (Wallace 2008), and in the Paris Basin three growth forms; arborescent, digitate and tabular. Another morphological distinction between the specimens in each basin is the branch thickness. Specimens of *Acropora anglica* and *A. roemeri* from the Hampshire Basin have a sturdier growth form than species from the Paris Basin, with an average branch

thickness of 1.16 cm and 0.79 cm respectively for all species found (Fig. 3). Another significant difference is the larger amount of infilling sediment in the Hampshire Basin specimens probably reflecting the finer grained nature of the lithology from the Hampshire Basin and the larger void structures produced by the larger, coarser skeletal structures in specimens.

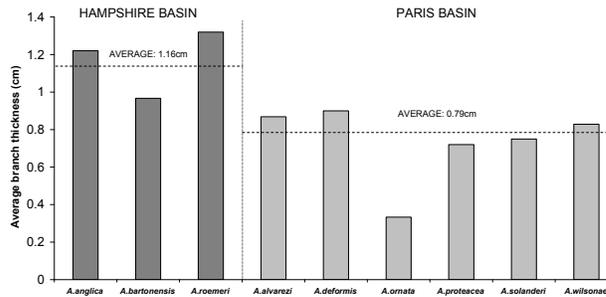


Figure 3: Variation in branch thickness shown between each species, and overall between the two basins (n=71)

Skeletal mineralogy; preservation, diagenesis and infilling

Preservation of original skeletal aragonite mineralogy is highly unusual due to the chemical instability of aragonite and its frequent alteration to secondary calcite. The combination of various methods has shown the exceptional mineralogical preservation and lack of taphonomic alteration of specimens from coral samples from both basins.

Using X-ray powder diffraction, over a 25° to 37° 2θ range, the majority of samples recorded seven main peak intensities. The main carbonate mineral peaks were four aragonite peaks (3.396Å, 3.273Å, 2.700Å, and 2.481Å) and one calcite peak (3.035Å). In addition to these, one quartz peak (3.343Å) and one gypsum peak (2.867Å) were recorded. Three samples show no peak for calcite (below 1% detection limit) and can be regarded as 100% aragonite with respect to their carbonate mineralogy.

Peak height analysis allowed the ratio for aragonite peak intensity to be determined. For *Acropora* specimens these ranged from 0.8299 ± 0.04 to 1 ± 0.05 , with a maximum of 1. For *Lobopsammia* specimens these ranged from 0.9770 ± 0.05 to 1 ± 0.05 . From this, the Milliman (1974) calibration curve allowed these values to be converted to percentage aragonite with respect to calcite. For *Acropora* specimens the percentage aragonite ranged from $92.55\% \pm 1.8$ to $100\% \pm 2.2$, and for the *Lobopsammia* specimens from $98.88\% \pm 2.1$ to $100\% \pm 2.2$.

The additional peaks seen in XRD across the 25° to 37° 2θ range, representing quartz and gypsum, are from infilling sediment or surface weathering (gypsum). In thin section and SEM, the quartz is seen

infilling voids within the coral fabric together with minor components of clinopyroxene, biotite, glauconite and chert (Fig. 2e & f). The grains are subangular to subrounded and infilling corallites trapped particularly by intact septal structures.

All the *Acropora* specimens show some degree of cementation. The combination of thin sections, XRD, SEM and CL techniques indicates this as a minor component and confined to specific areas of the specimen. In thin section and CL there is evidence of both early aragonite cement and later calcite cement precipitation, infilling and lining porous areas. Bioerosion is minor with two of the *Lobopsammia* corals showing boring molluscs identified by their foliated internal structure.

In summary post-depositional modifications of the coral skeleton include entrapment of glauconitic fine grained sands and the precipitation of aragonite and calcite cements within the porous skeletal structure.

Stable Isotopes

For *Acropora* specimens the total variation is about 1.5‰ between -6.84‰ to -5.31‰ for δ¹⁸O (Fig. 4). The range of δ¹³C is between -4.17‰ to -1.63‰, showing a total variation of about 2.5‰. For *Lobopsammia* specimens the total variation is about 1.0‰ between -5.90‰ to -4.86‰ for δ¹⁸O (Fig. 4a). The range of δ¹³C is between -3.92‰ to -0.79‰, showing a total variation of about 3.1‰.

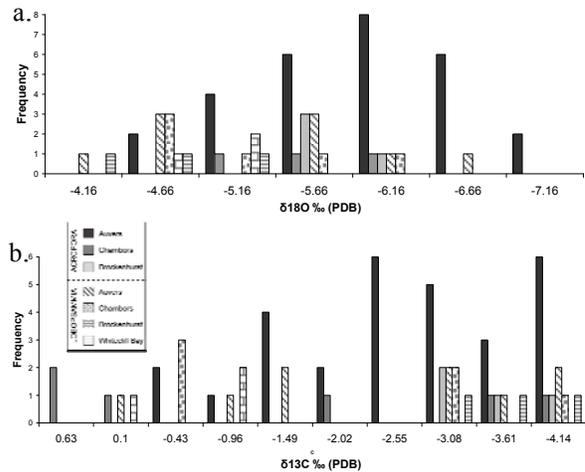


Figure 4: Frequency Histogram showing the distribution of a) oxygen and b) carbon isotope ratios for each locality of both *Acropora* and *Lobopsammia* specimens (n=60)

Carbon shows the larger variability in isotopic values, probably a function of the multiple factors which can effect this value (e.g. Zachos, 2001) (Fig. 4b). The *Acropora* specimens show a wide distribution with a skew towards isotopically lighter values. The *Lobopsammia* specimens show a weaker trend with a similar wide distribution of isotopic

values over a comparable range to *Acropora* specimens.

Discussion

Acropora is presently found within the modern reef coral limits, in all three major oceans of the world. The genus exists in a wide range of depths, reef zones and hydraulic regimes, primarily reflecting its ability for rapid growth. The fossil record shows that *Acropora* existed up to ~49 degrees north during the Eocene in the Hampshire and Paris basins. It is envisaged that in both basins *Acropora* occurred within isolated thickets/colonies, possibly forming more laterally extensive veneers, such as those seen in the marginal settings of Brownard County, Florida (Perry and Larcombe 2003). The relatively sparse distribution of specimens, and preservation as broken fragments in fine grained clastic sediments indicates that active reef accretion or mass reefal build-ups were unlikely to have occurred in either basin. If these specimens were derived from a reefal structure then unusually high hydraulic conditions would be needed to demolish evidence of this structure but to selectively preserve a limited number of pristine specimens. Additionally, the dominance of zooxanthellate and solitary corals, in modern settings typifies marginal environments, and the lack of other reef-building biota supports the absence of any reef.

The palaeoenvironmental settings are different within the two basins. In the Hampshire Basin, corals are found within siliciclastic storm beds in a relatively protected mid-shelf environment, below-wave base. Corals in the Paris Basin are found within predominantly carbonate-dominated beds and a mid-ramp environment is inferred. *Acropora*'s ramose, branching habit renders the skeletal remains subject to fragmentation, through bioerosion, hydraulic energy, and rolling and abrasion by transportation. However, the preservation of these fragments, up to 4cm in length, with intact morphological features, supports a lack of transportation and reworking of the fossils. The lack of abrasion features shown by specimens from both basins indicates minimal transportation implying low hydraulic energy, protection from bioerosion and additionally rapid burial. Morphologically the sturdier growth forms come from the Hampshire Basin implicating higher wave energy in this basin relative to the Paris Basin

The pristine morphological and mineralogical preservation, and lack of bioerosion, of the specimens from both basins supports rapid burial following fragmentation of the coral branches. This infers high sedimentation rates. Rapid rates of sedimentation were required to produce a geochemically enclosed system and sufficient burial to prevent bioerosion by benthic organisms. Post-depositional modifications of

the coral skeleton included entrapment of glauconitic sands and the precipitation of early aragonite and later calcite cement within the porous skeletal structure.

On the basis of modern distribution of zooxanthellate corals, the presence of *Acropora* within the two basins suggests tropical conditions persisted in Northern Europe during the Middle to early Late Eocene. This is supported by other palaeoclimatic indicators such as palaeobotanical studies (Collinson and Cleal 2001). This is confirmed by oxygen stable isotope values on specimens from basins indicating sub-tropical to tropical palaeoenvironments and the higher variation in carbon values reflecting the paralic environment in both basins.

The absence of reef rock and the existence of thickets and possible coral carpets suggests there was a lack of coral framework and raises the question as to whether this was a flourishing coral community or a disturbed/restricted state of development. The distribution of *Acropora* in the Hampshire and Paris basins during the Eocene is believed to have been at its northern limit. Combined with evidence that *Acropora* left these basins in the Late Eocene, existed for a geologically short period in each and that subsequently its northern limits retracted southwards suggests that this was a marginal setting. The lack of reefal build-ups however may have been due to evolutionary control rather than an ecological one as *Acropora* has not been found dominating reef frameworks until the Oligocene in Greece (Wallace and Rosen 2006).

In summary, the primary control on *Acropora*, and other coral genera, spatial and temporal distribution was primarily influenced by global and regional eustatic sea-level fall, climatic deterioration and local tectonics isolating both basins. Secondary controls included sediment supply and water movement. The existence of *Acropora* in the two basins reflects global climatic warm periods of the Eocene, its distribution reflects a complex interplay of local and regional factors. Global climatic and regional tectonic effects resulted in the loss of *Acropora*, and other corals, from the two basins by the end of the Late Eocene.

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