Corals and climate change in the Cenozoic; a case study based on the staghorn coral *Acropora*

by

Clare Hannah White

"If enough species are extinguished, will ecosystems collapse and will the extinction of most other species follow soon afterwards? The only answer anyone can give is: Possibly. By the time we find out, however, it might be too late. One planet, one experiment."
(Edward O. Wilson, 1992)

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Declaration

These doctoral studies were conducted under the supervision of Prof. Dan Bosence, Dr. Brian Rosen and Dr. Carden Wallace. The work presented in this thesis is the result of original research carried out by myself, in collaboration with others, whilst enrolled in the Department of Earth Sciences as a candidate for the degree of Doctor of Philosophy. This work has not been submitted for any other degree or award in any other university or educational establishment.

Clare Hannah White
June 26th, 2013

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 lack data from the geological record. This thesis documents the history of one individual taxon, *Acropora*, and demonstrates how a particularly important reef coral genus has responded to global change through its geological range. Existing fossil *Acropora* records have been databased, and revised as necessary to bring the names and stratigraphy into line with current classifications. Comparisons have been made with known patterns of climate change and with palaeogeographical reconstructions of availability of suitable habitat.

A taxonomic review provides new descriptions and records that provide evidence that the genus diversified rapidly after its appearance in the fossil record. The development of a new working taxonomy for fossil *Acropora* is based on how the surface characters used for modern species recognition correspond (or not) to characters seen in sectional preparations and computed tomography of fossil specimens. Field work in selected areas in France and England improves distributional data of *Acropora* and provides an understanding of *Acropora* taphonomy and palaeoecology. Unaltered coral and mollusc specimens from the Eocene of the Paris and Hampshire basins are assessed for their preservational state and diagenesis, and their stable isotopic and trace element compositions provide palaeoenvironmental data. Taxonomic uniformitarianism and geochemical data confirm that *Acropora* existed in high palaeolatitude tropical-like climatic conditions in Northwest Europe during the Eocene.

Overall the record suggests origination and diversification in the north African-Mediterranean region. Cenozoic global climatic cooling and palaeogeographical reorganisation led to a latitudinal restriction of the genus in the Miocene and to the emergence of *Acropora*-dominated communities from the Pliocene in the Caribbean and Southeast Asian regions. Non-framework building, high latitude coral assemblages have recently received increased attention as a potential refuge during global change, as a proxy for these changes and for testing the tolerances of these coral species (e.g. northern Gulf of California, Mexico, 29°N; Halfar *et al*., 2005). The fossil record of *Acropora* shows that during previous globally warm periods, the genus has survived in higher latitudinal positions than seen today in marginal environments, suggesting that this genus at least may have the potential to adapt and acclimatise to globally warm conditions deemed more environmentally marginal than those seen today. The fossil record appears to imply that warmer climates ameliorate pre-existing marginal and unfavourable environments (for z corals) by making them more suited to z-corals. The major difference at present, and for future predictions, is the unprecedented affect of human activity on these ecosystems. However, understanding a coral's ecological response to global climate change in the geological record undoubtedly helps to understand the future of coral reefs.

To my grandparents,
Bernard and Margaret White,
Michael and Nita Nobbs.
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CHAPTER 1. INTRODUCTION

CONTENT

The aim of this chapter is to introduce this thesis project. It gives a brief account of the background to this thesis and discusses the objectives and methodology of this study. The thesis structure is outlined.

1.1 INTRODUCTION

There is widespread concern about recent deterioration of living reef corals and tropical reefs. Much of this is related to coral bleaching which has had destructive effects resulting in an estimated 19% of the world's coral reefs having been lost and a further 35% are described as *seriously threatened* over the last decade (Wilkinson, 2008). One third of zooxanthellate reef-building coral species are now in categories with elevated risk of extinction (Carpenter, 2008). If the current trend in rising atmospheric CO_2 persists, levels are projected to rise from a preindustrial value of 250ppm to 700ppm by 2100 (Wilkinson, 2001). These projected changes will undoubtedly affect corals both directly, through alteration of seawater chemistry (Kleypas *et al*., 1999; Feely *et al*., 2004), and indirectly, through increased atmospheric and sea-surface temperatures. Global warming appears to have driven bleaching and other diseases in corals, and has combined with local-scale anthropogenic disturbances to elevate the extinction risk (Carpenter *et al*., 2008). The predicted responses include: the poleward movement of the isotherms currently associated with coral reef distributions and the distribution of reef corals including *Acropora*, a rise in mean SST within the present tropical-subtropical latitude ranges of reef corals, and some degradation of coral communities by local and regional episodes of higher temperature within the present warm-water zones (see Chapter 2).

Predictions of future responses of reefs to global warming are rarely based on data from the past on how reef organisms have responded to ancient climate changes. However, the ancient record of corals and reefs provides an unparalleled window into the effects of climate change through geological time and shows that reef coral distributions in particular are highly sensitive to climatic patterns, modulated by availability of suitable habitats. Today's reef-forming corals (i.e. order Scleractinia) have existed for ~240 million years during which time they have been repeatedly affected by climate changes due to many different causes, most of which are linked to upheavals of the carbon cycle (Veron, 2008). Although on long-term geological timescales reef ecosystems are clearly very persistent, the geological record also shows that on much shorter timescales, reefs can indeed be lost, that a large proportion of coral and other calcifying species can go extinct and that once lost, reefs can take thousands to millions of years to re-establish. This record can be used to constrain models of how reefs respond to climate change (Hughes *et al.,* 2003; Kiessling, 2005; Rosen 1999, 2000, 2002; Wilson and Rosen 1998). So far however, research emphasis has been on statistical and biogeographical syntheses, whereas the history of individual taxa would provide higher resolution data to test hypotheses on the effects of warming.

Acropora is believed to be a highly suitable exemplar genus for such a study because of its importance in present-day reef construction. It also has the largest number of living species of any extant reef coral genus (recent reviews recognise 113 (Wallace, 1999) or 180 (Veron, 2000) species). It is the only reef coral genus for which a morphological phylogeny has been published (Wallace, 1999), and now on its molecular taxonomy (Fukami *et al.*, 2000). Work by Wallace and Rosen (2006) shows that during the warmer climate times of the Eocene, *Acropora* occurred in localities in S. England and N. France, i.e. at relatively extreme palaeolatitudes in relation to its present-day distribution. Together with co-occurring species, the specimens in these particular English and French fossil assemblages are often aragonitic and are therefore potentially suitable for palaeoenvironmental studies based on stable isotopes.

Wallace and Rosen (2006) identified the importance of a collection of Eocene *Acropora* specimens from the Hampshire and Paris basins at the Natural History Museum, London (NHM). Using this collection they demonstrated the potential value of the fossil record in understanding evolutionary origins of modern biodiversity patterns. Following this, White (2006) conducted a pilot study to assess the feasibility of making palaeoenvironmental interpretations derived primarily from the geochemical signatures in the preserved skeletons.

Further taxonomic work within the fossil record of the genus was undertaken by Wallace (2008) based on re-examination of material in the collections of the Natural History Museum, London. The new descriptions and records contributed to evidence that the genus diversified after its appearance in the fossil record.

1.2 THE GENUS *ACROPORA*

The genus *Acropora* is one of the most widespread, abundant and species-rich of coral genera with over twice as many species than in other prolific scleractinian coral genera such as *Montipora* and *Porites* (Wallace, 1999; Veron, 2000). Recent revisions of the genus recognize 113 (Wallace, 1999) or approximately 180 (Veron, 2000) *Acropora* species. The genus, until the recent elevation to genus level of *Isopora*, consisted of two subgenera, *A. (Acropora)* and *A. (Isopora)* (Wallace, 1984; van Oppen *et al.*, 2001). Wallace (1999) using a phylogenetic approach, and Veron (Corals of the World VI,

2000) using morphology, have both grouped *Acropora* species into larger sub-generic categories ('species-groups'). Both schemes are based on skeletal morphology and shared skeletal characteristics. Veron (2000) identifies 38, whereas Wallace (1999) identifies 20 groups, with 19 in Indo-Pacific and 1 in the Caribbean.

The genus epitomises shallow tropical and sub-tropical worldwide coral reef environments typically recognised by its (usually) branching morphology in which its branches are almost uniquely formed round a leading axial corallite. The ability of the genus for fast, branching growth and high calcification rates results in it playing a crucial role in the structure and ecology of global reef structures through its contribution to reef accretion, either in fragment accumulations or as framework, hence forming habitats for other organisms (Aronson and Precht, 2001). The widely documented decline of *Acropora* (for example Precht *et al.*, 2004) has also been shown to result in the decline of reef accretion and loss of habitat for many marine species (Hughes, 1994, Jackson *et al.*, 2001). The association of the genus with shallow habitats and its distinctive branching morphologies have made the genus particularly vulnerable to disturbance events, while their rapid growth rates and branching structures are believed to have enabled populations to recover from such disturbances in a few years to decades (Gladfelter *et al.* 1978; Jaap *et al.* 1988).

Encompassing the genus is a vast array, and depth, of research conceivably not seen in any other scleractinian genus. *Acropora* has often been chosen as an exemplar species for coral systematic studies due to its potential use for modelling the evolution and development of modern reef coral faunas, principally due to its diverse and abundant nature (Wallace and Willis, 1994). The current taxonomic framework of the genus is being challenged through research utilising breeding trials, biogeographic and phylogenetic analyses, and genetic studies focused on exploring species boundaries (for example van Oppen *et al.*, 2001).

The diversity and abundance of *Acropora* together with its role in reef building make it an obvious choice as an exemplar genus for the scleractinian corals as outlined above. Below, the major taxonomic, morphological, ecological and reproductive features of the genus are reviewed.

1.2.1 Systematic Treatment

Phylum CNIDARIA Hatchek, 1888

The genus *Acropora* belongs to the phylum Cnidaria which consists of both solitary and colonial invertebrates including hydroids, jellyfish, sea anemones, and corals (Clarkson, 1986; Oliver and Coates, 1987; Benton and Harper, 1997). The phylum is characterised by radiobilateral symmetry, with the ectoderm and endoderm separated by mesogloea; the enteron has a mouth surrounded by tentacles with stinging cells (Benton and Harper, 1997). The three living classes of Cnidaria are Hydrozoa, Scyphozoa and Anthozoa. Oliver and Coates (1987) define 'true' corals as those of the class Anthozoa that possess massive, external, calcareous skeletons. Three subclasses are generally recognised but 'true' corals are limited to the subclass Zoantharia. Within this, the principal coral orders are Tabulata, Heliolitida (also included by some within the Tabulata), Rugosa and Scleractinia. All corals studied in this research belong to the Scleractinia, this being the only post-Palaeozoic order. Living scleractinians fall into two ecological groups. Zooxanthellate corals, (or z-corals) contain endodermal symbiotic dinoflagellate algae, or zooxanthellae in their polyps, and azooxanthellate (az-) corals are without these algae. It is not possible to observe directly this symbiosis in fossil corals, so where these two conditions can be inferred, it is more rigorous to refer to them respectively as z-like and az-like corals (Wilson and Rosen, 1998). However, many of the genera considered here are also extant and it is therefore reasonable to assume on the grounds of taxonomic uniformitarianism (Dodd and Stanton, 1990) that unless there is evidence to contrary, their modern condition also applied to their fossil counterparts.

Order SCLERACTINIA

The order Scleractinia is defined as aragonitic, solitary and colonial corals with relatively porous skeletons (Wells, 1956). They are often termed hexacorals due to their six protosepta and successive cycles of metasepta inserted in all interseptal spaces. The group first appeared in the mid Triassic (Stanley and Fautin, 2001) and now are the dominant reef-builders in the tropics and marginal-tropics (Wood, 1999).

Family ACROPORIDAE Verrill, 1902

The family Acroporidae includes the extant genera *Montipora* Blainville, 1830, *Anacropora* Ridley, 1884, *Astreopora* Blainville, 1830, *Acropora* Oken, 1915, *Isopora* Budd and Wallace, 2008 and, the only extinct genus in the family, *Dendracis* Milne Edwards and Haime, 1849. *Acropora* is the only member of the family currently found in the western Atlantic; the other genera are restricted to the Pacific and Indian Oceans, including the Red Sea (Chapter 3). The origin of the Acroporidae family is unclear but the septal structures of the group most closely resemble those of the Astrocoeniidae

(Vaughan and Wells, 1943), so perhaps sharing a common origin. First occurrence of the family was in the Late Cretaceous with the appearance of *Astreopora* (Hauterivian, Quebrada El Way, Chile (Prinz, 1991)).

Many of the old Cretaceous coral families failed to survive or were dramatically reduced following the Late Cretaceous worldwide collapse of many faunas (Rosen, 2000; Kiessling and Baron-Szabo, 2004). By the Eocene many new genera had evolved including from the family Acroporidae: *Acropora*, *Montipora* and *Dendracis*. *Dendracis,* is morphologically distinct from *Acropora* as it lacks an axial corallite, and disappeared in the Miocene. Last to evolve was *Isopora* and *Anacropora*, believed by Ridley (1884) to have evolved from *Montipora* relatively recently.

1.2.2 Morphological Characters

The genus is morphologically distinguished from other extant coral genera by the unique form of its polyp structure and its function dimorphism (see Chapters 4 and 5 for further details). This gives rise to branches formed by one or more central, or axial corallites, which bud off a second type of corallites, the radial corallites as the axial corallite extends and grows (Wells, 1956; Veron and Wallace, 1984; Wallace, 1999). *Acropora* is further distinguished from its confamilial genera (*Montipora*, *Anacropora* and *Astreopora*) by the distinct structures of its radial corallite walls (a wall being absent from *Montipora* and *Anacropora*, and undifferentiated from the simple conical tube in *Astreopora*). The genus exhibits a vast amount of morphological variability between species and additionally an enormous amount of intraspecific variability (Dana, 1846; Brook, 1893; Wallace, 1999).

1.2.3 Ecology

Acropora species occur in great abundances in reef habitats spanning the Indian and Pacific Oceans, and the Caribbean Sea. Although this is the most species-rich genus of scleractinian corals, diversity within the major oceanic realms varies dramatically with only 2 species (*Acropora cervicornis* and *A. palmata*, with a previously recognised third *A. prolifera* now recognised as a hybrid, see Vollmer and Palumbi, 2002) in the western Atlantic and Caribbean compared with 74 in the Indo-West Pacific oceanic realm (Wallace, 2001). The dominance of *Acropora* in global shallow-reef habitats and the co-occurrence of many species have resulted in the assumption that they have similar ecological parameters and physiological requirements (Duncan, 1866; Wallace, 1999).

Acropora species are often associated with shallow, high-energy, reef-front environments. For example in the Caribbean Veron (2000) has described *Acropora cervicornis* as common on shallow outer-reef margins exposed to wave action. The habitat of *Acropora palmata* has also been defined with Hubbard (1988) using the occurrence and morphologies of *Acropora palmata* as an indicator of wave and storm prevalence on reefs. Because this species is adapted to high light intensities and, therefore, water depths typically less than 10 m, its fossil distribution has been widely used to interpret rates of sea level rise (Blanchon and Shaw 1995; Montaggioni and Faure, 1997). Although these habitats and reef locations are where *Acropora* is found in greatest abundance species are found in deeper non-reefal habitats (e.g. *Acropora russelli* on deep sandy slopes, Wallace, 1999).

1.2.4 Reproduction

Species of the genus *Acropora* are hermaphroditic producing positively buoyant bundles of eggs and sperm, released from the polyp mouth, which collect and break apart at the surface where fertilisation occurs (Wallace, 1994). This is in contrast to *Isopora*, recently elevated from subgenus to genus status (Wallace *et al.*., 2007; Buss and Wallace, 2008), which broads planula larvae (Kojis, 1986). *Acropora* spawns gametes synchronously in mass spawning events. The existence of these simultaneous or near simultaneous mass spawning events of up to 76 species occurring in sympatry (Wallace, 1999) results in the potential for interspecific hybridisation (Vollmer and Palumbi, 2002). Willis *et al.* (1985) reported 35 sympatric *Acropora* species releasing gamete bundles over a two hour period on the Great Barrier Reef providing an opportunity for hybridisation. In the Indo-Pacific region introgression can also occur through backcrossing with a range of other species (Willis *et al.*, 2006). This not only occurs in the species-rich Indo-Pacific, as van Oppen (2000) suggested on the basis of molecular work that *A. prolifera* is a hybrid of *A. cervicornis* and *A. palmata*.

Asexual reproduction additionally occurs by fragmentation (Highsmith, 1982) and the redistribution of branches which can have a significant influence on its survivorship and propagation, particularly in response to physical disturbances such as storms. The degree to which this occurs has been suggested by Wallace (1985) to be dependent on colony shape with open-branch, indeterminate growth more likely to increase the number of colonies following fragmentation compared with symmetrical, determinate growth. Recruitment occurs through new colonies entering a coral population as both sexually produced larvae and asexual cloned fragments.

1.3 AIMS AND HYPOTHESES OF THE RESEARCH

The overall aim of the research presented in this thesis is to examine whether the short term, present-day and predicted future decline of *Acropora* relate to anthropogenic influences, or whether similar fluctuations in species occurrence have occurred in the past that are likely to be due to changes in climate and habitat space. This is accomplished by the compilation and analysis of the taxonomic, stratigraphic, evolutionary, and biogeographical history of the genus *Acropora* and to establish how this relates to known patterns of Cenozoic climate change and availability of suitable habitats. Specifically, the hypotheses and objectives are as follows:

- **To investigate how the surface characters used for modern species recognition correspond (or not) to characters seen in sectional preparations of fossil specimens in order to develop a working, integrated (i.e. living-and-fossil) taxonomy for *Acropora*.**

  Background

  Internal characters appear to have been used very little for *Acropora* taxonomy at genus- and species-level in either the modern or fossil record. Scanning electron microscopy (SEM) and ultra-thin sections have been used to image the microstructure of coral genera to propose models for the growth of coral skeletons (Barnes, 1970; Nothdurft and Webb, 2007). In the broad field of palaeontology, micro-CT (micro computerised tomography) has had a transformative impact on morphological research in general, and vertebrate studies in particular. Dodge (1980) is reported to be the first to suggest the use of computerised tomography (CT) for the study of the growth of corals and this was followed by the use of CT as a method for surveying corals (Logan and Anderson, 1991; Bosscher, 1993). Most recent applications include understanding external deciding factors in growth and morphology of reef corals, and how morphology responds to environmental conditions. It has been demonstrated that morphological variation can be quantified, and that biologically relevant morphological characteristics, like branch-spacing and surface/volume ratios, can be computed and modelled (Kaandorp *et al*., 2005; Kruszynski *et al*., 2007).

Fossil specimens are often broken, highly abraded and lack the surficial characters used to identify *Acropora* specimens to species-level. Here these methods (serial and thin sectioning analysis, SEM and CT) are used for the first time in the taxonomy of modern and fossil *Acropora* to assess the degree to which internal manifestations of key surface characters can be identified and aid genus- and species-level descriptions. Additionally, these methods have been used to assess the preservation and diagenesis of specimens.

- **To integrate as far as possible the different approaches that are currently used for the taxonomy of modern and fossil *Acropora* respectively.**

  Background

  It is rare for fossil *Acropora* to be identified to species level. Earlier descriptions of *Acropora* species were mostly named *Madrepora*, or were classified with different genus names (e.g. *Dendracis haidingeri* in Reuss, 1864). Felix (1925) listed 114 species of *Madrepora* described from Paleogene and Neogene coral occurrences. It is, however, unclear how many of these species are true *Acropora* and which are not. A literature summary by Wallace (1999) accepted only 14 fossil species. Wallace and Rosen (2006) then showed from a study of a selection of fossils at the Natural History Museum, London, that there were up to nine Eocene precursors of the 20 currently recognised living species groups of *Acropora*. Based on this work, and new approaches established in this thesis, the aim was to revise the taxonomy of fossil *Acropora* specimens from the Eocene of the Hampshire and Paris basins using the integrated approach developed (as above).

- **To construct a database and a time-series of global distribution maps of *Acropora* throughout the Cenozoic to assess to what extent distribution patterns can be related to changes in global climate and palaeogeography.**

  Background

  This was addressed by using a combination of primary research and data from the literature and subject to the limitations encountered in integrating the different taxonomic approaches. *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 extremely widespread, found throughout the Indian, Pacific and Caribbean oceans, and speciose (recent reviews recognise 113 (Wallace, 1999) or 180 (Veron, 2000) species). The genus also has an extensive fossil history, which is becoming more accessible as new spatially and temporally focused studies provide more data and finer resolution (e.g. Carbone et al. 1994; McCall et al. 1994; Wilson and 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. This thesis aims to describe the long-term history of *Acropora* and to test the implications for the evolution and origins of present day biodiversity patterns of reef corals and for predicting their response to future climate change

- **To complement the global palaeoenvironmental evidence obtained from *Acropora* records by using evidence from sedimentology and stable isotope geochemistry of fossil material from the Anglo-Paris Basin to obtain higher resolution (local and regional) information about the palaeoenvironments of fossil *Acropora*.**

Background

A key problem is that Duncan (1866) originally suggested the presence of a reef in the Eocene of the Hampshire Basin, saying ‘now the Brockenhurst beds must be admitted amongst the strata whose remains indicate the former existence of coral reefs exposed to a furious surf and the wash of a great ocean’. On the basis of taxonomic uniformitarianism, *Acropora* is commonly used (as Duncan here) as an indicator of reefal accretion in the fossil record. However, although commonly associated with reefs, *Acropora* today is not restricted to reefal biotopes (Wallace 1999; Veron 2000). Wallace and Rosen (2006) suggested there was insufficient stratigraphic and 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. A further problem with Duncan’s contention is the contemporaneous high palaeolatitude (see Figure 6.1) of the Hampshire Basin which is outside the limits of modern reef corals. Perhaps *Acropora* was living in a non-reefal environment in the Hampshire Basin, and perhaps *Acropora* was not a reef-builder anywhere at that time. The aim here was to use sedimentological and geochemical evidence to resolve these questions. Multiple approaches are used in this thesis. Fieldwork at selected localities provides detailed sedimentological and palaeoenvironmental data. A taphonomic and diversity study of corals independently aids palaeoenvironmental interpretations. A variety of quantitative and qualitative techniques (hand and thin section microscopy, x-ray diffraction, cathodoluminescence, scanning electron microscopy and stable isotope, and trace element analysis), allows an assessment of preservation and diagenesis, which aids palaeoenvironmental interpretations.

- **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 corals and reefal carbonates up until the latest Oligocene to earliest Miocene. Can a global view of *Acropora's* diversity and palaeogeography be used to solve this anomaly?**

  Background

  Today the genus is found within all three major oceans of the world with a greatest diversity in the Indo-Pacific oceanic realm. This region lacked most zooxanthellate coral genera ('z-corals') and z-coral-dominated carbonates up until the latest Oligocene to earliest Miocene (around 26 Ma), a phenomenon dubbed the 'Palaeogene gap' by Wilson and Rosen (1998). On the other hand, previous literature shows that, counterintuitively in relation to its modern distribution, *Acropora* seems to have originated and diversified in a North African-Mediterranean region (Wallace and 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). Wilson and Rosen (1998) ascribed this to changing palaeographies through the Cenozoic. The aim here was to see how far this palaeobiogeographical pattern holds in the light of the more complete compilations made in this thesis.. This is primarily undertaken through the database and analysis of existing fossil *Acropora* records, revised as necessary to bring the names and stratigraphy into line with current classifications.

- **Since the high-latitude Eocene occurrences of this reef-building coral are compatible with the widely recognised Eocene warm climate in Northwest**

Europe, stable isotope geochemistry of Eocene specimens of *Acropora* was used to discover if this was reflected in the specimens themselves.

Background

A main aim of this thesis is to add palaeoenvironmental context to high-latitude Eocene occurrences of *Acropora* in order to test hypotheses on the effect of an Eocene phase of climatic warming in Northwest Europe. Much of our understanding of coral reef ecosystems from the geological past is based on taxonomic uniformitarianism, but by combining this with independent data, like geochemistry, it is possible to make higher resolution predictions about future responses. One approach is to use taxonomic uniformitarianism. By using the quantitative relationship between present-day reef coral taxonomic richness and minimum prevailing surface sea-water temperatures (the so-called 'energy hypothesis'), Rosen (1999) used the 'energy hypothesis' to provide a working model of the global relationship between taxonomic richness and prevailing minimum sea surface temperatures. In this approach reef coral diversity in ancient records as a proxy for inferring minimum palaeotemperatures, in this case for Mediterranean waters during the Miocene. Bosellini and Perrin (2008) followed up this work applying the same approach to a much larger database, from 23 Eocene-Miocene localities of the Mediterranean region.

A second approach here is the use here of stable isotopic and trace element indicators of environmental conditions, which are independent of taxonomic uniformitarianism. Keeping these two types of information separate does not strictly a test of one against the other, but provides potential corroboration and 'reciprocal illumination' as shown in this thesis.

This thesis therefore presents the first summary of the distributional history and palaeoenvironmental context of the ancient occurrence of *Acropora*, using (a) stratigraphical, taphonomic, palaeoecological and sedimentological information, (b) stable isotope work on the *Acropora* specimens, and (c) published regional and global palaeoclimate models for the Cenozoic. This project was designed to demonstrate how one particular important reef-coral genus has responded to global change throughout its geological time-span. This potentially provides much-needed information to complement predictions on the fate of modern coral reefs which, to date, has been based largely on living corals and reefs.

1.4 MATERIAL

For the database, *Acropora* records were taken from various sources (see Chapter 3) from global Cenozoic localities (Fig. 1.1).

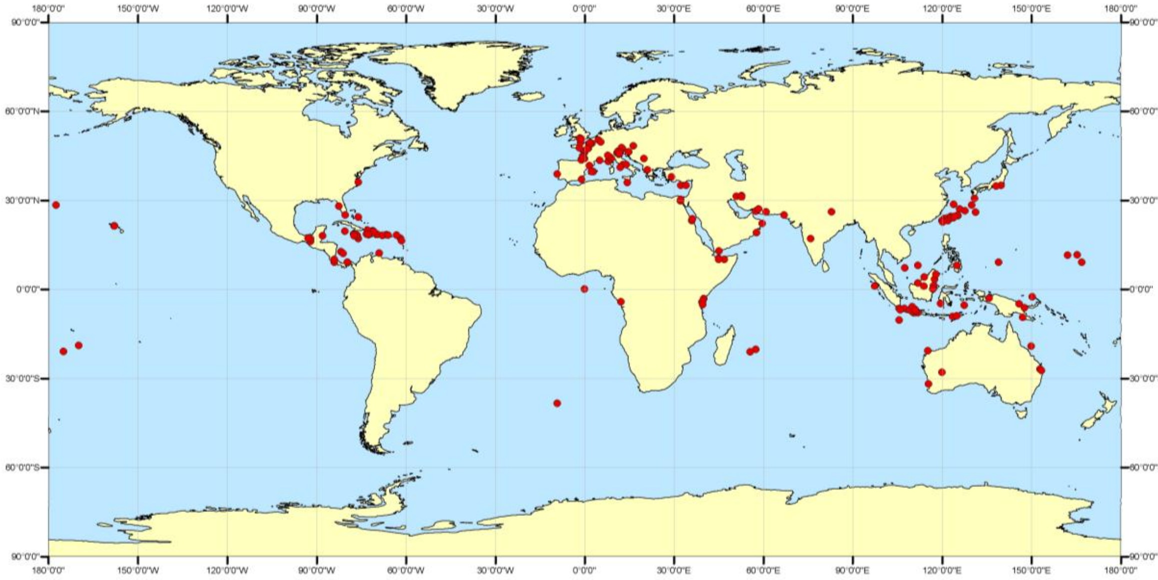


Figure 1.1. Global Cenozoic distribution of <u>Acropora</u> records used in this thesis.

Newly obtained *Acropora*, and other coral, specimens have been collected during this thesis and will be housed at the Natural History Museum (NHM), London, following completion of this thesis. Temporary specimen numbers assigned for this thesis will be kept alongside NHM numbers being assigned. Many of the specimens used for taxonomic and geochemical analysis in this thesis have come from localities in France and England such as quarries or railway cuttings which are now inaccessible and hence there is dependence on what has been collected in the past. This has made the collection of Eocene *Acropora* fossil fragments, and associated taxa, in the collections at the Natural History Museum (NHM), London, vital to this research. Specimens used for this research have been collected, presented and curated at the NHM throughout the twentieth century. Consequently the collection has been collected/compiled by various workers and there is a reliance on the accuracy, and a need for standardisation, of the stratigraphic, geographical and taxonomic information recorded during documentation of these specimens.

1.5 METHODS

The methods used in this thesis attempt to reconstruct the palaeobiogeographic history of the genus (Fig. 1.2). This includes: A. tracing the distribution of the genus by databasing all Cenozoic records and conducting a taxonomic review of specimens and, B. adding palaeoenvironmental context through geochemical analysis and a taphonomic and palaeoecological study.

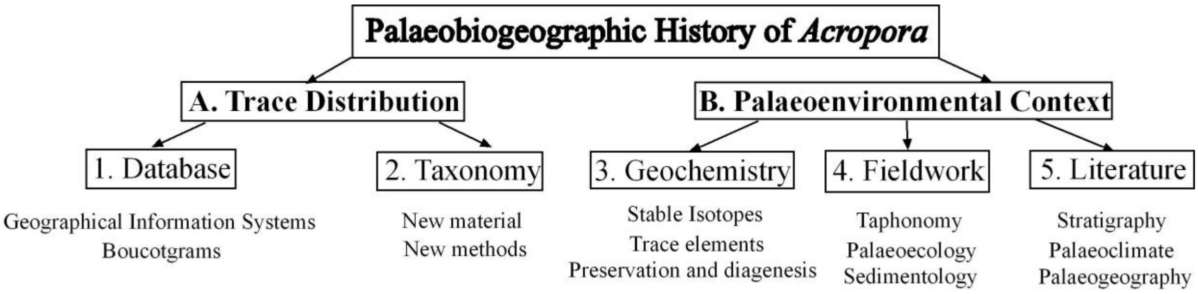


Figure 1.2. Overview of methods used within this thesis to accomplish an understanding of the palaeobiogeography of Acropora

1.5.1 Database

A database of existing fossil *Acropora* records, revised as necessary to bring the names and stratigraphy into line with current classifications respectively, was compiled. A complementary stratigraphic approach has been used to generate spatio-temporal plots (‘*Boucotgrams*’, named for Art Boucot) and a series of GIS maps of the fossil record of *Acropora,* to identify extinct distributions and hence the changing patterns in its distribution through the Cenozoic.

1.5.2 Field work

Field work was undertaken at fossil localities in the Hampshire and Paris basins. Field work in selected areas in France and England improved the distributional data of *Acropora* and in providing a limited understanding of *Acropora* taphonomy and palaeoecology. This is highlighted below:

- March 2006: Isle of Wight, Hampshire Basin, UK
- September 2007: Mainland Hampshire Basin, UK
- September 2009: Paris Basin, France

Fieldwork included logging of sedimentary sections, examination of sedimentary structures, examination of facies variations and unconformity surfaces. Table 1.1 shows the geological locations visited for this study.

LOCALITY	BASIN	LAT-LONG	DESCRIPTION
Fleury-la-Riviere	Paris	49'06'13N, 3'50'50E	Series of pits, some recently dug, on the edge of forest
Chalons-sur-Vesle	Paris	49'17'263N, 3'55'430E	Large old quarry/sand pit in park area
Cauroy-les-Hermonville	Paris	49'20'55N, 3'55'31E	Large recent quarry with multiple exposures
Vendrest	Paris	49'02'48N, 3'05'34E	Roadside small quarry, time limited access
Les Guepelle (La Chapelle-en-Serval)	Paris	49'05'067N, 2'32'243E	Large sand quarry closed to public
Auvers-sur-Oise	Paris	49'04'16N, 2'10'38E	Forest locality with old excavations related to previous quarry area
Vigny	Paris	49'04'17N, 1'54'55E	Area of outstanding natural beauty, protected area with huge quarry
Fercourt	Paris	49'18'975N, 2'15'133E	Recently dug pits, excavations, on either side of the road in woodland
St.Vaast-Les-Mello	Paris	49'16'00N, 2'23'21E	Bike track entry to huge disused quarry
Cuise-la-Motte	Paris	49'23'08N, 3'00'35E	Quarry outcrop
Saint Gobain	Paris	49'35'423N, 3'21'113E	Old railway cutting in forest, near Barisis
Whitecliff Bay, Isle of Wight	Hampshire	50'40'00N, 1'06'00W	Cliff and limited foreshore dependant on tides
Alum Bay, Isle of Wight	Hampshire	50'39'50N, 1'33'57W	Cliff faces and isolated chalk stacks.
Lyndhurst, Brockenhurst	Hampshire	50'52'24N, 1'34'34W	River beds and banks
Barton Cliffs, Barton-on-sea	Hampshire	50'44'16N, 1'40'33W	Cliffs and foreshore
Bracklesham Bay	Hampshire	50'45'51N, 0'51'28W	Foreshore with erosional pedestals dependant on tides

Table 1.1. Fossil localities studied during this thesis from the Hampshire and Paris basins

1.5.3 Museum visits

Many museum visits were conducted during this thesis to study coral collections, along with other fauna, from global *Acropora*-bearing localities (Tab. 1.2). Faunal lists were compiled and specimens photographed, and loaned from these institutes if further studies were needed. For each institute abbreviations are used throughout this thesis (Appendix 7).

LOCALITY	COUNTRY	COLLECTIONS STUDIED
Natural History Museum, London	UK	Recent and fossil worldwide coral specimens; Paris, Hampshire and Aquitaine Basin specimens
Royal Holloway University, Surrey	UK	Southeast Asia coral specimens
British Geological Survey, Nottingham	UK	Worldwide fossil coral specimens; Duncan (1866) *Acropora* types
Sedgwick Museum, University of Cambridge	UK	Hampshire Basin coral specimens
Oxford Museum of Natural History, Oxford	UK	Worldwide fossil coral specimens; Hampshire Basin coral specimens
Hampshire Museum, Winchester	UK	Hampshire Basin coral specimens
Dinosaur Isle Museum, Isle of Wight	UK	No coral specimens found*
Muséum national d'Histoire naturelle, Paris	France	Worldwide fossil coral specimens; Paris Basin coral specimens
Museum of Tropical Queensland, Townsville	Australia	Worldwide recent *Acropora* specimens
James Cook University	Australia	Worldwide recent coral specimens

Table 1.2 Museums visited and collections studied during this thesis.

* Coral collections from the Eocene Hampshire and Paris basins had previously been described as housed at the Isle of Wight Museum, Sandown, which is now closed with collections relocated to the Dinosaur Isle Museum, Isle of Wight.

1.5.4 Taxonomy

Training in coral taxonomy, particularly on *Acropora*, at the NHM and Museum of Tropical Queensland, Australia, allowed the identification of *Acropora* specimens to species level. Additionally, sectional preparations of fossil specimens and micro-computed tomography were used to develop of a working taxonomy for fossil *Acropora* based on how the surface characters used for modern species recognition correspond (or not) to characters preserved internally.

1.5.5 Geochemistry

An assessment of specimens for diagenetic alteration followed by stable isotope work on selected pristine, aragonitic specimens, for palaeoenvironmental information. Palaeoenvironmental context of the records using stratigraphical, taphonomic, palaeoecological and sedimentological information was reinforced by stable isotope and trace element work on the coral and molluscan specimens.

1.6 THESIS LAYOUT

This thesis begins with a review of the literature in chapter 2. An introduction to the modern global distribution of coral reefs and the factors affecting this distribution is followed by a review of climatic and non-climatic stresses to modern coral reefs. This is concluded by a historical overview of corals in crisis and the present responses of the genus *Acropora* to present anthropogenic-induced climate change, and the negative effects this has on the genus. Chapter 3 reconstructs the Cenozoic history of this genus using the newly compiled database of distributional data to provide an overview of fossil *Acropora* records and hence clarifying patterns of evolutionary change throughout its Cenozoic record. Chapter 4 introduces new methods for the development of a working taxonomy for fossil *Acropora* based on how the surface characters used for modern species recognition correspond (or not) to characters seen in sectional preparations and micro-CT scans of fossil specimens. Chapter 5 presents a fully revised taxonomy of the coral material described throughout this thesis. Of principle interest is the taxonomic content of the fossil record of this modern-day highly successful reef-building, coral genus *Acropora,* and its family, that are found in the Northern European area of the early Cenozoic. These identifications are based on re-examination of Middle-Late Eocene (Paris and Hampshire Basin) and Miocene (Aquitaine Basin) material from museum and private collections, and examination of material collected from field localities. Two type specimens, *Acropora roemeri* and *A. anglica*, have been newly located and re-described for the first time since their original description by Duncan (1866). This chapter discusses the diversity of Eocene *Acropora* specimens, and other members of the Acroporidae family, from the Hampshire and Paris Basin, and from the Miocene Aquitaine Basin. Chapter 6 summarises fieldwork at selected localities in the Eocene Hampshire and Paris basins to improve the distributional data of *Acropora* and understanding of *Acropora* taphonomy and palaeoecology. In chapter 7 estimates are made of the sea-surface temperatures from the Hampshire, Paris and Aquitaine basins based on coral taxonomic richness and by an assessment of specimens for diagenetic alteration followed by stable isotope and trace element work on selected specimens, for palaeoenvironmental information. Chapter 8 is a discussion of all the major results from this research and places it within the broader context of Cenozoic reef evolution. The principal conclusions and suggested future work of this study are listed in Chapter 9.

CHAPTER 2. CORAL REEFS AND GLOBAL CLIMATE CHANGE – A REVIEW

CONTENT

This chapter provides a review of the state of understanding about modern coral reefs, environmental change (driven by both natural and anthropogenic stresses), and the interactions between both. This aims to support discussions and conclusions drawn in future chapters with regard to the fossil record of the modern dominant reef building coral, *Acropora*.

2.1 OVERVIEW AND AIMS

Coral reefs have shaped and dominated ocean ecosystems since the first appearance of scleractinian corals in the fossil record in the mid-Triassic (~240Ma; Veron, 2000; Stanley, 2003). Molecular phylogenies suggest an origin predating these earliest fossils (~300Ma; Ramano and Palumbi, 1996; Romano and Cairns, 2000). During this period, these spectacular and diverse ecosystems have survived several mass extinction events including the most severe in Earth's history at the Permian-Triassic boundary (Stanley, 2003). Additionally these corals survived other periods of potential devastating environmental catastrophes. During the early Triassic when atmospheric CO_2 levels increased dramatically, reaching levels five times higher than today (Berner and Kothavala, 2001), corals survived and following this flourished, eventually dominating reefs of the Cenozoic. Therefore, although reefs are often regarded as environmentally fragile, the geological record shows they have long lived associations.

In order to predict the future of coral reef diversity, abundance and distribution it is necessary to understand their geological history. In combination with an understanding of previously recorded geological global climate change, an understanding of present anthropogenic change enables future predictions and an understanding of modern coral reef ecosystems. In fact, the geological record may provide us with hope for the resilience of coral reefs and benefits that future environmental changes may hold.

This chapter provides a review of the state of understanding about modern coral reefs, environmental change (driven by both natural and anthropogenic stresses), and the interactions between both. This aims to support discussions and conclusions drawn in future chapters with regard to the fossil record of the modern dominant reef building coral, *Acropora*, ultimately to provide an understanding of the geological record and additionally support predictions about the future of the genus.

2.2 CORAL REEFS AND REEF ORGANISMS

Coral reefs, and the organisms and communities which occupy them, are widely found within shallow marine tropical and subtropical areas of the world. These ecosystems contain a biological (the coral community) and geological (the reef structure) component with dynamic interactions between them.

Reefs have existed since the appearance of microbial mat communities around 3.5 billion years ago (Walther, 1983; Wood, 1999). During their Cenozoic record, a wide variety of skeletal algae and metazoans have dominated a variety of reef ecosystems with modern reefs being dominated by scleractinian corals and coralline algae.

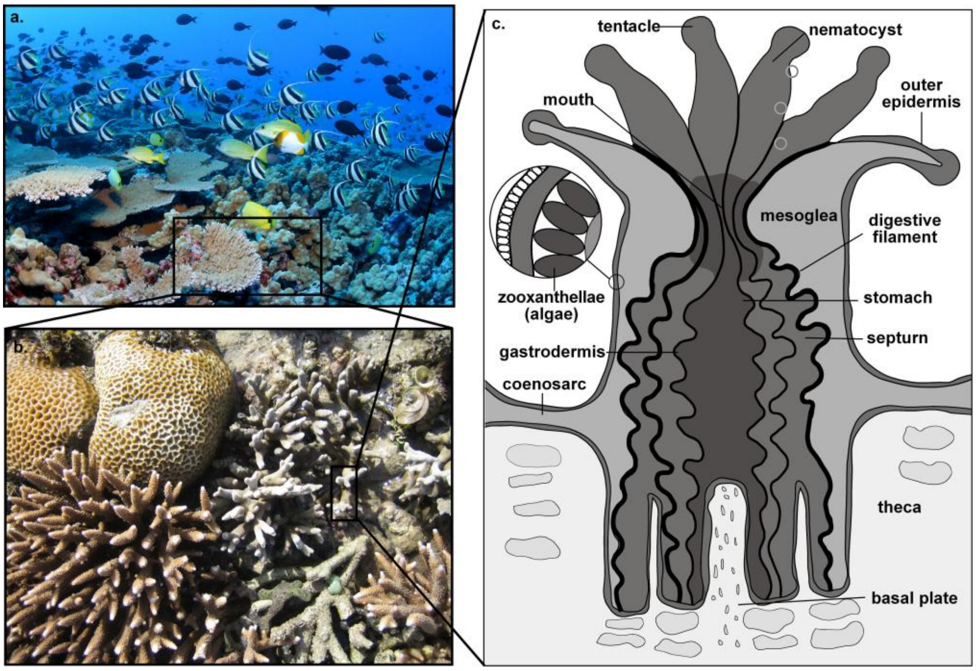


Figure 2.1. a. & b. Figures showing relationships of the polyp to the colony and of the colony to the reef ecosystem (Photos: Magnetic Island, Great Barrier Reef). c. Cross-section diagram of a polyp of typical reef-building coral, illustrating the presence of symbiotic microalgae (zooxanthellae) (adapted from Stanley, 2003)

The order Scleractinia consists of polypoidal marine invertebrates, which along with other groups including sea anemones, octocorals and sea pens, belong to the subclass Zoantharia, in the class Anthozoa of the Cnidaria phylum (Oliver, 1987; Stanley, 2003) (Fig. 2.1).

Within corals, there is a widely accepted ecological distinction based on the presence or absence within their endodermal cells of the symbiotic dinoflagellate alga, *Symbiodinium* (Trench, 1979) (Fig. 2.1c). Before the true identity of these symbionts was recognised, they were referred to as zooxanthellae and this term is still always used for them. Hence corals are now categorised as ‘zooxanthellate corals’ (or ‘z-corals’) or ‘azooxanthellate corals’ (or ‘az-corals’) (Schuhmacher and Zibrowius, 1985; Rosen 2000). The symbiotic relationship between the coral and dinoflagellates results from the zooxanthellae photosynthesising and releasing over 95% of the energy to the host coral (Muscatine, 1990). In return, the algae benefit from nutrients released as waste by the host coral. Additionally, there are complimentary benefits in carbon dioxide exchange believed to allow the rapid skeletal growth.

Prior to the adoption of these terms, two other terms had been in common use (and are still used by many authors), coined by John Wells (1933): 'hermatypic' and 'ahermatypic'. They are derived from 'herma' meaning mound or reef. Wells (1933) defined 'hermatypic' as corals that not only build reefs but also as species possessing zooxanthellae. In contrast, ahermatypic corals, according to Wells (1933), neither build reefs nor possess zooxanthellae. It is now widely accepted that there are issues with these distinctions principally because not all zooxanthellate corals build reefs and therefore these definitions breakdown. Rosen (1981, p. 106) proposed that the terms 'zooxanthellate' and 'non-zooxanthellate' (i.e. azooxanthellate) be divorced from criteria like reef dwelling or reef building. Moreover, for the fossil coral record, it is difficult to establish if a fossil coral ever possessed zooxanthellae, since the zooxanthellae are not preserved, nor if it was consistently a reef-builder or reef-dweller, since reefs have been defined in many different ways (see further below). So for the fossil record, Rosen (2000), suggested the terms 'z-like' for fossil forms resembling modern zooxanthellate corals and 'az-like' for fossil forms that are more similar to modern azooxanthellate corals (see also Wilson and Rosen 1998). In terms of diversity among the 1314 species currently known, they are almost equally split between z- and az-taxa, with 48.2% of the genera and 49% of the species being z-corals (Cairns, 1999).

The term 'reef' has had many scientific meanings from all-encompassing to subject specific. The term 'reef' originates from the Norwegian word 'rif', which describes a hazardous 'rib' of rock, shingle or sand that lies close to the surface of the sea surface (Wood, 1999; Schwartz, 2005). In a restrictive use of the word, 'reef' donates a rigid, wave resistant framework constructed by large skeletal organisms (Ladd, 1944). More recently, a broader definition has been proposed by Wood (1999): *a reef is a discrete carbonate structure formed by in-situ or bound components that develop topographic relief upon the sea floor*.

Modern reef morphology is dominated by a vast variety of coral skeletal geometries. Corals and reefs have existed for hundreds of millions of years and therefore house a wealth of information about the Earth's historical, environmental changes. Scleractinian corals and coralline algae first evolved during the mid Triassic and Cretaceous respectively (Stanley, 2003). Following a period of major extinction at the end of the Cretaceous, diversity in reef corals increased (Rosen, 2000; Rosen 2002;

Veron, 2000). Subsequently, the fish which characterise modern coral reef communities first appeared around 50 million years ago (Bellwood, 1996). During the Burdigalian (early Miocene), the fragmentation of the once pantropical Tethys Sea began separating corals into two major biogeographical provinces (Wilson and Rosen, 1998; Rosen, 2002). Present day reefs have accumulated during the last 10,000 years (during the Holocene) with the modern reef ecosystem forming a veneer over previous limestone accumulation (Buddemier *et al*., 2004).

2.3 MODERN GLOBAL DISTRIBUTION

Modern reefs are presently dominated by scleractinian corals, many of which are zooxanthellate (see above) and therefore restricted to shallow, clear tropical waters. Modern z-corals are not actually restricted to reefs but occur in various other shallow tropical and sub-tropical marine habitats. The distribution of reefs is dictated by a complex interplay of community dynamics and responses to physical and environmental changes. At present, corals, and the reefs they build are restricted to a narrow band circling the globe, defined by low latitudes limited to about 30 degrees north and south of the equator circling the globe (Fig. 2.2).

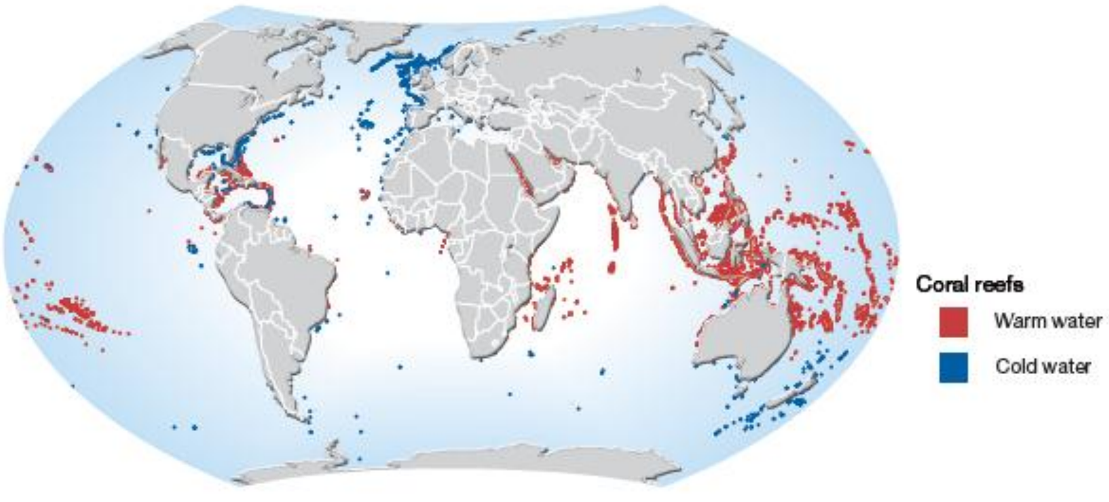
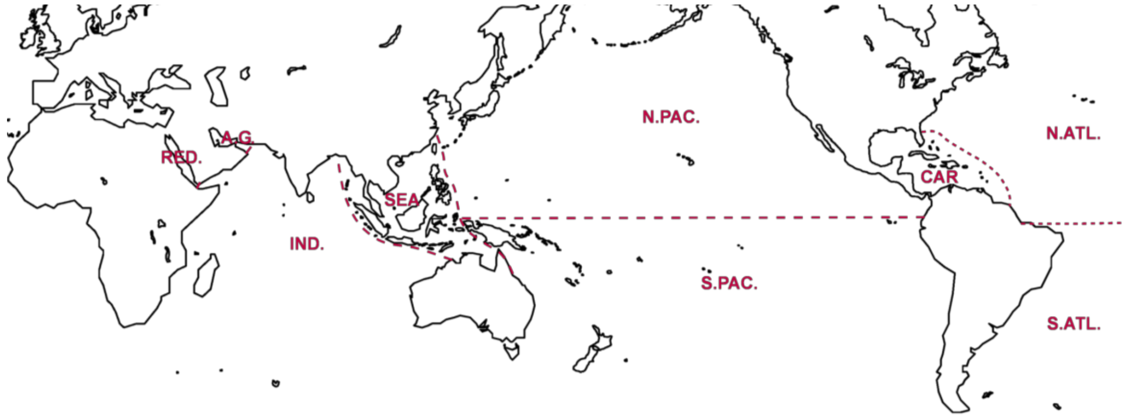


Figure 2.2. Global distribution of warm and cold water dominated coral reefs (Source: World Conservation Monitoring Centre of the United Nations Environment Programme, UNEP-WCMC)

A review by the World's Conservation Monitoring Centre of Smith's (1978) estimation of global reef area of 600 000km^2 has given a new estimate of global reef coverage of 255 000 km^2 (Spalding and Grenfell, 1997; Fig 2.3). It is believed this area accounts for less than 0.2% of the Earths oceanic area but importantly they house around 25% of all marine species (IUCN SSC Coral Reef Fish Specialist Group; Smith, 1978; Wood, 1999). It is estimated that over 900,000 species (plants, animals, microbiota) inhabit coral reefs (Reaka-Kudla, 1997). As a result of this diversity, coral reefs are widely described as the 'tropical rainforest of the sea'.



Region	Spalding and Grenfell (1997) area (×10^{3}km^2)	Smith's (1978) area (×10^{3}km^2)
Red Sea (RED.)	17	27
Arabian Gulf (A.G.)	3	12
Indian Ocean (IND.)	36	146
South East Asia (SEA)	68	182
Northern Pacific (N.PAC.)	17	76
Southern Pacific (S.PAC.)	91	77
Caribbean (CAR.)	20	57
Northern Atlantic (N.ATL.)	2	32
Southern Atlantic (S.ATL.)	1	8
TOTAL	**255**	**617**

Figure 2.3. Global and regional coral major reef areas comparing between Smith (1978) and Spalding and Grenfell (1997)

At present there are two major biological realms of coral distribution. One is centred on the Atlantic-Caribbean (250,000 km^2) and a second, the Indo-Pacific (1,250,000 km^2), with a third relatively minor Red sea region. Diversity is far lower in the Atlantic realm than within the Indo-Pacific, with the Pacific supporting 78 coral genera and the Atlantic 24 (Fraser and Currie, 1996). Although some coral genera are found in both provinces (e.g., *Montastraea, Porites* and *Acropora*) these provinces have few species in common (Veron, 2000).

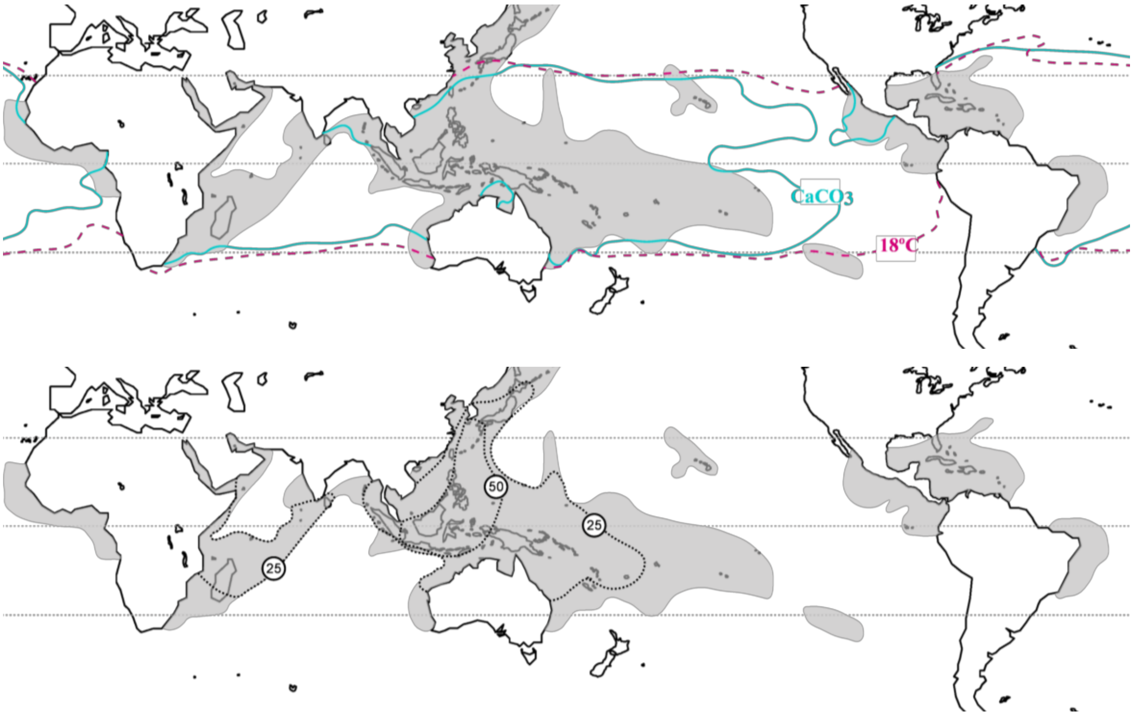


Figure 2.4 a. & b. General worldwide distribution of coral reefs, with contours indicating the number of genera. The area inside the 50 genera contour is essentially the high diversity "coral triangle" (the Southeast Asian centre of coral diversity). The blue area outside of the contour lines represents regions with at least 10 but fewer than 25 genera (adapted from Wilkinson, 2004, based on Veron, 1995). Coloured lines indicate critical boundaries of sea surface temperature (18°C) and aragonite saturation for coral reef accretion ($CaCO_3$) as given by Kleypas et al. *(1999).*

At present the Indo-Pacific accounts for 85% of the world's reefs and similar proportion of reef diversity (Veron, 1995) (Fig. 2.4). Only 17% of the total 111 reef building genera and none of the 18 coral families with reef builders are considered endemic to the Atlantic, whereas for the Indo-West Pacific the corresponding values are 76% and 39% (Veron, 2000). Within the high diversity Indo-West Pacific, coral diversity is at its highest around the Southeast Asia region, termed the 'Coral Triangle' (Fig. 2.5). This area lies in the waters of six countries in Southeast Asia: the eastern half of Indonesia, Philippines, Malaysia (Sabah), Timor-Leste, Papua New Guinea, and the Solomon Islands, occupying approximately 6.8 million km^2 (Hoeksema, 2007). Coral reefs cover over 100,000 km^2 of the Coral Triangle, which represents roughly one third of all the coral reefs in the world (Green and Mous, 2008). Within the Coral Triangle, the highest number coral species is found near the Bird's Head Peninsula of Indonesian Papua, which hosts 574 species (Veron *et al*., 2009). Individual reefs there have over four times the total number of species of reef-building corals than in the entire Atlantic Ocean.

Figure 2.5. Boundary of the 'Coral Triangle' (Veron et al*., 2009)*

Major biogeographic hypotheses have proposed mechanisms that lead to higher diversity in the Indo-Pacific, falling into four categories; i. *Centre of Origin*, ii. *Centre of Refuge*, iii. *Centre of Accumulation* and, iv. *Centre of Overlap* (Bellwood and Hughes, 2001). The *Centre of Origin* model (Fig. 2.6) invokes vicariance or sympatric speciation and predicts that the majority of small-range taxa should be found in the Coral Triangle and that all should be younger than more ancestral taxa with larger ranges, reflecting origins in this location with subsequent dispersal away from the centre. The *Centre of Refuge* model, providing a refuge from higher extinction rates in peripheral locations. The *Centre of Accumulation* (Fig. 2.6) model, small-range taxa should be young and peripherally distributed, reflecting peripheral origins with subsequent movement towards the centre some time later. The *Centre of Overlap* (Fig. 2.6) model predicts that sister taxa are distributed in and on either side of the Coral Triangle, the high diversity in this model being driven largely by vicariance in, and subsequent dispersal across, the Coral Triangle. However, origins are interpreted largely based on the geographic distribution patterns of extant taxa, especially 'endemics,' and there is little data on the age or evolutionary history of the component species. In reality, over geological time these models are not mutually exclusive and cumulatively they leave their mark to explain the present high diversity. This is discussed further in Chapter 3 as well as the significance of fossil coral assemblages outside the area, as these models have mostly been tested to date by using data only from living distributions.

Coral reefs diversity, and reef development, is largely absent from the Central Atlantic, and highly restricted along the western shores of Africa, and along the South Asian coastline between Pakistan and Bangladesh (Spalding *et al.*, 2001).

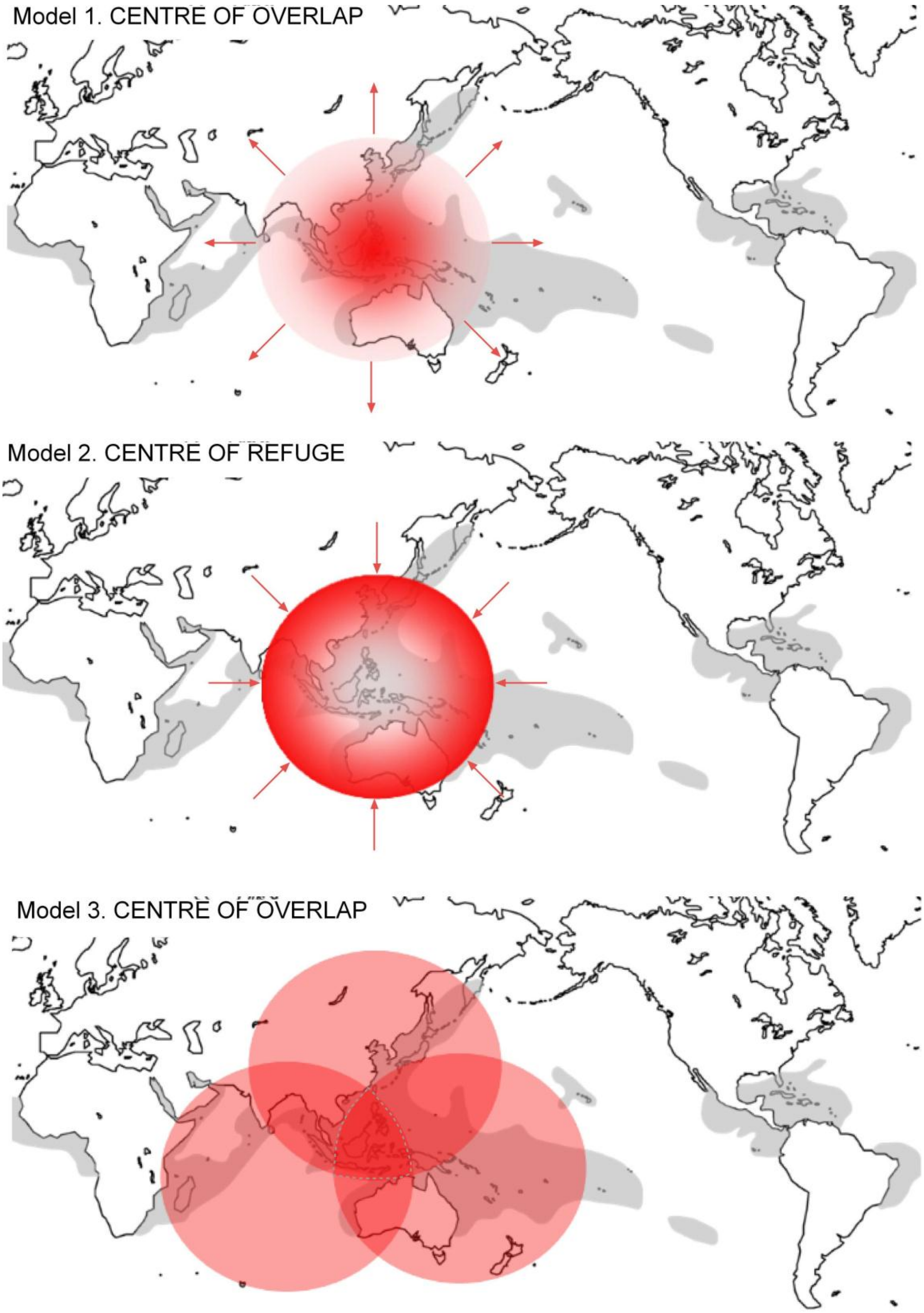


Figure 2.6. Three main categories of proposed mechanisms that lead to higher diversity in the Indo-Pacific

2.4 FACTORS AFFECTING THE DISTRIBUTION OF MODERN CORAL REEFS

The distribution of coral reefs worldwide is dictated by a combination of environmental factors. A summary of these factors collected from 1000 reefs indicates that there is a significant range for each variable, but there is also relatively minor variation around the means (Kleypas *et al*. 1999; Tab. 2.1).

Variable	*Min*	*Max*	*Mean*	*SD*
Temperature (°C)				
mean	21.0	29.5	27.6	1.1
minimum	16.0	28.2	24.8	1.8
maximum	24.7	34.4	30.2	0.6
Salinity (PSU)				
minimum	23.3	40.0	34.3	1.2
maximum	31.2	41.8	35.3	0.9
Nutrients $\mu mol\ l^{-1}$)				
NO_3	0.0	3.30	0.25	0.28
PO_4	0.0	0.54	0.13	0.08
Aragonite saturation (Ω_{arag})				
mean	3.28	4.06	3.83	0.09
Max depth of light penetration (m)				
mean	-9.0	-81.0	-53.0	13.5
minimum	-7.0	-72.0	-40.0	13.5
maximum	-10.0	-91.0	-65.0	13.4

Table 2.1 Environmental variables, the minimum (Min), maximum (Max), mean and standard deviation of sites (SD) for 1000 coral reef sites on ReefBase (taken from Kleypas et al.*, 1999 in McClanahan, 2002).*

2.4.1 Temperature

Few zooxanthellate corals can tolerate temperatures below 14°C (Wood, 1999). However, 50% of this corals exist in non-reef habitats with an average sea surface temperature of 14°C. Although rare, there are records of low temperature tolerance, both widespread taxonomically and geographically (Veron, 1995). *Siderastrea radians* has been found tolerating temperatures as low as of 4.5°C, if only briefly (Vaughan and Wells, 1943). The majority of reefs are restricted to waters that do not fall below 18°C and are therefore geographically restricted to low latitudes, ~30°N and S (see figure 2.4; Wells, 1956).

Hoegh-Guldberg (1994) reviewed numerous bleached scleractinian coral species from the French Polynesia and showed that acroporid species were most susceptible with 89-100% completely bleached. Marshall and Baird (2000) assessed the susceptibility of 4160 coral colonies on the Great Barrier Reef to bleaching and consistently observed severe bleaching of acroporids, suffering high mortality and only ~8% remaining alive. Coles *et al.* (1976) reported the upper thermal tolerance for two species, *Acropora formosa* and *A. hyacinthus* on the Marshall Islands as ~31°C. It is also evident that larvae of different species have a range of sensitivities to elevated temperatures. Negri *et al.* (2007) found that some Pacific acroporid species larvae, for example *A. millepora*, displayed significantly reduced fertilisation success and a higher frequency of embryonic abnormalities at 32°C. The present global distribution of corals falls generally within the 18°C monthly minimum seawater isotherm (Kleypas *et al.*, 1999). In the western Arabian Gulf, Coles and Fadlallah (1991) showed a series of cold fronts during 1988 and 1989 produced the longest period of sustained low water temperatures and resulted in severe mortality of *Acropora pharaonis* where minimum temperatures fell below 11.5°C on four consecutive days and mean daily temperatures were 13°C or less for more than 30 days. In the Caribbean region, colonies of *A. palmata* have experienced bleaching events (Lundgren and Hillis-Starr, 2008), but thus far have been less susceptible to temperature stress than other corals from the region such as *Montastraea* spp. and *Millepora* spp. (Wood *et al.*, 2008).

Coral growth rates can depend on both maximum and minimum seasonal temperatures (Slowey and Crowley, 1995), although the relationship between temperature and inhibition of coral reef growth is unclear. Yap and Gomez (1984) studied undisturbed colonies and transplants of the branching coral *Acropora pulchra* on a reef of Bolinao, northern Philippines. Temperature and day length correlated negatively with the growth and branching of the corals (Yap and Gomez, 1984). However, the stimulation of calcification by the elevation of temperature has been widely shown. Kajiwara *et al.* (1995) demonstrated the rate of calcification of *Acropora pulchra* peaks at 28.1°C, and the linear extension rate of *Acropora* specimens increases until 27.1°C and then declines at higher temperature (Reynaud-Vaganay *et al.*, 1999). Bleaching events, primarily believed to be the result of climatic warming, are an indication of extreme physiological stress and is often followed by death. Temperature changes directly influence the physiological processes of photosynthesis, and calcification, and in severe cases also survival (Crabbe, 2009). Current research shows that climate change will alter many aspects of what we know as coral reefs, however what remains unclear is exactly how, and what will be the result of these changes (e.g. Romaine *et al.* 1997, Ferrier-Pages *et al.* 1999).

2.4.2 Saturation state

Coral reef calcification depends on the saturation state of carbonate mineral aragonite of surface waters. A decrease in saturation state is predicted to reduce calcification rates, cause a shift towards calcite secretors, or give competitive advantage to non-calcifying reef organisms (Smith and Buddemeier, 1992). Tropical surface waters are at present supersaturated (Ω>1.0) with respect to all mineral phases.

Dissolved inorganic carbon occurs in three main components: carbon dioxide (CO_2), and majority is dissociated into bicarbonate (HCO_3^-) and carbonate (CO_3^{2-}). When CO_2 dissolves in water, it forms carbonic acid (H_2CO_3):

$$H_2O + CO_2 \leftrightarrow H_2CO_3$$

Carbonic acid is a weak acid that can lose hydrogen ion to form bicarbonate (HCO_3^-):

$$H_2CO_3 \leftrightarrow H+ + HCO_3^-$$

or further shed the remaining hydrogen ion to form carbonate (CO_3^{2-}):

$$HCO_3^- \leftrightarrow H^+ + CO_3^{2-}$$

(Buddemeier *et al.*, 2004)

The proportion of main components in preindustrial surface tropical seawater, in normal conditions (pH 8.0-8.2), is HCO_3^- 88%, CO_3^{2-} 11%, with the remainder existing as a combination of dissolved CO_2 and carbonic acid (Buddemeier *et al.*, 2004). Increasing atmospheric CO_2 drives more CO_2 into the ocean, lowering the pH, hence making it more acidic, and changing the proportion of the main components of the carbonate system (Hoegh-Guldberg *et al.*, 2007). Schneider and Erez (2006) observed that calcification by *Acropora eurystoma* was positively correlated with [CO_3^{2-}], and inversely correlated with [HCO_{3-}].

Suwa *et al.* (2010) summarised the effects of increased CO_2 on early life stages of *Acropora* spp. showing polyp growth and algal infection rates were significantly decreased at reduced pH levels. This study implied that future ocean acidification could result in reduced primary polyp growth and delayed establishment of symbiosis (Suwa *et al.*, 2010). Albright (2011) tested fertilisation, settlement, and post settlement growth of *Acropora palmata* and concluded that at predicted $p$$CO_2$ concentrations expected for the middle and end of this century results that ocean acidification has the potential to reduce fertilisation success by 12-13% and to decrease settlement success by 45–69%.

This may translate into a 52–73% reduction in the number of larval settlers on the reef (Albright, 2011). Renegar and Riegl (2005) measured growth rates of *Acropora cervicornis* branch tips maintained in the laboratory and concluded that coral skeletal growth declined 80% in branch tips at pCO_2 levels between 700 to 800 µatm. Several papers focused on other coral genera have described the negative relationship between calcification and CO_2, or a positive relationship with the aragonite saturation state (Gattuso *et al*., 1998; Marubini and Atkinson, 1999; Langdon *et al*., 2000; Leclercq *et al*., 2000; Marubini *et al*., 2003). However, Reynaud *et al*. (2003) showed for the branching scleractinian coral *Stylophora pistillata* that calcification was not affected by elevation of pCO_2 in colonies maintained at normal temperature (~25°C).

2.4.3 Nutrients

Corals are generally associated with waters characterised by low levels of inorganic nutrients (0.2 to 0.5 µM ammonium, 0.1 to 0.5 µM nitrate, and <0.3 µM phosphate, Furnas, 1991; nitrate and phosphate less than 2.0 µmol L^{-1}, Kleypas *et al*., 1999), and it is widely understood that significant increases in nutrient concentrations have negative effects on coral growth rates (Hallock and Schlager 1986, Stambler *et al*. 1991, Ferrier-Pagès *et al*. 2000). During seasonal influxes, high nutrient levels enhance the growth of macroalgae and degraded coral reefs generally exhibit a shift from high coral cover to low coral cover with an accompanying high cover and biomass of fleshy algae (Szmant, 2002). As a result of extreme weather events, such as hurricanes, there is an increase in coastal runoff and nutrient import into coastal areas. Harrison and Ward (2001) presented the first data on the effects on nutrient enrichment on fertilisation success of broadcast spawning corals, including *Acropora* spp. These laboratory results demonstrated that slightly elevated nutrient levels can adversely affect or block fertilisation and embryo development of the branching coral *Acropora longicyathus*. In addition water contaminants can also affect fertilisation, Harrison (1994) showed that fertilisation was reduced or blocked by low levels of oil hydrocarbons in *Acropora tenuis* gametes. Renegar and Riegl (2005) studied the growth rate of *Acropora cervicornis* branch tips after exposure to elevated nitrate (5 and 10 µM NO3–) and phosphate (2 and 4 µM P-PO43) levels. High concentrations of nitrate or phosphate resulted in significant decreases in growth rate, in both the presence and absence of increased pCO_2.

For other coral genera a significant decrease in calcification was also observed with elevated nutrient levels. Ferrier-Pagès *et al*. (2000) showed a phosphorus concentration of 2 μM resulted in a 60% decrease in the growth rate of *Stylophora pistillata* and *Montastraea annularis* also resulting in decreased calcification at nitrate concentrations of <5 μM (Bell and Tomascik 1993; Marubini and Davies 1996). Ferrier-Pagès *et al*. (2000) showed the greatest reduction in coral growth rate in the combined presence of nitrogen and phosphorus.

2.4.4 Light and Turbidity

Light, not temperature, is the most ecologically limiting of all physical environmental parameters (Falkowski *et al*. 1990; Veron, 1995). Most z- corals occur at light levels between 2-0.5% of the incident surface radiation (Lang, 1974; Fricke and Schumacher, 1983; Fricke and Meischner, 1985). As these corals derived most of their metabolic needs from their symbionts, light is an important limiting factor and appears to be a function of photosynthetically available radiation (wavelengths 400-700 nm; Dunne and Brown, 1996) and its attenuation with depth (Wood, 1999). Light also affects coral settlement (Maida *et al*., 1994; Mundy and Babcock, 1995) and competition with other organisms (Baynes, 1999). Light is intrinsically linked to depth, resulting in reef-coral extension rates declining logarithmically with depth (Kleypas, 1997). The depth to which light can penetrate water is dependent upon the turbidity and clarity of water. With depth coral colonies vary morphologically primarily to facilitate maximum light absorption (Fricke and Schumacher, 1983). Flattening of colonies has been shown to maximise the amount a colony is exposed to light from a single direction (Rosen, 1975; Insalaco, 1998; Rosen *et al*., 2002).

Anthony and Connolly (2004) using *Acropora valida* demonstrated that light and particle concentration (turbidity) are important determinants of species-specific physiological limits to growth. Kaniewski *et al*. (2008) investigated the effect of light variation on the morphology of *Acropora humilis* colonies. Specimens were studied along a depth gradient with light habitats ranging from 500 to 25 μmol photons m^{-2} s^{-1}, during 2006 at Heron Island, Great Barrier Reef, which showed branches of *Acropora humilis* in deep water were 40–60% shorter than in shallow water. Stromgren (1987) studied *Acropora pulchra* from an intertidal reef at Phuket, Thailand, grown at different depths in the sea and showed a linear relationship between irradiance and length growth, with a saturating level at 300–400 Wm^{-2}.

High turbidity acts as a light filter and can reduce damaging levels of ultraviolet radiation even in shallow water (Mobley, 1994; Bracchini *et al*., 2004) suggesting that turbidity may alleviate bleaching stress induced by both high temperatures and light conditions. Anthony *et al*. (2007) analysed the effects of irradiance, and sediment loading on coral survivorship in a controlled tank experiment using *Acropora intermedia* from the inner Great Barrier Reef lagoon. In summary, high sediment reduced mortality under high temperature and/or high light, potentially by alleviating light pressure and by providing an alternative food source for bleached corals.

Additionally, Stimson (1985) showed the importance of acroporid species to the light availability for other coral genera at Enewetak Atoll, Marshall Islands. Canopy forming *Acropora* species, such as *Acropora hyacinthus* and *A. cytherea*, produced shaded areas with illumination and irradiance levels at which most zooxanthellate corals do not occur. These table species are also associated with high mortality, Stimson (1985) suggested that though they caused local disturbances they also could contribute to enhanced coral diversity through the variation of shaded and unshaded areas.

2.4.5 Hydrographic exposure

Wave energy is a major constraint on the development of coral reefs and is an important factor in present day ecological zonation (Geister, 1977; Marshall and Davies, 1982; Done, 1983; Hubbard, 1988; Grigg, 1998; Yamano *et al*., 2003; Montaggioni, 2009). Fast coral growth rates are often associated with high hydrographic exposure with greatest diversity being found at the edge of continental shelves and on headlands (Wood, 1999). As wave energy increases, branching corals change from delicate to more robust forms and become oriented relative to the dominant wave direction (Hongo, 2009). Glynn *et al*. (1964) described the destruction of dense thickets of *Acropora palmata* on exposed reefs off La Parguera, Puerto Rico.

High wave agitation provides oxygen and nutrient flux, removes sediment and inhibits predation and herbivory (Hurd, 2000). Waves provide energy for the transport of water across reefs and the resuspension, and transport, of sediments along with circulation moving food through the reef, and removing waste from reef-building organisms, contributing to the cleaning of the coral polyps (Stoddart, 1969).

On Indo-Pacific reefs, the highest wave-energy settings (i.e., windward reefs) are characterised by corals with corymbose and tabulate forms or robust branches (Hong, 2009). For example, robustly branching *Acropora* (e.g., *A. robusta*, *A. danai*, *A.*

palifera, and *A. humilis*) and *Pocillopora* (e.g., *P. damicornis* and *P. verrucosa*) are dominant on reef crests, and *Millepora* is also present in high-energy settings. In contrast, living coral assemblages in lower-energy settings (i.e. leeward reefs) consist of massive corals. Additionally, Blanchon and Jones (1995) reported a delayed development of leeward reefs relative to windward reefs, also seen in fossil reefs (Blendinger, 1986).

2.4.6 Topography and substrate

Substrate availability is one of the most biogeographically limiting physical parameters for reef growth and biogeographic distribution (Veron, 1995; Wood, 1999). Substrates include living hard and soft corals, dead corals, rubble, sand, algae and sponges.

It is widely accepted that disturbances, such as hurricanes and tsunamis, can result in the mortality of *Acropora* communities, often degraded to rubble, which can easily be shifted by hydraulic energy and therefore hindering coral recovery (Fadli, 2009). However, the same disturbances can dislodge or move substrate making new habitat in previously uninhabitable regions. Tomascik *et al.* (1996) documented a rapid rate of coral community development, dominated by *Acropora*, on the sheltered andesitic lava flow of the 1988 volcanic eruption of Gunung Api, Indonesia. This disturbance provided a complex and initially predator free substrate for acroporids to colonise.

2.5 REEFS IN CRISIS

Coral reefs have been widely documented as offering both substantial economic and scientific value which explains the concern about their widespread global deterioration and being described as in 'crisis' (Hoegh-Guldberg, 1999; Carpenter *et al.*, 2008). The dramatic increase in coral mortality and reef degradation over the last 20-50 years is believed to be result of a complex interplay of environmental stresses, both natural and anthropogenic (Pandolfi *et al.*, 2003). By 1998, it is believed 11% of the world's reefs had been destroyed by human activity, with a further 16% being destroyed by the coral bleaching during 1997-1998 (Wilkinson 2000, 2002). In addition to the worldwide reef crisis, individual reefs and regions have exhibited extreme and varied responses to a variety of stresses. At present, an estimated 30% of reefs are already severely damaged and close to 60% are predicted to be lost by 2030 (Wilkinson, 2002). The conservation status of 845 zooxanthellate reef-building coral species was assessed by using International Union for Conservation of Nature Red List Criteria (Carpenter *et al.*, 2008). Of the 704 species that could be assigned conservation status, 32.8% are in categories with elevated risk of extinction. Declines in abundance are associated with bleaching and diseases driven by elevated sea surface temperatures, with extinction risk further exacerbated by local-scale anthropogenic disturbances. The proportion of corals threatened with extinction has increased dramatically in recent decades and exceeds that of most terrestrial groups.

The Caribbean region has been significantly hit by this combination of both natural and human disturbances. Gardner *et al.* (2003) recorded that this region shows massive region-wide decline, with a reduction of 80% in the last three decades of coral cover, from 50% to around 10%. The Caribbean has the largest proportion of corals in high extinction risk categories (Carpenter *et al.*, 2008). This has been accompanied by a dramatic phase shift to an ecosystem dominated by macroalgae (Hughes, 1994; Szmant, 2002).

The Great Barrier Reef, the largest continuous coral reef in the world (2100km, Hoegh-Guldberg, 1999) and commonly regarded as the closet to 'pristine', is showing system-wide decline. A combination of terrestrial runoff, over-harvesting and climate change are contributing to its degradation. Modern management of the Great Barrier Reef began in 1975 with the establishment of the Great Barrier Reef Marine Park Authority, which protected 5% of the park from fishing, now increased 33% in 2004

(Bellwood *et al*., 2004). Since 1990, coral growth in the Great Barrier Reef has slowed to the most sluggish rate in the past 400 years. Research indicates that calcification, or the deposit of calcium carbonate, by these corals has declined by 13.3% throughout the Reef since 1990, and that such a decline is unprecedented in at least the past 400 years.

Acropora plays a significant role in reefal ecosystems worldwide contributing to the structural and functional integrity of these systems. The characteristic elevated calcium carbonate rates and branching morphology make *Acropora* a fundamental genus to reef accretion and framework construction, providing habitat and food for marine ecosystems, as well as protection for coastal areas (Wallace, 1999; Aronson and Precht, 2001). The decline of the genus worldwide has led to acroporid species (*Acropora palmata, A. cervicornis* and *A. prolifera*, a hybrid of *A. palmata* and *A. cervicornis*; Vollmer and Palumbi, 2002) being designated as candidates under the Endangered Species Act (Diaz-Soltero, 1999). Disturbances of various types have been invoked to explain the changing face of worldwide coral ecosystems and the mass mortality of acroporids.

2.6 CLIMATIC AND ENVIRONMENTAL CHANGE

Since the late nineteenth century, the Earth's average temperature has risen by 0.4-0.8°C and this is largely attributed to the concurrent increase in greenhouse gas concentrations (Buddemeier *et al*., 2004). If this current trend persists, atmospheric CO_2 levels are projected to rise from preindustrial values of ~250ppm to ~700ppm by 2100 (Houghton, 2001; Fig. 2.7). These projected changes will undoubtedly affect corals both directly, through alteration of seawater chemistry (Kleypas *et al*., 1999; Feely *et al*., 2004) and indirectly, through increased atmospheric temperatures. During the twentieth century increasing atmospheric CO_2 has driven an increase in average sea surface temperature by 0.74°C, sea level by 17 cm, depleted carbonate concentrations by ~30 μmol kg^{-1} and increase in acidity by 0.1 pH unit (Solomon, 2007).

VARIABLE	**OBSERVED**		**PROJECTED**	
	1880	**2000**	**2050**	**2100**
CO_2 (ppmv)	280	367	463-623	478-1099
Global mean temperature (°C)				~+1.0-3.0
Sea level (m)		+0.07-0.15	+0.05-0.32	+0.09-0.88

Figure 2.7. IPCC global average climate change observations and projections (Buddemeier, 2004)

The following is a summary of both the chronic and acute stresses on the coral reef community caused by the present and predicted global climate changed outlined above, and also a wide range of environmental, non climatic factors, which have the potential to stress coral reefs.

2.7 CLIMATIC STRESSES TO CORAL REEFS

Despite the recent attempts to control escalating atmospheric carbon levels, it is predicted that they will continue to increase beyond 2100. It is projected to reach two times the preindustrial levels of about 270ppm by the year 2070, and approximately 700ppm by 2100. Translation of the expected global warming (about 2°C by 2100) into regional sea-surface temperature (SST) is difficult because of uncertainty about the physical controls on tropical SST but outcomes probably include: a. poleward movement of the isotherms currently associated with coral reef distributions, b. some rise in mean SST within the present tropical-subtropical latitude ranges, c. some further degradation of coral communities by local-to-regional episodes of higher temperature. Predicted rates of sea-level rise (15-95cm by 2100) are well within ranges in the geological past and measurements of accretion rates for unstressed reefs. However, combined effects of decreased calcification rates and other stresses may diminish the ability of reefs to keep up with rising sea level. Changes in atmospheric CO_2 are predicted to significantly change the carbon chemistry of surface ocean waters, especially decreasing pH and carbonate ion concentration, which will resultantly reduce the calcium carbonate saturation state.

2.7.1 Coral bleaching

Over the last 100 years, the Earths climate has increased by 0.6°C with main periods between 1910-1945, and from 1976. Six periods of mass coral extinction have occurred since 1979 and incidence is increasing in frequency and intensity (Walther *et al.*, 2002). The most severe event in 1998 resulted in the loss of 16% of the world’s reef building corals. This global bleaching event had major effects in the Arabian/Persian Gulf, Eastern Africa and throughout the Indian Ocean, in Southeast Asia, parts of western Pacific and the Caribbean and Atlantic region (Wilkinson, 2004).

The phenomenon of coral bleaching was first described by Glynn, 1984, and results in depressed growth and increased mortality. Symbiodinium cells are generally intracellular, located in the endoderm, and their elimination arises either from expulsion from the cell or the accompanied cell death (Douglas, 2003). The resultant whitening of corals appears to the naked eye when 70-90% of the algae are lost (Fitt *et al.*, 2000).

Specifically to the genus *Acropora*, fast growing branching corals are recognised as the most susceptible to bleaching and consequently suffer rapid bleaching and high mortality (Baird and Marshall, 2002). Hoegh-Guldberg and Salvat (1995) showed mass bleaching events have been occurring every 3 to 4 years since 1979 in Moorea, French Plynesia with *Acropora* spp. showing the most affected with severe bleaching (89-100% of colonies completely bleached). Although the genus is widely shown to be highly susceptible to bleaching it is also described as a genus displaying the ability to adapt and change thermal tolerance to bleaching events. Maynaerd *et al*. (2008) showed that the genus, along with branching *Pocillopora* and *Porites,* increased in thermal tolerance following the 1998 mass bleaching on the Great Barrier Reef. In the subsequent bleaching event of 2002 affecting the area, *Acropora* previously described as the most susceptible to thermal stress showed the greatest increase in tolerance. Other studies describing an increase in thermal tolerance between bleaching events include those from the Galapagos Islands (Podesta and Glynn, 2001) and on Costa Rican reefs (Jimenez *et al.*, 2001).

There are multiple possible mechanisms for this adaptive nature providing resistance and protection to increased temperature and light. Coles and Brown (2003) summarised these to include inducible heat shock proteins that act in refolding denatured cellular and structural proteins, production of oxidative enzymes that inactivate harmful oxygen radicals, fluorescent coral pigments that both reflect and dissipate light energy, and phenotypic adaptations of zooxanthellae and adaptive shifts in their populations at higher temperatures. Berkelmans and van Oppen (2006) showed in laboratory experiments that by shuffling existing types of symbiont already present in coral tissues to symbiont type D, *Acropora millepora* could increase its level of tolerance by around 1-1.5ºC. Thus the genus has been shown to have the ability to thermally acclimatise.

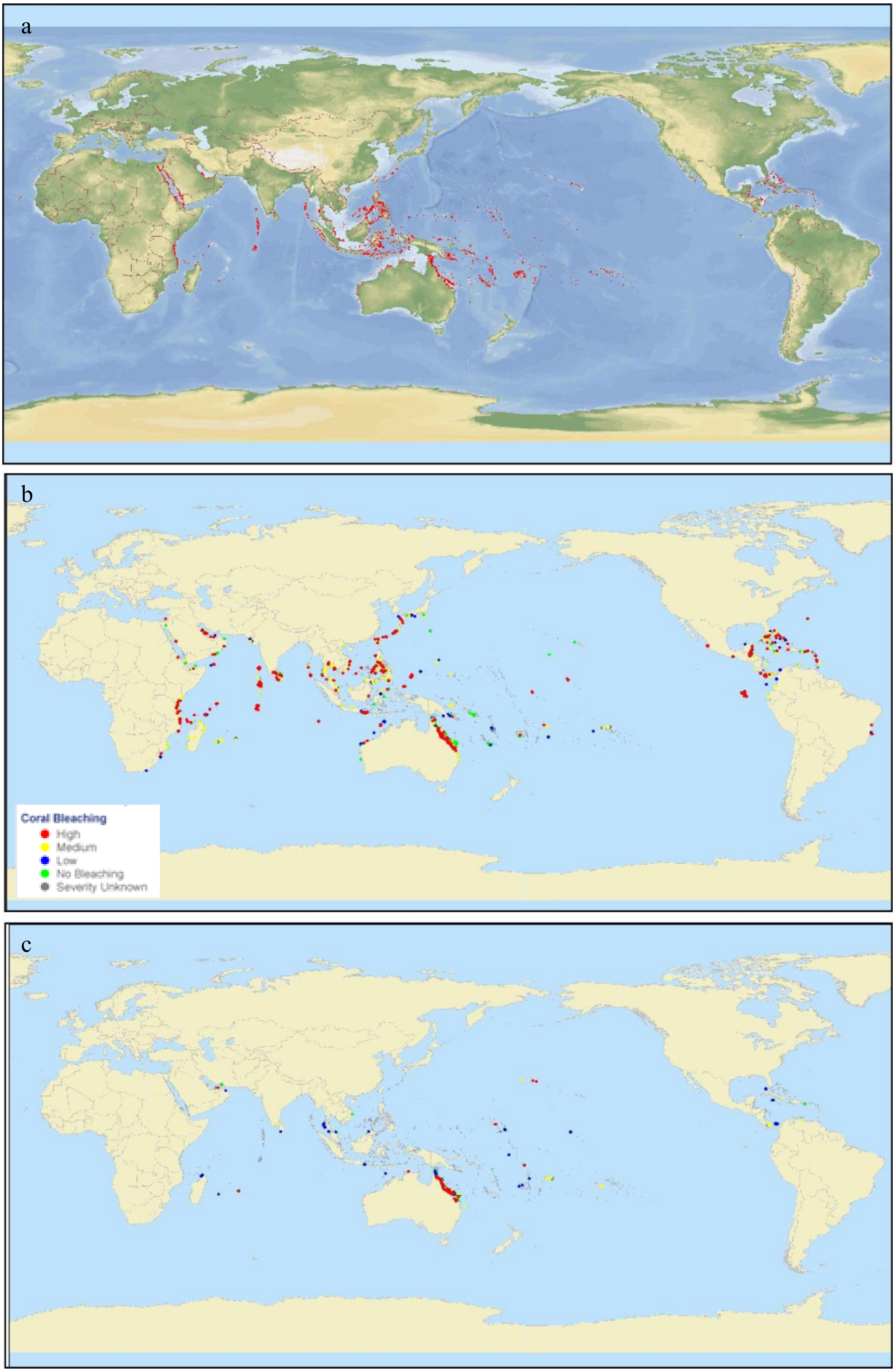


Figure 2.8. a. Distribution of coral reefs worldwide, b. Levels of coral bleaching in 1989, c. Levels of coral bleaching in 2002 event (maps generated in ReefGIS, ReefBase).

Bleaching is driven by a variety of mechanisms, but primarily by elevated sea water temperature resulting from global climatic warming (Brown, 1997). Triggers include extreme temperature, high irradiance, prolonged darkness, heavy metals flux and pathogenic micro-organisms (Brown, 2001; Rosenberg and Ben-Haim, 2002). Frequent or severe bleaching results in reduced growth and reproductive capacity, and disease resistance (Hoegh-Guldberg, 1999).

Future estimates suggest coral bleaching of reefs worldwide could become annual or biannual by 30-50 years if there is no increase in the thermal tolerance of corals (Brown, 1997). The ability for corals to survive these projected global warming trends, and extreme events, will depend on their ability to adapt and acclimatise. Tansplant experiments by Baker (2001) have supported the view that bleaching might offer a high-risk ecological opportunity for reef corals to get rid of suboptimum algae and acquire new symbiotic algal partners. This ecological gamble is supported by the ability of some corals to associate with a range of zooxanthella types (Rowan, 1995; van Oppen *et al.*, 2001). Traditionally, it has been thought that corals are associated with a single zooxanthellae type but it now appears that they can also be associated with several symbiont types simultaneously. Studies on the Great Barrier Reef indicate that coral colonies are dominated by one type of symbiont with additional low background levels of another (Ulstrup and van Oppen, 2003). Research suggests that corals with clade D symbionts are more resilient than some species with clade C symbionts (Glynn *et al.*, 2001; Rowan, 2004). If subjected to repeat bleaching, corals harbour more clade D-type symbionts (Baker *et al.*, 2004).

Particularly significant to this thesis is that recent monitoring of natural bleaching events reveals interspecific and intraspecific variation in the degree of bleaching. Branching forms exhibited by many *Acropora* species, generally bleach more strongly than massive corals (McClanahan *et al.*, 2001). Susceptible taxa are often numerically dominant in reefal ecosystems and therefore as a resulting of mass mortality due to bleaching there is a large loss in total coral cover (McClanahan *et al.*, 2001).

2.7.2 Global warming and reef distribution

The global latitudinal limit of reef building corals appears primarily restricted by an annual minimum temperature of 18°C (Kleypas, 1999). Historically, changing distributions of reef building corals in response to climate change have been demonstrated off the east coast of Florida. Following the warmer periods of the early-middle Holocene to present, the distribution of the dominant reef building coral, *Acropora*, has been shown to contract due to global climatic cooling (Precht and Aronson, 2004).

Around 18°C, sea surface temperature gradients are very steep and therefore the coupled doubling of CO_2 and climatic warming will only cause the 18°C contour to shift poleward by a few hundreds of kilometers (Kleypas, 2001). The latitudinal distribution of these reef building corals will also be restricted by other factors such as light availability and reef building maybe temporarily suppressed by elements of the changed climate (e.g. recurrence of temperature anomalies, changes in aragonite saturation state).

2.7.3 Reduced calcification

Changes in atmospheric CO_2 are predicted to significantly change the carbon chemistry of surface ocean waters, especially decreasing pH and carbonate ion concentration, which will reduce the calcium carbonate saturation state. One third of all anthropogenic CO_2 inputted into the atmosphere is absorbed by the ocean (Houghton *et al*., 2001). Resulting from projected increases in atmospheric CO_2 there will be a reduction in ocean pH, hence a reduction in carbonate ion concentrations, leading to a decrease in skeletal deposition (Caldeira and Wickett, 2003). Since the industrial revolution, atmospheric CO2 has increased by 31%, a level which has no been seen for the last 420,000 years (Petit *et al*., 1999), and probably not for the last 24 million years (Pearson and Palmer, 2000). The rate of increase of CO_2 concentration has been about 0.4% per year over the last two decades (Houghton *et al*., 2001). Laboratory experiments suggest a doubling in atmospheric CO_2 will decrease coral calcification and growth rates by 11-40% (Gattuso *et al*., 1999; Langdon, 2002; Reynaud *et al*., 2003), following an estimated decrease in reef calcification of 6-14% from preindustrial atmospheric CO2 level of 280ppmv to present day 370ppmv (Kleypas, 1999). These reduced growth rates will lead to a reduced resilience to other stresses including erosion. Overall the picture is of the negative effects of increased atmospheric levels of CO_2 but some corals are showing a level of resilience. Massive *Porites* corals have increased their calcification rates in response to the increased sea surface temperatures, and are not responding yet, to the decreased carbonate ion concentrations (Lough and Barnes, 2000).

2.7.4 Sea level

Predicted rates of sea-level rise (15-95 centimetres by 2100; Houghton *et al*., 2001) are well within geological ranges and measurements of accretionary rates for unstressed reefs (Smith and Buddemeier, 1992; Houghton *et al*., 2001). However, decreased calcification rates, combined with other stresses, may diminish the ability of reefs to keep up with rising sea level.

An understanding of the environmental requirements of the genus *Acropora* has been key to reconstructing historical sea level changes. Lighty *et al*. (1982) showed that due to its restricted depth range *Acropora palmata* the species is a reliable reference for reconstructing the history of Quaternary sea level change. Blanchon and Shaw (1995) described *Acropora palmata* reefs from the Caribbean-Atlantic region documenting three catastrophic sea-level–rise events during the last deglaciation. During Holocene sea level changes, variation in coral community and reef growth rates were driven principally by increasing water agitation due to the decrease in accommodation space (Montaggioni and Faure, 1997). Miller (2002) proposes although the geological history of *Acropora* spp suggests coral reef formation under high sea-level conditions has successfully occurred without the genus, it is clear that the predicted absence of these species will severely compromise the ability of reefs to survive anticipated sea level rise.

2.7.5 ENSO and extreme weather

Extreme temperature events have been increasing in both frequency and severity since the beginning of the twentieth century when records began (Parmesan, 2006). Particularly strong was the 1997-1998 El Nino which caused bleaching in every ocean. Regionally extreme events can result in coastal reef environments having greater incidences of high turbidity, nutrient loading and other pollution episodes. There are also predicted significant changes in ENSO and tropical cyclone climatology, although present research does not show a clear consistent picture. Tropical cyclones are predicted to increase in intensity by 10-20% by 2070, with a possible poleward extension of storm tracks and an increase in surface winds by 3-10% (Knutson *et al*., 2001; Knutson and Tuleya, 2004).

Disturbance events such as strong winter cold fronts and hurricanes have been seen to result in the mortality of *Acropora* communities. Largely as a result of the branching morphology and shallow water habitats, the genus is particularly susceptible to these disturbances. However, the ability for rapid growth rates and asexual reproduction following fragmentation is beneficial in recovery from these events. In the Dry Tortugas 1978 cold water event there was extensive mortality of the genus (Jaap *et al*., 2008).

A single event, such as extreme weather can result in multiple stressers on a coral community. Hurricane Allen in 1980, Jamaica caused extensive damage to the branching coral cover. Hughes and Connell (1999) described how corallivores out survived their prey and therefore led to the further demise of these corals.

Storms damage corals both directly through wave action but also indirectly through light attenuation by suspended sediment and abrasion by sediment and broken coral. Gardner *et al*. (2005) showed that coral cover on Caribbean reefs from 1977-2001 decreased by 17% on average in the year following a hurricane, with no recovery for at least 8 years post-impact.

2.7.6 Ocean circulation

Changes in the thermohaline circulation are poorly understood and difficult to assess. Circulation, both at local wind driven and global thermohaline, is intrinsically linked and will change with predicted climate change. Lund *et al*. (2006) suggested the Gulf Stream weakens with cooling and strengthens with warming, having been weakest (by ~10%) during the Little Ice Age and strongest during 1,000-1,100 yr BP, the Medieval Warm Period. Modelling has suggested a 30-40% reduction of the thermohaline circulation by the end of this century (Gent, 2001). Research has predicted an outcome of future slowdown or shutdown of the thermohaline circulation such as an increase in major floods and storms, a collapse of plankton stocks, warming or rainfall changes in the tropics or Alaska and Antarctica (including those from intensified El Niño effect), more frequent and intense El Niño events, or an oceanic anoxic event. (Schiermeier, 2006).

2.8 NON CLIMATIC EVENTS

2.8.1 Disease

Disease epidemics are a serious threat to coral reefs worldwide (Epstein *et al*., 1998; Harvell *et al*., 1999; Rosenberg and Ben-Haim, 2002). Widespread disease has been described as a major contributor to the decline of coral communities associated with pathogens including bacteria, cyanobacteria, fungi, and protists and with abiotic stressors including elevated seawater temperature, sedimentation, eutrophication, and pollution (reviewed by Sutherland *et al*., 2004). With the degradation of corals due to increased sea surface temperatures, resulting stressed and bleached corals are more susceptible to disease. Human activity is believed to at least be partly responsible for recent outbreaks (Wilkinson, 2004).

The Caribbean region has been described as a disease 'hot spot' (sensu Weil *et al*., 2006) due to the frequency of epizootic events, geographic distribution and the range of hosts which results in significant mortalities (Green and Bruckner, 2000). In contrast, in the Indo-Pacific relatively few events are reported with limited geographical range however the number appears to be increasing (Weil *et al*., 2006) (affect more than 150 species of Caribbean and Indo-Pacific corals; and new diseases are being added to the 29 described diseases; Sutherland *et al*., 2004). Regionally, in the Caribbean two specific outbreaks of disease have had a major impact on *Acropora*-dominated reefs (Richardson and Aronson, 2002). In the early 1980's a disease, carried by ocean currents, killed ~95% of long black-spined sea urchins, *Diadema antillarum* (Lessios, 1988). The loss of this herbivore resulted in the switch from coral-dominated to seaweed-dominated surfaces (Buddemeier, 2004).

The potential for disease outbreaks to impact coral reef ecosystems has been shown by acroporid corals. In the 1980s and 90s, the major reef building corals of the Caribbean region, *Acropora cervicornis* and *A. palmata,* were affected by white band disease causing unprecedented changes in Caribbean reefs community structure, and candidacy of these species for listing under the Endangered Species Act (Aronson and Precht, 2001). White pox disease (also termed acroporid serratiosis, Patterson *et al*., 2002, and patchyhecrosis, Bruckner and Bruckner, 1997) was first documented on the Keywest Florida in 1996 (Holden, 1996). The disease is seen exclusively affecting *Acropora palmata* throughout the Caribbean characterised by white patches or lesions. The disease is highly contagious as shown by the rapid spread of the disease on reefs of the Florida Key National Marine Sanctuary in the 1990's (Patterson *et al*., 2002). Shinn *et al*. (2000), first proposed a link between both African and Asian dust and temperature being associated with coral disease outbreaks, yet firm connections still has to be established (Shinn *et al*.2000; Garrison *et al*., 2003).

As a result of disease outbreaks, reduced growth rates have been observed in reef corals resulting in a reduced capacity to keep up with predicted sea level rises (Aronson and Precht, 2001). Socioeconomically, this reduced growth of reefs can affect their ability to protect shorelines and additionally the degradation of the reefal ecosystem can lead to a loss of resources including fisheries.

2.8.2 Predator plagues, invasive species and corallivores

Invertebrate corallivores have been largely recognised in the Pacific with echinoderms such as *Acanthaster planci* and *Eucidaris thouarsii*. Crown-of-thorns starfish (COTS; *Acanthaster planci*), are believed to have been initiated and exacerbated by human factors including over-fishing and nutrient runoff from land promoting the planktonic stages of the starfish. Outbreaks are also influenced by natural factors including river floods in wet years. The highest densities of COTS in recent years have been in Tanzania, Kenya, and on the Great Barrier Reef (Carpenter, 1997; Wilkinson, 2004). Recovery rates to COTS outbreaks are species-specific and therefore results in shifts in community structure. COTS feeds on several common species of hard coral, particularly *Acropora* spp., showing a clear preference for tabular forms and those corals that are least well defended (De'ath and Moran, 1998; Pratchett, 2001). Corallivorous gastropods such as *Drupella spp*. in the Indo-Pacific and *Coralliophila abbreviate* in the Caribbean have been seen affecting corals.

Invasion of non-native species is both ecologically damaging and economically costly. Human activity such as ballast water exchange from cargo ships and aquarium related incidents with imported individuals being introduced into the wild. For example, a species of lionfish (*Pterois volitans*) common to the Indo-Pacific regions that was thought to have been introduced from a home aquarium in 1992 has established populations all along the southeastern coast of the United States of America and for reef areas, it is now quite common in Bermuda (Whitfield *et al*., 2002).

Degrading reefs have been shown undergo a 'phase shift' where the abundance of corals decline and there is a transition to macroalgae dominance (Jamaica, Idjadi *et al*., 2006; Indo-Pacific, Bruno and Selig, 2007; GBR, Hughes *et al*, 2007; Belize, Bruno *et al*., 2009). In the Caribbean region a reduction of up to 98% live coral cover has been recorded (reviewed by Bruno *at al*., 2009 and Miller *et al*., 2002) believed to be due to both reduced herbivory and increased nutrient input. For example, following the 1980 collapse of *Acropora* communities in Belize relating to white band disease, macroalgal abundance increased by 300 and 1200% respectively at Glover reefs Atoll and Carrie Bow Cay respectively (Vargas-Angel *et al*., 2003). These phase shifts in coral communities to macroalgal dominated communities, and a reduction in coral reef accretion, have resulted in the exclusion of coral larvae from settlement areas by macroalgae (Hughes *et al*., 2007)

2.8.3 Over-fishing

Over 4,000 species of fishes (>25% of all marine fishes) inhabit shallow coral reefs (Spalding *et al*., 2001), along with a large number of marine plants and invertebrates, many of which are exploited for human use. The removal of resources and over-fishing of coral reef ecosystems is often accompanied by destructive fishing practices, such as bomb fishing and cyanide which can permanently damage and ultimately lead to the death of corals. Bryant *et al*. (1998) estimated over-fishing as a medium to high threat to over 38% of the world's reefs. Components of the reef ecosystem are also removed for souvenirs and decorations, primarily as part of the tourist and aquarium trade. Unsustainable fishing has lead to a reduction in fish populations and overexploitation of reef fishes is possible due to their relatively slow growth rates, late maturity and irregular recruitment.

In Belize, since the 1980s, low levels of herbivory have been attributed to overfishing of herbivorous fishes (McClanahan and Muthiga, 1998). This has resulted in a change from *Acropora*-dominated coral ecosystems to fleshy algal dominance over the past two decades.

2.8.4 Sediment and nutrient loading

Sediment interferes with feeding of polyps and costs the colonies energy to remove. Rapid and prolonged sediment loading can be fatal if corals cannot shed sediment fast enough, with increased suspended sediment there is increased turbidity and reduced light penetrating the water column. The negative effects of the accumulation of sediments on corals can be exacerbated by wave action that repeatedly resuspends sediments into the water column (Rogers, 1990; Rice and Hunter, 1992).

Through their algal symbiosis corals can thrive in nutrient poor tropical oceans. Reefs are damaged by excess nutrients (eutrophication) that favour the growth of macro-algae especially when the populations of grazing fishes and sea urchins are reduced. Increased phytoplankton growth in seawater reduces light energy penetration, adversely to the light-dependent corals, favours the growth of other competitors of corals, especially those that bore into coral skeletons, such as sponges, molluscs, worms and burrowing algae, and probably make corals more susceptible to disease (Wilkinson, 2004). All reefs near human populations or adjacent to large land masses suffer degradation from nutrient pollution. Crabbe and Smith (2005) tested the influence of high sedimentation rates, resulting from high human activity, on coral growth of *Acropora valeniennesi* corals from fringing reefs of Sulawesi, Indonesia. Branching angle measurements of *Acropora valenciennesi* indicates that during higher sedimentation rates, and consequent lowered light levels, result in nearly vertical earlier on in its colony development.

Nutrient input, sedimentation, and runoff have also been implicated as potential contributing factors in the initiation and elevated virulence of a disease, although few quantitative data have been published (Bruckner *et al*., 1997; Harvell *et al*., 1999; Kim and Harvell, 2002; Richardson and Aronson, 2000).

2.9 MULTIPLE STRESSORS AND RECOVERY OF *ACROPORA* COMMUNITIES

For many *Acropora* dominated ecosystems their decline worldwide can be attributed to a wide variety of factors acting both simultaneously and subsequently. In the Caribbean *Acropora palmata* and *A. cervicornis* have been recognised as the primary reefal framework builders forming a generalised zonation pattern also seen in the Pleistocene and Holocene (Hubbard, 1988; Aronson and Precht, 2001; Precht and Miller, 2007). However, by the 1980's Aronson and Precht described how this pattern with *Acropora* dominating coral reefs had disappeared. This transition has fundamentally been driven by mass coral mortality, particularly of *Acropora*. Miller *et al*. (2002) described the widespread decline of *Acropora palmata* and *A. cervicornis*, 93% and 98% respectively over the last 30 years in the Florida Keys. This has been attributed to, but not exclusive to, storms, disease, mass bleaching, water quality decline and physical damage caused by ship grounding. Boward County, in 2002, showed evidence of white band disease, predation by the corallivous worm *Hermodice carunculata*, and a series of Hurricanes (including Irene, 1999, and Katrina, 2005).

The widespread and prolific coral mortalities resulting from many interacting factors has resulted in a significant change in the function and structure of global coral reefs (Bruckner *et al*., 2002; Weil *et al*., 2006). The ability of *Acropora* communities to recover from these multiple stressors has been aided by the ability of the genus for rapid growth and asexual reproductive strategy following fragmentation. However, Knowlton (2001) suggested that the rarity of *Acropora*, specifically in the Caribbean, has resulted in the genus experiencing an Allee effect (low populations demise and therefore colonies are too far apart leading to reproductive failure).

There is evidence, at all scales and from a wide range of sources (geological and biological; field, laboratory and aquarium; theoretical and experimental), that corals as a group of organisms possess a wide range of adaptive and acclimative mechanisms, and that most of these mechanisms appear relatively robust and/or resilient in the face of stress. Coral community structure is dynamic on scales of years to centuries, and this dynamism may provide long-term resilience (or community adaptation) in response to stresses, including global environmental change. However, the unprecedented variety, rates and magnitudes of chronic anthropogenic alterations of modern reef environments may undermine this resilience.

2.10 LESSONS FROM THE PAST; HISTORICAL VIEW OF CORALS IN CRISIS

Reefs and other shallow-shelf carbonates are considered as good tracers of the ancient tropics and subtropics (Ziegler *et al*., 1984), and the latitudinal range of reefs is commonly thought to indicate palaeoclimate (Frakes *et al*., 1992; Johnson *et al*., 1996). Reefs changed substantially in abundance, composition, palaeogeographic distribution, geometric attributes and biodiversity during their geological history. Biological controls appear to either buffer the reef system or to amplify the responses to global change on timescales of millions of years (Kiessling, 2005).

2.10.1 Phanerozoic environmental change

Phanerozoic rates and magnitudes of environmental change have controlled reef building and decline over geological timescales. The mineralogy of inorganically precipitated calcium carbonate has switched between calcite and aragonite with three periods of 'aragonite' seas and two of 'calcite' seas (Sandberg, 1983; Porter, 2010). Aragonite I, Calcite I and Aragonite II are within the Palaeozoic, Calcite II occurred from the Jurassic-Oligocene and Aragonite III began during the Oligocene and remains today. There have been significant changes in the mean salinity of the ocean accompanying a general decline throughout the Phanerozoic. For the Cenozoic pH has been established with a value of 7.4 at the beginning of the Paleogene. In the Miocene pH increased to a peak of 8.3 before declining to the current 8.1 today (Pandolfi and Greenstein, 2007).

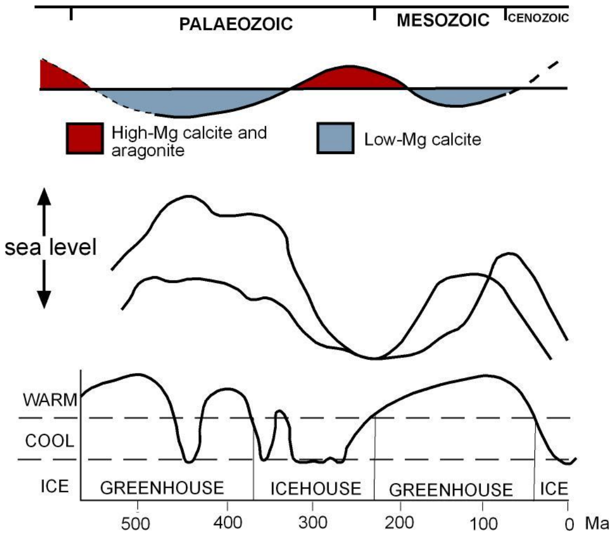


Figure 2.9. Mineralogy of marine abiogenic precipitates through the Phanerozoic compared with sea level change and global ice volumes (from Tucker, 1992).

The Phanerozoic has been divided into various icehouse and greenhouse periods on the basis of the Earth's glacial record (Veevers, 1990; Fig. 2.9). Greenhouse intervals occurred during the early-mid Palaeozoic and between Jurassic-Paleogene time, characterised by high sea levels, rapid sea floor spreading, elevated CO_2 concentrations and elevated sea surface temperatures. In contrast, icehouse intervals were times of lower sea level, continental glaciation, lower concentrations of atmospheric CO_2 and lower sea surface temperatures. Sea level variations of up to 200 meters can accompany transitions of icehouse to greenhouse (Hurley and Fluegman, 2003).

During the early Palaeozoic, atmospheric CO_2 was twenty five times higher than today (Fischer, 1981; Berner and Kothavala, 2001). Near the end Devonian (~360 Ma), the rise of vascular plants led to a large drop (~306 ppv; Robinson, 1991). By 325 Ma, reduction in CO_2 levels sufficiently plunged to result in the onset of an icehouse period which lasted 145 million years into the mid Jurassic. During the late Cretaceous CO_2 levels were five to six times present values, which persisted for 150 million years. Icehouse state began again in the early Oligocene, 33.5 Ma, which continues today (Zachos *et al.*, 1996; Lear *et al.*, 2000).

2.10.2 Phanerozoic reef response

Coral reefs have shaped and dominated ocean ecosystems since the first appearance of scleractinian corals in the fossil record in the mid-Triassic (~240Ma; Veron, 2000; Stanley, 2003). They provide the potential for a long term record of the effect of global climate change. Future increases in atmospheric CO2, and resultant global warming, are expected to exceed the rate and magnitude seen during corals Cenozoic history. However, the geological record does provide a baseline for the interactions and responses of corals and natural environmental change before assessing the impact of anthropogenic stresses.

The oldest known reefs are constructed by microbialites which first appeared ~3.4 Ga and existed as finely layered structures, stromatalites (Walter, 1983; Allwood *et al.*, 2007). During the early Cambrian, the evolution of calcification resulted in the increased morphologic potential of individual organisms and additionally in the physical fabric of benthic communities (Rowland and Gangloff, 1988). During this period heavily calcified structures were preserved when the first biotically diverse metazoan-algal reefs formed subtidally.

The total latitudinal range of reefs increased significantly throughout the Phanerozoic (Kiessling, 2001). The tropical reef zone has often been constricted after mass-extinction events, particularly after the late Early Cambrian, the latest Devonian, the Permian-Triassic, and the Triassic-Jurassic events. Microbial and coralline-sponge reefs occurred in significantly lower latitudes than coral reefs throughout the Phanerozoic, and bryozoan reefs were always more likely to grow in higher palaeolatitudes. Algal reefs tended to become more abundant globally during icehouse intervals. Development of a pronounced high-latitude reef zone is closely linked to climatic cooling. Many extant species records extend to the Pliocene, with some believed to have originated in the Eocene (Rosen, 1984). Best approximation of scleractinian coral extinction rates at the K–T boundary is 30±8% at the genus level (Kiessling and Baron-Szabo, 2004). But corals appear to have benefited from the end-Cretaceous mass extinction. Late Cretaceous shallow tropical shelves were often dominated by rudists, abundant nearly everywhere on carbonate platforms, sometimes forming reefal structures (Johnson *et al.*, 2002). During this period corals were also common, but rarely achieved rock-forming abundance. By the Paleocene corals dominated the global reef factory (Kiessling *et al.*, 1999). Global distributions of rhodalgal facies peaked in the late-early to early-late Miocene and commonly replaced coral-reef environments, accompanied by a decline in other carbonate-producing phototrophs (Halfar and Mutti, 2005). It is believed the dominance of red algae over coral reefs was triggered in the Burdigalian by enhanced trophic resources associated with a global increase in productivity, as evidenced by a long-term shift toward higher carbon isotope values. At times during the Pleistocene and Holocene species extended their latitudinal maximum, altering the coral belt, in response to climatic change. In the late Pleistocene, corals extended up to 500km further south along the west coast of Australia than where they are found today (Playford, 1983). The Pleistocene demonstrates the sensitivity of reef communities with the extinction of two widespread species of Caribbean reef corals, *Pocillopora* cf. *palmata* and a form of the *Montastraea* "*annularis*" species complex, believed to be in response to the sea level drop at the Last Glacial Maximum, resulting in a threshold of habitat reduction, and disruption of coral metapopulation structure (Pandolfi, 1999).

2.11 SUMMARY: THE FUTURE OF CORAL REEFS AND MODERN *ACROPORA* RECORD

Present anthropogenic-induced climate changes, and the negative effects of this on coral distribution and diversity, are widely substantiated. Underlying this are additionally the natural physical controls, seen also in the geological record, including seawater chemistry, sea level, sea surface temperature and global atmospheric CO_2 levels. Here, is summarised the nature and distribution of these factors and the effect they have on the ecology of coral reefs. In particular, the coral *Acropora* is considered a modern environmental indicator genus, vulnerable to anthropogenic and natural induced stress. There are many modern examples of the responses of the genus to both natural and anthropogenic factors.

Two cold-sensitive species *Acropora cervicornis* and *A. palmata*, are the dominant reef-builders of the Caribbean. Precht and Aronson (2004) demonstrated range shifts in this region by the genus, mirroring terrestrial range shifts. In the middle Holocene temperatures were warmer than today (Gagan *et al.*, 1998) which resulted in *Acropora* dominating reefs found as far north as Palm Beach County, on the east coast of Florida. Following this, the northern limit retracted to the Biscayne Bay, south of Miami, believed to be in response to climatic cooling. Despite other stresses placed presently on these two species, their northerly extent has again expanded, coincident with increased sea temperatures now found in the northern Gulf of Mexico. Future poleward shifts of the genus are predicted to be limited by light availability (Hoegh-

Guldberg, 1999), however small range shifts may provide new refugia against future sea surface temperature changes (Parmesan, 2006).

The genus also shows evidence of phase shifts which result from temperature increases and corals being unable to adapt or acclimatise. Typically in this scenario corals are replaced altogether by another organism. In the Caribbean large scale degradation has been seen of the previously dominant reef building species of *Acropora* and a phase shift towards a community dominated by macroalgae. In Jamaica, the effects of over-fishing, hurricane damage, and disease have combined to destroy most corals, whose abundance has declined from more than 50% in the late 1970s to less than 5% today (Hughes, 1994). The resultant dramatic phase shift has occurred, with a system now dominated by fleshy macroalgae of more than 90% cover.

Reef building corals are not all equally sensitive to the influence of increased temperature and may result in a strategy response with hardier species replacing less hardy species. This is already beginning to operate worldwide with different mortality in many reefs (Hoegh-Guldberg and Salvat, 1995) and a decrease in abundance of some species (Glynn and de Weerdt, 1991). For example corals with thicker tissues and more massive forms, e.g. *Porites*, are relatively resistant to temperature stress, and if they do bleach, tend to recover with little or no increase in mortality (Salvat, 1991; Wooldridge *et al*., 2005). In contrast thinner tissued corals, often with branching forms, like *Acropora* exhibit a greater sensitivity to low level or chronic bleaching events (Glynn, 1993; Loya *et al*., 2001).

The thermal threshold of corals to withstand high temperature stress, and resultant bleaching, varies geographically with corals closer to the equator having thermal thresholds for bleaching as high as 31ºC while those at higher latitudes may bleach at 26ºC (Jokiel, 2004). Additionally to geographical location and growth forms, the potential for corals to adapt and acclimatise is dependent on acquiring increased thermal tolerance as a result of changing the dominant symbiont type within their tissues from *Symbiodinium* type C to D. Berkelmans and van Oppen (2006) showed that by shuffling existing types of symbiont already present in coral tissues to symbiont type D, *Acropora millepora* could increase its level of tolerance by around 1-1.5ºC. Thus the genus has been shown to have the ability to thermally acclimatise.

Coral diseases have the potential to threaten biodiversity and shift the structure of reef communities by diminishing their resilience to physical factors. In the Caribbean region outbreaks of coral disease have resulted in massive losses of corals, particularly of species of *Acropora* in the 1970s and 80s. For example in Belize, until the 1980s *Acropora cervicornis* was the dominant species when white band disease resulted in the complete mortality of the species (Aronson and Precht, 1997). *Agaricia tenuifolia* quickly replaced *Acropora cervicornis* in the early 1990s but was wiped out by increased water temperatures of 1998. In the Florida Keys, white pox disease has decimated *Acropora palmata* with losses of living corals typically in excess of 70% (Patterson *et al*., 2002).

Evidence seen today and in the Quaternary record of the genus, *Acropora,* shows it to be responding to environmental change. Some traits of the genus such as *fast growth rates*, *dominant symbiont adaptation*, to increase thermal tolerance, and *morphological variation*, to withstand changes in the hydraulic regime, indicate that this genus shows resistance to change. However other traits, such as its *susceptibility to diseases* and *thin tissue structure*, make the genus more vulnerable to bleaching events, implying that the genus is relatively less tolerant to environmental change. Hence, based on the modern record the future of the genus remains inconclusive.

Some of the physical changes which are projected to occur, have occurred repeatedly in the geological past. Reefs may have diminished in response to these changes but have often rebounded. This offers us hope for the present day worldwide deterioration of coral reefs. Acclimative and adaptive responses which are being acquired by modern coral communities must have been used in the geological record. Hence data on the past response of marine ecosystems to climate change have become increasingly relevant. The major difference at present and for future predictions is the unprecedented affect of human activity on these ecosystems. However understanding corals ecological response to global climate change in the geological record, and understanding the levels of anthropogenically induced change and the responses of coral reefs, will undoubtedly help to understand the future of coral reefs.

CHAPTER 3. GLOBAL DISTRIBUTION OF *ACROPORA* IN THE FOSSIL RECORD

CONTENT

This chapter aims to reconstruct the Cenozoic history of the genus, *Acropora*. The principal aim of this chapter is to test hypotheses relating to the effect of major physical-environmental perturbations on the distribution and diversity of the genus *Acropora* throughout its fossil record.

3.1 INTRODUCTION

There is widespread concern about recent deterioration of living reef corals and tropical reefs. Much of this is related to coral bleaching which has had destructive effects on about 25% of the world's coral reefs over the last decade (see Chapter 2). Global warming appears to be the underlying cause of this. However, predictions of future responses of reefs to global warming lack data from the past on how reef organisms have responded to ancient climate changes. The ancient record of corals, and reefs, shows that reef coral distributions in particular are highly sensitive to climatic patterns, modulated by availability of suitable habitats. So far however, research emphasis has been on statistical and biogeographical syntheses whereas the history of individual taxa would be expected to provide higher resolution data to test hypotheses on the effects of warming. *Acropora* (Paleocene-Recent) is a highly suitable exemplar genus for such a study as it has the largest number of living species (c.120) of any extant reef coral genus and today occupies a narrow ecological niche on tropical reefs (Wallace, 1999).

Overall this work aims to reconstruct the Cenozoic history of this genus. Firstly, this chapter will give an overview of fossil *Acropora* records and hence clarify patterns of evolutionary change of the genus throughout its record, primarily regulated by environmental change, and the effect of habitat fragmentation through regional and global tectonics. The principal aim of this chapter is to test hypotheses relating to the effect of major physical-environmental perturbations on the distribution and diversity of the genus *Acropora* throughout its fossil record. Ultimately this is hoped to reveal a greater understanding of possible future responses of this coral genus, and their associated ecosystems, to future climatic perturbations and other anthropogenic global change.

Digital databases provide an essential tool for investigating large-scale spatial and temporal palaeontological questions in the Earth Sciences. The *Acropora* database presented here is an electronic database documenting the Cenozoic distribution of *Acropora* records worldwide. It has been developed within a series of interlinked spreadsheets. The primary purpose of this database is to describe and investigate the evolution of the genus in relation to palaeoclimate and tectonic changes. Using both graphical representation, through 'Boucotgrams' (see section 3.3.3), the mapping capabilities of Geographic Information System (GIS), and statistical analysis, the distribution of the genus and individual species has been documented for the fossil record.

3.2 BACKGROUND

Palaeontological collections offer an extensive amount of data on the spatial and temporal changes, taxonomic information, and biotic occurrences through the geological record. On the global scale, palaeontologists have focused much research on questions relating to global diversity estimations and macroevolutionary issues. Much of this work is based on compilation of taxonomic databases that can be used to investigate changes in diversity, biotic composition, and origination and diversity dynamics (Sepkoski *et al*., 1981). Global diversity curves have been used to exhibit trends and aid analysis. Most famous of these compilations, summarising the history of biodiversity on the global scale, is Sepkoski's (1981) genus level compendium, the goal of which was to estimate global origination rates and assess key periods of mass extinction and origination. Since this research, many subsequent databases have followed, which are largely web-based, with many analysing global- regional- and local-scale dynamics. Various authors have worked on summarising biotic macroevoltionary changes (i.e. Benton, 1995, paleobiology database) and in particular within the marine record of the geological record (i.e. Valentine, 1969; Sepkoski, 2002; Stanley, 2007; Alroy *et al*., 2008). Typically diversity curves from these assessments show changes through the geological record which have usually been based on literature sources. As well as palaeontological records being tackled in their entirety, focussed studies of selected classes, families and group of taxa have also been databased (Dinobase, Tetrapods, Neptune, Brachiopod World Database, fosFARbase). Additionally, some work has been within limited spatial (Alaskia Paleontological Database, Austrofossil) and temporally focused subjects, or a combination of a spatial and temporal restriction (Mesozoic Fish Reference, MIOMAP, GONIAT). Furthermore, museum based collections are also summarised through databases (Yale Peabody Musuem, PaleoBase, UCMP). Particular to corals, the Neogene Marine Biota of Tropical America (NMITA) is a web-based taxonomic database containing data that has been used to analyse Tropical American biodiversity over the past 25 million years (Budd *et al*., 2001) and for assessing the state of modern coral reefs there is the World Atlas of Coral Reefs which provides new global estimates for coral reefs world-wide and presents reef area estimates.

Attempts at summarising diversity on a global, regional and local scales such as the Sepskoski curve have recently come under attack questioning the robustness of their records along with, for similar reasons, compilations both spatial and temporally more restricted, as outlined above. Analysis now indicates that, if not rigorously assessed, the fossil record may provide a misleading signal of biodiversity changes throughout the geological record.

An important issue first outlined by Raup (1972, 1976) was an obstacle called the 'rock problem'. It has been widely recognised that different geological periods yield different numbers of fossils principally due to the different amounts and types of sedimentary rock being formed. Additionally, a palaeolatitudinal sampling bias of these fossils is affected by a skew of onshore rocks being preserved in the northern hemisphere affecting the collecting opportunity. Other issues include historical, political and economic factors which have also produced a bias towards collecting from the northern hemisphere, in particular to records from western Europe and northern America, where fossil collecting has been much more extensive and for longer. Throughout this work, collections have shown that regions such as Southeast Asia are under-sampled, and have preservational issues, and a lack of recent work on collections and publications. Furthermore, publications relating to the fossil content of this area are often non Anglophone and date well back into the nineteenth century. In relation to the wealth of databases outlined above, many of these are worked on by multiple authors which can produce a lack of clarity in standardisation, particularly with respect to taxonomy and stratigraphy. In relation to taxonomy, the 'monographic effect' (Raup and Boyajian, 1988) also causes problems due to the effect of periodic taxonomic revision. Another problem is that these records are often based on both specimen and literature based records with no transparency or distinction between the two.

What follows is what is believed to be the first attempt to follow the distribution and ecological record of one individual coral genus through its geological record. Issues such as those due to collecting and preservational bias are assessed and wherever possible taken into account. Taxonomy and stratigraphy are brought into line with current classifications with a clear distinction being made between specimen- and literature-based records.

3.3 METHODOLOGY

3.3.1 Database methodology

Database outline

Records of the location and occurrence of *Acropora* have been amalgamated into a database from various sources (Fig. 3.1). Data were entered from 2006 and concluded in 2009, creating an archival database, hence a synoptic representation of the data up until 2009 with taxonomic, spatial and temporal information brought into line with current classifications as described below. There are currently 308 records within the database. Sources for the database include primary literature, secondary literature, museum and academic institution collections, online databases and collections, private collections and fieldwork undertaken during this PhD.

The reliability of each of these sources is discussed in 3.3.2. First order selection and incorporation of *Acropora* records into the database is based on both knowing the geographical source of a specimen, at least to country level, and temporal (stratigraphical) information, at least to Epoch level.

Data were entered on a PC platform within a series of interlinked Microsoft Excel spreadsheets. This programme was selected in preference to those purely designed for databasing, such as Microsoft Access, as it allowed simple statistical analysis and graphical representation within the programme.

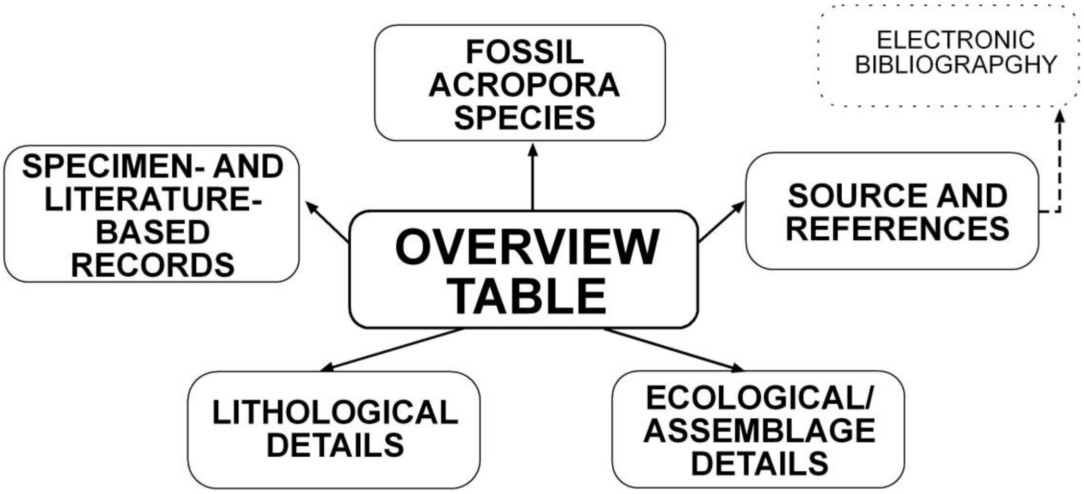


Figure 3.1. Main components of the database and outline of information entered for each record

For each occurrence details are entered that include: source, taxonomic name, present day latitude and longitude, age, geological occurrence, taphonomic information, palaeoenvironmental and ecological data. Further information about these details can be found within the sub-spreadsheets (Tab. 3.1).

SPREADSHEET	INFORMATION	FILE
Main spreadsheet		
♦ Overview	Core details of spatial, temporal, source and taxonomic detail	Appendix 1
Sub-spreadsheets		
♦ Source	Literature (both primary and secondary), collection, database or fieldwork source details	Appendix 1
♦ Specimen	Spatial, temporal, taxonomic and descriptive information	Appendix 1
♦ Lithology and palaeoenvironment	Lithological description and palaeoenvironmental implications from primary, secondary, voucher specimen labels and fieldwork	Appendix 1
♦ Assemblage	Coral assemblage and notable coral composition	Appendix 1

Table 3.1. Details of main spreadsheet and subsheets

3.3.2 Material and Data

Data acquisition, sources and basic database information

In total 308 records were entered into the database sourced from primary literature, secondary literature, museum and academic institution collections, online databases and collections, private collections and new fieldwork (Fig. 3.2). The data extraction and entry involved was from published and unpublished sources, and is either specimen based or non-specimen based. An attempt was made to locate all peer reviewed references and also included information from Masters and PhD dissertations. Where based on primary bibliographic references, attempts were made to locate specimen details. Records had to have sufficient spatial information, grounded to at least country resolution, and temporal information, some of this being available in the publications. Museum, institute and private collections, mostly unpublished, were only included if sufficient temporal and spatial information was recorded alongside the specimen, or could be located through any collecting references on voucher specimen labels. As well as visiting various collections, contacting curators for collections lists, some records were also included on the basis of surveying online databases and suites of images.

These included examples such as the Alan Morton Collection (www.dmap.co.uk/fossils).

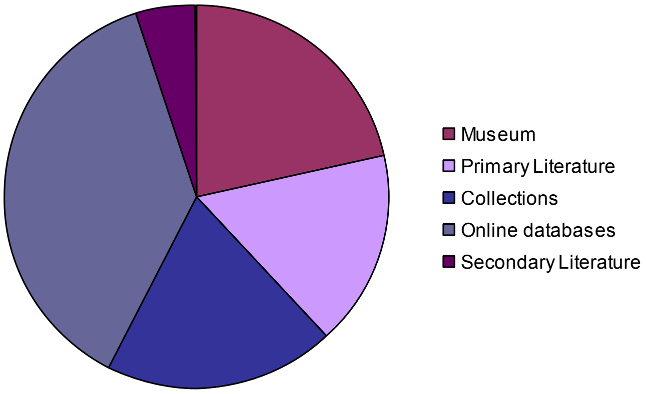


Figure 3.2. Proportion of contribution of records from various sources to the overall database

In order to judge the robustness of these records, each source is attributed to one of three confidence levels (Tab. 3.2).

RECORDS	**CONFIDENCE LEVEL**	**SOURCES** (examples)
Specimen based, seen by working group	**1**	Museum and personal collections and primary literature
Specimen based, but not seen by the working group	**2**	Museum and personal collections, online databases and primary and secondary literature
No specimen details	**3**	Primary and secondary literature

DECREASING CONFIDENCE

Table 3.2. Confidence levels used and respective examples of each type of source

These are, from lowest confidence to highest, 1.) those that are specimen based, therefore having their taxonomic details verified during this thesis (or previously by the working group) and hence the highest confidence level, 2.) records which have specimen details, either within the literature, collections or a database, but have not been seen by the working group, and finally, 3.) records which are purely grounded within the literature and are not supported by specimens details.

Records in this database have been independently compiled by the author of this thesis. The 'working group' refers to an extended group of predominantly European-based coral workers and is defined in order to qualify the increased confidence in the records gathered during this thesis that have information associated with the 'working group' (for example as the fossil identifier or collector). This group have experience in the identification of *Acropora* fossil specimens and many have worked in line with taxonomic classifications of fossil *Acropora* reviewed in Chapter 5. For example the *Acropora* record from the Scrima Cavallo section, Maiella reef blocks, Italy (Database ID 92), is literature based, however the confidence in the record has been raised by the work of Francesca Bosellini identifying the specimen originally. Another example is the museum specimen from the Miocene Aquitaine Basin at the Muséum National d'Histoire Naturelle, Paris. On the basis of this record being entered from a museum catalogue and therefore has not been visually confirmed during this thesis it would be assigned to the lowest confidence level. However, the label information lists the collector as JP Chevalier another worker experienced in *Acropora* identification therefore the confidence in the validity of this record is raised. Therefore, those records extracted and compiled for this chapter from museum databases or literature, authored by the members, have elevated confidence levels due to their experience working with the genus. Further to the supervision team of B Rosen, D Bosence and C Wallace, these workers include F Bosellini, C Perrin, Ken Johnson, M Wilson, F Schuster, in addition to this there is a legacy of coral workers including JP Chevalier, C Chaix and B Cahuzac who have also worked extensively on fossil *Acropora* specimens. In summary, those records extracted and compiled for this chapter from museum databases or literature, authored by the members, have elevated confidence levels due to their experience working with the genus. Contrary to this, those records which are specimen based but have been identified/collected by other authors is assigned a lower confidence level (2, see table 3.2)

Additionally, basic information is included such as an assigned database identification number, the number relating purely to the order of entry of records, the origin of information (i.e. NMITA, Reference, NHM), the type of information (i.e. Database, Museum collection, Journal, Thesis) and the primary, and any additional, references associated with the record. Source details are further expanded on in the sub-spreadsheet making each record traceable and transparent. The basic information of the assigned database identification number is carried over to each secondary sub-spreadsheet making these sub-spreadsheets always connectable to the primary spreadsheet (abbreviations relating to different sources are summarised in Appendix 7).

Specimen detail

Specimen details, when present, are taken directly from literature information or, where studied first hand, from specimen labels. Additionally, information was provided by curators where collections could not be studied first hand. In the primary database a specimen's taxonomic classification is listed based on the original recorded taxonomic detail, for example the voucher specimen labels or primary literature identification. No attempt is made in the primary database to reclassify or update taxonomic information. The number of specimens is also listed, particularly from literature sources where many specimens may have been collected from a particular locality. The source of the specimens was also recorded by specimen number and specimen holdings (i.e. Museum code, private collection reference).

Expanding on this, the taxonomic sub-spreadsheet provides full specimen details and is linked to the primary spreadsheet by the database identification number. In some cases there are more than one specimen entries under an individual identification number, where more than one specimen had been collected from the same locality and of the same age, therefore only warranting one record in the primary database. Only specimens personally studied or, in few cases, illustrated sufficiently well to understand taxonomic details are recorded in this sub-spreadsheet.

In the secondary sub-spreadsheet the main areas covered are specimen details, label details, re-identification, morphological characteristics, geochemical details and recording of the specimens. Within this workbook, individual sheets are assigned to each specimen-holding institute or source, for example fieldwork, with each sheet containing the headings and information outlined below. Under specimen details an identification number from the primary spreadsheet, specimen number (usually assigned by collector or holding institute), and location of specimen (the collection location or institute) are listed. Label details are included only if from original information on the specimen labels. This detail includes geographic (location and country on the label), stratigraphic (lithology), dating (chrono, litho or biostratigraphic ages), collection details and original taxonomic identification. Geographic, stratigraphic and age of the specimens are updated, as discussed under sub headings below, to bring into line with present schemes but these updates are only listed in the primary spreadsheet, alongside the raw original label information.

Original taxonomic information has been updated and this is listed under the column 're-identification' within this sub-spreadsheet following the taxonomic standards outlined below and in Chapter 5. On a generic level many specimens identified in this work as *Acropora* were labelled *Madrepora* (a synonym for *Acropora* used widely by nineteenth century authors and collectors) and hence are listed as *Acropora* at generic level in the re-identification. Specimens, where preserved well enough and were available, were re-identified to species level (see Chapter 5 for taxonomic identifications). Comparisons were also made with the modern *Acropora* record, listing most similar extant species and hence species group.

Under 'morphological characteristics' a general description of the specimen is listed with attention paid to the overall specimen, including corallite contribution to each branch and overall implied colony growth form, and the specimen's preservation. Measurements of individual branch thickness and length of the specimen are recorded. Details with respect to radial corallite shape, size and distribution are recorded, and, separately, coenosteum wall structure, on and in between radials, are listed using terms outlined in Chapter 5.

'Geochemical information' outlines the main results from any geochemical analyses undertaken as part of this thesis and provides links to the main source of information and results. Detailed descriptions of thin sections include information on the morphological characteristics and, infilling sediment and diagenesis (composition, amount and areas affected). A total percentage of aragonite composition is listed under x-ray diffraction (XRD) and linked to the original spreadsheet of results. Main cathodoluminescence results are summarised, linked to the raw data and images for each specimen. Isotopic data is listed and connected to results spreadsheets.

Finally in this sub-spreadsheet links are provided to all images collected with respect to hand specimens, thin sections and geochemical work.

Taxonomic standards

Taxonomic standards are discussed in detail in Chapter 5. Importantly, for the database original identifications (from literature and collection resources, and label details) and re-identifications, undertaken as part of this thesis, were both recorded with a clear distinction between the two. For general coral taxonomy, as found in the basin assemblage sub-spreadsheets, standard taxonomic references were followed, e.g. Veron (2000). Taxonomic work specific to the genus *Acropora*, and its family Acroporidae, follow modern work on the genus by Wallace (1999).

Temporal framework

Age assignments were taken from the original publication or specimen label. These were updated to conform to the International Commission on Stratigraphy (Ogg *et al.*, 2008). For certain regions, local biostratigraphic schemes were used such as for Southeast Asia (BouDagher-Fadel, 2008). Where possible Biozone, Age/Stage, Epoch and/or Period were entered, as well as geographically localised terms, for example Auversian (stage name from Auvers-sur-Oise in the Paris Basin). Another column summarising this, contains the maximum and minimum chronostratigraphic age in millions of years (Ma). Finally under the heading of age, is the category of 'time slice' which is a series of ten time-slices encompassing the time period between the Paleocene-Present. These time-slices (Late Paleocene-Early Eocene, Middle Eocene, Late Eocene, Early Oligocene, Late Oligocene, Early Miocene, Middle Miocene, Late Miocene, Plio-Pliestocene) are representative of each map-age slice used during the graphical representation on palaeogeographic maps. Thus, the time slices represent time intervals that may embrace several stages or transit system boundaries but also may cut stages.

Spatial framework

Present-day latitudes and longitudes of localities are rarely reported especially in older literature and museum collections. Commonly, geographical positions are quoted by outcrop, township or area, with occasional geographic descriptions being given. Therefore, depending on the level of geographical accuracy quoted or attained, through further investigation, a level of confidence has been established (Tab. 3.3).

ACCURACY	DETAILS	CONFIDENCE LEVEL	SUGGESTED RADIUS ERROR WITH LOCALITY POSITIONING
Exact	Latitude and longitude quoted	1	0.1km
Outcrop	Geological-outcrop details given	2	0.5km
Township	Latitude and longitude is inferred	3	1km
Area		4	5km
Region		5	10km
Country		6	Country-specific

Table 3.3. Details of geographical levels of confidence associated with accuracy of inferred and quoted geographical position recorded in the database

In some cases only a broad geographic description is given in publications and such localities were assigned a latitude and longitude that corresponded with the geographic description. They are therefore only approximations of their true positions, and in the worst cases are plotted at the centre of the country in which they occur. Where quoted as coordinates these were converted to longitudes and latitudes. On the larger scale a field is found in the primary spreadsheet to enter the oceanic realm in which each record is found.

Present day longitudes and latitudes were processed using GETECH software, University of Leeds, to obtain a reconstructed palaeolongitude and palaeolatitude for each record. These were used later in conjunction with a GIS programme to plot palaeodistribution maps for each time-slice.

Lithological framework

Lithological information is found in the primary spreadsheet but also within some of the sub-spreadsheets. Stratigraphic information was reviewed and brought inline with current classifications. Headings in relation to the stratigraphic units yielding the specimens included Group, Formation and Member. Basic description/comments about the stratigraphy are made. Where stratigraphic information was lacking, particularly from specimen labels, secondary sources and literature were used to support the primary source, and inferences were made about the stratigraphic aspects of the record.

Ecological information and basin assemblage

Information is found within both the primary and sub-spreadsheets on both general basinal trends as well as the locality-specific information that is summarised. Within the primary spreadsheet, basic information includes details under headings of coral assemblage and coral facies. Additional to this, the coral bearing unit sub-spreadsheet lists details about the coral assemblage of each *Acropora*-bearing lithology added to the database. Using, primarily, the *Treatise on Invertebrate Paleontology, Part F*, (Wells, 1954) information on morphological trends, colonial form, palaeoecology and taxonomic updates were added for each coral genus within the assemblage. Headings include genus and species name, any renaming or re-identification, source (including specimen number), order, family, azooxanthellate or zooxanthellate, extant or extinct and colonial or solitary.

Palaeoenvironmental

Within the primary spreadsheet, published primary literature was used to summarise previous palaeoenvironmental information, with secondary literature and sources supplementing this.

3.4 ASSESSMENT OF DATA

In this section the graphical representation and statistical analysis of the database are integrated to provide comprehensive spatial and temporal analysis of the Cenozoic *Acropora* specimens.

3.4.1 Graphical representation

Two simple methods were used to graphically represent the fossil distribution of the genus; a series of 'Boucotgrams' (see below) and Geographical Information Systems (GIS) maps. The aim of these is to summarise and access the changing spatial/temporal distribution of *Acropora* through the Cenozoic on varying scales, the 'Boucotgrams' mainly summarising global variation through time and the GIS maps summarise spatial distributions at both global and regional scales.

The 'Boucotgram'

In the book 'Evolution and Extinction Rate Controls' (1975) Boucot introduced the concept of simple spatial-temporal diagrams to illustrate various theoretical models of historical-biogeographical distribution patterns (Fig. 3.4). Boucot principally used the method for assessing distributions of brachiopods.

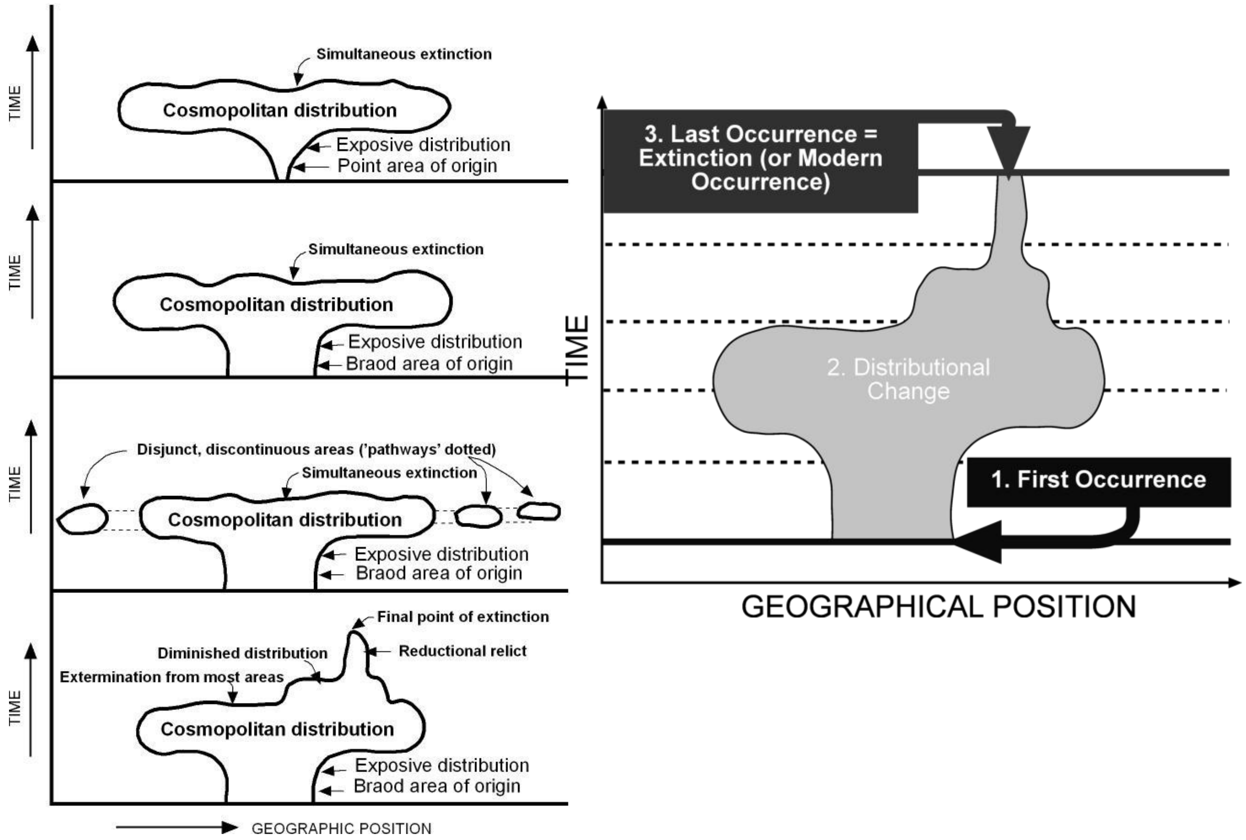


Figure 3.4. Spatial-temporal diagrams to illustrate various models of historical-biogeographical distribution patterns (Boucot, 1975) and summary of main features of the plot (Rosen, unpublished).

Boucot's models simply plot a synthesis of geographical position against time, and (by implication) surround the data in an encompassing envelope. This kind of plot has been adopted here after Rosen (unpublished) and modified here in order to plot real data in quantified axes. The resulting diagrams are named 'Boucotgrams' after Art Boucot, and his original concept.

For the database each record was plotted on a graph of time against both palaeolatitude and palaeolongitude. Each record plotted was coded by a relative source confidence level. Error bars were placed on each record for both the spatial and temporal axis.

Geographical Information Systems (GIS)

The mapping capabilities of GIS were used to illustrate the changing distribution of the genus, and additionally individual species, through a series of Cenozoic time slices. ArcGIS was used with a series of GIS files (ArcGIS 9x mxds, layers and shapefiles).

Latitudes and longitudes were converted to palaeolatitude and palaeolongitudes as described above.

Within the GIS time slices, records are separated into four fundamental classes based on their distribution within a particular time interval (Fig. 3.5; Foote, 2000): (1) records which cross the bottom of the time interval and whose last appearance is within the interval, bL; (2) records that first appears during the interval and crosses the top boundary, Ft; (3) records that range through the entire interval and crosses both boundaries, bt; (4) records confined to the time interval and first and last appearances occurred within the interval, FL.

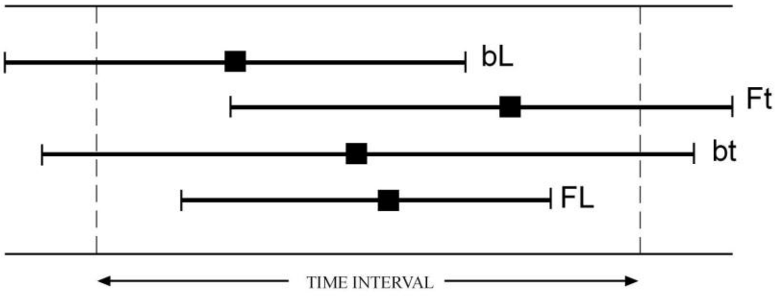


Figure 3.5. Illustration of four fundamental classes of records during a particular time interval

For each time slice a measure of the sum of records can be made along with the maximum and minimum occurrence age of each record (Tab. 3.4).

MEASURE	**DEFINITION**
Total records	$N_{bL} + N_{Ft} + N_{bt} + N_{FL}$
Bottom boundary crossers N_b	$N_{bL} + N_{bt}$
Top boundary crossers N_t	$N_{Ft} + N_{bt}$
Number of new records	$N_{FL} + N_{Ft}$
Number of end records	$N_{FL} + N_{bL}$
Estimated mean standing records	$(N_b + N_t) / 2$

Table 3.4. Definitions of the main measures of the records within a particular time interval (adapted from Foote, 2000) (N-number of records, for all other symbols see text above).

The number of new records documents the number of records which have a maximum possible age of each record within the time interval and additionally is either confined to the time interval or crosses the top boundary. The number of end records, documents the number of records with a minimum possible age of each record within the time interval and is either confined to the time interval or crosses the bottom boundary.

Overall distribution of reefs dominated by corals and other taxa (from Kiessling *et al*., 2003) are also plotted for each time slice on a series of maps for comparison.

Statistical analysis

To analyse this data a series of statistical treatment was applied. Each time slice was treated a series of 'bins'. Raw data was compared but additionally first differences were compared between different stages (the value for a stage, minus the value for the preceding stage). Comparisons of the raw data tend to emphasize similarities and differences in the general, long-term trends, whereas the focus on short-term, stage-to-stage changes. To measure the degree of positive association between each of the data sets, Pearson's linear product-moment correlation coefficient was used. Because the data are not normally distributed, the statistical significance of these correlations was assessed using Spearman's rank correlation coefficient.

Comparison with other records

The distribution of the *Acropora* records is compared and related to recent reconstructions of Cenozoic global climate (Pearson and Palmer, 2000; Pearson *et al*., 2001; Zachos *et al*., 2001), palaeogeography (Scotese, 2001) and carbonate platform area (Kiessling *et al*., 2003).

3.4.2 Identifying signal bias

It is widely accepted that the Phanerozoic marine fossil record not only reflects a response to palaeoclimatic-tectonic conditions but there is also a component based on preservational and archival factors (i.e. Kiessling, 2005; Smith, 2007). Incomplete preservation, heterogeneous geographic sampling, uncertainties in palaeogeographic reconstructions and inconsistencies of reef definitions bias global reef patterns observed in the geological record. This sampling bias is added to a biological habitat area effect, which is thought to be of paramount importance for modern reefs. In the database created here it is important to account for, and acknowledge, the influence of this artefactal signal (Tab. 3.5). The true palaeobiogeographical record reflects a reef's highly sensitive nature to global and local climatic influences. Also influential on this signal is the availability of habitat, primarily tectonically influenced and additionally, and consequentially influenced by, ocean circulation variations, sediment input, nutrient supply and substrate availability. The artefact signal reflects collecting and preservational bias, poor taxonomy and incomplete spatial and temporal data.

	Signal	*Details*	*Extraction*
1. Palaeosetting	Palaeoclimatic	• Modern coral reefs are found within a restricted climatic belt • Weathering rates and hence sediment supply and therefore water light penetration affecting coral growth and colony form • CO_2 levels affect CCD depth	• Comparison with climatic and palaeogeographic reconstructions for the Cenozoic
	Tectonic	• Ocean circulation patterns dictate dispersal • Availability of habitat modulates coral reef distribution	
2. Artefact	Poor taxonomy	• Artefacts produced by a reliance on different taxonomist's identifications • Monographic effects (increase in diversity associated with increased taxonomic attention)	• Develop a working morphologically-based taxonomic framework suitable for use by other taxonomists • Identify confidence levels in record sourcing
	Poor/uneven stratigraphic resolution	• Influences species distributions and understanding of evolutionary patterns	• Constrain and quantify error
	Preservation potential/bias	• Loss of rock record due to tectonic activity i.e. subduction of oceanic crust and erosion • Rate and type of sedimentation • Species occurrences/preservation related morphological robustness	• Compare distribution with global carbonate distribution and preservation • Compare stratigraphic and species-related preservational controls
	Collecting bias	• Primarily influenced by socioeconomic factors (e.g. oil exploration which would give rise to more Middle East records)	• Qualify collecting motivation primarily based on collection records

Table 3.5. Summary of influence on the fossil record including both a palaeosetting and artifactual signal

Preservation bias

The fossil marine record is widely accepted to be biased due to the reduced preservation potential of southern hemisphere rock record (Smith, 2001). It is important to identify within the database if the southern latitudinal record reflects a lack of records due to tectonic-related and erosional loss of carbonates, or is there a real latitudinal restriction of *Acropora* just in the southern hemisphere. The most comprehensive review of Phanerozoic carbonates distribution is Wolfgang Kiessling's database of Phanerozoic reefs. By plotting this database alongside the fossil *Acropora* database an attempt can be made to identify any preservational bias created by missing carbonate developments.

Collecting bias

The comparison of records from the different localities throughout the Cenozoic is dependent on the quality of collections made from different localities. Attempts have been made here to identify any collectional bias introduced by limited sampling and taxonomic factors established by restricted collecting. Bias of the collector includes motivation and method. Rarefaction allows the calculation of the species richness for a given number of sampled individuals and allows the construction of so called rarefaction curves. This curve is a plot of the number of species as a function of the number of individuals sampled. When collecting common, abundant fossils they are typically found and collected first with rare taxa often being missed. Sample bias can be controlled by socioeconomic factors with reefs and research more likely to be undertaken in rich countries, irrespective of geological and ecological controls. Varying taxonomic methods, and protocols, can lead to misidentifications and an attempt has been made here to rationalise the consequences of this with respect to the genus *Acropora* (Chapter 5).

Taxonomy – the Monographic Effect

The monographic effect results from the increased taxonomic attention, generating bias if it is non random. In each basin the original identifications show limited species diversity. For example revisions by Wallace (2008) lead to increasing the diversity in the basins studied. There is also the potential over splitting of the genus, and a coral assemblage as a whole. This shows that caution should be taken when comparing basins and assemblages where different levels of taxonomic revision have taken.

3.5 RESULTS

Here follows a review of the Cenozoic record of *Acropora* fossil records. Firstly these results summarise the scope of the database, and therefore the overall Cenozoic fossil record of the genus as implied by the *Acropora* database. An overview of the major global distributional changes of the genus are summarised by two 'Boucotgrams', one of palaeolatitude and the other of palaeolongitude both plotted against time.

A series of time slices, indicate important stages of palaeogeographic evolution of the genus from the Paleocene through to the Holocene. These periods are compared with climatic and palaegeographic reconstructions of these periods to allow inferences to be made about the possible driving mechanism of these trends and patterns. Also included is a discussion of artifactal driven patterns.

3.5.1 Modern *Acropora* record

The modern distribution of *Acropora* has undeniably been shaped by global, regional and local climatic and tectonic events over geological time. Principally oceanic circulation, bathymetry, salinity, runoff/sedimentation, light intensity, temperature control the distribution of corals as reviewed above. However the aim of this section is to summarise a snapshot at the present and, predicted, future biogeographic patterns of the genus (Fig. 3.6).

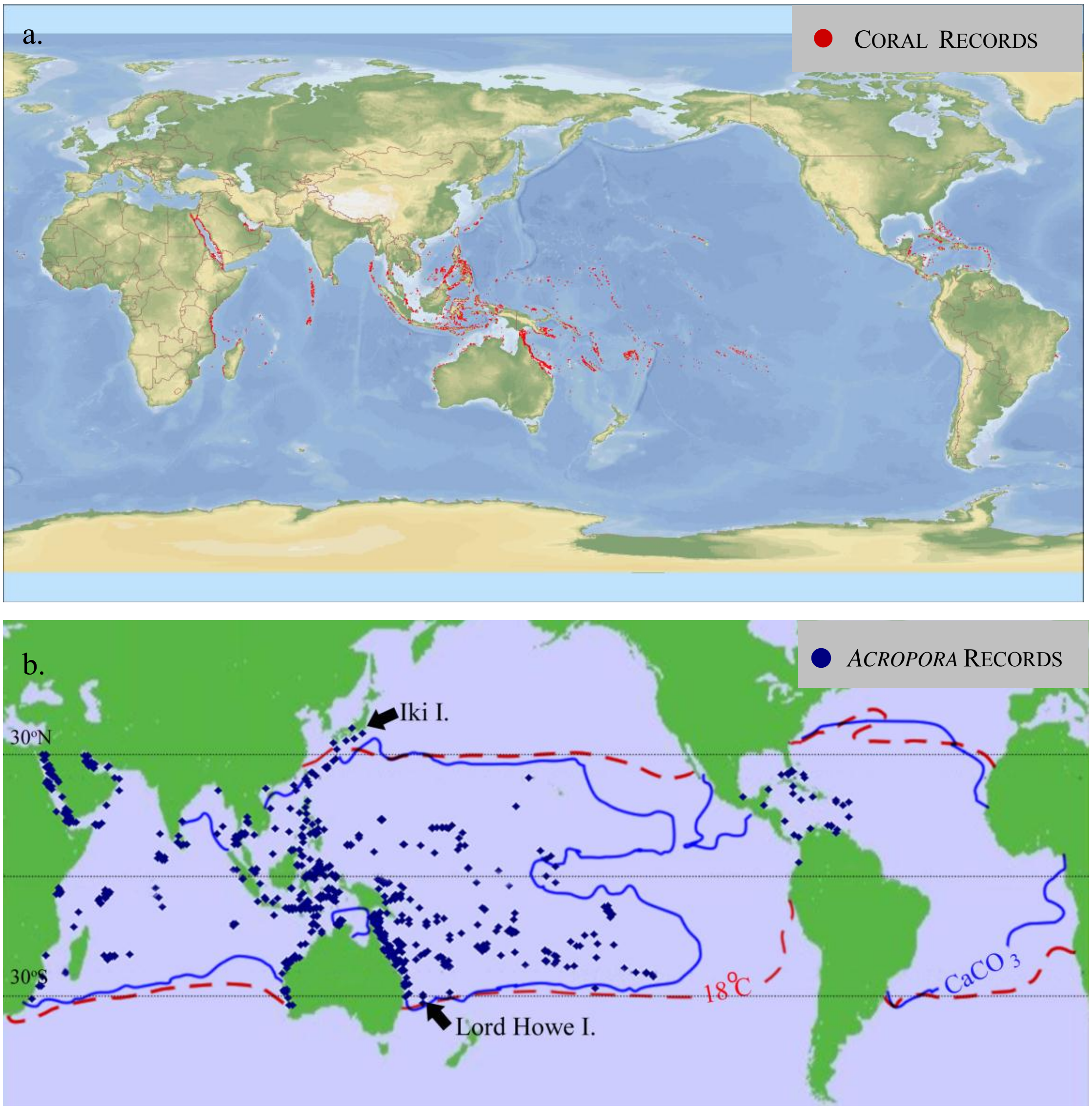


Figure 3.6 a. Worldwide coral distribution (data from Tupper et al.*, 2010, ReefBase), b. Present distribution of Acropora. Lines indicate critical boundaries of SST (18°C) and aragonite saturation for coral reef accretion ($CaCO_3$) as given by Kleypas* et al. *(1999). Highest north and south latitude reefs; Iki Island and Lord Howe respectively (modified from Wallace and Rosen, 2006).*

Modern Palaeogeographic distribution

Reef-building corals are currently found scattered throughout the tropics and subtropics (Fig. 3.6a). Although some coral reefs are found approaching 40° north and south, few well developed coral reef systems are found beyond 30°. *Acropora* is the most widespread, diverse zooxanthellate coral genus with some 130 species found within the three major oceans of the world, occurring in the two major oceanic realms, the Atlantic and Indo-Pacific. *Acropora* is found within the highest latitudinal reefs of Iki Island in the north and Lord Howe in the south, however the genus is not always tied to reef occurrence and this thesis deals with coral records rather than just reef records (Fig. 3.6b).

Following the closure of the Tethys Ocean, the waters of the Indian Ocean and Western Pacific became separated from those of the Atlantic and far eastern Pacific (Biju-Duval, 1977; Scotese *et al*., 1988; Spalding *et al*., 2001). From this point onwards coral reef communities developed distinctive characteristics. Because of both different climatic and tectonic controls within the Atlantic region, diversity in this region is low and only seven genera are shared between the Atlantic and Indo-Pacific (Belasky, 1996). In comparison with the low diversity Atlantic area, the Indo-Pacific region is widely recognised for its high coral diversity. Within this, the area of Southeast Asia is known for its outstanding diversity focus. Within these two major oceanic realms, the distribution of *Acropora* is similar to the modern global reef coral distribution. In the Indo-Pacific over 100 species are found (Wallace, 1999), comparative to the low diversity Atlantic region which has only three species of *Acropora* in the modern record; *A. palmata, A. prolifera and A. cervicornis*. It has been recently suggested that *A. prolifera* is a hybrid of the other two species (van Oppen *et al*., 2000).

Amongst the high-latitude scleractinian communities including *Acropora*, the highest latitudinal sites supporting reef (*sensu strictu* Wood, 1999) formation in northern and southern hemispheres are Iki Island, Japan (33°48'N, Yamano *et al*., 2001) and Lord Howe Island, Australia (31°33'S, Harriot *et al*., 1995). The Iki Islands are composed of Oligocene to early Miocene sedimentary rocks, covered by early to middle Pleistocene volcanic rocks (Nagaoka, 2001; Fig. 3.7).

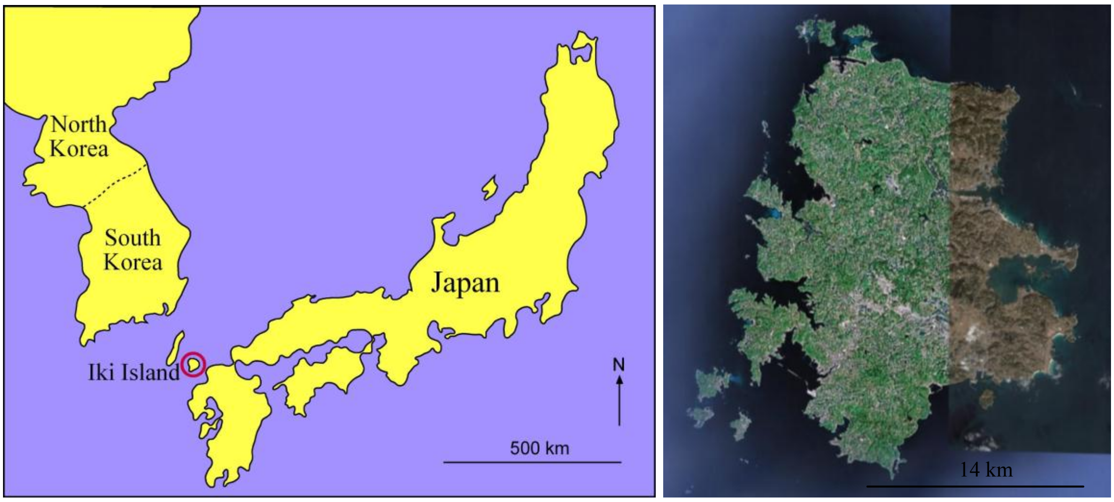


Figure 3.7. Location of Iki Island, Japan, with satellite view (Google Earth).

Within this area the highest latitude coral reef has been described (Yumano *et al.*, 2001). It covers an area of 900m^2, was established at least 1400 years B.P. and is predominantly composed of faviid corals and mud infillings. Coral diversity is low, with 39 species of 22 zooxanthellate coral genera, amongst which 4 species of *Acropora* have been identified (Veron 1992, 2000). The mean annual water temperature of the surrounding sea is 20°C (Natsukari and Takita, 1972). In the near-shore Kurosaki area of Iki Island the mean water temperatures fall to a low of around 13.3°C in March and a high of 26.2°C in August.

At the most southerly point of coral reef accumulation, Lord Howe is a volcanic island, over 1000 km south of the Great Barrier Reef, with a reef structure extending 6 km along its west side (Woodroffe *et al.*, 2005; Fig. 3.8). A few fringing reefs are along the east coast of mainland Australia, with development limited to around 22°S along the inner GBR, but offshore islands are found having wide fringing reefs like those seen on Lord Howe Island (~32°S) (Veron and Done, 1979).

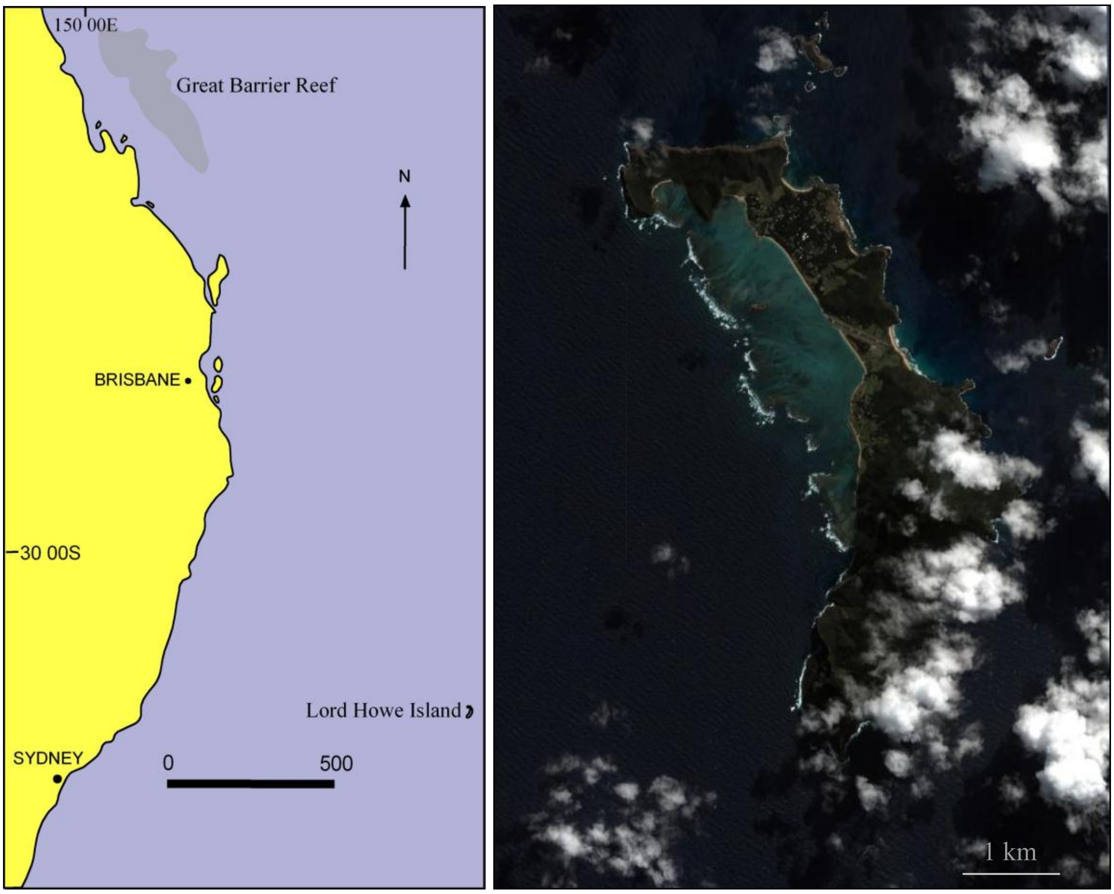


Figure 3.8. Location of Lord Howe Island, Great Barrier Reef, Australia, with satellite image (Google Earth)

As at Iki Island, biodiversity is low with many species at their ecological limit. Harriott *et al*. (1995) recorded 83 coral species, with 13 species of *Acropora*. Communities here are maintained by the south flowing East Australia current bringing warm waters and new larval recruits (Woodroffe *et al*., 2005). Mean annual sea surface temperature varies between 18°C and 23°C.

Modern Palaeoecology

The genus *Acropora* is not only recognised for its fast growing nature, but additionally its resilience to a huge range of physio-chemical conditions. Reflecting this, species occur in great abundance in a vast array of reef habitats with many species coexisting. However there are some species which are associated with unusual environments, for example *A. torihalimeda* on submerged *Halimeda* algal banks and *A. russelli* on deep sandy slopes (Wallace, 1999). Undoubtedly hydrodynamic regime (Bottjer, 1980), and other physio-chemical conditions, have an influence on the species that dominate but more so on the type of colonial growth form, and therefore on the species-groups which dominate. Additionally inter-genera competition plays a role in dictating the diversity and species of an area.

3.6 OVERVIEW OF FOSSIL RECORD

3.6.1 Summary of scope of data

In total 308 records were recorded within the database. Of these records, 126 are assigned to confidence level 1, 148 to confidence level 2 and 34 to confidence level 3 (Fig. 3.13a). Temporally, the specimens extend from the Late Paleocene to Recent (3 Paleocene, 28 Eocene, 29 Oligocene, 110 Miocene, and 150 Plio-Pleistocene; Fig. 3.7). Spatially, the records cover 36 countries (Fig. 3.13b). Forty species are recorded, as discussed in Chapter 5, with the first extant species being recorded in the Miocene.

MEASURE	PALEOCENE	EOCENE	OLIGOCENE	MIOCENE	PLIOCENE	PLEISTOCENE
Total records	3	28	29	110	87	63
Bottom boundary crossers N_b	0	1	3	0	16	12
Top boundary crossers N_t	1	3	0	16	12	-
Number of new records	3	27	26	110	71	-
Number of end records	2	25	29	94	75	63
Estimated mean standing records	0.5	2	1.5	8	14	-

Table 3.6. Summary of temporal distribution of records within each time epoch

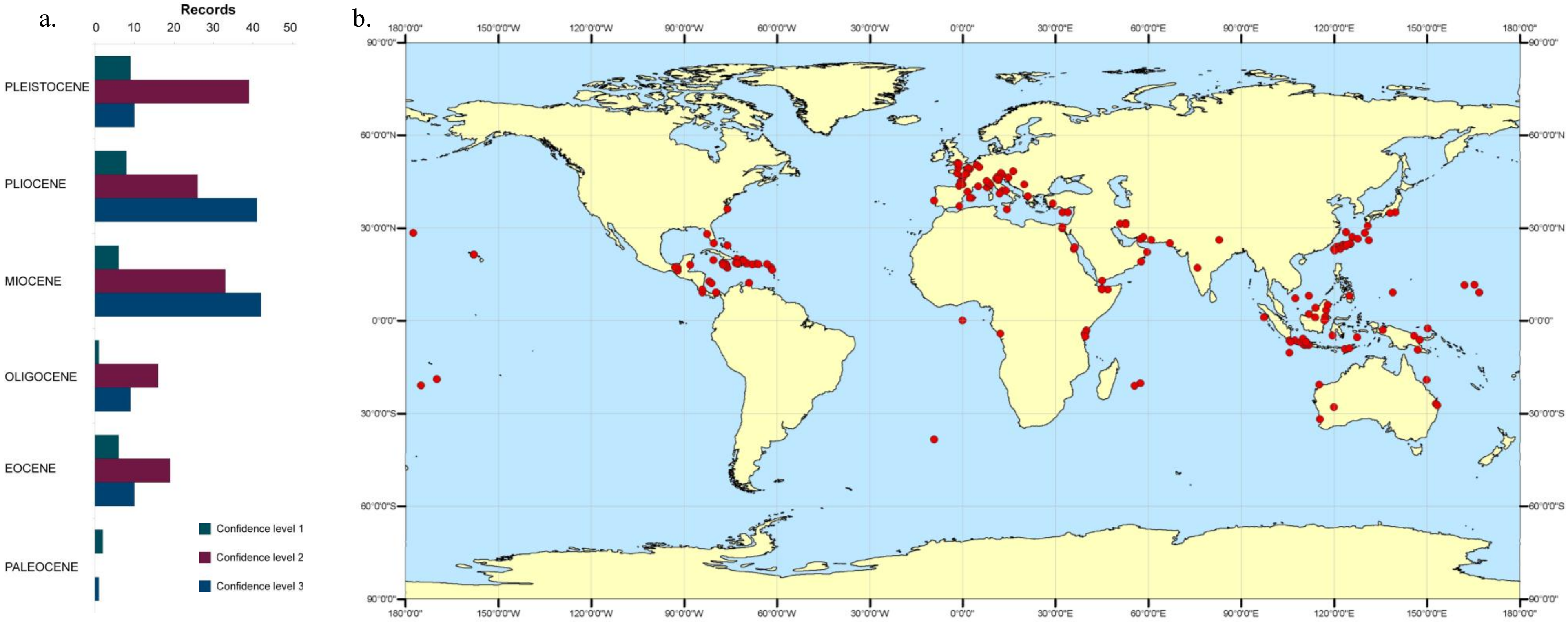


Figure 3.9. a. Distribution of Acropora records within the Cenozoic fossil record with breakdown into respective confidence levels, and b. map of distribution of all data points within the database showing coverage of the records.

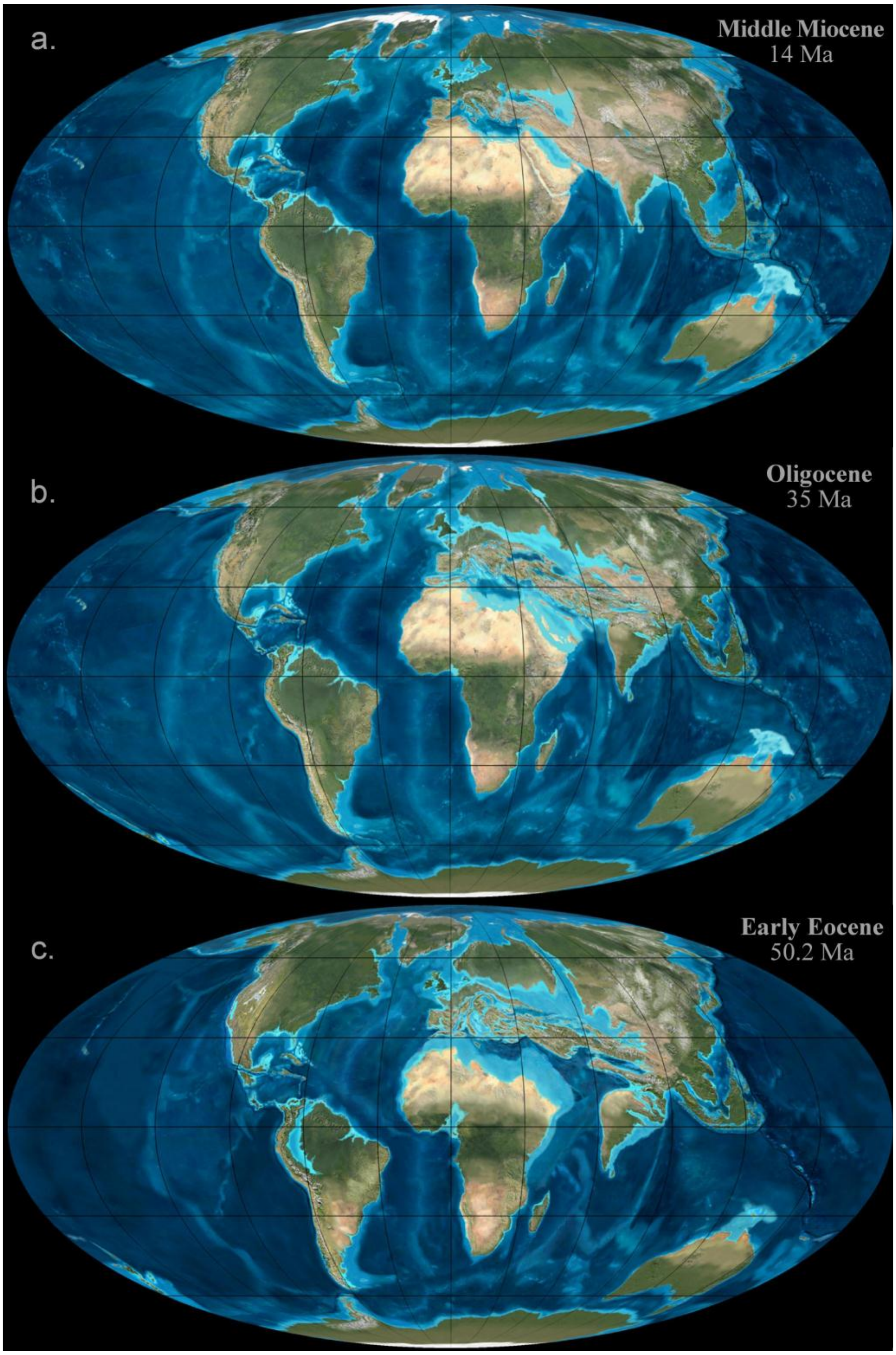


Figure 3.10. Early Eocene-Middle Miocene palaeogeographic reconstructions (Scotese et al.*, 2002)*

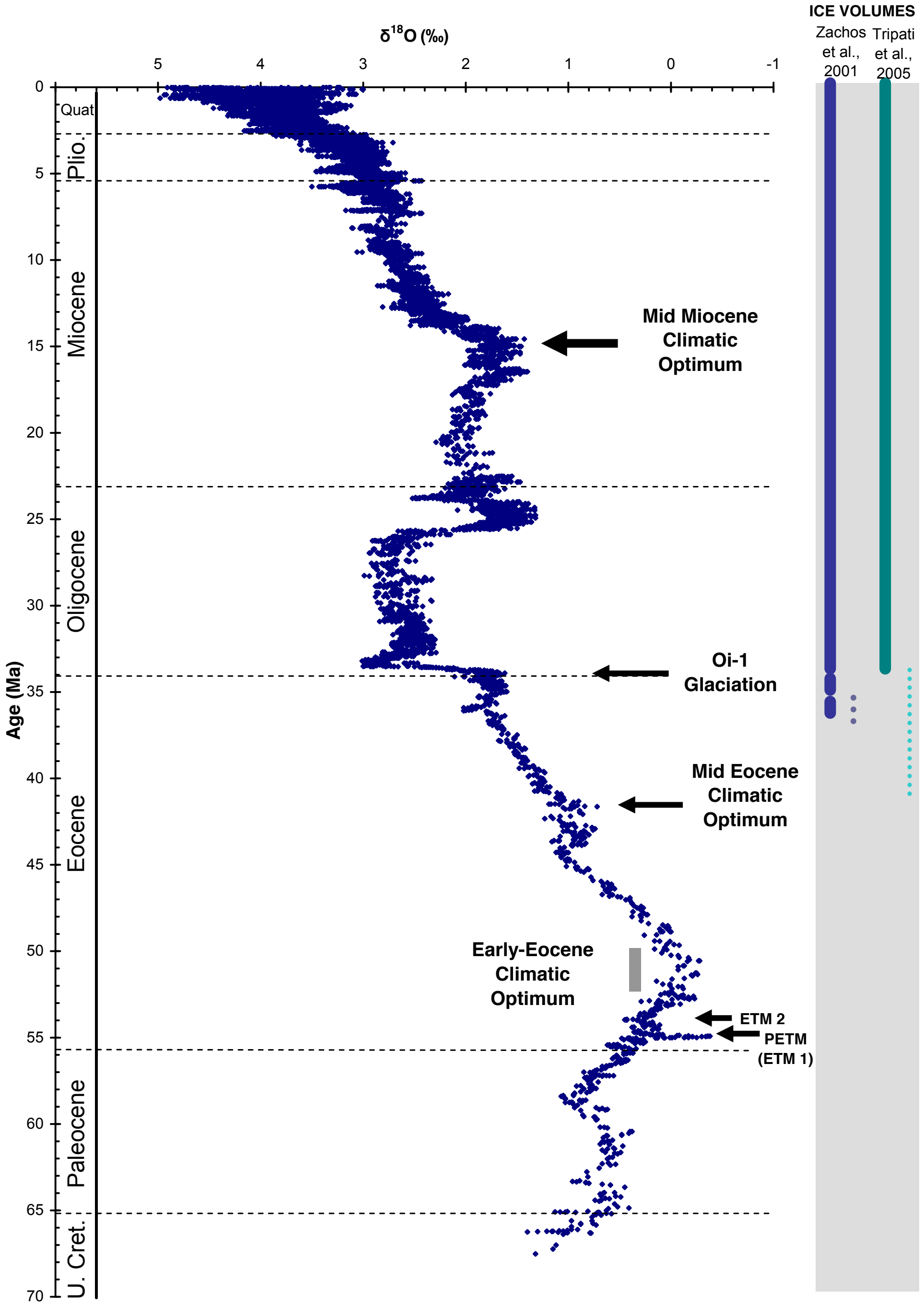


Figure 3.11.Global deep-sea oxygen isotope records (data from Zachos et al.*, 2001, compiled from more than 40 DSDP and ODP sites) reflecting both temperature and ice volumes. Tripati* et al. *(2005) show major ephemeral ice volume accumulation occurred at 42, 39 and 36 Ma. Zachos* et al. *(2001) provide a rough qualitative representation of ice volume relative to the LGM, with dashed bars representing periods of minimal ice coverage (50%), and the full bar representing close to maximum ice coverage (>50% of present), this is not quantified by Tripati* et al. *(2005). Dotted vertical bars represent the presence of ephemeral ice-sheets, in the case of Zachos* et al. *(2001) quantified as small, and for Tripati* et al. *(2005) variable in size.*

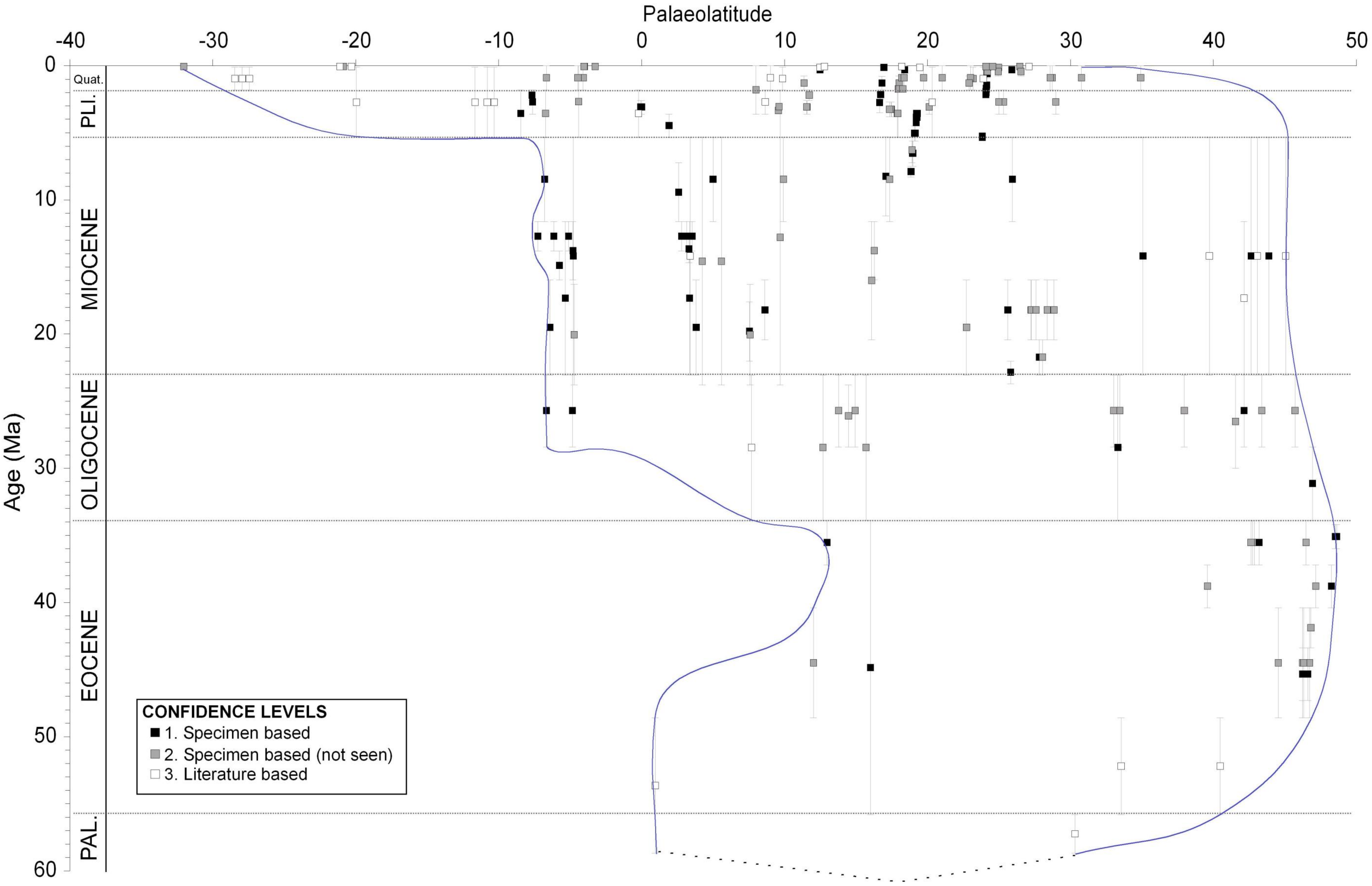


Figure 3.12. Boucotgram of palaeolatitude against time showing all known Acropora records from the Cenozoic

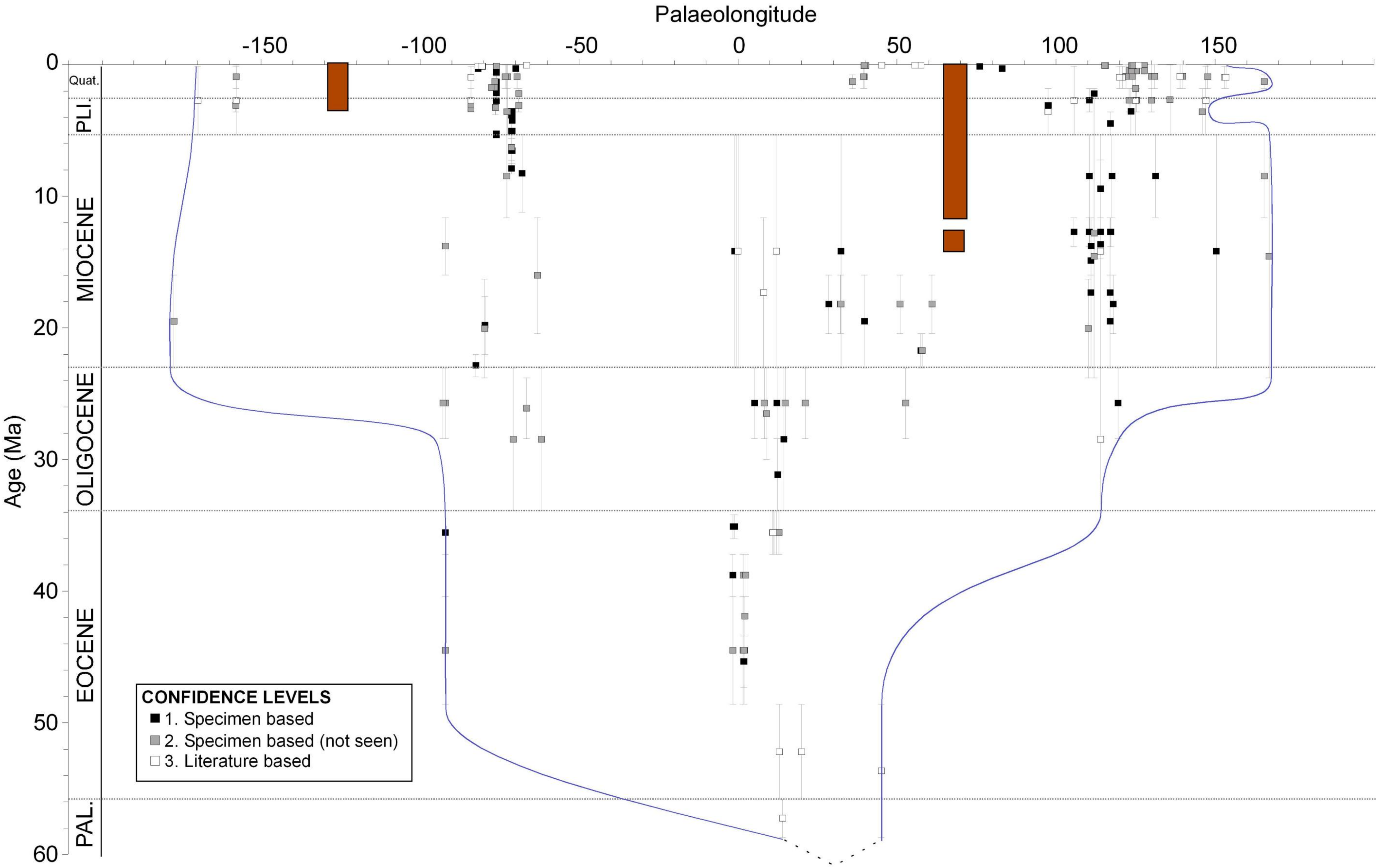


Figure 3.13. Boucotgram of palaeolongitude against time showing all known Acropora records from the Cenozoic (brown bars show presence of land bridges)

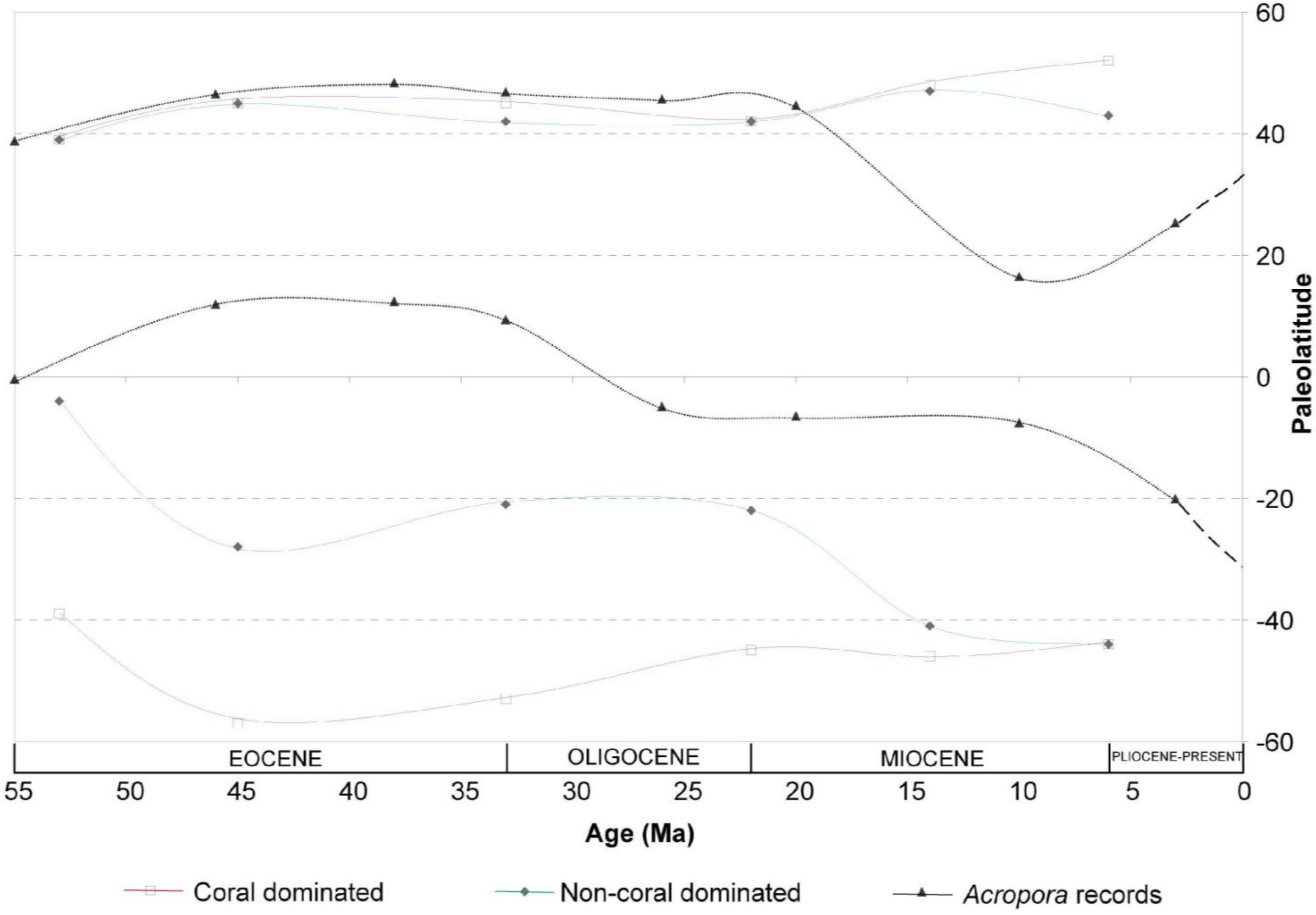


Figure 3.14. Maximum palaeolatitudinal extent of Acropora *records compared with coral-dominated and non-coral dominated reefs (maximum reefal extent from Kiessling et al., 2003)*

3.6.2 Evolution of *Acropora*-bearing Cenozoic oceanic realms

Considering corals physio-chemical sensitivity, in order to fully understand the evolution of *Acropora* in the fossil record, its distribution needs to be evaluated in a palaeogeographic (Fig. 3.10) and climatic (Fig. 3.11) context, along with its relationship to trends in Cenozoic coral evolution. Here a series of time-slices, illustrated using palaeogeographic maps, show the changing distribution of the genus throughout its Cenozoic fossil record.

Paleocene-Early Eocene (65.5-48.6 Ma)

Global setting

The Early Paleogene is characterised by warm, generally ice-free conditions (Zachos *et al*., 2001; Fig. 3.11). A warming trend, which started in the Late Paleocene, culminated in the warmest global temperatures of the Cenozoic Era in the Early Eocene time, the 'Eocene climatic optimum'. Superimposed on this is a six million year period of gradual warming known as the Paleocene-Eocene Thermal Maximum (PETM, Katz *et al*., 1999), also referred to the ETM1 (Sluijs, 2006) and formerly IETM/LPTM (Zachos *et al*. 1993), which lasted around 20,000 years and is associated with a rapid and transient rise in sea-surface temperatures of 4-5° in low latitudes and 8-10° in high latitudes (Zachos *et al*., 2003). Additionally during the Early Eocene period there are a group of other perturbations, or hyperthermal events, including the Elmo event. Importantly for corals, these events were associated with carbon being released into the ocean/atmosphere system, the PETM being the most severe of these (~1050-2100Gt, Dickens *et al*., 1997; Bowen *et al*., 2004). This period may also be crucial to understanding future responses of corals to increasing levels of anthropogenic carbon, comparable to those of this key geological period.

Initial research, Zachos *et al*. (2001), estimates 20-26°C sea surface temperatures for the Eocene, which has been recently been revised through work on exceptionally well-preserved planktic foraminifera from Tanzania (Pearson *et al*., 2007), that estimates Late Cretaceous and Eocene tropical SST to be at least 28–32°C.

During the Paleocene-Eocene, the globe was tectonically different from today (Fig. 3.10). This period was geographically dominated by the wide Tethys Ocean that extended through the Middle East and Mediterranean to the North Atlantic gateway between North and South America. The Isthmus of Panama did not yet connect North and South America, allowing circulation between the Pacific and Atlantic oceans (Ivany *et al*., 2003). The Pacific mid-ocean ridge system began realigning and India collided with the south Asian coastline at about 37 Ma (Ali and Aitchison, 2008). Further, the Drake Passage (water between the southern tip of South America at Cape Horn, Chile and the South Shetland Islands of Antarctica) was shut, preventing the thermal isolation of Antarctica (Scher and Martin, 2006). This, combined with higher CO_2 levels, meant that there were no significant polar ice sheets, with the globe being essentially ice free (Zachos *et al*., 2001).

Sea level is predicted to have risen 70-100m between 60-50 Ma during the Late Cretaceous, estimated by Miller *et al*. (2005) to be 50-70 m above present. Ocean circulation patterns changed dramatically at the beginning of the PETM with global-scale current directions reversing, which persisted for 40,000 years (Nunes and Norris, 2006). As a result of this, Atlantic deep waters flowed from the north to the south, compared with the usual south to north.

Carbonate platform and reefal distribution

Although over half the genera of scleractinian corals are estimated to have become extinct at the end of the Cretaceous, nine genera of living photosymbiotic corals survived the extinction event into the Paleocene and all either became, or were closely related to, important reef-builders in the Cenozoic (Rosen and Turnsek, 1989; Rosen, 2000).

During the Paleocene, carbonate platforms and reefs were rare with the most extensive reefs being established in the middle to late Paleocene, composed of low diversity coral assemblages (Kiessling *et al*., 2003). Coralline algae were relatively unscathed across the K/T boundary and, together with sponges, are largely responsible for the construction of most Paleocene reefs (Wood, 1999). Coral groups appearing during the Early Eocene were the poritids, actinacids and the faviids (McCall *et al*., 1994).

Importantly the total carbonate platform area was related to the global setting, with increased temperature and CO_2 input leading to shallowing of the lysocline, today at 4 km. In part of the south east Atlantic, the lysocline rose by 2 km in just a few thousand years (Zachos and Kump, 2005).

Acropora distribution

The Paleocene-Early Eocene period contains the first occurrences of the genus, *Acropora*, and hence offers clues to the origination, and earliest diversification, of the genus (Fig 3.12, 3.13). Records are extremely sparse, with only three records from the entire period. These records are geographically restricted to the North Africa-Mediterranean region (Fig. 20, 21). The single record from the North Africa region is from Horizon SK 57 and SK 64, of the Lower Aurada Limestone, Berbera-Sheikh, Somalia, dated as Thanetian stage of the Late Paleocene (Database ID 89; Fig. 3.15). This specimen-based record is a collection of 4 specimens housed at the Università degli Studi di Roma Sapienza, Italy, and was first described as *Acropora tergestina* by Carbone *et al*. (1994). This material has been borrowed from the University of Modena, on re-examination, the verification of these specimens as *Acropora* is problematical. All specimens lack the diagnostic axial corallite due to either recrystallisation of the area, making it hard to determine, or due to dissolution of the area. As a result, the entire skeletal area within the centre of the branch is missing. However, the coherent change in the central branch area appears to imply the presence of central axial corallite.

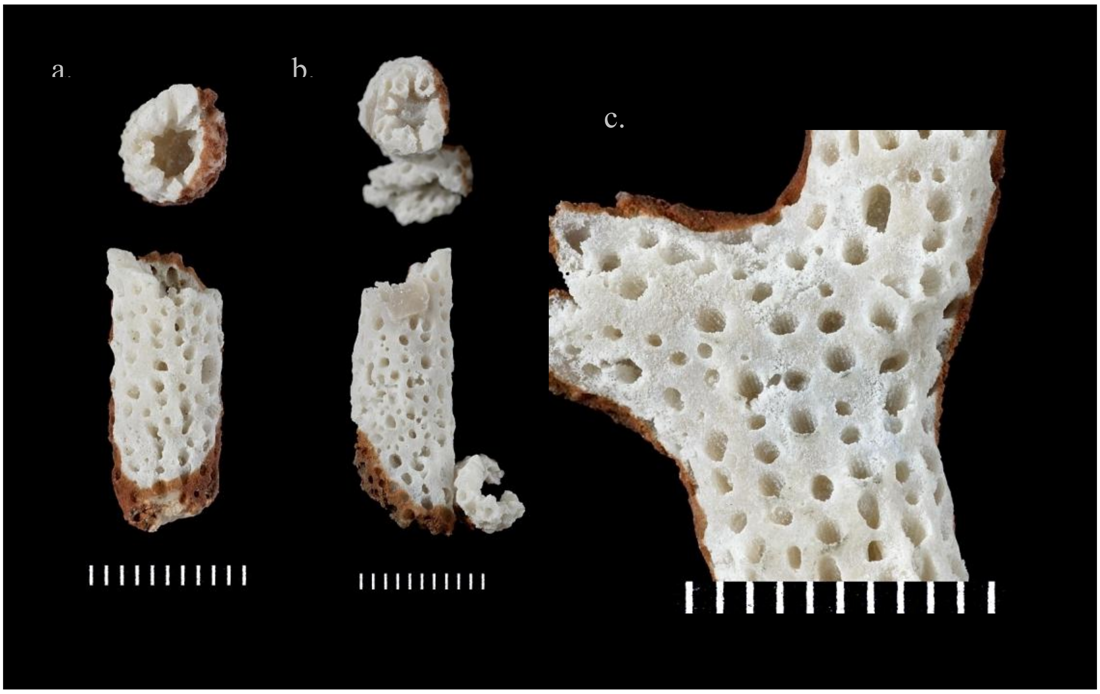


Figure 3.15. Selection of three specimens from the Thanetian collection, Somalia, showing a. persuasive dissolution and, b. recrystallisation of the axial corallite area, c. main branching pattern with alignment of radial corallites (specimens loaned from the University of Modena).

Another early record is from Scrima Cavallo section, Maiella reef blocks, Avella, Italy, dated as Thanetian, Late Paleocene (Vecsei and Moussavian, 1997; Moussavian and Vecsei, 1995; Database ID 92). This record is specimen-based and is only illustrated through a thin section, but has been identified in hand specimen by a member of the working group (Francesca Bosellini).

Finally, are records of specimens from the Late Paleocene of Austria. This is recorded in both the thesis of Tragelehn (1996) and new specimens recorded in Baron-Szabo (2006) (Database ID 288). Although illustrated in Baron-Szabo (2006) as *Acropora*, the thin section illustration appears to have been misidentified, principally as it lacks the characteristic axial corallite and other typical structures of the genus, and would question whether this record is of *Acropora*.

Comparison with coral distribution

When compared with Kiessling's (2003) quoted maximum latitudinal coral reef extent for the Early Eocene, maximum northerly distribution of *Acropora* during this period appears to closely follow this (Fig. 3.18, 3.22). However, the southern hemisphere record is much more restricted than the maximum extent of reefs dominated by non-coral organisms, but follows the extent of coral reefs. Like *Acropora's* distribution at this time, coral reefs dominate the North African-Mediterranean region, with the exception of additional records from the Indian Ocean region.

Robustness of record

The confidence in the records associated with this period includes one specimen re-examined, one specimen-based record and seen by a member of the working group, and additionally one which is specimen-based but has not been seen by the working group.

There appear to be problems with the taxonomic robustness of some these records due to either preservational problems or misidentification. Their preservation possibly reflects the age of these specimens, since preservational potential deteriorates with increasing age.

Additionally, the lack of southern hemisphere records appears to imply either a collecting or preservation bias. However a comparison with the reefal extent during this period confirms the limited spatial restriction of all coral reefs. This does not appear to be a preservational bias as reefs dominated by other organisms occur further to the south, although this may still reflect the different amounts of work undertaken in these regions and therefore a sampling bias towards northern hemisphere regions.

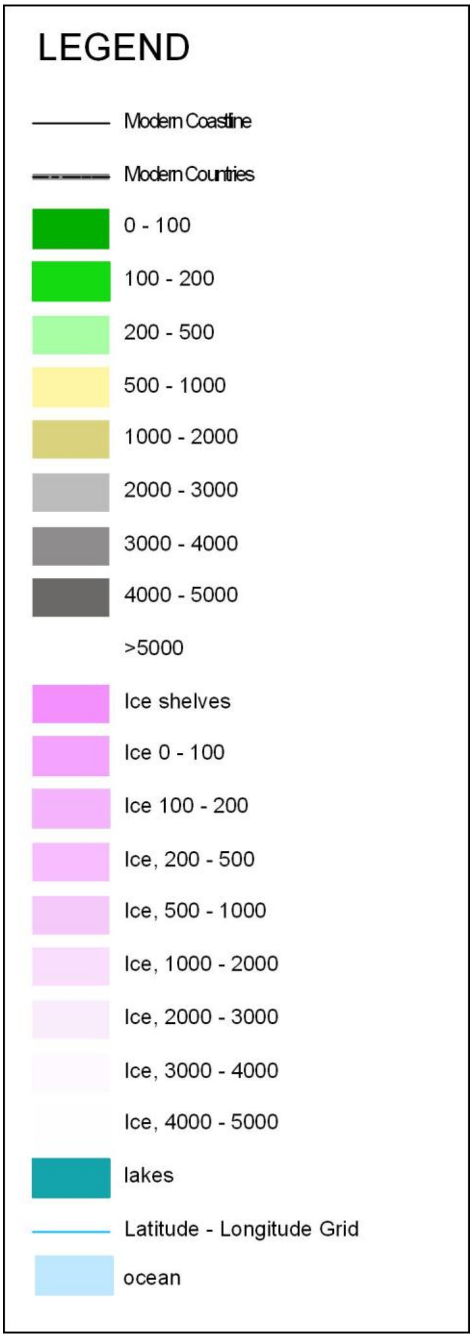
Discussion: Paleocene-Early Eocene record

The distribution of *Acropora* during the Paleocene-Early Eocene is spatially and compositionally very restricted with only three records from the North African-Mediterranean region (Fig. 3.16, 3.17). This reflects the global picture of low carbonate platform areas and rare coral reefs with low diversity assemblages. Coral reefs, like the distribution of *Acropora*, were largely restricted to the North-African-Mediterranean realm.

Undoubtedly, the global setting played an important role in restricting the distribution of the genus, and other corals, during this period. Global climate was generally warmer than today, possibly explaining the higher latitudinal extent of reefs compared with today. This offers clues to possible future responses of coral reefs, and the genus, to the predicted climate warming. This period is also associated with catastrophic changes (e.g. PETM) during this period which probably forced corals into marginal areas at the limit of their ecological tolerances. These catastrophic changes were rapid (for example during the PETM global temperatures rose by about 6 °C over approximately 20,000 years) and geologically short-lived (with the $\delta^{13}C$ record during the PETM recording a duration of around 120,000 years,) and never stabilised, suggesting that it would have been improbable that this genus and other corals could adapt to survive these changes (Sluijs, 2006). Therefore it is probable that corals during this time, a period associated with the re-establishment of coral communities following the K/T extinction, may have been subjected to a series of climate-related extinctions, leading to a series of transient coral assemblages.

Tectonically, the availability of habitat would have been a key limiting factor to the distribution of the genus. Regionally, Southeast Asia, the modern diversity focus of the genus, lacked corals with a 3000 km deep water divide between Australia-New Guinea block and Southeast Asia. As a result of the northward subduction of Indian-Australian lithosphere beneath Sunda-Java-Sulawesi arcs, this area was gradually reduced throughout the Paleogene (Hall, 2002), and with this came the creation of a series of small basins, therefore creating suitable habitat (Wilson and Rosen, 1998; Wilson, 2002). In the Caribbean region, the Isthmus of Panama was still open, and with the exception of corals from the Late Paleocene of Alabama, the first recorded Cenozoic coral assemblages were from the Early Eocene and showed very low diversity (Johnson *et al*., 2008). *Acropora* shows no records from this region during this period and the distribution implies the genus diversified from the western Mediterranean into this area. The North African-Mediterranean region, in comparison with the two present day oceanic realms, comprised a series of small basins, archipelagos, providing ample habitat for corals to originate and diversify.

In summary *Acropora's* distribution during this key period in the history of the genus, was spatially very restricted. The existence of no other records, implies the genus both originated and, as shown in Chapter 5, diversified in the North-African Mediterranean oceanic realm. The genus's distribution was responding to both restrictive processes, lack of habitat in the Southeast Asia region but additionally driving forces, compelling the genus and other corals into higher latitudes than seen today, global climatic warming. It is suggested an important controlling factor on the distribution was an increase in seawater temperatures during the Paleocene-Eocene with the genus resultantly having a much more northerly latitudinal extent than is seen today. This undoubtedly provides clues to the future responses, and possible diversification of the genus, and other corals, into highly latitudinal positions, where habitat availability permits. It additionally shows that in the face of gloomy forecasts for the future of coral reefs, there has been a period where corals have survived during periods of rapid global warming.



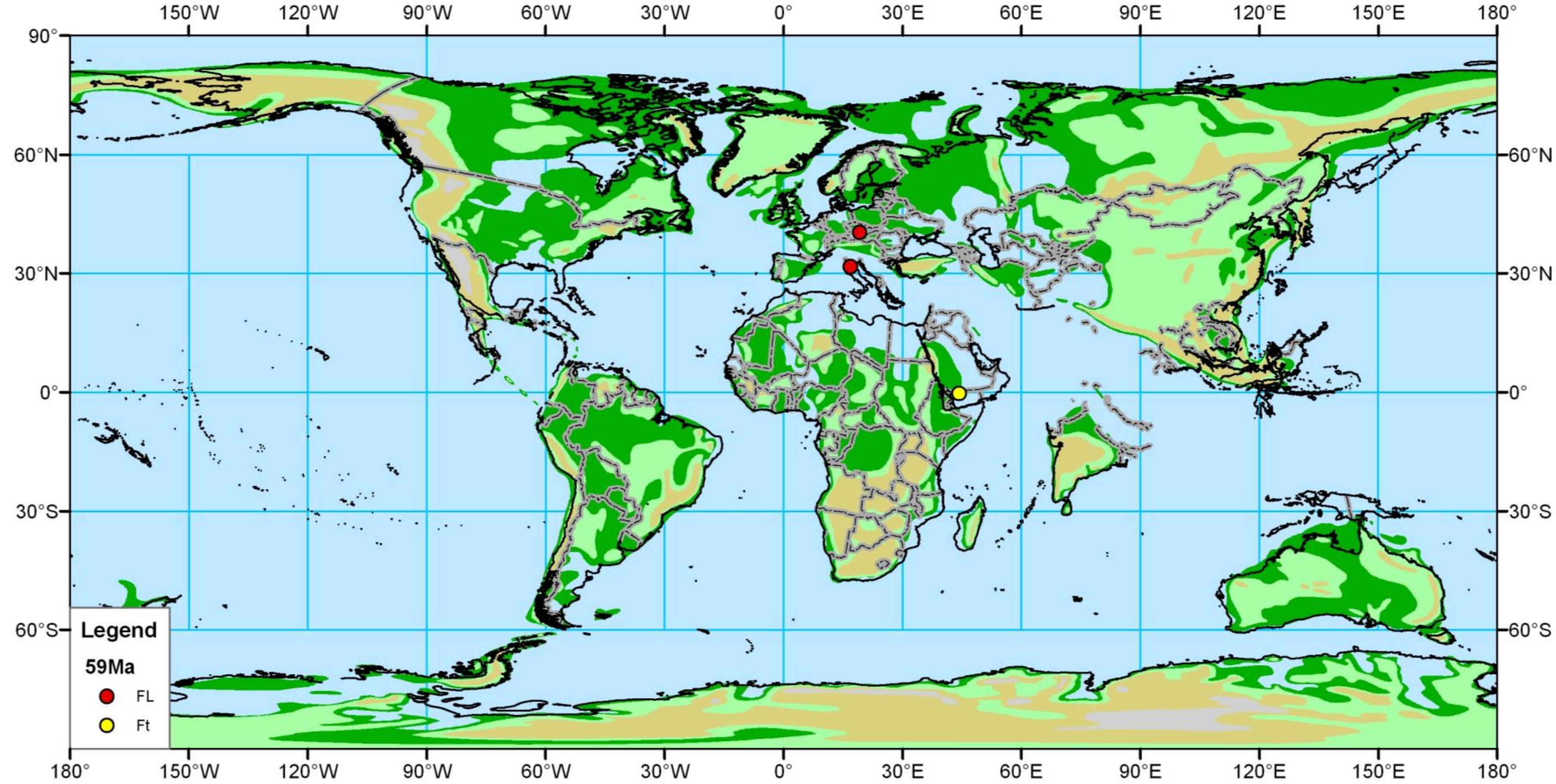


Figure 3.16. Late Paleocene occurrences of <u>*Acropora*</u> *(records that first appears during the interval and crosses the top boundary, Ft records confined to the time interval and first and last appearances occurred within the interval, FL)*

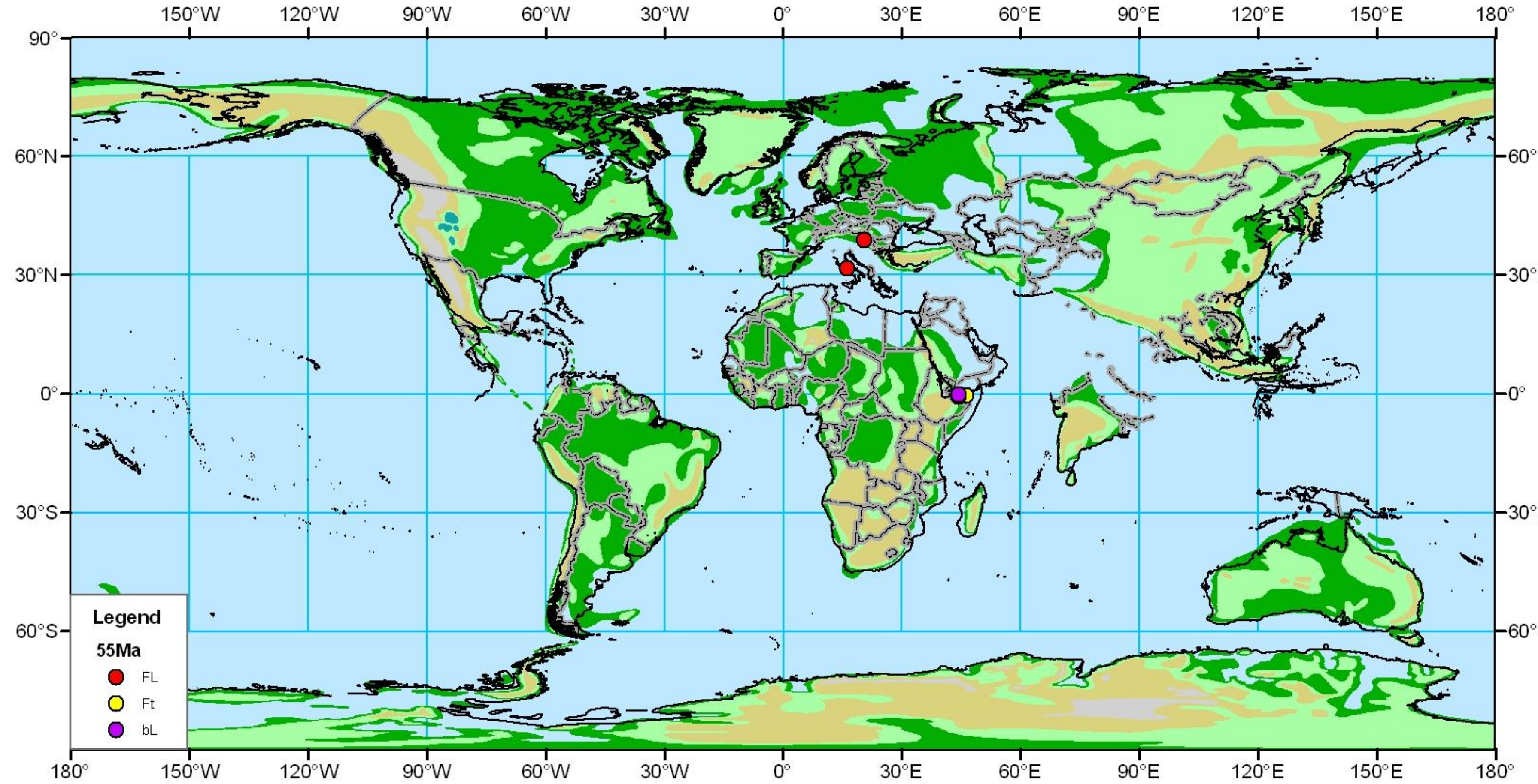


Figure 3.17. Early Eocene occurrences of Acropora (records that first appears during the interval and crosses the top boundary, Ft records confined to the time interval and first and last appearances occurred within the interval, FL, records which cross the bottom of the time interval and whose last appearance is within the interval, bL)

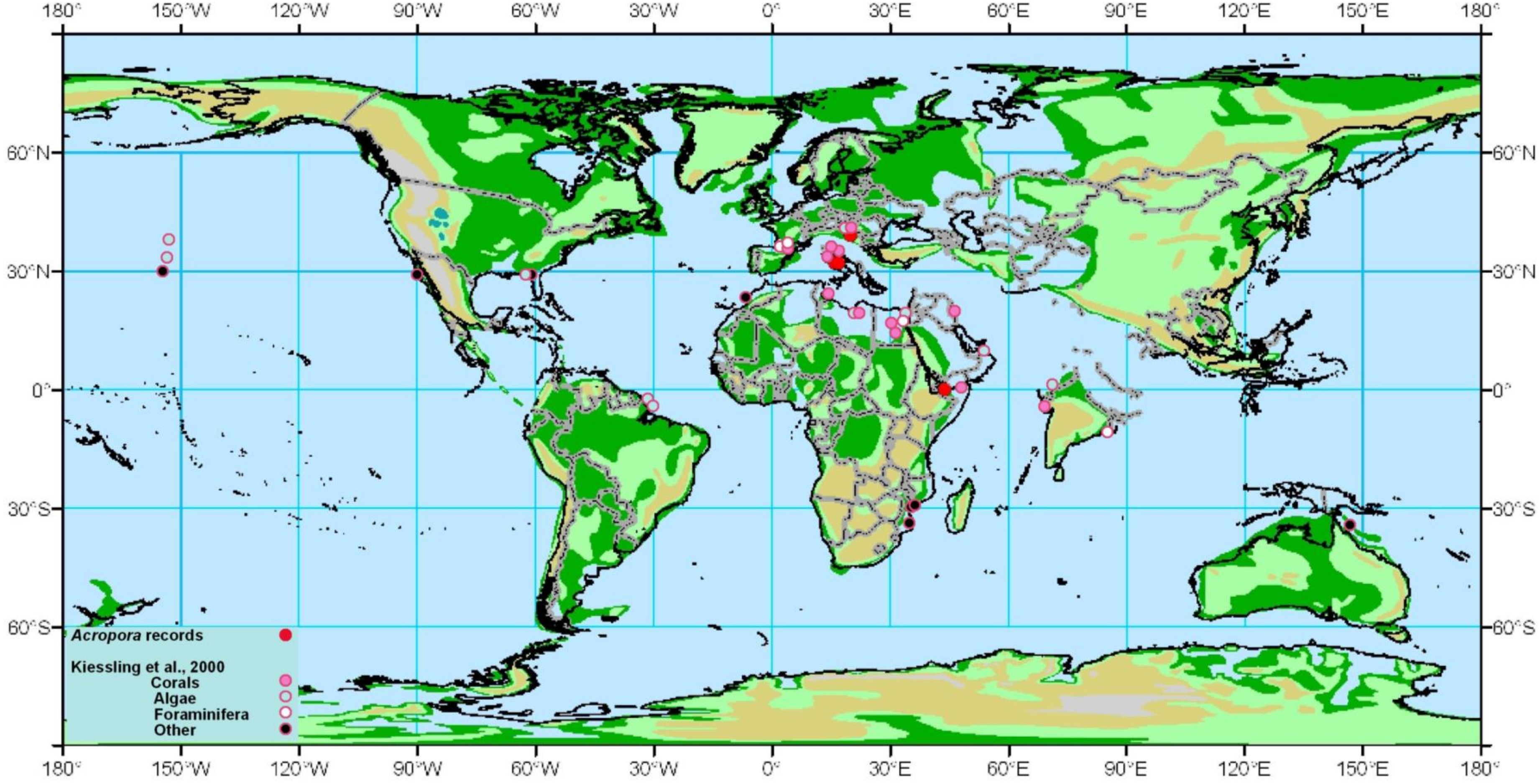


Figure 3.18. Late Paleocene-Early Eocene occurrences of reefs (non-Acropora occurrences from Kiessling et al.*, 2000)*

Middle -Late Eocene (48.6-33.9 Ma)

Global setting

The Middle to Late Eocene experienced the peak of early Cenozoic warming with the 'Eocene Climatic Optimum' (Zachos *et al*., 2001; Fig. 3.11). This was followed by the start of a trend in climatic deterioration, culminating in the build-up of both transient, and by the end of the Eocene, permanent, ice sheets labelled as the 'Oi-1 glaciation' (Zachos *et al*., 2001). This cooling is believed to have been triggered by the Arctic Ocean Azolla event (~49 Ma) and the formation of the Antarctic circumpolar current (Brinkhaus *et al*., 2006). The temperature gradient from the equator to pole was dramatically reduced compared with the present, with temperate regions showing the greatest difference and the tropics appearing similar to today (Greenwood and Wing, 1995). Evidence from planktonic foraminifera oxygen isotopes from deep sea cores indicates a sea surface temperature cooling of between 5-10° from the Early Eocene to Early Oligocene (Zachos *et al*., 2001), although work by Pearson *et al*. (2007) on drill cores from Tanzania now suggests a much more stable warm climate through the Eocene.

Tectonically, during the Eocene period, plate reorganisation was accompanied by a reduction in seafloor spreading rates (Zachos *et al*., 2001; Fig. 3.11). India continued to move northwards colliding with Asia, resulting in the formation of the Tibetan Plateau and the Himalayas. Australia and Antarctica remained connected until ~45 Ma, after which they began to separate resulting in changing circulation patterns causing the Antarctic region to cool, and the creation of ephemeral, and finally at the end of the Eocene, permanent ice-sheets (Zachos *et al*., 2001; Tripati *et al*., 2005). Prior to this Oi-1 glaciation, high-latitude (45 to 70 degrees in both hemispheres) sea surface temperatures were ~20°C and cooled by an average of ~5°C during the Late Eocene-Oligocene climatic transition (Liu *et al*., 2009).

In the Tethys realm, the uplift of the Alps, and the following collision of India with Asia, led to the loss of the western Tethys Sea and creation of the Mediterranean, with a series of basins with island archipelagos remaining to the north (Paratethys) along with an enlarged Indian Ocean (Rogl, 1999). Intracontinental seas covered large areas of the Eurasian platform and of western Asia.

From the Early Eocene (~50Ma) sea level is thought to have fallen by ~70-100m (Miller *et al*., 2005).

Carbonate platform and reefal distribution

Carbonate platform area changed dramatically throughout the Eocene. In the Middle Eocene, platform area reached a peak which was followed by a dramatic decline from the Late Eocene-Early Oligocene of carbonate platform areas and coral communities (Kiessling *et al*., 2003). Carbonate production was dominated by benthic foraminifera and calcareous algae, with coral reef deposits, especially in Southeast Asia being rare (Wilson and Rosen, 1998; Wilson, 2005). By the end of the Eocene all modern coral families had appeared with new radiations in scleractinian corals occurring throughout the Tethys region (Crame and Rosen, 2002).

Acropora distribution

Middle Eocene rocks preserve the most northerly palaeolatitudinal extent of *Acropora* with records from the Hampshire Basin, Southern England (palaeolatitiude ~49°N; Fig. 3.12). Other records from the North African-Mediterranean realm include abundant collections of specimens from France from the Paris Basin and additionally a literature-based record from the Sabassona reef, Vic Basin, Northeast Spain (Taberner and Bosence, 1985, Database ID 128). Additionally there is a literature-based record (Latham, 1929), of *Acropora* from Somalia during this period (Database ID 299-300). The concentration of records from the Hampshire and Paris basins are specimen based and are re-examined in this thesis (Chapter 5). The single record from the Vic Basin is specimen based and has been seen by a member of the working group. The Middle-Late Eocene also has the first record of *Acropora* in the Caribbean. These specimen based records in Frost and Langenheim (1974) are from the Ixtaclum Shale, Simojovel road section, near Chiapas, Mexico (Database ID 129) (Fig. 3.20).

By the Late Eocene, the most northerly palaeolatitudinal extent remained with specimens from the Hampshire Basin (Database ID 239 and 237). There are no *Acropora* records from the latest Eocene Paris Basin. *Acropora* was widespread throughout Europe, again being present in the Santa Giustina Limestone, Veneto

(Database ID 244), and the Nago Limestone, Trentino (Database ID 134), both in northern Italy. Other localities from Europe included records from Spain, the La Tossa Formation, Barcelona (Alvarez, 1997; Database ID 94) and from Son Sastre, S'Aresterta and Cala d'Egos in Mallorca (Alvarez, 1989; Database ID 285-287), and also two records from Graux (Database ID 309) and Mary pres Meaux (Database ID 308) in Belgium (Fig. 3.21).

Comparison with coral reef distribution

The Middle to Late Eocene northerly distribution of *Acropora* again follows that of the coral reef distribution for this period, but with *Acropora* occuring at marginally higher latitudes. During this period *Acropora* exhibited its most northerly palaeolatitudinal extent within its fossil record (~50°N). Within these high palaeolatitude occurrences of *Acropora* there is no evidence, or record, of a coral reef (*sensu stricto* Wood, 1999) and it is interpreted to have existed as coral thickets or, at a maximum extent, coral veneers (see Chapter 6).

Southerly palaeolatitudinal extent is restricted in comparison with both coral dominated reefs, and those dominated by other organisms. However, during this period the southerly palaeolatitudinal extent of coral reefs does become more restricted and there are no records from the southern hemisphere.

Robustness of record

Due to the focus of this thesis, in the Hampshire and Paris basins, there is a clustering of numerous specimen-based records from localities recorded from these basins. This reflects several biases including a preservational one, with preservation favoured due to the sedimentological setting of these corals (see Chapter 6), and a collecting bias, resulting from socio-economic factors favouring collecting by nineteenth century amateur palaeontologists in this region.

Collections from the NW European region are the only fossil *Acropora* that have been extensively been studies (Wallace and Rosen, 2006; Wallace, 2008) and hence suffer from the monographic effect.

Discussion

The Middle-Late Eocene saw the most northerly extent of *Acropora* in its entire Cenozoic history. This coincided with a period of global climatic warming when, globally, carbonate platform areas were at a peak. Following this period, global climate began to cool, culminating in the build-up of permanent ice sheets at the start of the Oligocene. Coincident with this cooling, areas of shallow water carbonates decreased. Counterintuitively, during this period *Acropora* remained in the high latitude, non-reefal setting of the Hampshire Basin. However regional tectonics and global climate change led to isolation of the Paris Basin and loss of records from this basin. The creation of a series of intracontinental basins in the Paratethys created increased potential habitat in the south-eastern Europe area resulting in new records being found in this region.

In Southeast Asia reefs deposits were scarce with no *Acropora* records from here during this period (Fig. 3.19). The Southeast Asia region still remains relatively understudied, with corals poorly preserved and rare but with more focused collecting may result in the record of *Acropora* in this region being extended. Following the first occurrence of corals in the Caribbean region, *Acropora* is found in the Ixtaclum Shale, Mexico.

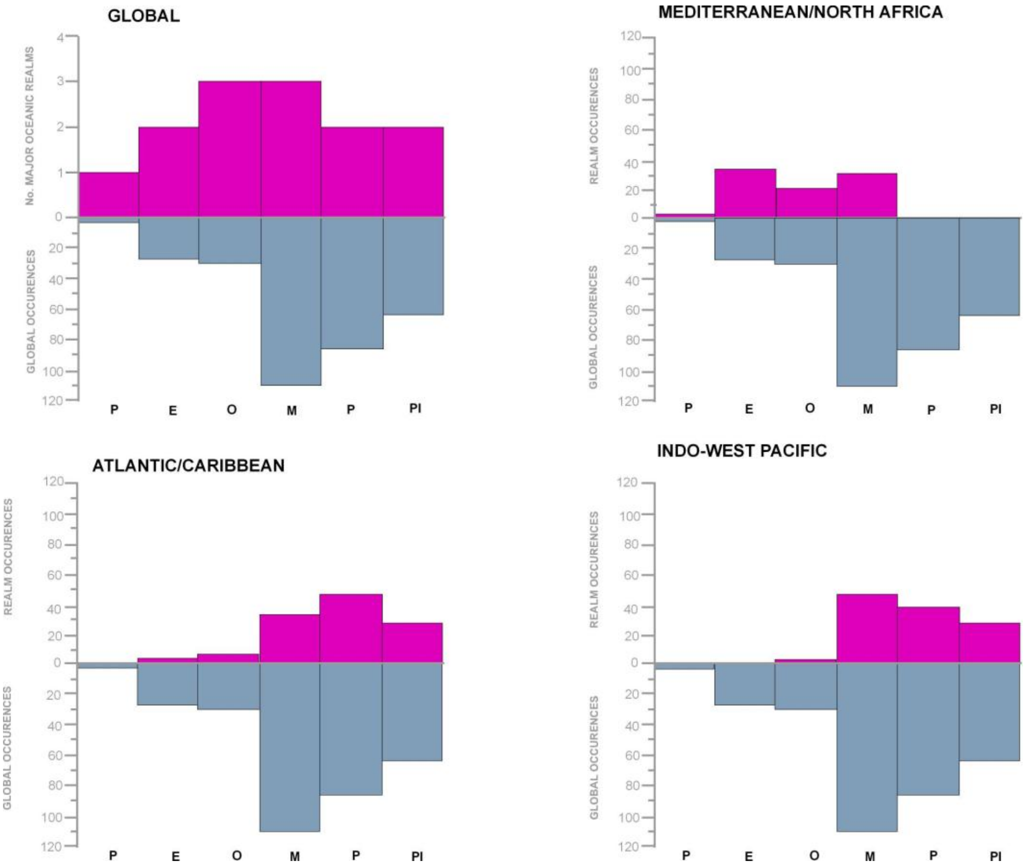


Figure 3.19. Distribution of Acropora in each oceanic realm throughout the Cenozoic

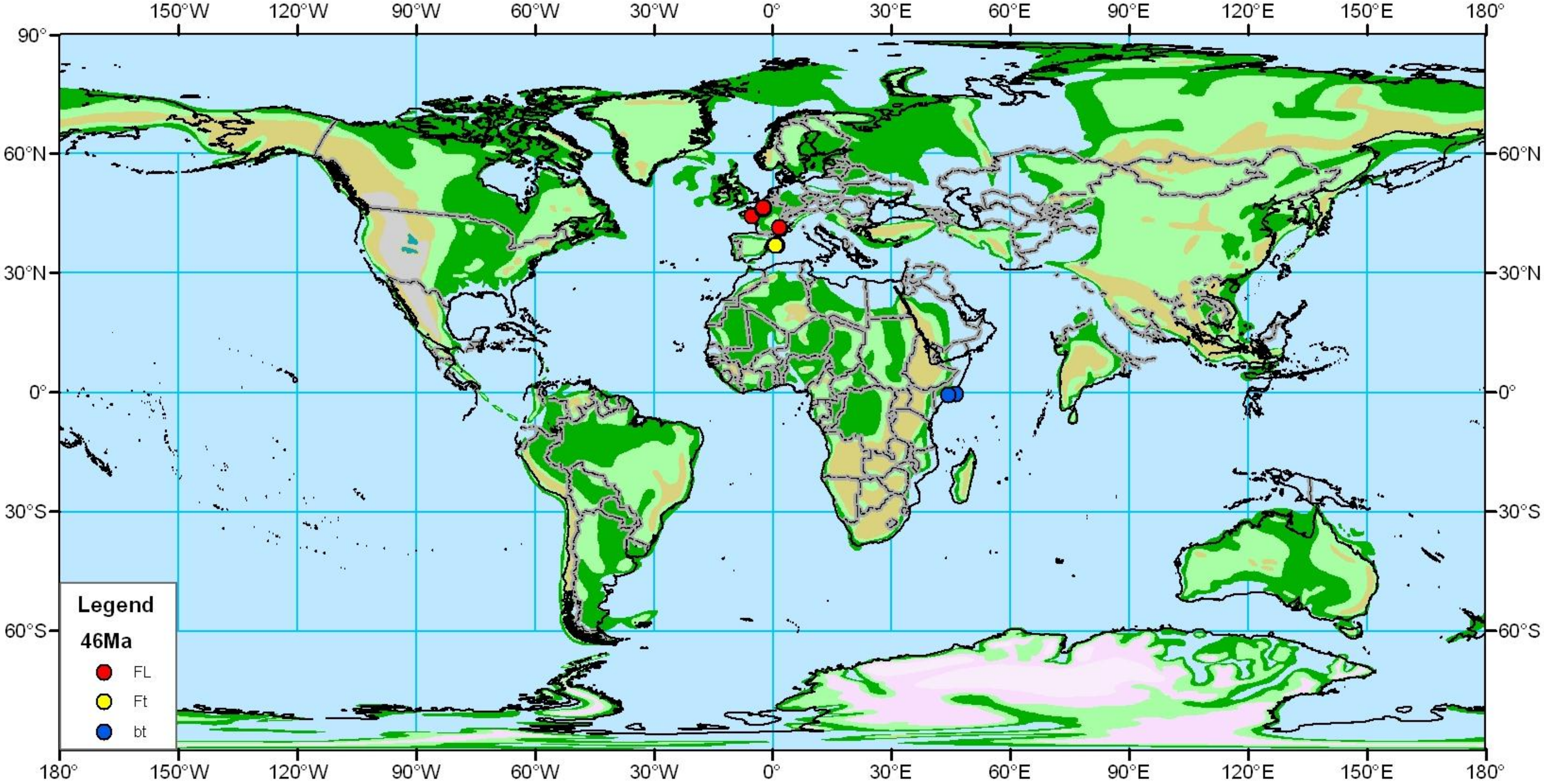


Figure 3.20. Middle Eocene occurrences of *Acropora* *(records that first appear during the interval and cross the top boundary, Ft; records confined to the time interval and first and last appearances occurred within the interval, FL; records that range through the entire interval and crosses both boundaries, bt)*

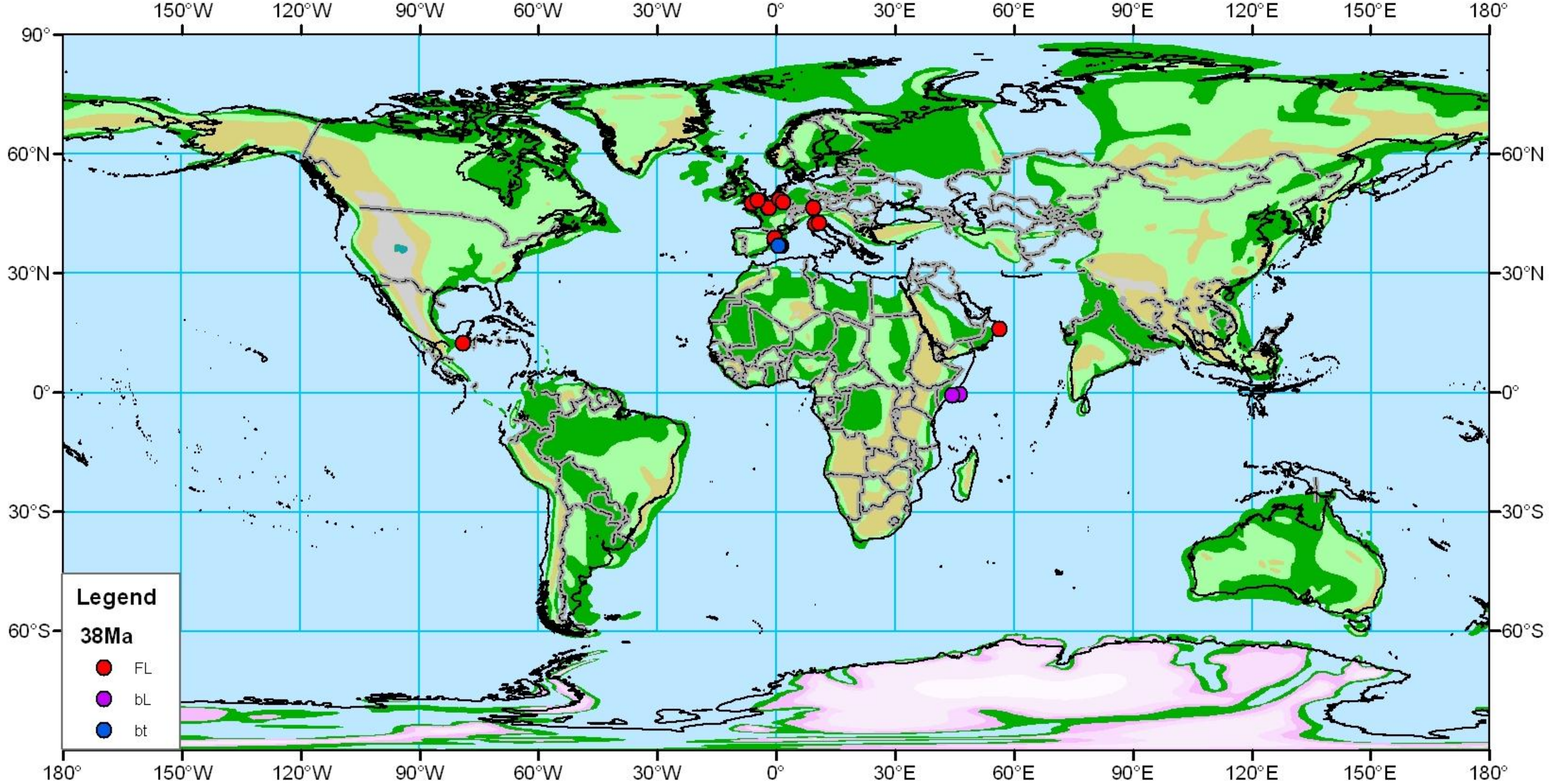


Figure 3.21. Late Eocene occurrences of Acropora (records confined to the time interval and first and last appearances occurred within the interval, FL; records which cross the bottom of the time interval and whose last appearance is within the interval, bL; records that range through the entire interval and crosses both boundaries, bt)

Oligocene (33.9-23.03 Ma)

Global setting

The Oligocene climate continued with the Paleogene trend of a general temperature decline from the greenhouse Eocene world to the early Oligocene icehouse world (Miller *et al.*, 1991; Fig. 3.11). This period was when Earth's climate shifted from a relatively ice-free world to one with substantial ice sheets in Antarctica (50% of that of the present-day), following smaller, transient glaciations in the Middle Eocene. High-latitude (45° to 70° in both hemispheres) temperatures before the climate transition were ~20°C and cooled by an average of ~5°C (Liu *et al*, 2009). During the latter part of the Oligocene a warming trend reduced the extent of Antarctic ice (Zachos *et al.*, 2001).

Mountain building continued in western North America, and the Alps continued to rise in Europe as the African plate pushed northwards into the Eurasian plate, isolating remnants of the Paratethys Sea with a brief marine incursion marking the Early Oligocene in Europe. During the Oligocene, South America finally detached from Antarctica and drifted northwards towards North America, allowing the Antarctic Circumpolar Current to flow, with rapid cooling of the Antarctic continent.

Coincidental with this period was the deepening of the calcite compensation depth (Merico *et al.*, 2008).

Carbonate platform and reefal distribution

Coral communities declined near the Eocene-Oligocene boundary, but extensive platform-rimming reefs comprising scleractinian corals and coralline algae were present by the Oligocene, with the Late Oligocene being a time of widespread and massive reef development (James, 1983; Kiessling *et al.*, 2003). By the late Paleogene, carbonate platform area had become most spatially extensive in the North African-Arabian region with large areas of shallow water carbonate production also in the Gulf of Mexico (Kiessling *et al.*, 2003). Diverse coral reefs and a tropical mollusc fauna flourished along the northern coast of Western Tethys (Schuster, 2002; Harzhauser *et al.*, 2007).

The two modern major oceanic realms, Southeast Asia and the Caribbean, appear to have very different preserved reefs of Oligocene age. In the Early Oligocene, Caribbean reefs are poorly known with only one reefal assemblage being reported during this period from Chiapas, Mexico (Budd, 2000). In contrast to this, during the Late Oligocene, reefs of the Caribbean region were well-developed with a moderately diverse fauna (Budd, 2000; Johnson *et al*., 2008). Both in the Eocene and Oligocene Caribbean faunas appear to consist of mostly cosmopolitan taxa whose distribution extended at least to the western Tethyan realm. Edinger and Risk, 1994, documented a 50% decrease in Caribbean 'hermatypic' corals in the latest Oligocene-Early Miocene (Oligocene/Miocene Transition, OMT-Johnson *et al*., 2008) possibly in response to the glaciation which ended the warm interval of the Late Oligocene. Large reefal build-ups are common in the Oligocene, including the Antigua Formation of Antigua (Weiss, 1994), the White Limestone of Jamaica (Stemann, 2004), and the Lares and Juana Diaz Formations of Puerto Rico (Frost *et al*., 1983).

In contrast, the Late Oligocene in the Southeast Asia realm had little reef building and a low diversity of reef builders (Wilson and Rosen, 1998; Wilson, 2002). During most of this period, and the Eocene, corals are rare, with solitary or isolated colonial forms present in shallow and sometimes muddy coastal deposits with patch reefs. Reefal build-ups or reef rimmed margins only start to be reported from the later part of the Oligocene (Wilson, 2008). There was a marked increase in the extent of carbonates, and a change from larger foraminifera and coralline algal deposits to coral dominance, around the Oligo-Miocene boundary (Wilson and Rosen, 1998). In summary, Johnson *et al*. (2008) suggested these two major oceanic realms were ecologically discordant response to local and regional changes rather than responding to the global environmental setting (see also Rosen, 2002).

The Oligocene–Miocene transition (OMT) was an important time of regional biotic change in the Caribbean. During this time, there was extinction of a widespread Oligocene Tethyan reef biota and the origin of many lineages of reef corals that are characteristic of the western Atlantic today (Vaughan, 1919; Frost, 1977; Budd, 2000). For example, the Late Oligocene biotas of Antigua (Johnson, 2007) and Puerto Rico (Frost *et al*., 1983) are distinct from early Miocene units in Panama (Johnson and Kirby, 2006), Florida (Weisbord, 1973), and Trinidad (Johnson, 2001). Typical Oligocene taxa include globally extinct genera, such as *Antiguastrea* and *Astrocoenia*, as well as taxa such as *Diploastrea* and *Favites*, which are now extinct in the Western Atlantic but have living representatives in the Indo-West Pacific (Budd, 2000). In contrast, Miocene reef-coral assemblages are dominated by lineages that comprise the extant western Atlantic fauna, including *Porites*, *Montastraea*, and the plate-forming, agariciid genera.

The OMT also coincides with a regional decline in reef building that persisted until their re-establishment following Plio–Pleistocene environmental change in the region (Johnson *et al*., 2008).

Acropora distribution

The Oligocene period shows the most globally extensive distribution of *Acropora* with records in all three major Cenozoic oceanic realms: Indo-West Pacific, Caribbean and Tethyan realms (Fig. 3.12, 3.13). In the Tethyan realm, the northerly latitudinal extent of *Acropora* during this period had contracted compared with the Eocene. This principally resulted from the termination of carbonate deposition, and loss of the diverse suite of Eocene corals, in the Hampshire and Paris basins. The most northerly latitudinal occurrences of *Acropora* during the Early Oligocene in the Tethyan realm are specimen-based records from the Bavaria region, South Germany (palaeolatitude 47°N; Database ID 241; Fig. 3.12). Although no records are known from the Paris Basin, records are found in the Upper Oligocene, southern France area of the La Teoulere reef, Landes (Cahuzac and Chaix, 1994, 1996, Database ID 264) and the Carry-Le-Rouet section, Marseille (Chevalier, 1961; Monleau *et al*., 1994; Database ID 222). Extensive records are abundant throughout the Oligocene in Italy (i.e. Lower Oligocene-Vicenza, Geister and Ungaro, 1977, Database ID 257; Upper Oligocene-Cairo Montenotte, Pfister, 1985, Database ID 137-8, Piemont, Pfister, 1985, Database ID 258) where coral assemblages are believed to have thrived in varied environments including permanently or episodically turbid waters as a result of terrigenous input (Silvestri *et al*., 2008; Silvestri and Quaranta, 2009). Other Tethyan records include the Lower Oligocene of Mallorca and Upper Oligocene of Spain, Greece, Slovenia and Malta. *Acropora* seemed common in late Rupelian/Chattian coral assemblages described from Liguria (Database ID 221) and Piemont (Pfister 1980, 1985; Database ID 258) and in Chattian coral layers of southern France (Chevalier, 1962, Monleau *et al*., 1994; Database ID 222). Pfister (1985) described reef limestones with abundant rubble of encrusted *Acropora* branches from northern Italy. Massive, tabular *Acropora* colonies are also present but rare. However, the dominant genera of the different coral associations described by Pfister (1985) are *Goniopora*, *Actinacis*, and *Astreopora*. The coral occurrences of southern France (Carry-le-Rouet, Provence) are mainly composed of allochthonous layers formed by branches of *Porites* and *Acropora* and autochthonous isolated, massive colonies (Chevalier, 1961). Significantly, the first record of *Acropora* dominating a reef structure as seen in many modern reefs comes from the shallow subtidal environments of the Mesohellenic Basin (Late Oligocene, 28–23 Ma) in Greece (Schuster, 2002; Database ID 220).

Within the Caribbean realm *Acropora* records are found in the Upper Oligocene of the Pueblo Nuevo reef (Frost and Langenheim, 1974; Database ID 130) and La Quinta Formation (Frost and Langenheim, 1974; Database ID 139), Chiapas area, Mexico. Records are also found in Jamaica (Stemann, 2004; Database ID 259-260), Antigua (Frost and Weiss, 1979; Database ID 135), Puerto Rico (Edinger and Risk, 1994, Database ID 141) and Haiti (Vaughan *et al.*, 1921; Database ID 202).

The first records of *Acropora* in the Indo-Pacific realm are from the Oligocene. Records are found from Borneo (Fritsch, 1878; Database ID 95) and Tonasa Formation, South Sulawesi (Wilson and Rosen, 1998; Database ID 132) (Fig. 23 and 24).

Comparison with coral distribution

The Oligocene maximum northerly extent of *Acropora* coincides with that of the coral reef distribution for this period (palaeolatitude ~40°N), with *Acropora* occurring at marginally higher latitudes. Carbonate platform areas had become most widespread in the North African-Arabian region which is also reflected in the density of *Acropora* records from this region, and the massive widespread global reef development.

The southern latitudinal extent of *Acropora* significantly expanded in the Oligocene (~10°S), resulting in the genus extending for the first time into the Southern Hemisphere. Simultaneously, reefs dominated by corals retracted (~20°S), accompanied by the retraction of non-coral dominated reefs.

Robustness of record

For socioeconomic reasons collecting has focused on the Atlantic-Caribbean and Mediterranean-North African realms rather than the Indo-Pacific for Oligocene outcrops. Some missing taxa may truly not have been preserved anywhere, whereas others may exist as fossils but have not yet been discovered and/or properly identified by palaeontologists. Few coral workers have targeted the SE Asian region and a resulting sampling bias is introduced by a bias against targeting corals at localities. Poor preservation of corals and reef systems from this region has created difficulties in identification, especially to species level. Owing to these biases in sampling intensity, tropical Indo-Pacific taxa almost certainly have a significantly lower probability of being recorded as fossils than do taxa from higher latitudes.

Discussion

By the early Oligocene high latitudinal regions experienced cooling (Zachos *et al*., 2001) resulting in the latitudinal restriction of warm water biota (Montaggioni and Braithwaite, 2009). Counterintuitive to this Perrin, 2002, showed that during this period scleractinian corals maintained high diversity as seen previously in the Eocene also reflected in the distribution of *Acropora* records. The maximum northerly extent of *Acropora* coincides with that of the coral reef distribution (palaeolatitude ~40°N), with the genus occurring at marginally higher latitudes. There are numerous records of *Acropora* throughout the Arabian Peninsula (Schuster, 2002) and globally, records of *Acropora* are widespread in tropical areas of all three fossil oceanic realms; Indo-West pacific, Atlantic-Caribbean and North Africa-Mediterranean (Fig. 3.22).

Stanley, 2006, suggested that a rise in Mg/Ca ratios resulted in increased reef-building capacities with reef distribution extending throughout the Tethys, Southeast Asia and eastern Pacific. In the late Oligocene reef coral faunas began to diversify and taxonomic richness increased with a surge in reefal development (Montaggioni and Braiithwaite, 2009). Importantly, the first record of *Acropora* dominating a reef is recorded from the late Oligocene in Greece (Schuster, 2002).

The first record of *Acropora* in the Indo-Pacific are from the Oligocene reflecting a change in the style of carbonate deposition in the region, coinciding with a reduction in the deep-water throughflow between the Pacific and Indian Oceans (Kuhnt *et al*., 2004) and marine incursions and therefore habitat creation in the area (Wilson and Rosen, 1998; Wilson, 2002).

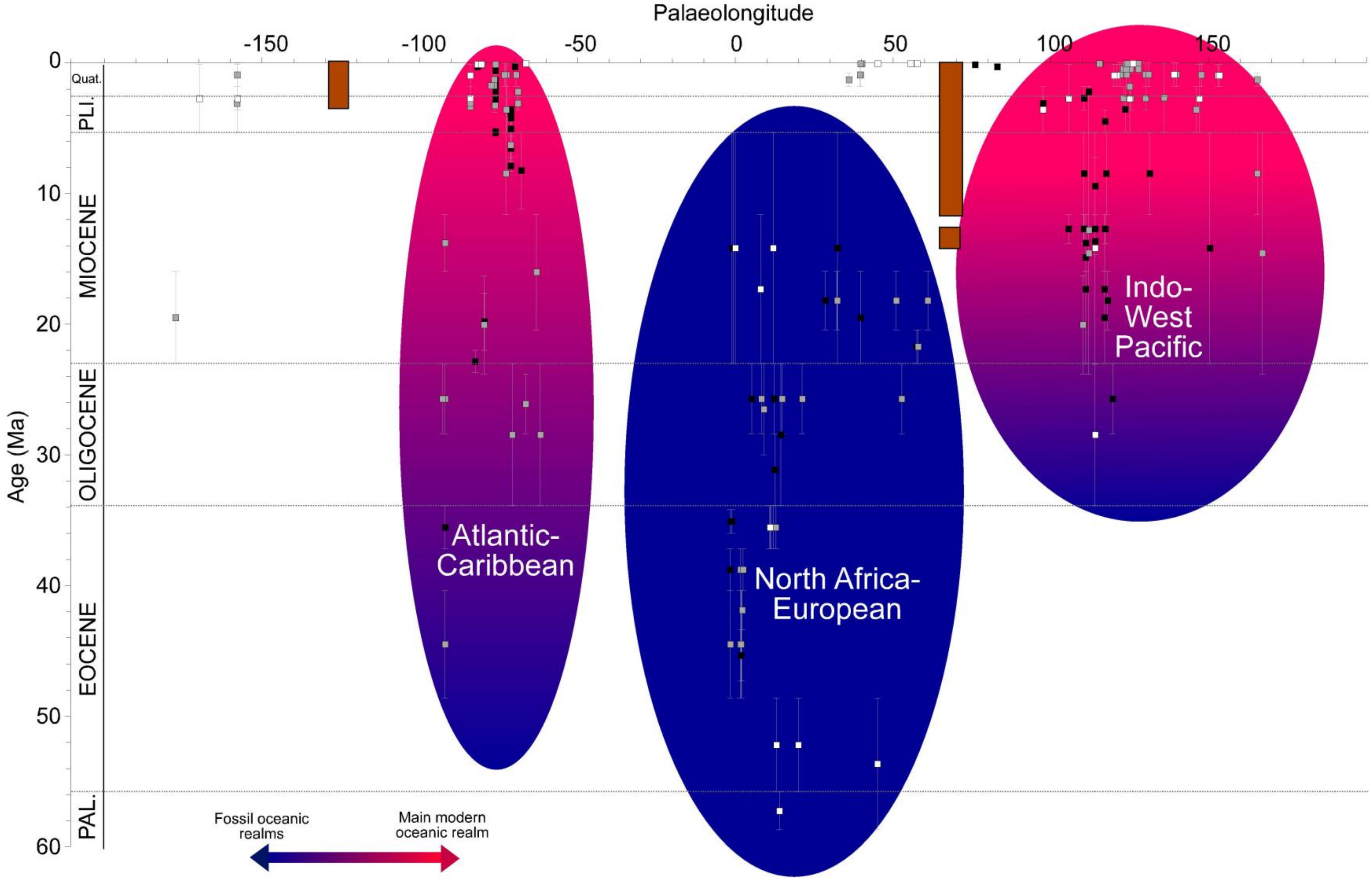


Figure 3.22. Illustrated boucotgram showing the establishment of the major oceanic realms

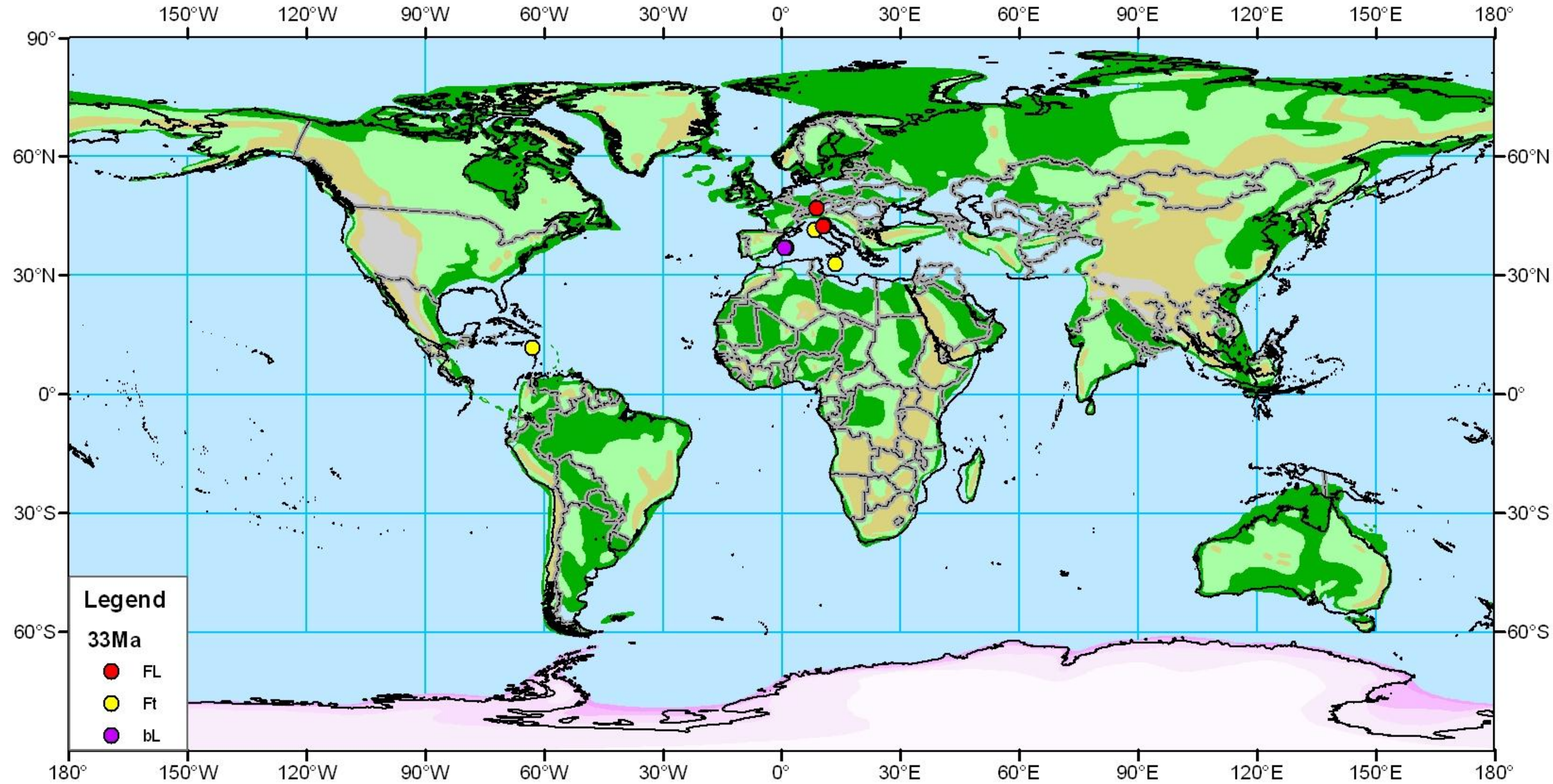


Figure 3.23. Early Oligocene occurrences of <u>*Acropora*</u> *(records that first appears during the interval and crosses the top boundary, Ft; records confined to the time interval and first and last appearances occurred within the interval, FL; records which cross the bottom of the time interval and whose last appearance is within the interval, bL)*

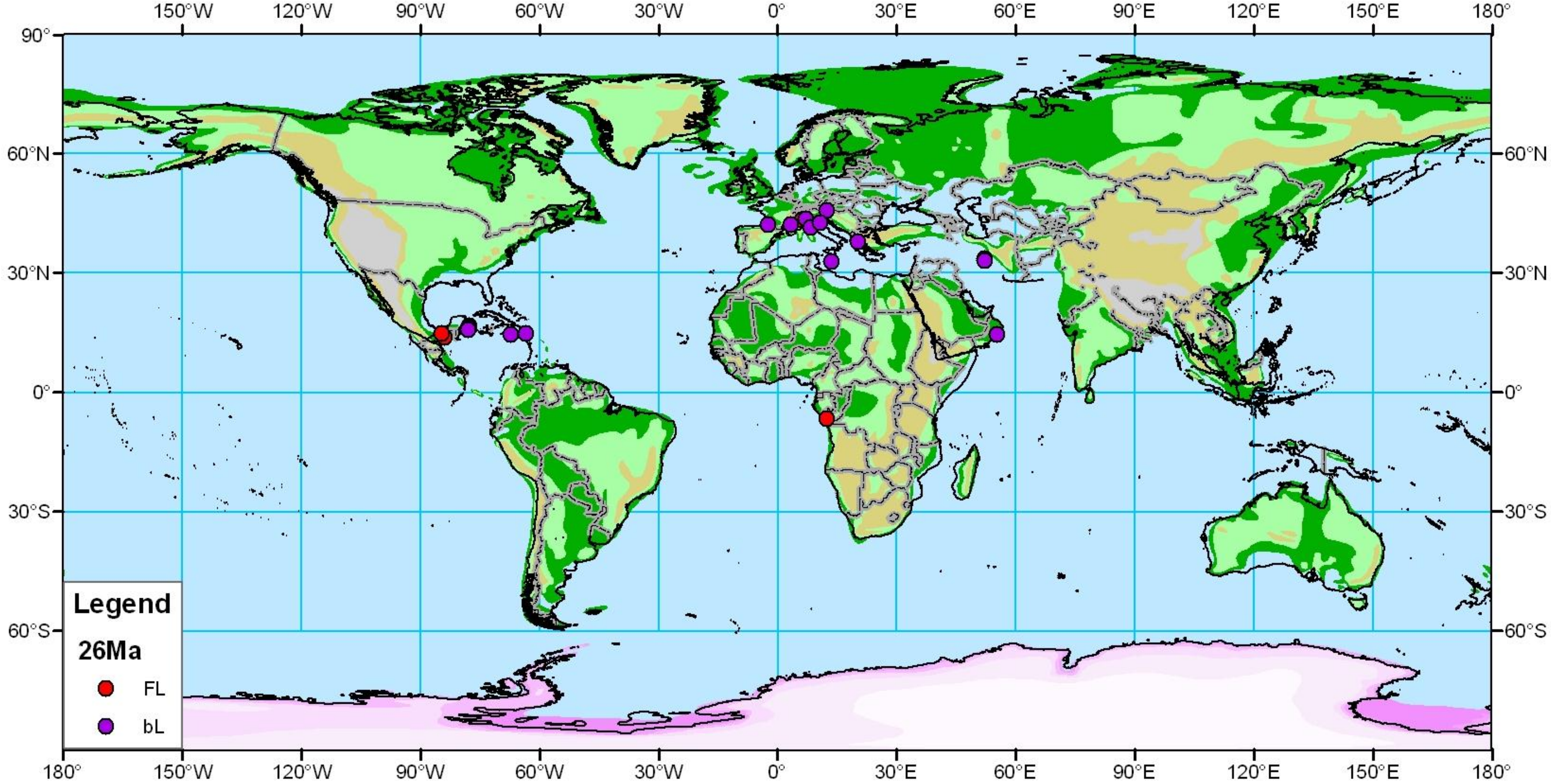


Figure 3.24. Late Oligocene occurrences of Acropora (records confined to the time interval and first and last appearances occurred within the interval, FL; records which cross the bottom of the time interval and whose last appearance is within the interval, bL)

Miocene (23.03-5.33 Ma)

Global setting

From the Late Oligocene through to the Middle Miocene global ice volume remained low with the exception of several brief periods of glaciations (e.g. M1-events) (Fig. 3.11). A global warm phase occurred in the middle Miocene, ~15 Ma, (Middle Miocene Climate Optimum, MMCO; You *et al.*, 2009) with a global annual mean surface temperature of 18.4°C, about 3°C higher than present (You *et al.*, 2009). This was followed, at ~10 Ma, by gradual cooling and the reestablishment of a major ice sheet on Antarctica (Zachos *et al.*, 2001). In the south-western Pacific between 14.2-13.8 Ma region planktonic foraminifera indicate a sudden cooling of between 6-7°C (Shevenell, 2004).

In the Miocene continents drifted towards their present position with the land bridge between south and north America and the eastward connection of the Mediterranean with the Indian Ocean being the main major features of difference (Fig. 3.10). Two important geological events had a major influence on the climate of the period; the uplifting of the Tibetan plateau and the desiccation of the Mediterranean Sea. Indentation continued following the collision of India with Asia and culminated in the greatest period of uplift of the Tibetan Plateau in the Miocene (Chung *et al.*, 1998). Throughout the Paleogene, the Tethys Sea, precursor to the Mediterranean, covered parts area of Europe and North Africa. Europe was an archipelago with shallow seas and small intercontinental basins. The Tethys Sea remained an open east-west connection between the present- day Atlantic and Pacific Oceans via the Mediterranean until approximately the mid-Miocene (Rogl and Steiniger, 1984), although it seems likely that there were several closures and reopenings from the late Oligocene or early Miocene (Rosen, 1988). Following the gradual narrowing of the eastern end of the Tethys Sea, it became cut off completely from the Indian Ocean. This resulted in a large marine basin being formed that encompassed the Mediterranean, Black Sea and Caspian Sea, that was almost cut off from the Atlantic Ocean. However, between 5.96 and 5.33 Ma, in the Messinian salinity crisis occurred, resulting from the closure of marine gateways between the Atlantic Ocean and the Mediterranean Sea. Different causes for this isolation have been debated (e.g. Duggen *et al.*, 2003). Recently Duggen *et al*. (2004) proposed a geodynamic model to illustrate how mantle processes affected western Mediterranean palaeogeography over ca. 20 Ma, causing a change in the location of marine gateways connecting the Mediterranean Sea with the Atlantic Ocean. Changes in palaeogeography culminated with the isolation and desiccation of the Mediterranean Sea in the Messinian, triggering the Messinian Salinity Crisis.

Carbonate platform and reefal distribution

Neogene carbonate platform areas were widespread but dispersed (Kiessling, 2005). Equatorial platforms were largely bioclastic with common reefal debris. Through the Miocene, European platforms continued to decline with relict platforms in the Paratethys region attaining a pronounced cool-water aspect. Miocene carbonates in the Mediterranean are dominated by organic buildups of rhodalgal and coral-reef facies with local stromatolitic mounds, azooxanthellate coral mounds and oyster banks and occur in a wide variety of tectonic settings and substrates (Esteban, 1996). Coral reefs in this region reflect the transition between Early Miocene open-oceanic, humid-tropical conditions and Late Miocene landlocked, semi-arid and marginally subtropical environments. Coral diversity decreased from Early to Late Miocene times (Rosen, 1999) with low-diversity reefs of latest Miocene age in the western Mediterranean. These were essentially monogeneric, constructed of *Porites* and encrusting coralline algae (Bosellini and Perrin, 2008; Fig. 3.25).

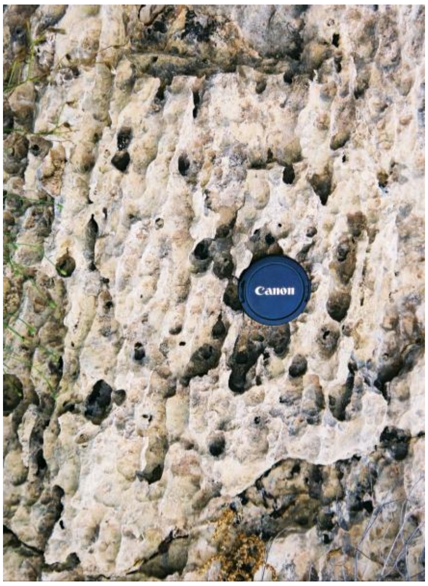


Figure 3.25. Branching Porites corals, monogeneric reef. Lucainena, Sorbas Basin (Spain), Late Miocene (Messinian), Lens cap = 50 mm

In the Southern Hemisphere, cold-water carbonate platforms had a similar composition although bryozoans appear more important (Kiessling *et al*., 2003).

The Tethys Ocean finally closed (Langhian) and the Mediterranean formed as a separate sea. Two barriers also developed and began the differentiation of the Indo-Pacific and Caribbean coral faunas. A ‘soft’ marine barrier in the Eastern Pacific is believed to have developed in the Miocene which was later joined by a ‘hard’ barrier due to the uplift of the Isthmus of Panama in the Pliocene (Coates and Obando, 1996; Collins *et al*., 1996). The other barrier was the emergence of the African-Asian land barrier which became the Middle East around the late Oligocene-Miocene (Rögl and Steiniger, 1984). Reefs were abundant with some early Miocene reefs being characterised by large, cylindrical solitary corals which are quite absent in reefs today (McCall *et al*., 1994).

In the Caribbean, Miocene coral communities are more common in small patch reefs, fringing reefs, or siliciclastic-dominated settings in units such as the Anguilla Formation (Budd *et al*., 1995), the Tamana Formation of Trinidad (Johnson, 2001), or the La Boca and Valiente Formations of Panama (Coates *et al*., 2003; Johnson and Kirby, 2006). Reef building was suppressed in the Caribbean for 20 myr, but there is no evidence for declining coral growth rates during this interval (Johnson and Perez, 2006), suggesting that lack of carbonate accumulation was not a function of reduced coral growth rates.

Acropora distribution

During the Miocene, three main reef provinces, Mediterranean, Caribbean, and Indo-Pacific, developed from splitting of the previously extensive Tethyan province. The most northerly latitudinal extent of *Acropora* records that are specimen-based are from the Loire (Database ID 273-274) and Aquitaine basins (e.g. Database ID 265-271), France, found largely within numerous marine littoral deposits (~45°N). Other records found within this realm include northern Italy (Liguria, Piedmont and Vicentin Lessini Shelf), Cyprus (Terra Reefs, Pakhna Formation, Follows *et al*., 1996, Database ID 261), Portugal (Chevalier, 1964, Database ID 301-2), Iran (Database ID 153, 157, 214-215, 219 and 249), Turkey (Hakyemez, 1989, Database ID 304), Egypt (Schuster, 2002, Database ID 217-218), along with a record from the Pemba Island, East Africa (Database ID 250), and a record from Pakistan (Duncan, 1880, Database ID 292), the

Indian Ocean sub-realm. The Gulf of Suez (Eastern Desert, Egypt) specimens have a similar palaeoenviromental setting to those found in the Hampshire Basin (Eocene) found within deposits of calm, low energy environment forming thickets and, in places, small patches.

Records became more widespread and abundant in the Indo-Pacific and Atlantic-Caribbean realms throughout the Miocene. In the early Miocene Indo-Pacific realm specimen-based records come from Sabah (Database ID 45-49), Java (Database ID 14-15, 21-22, 37-44, 87-88, 146, 281-282, 296, 298), Borneo (Database ID 1, 13, 23-25, 27-28, 100, 126-127, 142-143, 284), Papua New Guinea (Hohnen, 1978, Stewart and Sandy, 1988, Database ID 240), Japan (Ozawa at al., 1995, Database ID 263) and the Eniwetak Atoll, Marshall Islands (Wells, 1964, Database ID 144-145). In the Caribbean, specimen-based records include Panama (Vaughan, 1919, Database ID 52, Johnson and Kirby, 2006, Database ID 147-151), Hawaii (Grigg, 1988, Database ID 152), Anguilla (Budd *et al.*, 1995, Database ID 154-156), Columbia (Geister, 1975, Database ID 291) and Maryland (Cope, 1868, Database ID 293) (Fig. 3.26 and 3.27).

The Late Miocene period of coral growth was interrupted when hypersaline conditions became established in the Mediterranean region and ultimately resulted in complete disappearance of *Acropora* from this region. Two distinct modern realms became established; Indo-Pacific and Atlantic-Caribbean. In the late Miocene Indo-Pacific realm specimen based records are from Borneo, Java, Bikini Island, Marshall Islands (Emery *et al.*, 1954, Wells, 1954, Database ID 158). In the Caribbean, specimen-based records are from the Isla de Mona Reef complex, Puerto Rico (Budd *et al.*, 1994, Gonzalez *et al.*, 1997, Database ID 277), Dominican Republic (Budd and Johnson, 1999, Database ID 159, Saunders *et al.*, 1986, Database ID 54-59, 62-66), Bahamas (Budd and Kievman, in review, Database ID 60-61), Mexico (Frost and Langenheim, 1974 , Database ID 131) and Haiti (Butterlin, 1960, Database ID 198) (Fig. 3.27 and 3.28).

Comparison with coral distribution

The records of *Acropora* are more latitudinally restricted than the oldest records in the Late Paleocene. The maximum northerly extent of *Acropora* in the Early Miocene is similar to that of the northerly extent of both coral and non-coral dominated reefs. However, following this, the latitudinal extent of the genus in the northern hemisphere

(~18°N) retracted drastically, principally as a result of the loss of the genus from the Mediterranean realm. In the southern hemisphere, the latitudinal extent of the genus remained the same as that of the end of the Oligocene (~10°S). This is more restricted than the extent of coral and non-coral dominated reefs which expanded their latitudinal limit southwards (~45°S).

Robustness of record

Much more is known about the Tethys and Caribbean areas, than about the Indo-Pacific, partly because there are relatively few well preserved Indo-Pacific reefs of this period, and although Miocene reefs in this area are abundant, have been little studied. Two compilations, Ken Johnson SEA and NMITA (Budd *et al.*, 2001), produce a bias in the density of records from the Atlantic-Caribbean and Indo-Pacific resulting from the recent revision of coral assemblages within each region.

Discussion

By the Mid-Miocene (16–12 Ma) 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; Bosellini and Perrin, 2008). Non-reefal occurrences of *Acropora* which had been common throughout the Mediterranean region had become rare to be followed by a period of abundant *Acropora* dominated reefal deposits of the Indo-Pacific and, more so, the Caribbean.

The Miocene (21-6 Ma) of the Indo-Pacific is a period of pronounced first occurrences of reef coral species, and the complete reorganisation of coral communities. The collision of Australia/New Guinea with the islands off the Asian continent, which began in the Early Miocene (Audley-Charles, 1981; Hall and Holloway, 1998) may have further contributed to this period of evolutionary diversification. This Miocene diversification is also demonstrated by the genus with the emergence of Caribbean species which is likely to coincide with the effective isolation between Caribbean and Indo-Pacific *Acropora* species. The earliest *A. cervicornis* and *A. palmata* fossils are approximately 6.6 Ma (Budd and Johnson, 1999) and 3.6–2.6 Ma (McNeill *et al.*, 1997) respectively and appear to represent the most ancestral extant species of the genus.

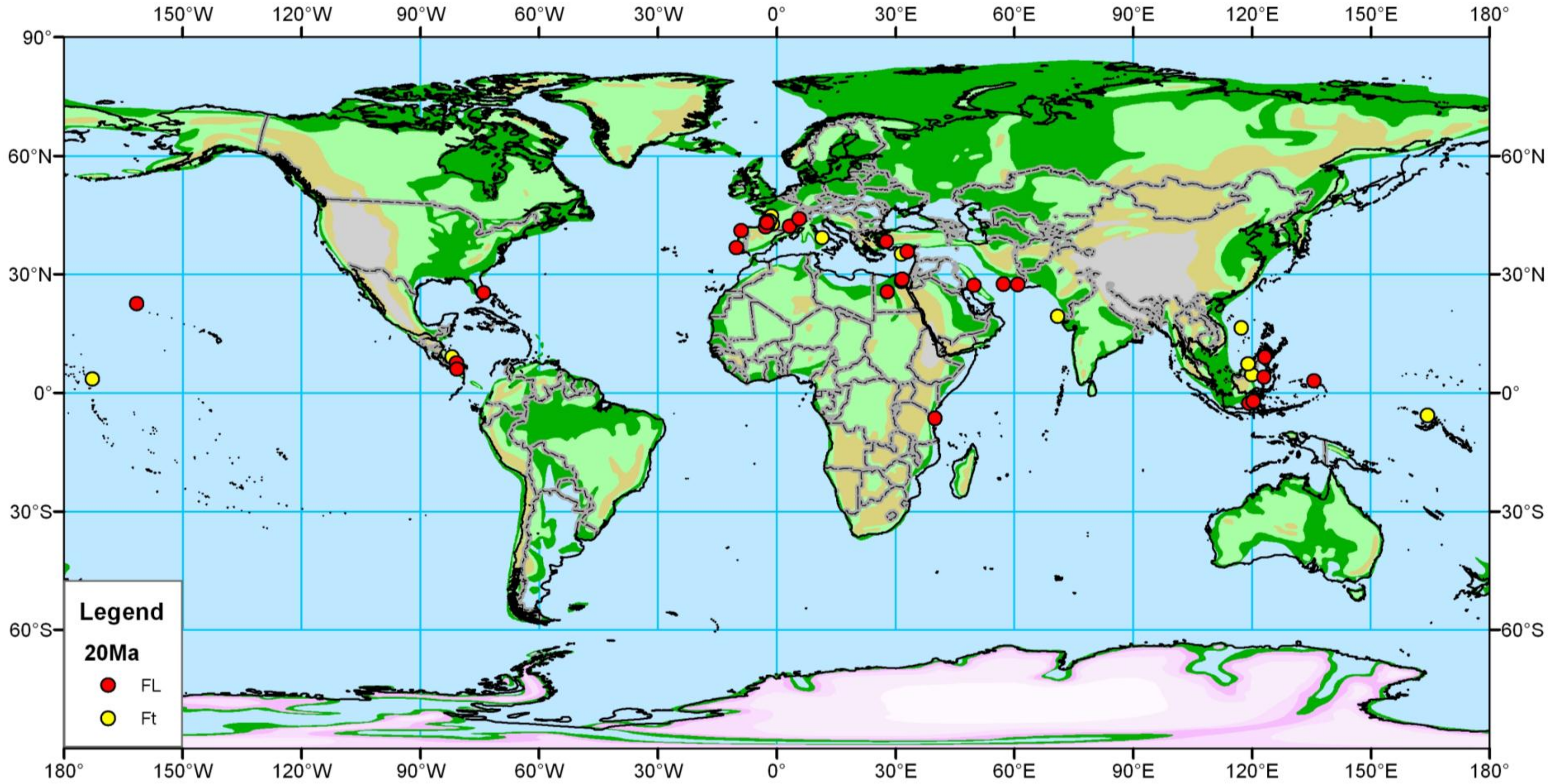


Figure 3.26. Early Miocene occurrences of <u>*Acropora*</u> *(records that first appears during the interval and crosses the top boundary, Ft; records confined to the time interval and first and last appearances occurred within the interval, FL)*

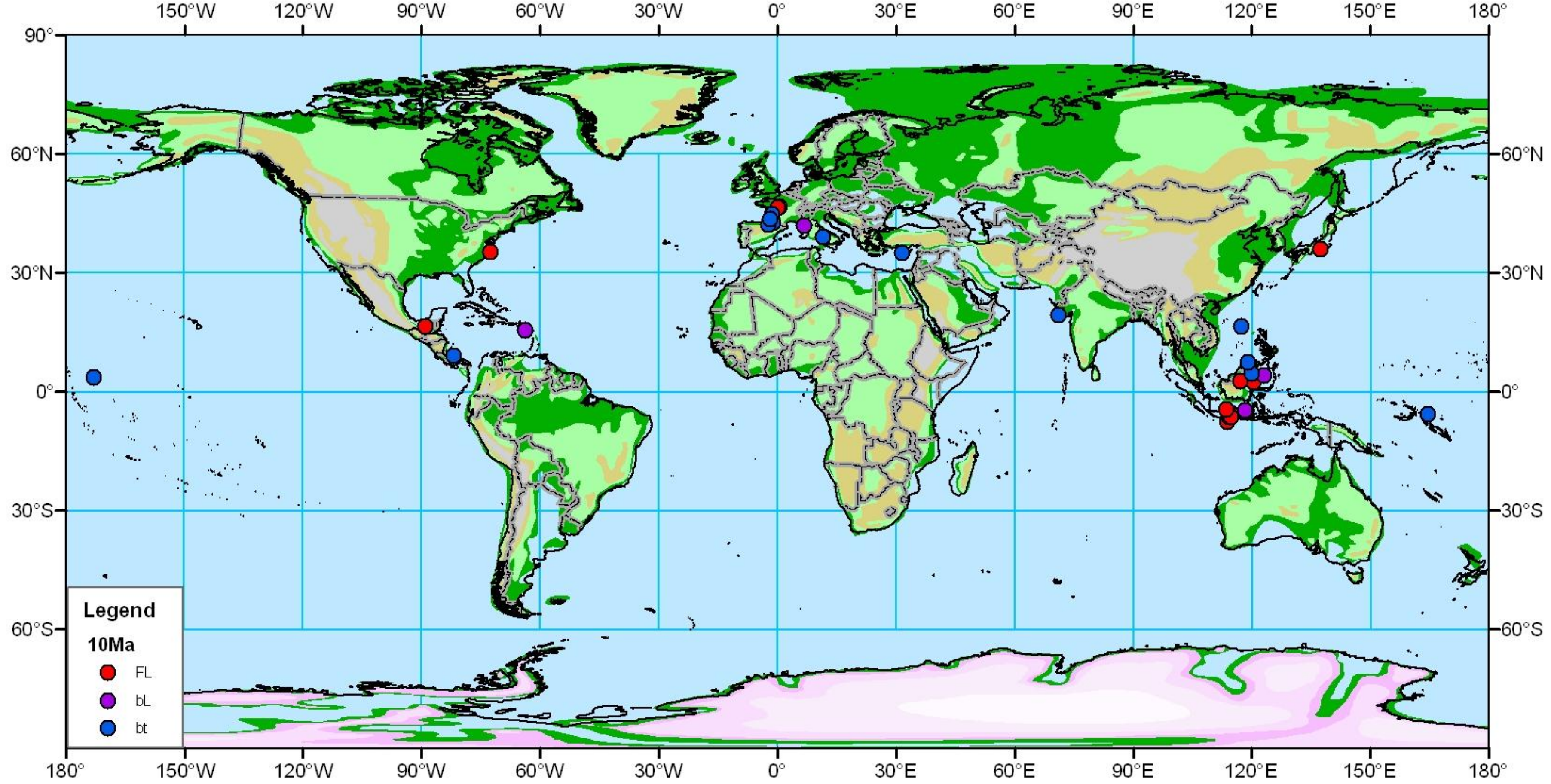


Figure 3.27. Middle Miocene occurrences of <u>*Acropora*</u> *(records confined to the time interval and first and last appearances occurred within the interval, FL; records which cross the bottom of the time interval and whose last appearance is within the interval, bL; records that range through the entire interval and crosses both boundaries, bt)*

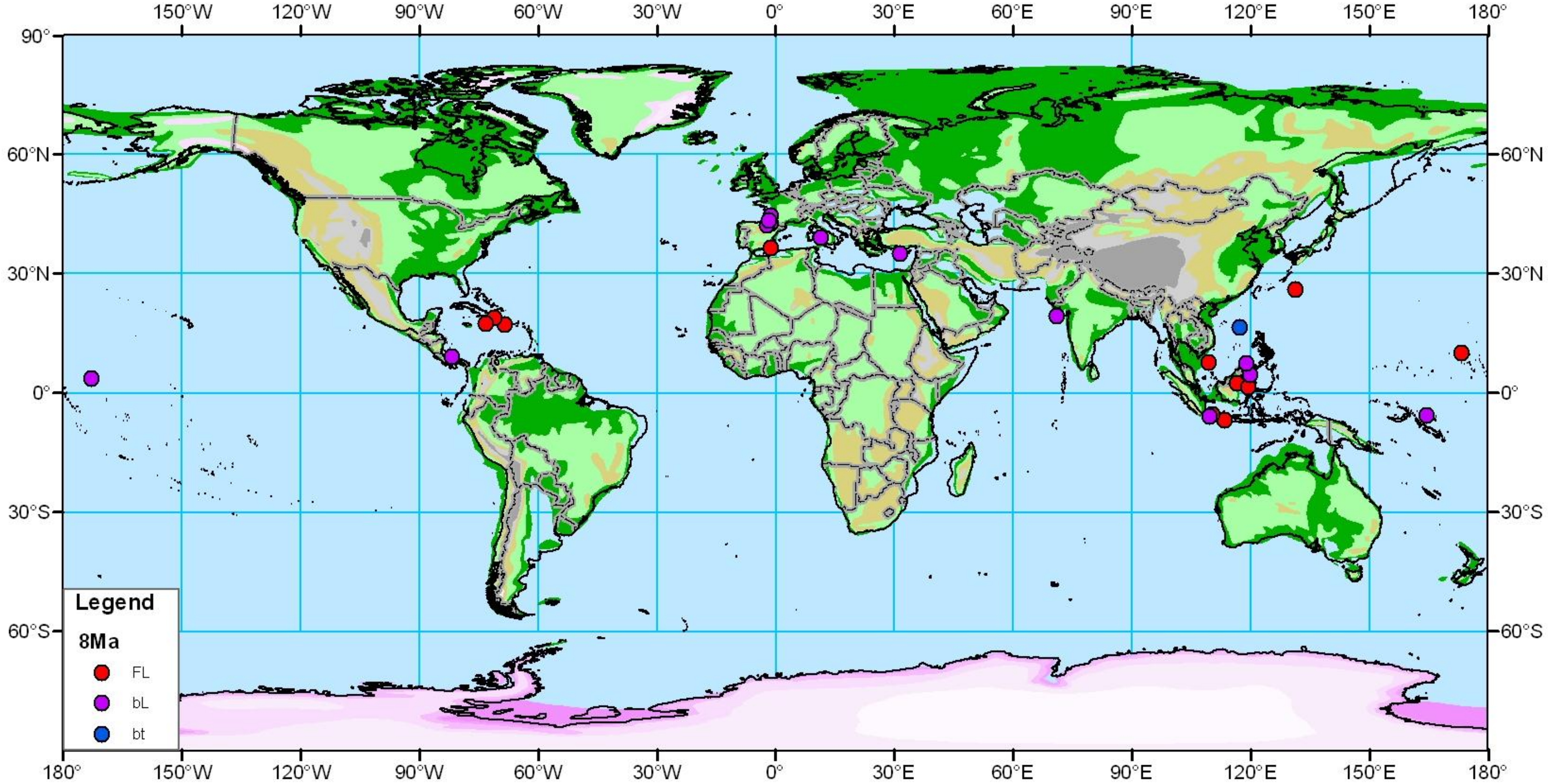


Figure 3.28. Late Miocene occurrences of Acropora (records confined to the time interval and first and last appearances occurred within the interval, FL; records which cross the bottom of the time interval and whose last appearance is within the interval, bL; records that range through the entire interval and crosses both boundaries, bt)

Plio-Pliestocene (5.33-0.0117 Ma)

Global setting

The Early Pliocene is marked by a slight warming trend until 3.2 Ma, when $\delta^{18}O$ again increased reflecting the onset of the Northern Hemisphere Glaciation (NHG) (Zachos *et al.*, 2001; Fig. 3.11). Mid-latitude glaciation was probably also underway before the end of the epoch. Palaeogeographically, the Pliocene was marked by continents continuing to move from positions possibly as far as 250km from their present locations to positions only 70km from their current locations. South America became linked to North America through the Isthmus of Panama during the Pliocene (Bartoli *et al.*, 2005). Beginning in the lower Miocene, the "Horn of Africa" began to separate from the Arabian Peninsula (Swartz and Arden, 1960). During the Pliocene the Red Sea and Gulf of Aden were joined. In Southeast Asia most of Sumatra and Java were elevated above sea level and attainted their present size only since 5 Ma, and much of East Java continued to be the site of marine deposition until late in the Pliocene or even Pleistocene (Hall, 2009).

In the Pleistocene, the modern continents were essentially in their present positions, the plates upon which they sit probably having moved no more than 100km relative to each other since the beginning of the period. Early Pleistocene climate varied with a period of 41 kyr in relation to variations in Earth's obliquity (Crowley and Hyde, 2008). Variability increased, ~ 900 kyr ago, and oscillated primarily at a period of ~100 kyr, suggesting that the link was then with the eccentricity of Earth's orbit.

Carbonate platform and reefal distribution

Compression of the climatic belts and the rise of the Isthmus of Panama restricted reef growth to the Caribbean and Indo-Pacific regions. In the Caribbean during the Plio-Pleistocene there was a major episode of coral turnover which strongly affected the reef coral families *Pocilloporidae* and *Agariciidae* (Budd *et al.*, 1994). During the turnover episode, no new genera or higher taxa arose. Instead, new species originated within the surviving Caribbean genera at approximately the same time as the extinctions, including many dominant modern Caribbean reef-building corals (e.g. *Acropora palmata* and the *Montastraea annularis* complex).

Acropora distribution

Acropora records are found within the Plio-Pleistocene within a similar extent as seen today with two major oceanic realms of the Indo-Pacific and Atlantic-Caribbean (Fig. 3.29). Like today, records suggest the highest abundance was in the Indo-Pacific similar to the abundance of *Acropora* in modern oceanic realms.

It is commonly assumed that the species composition of extant reef corals, including *Acropora*, has been most strongly influenced by Neogene evolutionary events, particularly the Panama closure and Plio-Pleistocene sea level fluctuations of the last two million years (Stehli and Wells, 1971; Potts, 1985; Veron, 1995; Fukami *et al*., 2000). The emergence of *Acropora* in the Caribbean as a dominant genus began during the Pliocene with a late Pliocene first appearance of the Caribbean reef-building coral *Acropora palmata* (McNeill *et al*., 1997) and became increasingly abundant during the Pliocene as slower-growing *Stylophora* and *Pocillopora* species became extinct (Johnson, 2008).

Robustness of record

There appears to be problems of taxonomic robustness of these records due to either preservational problems or misidentification. However, as their preservation undoubtedly reflects the age of these specimens, preservational potential should be higher for these specimens. Although a big problem for Quaternary coral taxonomy is that many limestones of this age are or were emergent, leading to recrystallisation in the vadose zone.

Discussion

The Caribbean region was probably populated by dispersal of the Mediterranean fauna until the loss of corals from this region and changing circulation patterns in the Miocene

(Budd, 2000). Plio-Pleistocene sea level changes would have also led to changes in intensity and direction of sea surface currents and, as a consequence, the repeated isolation and reconnection of populations and species (Veron, 1995; Benzie, 1999). With sea level rise, new habitats were created, and a combination of founder effects and selection may have caused many new species to evolve (Potts, 1983). Southeast Asia is the current location of the greatest diversity of *Acropora,* and other modern Indo-Pacific reef coral genera, it was during this period that diversification in the Indo-West Pacific occurred following differentiation of Caribbean and Indo-West Pacific. Hence, this centre of diversity is a relatively young phenomenon.

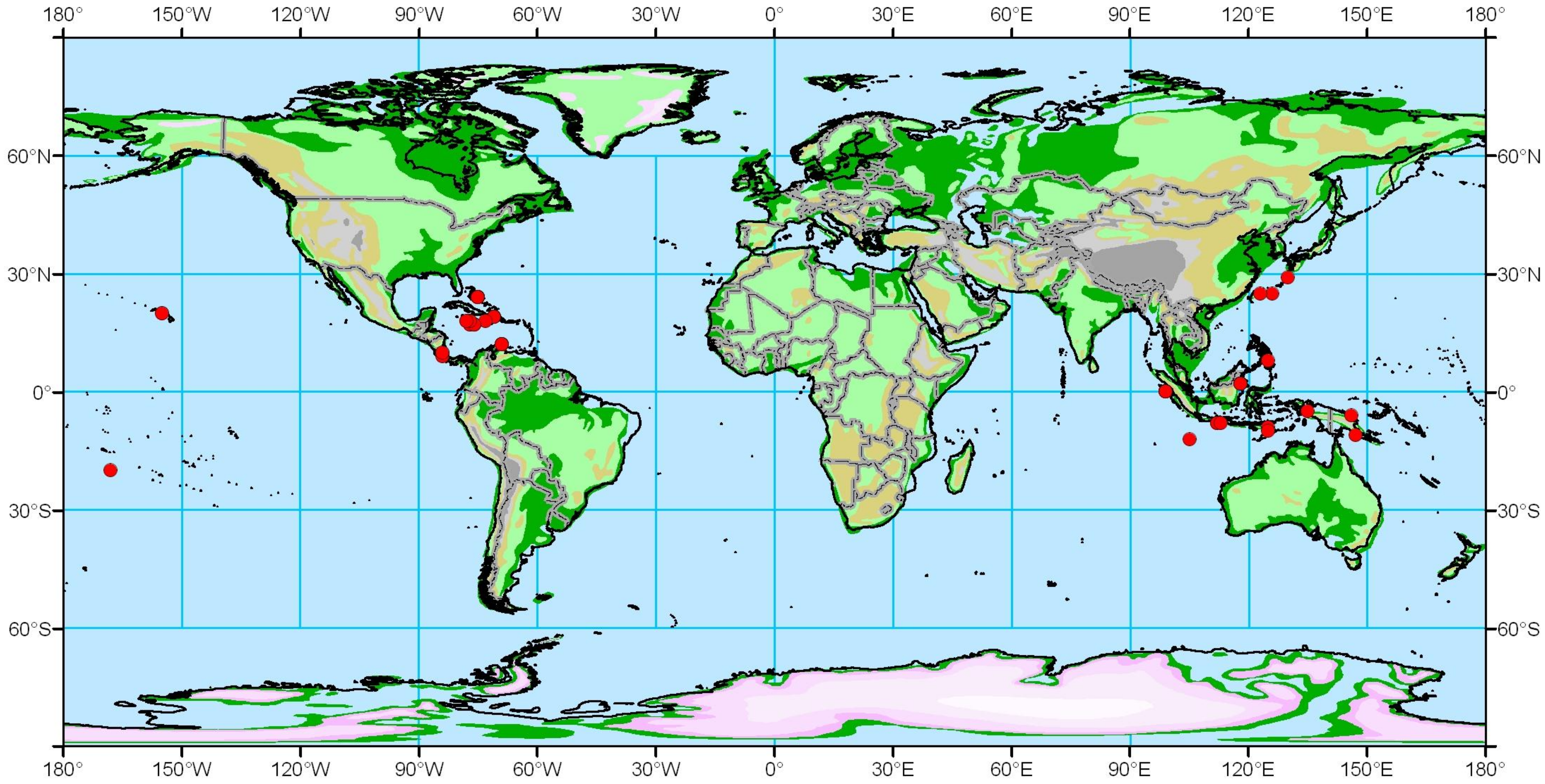


Figure 3.29. Plio-Pleistocene occurrences of <u>Acropora</u>

3.7 CENOZOIC RECORD OF THE ACROPORIDAE FAMILY

The Cenozoic *Acropora* record is compared here with the distribution of records of other members of the Acroporidae family which have widespread geological records; *Dendracis* and *Astreopora* (for details see Chapter 5). *Astreopora* is an extant member of the family and *Dendracis* is the only extinct member in this family.

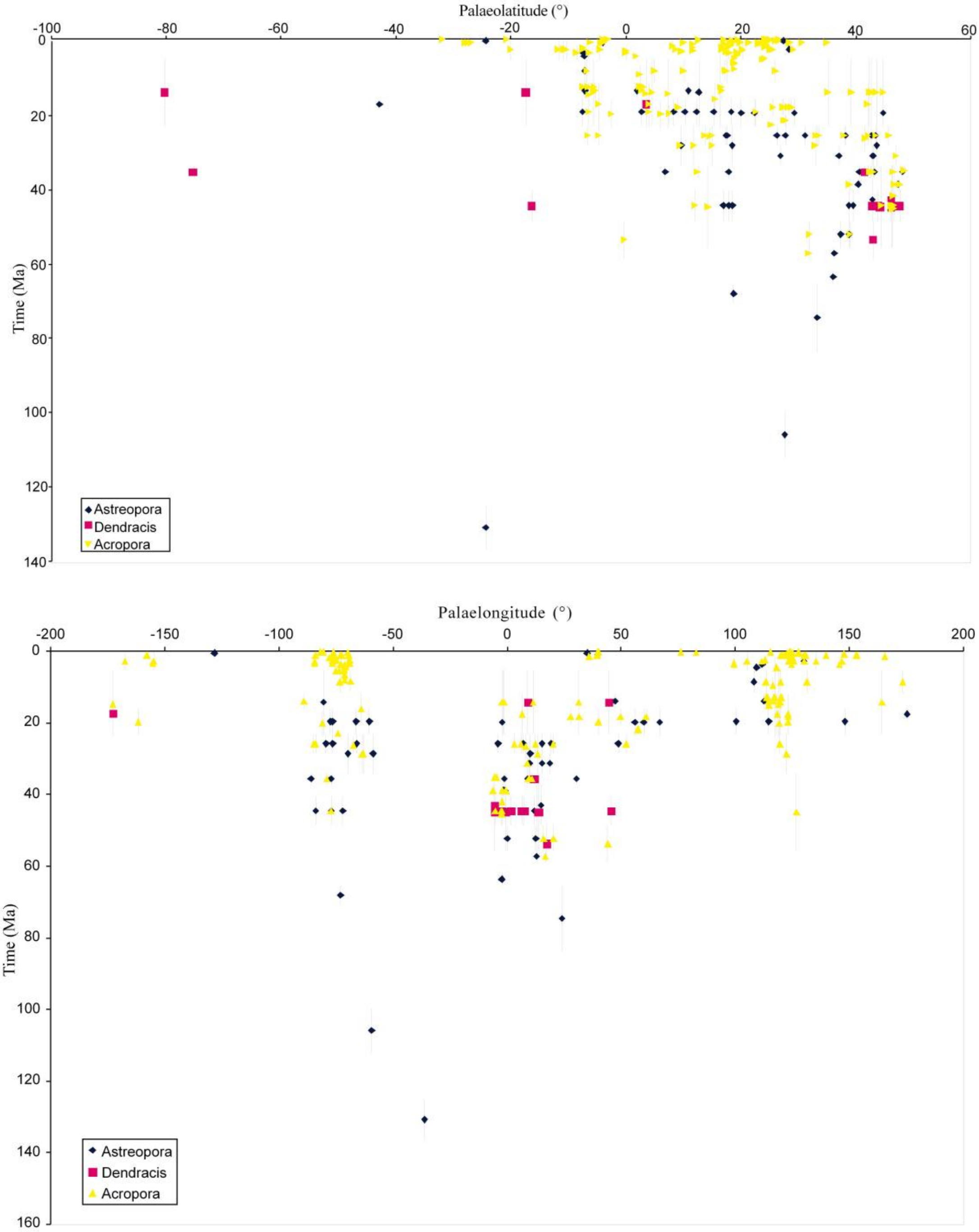


Figure 3.30. Boucotgrams showing the distribution of other members of the Acroporidae family (<u>Dendracis</u> and <u>Astreopora</u>) compared with <u>Acropora</u>, a. palaeolatitude against time, b.

palaeolatitude against time. <u>*Astreopora*</u> *is presently found within the modern coral limits of ~32ºN and S. (Appendix 2 and 3).*

Both Bougotgrams (palaeolatitude and palaeolongitude versus time; Fig. 3.30) show the first occurrence of the family was in the late Cretaceous (Hauterivian-Barremian; 136.4-125.0 Ma) with the appearance of *Astreopora* (Quebrada El Way, Chile; Prinz, 1991). This suggests an origination in the Cretaceous South American area, counterintuitively to the suggested origination and diversification of *Acropora* in the North African-European region. The earliest appearance of *Dendracis* was in the Thanetain-Ypresian (Late Paleocene-Early Eocene) of Somalia (Carbone *et al.*, 1993).

In the northern hemisphere, the maximum palaeolatitudinal extent of the *Astreopora* and *Dendracis* followed that of *Acropora,* coexisting in the high latitude Middle Eocene localities of the Paris Basin. In the Hampshire Basin, *Dendracis* is found in the Middle Lutetian E7 bed, Earnley Formation, Bracklesham Bay, however like *Astreopora* it never coexists in this basin with *Acropora*. Apart from a single record from Marshall Islands (Wells, 1964), all records of *Dendracis* are from restricted palaeolongitude (~10°W-50°E), and are restricted to palaeolatitudes (~20°S-50°N) in a North African-European region. The last records of *Dendracis* are from the Miocene (Madagascar, Colligon and Cottreau, 1927, and Marshall Islands, Wells, 1964). The main difference between the genera *Acropora* and *Dendracis* is the presence of an axial corallite in the former and the extinction of the *Dendracis* is suggested to be related to a poor potential for morphological variation compared with *Acropora* (see Chapter 5).

The records of *Astreopora* show similar distribution to *Acropora* after an apparent origination in South America. The Middle Eocene localities in the Paris Basin represent the most northerly latitudinal extent (~48ºN) of *Astreopora* in its entire history.

3.8 SUMMARY OF MAIN FEATURES OF *ACROPORA* CENOZOIC RECORD

- ***Late Paleocene-Early Eocene***
    - ❖ Oldest records of *Acropora* are from the North Africa-Mediterranean region; the late Paleocene of Italy (Moussavian and Vecsei, 1995), Austria (Tragelehn, 1996) and Somalia (Carbone *et al*., 1994).
    - ❖ On fossil evidence alone, *Acropora* originated and first diversified (see Chapter 5) in the Mediterranean-North African region.

- ***Middle-Late Eocene***
    - ❖ The Middle-Late Eocene localities in the Hampshire and Paris basins represent the most northerly latitudinal extent (~48ºN palaeolatitude) of *Acropora* in its entire history.
    - ❖ These non-reefal high latitudinal occurrences coincide with a period of global warming in the Middle Eocene.

- ***Oligocene***
    - ❖ Time of most spatially extensive distribution of *Acropora* with records in all three major Cenozoic oceanic realms; Indo-West Pacific, Caribbean and Tethyan realms
    - ❖ First record of *Acropora*-dominating a reef is from Late Oligocene in Greece (Schuster, 2002).

- ***Miocene***
    - ❖ The Caribbean region was probably populated by *Acropora* spreading from the Mediterranean region until circulation patterns changes in the Miocene, and its z-coral fauna declined and finally became extinct.
    - ❖ By the middle Miocene, *Acropora* was extinct in the Mediterranean region due to changes in the palaeogeography culminating in the isolation and desiccation of the Mediterranean Sea in the Messinian.
    - ❖ Following the palaeolongitudinal expansion of occurrences at the Paleogene/Neogene boundary, the genus had become established in both the modern realms of the Atlantic-Caribbean and Indo-West Pacific.

- ***Plio-Pleistocene***
    - ❖ Genus became more spatially widespread and diversified in both the Atlantic-Caribbean and Indo-West Pacific following Miocene isolation between Caribbean and Indo-Pacific *Acropora* species.

3.9 CONCLUSION

Together with numerous other organisms, corals (both zooxanthellate and azooxanthellate) show highest taxonomic richness today in SE Asia and adjacent regions ('The Coral Triangle'). Numerous ideas have been proposed to explain this modern pattern (see Chapter 2), but in essence they fall into three groups: the region has behaved as (1) a source of new taxa ('Centre of Origin'), (2) a sink or refuge for taxa which have originated externally, or additionally, to the centre ('Centre of Accumulation'), and (3) a region of overlapping patterns whose foci lie outside SE Asia ('Centre of Overlap'). These ideas are notoriously difficult to test, regardless of the organisms concerned, and there is no clear consensus from phylogenetic studies, either molecular or morphological. Data for these studies have been derived entirely from living taxa, so they are not based on ancient distribution patterns beyond the areas sampled.

This work has used a complementary stratigraphic approach to generate spatio-temporal plots ('Boucotgrams', named for Art Boucot) and time-slice maps of the fossil record of *Acropora,* to identify palaeobiogeographic distributions through the Cenozoic. Although some of the patterns must be due to sampling bias, they suggest that *Acropora* (along with numerous other reef coral taxa) did not occur in SE Asia and the Atlantic-Caribbean during the early Cenozoic, but were common during the Paleogene to early Neogene in Europe and Northeast Asia. *Acropora's* fossil record indicates that it originated and diversified in a North African-Mediterranean region (Wallace and 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 maximum latitudinal extent of the genus was in the Middle Eocene (palaeolatitude ~49°N), these high latitudinal occurrences coincide with a period of global warming in the Middle Eocene. *Acropora* became extinct in Europe during the Neogene, but emerged relatively recently in the SE Asia region. This suggests (1) a centre of diversity from Europe and adjacent regions to SE Asia during the Oligocene-Miocene and (2) that at least part of the taxonomic structure of the modern SE Asia hotspot consists of taxa accumulated from Europe and elsewhere (cf. Centre of Accumulation).

This is the first study attempting to compile the stratigraphic history of a single z-coral genus which is widespread, diverse and ecologically important today. The patterns here suggest that *Acropora* is therefore is a good exemplar genus for understanding the origins and history of the modern reef coral fauna, especially (and topically) in relation to climatic changes.

CHAPTER 4. NEW MULTIDISCIPLINARY APPROACHES TO A MORPHOLOGICAL-BASED TAXONOMY IN THE GENUS, *ACROPORA*

Contents

4.1 OVERVIEW

Currently, species of *Acropora* within the modern record are designated according to Linnean or Lamarckian categories, using morphology, growth form and physical characteristics (see Wallace (1999) and Chapter 5 for details). As with other coral genera, taxonomists working on the genus have adopted new morphology-based techniques. While most palaeontologists do not attempt to identify fossil *Acropora* to species, some have now been described (Wallace and Rosen, 2006; Wallace, 2008; this thesis). Many of the specimens in Chapter 4 from the Paris and Hampshire basins, and the fossil record, have retained surficial features such as coenosteum, radial corallites and clues to the form of the colony, enabling the specimens to be sorted to species group level (Wallace and Rosen, 2006). Although not a formal taxonomic category, this level has useful resolution into putative morphological clades of extant corals (Wallace, 1999; Wallace, 2008).

Many species of *Acropora* have a branching, relatively fragile habit, with synapticula-based skeletal features and projecting corallites. Its skeletal remains are prone to fragmentation, rolling and wearing. Resultantly, many specimens have lost many of the surficial features otherwise seen in Hampshire and Paris basins specimens. Taphonomic alteration through both reworking and transportation often result in preservation in the form fragments or rubble. Fragmentation leads principally to the loss of colony growth form, and with rolling and wear, there is a loss of characters including coenosteum type and the shape, size and arrangement of radial corallites.

This chapter attempts to recognise to what extent these surficial diagnostic characters are still preserved internally within the coral fragments and hence strengthen identifications of fossils at genus- and species-level. Hitherto, internal characters appear to have been used very little for *Acropora* for genus- and species-level identifications in the modern and fossil record. The methods used here for studying internal features include serial and thin section analysis, and micro-computed tomography (micro-CT) both of which have aided taxonomic descriptions in Chapter 5.

4.2 BACKGROUND

Serial- and thin-sectioning are commonly used in the study of fossil and recent reef ecology and sedimentology (see Chapter 6 and 7). Sectioning provides unique information in reef studies and is necessary for the petrographical analysis of sediment, cement and organisms. Problems with sectioning principally are the result of its destructive nature especially in serial sectioning. Matrix is washed out, pieces break off and centimetres of rock are ground away in the cutting process. Thin sectioning of corals has been widely used in order to assess the state of preservation of original skeletal material (see Chapter 7). Diagenesis is a major source of error in palaeoclimatic reconstructions from coral geochemical records and to avoid such spurious results, thin section analysis is used to screen coral material prior to geochemical analysis. For taxonomic studies thin sections are routinely made, however are rarely published. Scanning electron microscopy (SEM) and ultra-thin sections have been used to image the microstructure of coral genera to hypothesise models for the growth of coral skeletons (Barnes, 1970; Nothdurft and Webb, 2007).

A relatively novel method for imaging corals internally is micro-CT (micro computerised tomography). Soon after the use of medical Computerised Axial Tomography (CAT) scanners for medical imaging in the 1970s, machines and protocols were adapted in the 1980s for application in the engineering and materials sciences (Petrovic *et al*. 1982; Hainsworth and Aylmore 1983), and in the earth and planetary sciences (Arnold *et al*., 1982; Haubitz *et al*. 1988; Kenter, 1989). In the broad field of palaeontology, CT has had a transformative impact on morphological research in general, and vertebrate studies in particular. The introduction of high-resolution scanners expanded those applications and as a non-destructive technique, CT has allowed three dimensional examination of fossils often too rare to be examined by serial sectioning, and those that for a variety of reasons cannot be prepared (e.g. extracted from rock they are embedded in) by traditional means. For corals, X-radiography was originally used to identify growth banding (changes in skeletal density) (Logan and Tomascik, 1991). Dodge (1980) is reported to be the first to suggest the use of CT for the study of the growth of corals and this was followed by the use of computerised tomography (CT) as a method for surveying corals (Logan and Anderson, 1991, Bosscher, 1993). Most recent applications include understanding external deciding factors in growth and morphology of reef corals, and how morphology responds to environmental conditions. It has been demonstrated that the morphological variation can be quantified, and that biologically relevant morphological characteristics, like branch-spacing and surface/volume ratios, can be computed (Kaandorp *et al*., 2005; Kruszynski *et al*., 2007). In a CT scan, this information, important to the understanding of ecological and sedimentary processes, can be viewed easily and quantified in three dimensions. Digital images therefore preserve depositional relationships (e.g. grain to grain contacts), saving information which would otherwise be removed through thin section analysis. Digital images can be imported into computer programmes such as ImageJ (Abramoff *et al*., 2004) or NIH Image (developed at the U.S. National Institutes of Health and available on the Internet at http://rsb.info.nih.gov/nih-image) where aspects of coral biology (e.g. polyp size and growth rings) and ecology (e.g. bioerosion rates) can be quantified. Computed tomography (CT) provides non-destructive three-dimensional visualisation and characterisation, creating images that map the variation of X-ray attenuation within objects, which relates closely to density.

4.2 DISCUSSION OF FIDELITY OF MORPHOLOGICALLY RELATED TAXONOMIC RECORD

Through the study of the morphology of coral taxa species diversity and abundances can be determined. From 3D morphometric information the aim is to establish a series of morphospecies. This is complicated by the factors outlined below which have been recognised during the study of the modern coral collections at the Museum of Tropical Queensland and the Natural History Museum in the course of this thesis project.

Some frequently observed sources of variation within these specimens include variations of morphology with water depth, regional variations (possibly based on water chemistry) and habitat-related variations. Features of colonial coral skeletons result from a complex interplay of both genetic and environmental processes. Therefore differences within a phenotype can be explained as a result of changing environmental conditions and genetic variation due to disruption of gene flow between populations, with subsequent speciation into biological species (Bottjer, 1980). Phenotypic plasticity is the sum of multiple phenotypic expressions by a single genotype in response to environmental factors. This is displayed by many taxa including plants, sponges (Palumbi, 1984), molluscs (Trussell, 1996), algae (Fowler-Walker *et al*., 2006) bryozoans (Yoshioka, 1982) and anthozoans (Bruno and Edmunds, 1997; Gleason, 1992). The ability to adapt in this way has important evolutionary implications allowing a variety of genotypes to display various phenotypes within a particular environment and therefore maintaining genetic diversity. Branching corals may generate complex morphological variations (Shaish *et al*., 2007).

Within the taxonomy of corals the majority of studies are based on morphology (Linnaeus, 1758; Vaughan and Wells, 1943; Veron *et al*., 1977) and hence plasticity has complicated and caused the instability of species classifications. Many genera have remained relatively unstudied with research generally focusing on the faviids. However, within branching colonies, in general, studies have focused on responses of corals to changing hydraulic regime (Bottjer, 1980), temperature, sea water chemistry, sediment supply and various other environmental factors. Variation within the genus, *Acropora,* has been seen in response to various environmental forcings (Wallace, 1979, Yapand Gomez, 1981, Oliver *et al*, 1983, Willis *et al*., 1997). In particular causes of morphological variation including depth, regional variations due to seawater chemistry and habitat-related variation have been highlighted (Wallace, 1999). In response to depth *Acropora* colonies (e.g. *Acropora tenuis, A. latistella, A. aculeus, A. solitaryensis, A. florida*) show a flattening of colony shape, a reduction in radial corallite crowding and decrease in skeletal density (see Chapter 2 and Wallace, 1999).

Another potential problem has been shown here and in Chapter 4 to be the variation of skeletal structure within an individual colony. The majority of fossil specimens are small in length (cms) and probably represent only a very small area of the overall colony form.

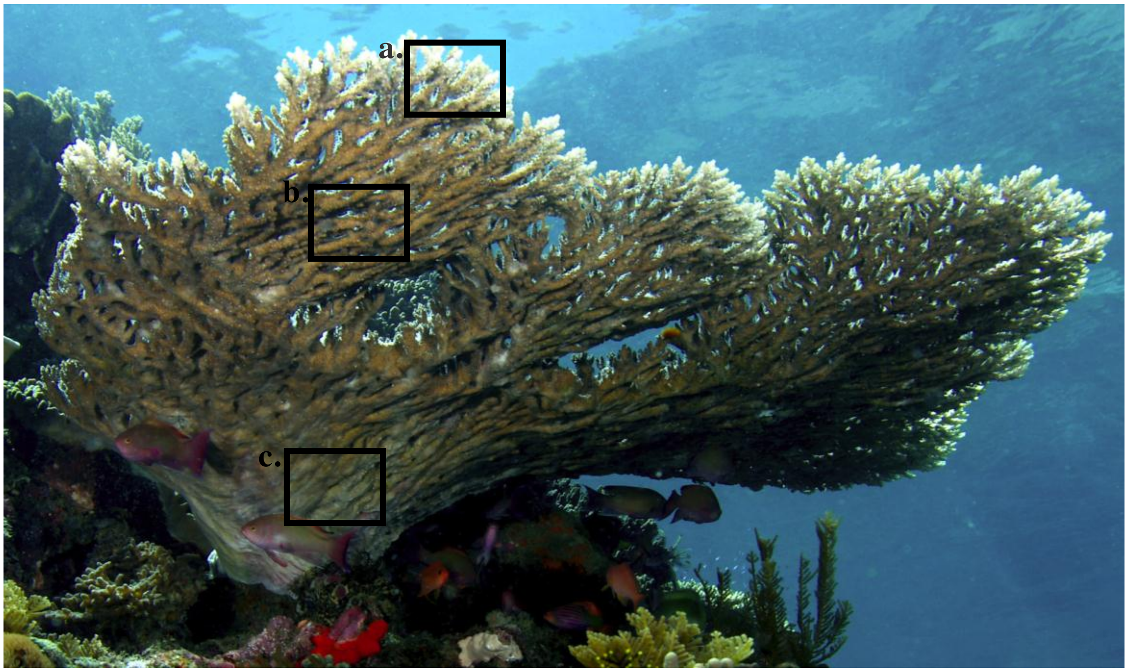


Figure 4.1. Modern Acropora latistella colony showing three areas of intra-colony variation a. fragile tips showing 'rosette' branching associated with the fossil species Acropora proteacea, b. main branch area and, c. sturdy basal area (Photo: Nick Hobgood).

Many are fragments of longer branches and do not show evidence of branch tips, so assigning them to a position within the branch or colony can be difficult. For example fragments from species within a tabular colony form can vary (Fig. 4.1). Sturdy fragments may represent the basal part of a colony (Fig. 4.1c) whereas a more delicate, fragile form may represent areas close to the growth tip within the same colony (Fig. 4.1a). The underside of tabular specimens also shows a relative scarcity of radial corallites and a reduction in crowding of radial corallites and, if this is only seen as a fragment from this area, it could be believed to represent a different species. Both of these issues need to be kept in mind when dealing with the taxonomy of fossil specimens.

4.3 METHODS

Widely recognised as a method to determine species diversity and abundance is the study of the morphology of coral taxa (systematic palaeontology). A typical application of morphometric techniques is to distinguish morphospecies, separated, defined and compared using morphometric information. In both the recent coral record (Wallace, 1999), and more recently the fossil record (Wallace and Rosen, 2006; Wallace, 2008; this thesis), of *Acropora,* the use of surface characteristics are fundamental and predominantly used in the taxonomy of the genus. Here methods and techniques are introduced for addressing the internal characteristics of fossil material, and the examples are presented of results which are then used throughout this thesis.

4.3.1 Thin sectioning

Transverse and longitudinal thin sections were prepared of fossil and modern *Acropora* specimens for observation using optical microscopy. Methods for sectioning are described in Appendix 9. Modern specimens were selected for sectioning from the Worldwide *Acropora* Collection (with over 20,000 specimens, located in the Museum of Tropical Queensland (MTQ), Australia) and nominated as the 'most similar extant species' (*sensu* Wallace, 2008) for each fossil species, based on comparisons with the collections (as listed in Chapter 4). Thin sections were imaged and montages compiled of the overall thin section.

Attempts were made to quantify the internal structure of the coral skeleton using digital images which were imported into the program Image J. The internal branch growth structure of *Acropora* is highly porous. Principally, the porosity is a function of the main aragonite framework to pore space ratio created by other morphological features including vuggy coenosteum and elongate channel framework from corallite features (Tab. 4.1). Additionally, this overall porosity in fossil specimens not only relates to the skeletal framework and primary growth-related porosity but also to a series of post-mortem processes including sediment and cement infilling.

Main feature	Comments	Macro-pore spaces
Skeletal component	Main $CaCO_3$ framework	↓
Primary porosity	Growth-framework porosity related to coenosteum and corallite pores	↑
Secondary porosity	Enlargement of primary porosity through dissolution	↑
Reduction of primary and secondary porosity	Sediment fill and carbonate cements	↓

Table 4.1. Main features in thin section and their relation to porosity (arrows in right-hand column indicate either an increase or decrease in the macro-pore space)

By quantifying and determining the porosity in thin section it may be possible to interpret which factors are responsible for the preserved structure. Traditionally, quantitative determination of porosity from thin section can either be done through point counting or visual estimation. A valuable method is computer-assisted providing an accurate and quick porosity determination using 2D, digitised image of thin sections described by White *et al.* (1998). This allows open pore space and additionally cement-filled closed pore space to be recognised and differentiated. The methodology used here to quantify the different skeletal components has previously been used to characterise carbonate pore systems through digital image analysis for hydrocarbon reservoir characterisation (e.g. Anselmetti *et al.*, 1998; White *et al.*, 1998; Tab. 4.2).

Stage	Details	Package & apparatus
1. Image acquisition	Plane polarised light	Nikon
2. Image enhancements	Histogram balancing and filtering	Adobe Photoshop
3. Mosaic constructions	Stitching of images minimising distortion	Adobe Photoshop
4. Guided classification		ImageJ
5. Calculation of shape properties	Pore-Matrix area quantification	ImageJ

Table 4.2. Summary of stages of computer-assisted accurate and quick porosity determination using 2D, digitised image of thin sections

4.3.2 Micro-CT

A detailed description of the principles and operations of an X-ray CT scanner can be found in ASTM publication E1441-92a (ASTM, 1992). Computed tomography (CT) is the process of imaging an object from many directions using penetrating radiation (e.g. X-rays) and using a computer to calculate the interior structure of that object from these projected images.

Sample preparation is minimal for CT scanning. Specimens were mounted in blocks of oasis (florist foam) and attached to the scanning stage. Samples must be within the field of view and unable to move during scanning. Coral specimens were scanned using an HMXST 225 CT system (Metris X-Tek, Tring, UK) at the Department of Mineralogy, EMMA Division, The Natural History Museum, London (Fig. 4.2).

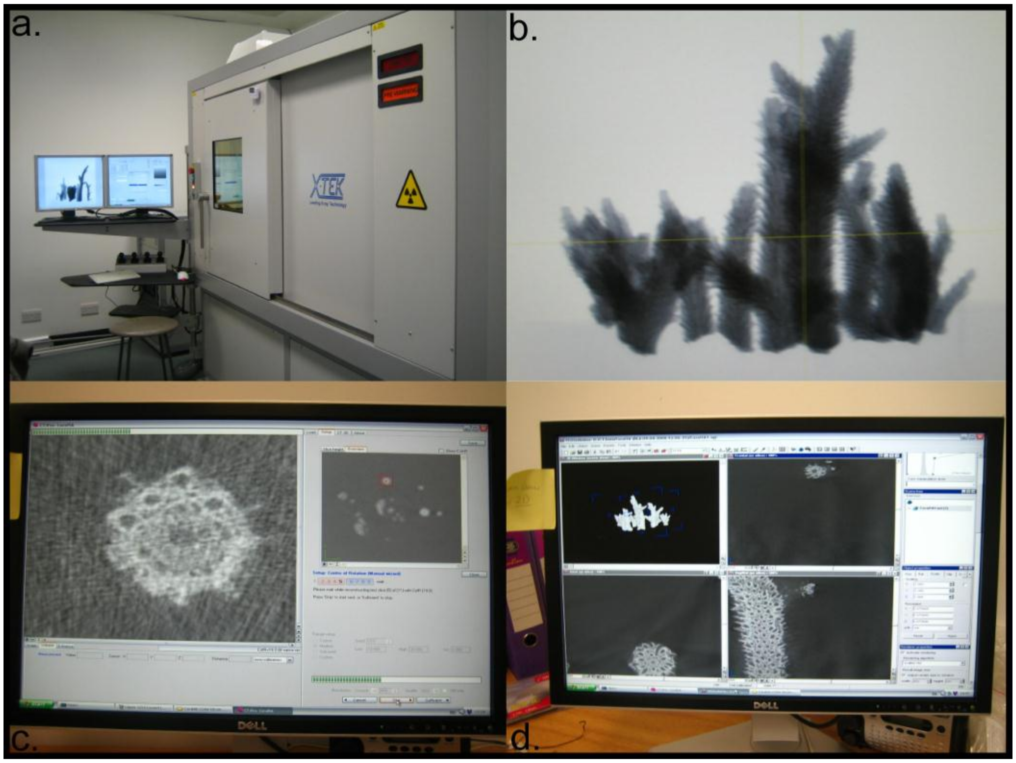


Figure 4.2. Micro-CT Methodology - Equipment used for image acquisition, a. HMXST 225 CT system, b. single projection across a sample with multiple specimens, and processing, reconstruction and visualisation, c. CT PRO software, d. VG Studio Max 2.0, both on a PC platform.

The X-rays were generated from a tungsten target using a voltage and current of between 80-180 kV and 10-200 μA, respectively. The sample is rotated through 360° on a precision turntable. A total of 720 angular projections for each sample were collected at 0.5° intervals in a single 360° rotation. Micro-CT slices were reconstructed using CT PRO software (Version 2.0, Metris X-Tek, Tring, UK). The data were visualized, reconstructed and rendered using VG Studio Max 2.0 (Natural History Museum, London). For details of each scan see Appendix 7.

4.4 MATERIAL

Nine fossil specimens from the Eocene Hampshire and Paris basins, and seven modern specimens were thin sectioned (Tab. 4.3). A series of experimental attempts at the thin sectioning the specimens collected from the Worldwide *Acropora* Collection, Museum of Tropical Queensland, resulted in certain specimens being deemed unsuitable for thin sectioning, principally being too fragile or the branching form making it difficult to section.

All fossil specimens, including proposed types from this thesis and previously published types, identified in Chapter 4 were scanned using the micro-CT scanner along with 47 modern specimens. A selection of the main features from these is presented here.

Specimen No.	Holding	Label Information					Collector	Identification in this thesis
		Locality		Age	Stratigraphy	Original Identification		
AZ2902	NHM	Auvers (Oise)	France	Middle Eocene, Late Lutetian	Sables d'Auvers	*Acropora sp.*	Steve Tracey Colln. (pres. 2005)	*Acropora wilsonae*
AZ2903	NHM	Auvers (Osie)	France	Middle Eocene, Late Lutetian	Sables d'Auvers	*Acropora sp.*	Steve Tracey Colln. (pres. 2005)	*Acropora wilsonae*
55687a	NHM	Auvers	France	Middle Eocene	-	*Acropora solanderi* (Defrance)	No label details	*Acropora alvarezi*
46824b	NHM	Auvers	France	Eocene	-	*Madrepora solanderi (Defrance)*	No label details	*Acropora wilsonae*
46824a	NHM	Auvers	France	Eocene	-	*Madrepora solanderi (Defrance)*	No label details	*Acropora wilsonae*
50236d	NHM	Auvers	France	Eocene	Jarisien B2	*Madrepora solanderi (Defrance)*	No label details	*Acropora wilsonae*
49583c	NHM	Brockenhurst	UK	Eocene	Mid-Headon Beds	*Madrepora sp.*	F.E.Edwards Colln.	*Morphotype 1*
R52048	NHM	Chambors	France	Eocene	Upper Calcaire Grossier	*Acropora sp.*	A.G.Davis Colln. (purch. 1957)	*Acropora proteacea*
R52050	NHM	Chambors	France	Eocene	Upper Calcaire Grossier	*Acropora sp.*	A.G.Davis Colln. (purch. 1957)	*NOT ACROPORA*
G46845a	MTQ	Banda Sea, Sekaro (Turtle) Is., 05'35'S 127'28'E	Indonesia	Modern	-	*Acropora aspera*	C. C. Wallace (20.10.1993)	*Acropora aspera*
G46844a	MTQ	Banda Sea, Sekaro (Turtle) Is., 05'35'S 127'28'E	Indonesia	Modern	-	*Acropora pulchra*	C. C. Wallace (20.10.1993)	*Acropora pulchra*
G35057	MTQ	Chesterfield Atoll, Long Island, QLD	Australia	Modern	-	*Acropora abrotanoides*	C. C. Wallace	*Acropora abrotanoides*
G46844b	MTQ	Banda Sea, Sekaro (Turtle) Is., 05'35'S 127'28'E	Indonesia	Modern	-	*Acropora pulchra*	C. C. Wallace (20.10.1993)	*Acropora pulchra*
G37359	MTQ	Magnetic Island, QLD, 19'08'S 146'50'E	Australia	Modern	-	*Acropora pulchra*	C. C. Wallace (27.10.1991)	*Acropora pulchra*
G51489	MTQ	N Halmahera, N loloda Is, Doi Island, 02'15'N 127'45'E	Indonesia	Modern	-	*Acropora russelli*	C. C. Wallace (2.6.1996)	*Acropora russelli*
G37361	MTQ	Magnetic Island, QLD, 19'08'S 146'50'E	Australia	Modern	-	*Acropora hyacinthus*	C. C. Wallace (27.10.1991)	*Acropora hyacinthus*

Table 4.3. Thin sectioned fossil and modern specimen details (for abbreviations see Appendix 6).

4.5 RESULTS

This section summarises the main results of studying the internal features of the skeletal remains of the genus, *Acropora,* in the modern and fossil record. The internal manifestation of examples of the main surficial characteristics used in species- and genus-level identification are described with a comparison between the fossil material characteristics and examples from the modern species group equivalents.

4.5.1 Contribution of skeletal components to internal structure

Digitisation of thin section images allowed the quantification of the overall internal structure of the coral skeleton using the programme Image J (Fig. 4.3). ImageJ is a freely available java-based public-domain image processing and analysis program developed at the National Institutes of Health. *Acropora* specimens are highly porous and void areas were quantified and represent the contribution of void areas created by corallites and the vuggy, coenosteum area.

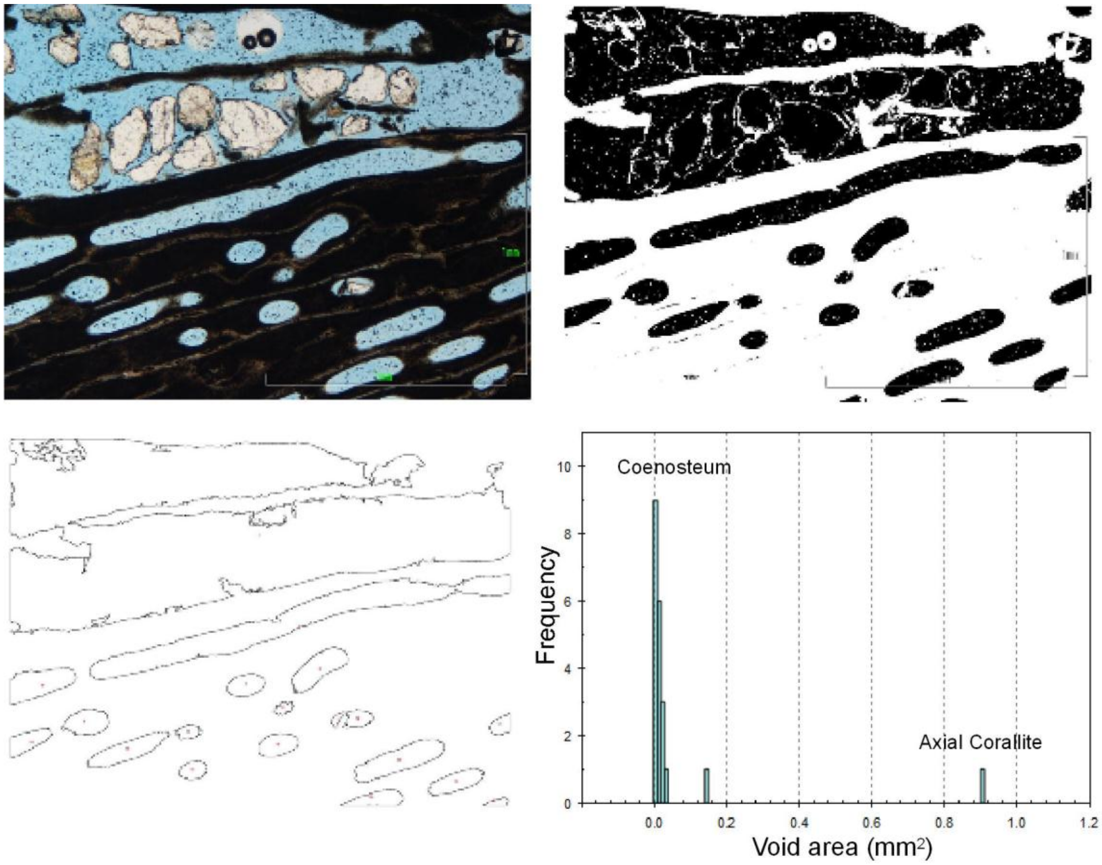


Figure 4.3. a. Part of thin section of fossil Acropora, b. binarised image, c. analysed megapore space, d. histogram showing difference size of void representing coenosteum voids and voids created by corallite areas.

All the thin section montages of fossil specimen were digitised and analysed. Although there was variation between each species dependent on the contribution of different coenosteum and corallite types, this was also dependant on the cutting plane of the section. Another problem with fossil specimens was the wear of radial corallites and flattening of the branch wall meant a true representation of the contribution of radial corallites to the branch thickness was unachievable. Attempts were made to quantify this area using CT scans but, due to the porous nature of the specimens, this could not easily be achieved. It could be done however if the specimens were then embedded and rescanned.

4.5.2 Internal morphological features

The microstructure of coral skeletons of *Acropora* specimens has been studied here in thin section.

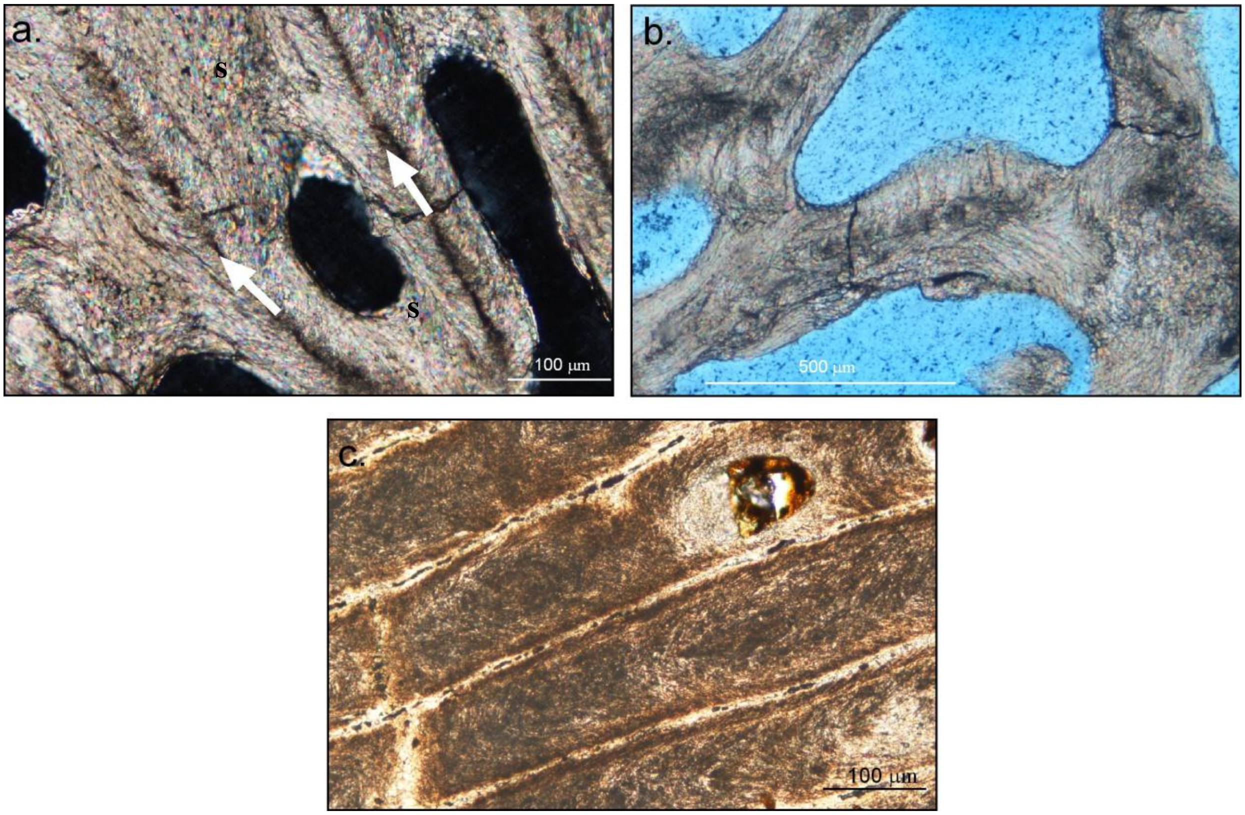


Figure 4.4. a. Longitudinal section through two costae (white arrows) illustrating shingle microstructure (s) filling space between costae, b. Trabecula composed of skeletal fibres that

radiate from the centres of calcification (dark area) (blue resin dye in pore space), c. Fossil specimen with clear remnants of trabecula.

These sections show coenosteal walls formed by skeletal growth involving fibrous trabeculae (Fig. 4.4), followed by the filling of inter-trabecular spaces by individual elongated bundles of fibres, resulting in a 'shingle-like' appearance (previously shown in coral specimens by Sorauf, 1996; Nothdurft and Webb, 2007) (Fig 4.4a).

The principal diagnostic feature of the genus is the dimorphism of corallites; radial and axial corallites (Chapter 4; Fig. 4.5). The wall of the axial corallite is formed by synapticular rings, which are often difficult to identify (Fig. 4.5b). Non-destructive micro-CT scans here shows the inner part of the wall of each corallite does not stand free and the outer walls extend outward around the branch forming a distinct rosette around the axial corallite (Fig. 4.5b). The radial polyp shafts appear not to extend all the way into the axial polyp shafts, suggesting that axial polyps build a wall closing off any direct hole between the axial and radial polyp shafts.

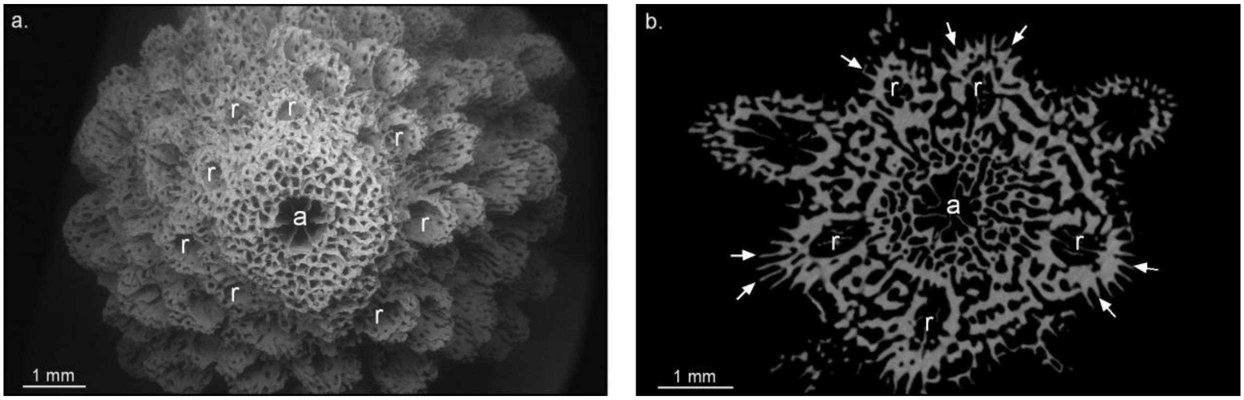


Figure 4.5. a. Scanning electron photomicrograph of modern <u>Acropora</u> specimen showing distal view of a branchlet showing axial corallite and smaller radial corallites (r). b. Micro-CT slice through the transverse section through a branchlet. Axial corallite is in centre (a) with prominent septa. Radial corallites (r) surround the axial corallite and have costae (white arrows) that extend outward from the lip.

Thin sections and CT scans of fossil and modern specimens through the longitudinal, maximum growth axis show the axial corallite extending throughout the branch length, a diagnostic of the genus and the first character looked for when identifying fossil specimens to genus level (Fig. 4.6 and 4.7).

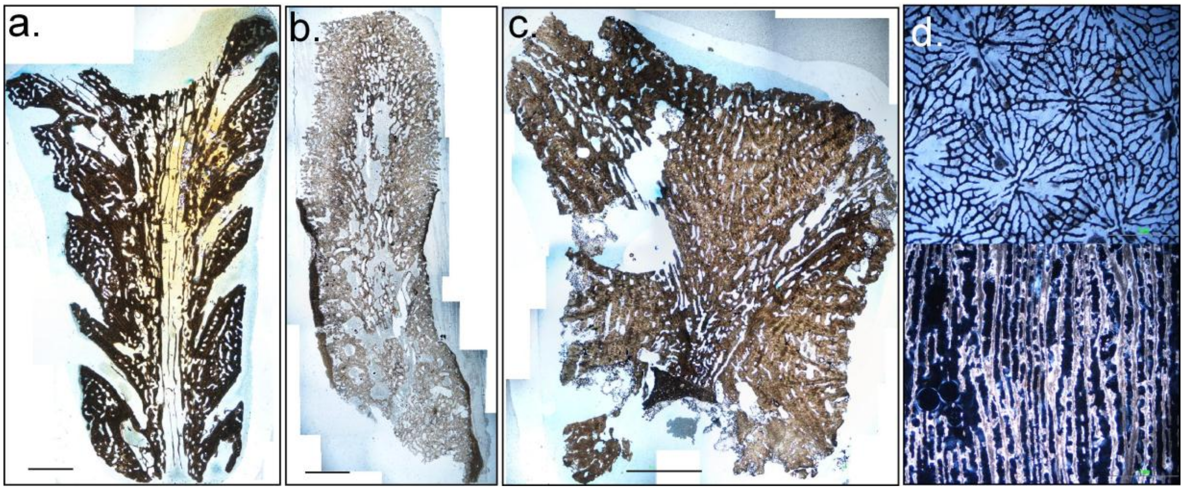


Figure 4.6. Thin sections of different genera; a. Acropora, b. Porites, c. Lobopsammia, d. Solenastrea (top-transverse and bottom-longitudinal) (a-c. scale=4 mm), showing the variation in internal morphological features.

Figure 4.7 shows the benefit of thin sectioning for genus level identifications. Both specimens (NHM AZ2904 and NHM R52050) were sectioned as they showed limited evidence of the diagnostic axial corallites resulting from the abrasion of the branch tip areas. Specimen R52050 also showed no surficial evidence of any radial corallites, probably reflecting preservation. However, its characteristic 'rosette' branching structure did appear to imply that the specimen belonged to *Acropora proteacea*. Thin sectioning showed the presence of an axial corallite within specimen AZ2904, and the presence of two sizes of radial corallites indicated it belonged to *Acropora wilsonae* (see Chapter 3). The other specimen showed no evidence of an axial corallite, and on the basis of this it is now not believed to belong to the genus, *Acropora*.

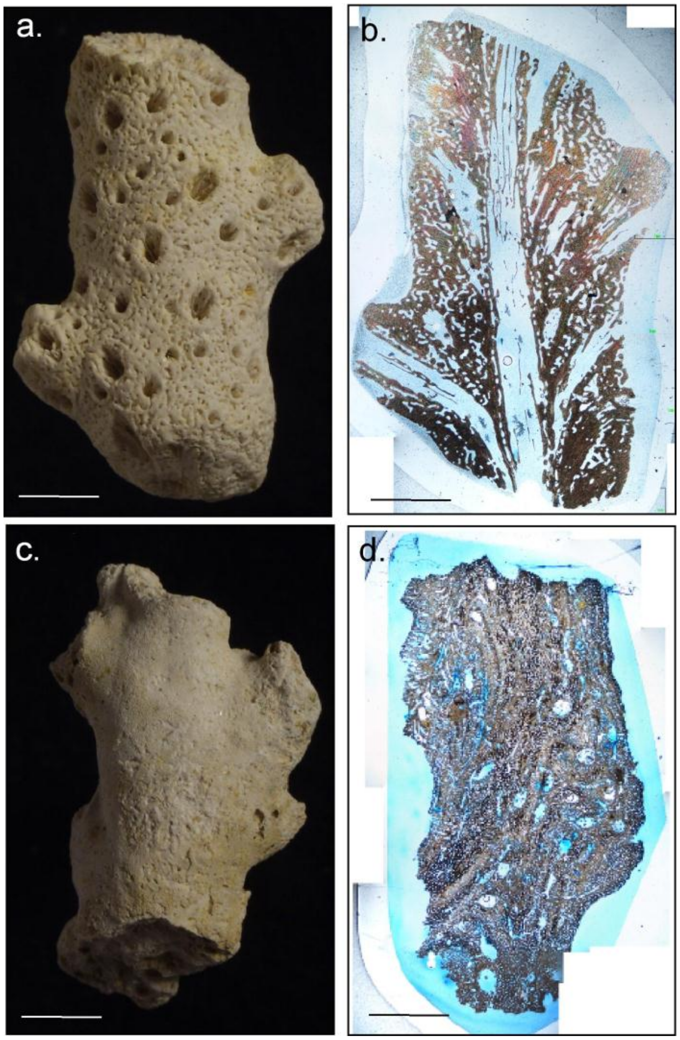


Figure 4.7. Fossil specimens a. AZ2904 Acropora wilsonae and b. longitudinal thin section through its axial corallite, b. R52050 Unidentifiable coral and b. longitudinal thin section (scale=0.5cm).

Slices parallel to these sections (tangential longitudinal section), outside the area of the axial corallite and within the rest of the branch, indicate the density and size of radials, with their shape being largely indeterminable (Fig. 4.7b and d; Fig. 4.8).

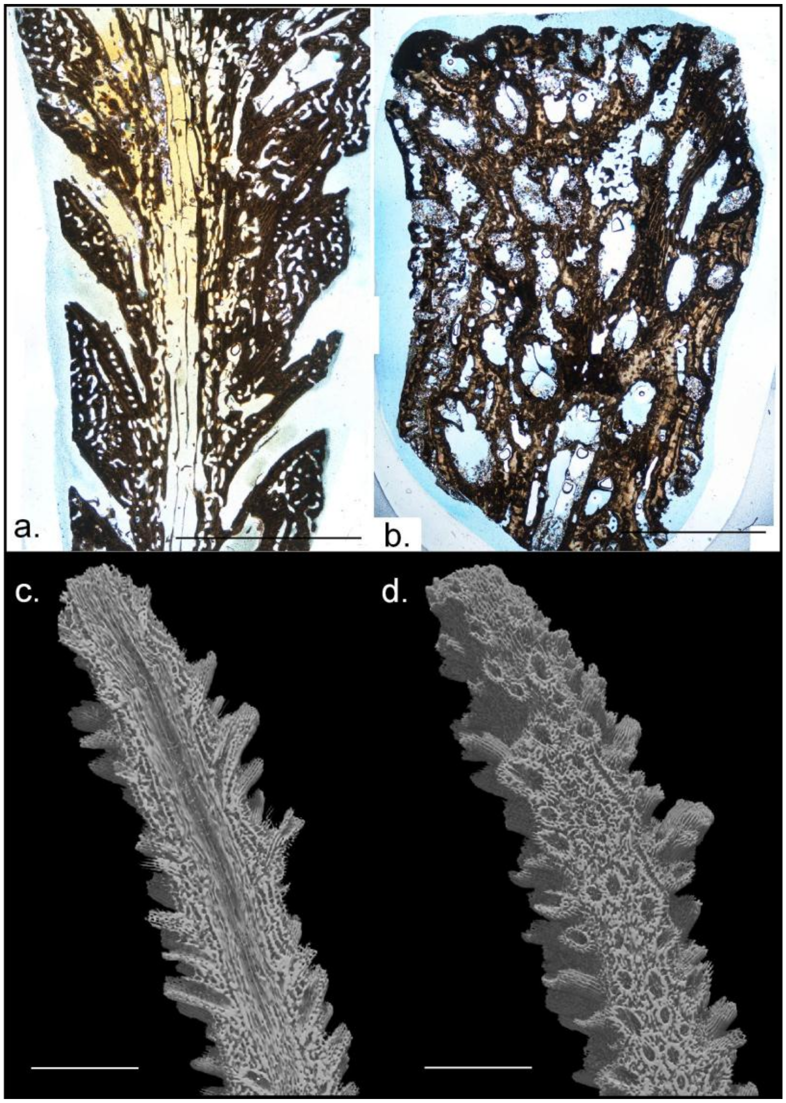


Figure 4.8 a-b. Thin sections of fossil specimens through, a. the axial corallite of specimen NHM R40833, b. area parallel to the axial corallite of specimen NHM R55687a; c-d. Micro-CT slice through modern specimen of, c. axial corallite, d. area parallel to c. showing radial corallites (scale=1 cm).

Even when specimens have surficially lost evidence of the shape of the radial corallites due to surface abrasion, the angle at which the radial corallites extend from the central branch area through the coenosteal area implies the type of corallite. In CT scans it is possible to quantify the size and crowding of the radials.

The contribution of the axial corallite to the overall branch diameter has been shown to vary between species within both the fossil and modern examples, and is a main skeletal character. Axial corallites can be a major component of the overall branch diameter (e.g.

Acropora robusta species group, and in the fossil *Acropora britannica* and *Acropora deformis*), show equal contribution (e.g. *Acropora cervicornis* species group, and in the fossil record *Acropora alvarezi* and *Acropora wilsonae*; Fig. 4.9a-e.) or radials being a major component (e.g. *Acropora hyachintus* and *Acropora latistella* species group, and in the fossil *Acropora proteacea* and *Acropora lavandulina*; (Fig. 4.9f-i.).

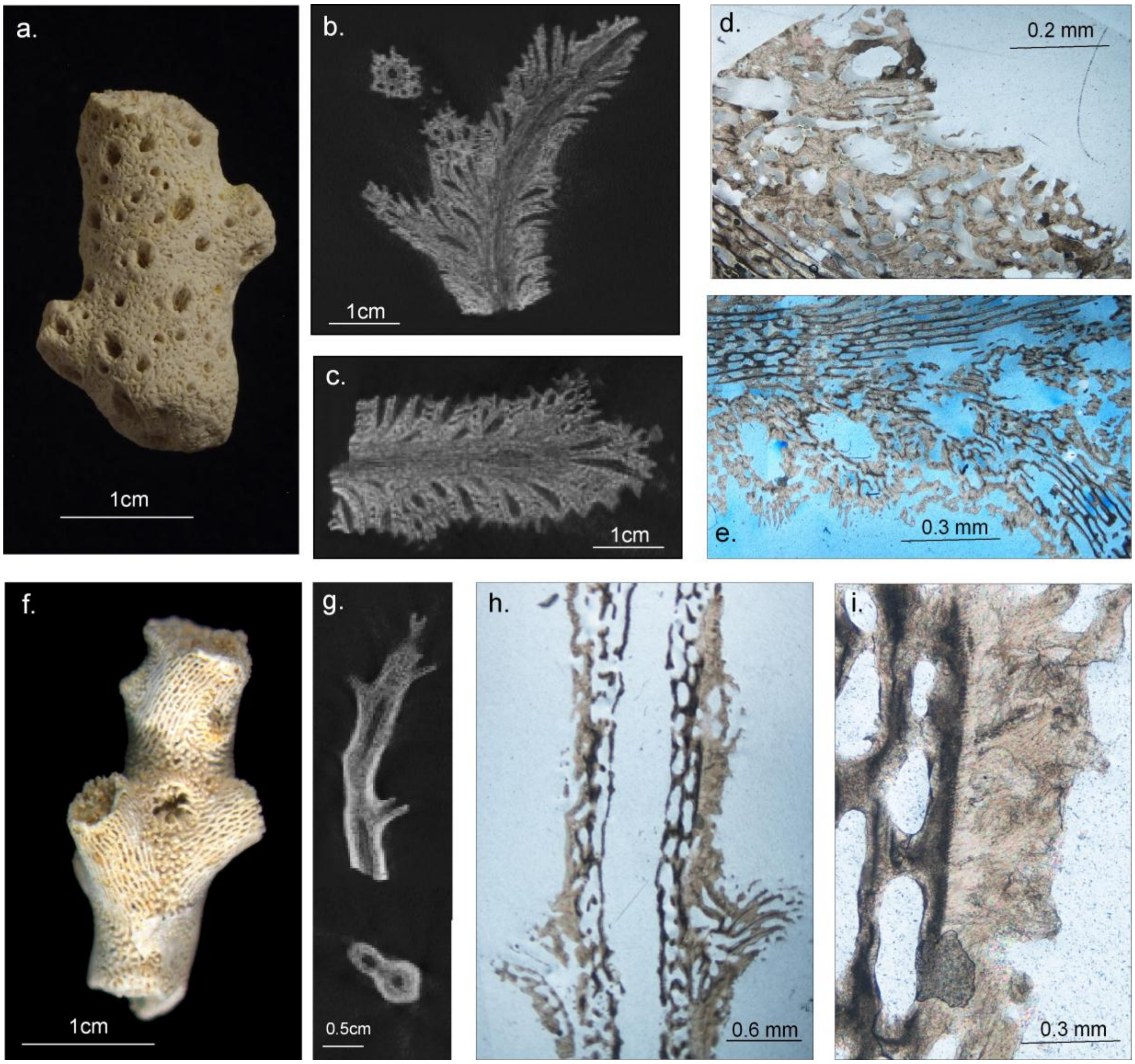


Figure 4.9. a-e. Fossil species <u>Acropora wilsonae</u> and f-i. fossil species <u>Acropora ornata</u> and features of modern species group equivalent. a. <u>Acropora wilsonae</u> NHM AZ2902, b-c. micro-CT slice through the longitudinal section through a branchlet of <u>Acropora aspera</u> MTQ G35057 and MTQ G51491, d. thin section of fossil species <u>Acropora wilsonae</u>, e. thin section of <u>Acropora aspera</u> MTQ G35057. f. <u>Acropora ornata</u> NHM R40832, g. micro-CT slice through the longitudinal

and transverse section of branch of Acropora russelli MTQ G51489 and, h-i. thin sections of longitudinal section of specimen.

An important surficial characteristic of *Acropora* used for species determination is the type of coenosteum on the radial corallites and between them (Fig. 4.10a-b). As shown in Chapter 4, in the fossil record, basic coenosteum variation of both reticulate and costate structures are shown by the specimens from the Hampshire and Paris basins with the majority of species displaying costate coenosteum on the radial walls and reticulate coenosteum between. The exception to this is the fossil species *Acropora ornata* showing costate coenosteum on and between radials (Fig 4.9f). This is also shown by a comparison of thin sections of their corresponding modern species group specimens of *Acropora aspera* (corresponding to the fossil species *Acropora wilsonae*; with reticulate coenosteum on radials, and costate between) and *Acropora russelli* (corresponding to the fossil species *Acropora ornata*; with costate coenosteum on and between radials). In thin section, the costate coenosteum between the radials (Fig. 4.9d-e), compared with the reticulate structure (Fig. 4.9h-i), shows a comparatively denser, less vuggy texture, also shown in the CT scans with *Acropora russelli* showing a denser, brighter coenosteal wall area (Fig. 4.9g).

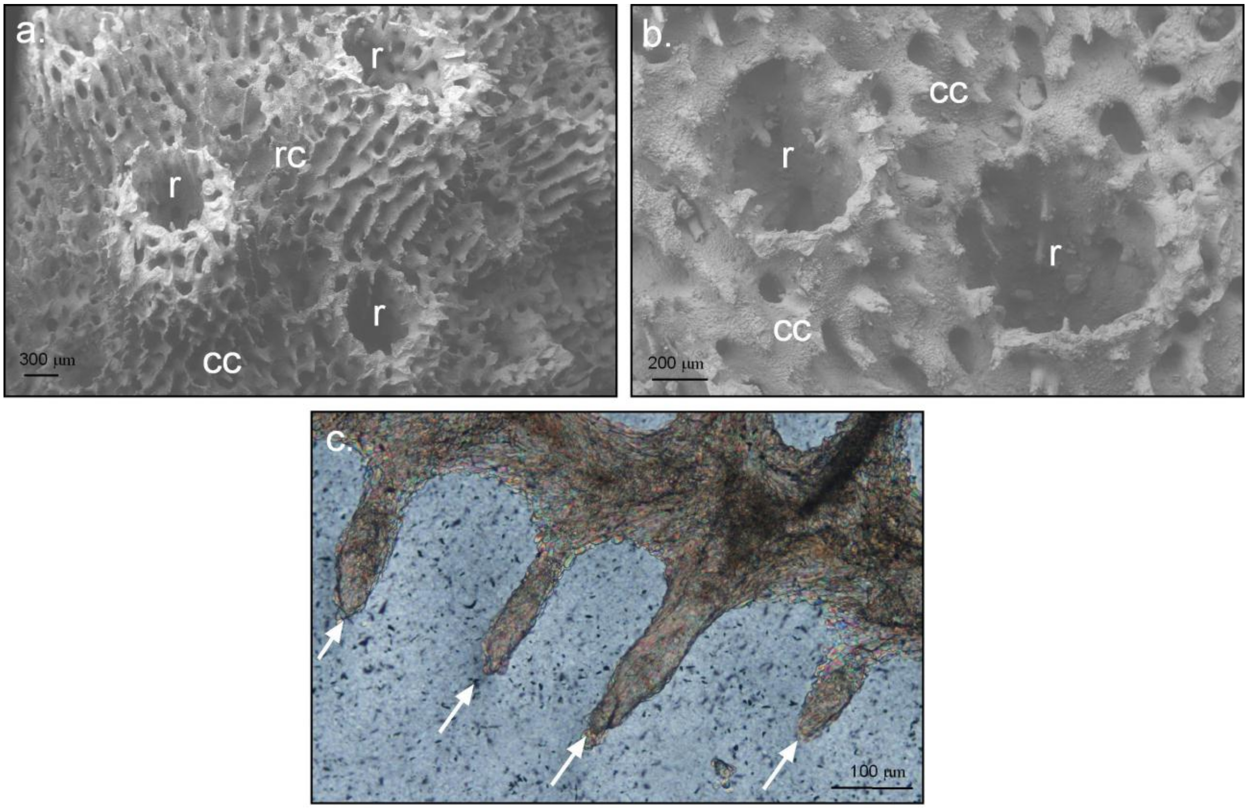


Figure 4.10. a. Scanning electron photomicrograph of costate coenosteum (cc) on the radial corallite walls and between the radials reticulate (rc). b. Scanning electron photomicrograph of radials reticulate (rc). c. Thin section showing costae, indicated by white arrows, consisting of trabeculae with subsequent filling of intercostal space by shingled microstructure

Thin sections of modern specimens show surficial evidence of coenosteum type with spinules successfully sectioned, indicative of a costate coenosteum (Fig. 4.10c). The shingle texture described from the microstructural features in figure 4.4 can be seen infilling between the costae. However, no clear evidence of these spinules was seen in fossil thin sections, principally due to the abrasion of branches (Fig. 4.11).

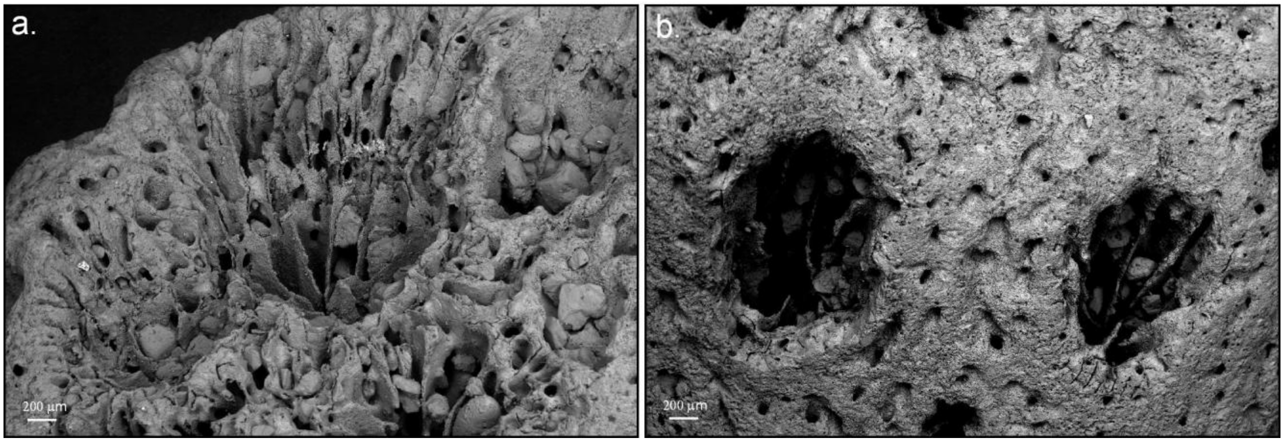


Figure 4.11. a-b Scanning electron photomicrograph of a. sediment infilling of coenosteum and corallites and, b. loss of surface coenosteum structure due to abrasion.

In the study of modern coral species, colony growth form is established from the study of in-situ, living colonies (Wallace, 1999). In the fossil record, whole colony form is rarely preserved in entirety but indicators can often be seen, for example the 'rosette' branching structure of the fossil species *Acropora proteacea* (Chapter 5). This is most reminiscent of the modern species group, the *hyacinthus* group, which commonly forms tables and overlapping plates (Wallace, 1999; p.256). In thin sections of both modern and fossil material these indicators of colony form are rarely deduced, primarily as a result of thin sections only being able to image a two dimensional section of a single plane. Micro-CT slices of the internal morphology of specimens did give some indication of the branching structure (Fig. 4.12), hence an indicator of colony form. In particular, the relationship between axial corallites at branching points can be seen (Fig. 4.12) with centrifugal budding.

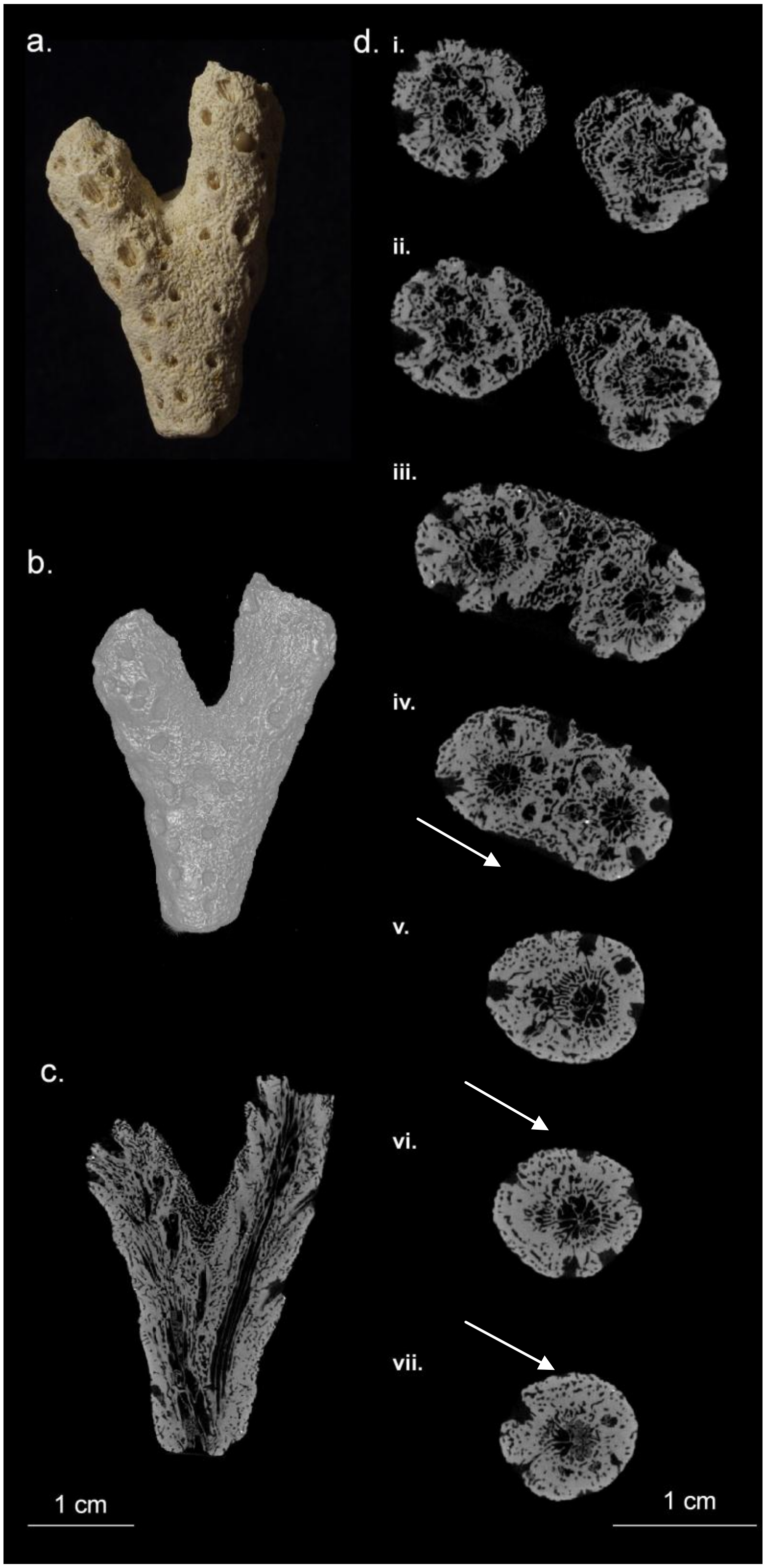


Figure 4.12. a. Fossil specimen NHM AZ2904, b. 3D reconstruction of specimen and micro-CT slices through c. the longitudinal section and d. transverse sections (arrows indicate budding area with the development of a secondary axial corallite, slices i to vii from top to bottom of specimen).

Aside from taxonomic reasons for imaging the internal structure of specimens, a secondary motivation is to asses the preservation of these specimens. The use and features of thin sections is described in section 4.5.2, and here, is an example of the use of CT imaging of a relatively poorly preserved specimen from the Eocene Hampshire Basin. Although superficial preservation is poor the imaging of axial corallites (Fig 4.13c) facilitates the identification of the specimen to genus level as *Acropora*.

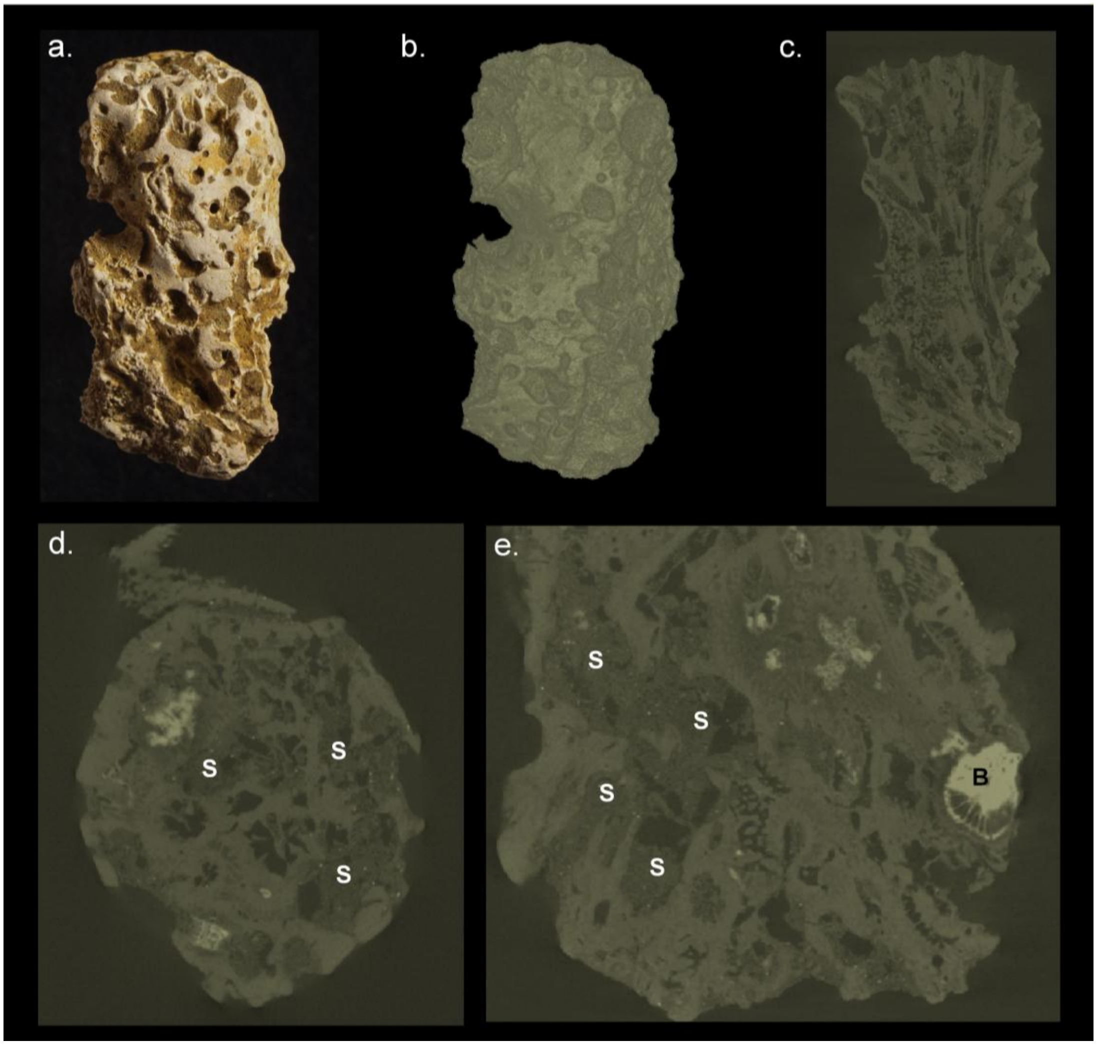


Figure 4.13. a. Fossil <u>Acropora</u> specimen NHM 49583a, b. 3D reconstruction of specimen and micro-CT slices through c. the longitudinal section showing axial corallites which aided the identification and d-e. slices showing areas of sediment infilling (s) and boring (B).

4.6 DISCUSSION

This chapter has attempted to describe the degree to which surficial characters, often lost in the fossil record, are represented in the internal skeletal structure of specimens. This has firstly been targeted in the modern record where characters are identified on the surface, and so can be compared internally, and secondly in fossil specimens where the surface characters are lost. However, when compared with the internal manifestation in modern specimens, fossil material can be identified. This previously has not been attempted within the genus for either the modern, or fossil, material. This approach has used two methods (thin section analysis and micro-CT scans), the success and suitability of these methods is compared below followed by a summary of the degree to which morphological characters could, or not, be identified.

4.6.1 Comparison of methods

Both methods of thin sectioning and micro-CT scanning were successfully used here to image the internal features of *Acropora* modern and fossil specimens. Different benefits to both methods were seen (Tab. 4.4). The main issue with thin sectioning is the highly destructive nature with a large proportion of the specimen being lost, and therefore internal information, during the sectioning process. The targeting of the axial corallite area is also problematic with branches often being curved and therefore a 2D slice only represents a restricted area of the axial corallites, making verification of it, and its extent throughout the branch sometimes unachievable. Thin sectioning does allow a true representation of the microstructure which can aid diagnosis of coenosteum type. Non-destructive micro-CT scanning allows internal imaging of specimens too rare or fragile to be examined by serial sectioning, and those that for a variety of reasons cannot be prepared (extracted from their surroundings) by traditional means. Specimens can be imaged as both 2D slices and 3D images allowing the main morphological features to be visualised. Diagenetic and preservation features (see Chapter 7 for details) are difficult to resolve in CT but can be resolved in thin section analysis.

	THIN SECTIONS[Δ]	CT-SCAN *
MAIN MORPHOLOGICAL FEATURES		
Radial Corallites	Only selection cut by thin sectioning and sliced through in different parts of those that the sectioning does cut	Good representation of features with limited morphological data lost due to resolution problems.
Axial Corallites	Section through centre of corallite preserved with limited septal features	
Coenosteum	Preserved internal features seen as vuggy porosity	
Branching nature	Detail lost by angle of thin sectioning	
Overall	2D	2D/3D
DIAGENETIC FEATURES		
Sediment fill & Cement	Limited preserved in thin section. Easily identified by thin section characteristics	Difficult to resolve on grey scale
Bioerosion	Only preserved if within the thin sectioning area. Difficulties identifying depending on cutting angle	True representation of features with limited morphological data lost due to resolution problems.
TECHNIQUE		
Nature	**Highly destructive**	**Non destructive**
Size (object)	Standard thin section (Length 3mm Width 2mm)	Length 5mm- c.380mm Height c. human skull
Timing	Dependant on departmental resources (RHUL: 6 weeks)	6-52 minutes per scan plus processing (plus booking and waiting time at NHM)
Resolution		Within object: 5µm
Image	True representation of sectioned area	Artifacts, Fossil preservation can be problematic (including pyrite inclusions)

[Δ] Royal Holloway University of London, * Natural History Museum London

Table 4.4. Comparison of the two methods used for the internal imaging of Acropora specimens

In summary the application of high-resolution X-ray CT scanning has the capability to illustrate internal morphological structures of corals that otherwise could only be studied by destruction of the specimen. Traditional sectioning by a diamond saw requires that the angles and positions of cutting be predetermined. If serial sections are made the specimen is destroyed. CT scanning is non-destructive, relatively quick, and allows specimens to be viewed from many different angles and in 3D reconstructions.

4.6.2 Internal morphological features

In the literature, aspects of the internal and external morphology of corals tends to be considered separately and for different reasons (externally for taxonomic reasons and internally to propose models related to biomineralisation). This chapter demonstrates the development an understanding of the morphology of fossil *Acropora* based on how the surface characters used for modern species recognition correspond (or not) to characters seen in thin section preparations and micro-CT scans of fossil and modern specimens. Primarily, verification of *Acropora* at genus-level is shown through the presence of an axial corallite and this can also be observed internally using these methods. Amongst the specimens studied from the Hampshire and Paris basins the internal morphological details include the radial corallite size (one, graded or two sizes), implied shape and crowding (radials not touching, some touching or crowded) of radial corallites (Fig. 4.14). At least two types of coenosteum (costate and reticulate) can be recognised and the relative contribution of axial to radial corallites to the branch diameter and variations on other *Acropora* characters, as shown in figure 4.15.

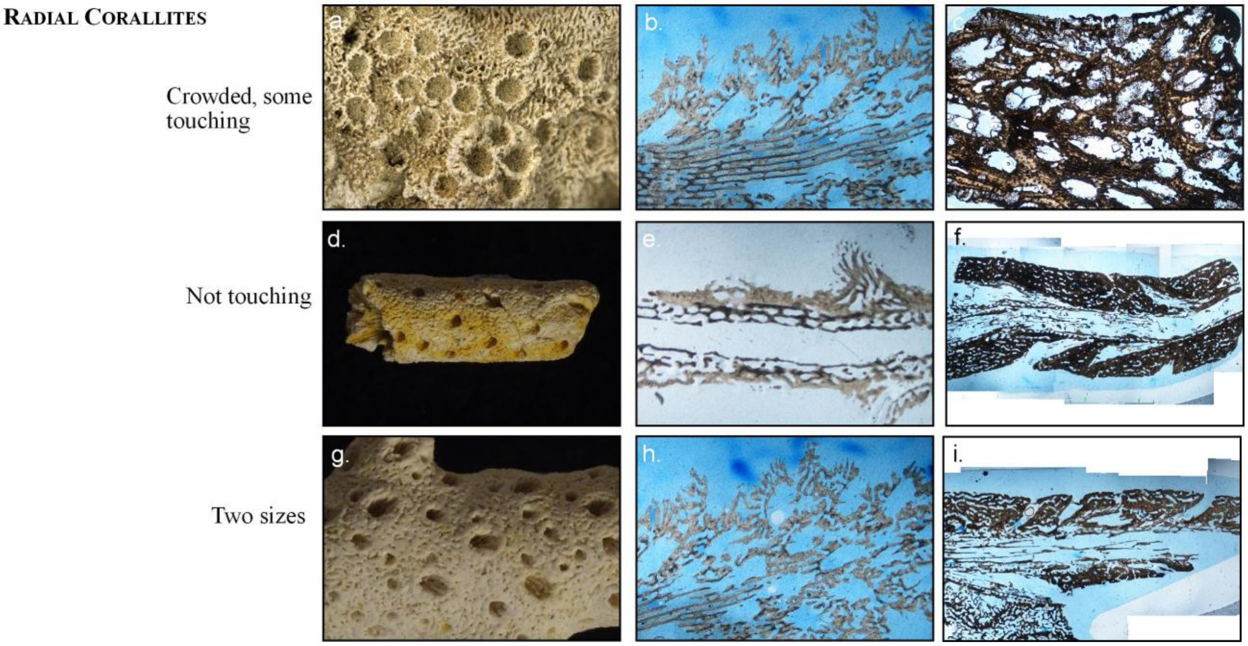


Figure 4.14. Variation in thin sections shown by radial corallites, a-c. Crowded, some touching a. Acropora roemeri SGW C 25746, b. Acropora aspera c. Acropora roemeri NHM R49583c, d-f. Not touching d. Acropora proteacea NHM R52048 e. Acropora hyachinthus f. Acropora wilsonae

AZ2903, g-i. Two sizes g. Acropora wilsonae NHM AZ2902 h. Acropora aspera i. Acropora wilsonae NHM R46824b

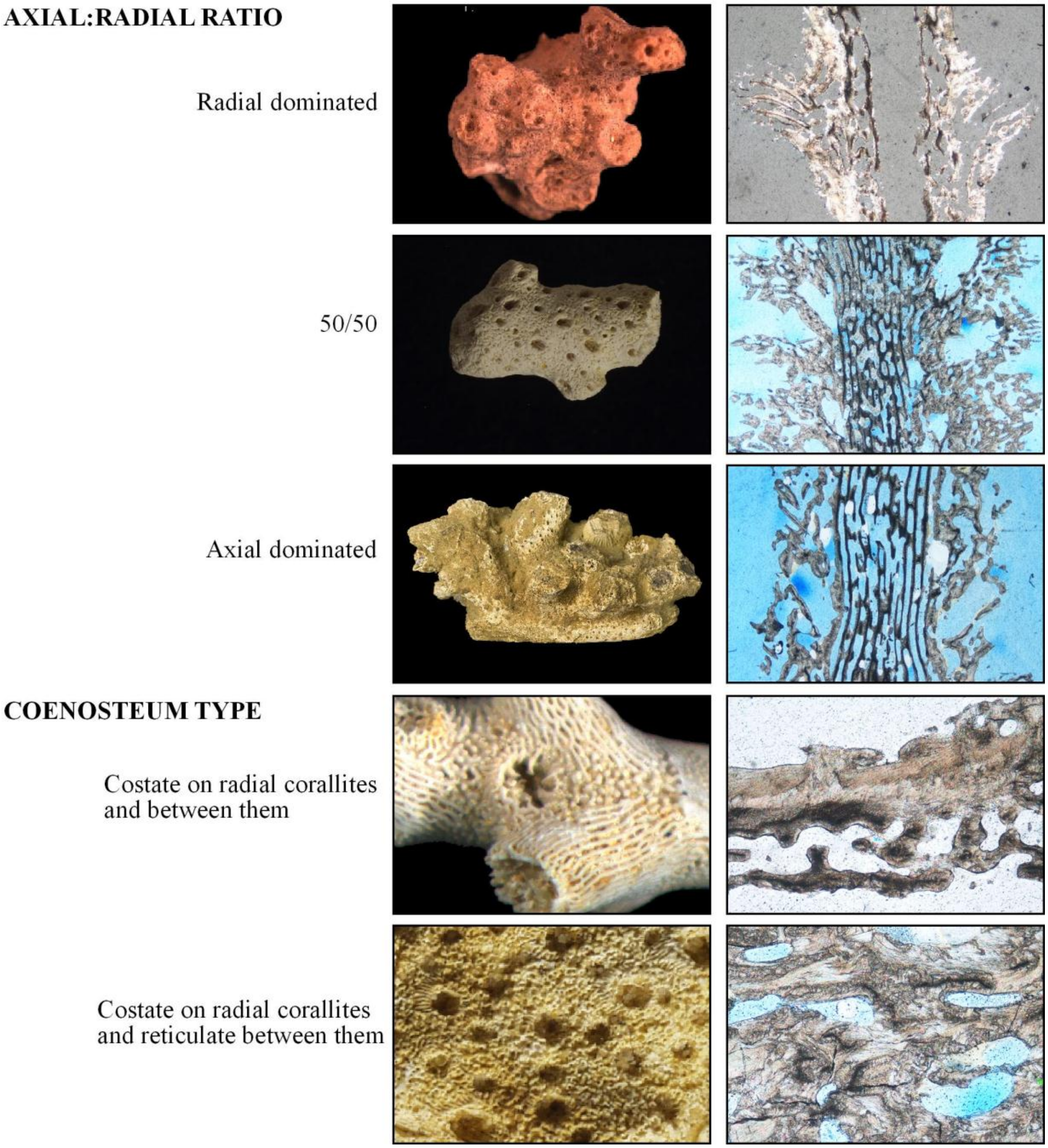


Figure 4.15. Axial:Radial ratio within branch a-b. Radial dominated c-d.Equal contribution e-f. Axial dominated; Coenosteum type g-h.Costate on and between radial corallites, i-j.Costate on radial corallites and reticulate between corallites.

In summary these methods have shown that a range of surface characteristics correspond to characters seen internally including coenosteum and radial corallites type. They provide clues to the colony form and show the contribution of axial and radial corallites to branch diameter (Tab. 4.5). Importantly in the fossil record, the preservation of these internal features appears to be good irrespective of modification and loss of surface characters due to reworking and transportation. Recrystallisation, sediment infilling and bioerosion may make characters harder to determine using these internal methods, however micro-CT scanning and thin sectioning have demonstrated that they can still be determined.

Morphological Features (from Wallace, 1999)	**MODERN SPECIMENS**				**FOSSIL**				
	Hand specimen	**Thin section through ac, longitudinal**	**Thin section through ac, transverse**	**Micro-CT (3D and 2D slice)**	**Hand specimen**		**Thin section through ac, longitudinal**	**Thin section through ac, transverse**	**Micro-CT (3D and 2D slice)**
Colony growth form	√	√	√	√	√ or X	All dependent on preservation of surficial characters*	X	X	√
Branch diameter	√	√	√	√	√ or X		√	√	√
Shape radial corallites	√	√	√	√	√ or X		X	X	√
Size radial corallites	√	√	√	√	√ or X		√	√	√
Radial corallite openings	√	X	X	√	√ or X		X	X	√
Arrangements radial corallites	√	√	X	√	√ or X		√	X	√
Radial corallite coenosteum	√	√	√	√	√ or X		√	√	√
Between radials coenosteum	√	√	√	√	√ or X		√	√	√
Axial:radial ratio	√	√	√	√	√ or X		√	√	√
Branch thickness	√	√	√	√	√ or X		√	√	√
Branch taper	√	√	X	√	√ or X		√	X	√
Max. branch length	√	√	√	√	X		X	X	√

*Table 4.5. Comparison of main Acropora characters identified using thin section analysis and micro-CT scans, using modern and fossil specimens (√-character present, X-character not present, ac-axial corallite). * Within each of the fossil specimens the degree of preservation of a specimen reflects the degree to which morphological characters are preserved.*

4.7 CONCLUSIONS

- Fossil specimens are often broken, highly abraded and lack the surficial characters used to identify modern *Acropora* specimens to species-level.
- Here the methods used to identify the internal manifestation of these features include serial and thin sectioning analysis, and micro-computed tomography (micro-CT).
- Highly destructive thin-sectioning provides details of microstructure in predetermined 2D slices whereas non-destructive micro-CT scans provide images of skeletal characters in 2D slices and 3D reconstructions.
- Surficial diagnostic characters are preserved internally within the coral fragments and hence assist identifications within the fossil at genus- and species-level.
- From this work, the CT and thin section analysis has aided taxonomic work described in Chapter 5 primarily through the verification of *Acropora* at genus-level shown through the presence of an axial corallite observed internally using these methods.
- Amongst the specimens studied from the Hampshire and Paris basins the internal morphological details include the radial corallite size (one, graded or two sizes), implied shape and crowding (radials not touching, some touching or crowded) of radial corallites, characteristics all used for species level descriptions described in Chapter 5.
- Additionally, these methods can be used to assess the preservation and diagenesis of specimens.
- In particular, the re-discovery and re-description, since their original descriptions, of *Acropora* type specimens (Chapter 5) has been aided principally through the micro-CT work described here. Due to the type-specimen status and, like other specimens described in Chapter 5, belonging to other institutions the non-destructive nature of CT analysis has aided specimen descriptions.

patterns here suggest that *Acropora* is therefore is a good exemplar genus for understanding the origins and history of the modern reef coral fauna, especially (and topically) in relation to climatic changes.

CHAPTER 5. TAXONOMY OF *ACROPORA* SPECIMENS AND OTHER CORALS FROM *ACROPORA*-BEARING LOCALITIES

CONTENTS

This chapter focuses on the taxonomy of the fossil coral material used in this research. Material has been studies from museum and private collection, along with new collections as part of this research.

5.1 ABSTRACT

This chapter summarises the taxonomy of the coral material described throughout this thesis. Of principle interest is the taxonomic content of the fossil record of this modern-day highly successful reef-building, coral genus *Acropora,* and its family, that are found in the Northern European area of the early Cenozoic. For this thesis 118 *Acropora* specimens were examined from museum, private, and new collections from fieldwork, with the majority of these specimens previously only described to genus level and at species-level they are dominantly labelled sp. or solanderi (Defrance). These specimens are listed in section 5.7 (species accounts) under 'material studied and included in the species'. Additional specimens from collections confirmed here as previously described correctly to species level are listed under 'other comparative material'. The new descriptions and records, of type material and new species, extend the morphological variation and geographical range of published records of the genus from the Mediterranean region (see section 5.5). Described are three new fossil species of *Acropora* and an additional twelve fossil species (*Acropora deformis, A. britannica, A. bartonensis, A. wilsonae, A. alverezi, A. proteacea, A. anglica, A. solanderi*, *A. roemeri*, *A. lavandulina, A. exarata* and *A. ornata*) from locations in England and France, extending the temporal and spatial history of many of these species. These identifications are based on re-examination of Middle-Late Eocene (Paris and Hampshire basins) and Miocene (Aquitaine Basin) material from museum and private collections, and examination of material collected from field localities. Two type specimens, *Acropora roemeri* and *A. anglica*, have been newly located and re-defined for the first time since their original description by Duncan (1866). Resulting from these descriptions previously described fossil specimens have been reassigned to these species (see section 5.7). Overall this collection of specimens represents a variety of morphological features including branching types, implied colony form, radial corallite shapes and coenosteal ornamentation. In addition to *Acropora*, other members of the Acroporidae family are reviewed, showing the diversity and distribution of the family within each basin. Finally, the taxonomy of coral specimens from *Acropora*-bearing localities, studied during fieldwork and collection visits, is also reviewed.

Counterintuitive to the present-day diversity focus of *Acropora* in the Indo-Pacific, this collection implies the genus originated in the early Cenozoic of Northern Europe. The variety of morphological characters, and respective species, suggests this

Cenozoic tropical fauna diversify in this region along with other members of the Acroporidae family.

5.2 INTRODUCTION

This chapter focuses on the taxonomy of the coral fossil material used in this research. Material has been studied from museum and private collections, along with new collections from fieldwork undertaken as part of this research. The species-level identifications are supported by designation of voucher specimens in this study. Specimens described here as new types (i.e. *Acropora morphotype 1*, section 5.7.2) will be renamed when the current work is prepared for publication in due course, along with the re-description of newly located type material. The re-discovery and re-description, since their original descriptions, of *Acropora* type specimens has been aided significantly through the micro-CT work described in Chapter 4. Due to the type-specimen status, and specimens belonging to a variety of institutions, the non-destructive nature of CT analysis has aided specimen descriptions. These detailed specimen-based descriptions provide taxonomic anchorage for coral names used in other chapters. Additional information about occurrence ranges, morphological variability and palaeobiodiversity is outlined. These new descriptions and records located for this thesis provide further evidence to test the hypothesis of early diversification of the genus, and its family, in the Eocene of Northern Europe.

All material described in the Species Accounts within the Systematic Treatment (see section 5.6 and 5.7) have been examined and newly described at both genus and species level and are listed as ‘material studied and included in the species’. Taxonomic descriptions of these specimens have not been previously published and include the proposal of three new species. These descriptions have extended the stratigraphic and geographical range of *Acropora* species as summarised in section 5.5.1.

5.3 BACKGROUND

Acropora is the most diverse and widespread extant coral genus with over twice as many species than in other prolific scleractinian coral genera such as *Montipora* and *Porites* (Wallace, 1994). The majority (83%) of the 109 extant hermatypic coral genera have fewer than 10 species per genus (Kenyon, 1997). Some 370 extant species have been described in the genus *Acropora*, 113 of which still stand today (Wallace, 1999). Although this is the most species-rich genus of scleractinian corals, diversity within the major oceanic realms varies dramatically with only 3 species (*A. cervicornis, A. palmata, A. prolifera)* in the Caribbean compared to 74 in the Indo-West Pacific oceanic realm, presently regarded as the centre of diversity for the genus (Wallace, 2001). There have been two full monographs on the genus, Brook (1893) in the nineteenth century and over a hundred years later Wallace (1999). Prior to, between and after the compilation of these monographs there has been a vast array of work, challenging previous taxonomic diagnoses particularly through the development of new taxonomic methods. Here, major taxonomic works are summarised both from research on modern material but also the limited work done within the fossil record.

5.3.1 Trends in taxonomy of modern material

A thorough review of trends in taxonomy of modern *Acropora* material can be found in Wallace (1999, p. 4). Below, is a summary of the major steps and influences on the taxonomic record of the genus along with further research since the publication of the recent Wallace (1999) monograph.

Early species-level designation in scleractinian corals used Linnaean or Lamarckian categorisation schemes basing diagnosis on morphology, growth form and physical characteristics, along with variability. These descriptive methods led to a wealth of descriptive works by nineteenth century authors based on material from the field and a series of expeditions, including the HMS *Challenger* expedition. Classic taxonomic publications on the genus of this period included Ridley (1884), Lamark (1916), Ehrenberg (1834) and Dana (1846). One of the most influential works from this period was Dana's (1846) Atlas of the US Exploring Expedition within which many of the morphological terms for the genus were first coined. In addition, a benchmark in coral taxonomy, and in particular work on the genus *Acropora*, was Brook's (1893) monograph in which types and material from European museums were examined and summarised.

The twentieth century saw a series of short publications on the genus dealing with regional aspects such as a major revision of Eastern Australian species (Wallace, 1978; Veron and Wallace, 1984) and of Indonesian diversity and biogeography (Wallace and Wolstenholme, 1998), and others dealing with information regarding biology and ecology of species of *Acropora*. Wallace (1999) outlined gaps in Brook's monograph because he had no access to Dana's types, and the types from America, and this led to the Wallace monograph, the first full monograph of the present-day forms of this genus since that of Brook (1893). In this new monograph, material from around the world was reviewed, and this consolidated new and old information from both centuries. Wallace (1999) summarised morphology and biogeographical ranges, testing hypotheses on phylogenetic relationships of species and transformations of characters through time.

Like other coral genera, taxonomists working on the genus have adopted and attempted new techniques to aid taxonomy within the genus. Geometric morphometrics have become important in coral taxonomy to distinguish morphospecies, separated, defined and compared using morphometic information (e.g. Budd and Klaus (2001) work on *Montastraea*). Since Wallace's (1999) monograph the explosion of molecular research into the twenty first century has led to the further review of the genus (Fukami *et al*., 2000; van Oppen *et al*., 2001; Wallace *et al*., 2007). Species boundaries, traditionally based on morphology, are being challenged based by genetics (Fukami *et al*., 2000). Research now focuses on redefining and challenging species boundaries, along with other aspects of coral biology, ecology and distribution applicable to the genus. These new molecular methods unfortunately will not aid the fossil record, where soft body parts are not preserved, therefore there is still a need for accurate and diagnostic morphological-based taxonomic studies. Undoubtedly a better understanding of the present state of *Acropora* will aid us in understanding the fossil record.

5.3.2 Trends in taxonomy of fossil *Acropora*

Despite over 100 years of research on the genus, the taxonomy of *Acropora* in the fossil record is still poorly understood. In the oldest monograph of *Acropora,* Brook (1893) failed to address the fossil species record at all, finding the type specimens scattered, imperfectly described, rarely figured and generally fragmented. Fossil *Acropora* specimens have often been regarded as inappropriate for classification beyond genus level due to their worn, and generally poorly preserved, nature. Beyond the presence of the diagnostic axial corallite, allowing generic level identification, in abraded specimens, very few features are adequately usually preserved in abraded specimens, for species-level identification.

Few authors have worked on the taxonomy of fossil *Acropora* and they have generally concentrated on particular geographical regions, or time ranges, particularly within the Quaternary fossil record. The European and North African fossil record includes taxonomic work in Spain (e.g. Alvarez, 1993), France (e.g. Defrance, 1826; Michelin, 1840), England (e.g. Duncan, 1866), Somalia (e.g. Oppenheim, 1901), and

Italy (e.g. Michelotti, 1838). The Caribbean fossil material was dominated by the taxonomic studies of Lamark (1816) and Vaughan (1919). In the south-east Asian region works have been dominated by Dutch geologists and in particular von Fritsch (1875), Felix (1921) and Gerth (1921), along with later work by Umgrove (1946). The majority of existing taxonomic records of English and French fossil *Acropora* are contained in Michelin (1840-47) and Milne Edwards and Haime (1850) for France and in Milne Edwards and Haime (1850-1854) and Duncan (1866) for England. Taxonomic research within the Hampshire and Paris basins (the main focus of this thesis) was largely undertaken by Duncan (1866) and Milne Edwards and Haime (1849). Since then, there appears to have been no further treatment of Eocene *Acropora* species from these two countries since the nineteenth century until Wallace and Rosen (2006) provided a modern species-group check list, and Wallace (2008) published species identifications and descriptions of new species from the Paris and Hampshire basins. However Wallace did not include redescriptions of the previous type specimens in these studies.

Duncan (1866) described two species *(Acropora anglica* and *A. roemeri)* solely from the Brockenhurst Bed (Eocene), Brockenhurst in the Hampshire Basin. He also recorded some early-named French species are recorded, not only in the Paris and Aquitaine Basin but also, from England, as well as elsewhere in continental Europe. Eocene *Acropora* species from these basins have also been described from locations in Italy (Michellotti, 1838; Oppenheim, 1901), Spain (Alvarez, 1994, 1997) and other localities around the Mediterranean (Michellotti 1838; Oppenheim 1912). Notwithstanding the apparently meagre record of described species to date, surveys of online databases and literature-based listings of museum collections indicate that there are vast amounts of fossil *Acropora* material (e.g. Museum Victoria, Australia, holds specimens from the Hampshire and Paris basins), and specimens of other acroporids which await species-level study.

5.4 METHODS AND MATERIAL

For this thesis 118 *Acropora* specimens were examined from museum collections (e.g. NHM, BGS, SGW, OM, MNHM, see Table 5.1 and Appendix 6 for institute abbreviations), in private and new collections from fieldwork from the Hampshire, Paris and Aquitaine basins, along with other *Acropora* specimens used as comparative material throughout the genus's Cenozoic history.

As shown in Appendix 4 the majority of these 118 *Acropora* specimens are only described to genus level and at species-level they are dominantly labelled sp. or solanderi (Defrance). Many of these specimens have not been redescribed since their collection or publication, and therefore here we utilise characters and character states used in morphological descriptions of modern coral specimens and novel imaging techniques (see chapter 4) to aid redescriptions of these specimens.

SOURCE	SYMBOL	NUMBER *ACROPORA* SPECIMENS	AQUITAINE BASIN MATERIAL	PARIS BASIN MATERIAL	HAMPSHIRE BASIN MATERIAL	SPECIES DESCRIBED IN THIS THESIS
Natural History Museum, London	NHM	30	√	√	√	*A. deformis, A. britannica, A. bartonensis, A. wilsonae, A. alverezi, A. proteacea, A. anglica, A. solanderi, A. roemeri, A. lavandulina, A. exarata, A. ornata*
Sedgwick Museum, Cambridge	SGW	6	X	X	√	*A. anglica, A. roemeri*
British Geological Survey, Nottingham	BGS	2	X	X	√	*A. anglica, A. roemeri*
Muséum national d'Histoire naturelle, Paris	MNHN		√	√	√	*A. lavandulina, A. exarata, A. solanderi*
Hampshire Museum, Hampshire	HM	0	X	X	√	-
Oxford University Museum	OUM	1	X	√	X	*A. lavandulina*
Isle of Wight Museum, Hampshire	IWM	0	X	X	√	-
Private collections	PC	3	X	√	√	*A. roemeri, A. anglica*
Fieldwork	FW	26	X	√	√	All species

Table 5.1. Summary of sources, amount and diversity within the Acropora material located for this research (X no specimens recorded, √ specimens recorded)

Additionally, acroporid corals, as well as corals from other families, collected from *Acropora*-bearing lithologies were studied from museums and private collections. Over 300 coral specimens were studied in detail, with identification being verified or revised where needed. Corals were also studied from lithological units which were temporally the same but spatially different, and from those lithologies pre and post the *Acropora*-bearing lithologies within the stratigraphy of both basins.

The *Acropora* specimens studied in taxonomic detail come mainly from the Eocene of the Paris and Hampshire basins, with a few specimens from the Miocene of the Aquitaine Basin. Within these basins material was examined from nine main locations, four in the Paris Basin, three in the Hampshire Basin and two in the Aquitaine: two Priabonian sites, Whitecliff Bay and Brockenhurst in England, two Bartonian, Auvers-sur-Oise in France and Barton in England, and two Lutetian sites Chambors and La Ferme de l'Orme in France, one Middle Eocene site, Fresville in France, and two Miocene sites, Gass and Bordeaux in France (Aquitaine Basin). Where possible type specimens were located, or if not, specimens were compared with literature sources and diagrams to aid interpretations.

Specimen details of accompanying labels or collecting information are quoted in Appendix 4. Museum based *Acropora* specimens are all labelled at genus level as either *Acropora* or as its common older synonym *Madrepora*. At species-level they are dominantly labelled *sp*. or *solanderi* (Defrance), with the exception of the type material restudied in this thesis. *Acropora solanderi* is a species which Duncan (1866) regarded as "an indifferent species", based on small, worn specimens, therefore leading to specimens often being labelled as *solanderi*, in effect, by default.

The fossils were examined using a Wild binocular microscope with eyepiece graticule, for the presence of diagnostic *Acropora* features preserved in fossil material, including branching type, radial and axial corallite structure, and coenosteum structure (cf. Wallace, 1999). Crib sheets were used for each specimen to record label details including any registration information, previous identifications and original age and location. This information was then entered verbatim into the specimen detail sub-spreadsheet of the *Acropora* Database in Excel. Measurements were recorded of overall specimen size, branch diameter, and outer and inner diameters of the radial corallite.

Total septal count and contribution of primary, secondary and tertiary septa, if present, were entered. Morphological characters of radials were described and coenosteum, on and between radials, recorded.

Terminology used for genus-level descriptions follows Wallace's (1999) scheme of morphological features used to describe modern acroporid specimens in (Tab. 5.2).

Character No.	Character	States
1	Colony form	massive foliose & variations ramose
2	Branching	axial non-axial no branching
3	Axial corallite (number per branch)	none one more than one
4	Corallite types	monomorphic dimorphic
5	Dissepiments	present absent
6	Columella	weakly represented absent
7	Corallite walls	solid porous
8	Coenosteum	solid reticular
9	Septa-columella union	present absent not applicable
10	External theca*	present not present
11	Mode of spawning*	brooded planula larvae gametes

*Table 5.2. Characters used in phylogenetic analysis of the family Acroporidae (Wallace, 1999) *not preserved in the fossil material*

For other coral genera, coral taxonomy and morphology followed standard taxonomic references and nomenclature (Veron, 2000). Coral growth forms were described as massive (>2 cm thick), robust branching (>2 cm maximum branch diameter), branching (<2 cm maximum branch diameter), tabular, foliaceous, or encrusting (<2 cm thick; in contact, or appeared to have been, with basal substrate).

Terminology for species-level descriptions in the *Acropora* fossil material follows Wallace (1999) as used for descriptions of Recent *Acropora* (Tab. 5.3). Where possible, species-level descriptions are also given here for other coral genera relevant to the present study.

Examples of these specimens and their features were photographed using a Zeiss Axiocam mounted on a Leica MZ16 microscope with Axiovision 3.0 software and a JEAOL JSM5410LV scanning electron microscope at the Natural History Museum, London (see section Systematic Treatment). Comparisons were made with material previously identified from the area (see Wallace, 2008) and modern material in the World Wide *Acropora* Collection (Wallace, 1999) and associated database located at the Museum of Tropical Queensland, Australia.

Specimen details, including voucher record details, are outlined in the systematic section below. Following completion of this research, specimens not already deposited in museum collections will be deposited in the Natural History Museum, London. Personal specimen numbers have been assigned to newly collected material and will be given additional Museum specimen numbers when registered there.

Character No.	Character	States	Coding
1	Branch formation	Around a single axial corallite	0
		Around more than one axial corallite	1
2	Predominant colony outline	Cuneiform	0
		Arborescent	1
		Hispidose	2
		Encrusting	3
		Elkhorn	4
		Corymbose (digitate)	5
		Table	6
		Arborescent-table	7
		Plate	8
3	Branch diameter	Axial-dominated	0
		Radial-dominated	1
		50/50	2
4	Coenosteum	Same on and between radial corallites	0
		Different on and between radial corallites	1
5	Radial corallite coenosteum	Costate or broken costate	0
		Reticulo-costate	1
		Reticulate	2
		Open spinules	3
		Dense spinules	4
6	Between radials coenosteum	Costate or broken costate	0
		Reticulate	1
		Open spinules	2
		Dense spinules	3
		Reticulo-costate	4
7	Radial corallite sizes	One size or graded	0
		Two distinct sizes	1
8	Radial corallite shape	Nariform	0
		Dimidate	1
		Lipped	2
		Tubular	3
		Appressed tubular	4
		Conical	5
		Rounded appressed	6
		Round tubular	7
		Immersed	8
9	Radial corallite openings	Elongate	0
		Oval to rounded	1
		Dimidate	2
		Cochleariform	3
		Horizontal lip	4
		Elongate lip	5
		Square	6
10	Axial:radial ratio	Few radials (up to 10 per axial)	0
		Many radials (more than 10 per axial)	1
11	Axial corallite outer diameter	Big (more than 5 mm)	0
		Medium (3.0-4.9 mm)	1
		Small (1.0-2.9 mm)	2
12	Radial corallites	Very large	0
		Large	1
		Medium	2
		Small	3
13	Branch thickness	Super thick (20 mm or more)	0
		Thick (10.0-19.9 mm)	1
		Medium thick (5.0-9.9 mm)	2
		Thin (2.5-4.9 mm)	3
		Super thin (less than 2.5 mm)	4
14	Branch taper (below growing tip)	Terete	0
		Tapering	1
15	Radial crowding	Radials don’t touch	0
		Some radials touch	1
		Radials crowded, touching	2

Table 5.3. Characters and character states used in the phylogenetic analyses and morphological description of the genus Acropora restricted and modified from Wallace (1999) for use here in the fossil record

5.5 RESULTS AND DISCUSSION

For a summary of coral diversity within the English and French basins with a focus on its palaeoenvironmental implications, see Chapter 6. Here follows a summary of general coral diversity, species diversity of *Acropora* and associated growth forms, the relationship of this to modern day *Acropora* and implications of preservational bias.

Of the 96 *Acropora* specimens studied from both fieldwork and collections (museum and private), 78 could be identified to species level. From the museum based material, the majority of specimens were previously identified as *Madrepora*, the generic synonym extensively used by nineteenth century authors (e.g. Dana, 1846; Brook, 1893). If identified to species level, the bulk of specimens are detailed as the fossil species *Acropora solanderi* (Defrance) with the exception of type specimens studied, with the rest identified as non-specific *Acropora*.

The main limiting factor for undertaking taxonomic work was the preservation of key morphological features (Fig. 5.1). The ramose structure of *Acropora* makes it poorly preserved in the fossil record, principally, because its branches often break post-mortem, so information about colony form and branch structure is lost. Also, post-mortem abrasion removes key diagnostic features including radial corallite features and coenosteum structure.

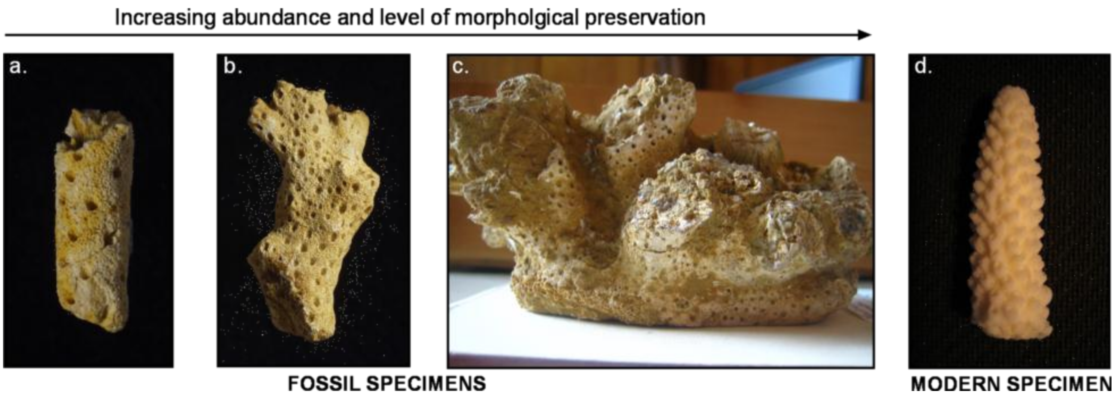


Figure 5.1. Comparison of specimen preservation between fossil (a-c) and modern specimens studied (d), with potential variation shown between specimens of preservation-related potential for species-level descriptions. a. Small fragment of specimen, clearly highly abraded and lacking both corallite and coenosteum features, b. Specimen showing branching structure, c. Clear table-like colonial growth form preserved, e. Comparative pristine modern specimen

Duncan (1866) described *A. solanderi* as ‘an indifferent species’, based on small, worn specimens. The problem with many of the museum-based specimens is that abrasion has led to the loss of morphological features that would provide character states for the fossil *Acropora* specimens. Duncan (1866) commented on specimens assigned to the species *A. solanderi* as ‘Many well-characterised species, were they worn and rolled, would present the appearance of the typical specimen’. Wallace (2008), proposed from examination of figures of Defrance’s (1828) type specimen that a diagnostic feature of this species is the tapering branch structure and hence was discernible from other species.

Overall, specimen source had a varied contribution depending on the accessibility of localities which were identified in museum collection and targeted for re-examination and collection during fieldwork (Fig. 5.2).

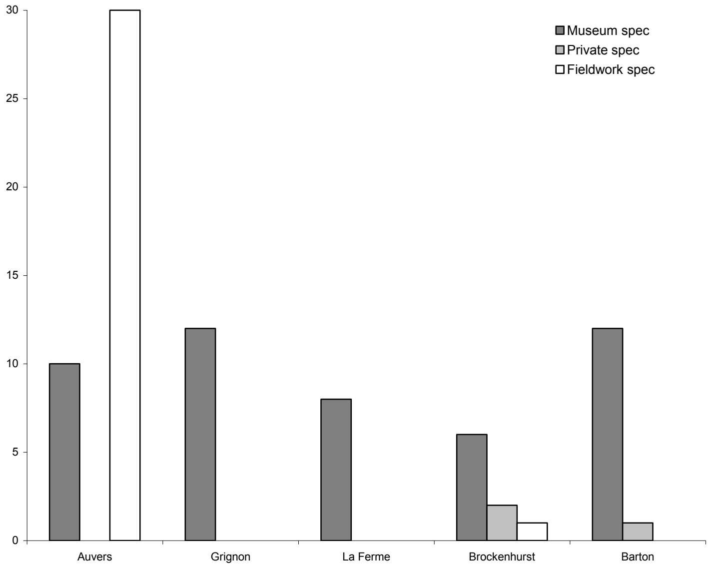


Figure 5.2. Contribution of specimens from various sources to the total number of specimens from each of the localities from the French and English basins.

Some localities have a high contribution of specimens from the field (e.g. Auvers-sur-Oise), relating to both abundance and preservation, other localities (e.g. Brockenhurst,), although fieldwork was carried out, specimens were sparse, poorly preserved or difficult to collect. Contribution was also dependent on the geographical and temporal focus of museum and private-based collections (Fig. 5.2).

5.5.1 Diversity of *Acropora* specimens

The material studied fell into 15 groups whose characters were consistent with separate species (Tab. 5.4). From these, twelve previously described fossil species were identified; *Acropora deformis, A. britannica, A. bartonensis, A. wilsonae, A. alverezi, A. proteacea, A. anglica, A. solanderi*, *A. roemeri*, *A. lavandulina, A. exarata* and *A. ornata* (see Systematic Treatment below). The collection also included some specimens which were unable to be identified or allocated to a new species, principally due to their poor state of preservation. These specimens are not dealt with further in this chapter. The remaining material is interpreted as representing three new species, two from the English deposits (morphotype 1 and 3) and one from France (morphotype 2).

SPECIES	AUTHOR	TYPE LOCALITY
A. britannica	Wallace, 2008	Brockenhurst, England
A. deformis	Michelin, 1840	Auvers-sur-Oise, France
A. alvarezi	Wallace, 2008	France
A. exarata	Michelin, 1840	France
A. solanderi	Defrance, 1828	Mary pres Meaux, Graux (Belgium); Auvers (France)
A. anglica	Duncan, 1866	Brockenhurst, England
A. wilsonae	Wallace, 2008	Paris, France
A. roemeri	Duncan, 1866	Brockenhurst, England
A. bartonensis	Wallace, 2008	Barton, England
A. proteacea	Wallace, 2008	Auvers, France
A. lavandulina	Michelin, 1840	Bordeaux and Dax (France); Turin, Italy
A. ornata	Defrance, 1828	Paris Basin, France
Morphotype 1	This thesis	Brockenhurst, England
Morphotype 2	This thesis	Auvers, France
Morphotype 3	This thesis	Brockenhurst, England

Table 5.4. Species from which material is described in this chapter with type localities and authors.

Of the fifteen species described six were found solely in the Paris Basin, one Paris Basin species (*Acropora solanderi)* was also found in the Hampshire Basin, with an additional six being described solely from the Hampshire Basin. One species was described from the Paris and Aquitaine basins (*Acropora lavandulina),* with one species (*Acropora exarata*) being only described from the Aquitaine Basin.

An important step in work on the taxonomy of fossil *Acropora* was the re-discovery of the Duncan (1866) type specimens of two species from the Hampshire Basin, now stored at the British Geological Survey (BGS), Nottingham. Previously these specimens had been housed at The Museum of Practical Geology, London, before the collection was distributed between the Natural History Museum (NHM), London, and the BGS in 1935. These type specimens had previously been lost and published taxonomic work had to be undertaken using solely the illustrations from Duncan (1866) (e.g. Wallace, 2008). Importantly, thorough re-examination of this type material led to the observation of additional characters and character states in the two species *Acropora anglica* and *A. roemeri* which had not been apparent or made clear from Duncan's original descriptions and figures (for full descriptions see Systematic taxonomy).

Duncan's *Acropora anglica* type specimen (BGS X/X 3/20) is a sturdy specimen with extensive broad branching pattern indicating a sturdy sub-arborescent colony growth form and two-sized of radial corallites. Duncan suggested that the *Acropora anglica* was similar to modern *Acropora crassa* (Edwards and Haime, 1860), now regarded by Wallace (1999) as a junior synonym of *Acropora abrotanoides* (Lamarck, 1816), a reef-edge species and member of the *A. robusta* species group (see Wallace 1999 p. 193).

Duncan's type specimen of his other species *Acropora roemeri* (BGS X/X 2/19), is a comparatively more delicate specimen and shows a growth form and coenosteum similar to those of the *Acropora humilis* 2 species group (Wallace 1999). This comprises a sturdy species which, on modern reefs, is seen in shallow reef fronts and high energy sites.

In addition to the re-examination of the types, three new morphotypes were identified. *Morphotype 1* is a single specimen (SGW C25799) from the Brockenhurst Beds, Brockenhurst. It is a sturdy, robust species like those already described from the Hampshire Basin. It shows clear evidence of an arborescent-table colony growth form. This is the first time this colony form has been seen in either basin and is associated in the modern *Acropora* record with the *muricata* group.

Morphotype 2 (FW P1A28) is a single specimen from the Sables d'Auvers, Auvers-sur-Oise designated a morphotype on the basis of its thick branch fragment and small radial corallites. The single branch is axial dominated and sturdy, a characteristic previously having only been found in the Hampshire Basin.

Material designated here as *Morphotype 3* was all material previously assigned to the species *A. roemeri* by Wallace, 2008. On the basis of location and re-examination of the type of *A. roemeri*, the specimens treated by Wallace appear to be a different species and are therefore assigned here to a separate morphotype, *Morphotype 3*.

Species	Characters														
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
alverezi	0	1	2	1	0	1	0	3	?			?	1	0	0
anglica	0	1	0	1	0	1	1	4					?R	1	1
bartonensis	0	2	2	1	0	0-1	0	4					?R	?	?
*britannica**	0	5	0	0	1	4	0	4					?R	0	2
*deformis**	0	5	0	1	0	1-2	0	4					2	0	0
lavandulina	0	5	1	1	0	0-1	0	3					2	1	0
ornata	0	?	1	1	0	4	0	3					?	?	0
proteacea	0	6	1	1	0	1	0	2					3	0	2
roemeri	0	6	2	0	0	0	1	4					?R	?	1
solanderi	0	1?	2	0-1	0-2	1	0	X					2	1	2
wilsonae	0	1	2	1	0	1	1	2					2	0	0
Morphotype 1	0	7	0	1	0	1	1	3	1				1	0	1
Morphotype 2	0	1	0	1	0	1	0	8	1			3	1	0	0
Morphotype 3	0	5	0	0	1	4	0	4					?R	0	2

Table 5.5. Matrix of character states and species for the phylogenetic analysis presented in this work. Characters taken from Wallace, 2008, updated in light of re-examination and with the addition of further specimens (Characters 10 and 11 were not preserved in the specimens studied but potentially could be in the fossil record). For character details see Table 5.3.

5.5.2 Diversity in growth forms and morphological characters

Overall this collection of specimens represents a variety of morphological features including branching types, implied colony form, radial corallite shapes and coenosteal ornamentation (Tab. 5.5). This is consistent with the previous assessments of the variety present in fossil *Acropora* fauna (Wallace, 2008) and further expands that seen in Paleogene *Acropora*.

Specimens show both branching types with several species showing terete (e.g. *Acropora alverezi*) and one showing tapering structure (*Acropora solanderi*). Colony form in modern coral taxonomy is a primary character widely used for species identification. However, in Paleogene *Acropora* material colony form is not directly observable, having been destroyed through fragmentation, but is implied by branching patterns and other indicators. Overall, six of the eleven standard colony forms (Wallace, 1999, p. 52) could be identified in the material (hispidose, arborescent, corymbose, digitate, tabular, arborescent tabular) (Fig. 5.3). Within the Paris Basin arborescent, table, corymbose and digitate colony forms can be identified. In the Hampshire Basin hispidose, arborescent and arborescent table colony shapes are seen. With only two species so far identified in the Aquitaine Basin, corymbose and arborescent colony form is exhibited.

One specimen shows the first evidence of a table type colony growth form in the Hampshire Basin, a form previously described in the Bartonian of the Paris Basin for the species *A. proteacea* (Wallace, 2008). The Hampshire specimen is distinct from the table species from the Paris Basin as it has a much more robust, sturdy form, a character seen in other species in the Hampshire Basin (e.g. *Acropora roemeri* and *A. anglica*). The Hampshire Basin coral is inferred to have been an arborescent table colony and is described below as *Morphotype 1* n. sp. This species is reminiscent of the modern muricata group, associated today with a reef crest environment. Wallace (2008) commented that this tabulate colony form had not previously been recorded outside the present-day Indo-Pacific, until her description of *Acropora proteacea,* and *Morphotype 1* confirms that this form was also present in more than one species.

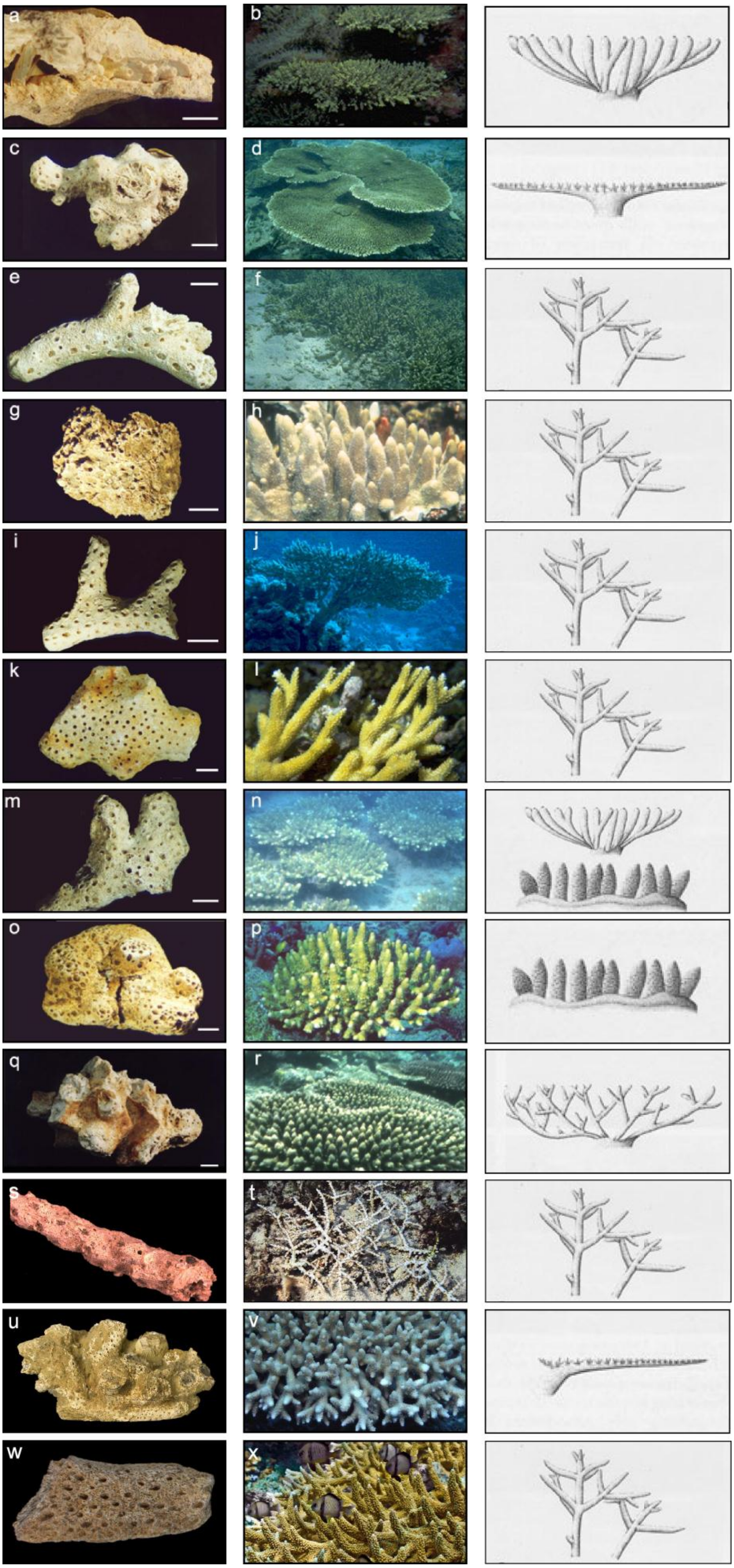

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Figure 5.3. Comparison between species in the fossil record (first column) with modern species and their assigned species groups (second column), and the main growth forms (third column) associated with each. a. & b. A. lavandulina (latistella group), c. & d A. proteacea (hyacinthus group) e. & f. A. solanderi (muricata group) g. & h. A. anglica (robusta group) i. & j. A. wilsonae (aspera group) k. & l. A. alvarezi, (cervicornis group) m. & n. A. alvarezi (humulis I group) o. & p. A. britannica (humulis II group) q. & r. A. bartonensis and A. roemeri (florida group) s. & t. A. ornata (elegans group) u. & v. Morphotype 1, (muricata group) w. & x. A. exarata (robusta group) (Photographs of fossil Acropora species taken as part of this thesis, examples of modern species groups from Wallace (1999), colony growth forms reproduced from Wallace, 1999)

A single, exceptionally preserved *Acropora* specimen was found in the Oxford University Museum. This specimen is labelled from the Eocene of Fresville, Cotentin area, northern France (OUM C1D101). This specimen is assigned here to the species *Acropora lavandulina*, and although this species had previously been described from the Middle Eocene (in this thesis, specimen NHM R54844), the label of the respective specimen gives its locality only as 'France'. This Oxford museum specimen therefore extends the temporal and spatial record of this species, as apart from the above two specimens its previous known distribution was Miocene of the Aquitaine Basin (France), south Portugal and north Italy.

These specimens from the Hampshire and Paris basins are a unique collection of specimens showing abundant morphological diversity. Apart from specimen-based records from the Paleocene of Somalia and Italy, these specimens offer clues about the early diversity of the genus. The previously unrecognised diversity of *Acropora* in the European region was first reported by Wallace and Rosen (2006) and Wallace (2008). This present study confirms, and expands, this work and the present specimens also extending the geographical ranges of *Acropora* species and additionally the coverage within previously recorded basins by the addition of new localities through the study of existing museum collections as well as new material from fieldwork.

In summary, specimens exhibit remarkable morphological variation, including at least six colony shapes, both determinate and indeterminate growth (sensu Wallace, 1999, p. 50–51), at least four types of radial corallite, four types of coenosteum and variations on other *Acropora* characters. Comparison with the modern *Acropora* species groups indicates that the genus had already diversified to a point where species groups could be determined. Although specimens from these collections are exceptionally well preserved, where other suitable material exists, study of fossil material from other regions of the Mediterranean, and the Caribbean region, will increase the known fossil diversity of this genus.

5.5.3 Diversity of rest of the Acroporidae family

Within the Hampshire, Paris and Aquitaine basins, two other acroporid genera are found; *Dendracis* and *Astreopora*. Within the Paris Basin both *Dendracis* and *Astreopora* are found but in the Hampshire Basin only *Dendracis* is found in Bartonian localities. In the Aquitaine Basin only *Astreopora* has been found.

Dendracis

This thesis provides the first review of the fossil record of *Dendracis* from available literature and specimens (detailed distribution discussed in Chapter 3). The aim was to locate types and museum material, and to examine and photograph these incidentally to *Acropora* during museum visits. In total 28 specimens were identified as *Dendracis* from museum collections, two specimens from private collections, but no additional material was found during fieldwork. No type specimens were located, the reasons for this are discussed below.

Historically, there are vast taxonomic problems understanding the genus *Dendracis*. This is largely due to the sparse nature of specimens with a spatially and temporally restricted fossil record. The literature is often based on previous misinterpretations and lacks specific specimen details. No type specimens are identified in the literature and they have not been located in the various museum collections studied. Many of the taxonomic problems with the genus appear to be due to the use of the generic name *Madrepora*. This name was used by nineteenth century authors for the genus *Acropora* as well as the genus *Dendracis*, and has also been applied to various *Oculinids*. On priority grounds it is now restricted in usage to an oculinid genus. Various early nineteenth century authors (e.g. Michelin (1840), Defrance (1828)) identified all three, now separate genera, as *Madrepora* with various species identifications. The species taken forward as the type species of the genus *Dendracis* appears to be that of *Madrepora gervillei* (*Madrepora gervilii* Michelin, 1840, and *Madrepora gervillei* Defrance, 1828). Although there are no specimen details or illustrations, it appears that this type specimen is likely to have been from Hauteville, Cotentin region, northern France, and was named after a collector, Monsieur Gerville, by Defrance (1828). However, the reasoning for this species of *Madrepora* later being assigned to *Dendracis,* and being taken forward as the type, still remains unclear. The various studied descriptions and illustrations show no evidence of the diagnostic lack of leading axial corallite in comparison with that found in *Acropora* specimens. This problem has been further complicated by the same species names being taken forward for both the genus *Acropora* and *Dendracis*, and lack of separation in descriptions. For example, *Madrepora ornata* (Defrance) has been assigned both to *Acropora* and *Dendracis,* in both cases with reference to Defrance's (1828) type of *Madrepora gervillei*. Without relocation of the apparently lost Defrance (1828) type specimen, this will not be clarified. For this reason, specimens studied here have been allocated to separate morphospecies and related to those described previously where possible. In the literature, the first use of the generic name *Dendracis* was by Milne Edwards and Haime (1949), the first mention of the lack of leading corallite was by Duncan (1866), in this description of *Madrepora gervillei*.

In addition to the taxonomic problems related to the generic name *Dendracis*, there are additional preservation-related issues. The only discernible morphological difference between the genus *Acropora* and *Dendracis* is the lack of a leading corallite in the later. However, in some specimens the area where the presence of an axial corallite needs to be checked has been lost due to dissolution of skeletal material or recrystallised making it difficult to decide between the two generic names (e.g. Russo Collection, Somalia, see Chapter 3). This has led to un-verifiable identification of many specimens and leaves a legacy of problems for future identifications.

Furthermore, the spatially and temporally sparse occurrence of specimens in collections, and during present fieldwork, hinders an effective taxonomic review. Chapter 3 summarises the global spatial and temporal ranges, and diversity, of *Dendracis* in the Cenozoic record as recorded here from the literature and collection sources. Records included in this summary have been determined as being taxonomically sound enough to be verified as *Dendracis*. On the other hand, where apparent records of *Dendracis* are specimen-based, they have been omitted here if absence of an axial corallite could not be confirmed during the present study. Therefore, re-examination of all available specimens is needed, whereas here we have tackled specimens only from the France and England. In summary, the genus had a limited record extending from the Paleocene through to the Miocene with specimens from Europe, Africa, East Indies and West Indies (Tab. 5.6 and Chapter 3).

	U. Cret		Lower Cenozoic (to Upper Miocene)											
Described/recorded species	South America	Eastern Europe	North America & North Atlantic	Central America and Caribbean	South America and South Atlantic	Northern Africa	Eastern Africa	Western Asia & Indian Ocean	South East Asia	Northern Europe	Southern Europe	Eastern Europe	Western Europe	Micronesia
ACROPORA														
A. esperanza Frost and Langheim, 1974											x			
A. tergestina Oppenheim, 1901							x							
A. ornata Duncan, 1866													x	
A. bancellsae Alvarez, 1997											x			
A. ramosi Alvarez, 1993											x			
A. lavandulina Michelin, 1840						x					x		x	
A. pachymorpha (?)													x	
A. haidingeri Reuss, 1864 (now lavandulina)														
A. bonelli Michelotti in Sismonda, 1871									x		x			
A. exarata Michelotti, 1838								x			x		x	
A. duncani Reuss, 1867								x	x					
A. panamensis Vaughan, 1919				x										
A. fennemal Gerth, 1921									x					
A. saludensis Vaughan, 1919			x	x										
A. microphthalma Verrill, 1869														x
A. humilis Dana, 1846														x
A. proteacea Wallace, 2008													x	
A. britannica Wallace, 2008										x				
A. bartonensis Wallace, 2008										x				
A. anglica Duncan, 1866										x	x			
A. roemeri Duncan, 1866										x	x			
A. alvarezi Wallace, 2008													x	
A. deformis Michelin, 1840													x	
A. wilsonae Wallace, 2008													x	
A. solanderi Defrance, 1828											x		x	
DENDRACIS														
D. micrantha Felix, 1884														
D. seriata Reuss, 1868											x			
D. mammillosa Reuss, 1868											x			
D. cantabridgensis Vaughan 1899				x										
D. meridionalis ?Colligon & Cottreau, 1927							x							
D. pacificus Wells, 1964														x
D. gervillei Defrance, 1828													x	
D. bifaria Azzaroli, 1958							x							
D. lonsdalei Duncan, 1866										x				
D. ornata Defrance, 1828													x	
D. solanderi ?Barta-Calmus & Chevalier, 1980													x	
D. haidingeri Reuss, 1864													x	
D. nodosa Reuss, 1868														
ASTREOPORA														
A. auvertiaca Michelin, 1844											x		x	
A. hexaphylla Felix, 1906	x	x		x								x	x	
A. esperanzae Frost & Langenheim, 1974	x			x							x			
A. panicea Michelin, 1840													x	
A. asperrima (?)													x	
A. michelini (?)													x	
A. leightoni Wells, 1932			x											
A. perexigua Oppenheim, 1914												x		
A. decaphylla Reuss, 1868						x					x			
A. tecta Catullo, 1856													x	
A. spinulosum Frost and Langenheim, 1974				x										
A. schedakena Darga, 1992													x	
A. meneghiniana d'Achiardi, 1866											x	x	x	
A. gatuncilloensis Budd, 1992				x										
A. antiguensis Vaughan, 1919				x										
A. subcylindrica Matheron, 1961													x	
A. densata Chevalier, 1961													x	
A. myriophthalma Lamarck, 1816														
A. goethalsi Vaughan, 1919				x										
A. hochstetteri Ruess, 1866								x	x					
A. solida (?)								x						
A. hemisphaerica Duncan, 1880							x	x						
A. sphaeroidalis Michelin, 1844													x	
A. stellaris Kühn, 1933								x						
A. walli Wells, 1934				x										
A. occidentalis Nomland, 1917			x											
A. sanjuanensis Durham, 1942			x											
A. duwamishensis Durham, 1942			x											
A. organum D'Ordigny														
A. compressa (?)													x	

Table 5.6. Summary of the palaeogeographic distribution of three members of the Family Acroporidae; Acropora, Dendracis and Astreopora (? denotes uncertainty and missing information)

In total 26 specimens were identified as *Dendracis*. Specimens studied all come from Bartonian and Lutetian Paris Basin localities, and Miocene Aquitaine Basin localities. Within the 26 specimens studied and identified as *Dendracis*, a variety of morphological characters were recognised. These specimens are taxonomically distinct from *Acropora* specimens such as *Acropora* having a colonial, ramose and finely branched nature, but the axial of the leading corallite being absent. Apart from those related to the absent leading axial corallite, the specimens show a similar variety of characters shown by fossil *Acropora* specimens.

Both basic coenosteum variation of reticulate and costate is shown by the specimens. Among the collection studied is a set of four specimens with exceptional coenosteum preservation showing costate radial walls and reticulo-costate interradial coenosteum. These specimens also show long, delicate radial corallites, a character which is shown by other *Dendracis* specimens (*Morphotype 1*).

Radial corallites show huge variation particularly in the size of corallites, and exhibit mixed, two distinct or one corallite sizes. Like *Acropora* species, these specimens also show variations in radial corallite shape. This variation can be seen in one specimen (NHM 55688a) which shows clear evidence of thickened, sub-immersed radials and in another (NHM R6024) which shows evidence of suppressed tubular form. A distinct feature of *Dendracis* specimens is the geometric arrangement and crowding of the radial corallites. This appears to show more variation than in the *Acropora* family with some specimens showing a clustering, crowding of corallites (Hors collection specimen, *Morphotype 2*) resulting in large areas of the coenosteum being barren of radials. In contrast other specimens show a distinct arrangement forming rows of radials (NHM R6024, *Morphotype 2*). Branch shape exhibits variation with some cases showing fluctuation in branch thickness along individual branches, maybe as a result of not having a controlling central axial corallite (*Morphotype 4*).

This collection of *Dendracis* specimens showed that they exhibit a large diversity in morphological characters and offer the potential for increased morphological diversity to be identified in their short Cenozoic fossil record. Based on the previous poor taxonomic protocol within the genus and absence of locatable type species, all species were designated as morphotypes. Therefore material studied fell into four groups whose characters were consistent with separate species.

Astreopora

Like other members of the Acroporidae family, *Astreopora* has a complex taxonomic history. The genus was originally named by Blainville (1830). Its long fossil record from the Early Cretaceous to its widespread extant range means an abundance of species have been described. Taxonomically, specimens from France at genus-level are largely labelled *Astrea*, a synonym used primarily by nineteenth century French authors. It should be noted that this has also been used as a synonym for *Stylocoenia* as found extensively in the collections studied (i.e. *Astrea emarciata*, *A. ameliana* from Michelin (1844). Another synonym includes of *Astreopora* is *Areacis* which was used by Milne Edwards and Haime (1849) and Michelin (1840). The specimens studied show diagnostic characters of the genus appearing colonial, massive, with tabulate dissepiments.

Amongst the coral collections re-examined from the Paris, Hampshire and Aquitaine basins, *Astreopora* is only found within the Lutetian and Bartonian of the Paris Basin. Four species were identified within collections (*Astreopora auvertiaca, A. asperrima, A. michelini*, *A. panicea*) with a further species described within the literature and collection records (*Astreopora sphaeroidalis*). Specimens in the collection identified as *Astreopora auvertiaca* (Michelin, 1844) show colonial, submassive, plocoid growth form, with compact septa in 2 or 3 cycles in 6 regular systems. Specimens identified as *Astreopora panicea* (Michelin, 1844) also show colonial, submassive, plocoid growth form, but distinctively have much smaller corallites.

5.5.4 Diversity of corals in the basins

The coral diversity within each basin from which corals have been studied here is discussed in detail in Chapters 6 and 7, particularly in a palaeoenvironmental context. However, briefly described here is the taxonomic detail of corals from each basin. Within this systematic taxonomy section specimens studied as part of collection visits and fieldwork, are reviewed. If specimens have not been re-identified they are not included in this section but taxonomic information can be found in the Basin Assemblage sub-spreadsheet of the *Acropora* Database.

Class	Order	Sub order	Family	Genus
ANTHOZOA				
	SCLERACTINIA	**FAVIINA**	OCULINIDAE	*Diplohelia*
			MUSSIDAE	*Circophyllia*
			MEANDRINIDAE	*Meandrina*
			FAVIIDAE	*Solenastrea*
		ARCHEOCAENIINA	ACROPORIDAE	*Acropora* *Dendracis* *Astreopora*
			ASTROCOENIIDAE	*Stylocoenia* *Astrocoenia*
		FUNGIINA	PORITIDAE	*Goniopora* *Porites*
			AGARICIIDAE	*Trochoseris* *Cyathoseris*
		DENDROPHYLLIINA	DENDROPHYLLIIDAE	*Lobopsammia* *Dendrophyllia* *Balanophyllia*
		CARYOPHYLLIINA	CARYOPHYLLIIDAE	*Caryophyllia*
			TURBINOLIIDAE	*Turbinolia* *Sphenotrochus*
			PARASMILINAE	*Parasmilia*
		OCTOCORALLIA		*Graphularia*
		OCULINIDAE		*Oculina*
HYDROZOA		**MILLEPORINA**		*Axopora* *Millipora*
		STYLASTERINA		*Distichopora*
UNCLASSIFIED				*Alveolites* *Stylophora* *Turbinaria*

Figure 5.4. Summary taxonomic classification of the coral assemblages found in Acropora-bearing lithologies in this thesis.

Some ~100 specimens of coral were examined and identified from the Paris and Hampshire basins. In addition, specimens from *Acropora*-bearing lithologies were recorded within the *Acropora* database (see Chapter 3 and 7). In total nine scleractinian coral families were identified, consisting of 29 coral genera (Fig. 5.4).

From the Bartonian locality in the Hampshire Basin five genera were recorded; *Dendrophyllia, Graphularia, Acropora, Paracyathus, Turbinolia*. From the Priabonian Hampshire Basin localities nine genera were recorded; *Axopora, Acropora, Dendrophyllia, Diplohelia, Goniopora, Oculina, Solenastrea, Balanophyllia and Lobopsammia*. In the Lutetian of the Paris Basin 16 genera are recorded; *Stylocoenia, Acropora, Turbinolia, Lobopsammia, Trochoseris, Chaelites, Diplohelia, Distichopora, Graphularia, Oculina, Sphenotrochus, Alveolites, Astocoenia, Astreopora, Circophyllia* and *Stylophora*. From the Bartonian Paris Basin localities 14 genera are recorded; *Dendrophyllia, Caryophyllia, Porities, Acropora, Meandrina, Turbinaria, Palmipora, Trochoseris, Lobopsammia, Stylocoenia, Goniopora, Parasmilia, Turbinolia, Astreopora*.

Overall the coral assemblages in the Paris Basin are more generically diverse than those in the Hampshire Basin. Despite the fauna of the Hampshire and Paris basins respectively consisting of only 8 in the Bartonian and 17 Priabonian in the Hampshire Basin, and 30 Lutetian and 22 Bartonian species in the Paris Basin, ecologically it forms a very diverse assemblage. These are characterised by a wide range of growth types (e.g. massive, branching, lamellar, columniform), a great variety of polyp integration types (e.g. plocoid, ceriod, meandroid) and dominated by colonial forms (with only 2 Bartonian and 1 Priabonian solitary taxon in the Hampshire Basin and 5 Lutetian and 4 Bartonian in the Paris Basin) (see Chapter 7 for more details).

Specimens that were located within collections and during fieldwork are outlined in Systematic taxonomy section below.

5.6 SYSTEMATIC TREATMENT

5.6.1 Phylum CNIDARIA Hatchek, 1888

The genus *Acropora* belongs to the phylum Cnidaria which consists of both solitary and colonial invertebrates including hydroids, jellyfish, sea anemones, and corals (Clarkson, 1986; Oliver and Coates, 1987; Benton and Harper, 1997). The phylum is characterised by radiobilateral symmetry, with the ectoderm and endoderm separated by mesogloea; the enteron has a mouth surrounded by tentacles with stinging cells (Benton and Harper, 1997). The three living classes of Cnidaria are Hydrozoa, Scyphozoa and Anthozoa. Oliver and Coates (1987) define 'true' corals as those of the class Anthozoa that possess massive, external, calcareous skeletons. Three subclasses are generally recognised but 'true' corals are limited to the subclass Zoantharia. Within this, the principal coral orders are Tabulata, Heliolitida (also included by some within the Tabulata), Rugosa and Scleractinia. All corals studied in this research belong to the Scleractinia, this being the only post-Palaeozoic order. Living scleractinians fall into two ecological groups. Zooxanthellate corals, (or z-corals) contain endodermal symbiotic dinoflagellate algae, or zooxanthellae in their polyps, and azooxanthellate (az-) corals are without this algae. It is not possible to observe directly this symbiosis in fossil corals, so where these two conditions can be inferred, it is more rigorous to refer to them respectively as z-like and az-like corals (Wilson and Rosen, 1998). However, many of the genera considered here are also extant and it is therefore reasonable to assume on the grounds of taxonomic uniformitarianism (Dodd and Stanton, 1990) that unless there is evidence to contrary, their modern condition also applied to their fossil counterparts.

5.6.2 Order SCLERACTINIA

The order Scleractinia is defined as aragonitic, solitary and colonial corals with relatively porous skeletons (Wells, 1956). They are often termed hexacorals due to their six protosepta and successive cycles of metasepta inserted in all interseptal spaces. The group first appeared in the mid Triassic (Stanley and Fautin, 2001) and now are the dominant reef-builders in the tropics and marginal-tropics (Wood, 1999).

5.6.3 Family ACROPORIDAE Verrill, 1902

The family Acroporidae includes the extant genera *Montipora* Blainville, 1830, *Anacropora* Ridley, 1884, *Astreopora* Blainville, 1830, *Acropora* Oken, 1915, *Isopora* Budd and Wallace, 2008 and, the only extinct genus in the family, *Dendracis* Milne Edwards and Haime, 1849. *Acropora* is the only member of the family currently found in the western Atlantic; the other genera are restricted to the Pacific and Indian Oceans, including the Red Sea (Chapter 3). The origin of the Acroporidae family is unclear but the septal structures of the group most closely resemble those of the Astrocoeniidae (Vaughan and Wells, 1943), so perhaps sharing a common origin. First occurrence of the family was in the late Cretaceous with the appearance of *Astreopora* (Hauterivian, Quebrada El Way, Chile (Prinz, 1991)) (Fig. 5.5).

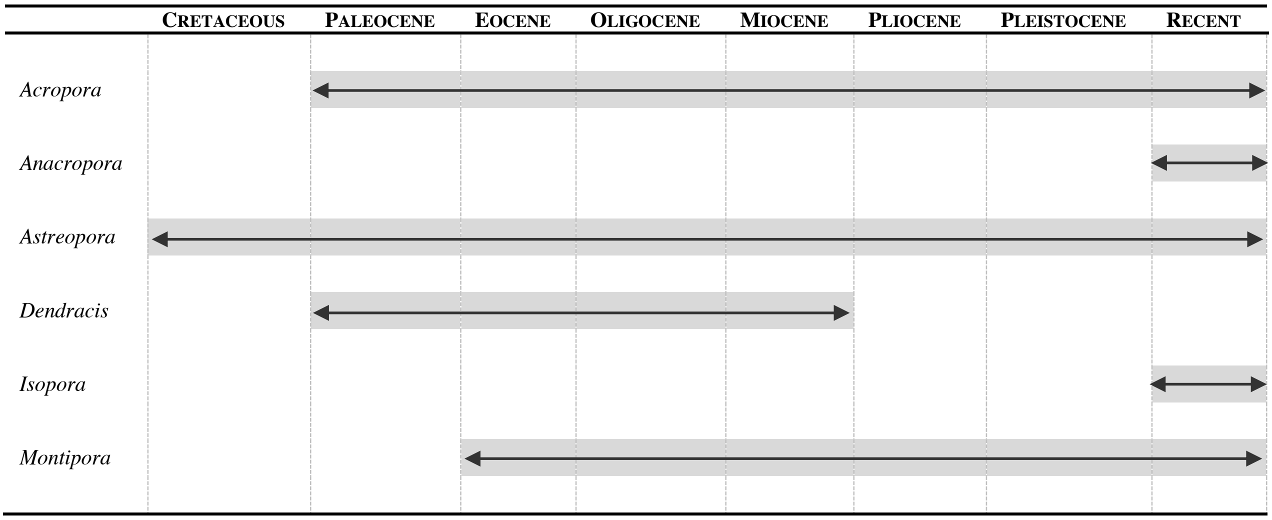


Figure 5.5. Summary of stratigraphic distribution of acroporid genera (see Chapter 3)

Many of the old Cretaceous coral families failed to survive or were dramatically reduced following the Late Cretaceous worldwide collapse of many faunas (Rosen, 2000; Kiessling and Baron-Szabo, 2004). By the Eocene many new genera had evolved including from the family Acroporidae: *Acropora*, *Montipora* and *Dendracis*. *Dendracis* is morphologically distinct from *Acropora* as it lacks an axial corallite, and disappeared in the Miocene. Last to evolve was *Isopora* and *Anacropora*, believed by Ridley (1884) to have evolved from *Montipora* relatively recently.

Recent phylogenetic trees from the analysis of the relationships among the genera of Acroporidae based on morphology alone appear to be increasing challenged by the use of molecular systematics (Fig. 5.6).

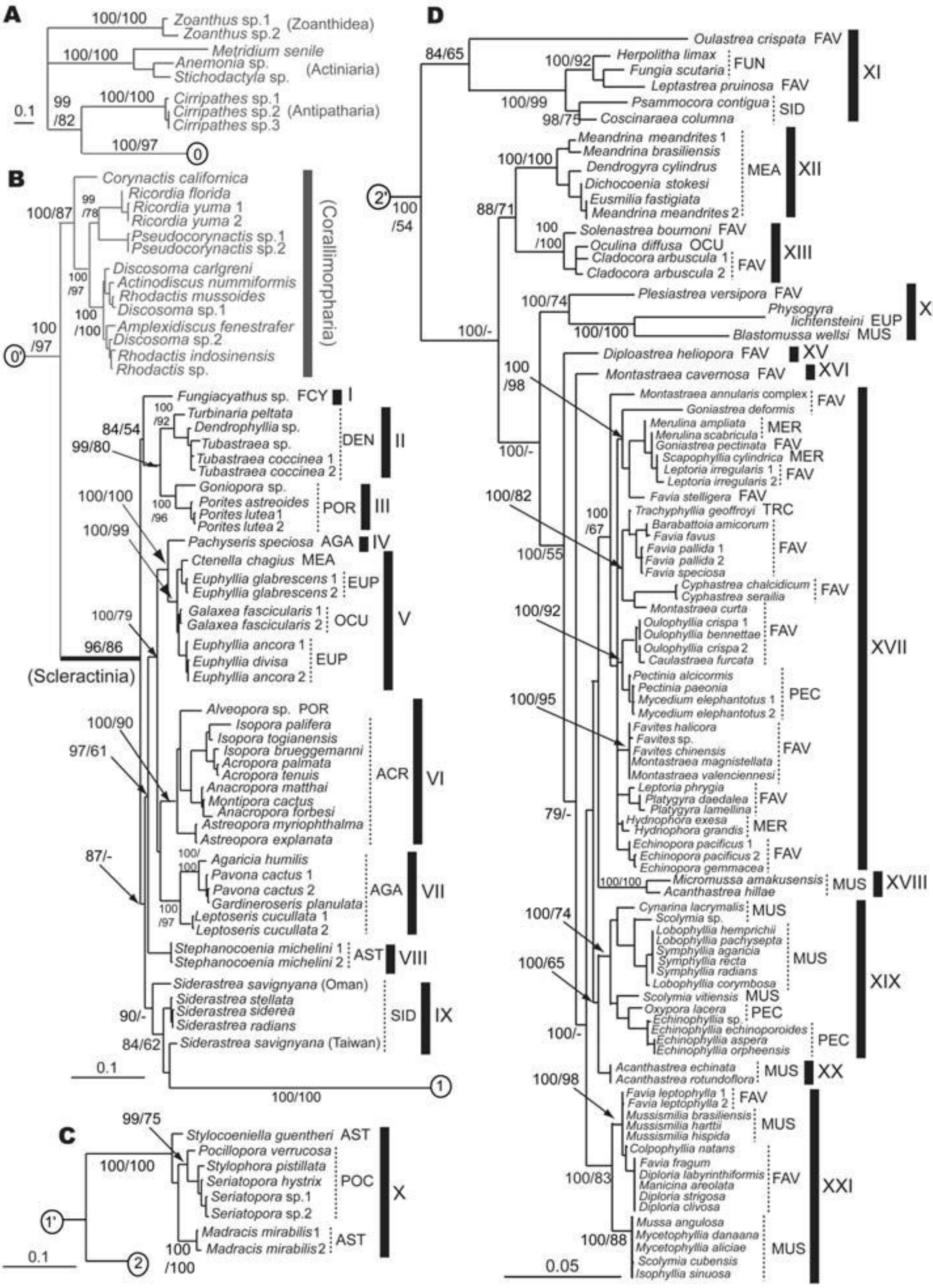


Figure 5.6. Phylogenetic relationships among scleractinian (mostly zooxanthellate) corals and outgroups. Topology was inferred by Bayesian analysis, based on combined mitochondrial cox1 and cob DNA sequences. Numbers on main branches show percentages of Bayesian probability (>70%) and bootstrap values (>50%) in ML analysis. Dashes mean bootstrap values <50% in ML. Numbers in circles show the connection of trees from A to D; for example, 19 in circle continues directly from 1 in circle. Bars in black indicate possible new family level groupings. Numbers (1, 2) following species names indicate that different colonies of the species had

different haplotypes. A. outgroups, B. complex corals and corallimorpharians, C. the family Pocilloporidae, D. robust corals. ACR: Acroporidae, AGA: Agariciidae, AST: Astrocoeniidae, DEN: Dendrophylliidae, EUP: Euphylliidae, FAV: Faviidae, FCY: Fungiacyathidae, FUN: Fungiidae, MEA: Meandrinidae, MER: Merulinidae, MUS: Mussidae, PEC: Pectiniidae, POC: Pocilloporidae, POR: Poritidae, OCU: Oculinidae, SID: Siderastreidae, TRC: Trachyphylliidae (Fukami et al.*, 2008).*

For example comparing molecular- (Fukami *et al.*, 2008) and morphological-based (Wallace, 1999) cladograms of the Acroporidae family show resemblances and disparities.

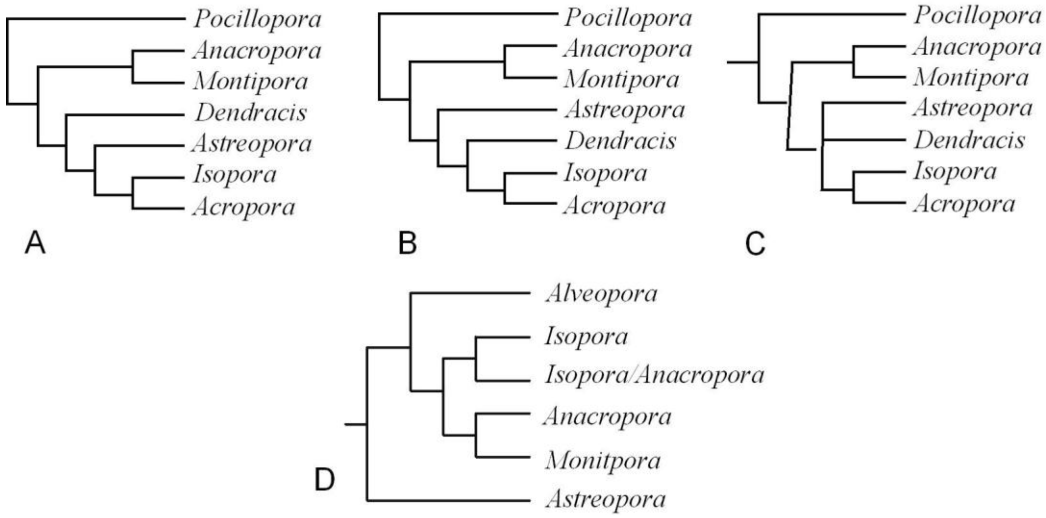


Figure 5.7. Acroporidae Family, comparison between A-C. morphology-based cladogram (from Wallace, 1999), and D. Extracted from molecular topology (Fukami et al.*, 2008).*

When comparing the two, 1. the morphology-based cladogram shows the genera *Anacropora* and *Montipora* are basal to Acroporidae, however the molecular shows *Astreopora* being basal, 2. first appearances in the morphology based cladogram show a first occurrence of the genus *Astreopora* which appears to be matched in the molecular-based cladogram (Fig. 5.7).

Diagnosis of the family Acroporidae Verrill, 1902

All members of the family are zooxanthellate. Genera in the family form massive or ramose, plocoid colonies by extratentacular budding (Tab. 5.7). Corallites are small, synapticulothecate, slightly differentiated from coenosteum. Septa do not extend above the corallite wall, in two cycles, constructed by simple spiniform trabeculae. Collumella is absent or weak. Dissepiments are thin and tabular when developed. Coenosteum extensive, flake-like, spiny, or striated.

	Acropora	***Anacropora***	***Astreopora***	***Dendracis***	***Isopora***	***Montipora***
Colony shape	Ramose, rarely massive or encrusting	Ramose	Massive or submassive	Ramose	Ramose	Submassive, foliaceous, ramose or encrusting
Axial of leading corallite	Present	Absent	Absent	Absent	Present	Absent
Corallite integration	Plocoid	Plocoid	Plocoid	Plocoid	Plocoid	Plocoid
Dissepiments	Absent	Absent	Tabulate	Absent	Absent	Absent
Synapticulae	Present throughout corallum		Absent	Present in vicinity of wall		
Columella	Absent	Absent	Absent	Absent	Absent	Weakly represented
Corallite wall	Synapticulothecal, porous	Solid	Parathecal-septothecal incomplete	Synapticulothecal	Porous	Porous

Table 5.7. Generic characters of the family Acroporidae, adapted information from older work, combined and presented here (Wallace, 1999, Veron, 2000).

5.6.4 Genus *Acropora* Oken, 1815

Heteropora Ehrenberg, 1834

Madrepora Ellis & Solander, 1786 and numerous 19th century authors

Acropora Oken, 1815; Verrill, 1902

Verrill (1902, p. 208) gives reasons for replacing the name *Madrepora* with *Acropora*, and Boschma (1961) gives a historical account of these names in support of an application to the International Commission of Zoological Nomenclature to validate *Acropora* (China, 1963).

Type specimen

Millepora muricata Linnaeus, 1758 by subsequent designation of the International Commission of Zoological Nomenclature (China, 1963). Neotype, specimen number G49167, from the Banda Islands, Indonesia in Museum of Tropical Queensland (Fig. 5.8, Wallace, 1999).

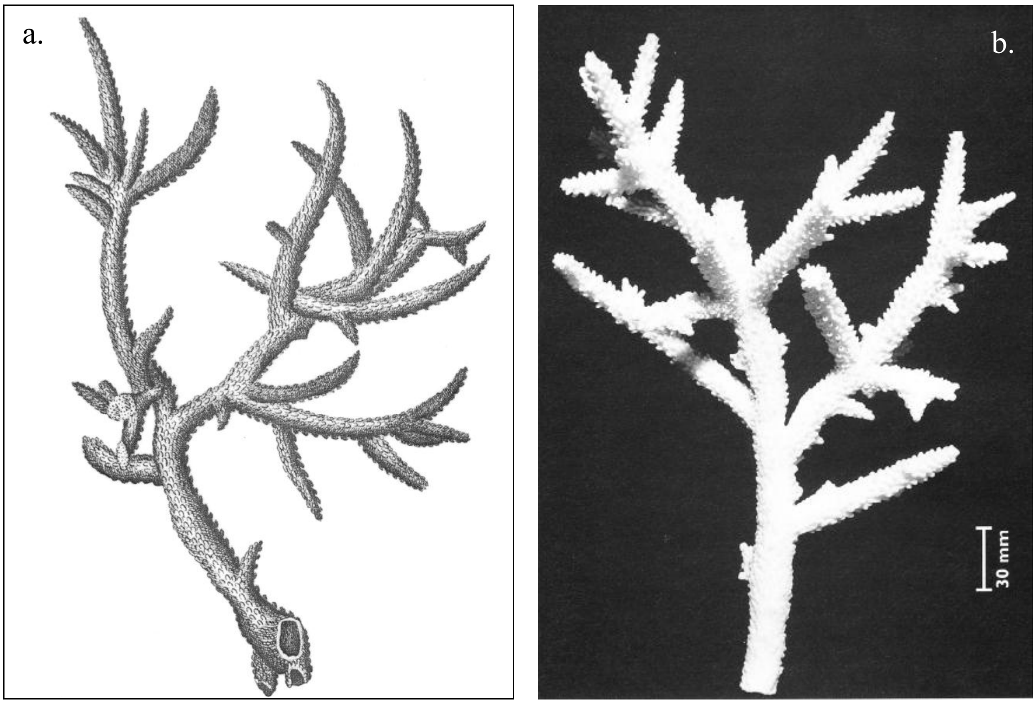


Figure 5.8. a. Acropora muricata (Linnaeus, 1758). Illustration from Rumphius, 1750, 'Herbarium Amboinense'. b. Acropora muricata (Linnaeus, 1758). Neotype specimen number G49167, from the Banda Islands, Indonesia in the Museum of Tropical Queensland (photo A. Elliott in Wallace, 1999).

Generic diagnosis by (Wallace, 2007, 2008)

Acroporidae which are ramose, rarely massive or encrusting. Branching with an axial or leading corallite larger than the more numerous radial corallites budded from it. United by light, reticulate, spinose or pseudocostate or costate coenosteum. Columella and dissepiments absent.

Summary of taxonomic history

The vast amounts of reefal research, both present and past, and *Acopora's* dominance in these environments, has led to an intrinsic need for work on *Acropora* taxonomy. This is exemplified by the monograph of Brook (1893) in which he treated all described species up to this time within the genus *Madrepora*, the name used for *Acropora* in the nineteenth century, and also included numerous new species of his own. Before Wallace (1999) this monograph was the only worldwide treatment of the genus (Veron and Wallace, 1984). It was not until 1963, following a submission to the International Commission of Zoological Nomenclature by Boschma (1961), that the name *Acropora* was officially validated (Wallace, 1999).

Wallace classified species of *Acropora* into species groups and provided a working phylogeny for them. Relationships between taxa are traditionally based on morphological features, summarised and analysed in morphology-based cladograms. Characters and characters states are organised in a character matrix which is then analysed to determine the most parsimonious distribution of shared characters and states amongst the sample set of taxa. The resulting cladogram shows the extent to which different taxa share their characters. Wallace (1999) and Wallace and Rosen (2006) presented cladograms for *Acropora* species groups (Fig. 5.9).

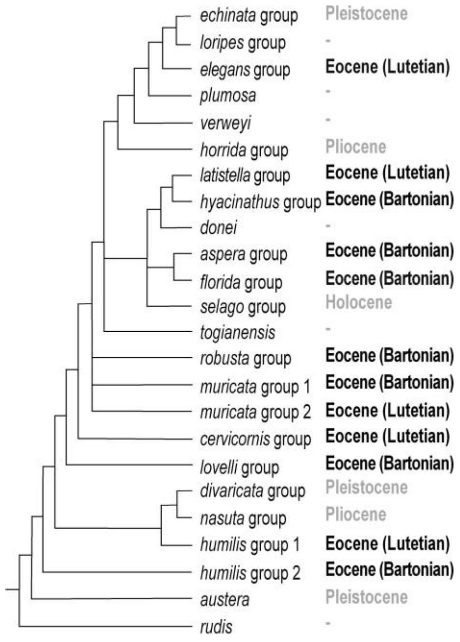


Figure 5.9. Morphology-based cladogram of species group relationships within the genus <u>*Acropora*</u> *updated in Wallace and Rosen (2006) from Wallace (1999). Highlighted are the earliest fossil occurrences updated from Wallace and Rosen (2006) with results from this thesis.*

Former taxonomic boundaries based on morphology alone are now being questioned by the increasing use of molecular systematics. Significantly, the molecular tree topologies generated by these bear little similarity to the results of recent cladistic analysis and are at odds with the fossil record (Fukami *et al.*, 2000; van Oppen, 2001, Fig. 5.10).

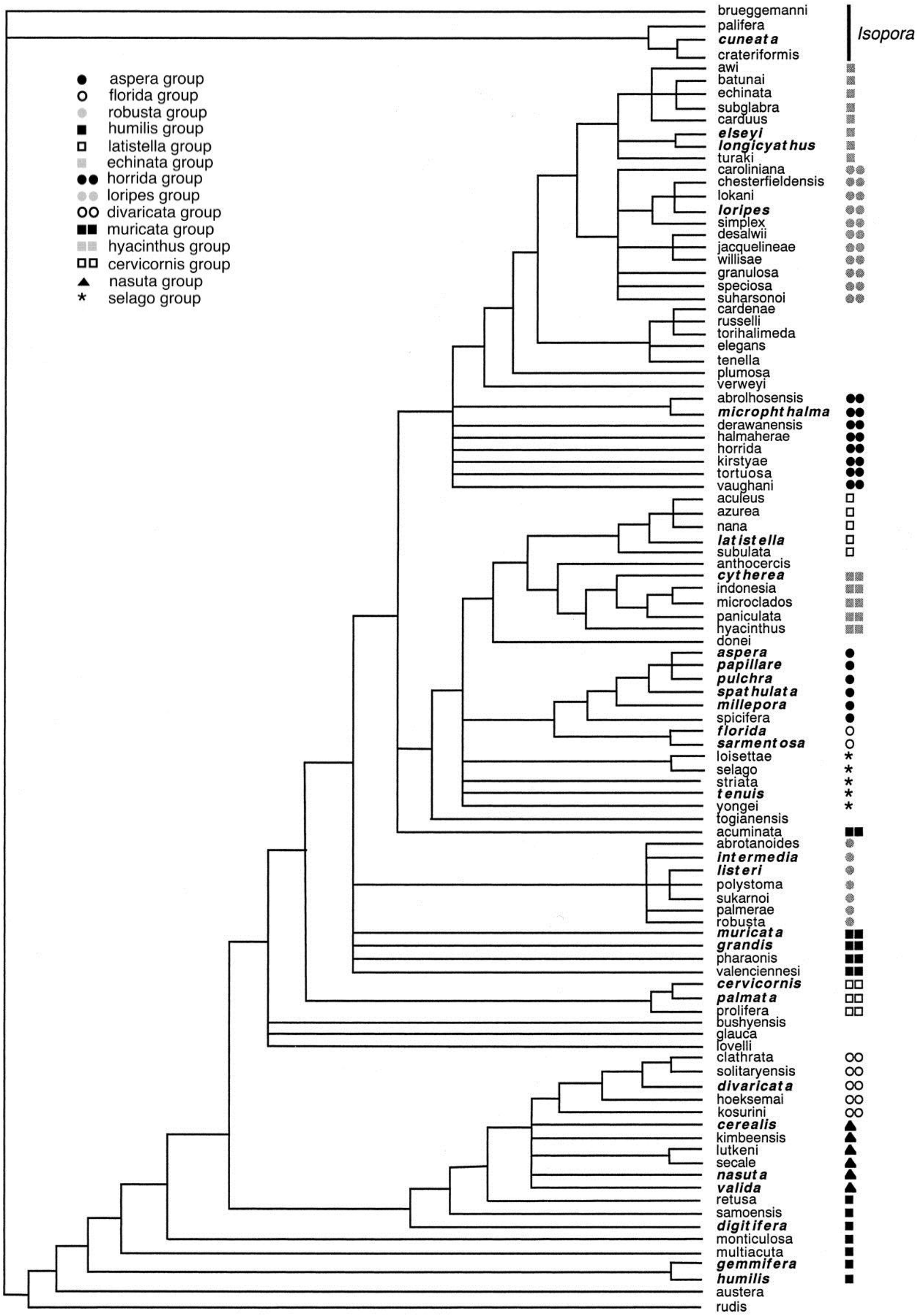


Figure 5.10. Parsimony consensus tree based on 23 morphological characters of the skeleton. Species that were used for the molecular phylogenies are in italics and boldface. Symbols represent species groups (van Oppen et al.*, 2001).*

Morphology, characters and terminology

Acropora is morphologically distinguished from other extant coral genera by the unique form of its polyp structure and its functional dimorphism. This gives rise to branches formed by one or more central or axial corallites which bud off a second type of corallite, the radial corallites, as the axial corallite extends and growth (Wells, 1956; Veron and Wallace, 1984; Wallace, 1999, Fig. 5.11-5.12). Axial corallites are cyclindrical and may reach several centimeters in length, while radial corallites occur in a variety of shapes and are never more than a few millimetres long. From its confamilial genera (*Montipora, Anacropora* and *Astreopora)*, *Acropora* is further distinguished by the distinctive structures of the radial corallite walls (a wall being absent from *Montipora* and *Anacropora,* and undifferentiated from a simple conical tube in *Astreopora)*.

In general, the terminology used here to describe morphological structures conforms to that used by Wallace (1999) for modern *Acropora* and is based on Dana (1846). The genus *Acropora* exhibits the characters of the family Acroporidae, characterised by synapticulotheca, simple septa and lacking both columella and dissepiments. The genus is primarily defined by its highly organised growth form, in which a central or axial corallite extends and buds off subsidiary or radial corallites growing from the tip (Oken, 1815; Wells, 1956; Wallace, 1978). This results in the axial corallite in each branch being the oldest one, and the newest corallites are the radials closest to the distal end of the axial one. This contrasts with other ramose corals which lack the axial-radial dimorphism, because the youngest corallites are all at the distal tip together.

Variability

The genus exhibits a vast amount of morphological variability between species but more problematically within species (intraspecific variation). Species can also display striking similarities to other species particularly in response to the same environmental factors. Most problematic within the fossil record is fragmentation of material making it difficult to distinguish inter- and intraspecific variation. With fragmentation of these colonies through the geological record problems arise when trying to determine growth form as different areas of colonies may be preserved, without it being obvious that they derive from the same colony or same species. The same characters seen in what remains of a colony, may also be exhibited by other species.

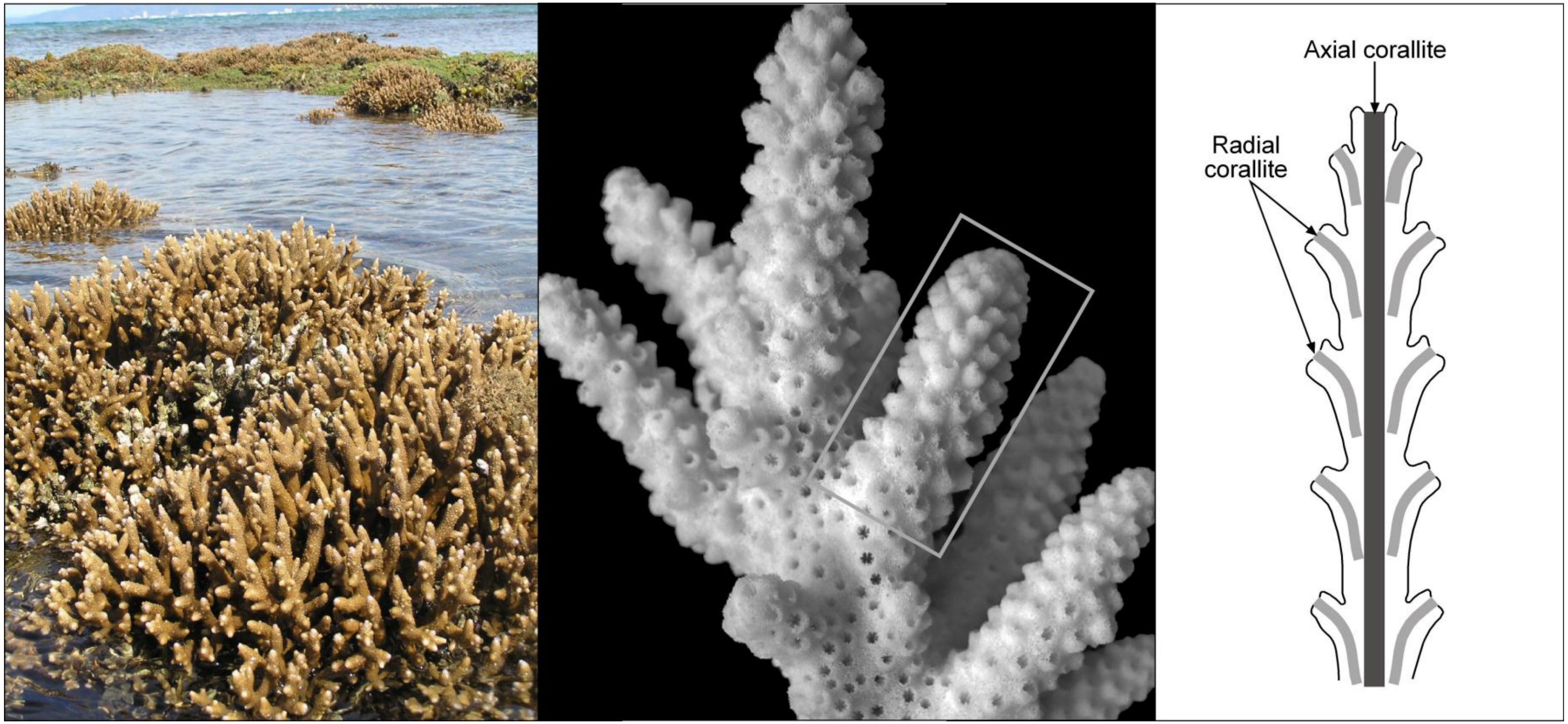


Figure 5.11. Skeletal morphology a. Example of colony form on the reef flats of Geoffrey Bay, Magnetic Island, GBR. Low, sprawling thickets dominated by Acropora pulchra Brook, 1891, and A. aspera Dana, 1846. Colonies appear corymbose or open arborescent, and are exposed during low tides, b. Part of specimen G 40906 Acropora sarmentosa (Brook, 1892), Bowden Reef, GBR, displaying hispidose branching (box refers to schematic section shown in c.), c. Schematic of main internal morphological features of an Acropora branch. Axial corallites are the central corallites which make up the axis of an Acropora branch, with radial corallites budding off from below the extending tip of the axial corallite.

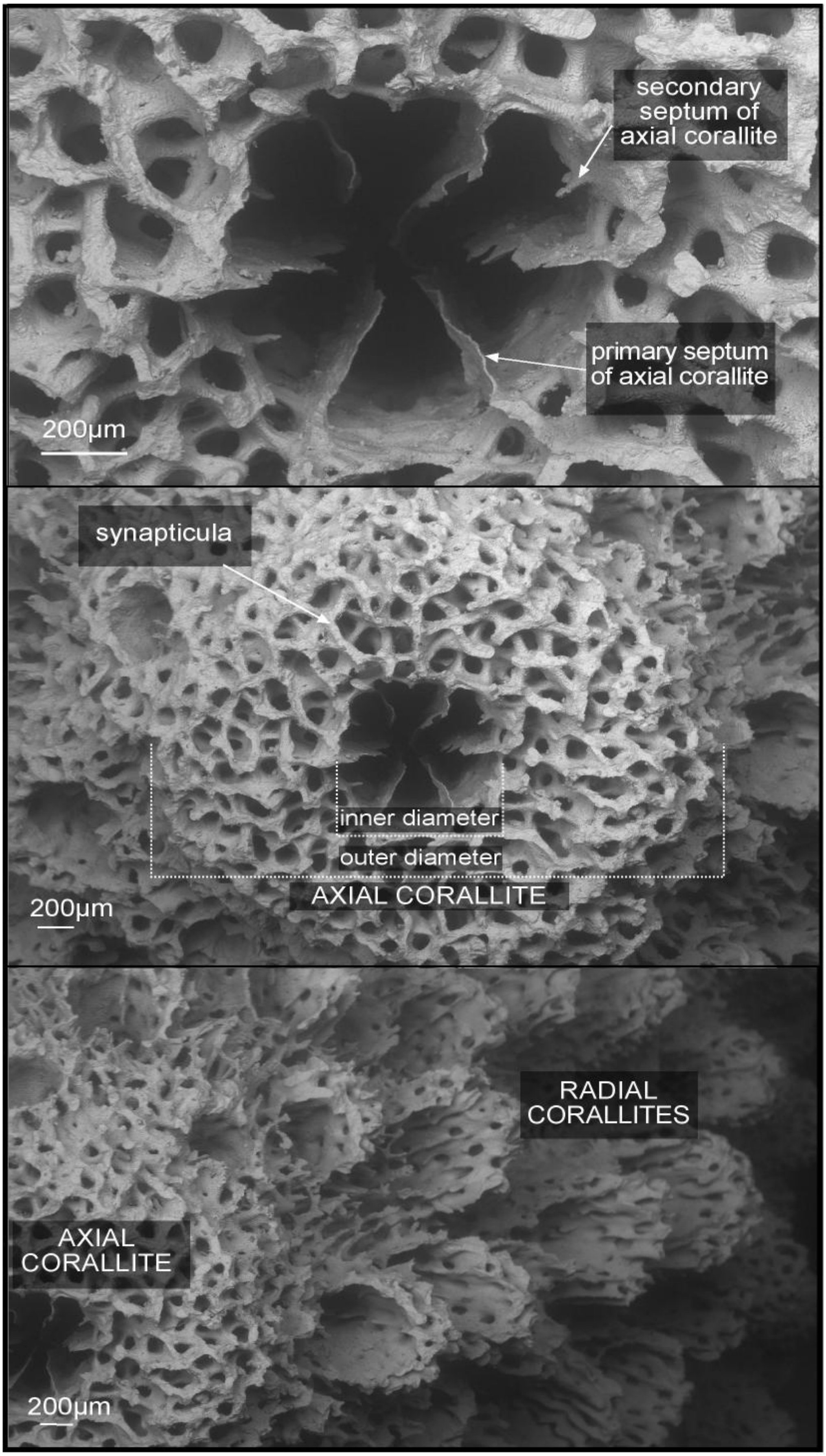


Figure 5.12. Main detailed morphological features diagnostic of the genus Acropora

Modern Species and Species Groups

Recent revisions of the genus recognize 113 (Wallace, 1999) or approximately 180 (Veron, 2000) *Acropora* species. The genus, until the recent elevation to genus level of *Isopora*, consisted of two subgenera, *A. (Acropora)* and *A. (Isopora)* (Wallace, 1984; van Oppen *et al*., 2001). Wallace (1999) phylogenetically, and Veron (Corals of the World VI, 2000) morphologically, have both grouped *Acropora* species into larger sub-generic categories ('species-groups'). Both schemes are based on skeletal morphology and shared skeletal characteristics. Veron (2000) identifies 38, whereas Wallace (1999) identifies 20 groups, with 19 in Indo-Pacific and 1 in the Caribbean.

5.7 SPECIES ACCOUNTS

5.7.1 Methodology and Protocol

Here follows a phylogenetic list of fossil *Acropora* species, and specimens newly assigned to these species, described from the Hampshire, Paris and Aquitaine basins. This revisionary taxonomy is presented according to the International Code of Zoological Nomenclature (Fourth Edition, Ride *et al*., 1999). In the species descriptions which follow, a protocol explained below, is used to distinguish between primary and secondary data where primary information has been updated. In the Specimen Detail sub-spreadsheet of the *Acropora* Database a verbatim copy of the information recorded by the collector is retained and is summarised here in (Appendix 4). Summarised below (Tab. 5.8) are the updated characteristics of locality details from the Eocene and Miocene localities from which fossil *Acropora* and *Dendracis* specimens have been collected.

		LOCALITY	REGION/COUNTRY	PALAEOLATITUDE$^{1.}$	ESTIMATE AGE (MA) $^{2.}$	RELATIVE AGE$^{2.}$	LITHOSTRATIGRAPHY^{3}
MIOCENE	AQUITAINE	GAAS	Aquitaine, France	41° N	23.03-5.332	Miocene*	-
		BORDEAUX	Aquitaine, France	43° N	23.03-5.332	Miocene*	-
EOCENE	HAMPSHIRE	BROCKENHURST	Hampshire, England	48° N	37.2-33.9	Priabonian, Late Eocene	Brockenhurst Bed
		WHITECLIFF BAY	Isle of Wight, England	48° N	37.2-33.9	Priabonian, Late Eocene	Brockenhurst Bed
		BARTON	Hampshire, England	48° N	40.4-37.2	Bartonian, Late Eocene	Barton Bed
	PARIS	AUVERS	Oise, Ile-de-France, France	47° N	40.4-37.2	Bartonian, Late Eocene	Sables Moyens
		CHAMBORS	Oise, Ile-de-France, France	47° N	48.6-40.4	Lutetian, Middle Eocene	Upper Calcaire Grossier
		FERME DE L'ORME	Yvelines, Ile-de-France, France	47° N	48.6-40.4	Lutetian, Middle Eocene	Upper Calcaire Grossier
		GRIGNON	Oise, Ile-de-France, France	48° N	48.6-40.4	Lutetian, Middle Eocene	Upper Calcaire Grossier
		VILLIERS ST. FREDERIC	Yvelines, Ile-de-France, France	48° N	48.6-40.4	Lutetian, Middle Eocene	Upper Calcaire Grossier
		FRESVILLE	Manche, Basse-Normandie, France	48° N	48.6-37.2	Middle Eocene*	-
		PARNES	Oise, Ile-de-France, France	47° N	48.6-37.2	Middle Eocene*	-
		PARIS BASIN*	Oise, Ile-de-France, France	47° N	48.6-37.2	Middle Eocene*	-

Table 5.8. Characteristics Eocene and Miocene localities from which fossil Acropora and Dendracis specimens have been collected (Poor precision of locality or age is indicated by an asterix and results in no lithostratigraphical information for these localities. Sources of information; [1.] Paul Markwick, GETECH, [2.] Gradstein et al.*, 2009, [3.] Information primarily from label information and updated from various sources).*

Taxonomic (information relating to the identification of the specimen), locality (where the specimen was found), stratigraphy (the geological context of the specimen), and provenance (how the specimen was obtained), verbatim data from the original label information, and registration details, are all distinguished from any interpretation made here, by placing the original information in brackets following after the interpreted information. For example, the only stratigraphic information on the label for specimen C25746 is 'Middle Headon' which can now be updated to 'Brockenhurst Bed', since this is the only coral bearing bed within this succession and in light of fieldwork carried out. Information which is now incorrect is still placed within brackets but also has the prefix 'non'. For example, specimen R54914 from the Brockenhurst Bed has label age information of 'Oligocene' where the Priabonian was originally placed. However, the Priabonian has now been placed in the Late Eocene (Gradstein *et al.*, 2009) and so the original Oligocene information is prefixed 'non' (i.e. Priabonian (non Oligocene)). Data with a high level of uncertainty, hence has poor geographical or temporal precision, and has been inferred here from basic label information, follows a question mark. For example, specimen NHM R54843 label has imprecise information of 'France, Middle Eocene'. On the basis of a knowledge of coral bearing lithologies found during the Middle Eocene of France additional locality information of '?Paris Basin' is tentatively added with the prefix of a question mark.

Specimens listed under each species have been newly studied here and included under their respective species. With the exception of the two types described below, and a few other specimens, this is the first time these specimens have been described to species-level (see Appendix 4 for original taxonomic label details). In addition to these specimens, specimens which were used as comparative material (primarily in Wallace, 2008) and which have previously been identified as this species are also listed. Material which has been listed as these species but which have not been seen in the present study, and therefore the identification could not be verified, is placed in brackets also under this subheading.

Strictly, the preservational state of a specimen is not part of a taxonomic description, but is included when it is important to indicate how it was constrained since taxonomic precision and conclusions, and additionally has bearing on the palaeoenvironmental interpretations in this thesis (see Chapter 6 and 7).

Where possible, following the approach of Duncan (1866), and Wallace (2008), comparisons and comments are made with the most similar modern *Acropora* species groups, based on morphological characters, and the environment within which these species groups are found today.

All specimens included under the subheading of ‘material studied and included in the species’ are newly described to species-level and assigned to these species with the exception of the two holotype specimens (*Acropora roemeri* and *A. anglica*) (see Appendix 4 for original label information where exists).

5.7.2 Fossil Acropora species accounts

Acropora [Madrepora] roemeri (Duncan, 1866)

PLATE 1

Madrepora roemeri Duncan, 1866, p. 51, pl.8, Figs 8-11
? *Acropora bartonensis* Wallace, 2008, p. 326, Fig 10
non *Acropora roemeri* (Duncan, 1866), Wallace, 2008, p.326, Fig. 9

Diagnosis updated from Duncan (1866)

Simple hispidose colony growth form. Branches are short and rounded with an equal contribution of axial and radial corallites to branch diameter. Radial corallites are probably tubular of one size or graded, some touching. Coenosteum on the radial corallite walls is costate and intercorallite coenosteum reticulate.

Type Locality Brockenhurst Bed (Mid Headon), Brockenhurst, England, Priabonian (from Duncan, 1866)

Material studied and included in the species

Holotype BGS X/X 2/19, Brockenhurst Bed (Mid Headon), Brockenhurst, Hampshire, England, Priabonian (Eocene)

SGW C25746, Brockenhurst Bed (Middle Headon), Brockenhurst, C26189, Brockenhurst Bed, Brockenhurst (Brockenhurst railway cutting), Hampshire, England, Priabonian **PC** AM MIWG2611, Brockenhurst Bed (Middle Headon), Whitecliff Bay, Isle of Wight, England, Priabonian.

Other comparative material

NHM 49583 Brockenhurst Bed (Middle Headon Beds), Hampshire, England, Priabonian, R18216 Brockenhurst Bed (Middle Headon Beds), Hampshire, England, Priabonian (Eocene), R18217 Brockenhurst Bed (Middle Headon Beds), Hampshire, England, Priabonian (Eocene), R54913 Brockenhurst Bed, Brockenhurst, Hampshire, England, Priabonian (non Oligocene), R54914 Brockenhurst Bed, Brockenhurst, Hampshire, England, Priabonian (non Oligocene).

Description

Holotype X/X 2/19. Intermittent areas of well preserved radials showing clear morphological features. Some areas appear relatively more worn with radials very abraded. Some details obscured by muddy infilling with sediment.

Overall size of the specimen 42.3 by 19.1mm. Joint area with eight branches arising from thickened, flattened basal section. Branches abraded and ends irregularly broken. Diameter of broken branches 8.4 and 9.2mm. Radial corallites rounded tubular, some appear sub-immersed, appear to be mixed sizes, crowded and touching. Equal contribution of axial and radial corallites to branch diameter. Average diameter of radials 1.4mm (1.2-1.6mm, n=3). Radial corallite walls dense costate (where well preserved) intercorallite walls reticulate.

SGW C25746. Well preserved specimen showing clear morphological features. Overall length of specimen 35mm, with a maximum width of 28.3mm. Joint area with multiple branchlets. Implied colony growth form is simple hispidose with fine, rounded branches. Appears to have a basal plate, possibly where attached to the substrate, with branches radiating upwards from it. Seven branchlets can be seen meeting at the basal plate, all broken. Average branch diameter 8.2mm (7.8-8.7mm, n=3). ~50/50 contribution of axial and radials to branch diameter. Axial corallites are worn and heavily infilled with sediment. Radials in two distinct sizes, some touching, crowded in places; appressed tubular with rounded openings; average radial corallite diameter 1.4mm (0.9-1.9mm, n=3). Coenosteum on radials costate; intercorallite coenosteum broken costate/reticulate.

SGW C26189. Fairly well preserved specimen infilled with sediment and with heavily abraded radial corallites. Specimen size 24.8 by 15.9mm. Joint area between three rounded branchlets. Equal contribution of axial and radial corallites to branch diameter. Branch diameters 8.3, 8.1 and 7.0mm. Radial corallites touching in some areas. Coenosteum on radials costate and reticulate between radials.

AM MIWG2611. Highly abraded specimen, overall 25mm length. Single branch with two broken-off branchlets, axial dominated with highly abraded radial corallites and wall structure.

Remarks

Wallace (2008) included no information about the type specimen of this species. In fact, Wallace's new species, *A. bartonensis* Wallace, 2008, appears to belong, or is very similar, to *A. roemeri,* whereas *A. roemeri* sensu Wallace, 2008, is a new species assigned here to *Morphotype 3*.

This species shows development of rounded branchlets in a simple hispidose colony form with branches evenly spaced around a main branch reminiscent of the modern *florida* group (see Wallace, 1999, p. 249). This group is found today subtidally and includes *Acropora florida*, one of the most common Indo-Pacific species (see Wallace, 1999, p. 249)

Acropora [Madrepora] anglica (Duncan, 1866)

PLATE 2

Madrepora anglica Duncan, 1866, p. 51, pl.8, Figs 1-7

Acropora anglica (Duncan, 1866), Wallace, 2008, p. 323, Fig 7

Diagnosis modified from Wallace (2008)

Sturdy, sub-arborescent colony form with tapering branches. Branches are dominated by axial corallite. Radial corallites appressed tubular, in two distinct sizes, sometimes touching. Coenosteum on radial corallites costate and intercorallite coenosteum reticulate.

Type Locality Brockenhurst Bed (Mid Headon), Brockenhurst, England (from Duncan, 1866)

Material studied and included in the species

Type: BGS X/X 3/20 Brockenhurst Bed (Mid Headon), Brockenhurst, Hampshire, England, Priabonian; **SGW** C29420 Brockenhurst Bed (Middle Headon Bed, lowest 2 feet [0.6m]), Whitecliff Bay, Isle of Wight, England, Priabonian C29419 Brockenhurst Bed (Middle Headon Bed, lowest 2 feet [0.6m]), Whitecliff Bay, Isle of Wight, England, Priabonian, C259911 Brockenhurst Bed, Brockenhurst, Hampshire, England, Priabonian

Other comparative material

NHM R49583 Brockenhurst Bed (Middle Headon Beds), Brockenhurst, Hampshire, England, Priabonian (Eocene), R2339 Brockenhurst Bed, Brockenhurst, Hampshire, England, Priabonian (Eocene),

Description

Holotype BGS X/X 3/20. Well preserved large specimen with some clear morphological features. Coenosteum and radial corallite features abraded in some areas. Sediment infilling, concretions, iron staining and molluscan borings also present.

Overall size of the specimen 107.7 in length, by a maximum width of 71.2mm. Broad, sturdy specimen with extensive branching pattern. Joint area with two main branches forming one, several branchlets (~18). Ends too worn and infilled with sediment to see details of axials. One side of the specimen is much more heavily branched (~10-14) with fewer branches on the other and appearing more rounded and appressed (~4) on the opposite side. Diameter of broken branches 15.1, 10.7 and 14.3mm. Axial corallites dominate branches. Radial corallites appressed tubular with rounded openings, not touching and appear two sizes. Diameter of radial corallites 0.8, 0.6 and 0.9mm. Radial corallite walls costate, interradial coenosteum predominantly reticulate with areas of more continuous form, broken costate.

SGW C29420. Poorly preserved specimen, heavily abraded and infilled with sediment. Overall specimen is 26.7 by 33.4mm. Branches axial dominated, 11.8 and 11.5mm diameter.

SGW 29419. Well preserved specimen, although with highly abraded surface causing loss of superficial morphological characters. Overall size of specimen 27.7 by 15.9mm. Arborescent colony form. Joint area between two branchlets to form a single main branch. Branches dominated by axials, with 11.0 and 11.8mm diameter. Radials appear to be in two sizes.

SGW C259911. Large, well preserved specimen. Infilled with large amounts of sediment. Superficial features abraded and radial corallites and coenosteum worn. Evidence of mollusc encrustation and borings, iron staining. Specimen overall 56.8 by 50.5mm. Colony form sturdy, arborescent. Rounded, sturdy, axial dominated branches.

Branch diameter 10.3, 12.7 and 13.8mm. Axial corallites worn and flush with branch walls. Some touching in two sizes. Coenosteum on radials costate.

Remarks

The type for this species has been newly located and re-examined for the first time since Duncan (1866). This species characteristically exhibits a sturdy, robust growth form with broad branches and two distinct sizes of radial corallites. Duncan described this species as being similar to the modern *Acropora crassa* (now a junior synonym of *A. abrotanoides)*, a member of the *robusta* group which is today associated with shallow, high water movement habitats such as the reef crest or edge, or patch reefs and shoals in high current locations (see Wallace, 1999, p.193 and 196).

Acropora alverezi Wallace, 2008

PLATE 3

Acropora alverezi Wallace, 2008, p. 321, Fig. 5

Diagnosis from Wallace (2008)

Colony growth form arborescent with terete branches. Equal contribution of axial and radial corallites to branch diameter. Radial corallites are one size or graded, not touching and tubular. Coenosteum on radials is costate with reticulate coenosteum between radials.

Type Locality NHM R35320 ?Paris Basin, France, ?Middle Eocene

Material studied and included in the species

NHM 50236a, Sables Moyens (Jarisien B2), Auvers-sur-Oise, Il-de-France, France, Bartonian (Eocene), 50236c, Sables Moyens (Jarisien B2), Auvers-sur-Oise, Il-de-France, France, Bartonian (Eocene), 55687a, Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian (Middle Eocene), R40831, Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian R52049, Upper Calcaire Grossier, Chambors, Ile-de-France, France, Lutetian, 55687c, Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian (Eocene), AZ2904, Sables Moyens (Sables d'Auvers), Auvers-sur-Oise, Ile-de-France, France, Bartonian (non Late Lutetian), 55687b, Sables Moyens, Auvers-sur-Oise. **FW** P1A09, Sables Moyens, Auvers-sur-Oise, Ile-de-France,

France, Bartonian (Middle Eocene), P1A10, Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian.

Other comparative material

NHM 35320 (Holotype) ?Paris Basin, France, ?Middle Eocene, R2209b Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian (Mid Gervillei, Eocene), R45675 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian (Eocene), R45676 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian (Eocene), R52067 Upper Calcaire Grossier, Chambors, Ile-de-France, France, Lutetian, R54831 Paris Basin, France, Middle Eocene, R54833 Paris Basin, France, Middle Eocene, R54861 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian (Eocene), R54849 Paris Basin, France, Middle Eocene, R54838 Paris Basin, France, Middle Eocene

Description

NHM 50236c. Joint area between two axial corallites with graded radial corallites. Coenosteum heavily abraded in places.

NHM 55687a. Single terete branch with multiple (~4) branchlets indicating an arborescent growth form. Radials graded and crowded, although not touching. Coenosteum costate on radials and reticulate between.

NHM 50236a. Joint area between two terete branches, one which further splits into two axial corallites. Radial corallites are graded with some touching. Radials and coenosteum heavily abraded.

NHM R52049. Single terete branch. Radial corallites graded with some touching.

NHM 55687c. Single terete with single branchlet at base and an incipient branchlet. Radial corallites graded, crowded and not touching.

NHM AZ2904. Joint area between two terete branches. Radial corallites multiple sizes. Coenosteum between radials appears reticulate.

NHM 55687b. Basal plate or appressed side, flat with few corallites. Multiple (~3) terete branchlets appear to radiate from appressed side. Radials graded with rounded openings, mostly not touching. Coenosteum on radials is costate with reticulate coenosteum between radials.

FW P1A09. Joint area with two branchlets off a main branch, single insipient branch on main branch. Overall size 24.6mm by 5.5mm (9.2mm joint area). Radial corallites two sizes, heavily worn, crowded

FW P1A10. Overall size 20.1mm by 5.5mm. Fragment of single terete branch. Radial corallites graded, heavily abraded, crowded with some touching. Coenosteum on radial corallites costate, and between reticulate.

Remarks This species is very common within the Paris Basin localities exhibiting relatively fine, terete branches and an arborescent growth form. It is similar to the species *Acropora wilsonae,* the distinction being made between the two by *wilsonae* exhibiting two distinct sizes of radial corallite. Additionally, the transverse section of individual branches appears to be different, with *alvarezi* exhibiting a circular shape, but *wilsonae* specimens often showing a more oval shape (this may however due to preservation factor). This oval branching shape is often associated with the species group *cervicornis*, implying sub-vertical growth.

***Acropora wilsonae* Wallace, 2008**

PLATE 3

Acropora wilsonae Wallace, 2008, p. 324, Fig. 8

Diagnosis from Wallace, 2008

Arborescent colony form with terete branches. Equal contribution of axial and radial corallites to branch diameter. Two distinct sizes of radial corallites, not touching and lipped. Coenosteum on radials costate and between radials reticulate.

Type Locality NHM R54847 Paris Basin, France, Middle Eocene

Material studied and included in the species

NHM R40833 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian (Eocene), AZ2902 Sables Moyens (Sables d'Auvers), Auvers-sur-Oise, Ile-de-France, France, Bartonian (non Late Lutetian, Middle Eocene), AZ2903 Sables Moyens (Sables d'Auvers), Auvers-sur-Oise, Ile-de-France, France, Bartonian (non Late Lutetian, Middle Eocene), 46824b Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian (Eocene) 46824a Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian (Eocene) 50236d Sables Moyens (Jarisien B2), Auvers-sur-Oise, Ile-de-France, France, Bartonian (Eocene) R40832, Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian (Eocene) R52052 Upper Calcaire Grossier, Chambors, Ile-de-France, France, Lutetian (Eocene) **FW** P1A13 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian

Other comparative material

NHM R54842 ?Paris Basin, France, Middle Eocene, R54848 Paris Basin, France, Middle Eocene, R2209c Sables Moyens (Middle Gervillei), Auvers-sur-Oise, Ile-de-France, France, Bartonian (Eocene), R45677 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian (Eocene), R45678 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian (Eocene), R52065 (listed but no label detail), R54837 Paris ?Basin, France, Middle Eocene

Description

NHM R40833. Single branch with multiple, abraded radial corallites. Radials two sizes. Thin, fragile structure.

NHM AZ2902. Single branch with multiple, abraded, not touching radial corallites.

NHM AZ2903. Single branch with highly abraded radial corallites and coenosteum structure. Two distinct sizes of radial corallites.

NHM 46824b. Two branches, one being a single terete branchlet. Radial corallites heavily worn but appear to be in two sizes and not touching.

NHM 46824a. Joint area between multiple (~5) axial corallites. Radial corallites heavily worn but appear to be in two sizes and not touching.

NHM 50236d. Three branches with multiple highly abraded radial corallites and coenosteum. Radials appear to be in two sizes.

NHM R40832. Two fused terete branches. Two distinct sizes of radial corallites, heavily abraded, mostly not touching.

NHM 52052. Single terete branch. Two sizes of tubular radial corallites, mostly not touching. Coenosteum costate on radials and reticulate between them.

FW P1A02. Fragment of single terete branch with one incipient branchlet. Overall specimen length 17.8mm and maximum width 5.0mm. Radial corallites in multiple sizes, mostly not touching; crowded, tubular. Coenosteum costate on radial corallites and reticulate between them.

P1A13. Joint area between two main broken branches and one incipient branch. Overall size 18.0mm by 6.1mm (9.2mm in joint area). Radial corallites appressed tubular with round openings, in two sizes. Coenosteum costate on radials and reticulate between them.

P1A21. Overall specimen is 21.8mm by 7.4mm, single branch with abraded joint area at the top. Radial corallites in two sizes, not touching but crowded. Coenosteum costate on radials and reticulate between them.

P1A22. Joint area, with 4 branchlets and one main branch and further evidence of an incipient branch on main branch. Overall size 27.2mm by 8.3mm (14.3mm in joint area). Radial corallites two sizes with rounded openings, not touching. Coenosteum on radials heavily worn but in between them appears reticulate.

Remarks See remarks under *Acropora alvarezi*

Acropora proteacea Wallace, 2008

PLATE 3

Acropora proteacea Wallace, 2008, p. 327, Fig. 11

Diagnosis modified from Wallace, 2008

Tabular colony form with terete branchlets. Branches often shows radial corallites arranged in a 'rosette' around axial corallites. Radial dominated branches. Radial corallites one size, touching and lipped. Coenosteum on radials heavily worn but in between them appears reticulate.

Type Locality NHM R18265 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian (Eocene)

Material studied and included in the species

NHM R52048 Upper Calcaire Grossier, Chambors, Ile-de-France, France, Lutetian (Eocene), R52050 Upper Calcaire Grossier, Chambors, Ile-de-France, France, Lutetian (Eocene).

Other comparative material

NHM Holotype 18265 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, (Lower) Bartonian (Eocene), R45679 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian (Eocene).

Description

NHM R52048. Joint area between two branchlets. Radials in two sizes, not touching. Coenosteum on radials costate and reticulate between them. Diagnostic rosette arrangement of radials around axial corallite.

NHM R52050. Highly abraded and lacking clear radial corallites and coenosteal morphological features. However, evidence of diagnostic 'rosette' branching pattern is visible where multiple (~5) branchlets arise from main slender branch.

Remarks Specimens have been assigned to this species on the basis showing the characteristic 'rosette' branching pattern and slender growth form of the branches. This is the only species from the Paris Basin for which a table growth form can be inferred and, with its characteristic rosette branching pattern, it is most similar to the modern species associated with the *hyacinthus* group.

Acropora [Madrepora] deformis (Michelin, 1840)

PLATE 3

Heliopora deformis Michelin, 1840, p. 164, pl. 45, Fig. 6
Acropora deformis (Michelin, 1840), Wallace, 2008, p. 316, Fig. 4

Diagnosis modified from Michelin (1840) and Wallace (2008)

Corymbose-digitate colony form with terete, axial dominated branches. Radial corallites one size, not touching, appressed with round openings. Coenosteum costate on radials, and reticulate between them.

Type Locality Avert, Valmondois (Seine et Oise)

Material studied and included in the species None

Other comparative material

NHM R54843 ?Paris Basin, France, Middle Eocene, R2209a Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian (Mid. Gervillei, Eocene), R54910 ?Paris Basin, France, Middle Eocene, R18266 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, (Lower) Bartonian (Eocene), R54911 ?Paris Basin, France, Middle Eocene, R55689 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian (Middle Eocene)

Acropora britannica Wallace, 2008

PLATE 3

Acropora britannica Wallace, 2008, p. 316, Fig. 3

Diagnosis from Wallace (2008)

Digitate colony with short vertical terete branchlets, around 5mm long and 8mm diameter, arising from a solid base; radial corallites all same size, appressed, crowded; coenosteum dense reticulo-costate on ad between radials.

Type Locality Brockenhurst Bed, Brockenhurst, Hampshire, England, Priabonian

Material described None

Other comparative material

NHM Holotype R54912 Brockenhurst Bed, Brockenhurst, Hampshire, England, Priabonian

Acropora [Madrepora] ornata (Defrance, 1828)

PLATE 3

Madrepora ornata Defrance, 1828, p. 8, pl. 28
Acropora ornata (Defrance, 1828), Wallace, 2008, p. 327, Fig. 13

Diagnosis from Wallace (2008)

Colony arborescent with cylindrical tapering branches; radial corallites tubular with round openings, all same size, not touching; radial corallite walls costate; interradial coenosteum reticulo-costate.

Type Locality Paris Basin, Lutetian

Material studied and included in the species

NHM 46822, Gass, Aquitaine, France, Miocene

Other comparative material

NHM R40382-40385, Upper Calcaire Grossier, Ferme de l'Orme, Ile-de-France, France, (Upper) Lutetian (Eocene)

Description

NHM 46822 Single tapering, cylindrical branch. Radial corallites tubular and rounded, appear the same size. Coenosteum is costate on and between radials.

Remarks This record from the Miocene of the Aquitaine Basin extends both the spatial and temporal record of the species having previously only been described from the Lutetian of the Paris Basin. The slender branch and long radial corallites are reminiscent of the modern species *Acropora russelli*, associated with calm, deep water locations

Acropora [Madrepora] solanderi (Defrance, 1828)

PLATE 3

Madrepora solanderi Defrance, 1828 p. 8 pl. 28

Acropora solanderi (Defrance, 1828), Wallace 2008, p. 322, Fig. 6

Diagnosis modified from Wallace (2008)

Slender, open, tapering branches. Equal contribution of radial and axial corallites to branch diameter. Radial corallites appressed tubular with lip, of mixed sizes, some touching. Radial corallite wall broken costate or reticulate, intercorallite coenosteum reticulate.

Type Locality Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian

Material studied and included in the species

FW P1A03 Sables Moyens, Auvers-sur-Oise. Ile-de-France, France, Bartonian, P1A05 Sables Moyens, Auvers-sur-Oise. Ile-de-France, France, Bartonian, P1A24 Sables Moyens, Auvers-sur-Oise. Ile-de-France, France, Bartonian

Other comparative material

NHM R54832 Paris Basin, France, Middle Eocene, R54839 Paris ?Basin, France, Middle Eocene

Descriptions

P1A03. Slender fragment of branch. Heavily worn but appears tapered. Overall size 15.2mm by 3.3mm. Radials are heavily worn but appear mixed in size.

P1A05. Fragment of single tapering branch. Overall size 21.7mm by 4.3mm. Radial corallites graded, of mixed sizes, some touching and heavily worn.

P1A24 Fragment of single tapering branch. Overall size 18.9mm by 4.0mm. Radial corallites are heavily abraded, appears to be in two sizes with few touching. Coenosteum on radial corallites costate and in between corallites is reticulate.

Remarks Many specimens within the collections studied are labelled '*Madrepora solanderi'*. Few, however, show the diagnostic tapering branch structure and therefore have been designated here to other species. All specimens placed in this species have been done so principally on the basis of their tapering branch structure.

Acropora [Madrepora] lavandulina (Michelin, 1840)

PLATE 4

Madrepora lavandulina Michelin, 1840, p. 67, pl. 14, Fig 2 a-b
Acropora lavandulina (Michelin, 1840), Wallace, 2008, p. 327, Fig. 12

Diagnosis modified from Michelin (1840) and Wallace (2008)

Corymbose(?) colony with tapering branchlets, around 45–50 mm long and 7 mm diameter. Radial corallites tubular with round openings, one size, not touching. Coenosteum costate on radial walls and reticulate to broken costate between radials.

Type Locality Turin, Bordeaux and Dax (Michelin, 1840)

Material studied and included in the species

NHM R18276, Bordeaux, Aquitaine, France, Miocene, R2416, ?Aquitaine Basin, France, Miocene **OM** C1D101 Fresville, Basse-Normandie, France, Middle Eocene **UREG** NHM France, Miocene

Other comparative material

NHM R54844 ?Paris Basin, France, Middle Eocene

Descriptions

NHM R2416. Specimen is a joint area between two branchlets, overall size of the specimen 28.4 mm by 7.3mm, maximum width of 22.4 mm in the joint area. Radials geometrically aligned in two rows, appearing conical in places.

OM C1D101. Overall length of specimen 18.1mm, with a maximum diameter of 5.2mm. Branch tapered and radial dominated. Radial corallites tubular with rounded openings, one size, not touching, crowded. Coenosteum on radials costate and broken costate between them.

NHM UNREG Material. Overall length 33 mm in length, by 7.2 mm, maximum width 18.4 mm in the joint area, consisting of a single branch with joint area between two branches. Radials rounded and tubular, one size, not touching. Coenosteum not preserved well enough to see.

Remarks *Acropora lavandulina* appears to have a close morphological similarity to that of *Acropora tergestina* (Oppenheim, 1901), from Somalia, with similar geometric row-like arrangement of radial corallites. This row-like arrangement is also shown by some *Dendracis* specimens.

The specimen OM C1D101 from the Middle Eocene, Fresville, Valognes (Cotentin region) spatially and temporally extends the record of the species in France, having previously only been described form the Miocene of the Aquitaine Basin, SW France.

Acropora [Madrepora] exarata (Michelotti, 1838)

PLATE 4

Madrepora exarata Michelotti, 1838, p. 186, pl. 6, Fig. 6
Madrepora exarata Michelin, 1840, p. 67, pl. 14, Fig 3a-b

Diagnosis

Colony form appears arborescent. Branches axial dominated, cylindrical and terete. Radial corallites are short with rounded openings, two distinct sizes, not touching. Radial corallite walls are costate, and reticulate between them.

Type Locality ?Aquitaine Basin, France, Miocene

Material studied and included in the species

NHM R18276, Bordeaux, Aquitaine, France, Miocene, R50912 Bordeaux (Graviere de Cante, Saucats), Aquitaine, France, Burdigalian, Miocene

Other comparative material None

Description

NHM R18276. Single branch with the beginnings of a joint area at the fragmented end. Branch is axial dominate and heavily abraded. At least two sizes of radial corallites. Coenosteum is too worn to observe characters.

NHM R50912. Joint area between two branches. Overall size 36mm by 24mm. Branches are axial dominated. Both coenosteum and radial corallites are heavily worn but radials appear to be in two sizes and mostly not touching.

Remarks Only two species have, prior to this work, been described from the Aquitaine Basin (*Acropora lavandulina, A. exarata*). This species exhibits a robust, sturdier nature, particularly in contrast to the slender branches of *Acropora lavandulina* specimens. Its broad branching structure, arborescent growth form and two sizes of radial corallite appears similar to species from the *robusta* group, whose species are associated with reef edge environments.

Acropora morphotype 1 n. sp.

PLATE 5

Diagnosis

Arborescent-table, sturdy form. Branches terete, rounded and axial dominated. Radial corallites tubular, two sizes, some touching. Coenosteum on radials costate and reticulate in between them.

Locality of proposed type. Brockenhurst Bed, Brockenhurst, Hampshire, England, Priabonian

Material studied and included in the species

SGW Proposed holotype C25799, Brockenhurst Bed, Brockenhurst, Hampshire, England, Priabonian

Other comparative material None

Descriptions

Proposed holotype SGW C25799. Specimen very well preserved although large amounts of brown infilling sediment obscuring some areas and features. Clear radial, axial and coenosteum features. Some iron staining, boring and encrusting molluscs.

Overall size 110.4mm by 70.4mm. Joint area with multiple branchlets. Flattened base implies arborescent table-like form. Axial dominated sturdy, rounded branches extending from a flattened base plate. Branch diameters 15.2, 10.1, 9.8, 10.8, and 12.7mm. Radials tubular with rounded opening, in two sizes, some touching. Coenosteum of radial corallites costate and reticulate between them.

Remarks A new species is proposed here on the basis of the arborescent-table colony growth form. No other material with this colony form has been published for either the Hampshire or Paris basins. The characters of this species suggest that it belongs with the extant *muricata* group.

Acropora morphotype 2 n. sp.

PLATE 6

Diagnosis

Colony growth form appears arborescent. Branches terete, with axial corallites dominating and branches rounded. Radial corallites immersed, small, mixed in sizes and not touching. Coenosteum on radial corallite is costate, and reticulate between them.

Locality of proposed type. Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian

Material studied and included in the species

Proposed holotype FW P1A28 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian

Other comparative material None

Description

Proposed holotype FW P1A28 Thick branch fragment, thickening into what may have been a larger main branch. Overall size 10.1 by 17.3mm. Branch is axial dominated. Radial corallites rounded openings, immersed, mixed sizes and small, 0.8, 0.4, 0.7, 0.6mm, not touching. Coenosteum on radials is broken costate and reticulate between them.

Remarks This is the first record of a sturdy specimen being recorded from the Paris Basin. It is additionally morphologically distinct by the small nature of the radial corallites. The specimen is a very small, broken fragment of a branch and is tentatively designated as *Morphotype 2*.

Acropora morphotype 3 n. sp.

PLATE 6

Acropora roemeri Dunan, 1866, Wallace, 2008
non *Madrepora roemeri* Duncan, 1866

Diagnosis

Colony simple hispidose. Radial corallites rounded tubular with round openings, in mixed sizes. Coenosteum costate on radial corallite walls and reticulate between them.

Material studied and included in this species

NHM 49583 Brockenhurst Bed (Middle Headon Beds), Brockenhurst, Hampshire, England, Priabonian (Eocene), R18216, R18217 Brockenhurst Bed (Middle Headon Beds), Brockenhurst, Hampshire, England, Priabonian (Eocene), R54913, R54914 Brockenhurst Bed, Brockenhurst, Hampshire, England, Priabonian (non Oligocene).

Descriptions

49583. Overall length 57mm. Joint region with six branchlets 5.5–11.5mm in diameter arising from a common branch, some with further small branchlets developed from them; five branches broken across, three small branchlets unbroken. Radial corallites tubular appressed with round openings or exert tubular with round openings, mixed sizes, very abraded, mostly not touching. At least four radial corallites with walls clearly visible; walls costate, intercorallite walls reticulate.

R18216. Overall length 47mm. Joint area with three branches arising from a common branch, all broken, 14mm in diameter. Radial corallites tubular with round openings, sizes are mixed but mostly two sizes, touching, very abraded. One area between two branches shows corallite with partial walls, radial corallite walls costate, intercorallite areas reticulate.

R18217. Severely abraded. Overall length 56mm. Section of branch, with evidence that one branch is complete with its base, 13mm diameter. Radial corallites mixed sizes, some touching.

R54913. Overall length 30mm. Abraded fragment of main branch, with six branchlets evenly distributed on one side; these appear to be short branchlets with only one ring of radial corallites; branchlet diameter 11mm. Radial corallites apparently tubular appressed on the branchlets, either immersed or exert between branches, in mixed sizes, mostly not touching. Coenosteum of radial corallite walls costate, broken costate or reticulate between them.

R54914. Severely abraded. Forked fragment, overall length 19 mm, with two broken branches which are apparently mostly complete, each forming another branch. Branch diameters 7 and 13mm.

Remarks Wallace's new species, *A. bartonensis* Wallace, 2008, appears to belong, or is very similar, to *A. roemeri*, whereas *A. roemeri* sensu Wallace, 2008, is a new species assigned to *Morphotype 3*.

5.8 SUMMARY OF NON-ACROPORA GENERA

Dendracis Milne-Edwards & Haime, 1849

PLATE 7 & 8

Madrepora gervillei Defrance, 1828, pl. 45, Fig. 8
Dendracis Milne-Edwards & Haime, 1849, p.451
Dendracis Carbone *et al*., 1993, p. 227, Fig. 11b-c
non *Acropora tergestina* (Oppenheim, 1901), Carbone *et al*., 1993, Baron-Szabo, 2006

Type specimen *Madrepora gervillei* Defrance, 1828, France, Eocene

Diagnosis from Baron-Szabo, 2006

Colonial, ramose, rarely massive or incrusting, plocoid; gemmation extracalicinal; corallites can be projecting, embedded in porous coenosteum, which becomes solid due to secondary thickening; columella absent; occurrence of dissepiments unclear; wall (?para-) synapticulothecal. No axial corallites.

Material studied

NHM R54905 Fresville, Basse-Normandie, France, Middle Eocene, R6024 Fresville, Basse-Normandie, France, Middle Eocene, R35340, Hauteville, Basse-Normandie, France, Middle Eocene R54903, R6023a-d Hauteville, Basse-Normandie, Middle Eocene, R6024a-d Fresville, Basse-Normandie, France, Middle Eocene, R55690a-c, R54901-2a-b, R54902a-b Parnes, Ile-de-France, France, Middle Eocene, R1998 ?Villieu, France, Lutetian, 55688a-d Grignon, Ile-de-France, France, Lutetian (Middle Eocene), R2420a-f Paris Basin, France, ?Middle Eocene, R40382-3 Ferme de l'Orme, Ile-de-France, France, (Upper) Lutetian (Eocene)

Other comparative material

PC François Rougerie Collection, ?Upper Calcaire Grossier, Villiers St Frédéric, Ile-de-France, France, Lutetian, François Rougerie Collection, Upper Calcaire Grossier, Ferme de l'Orme, Ile-de-France, France, Lutetian

Descriptions

R54905. Overall size 32mm, by 13mm maximum width. Corallites all distributed around what appears to be a broken 'branch' although branch is highly irregular in diameter. Two corallites appear to be dividing by intracalicular budding on either side of a directive septal plate. Coenosteum is same on and between radials, nobbly spinules sometimes slightly aligned. Corallites appear slightly oval, mostly same sized, evenly spaced and not touching. Total septal count 16-17, in more than two cycles of septa, but less than three complete cycles.

R35340. Overall size 47mm by 18mm. Branch appears broken and irregular in diameter. Coenosteum same on and between corallites with nobbly spinules which appear to be slightly aligned parallel to the branch. Corallites mostly same sized, evenly spaced and mostly not touching. Total septal count 13-16.

R6023. Slender branch with joint area at the base. Overall size 1cm by 2.2cm. Septa poorly preserved but one corallite appears to show two cycles. Corallites corallites directed slightly upwards, generally small with rounded openings. Coenosteum on and between radials costate. Four rows of radial corallites.

R6024. Curved branch with joint area between two branchlets. Corallites directed upwards in 10 rows, irregular with areas where corallites line up into rows. Corallites without obvious directives. Total septa 12-13. Coenosteum on and between corallites bears aligned spinules with forked tips, herringbone pattern. Around top of radial corallites spinules become joined up and coenosteum appears costate.

Distribution and Remarks

The genus is morphologically distinct from the genus *Acropora* principally in that it lacking the characteristic axial corallites of *Acropora,* but in many ways, it shows close morphological affinities to *Acropora* and similar kinds of variation. Within the specimens described above, four morphotypes, or even morphogroups, appear to be discernible. *Morphotype 1* has a clear distinctive costate coenosteum shown on both the radial corallites and in between, similar to in the *Acropora* genus to the species *ornata*. *Morphotype 2* has a clustered arrangement of radial corallites with large amounts of coenosteum between the clusters. *Morphotype 3* has a clear geometric arrangement of corallites in series, also exhibited by *Acropora* in the species *A. lavandulina*. Finally *Morphotype 4* has variable branch thickness randomly along a branch, a feature not shown by any *Acropora* species.

There are no *Dendracis* specimens examined from the Hampshire or Aquitaine basins. All studied specimens are from the Lutetian of the Paris Basin, and to the north of this in the Cotentin region of France.

Astreopora Blainville, 1830

PLATE 9

Type species *Astrea myriophthalma* Lamarck, 1816, Red Sea, Recent

Diagnosis (Wells, 1956)

Colonies are massive or subramose; no axial corallites. Coenosteum reticular, formed by outwardly inclined trabeculae, with spinose surface. Dissepiments tabular. Corallites are immersed or conical with short, numerous, neatly spaced septa. Corallite walls are slightly porous.

Material studied

NHM R40831 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian, R40830 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian, **FW** P1A59 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian, P1A60 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian, P1A61 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian, P1A62 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian, P1A63 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian, P1A64 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian, P1A65 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian, P1A20 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian, P1V01 Vendrest, Ile-de-France, France, Bartonian **OM** Fresville, Basse-Normandie, France, Middle Eocene

Distribution and Remarks *Astreopora* specimens examined here show a similar distribution to *Dendracis* specimens with no records from the Hampshire Basin, but concentrated in the Lutetian of the Paris Basin, and to the north of this in the Cotentin region of France, with the addition of Bartonian specimens from the Paris Basin and Miocene specimens from the Aquitaine Basin.

Within the specimens studied the characters identified were consistent with separate species four species being present; *Astreopora auvertiaca, A. asperrima* (NHM R35335, 3594)*, A. michelini* (NHM R35322), *A. panacea* (NHM 3593).

Montipora Blainville, 1815

Porites verrucosa Lamarck, 1816

Type specimen *Porites verrucosa* Lamarck, 1816 (in Veron, 1986)

Diagnosis (Wells,1956)

Submassive, foliaceous, ramose or incrusting; no axial corallite. Corallite walls porous. Columella feeble or absent. Coenosteum reticular with strong vertical trabecular elements, thin horizontal connections, surface spinulose or hirsute. No dissepiments.

Distribution and Remarks

No specimens were studied from the Hampshire, Paris or Aquitaine although the fossil record of *Montipora* does stretch back to the Eocene (e.g. Enewetak atoll, Marshall Islands (Wells, 1964)).

Anacropora Ridley, 1884

Type species *Anacropora forbesi* Ridley, 1884

Diagnosis (Wells, 1956)

Like Montipora but invariably ramose, with dense coenosteum. Columella feeble or absent. Colonies are arborescent with thin tapered branches, without axial corallites. All corallites are radial, small and immersed.

Distribution and Remarks

No specimens were studied from the Hampshire, Paris or Aquitaine as *Anacropora* seems only to have a relative recent origin. At present *Anacropora* is found in the Indo-Pacific realm, including the Red Sea (Veron, 2000; Fatemi and Shokri, 2001).

Isopora Studer, 1878

Type species *Acropora (Isopora) muricata*, Lamark, 1818

Diagnosis from Wallace (1999)

Multiple axial corallites, leading to thickened, wedge-shaped (cuneiform) branches; coenosteum a dense arrangement of meandroid elaborated spinules both on and between corallites.

Distribution and Remarks

Isopora is distinguished from *Acropora* by its supplementary axial corallites, brooding planula larvae and genetic distinctness. Wallace *et al*. (2007) proposed its elevation of the subgenus *Isopora* to genus following new molecular studies. The genus also differs from *Acropora* by having differing reproductive strategies (viviparity in *Isopora* and oviparity in *Acropora*). No specimens were studied from the Hampshire, Paris or Aquitaine basins as *Isopora* has only originated recently. *Isopora's* distribution at present is found widespread in the Indo-Pacific realm and was briefly present, and abundant, in the southern Caribbean (Mio-Pliocene) before becoming extinct (Budd and Wallace, 2008).

5.9 TAXONOMY OF SPECIMEN-BASED RECORDS OF OTHER CORALS FROM *ACROPORA*-BEARING LITHOLOGIES STUDIED IN THIS THESIS

This section gives taxonomic details of specimen-based coral records from *Acropora*-bearing lithologies which were studied along with *Acropora* specimens. For a full list of all coral recorded from each basin, based on both the literature and collections, see Chapter 5.

The taxonomy of coral specimens which been re-examined, and identified here, are given below. Corals were identified using a Wild binocular microscope with an eyepiece graticule. Examples of these specimens, and their characters, were photographed using a Zeiss Axiocam mounted on a Leica MZ16 microscope with Axiovision 3.0 software and a JEAOL JSM5410LV Scanning electron microscope at the Natural History Museum, London.

Specimens which were collected during fieldwork will be housed at the Natural History Museum, London, following the completion of this thesis.

Family DENDROPHYLLIIDAE Gray, 1847

Genus *Lobopsammia* Milne Edwards & Haime, 1848

PLATE 11 & 13

Diagnosis from Milne Edwards & Haime (1848) and Wells (1956)

Corallum consisting of small arborescent colonies produced by di- or tri-stomadeal intracalicular budding, permanent conditions being monocentric. Synaphculotheca granular costate.

Type species *Lithodendron cariosum* Goldfuss 1826 (subsequent designation of Milne Edwards and Haime, 1848)

Material studied

NHM R40672 Brockenhurst Bed, Whitecliff Bay, Isle of Wight, England, Priabonian, R14518 Brockenhurst Bed, Brockenhurst, Hampshire, England, Priabonian, 50596 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian, 55685b Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian, AZ2901 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian, R52054-6 Upper Calcaire Grossier, Chambors, Ile-de-France, France, Lutetian, R52060-1 Upper Calcaire Grossier, Chambors, Ile-de-France, France, Lutetian, **FW** P1A15 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian, P1A14 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian, IOW 01 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian, **BGS** Brockenhurst Bed, Whitecliff Bay and Brockenhurst, England, Priabonian.

Other comparative material

MNHM 174241 Upper Calcaire Grossier, Chaumont en Vexin, Ile-de France, France, Lutetian

Occurrence *Lobopsammia* is an extinct coral genus with a fossil record from the Middle Eocene-Middle Oligocene (Middle Eocene: France (Morellet and Morellet ,1945), Italy (Wells, 1956); Late Eocene: Czech Republic (Eliasova, 1974), England (Duncan, 1866); Early Oligocene: Germany, Italy (Cairns, 2001); Middle Oligocene: Germany(Wells, 1956)).

Remarks Where specimens could be identified to species level, the majority from the Hampshire and Paris basins were assigned to *Lobopsammia [Lithodendron] cariosa* (Goldfuss, 1827). Additionally, another species has been documented from the Middle Eocene of France, *Lobopsammia parisiensis* (Michelin, 1844). Budding in Lobopsammia is distomadeal and tristomadeal. Usually each budded corallite becomes individualised (monocentric), but *Lobopsammia parisiensis* is distinguished by maintaining its linkage between budded corallites (di- and tricentric) (Cairns, 2001). Specimens are recorded from the Lutetian and Bartonian of the Paris Basin, and from the Priabonian of the Hampshire Basin.

Genus *Dendrophyllia* de Blainville, 1830

PLATE 11

Type species *Madrepora ramea* Linnaeus, 1758

Diagnosis from Wells (1956), Cairns (2001)

Forms colonies by extratentacular budding from the edge zone. Extratentacular budding forms colonies of three general forms: arborescent colonies with axial corallites (group 1); small, bushy colonies with sparse branching from main stem (group 2); and dendroid colonies with sympodial branching (group 3). All three forms originate from single basal stem. Epitheca absent. Costate well developed corresponding to septa, covered with small hispid granules. Septa arranged in Pourtales plan; pali present or absent (absent in type species). Columella spongy or papillose, type species having both states. Tabular endothecal dissepiments may be present.

Material studied

BGS 170/12 Brockenhurst Bed, Brockenhurst, Hampshire, England, Priabonian

Other comparative material None

Occurrence *Dendrophyllia* is an extant genus with a fossil record dating from the Maastrichtian (e.g. Xizang, China (Loser and Liao, 2001), Jebel Faiyah, Oman (Baron-Szabo, 2000)).

Remarks Amongst the specimens studied a single species *Dendrophyllia dendrophylloides* has described from the Late Eocene Hampshire Basin by Milne Edwards and Haime (1848).

Family PORITIDAE Gray, 1842

Genus *Goniopora* Blainville, 1830

PLATE 11 & 13

Goniopora Blainville, 1830
Litharaea Milne Edwards and Haime, 1849
Goniaraea Orbigny, 1849
Rothastrea Eliasova, 1989
Goniopora Baron-Szabo, 2002

Type species *Goniopora pedunculata* Quoy and Gaimard in Blainville, 1830, Recent, New Guinea

Diagnosis from Wells (1956)

Colonial, extracalicular budding. Massive, columniform or ramose, rarely encrusting. Septa generally in 3 cycles, formed by 4 to 8 trabeculae.

Material studied

FW P1A18 Sables Moyens, Auvers sur Oise, Ile-de-France, France, Bartonian, **NHM** R1819-20 Brockenhurst Bed, Brockenhurst, Hampshire, Priabonian, R55680 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian, R4825 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian, R4822 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian

Other comparative material

MNHM 69761 Sables Moyens, Le Guepelle, Ile-de-France, France, Bartonian

Occurrence *Goniopora* is extant with a long fossil record ranging from the Late Cenomanian (e.g. Klokocov, Czech Republic (Eliasova, 1989); Austria (Baron-Szabo, 2001)) to present day.

Remarks From the Paris and Hampshire basins four species of *Goniopora* were identified in the specimens studied from *Acropora*-bearing lithologies; *Goniopora ameliana, G. websteri and G.crenulte and G. hebeti*. Specimens are from the Bartonian of the Paris Basin and Priabonian of the Hampshire Basin.

Family AGARICIIDAE Gray, 1847

Genus *Trochoseris* Milne Edwards & Haime, 1849

PLATE 12 & 13

Anthophyllum Michelin, 1844

Trochoseris Milne Edwards and Haime, 1849

Diagnosis from Wells (1956)

Solitary, turbinate-patellate, expanding rapidly from base of the attachment; calices broad and shallow, calciular pit elongated.

Type species *Anthophyllum distortion* Michelin 1844 Eocene, France

Material studied NHM R18246-52, R55681, R50597, R40836 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian, R52059 Upper Calcaire Grossier, Chambors, Ile-de-France, France, Lutetian **FW** P1A19 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian

Other comparative material None

Occurrence Extinct genus with a fossil record from the Late Barremian (e.g. Ocozocoautla, Chiapas, Mexico (Filkorn *et al*., 2005) to the Burdigalian (e.g Makran, Iran (McCall *et al*.,1994))

Remarks Where identified to species level, specimens are been assigned to *Trochoseris distorta* (Guettard, 1770). Specimens are restricted to the Bartonian and Lutetian of the Paris Basin.

Genus *Pavona* Lamark, 1801

PLATE 13

Madrepora cristata Ellis & Solander, 1786
Hydnophorabacia d'Achiardi 1875
Reussastraea d'Achiardi 1875

Type species

Diagnosis from Wells (1956)

Massive to foliaceous with bifacial fronds. Corallite walls absent. Collines radiating, discontinuous

Material studied

FW P1A17 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian

Other comparative material None

Occurrence *Pavona* is extant with a fossil record going back to the Selandian of Sind, Pakistan (Duncan, 1880)

Family MUSSIDAE Ortman, 1890

Genus *Circophyllia* Milne Edwards and Haime, 1848

PLATE 13

Anthophyllum truncatum Goldfuss, 1826

Diagnosis from Wells (1956)

Solitary, turbinate or trochoid, fixed or free. Septothecate, costate. Septa with one broad peripheral fan system and several smaller inner ones.

Material studied FW P1A58 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian

Other comparative material None

Occurrence *Circophyllia* is an extinct coral genus with records from the Eocene-Oligocene (Eocene**:** Papua New Guinea (Gregory and Trench, 1916), France (as above); Oligocene: Berbera, Somalia (Latham, 1929)).

Remarks Specimens described to species level are assigned to *Circophyllia truncata* (Goldfuss, 1826).

Family FAVIIDAE Gregory, 1900

Genus *Montastraea* Blainville, 1830

PLATE 13

Orbicella Dana, 1846
Phyllocoenia Milne-Edwards & Haime 1848
Heliastreopsis Chevalier, 1954

Type species *Astrea guettardi* Duncan, 1826, p. 379

Diagnosis from Wells (1956)

Colonial massive, plocoid. Gemmation extracalicinal. Costosepta compact, radially arraged, coarsely granulated laterally. Columella rudimentary spongy. Perithecal wall well-developed. Endothecal dissepiments thin, very abundant. Wall parathecal.

Material studied P1A16 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian

Other comparative material None

Occurrence *Montastraea* is an extant coral genus with records back to the Late Aptian of Baja California, Mexico (Allison, 1955).

Remarks Literature-based records are been assigned to species level as *Montastraea (Phyllocoenia) irregularis* from the Paris Basin.

Genus *Solenastrea* Milne Edwards and Haime, 1849

PLATE 11 & 13

Dachiardia Duncan, 1880

Type species *Astrea turonensis* Michelin, 1847, p. 312

Diagnosis from Wells (1956)

Plocoid; extramural budding; absent or extremely weak costae; trabecular and discontinuous columella with reduced paliform lobes; septothecal wall structure.

Material studied

NHM P1A40 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian, **BGS** Brockenhurst Beds, Whitecliff Bay, Isle of Wight, England, Priabonian

Other comparative material None

Occurrence *Solenastrea* is extant with a fossil record stretching back to the Late Eocene (e.g Fly River, Papua New Guinea (Gregory and Trench.,1916), Yogyakarta, Java (Gerth, 1933)).

Remarks With the Eocene records from Papua New Guinea and Late Eocene records from Indonesia, these specimens may be the oldest records of the genus.

Family CARYOPHYLLIINA Vaughan & Wells, 1943

Genus *Turbinolia* Lamarck, 1816

PLATE 11 & 13

Type specimen *Turbinolia sulcata*, Lamarck 1816

Diagnosis from Wells (1956)

Corallum trochoid-conical, elongate and slender. Wall perforated or externally pitted between costae. Interseptal costae in some species. Styliform or slightly compressed columella formed by fusion of primary septa.

Material studied

FW P1A41-45 Sables Moyens, Auvers-sur-Oise, Ile-de-France, France, Bartonian

Other comparative material

HM G2003.14.1 Barton Beds, Barton, Hampshire, England, Bartonian

Occurrence *Turbinolia* is extinct with a fossil record from the Eocene through to the Early Oligocene (Eocene-USA, Mexico, Ukraine, England, Nigeria, France, Columbia, Oligocene-Greenland)

Remarks Within the specimens studied identified here no attempt was made to determine species-level identifications. However, from both the Paris and Hampshire basins a wealth of species have been described including; *Turbinolia sulcata, T. affinia, T. forbesi, T. fredericiani, T. humili* and *T. bowerbanki*.

Genus *Diplhelia* Milne Edwards and Haime, 1850

PLATE 11

Diplohelia Milne Edwards and Haime, 1857

Diagnosis from Wells (1956)

Dendroid with coalescing branches. Paliform lobes opposite first two cycles of denate septa.

Material studied

NHM R18223-8 Brockenhurst Bed, Brockenhurst, Hampshire, England, Priabonian

Other comparative material

MNHM 175626, 177743, 178546 Upper Calcaire Grossier, Chaumont en Vexin, Ile-de-France, France, Lutetian 174243, 176089, 179214 Upper Calcare Grossier, Grignon, Ile-de-France, France, Lutetian

Occurrence *Diplhelia* is extinct and appears to have a short fossil record Eocene-Miocene (Eocene: France, England; Miocene: Djunggrangan, Java (Osberger, 1954), Piedmont, Italy (Chevalier, 1961))

Remarks A single specimen of *Diplhelia raristella* Milne Edwards and Haime, 1850, is identified here.

Family ASTROCOENIIDAE Koby, 1890

Genus *Stylocoenia* Milne-Edwards and Haime ,1849

PLATE 12

Type species *Astrea emarciata* Lamarck, 1816, Eocene of France

Diagnosis from Baron-Szabo (2006)

Colonial, ramose, massive or incrusting, cerioid; columniform projections arise at junctions of adjacent corallites; gemmation extracalicinal; costosepta compact, thin, laminar, acute dentations laterally; columella styliform; endothecal dissepiments tabular; wall septothecal.

Material studied

NHM R52053 Upper Calcaire Grossier, Chambors, Ile-de-France, France, Lutetian

Other comparative material

MNHM 67663, 69710 Upper Calcaire Grossier, Le Bois-Gouet, Pays-de-la-Loire, France, Lutetian, 69630, 69628-9 Upper Calcaire Grossier, Beynes, Ile-de-France, France, Lutetian

Occurrence *Stylocoenia* is extinct with a fossil record stretching from the Paleocene-Middle Miocene (Paleocene: Italy, Pakistan, Somalia; Eocene: Bosnia, Czech Republic, France, Spain, Jamaica, Haiti, Germany, Indonesia, Pakistan, Egypt; Oligocene: Somalia, Jamaica, Iran; Miocene: France, Italy)

Remarks *Stylocoenia* specimens within the collections are often labelled *Astrea* (a synonym for the genus, commonly used by nineteenth century authors). three species are identified here; *S. ameliano, S. emarciata* and *S. monticularia*.

Class HYDROZOA

Family AXOPORIDAE Boschma, 1951

Genus *Axopora* Milne-Edwards & Haime, 1850

PLATE 11 & 13

Type species *Geodia pyriformis*, Michelin 1844

Diagnosis from Wells (1956), Cairns (1983)

Colony encrusting, forming lumpy protuberances or arborescent. Calcified hydrozoans with long spinose gastrostyles and with no skeletal evidence of dactylozooids (dactylopores) or gonophores (ampullae).

Material studied

FW P1A33-36 Sables Moyens, Auvers-sur-Oise, Ile-de-France, france, Bartonian, **BGS** 170/12 Brockenhurst beds, Whitecliff Bay, Isle of Wight, England, Priabonian

Other comparative material None

Occurrence *Axopora* is extinct with a short fossil record in the Eocene-Upper Miocene (Eocene: England, France, Hungary, South West Africa (Cairns, 1983); Oligocene: Hungary, Germany; Miocene: New Zealand (Cairns, 1983)).

Remarks Three species from the Hampshire and Paris basins are described in the fossil record *Axopora deformis, A. solanderi* and *A. michelini*. In addition to the specimen based records *Axopora* has been recorded from the Barton Beds, Barton, *Axopora michelini* (Burton, 1933).

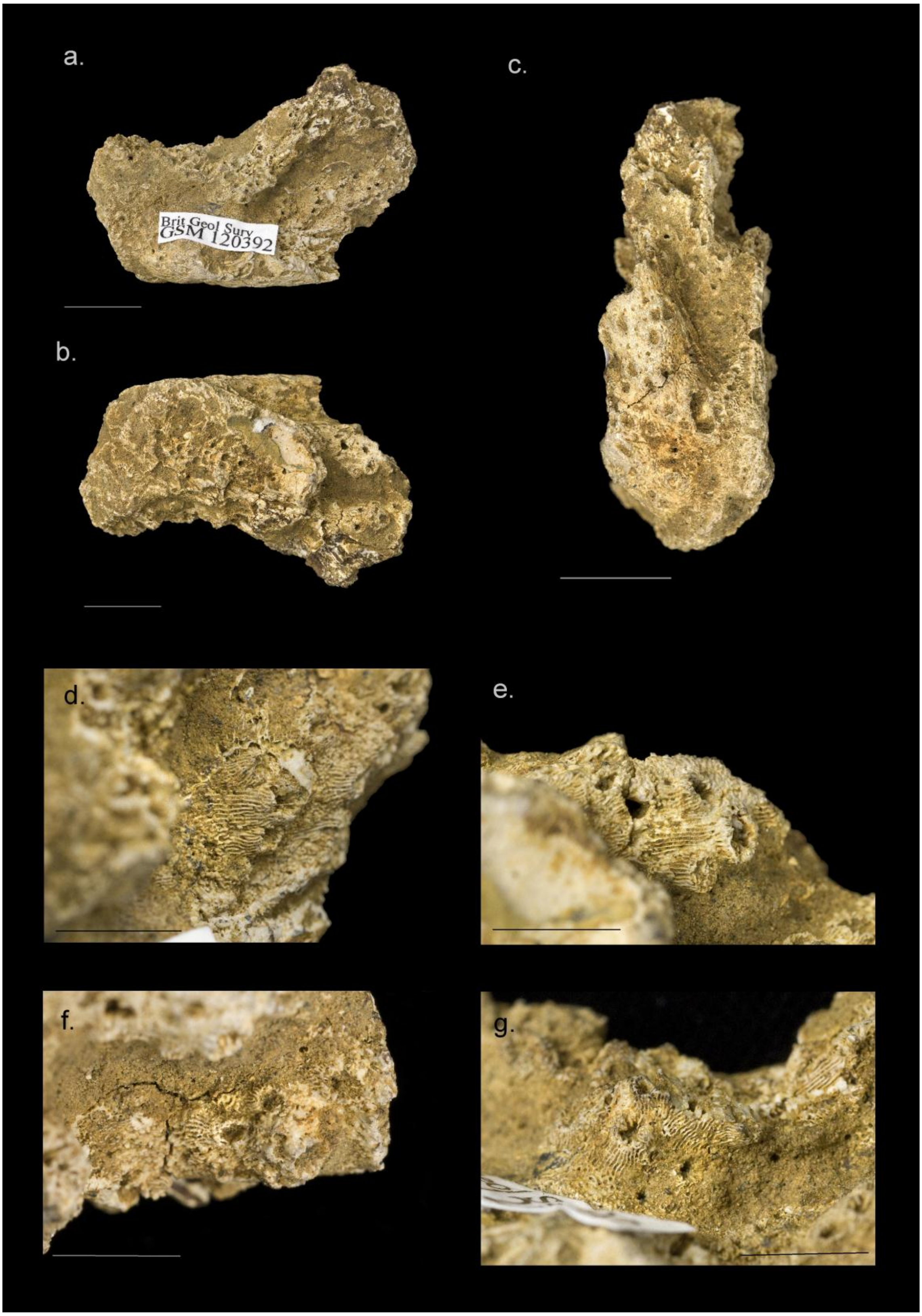


PLATE 1. ***Acropora roemeri*** **BGS X/X 2/19**

Brockenhurst Bed, Brockenhurst, Hampshire, England, Priabonian

Morphological characteristics: a-c. Overview of specimen, simple hispidose branches with an equal contribution of axial and radial corallites to the branch diameter, d-f. Radial corallites, one size, often touching with costate coenosteum on radials and resticulate between (Scale-1cm).

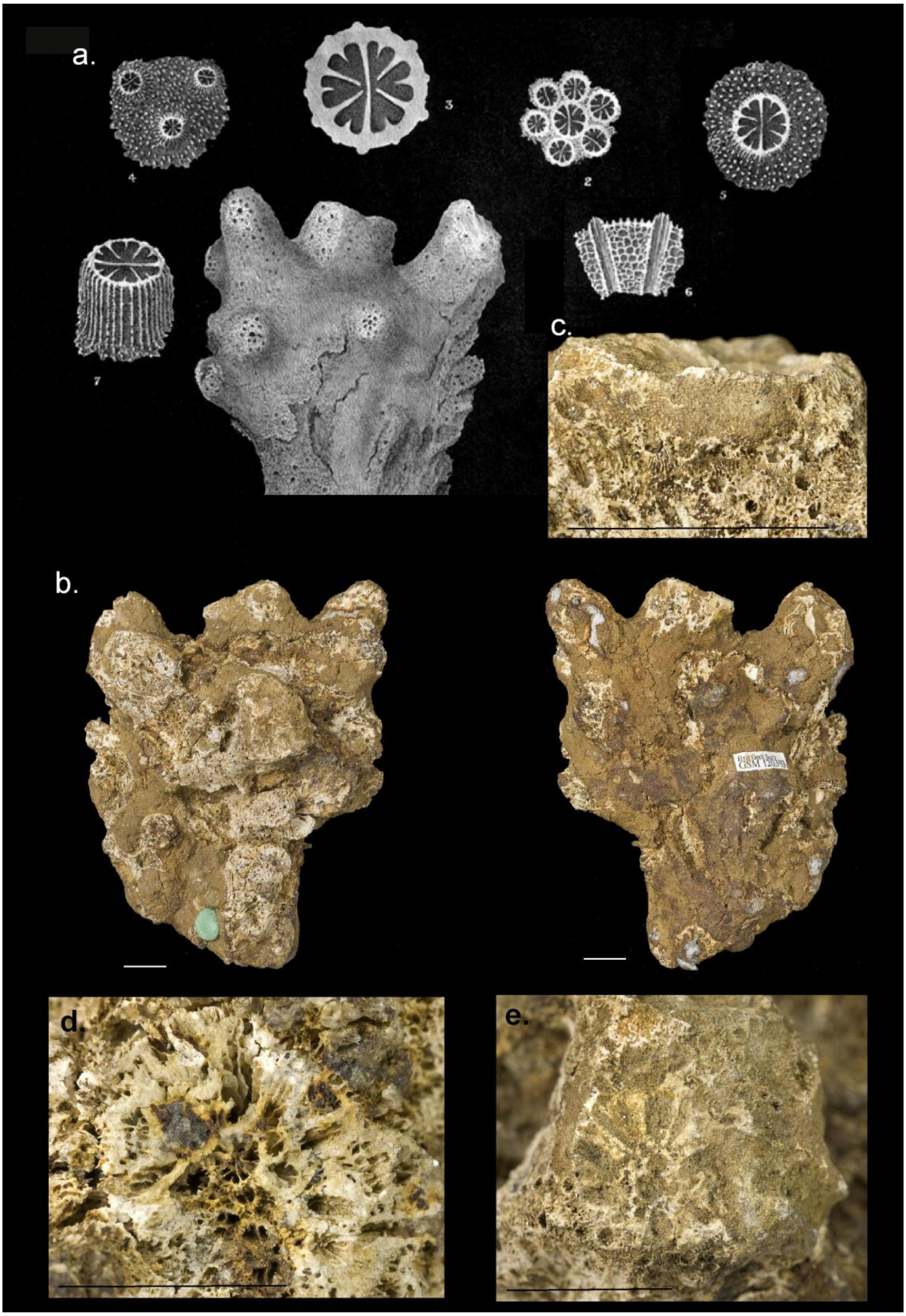


PLATE 2. ***Acropora anglica*** **BGS X/X 3/20**

Brockenhurst Bed, Brockenhurst, Hampshire, England, Priabonian

a. *Madrepora anglica* Duncan, 1866, p.51, pl.8, Figs 1-7; Morphological characteristics: b. Overview of specimen with sturdy, sub-arborescent colony form, c. radial corallites two distinct sizes with some touching, d-e. branches are axial dominated (Scale-1cm).

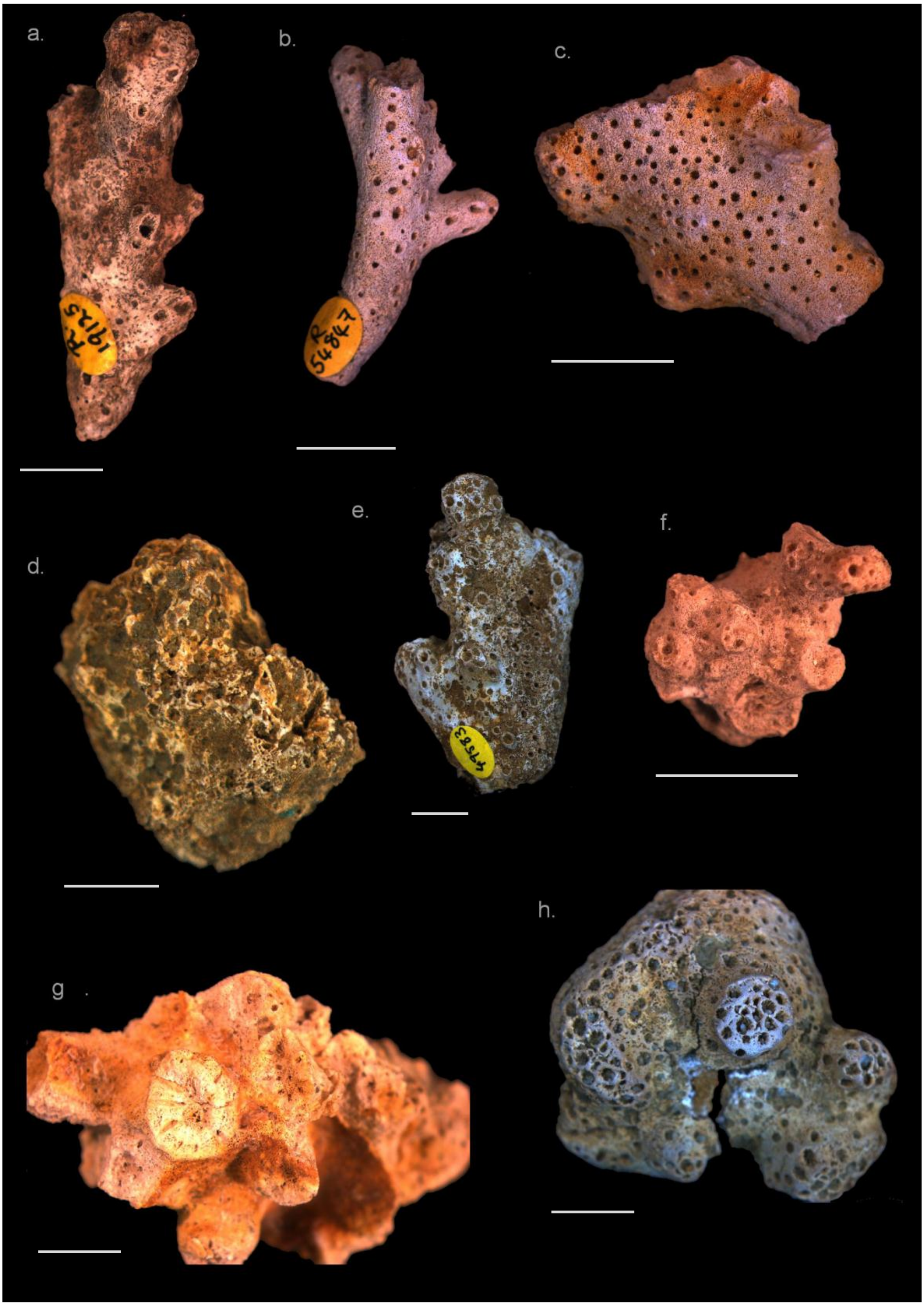


PLATE 3. *Acropora* species from the Hampshire and Paris basins

a. *A. bartonencis*, NHM R19125, b. *A. solanderi*, NHM R54847 c. *A. alvarezi*, NHM R35320, d. *A. anglica*, NHM R2339, e. *A. roemeri*, NHM 49583, f. *A. proteacea*, NHM R18265, g. *A. deformis*, NHM R54910, h. *A. britannica*, NHM R54912 (Scale 1cm).

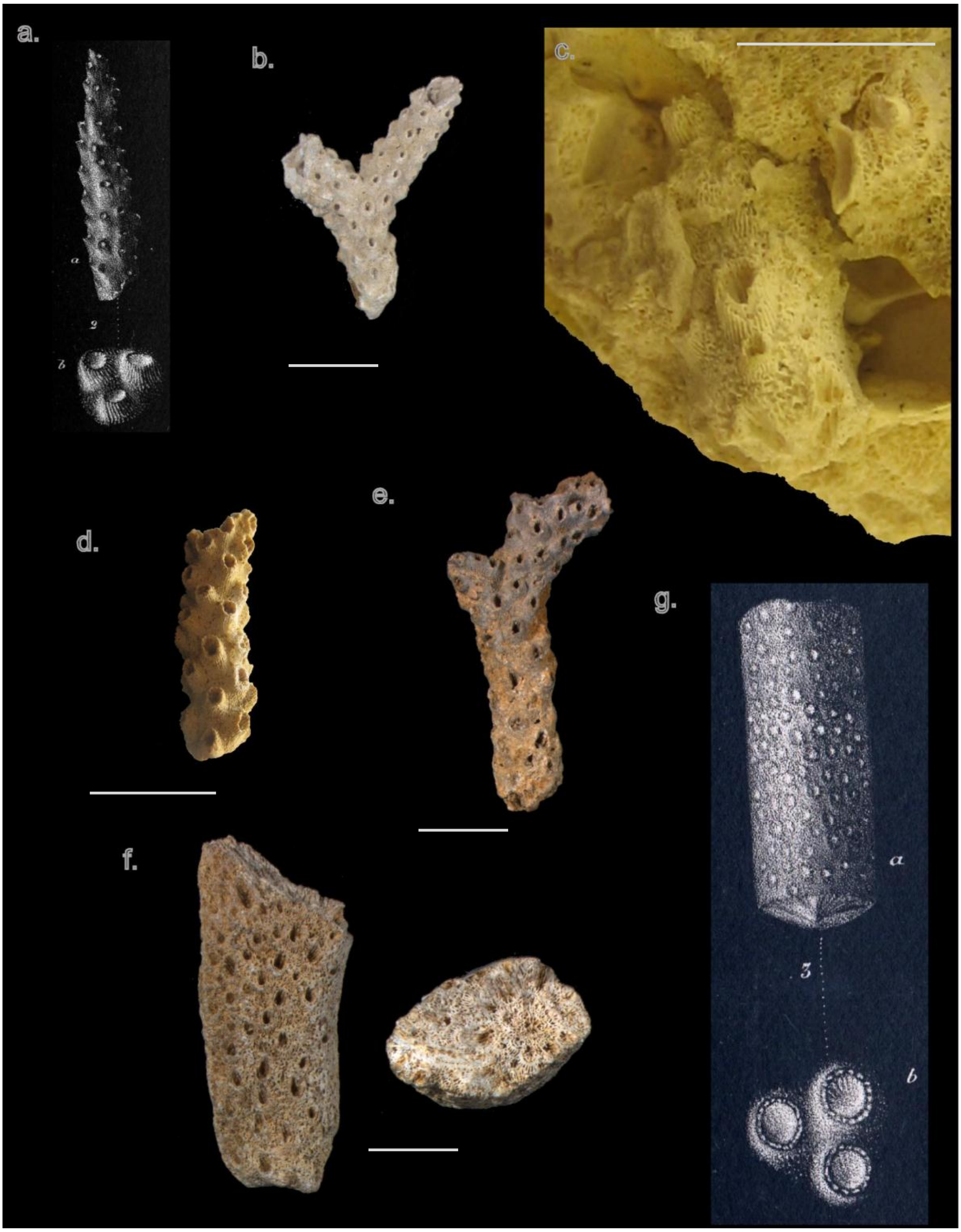


PLATE 4. *Acropora lavandulina* (a-e) and *Acropora exarata* (f-g), Aquitaine Basin

a. *Madrepora lavandulina*, Michelin, 1847, b. NHM R2416, France, Miocene, c. NHM R54844, France, Mid Eocene, d. OM, Fresville, Mid Eocene, e. NHM UNREG, France, Miocene, f. R18276, g. *Madrepora exarata*, Michelin, 1947 (Scale 1cm)

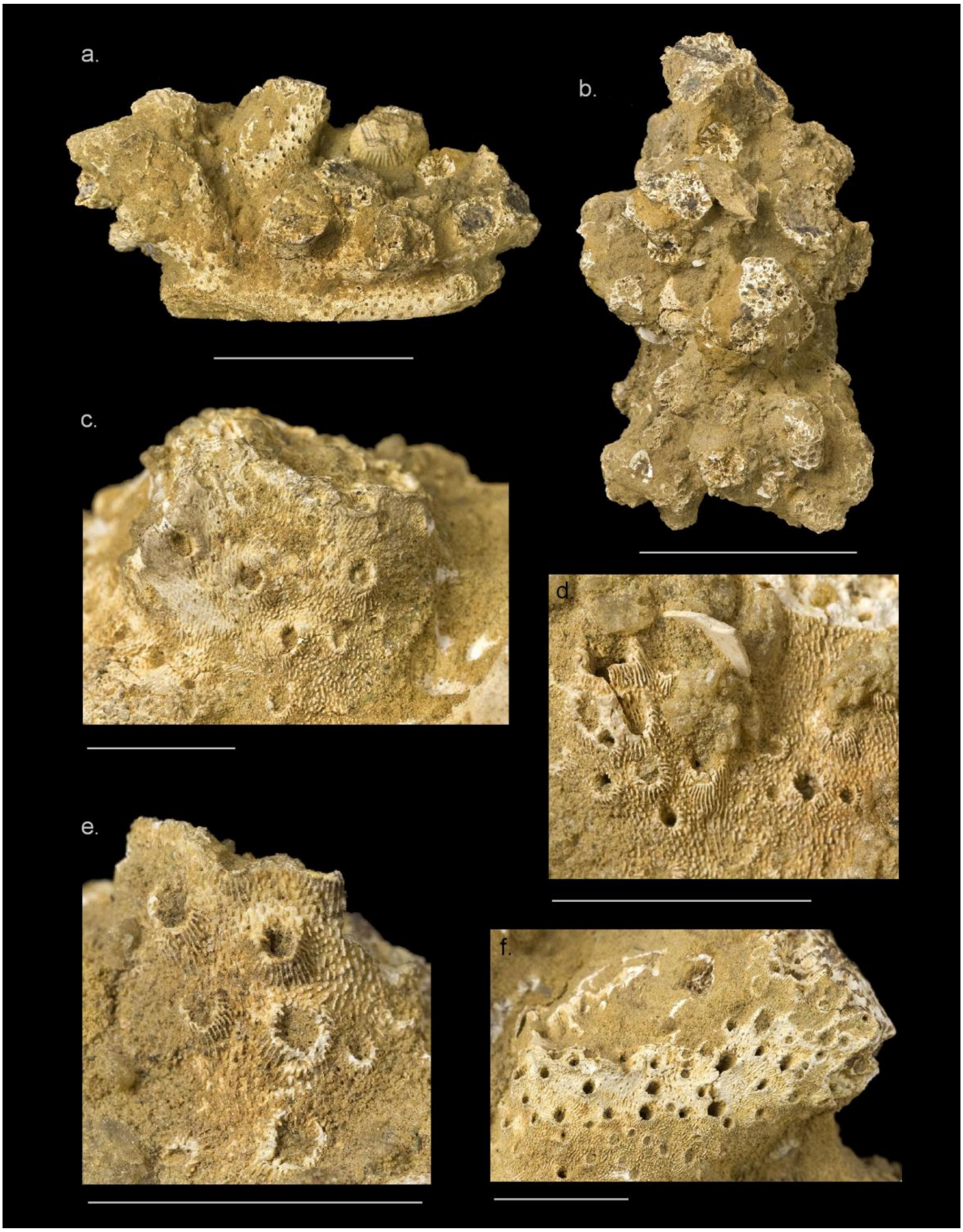


PLATE 5. ***Acropora* morphotype 1, SGW C25799**

Brockenhurst Bed, Brockenhurst, Hampshire, England, Priabonian

a. & b. Overview of specimen with sturdy arborescent table growth form and axial dominated branches. c. Radial corallites are tubular with rounded openings d. Morphologically the specimen has exceptional preservation although there are areas of sediment infilling, fragmentation of the skeletal structure and molluscan borings. e. & f. Radial corallites are mixed sizes , tubular with rounded openings and touch in crowded areas. Coenosteum on inter-radial areas is reticulate or broken costate and on radial corallites is costate (Scale a-b 5cm, c-f 1cm)

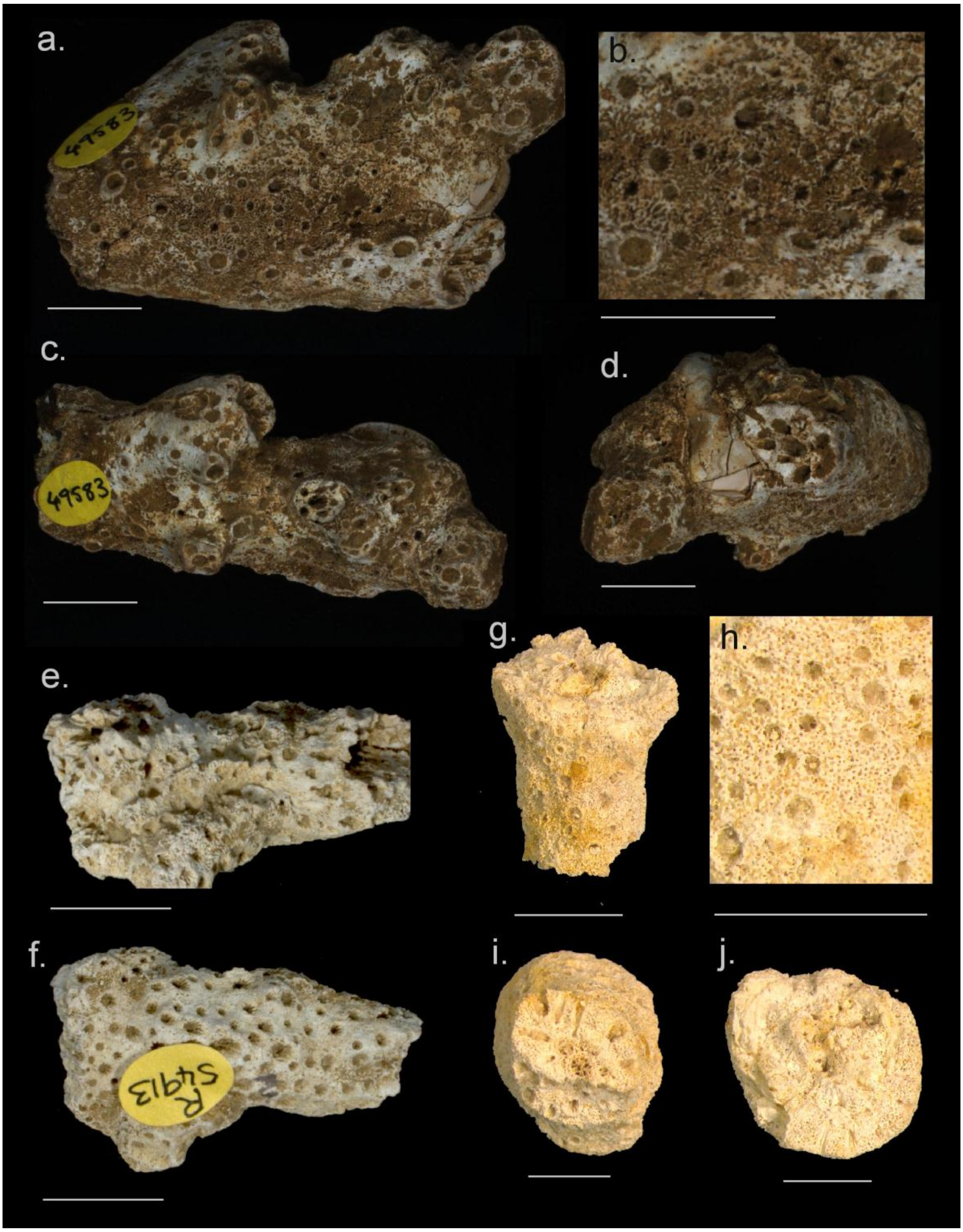


PLATE 6. *Acropora* morphotype 2 and 3, Paris Basin

a-d NHM 49583 morphotpye 3, a. colony hispidose, b. radial corallites mixed sizes, c. simply hispidose branching, equal contribution of axial and radial corallites; e-f. NHM R54913 morphotype 3, showing simple hispidose colony form; g-h. FW P1A28 morphotype 2, g. thick branch fragment, colony growth appears arborescent, h. readial corallites are small, mixed sizes and generally immersed, i-j. branches terete and axial dominated (Scale-1cm).

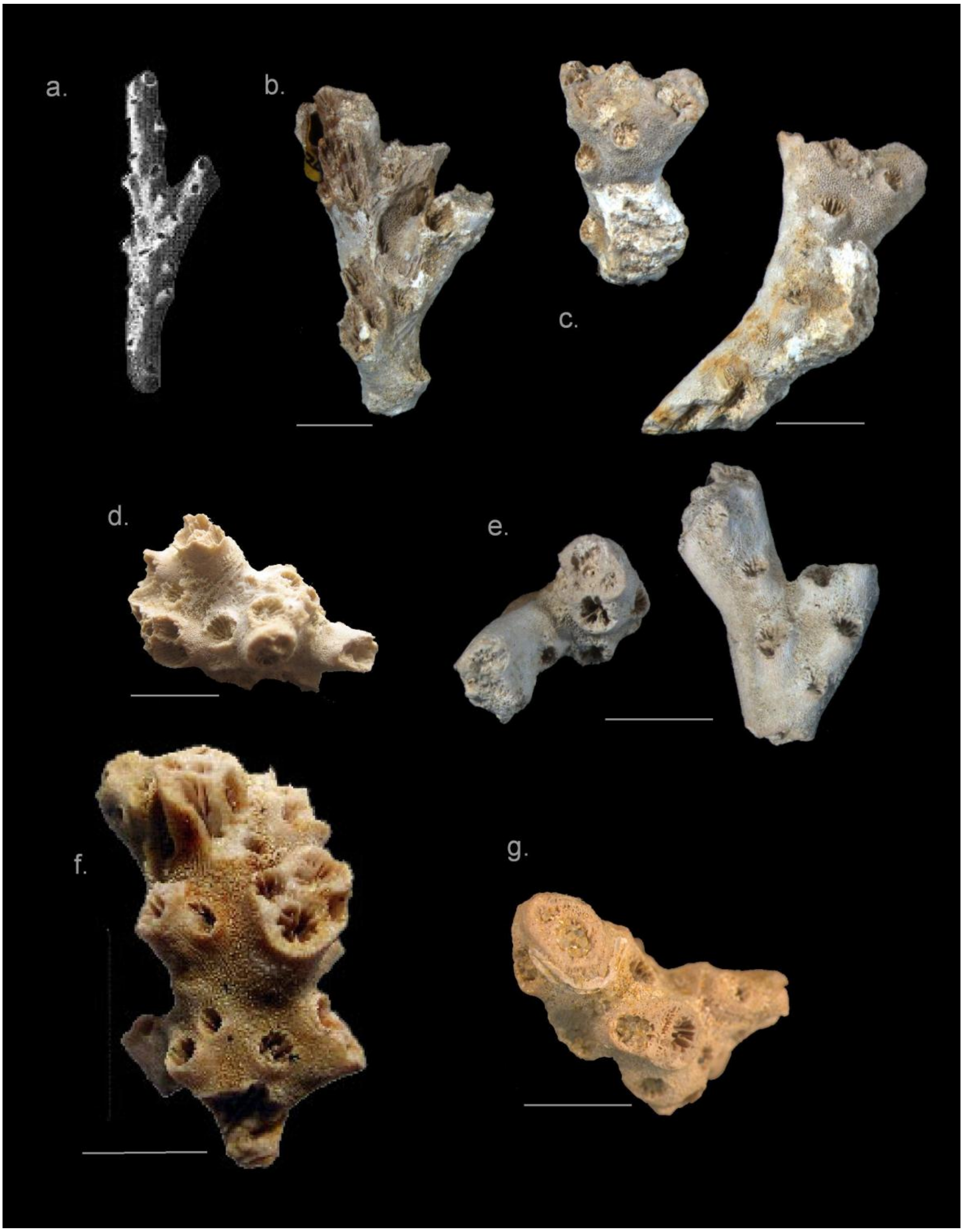


PLATE 7. Genus *Dendracis*, Paris Basin

a. *Dendracis ornata*, Fischer, 2000, b. NHM R2420 c. NHM 55688a, Grignon, M. Eocene d. NHM 55688b, Grignon, M. Eocene, e. OM, Freville, M. Eocene, f. PC Hors collection, g. NHM 55688c, Grignon, M. Eocene (Scale-1cm).

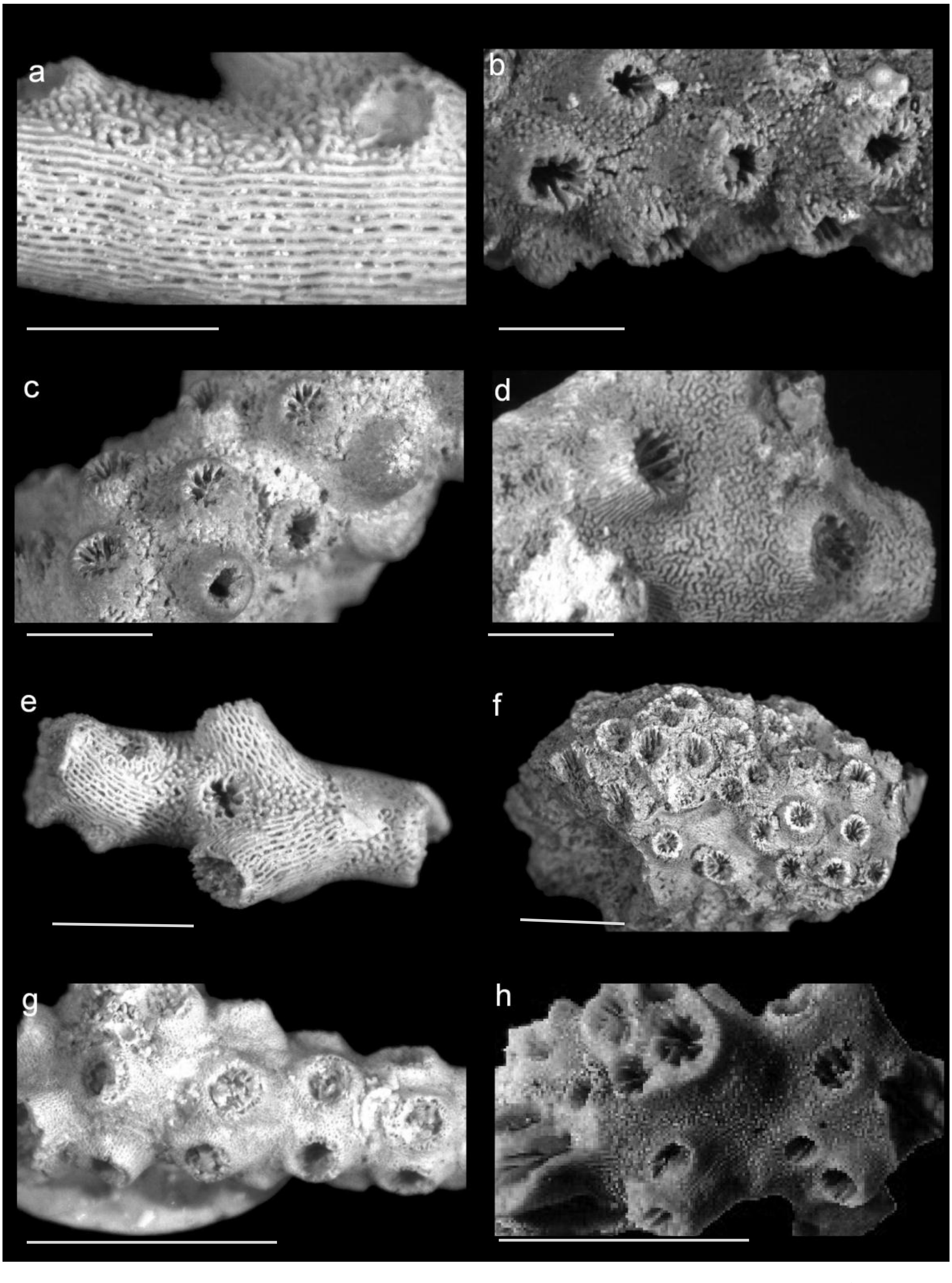


PLATE 8. Variation in morphological features shown in the fossil *Dendracis* specimens studied

a. NHM R40382, Ferme de l'Orme, Upper Lutetian, b. NHM R6024, Fresville, Eocene, c. NHM R35340, Hauteville, Middle Eocene, d. NHM 55688, Grignon, e. NHM R40382, Ferme de l'Orme, Upper Lutetian, f. NHM R54903, Hauteville, Middle Eocene, g. NHM R54902, Parnes, Middle Eocene, h. PC Hors collection (Scale a-d 0.5 cm, e-h 1cm).

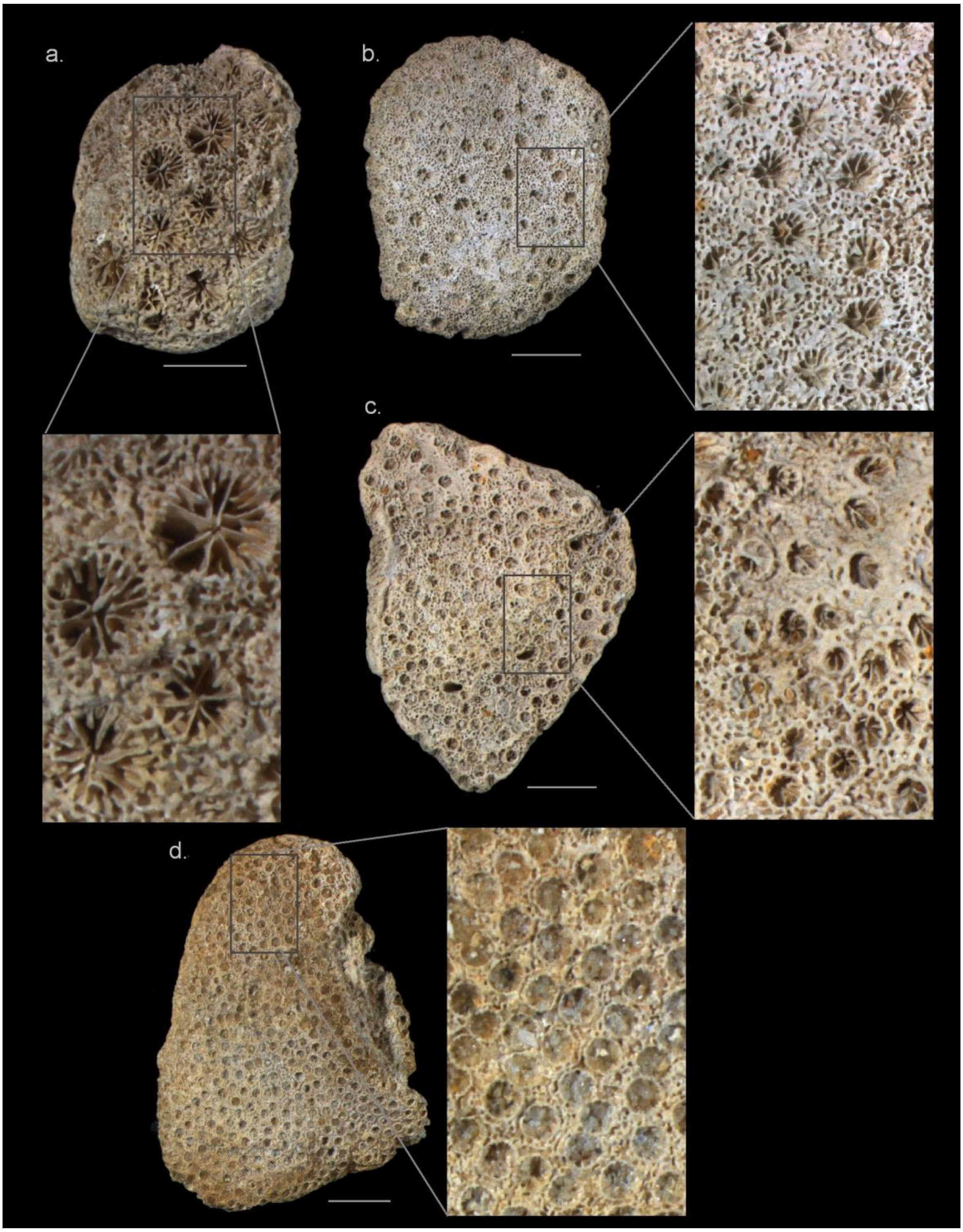


PLATE 9. Genus *Astreopora*, Paris Basin

a. *Astreopora michelini*, NHM R35322, b. *Astreopora asperrima* NHM R35335c, *Astreopora panicea*, NHM 3593, c. *Astreopora asperrima* NHM 3594.

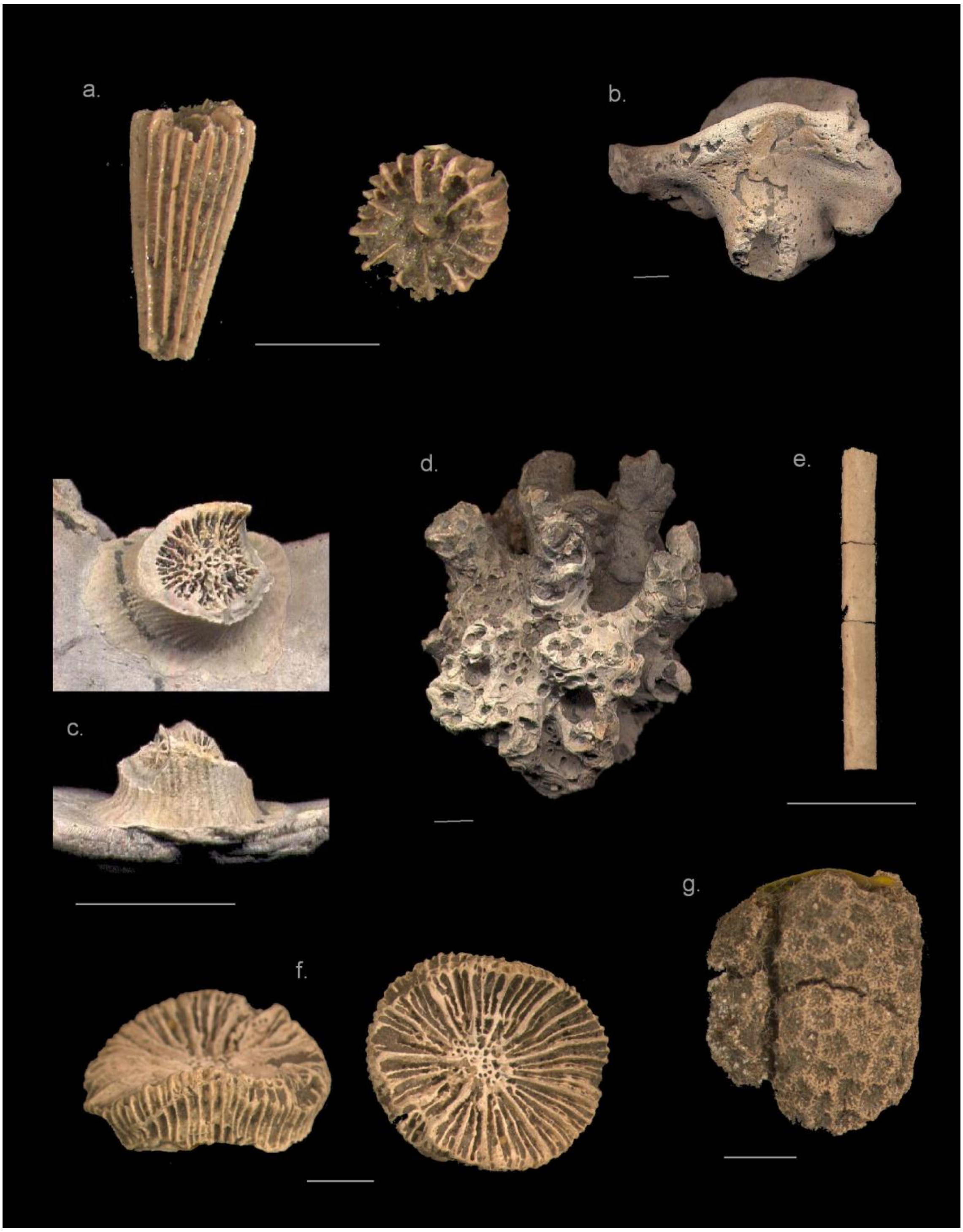


PLATE 10. Bartonian Corals, Hampshire Basin, England

a. NHM 49701, *Turbinolia bowerbanki*, b. PC AM *Axopora* sp., c. PC AM *Dendrophyllia dendrophylloides*, d. PC AM *Oculina ?conferta*, e. NHM 49586 *Graphularia wetherellii*, f. NHM 49685 *Paracyathus haimei*, g. NHM *R14570 Goniopora* sp. (Scale 0.5cm)

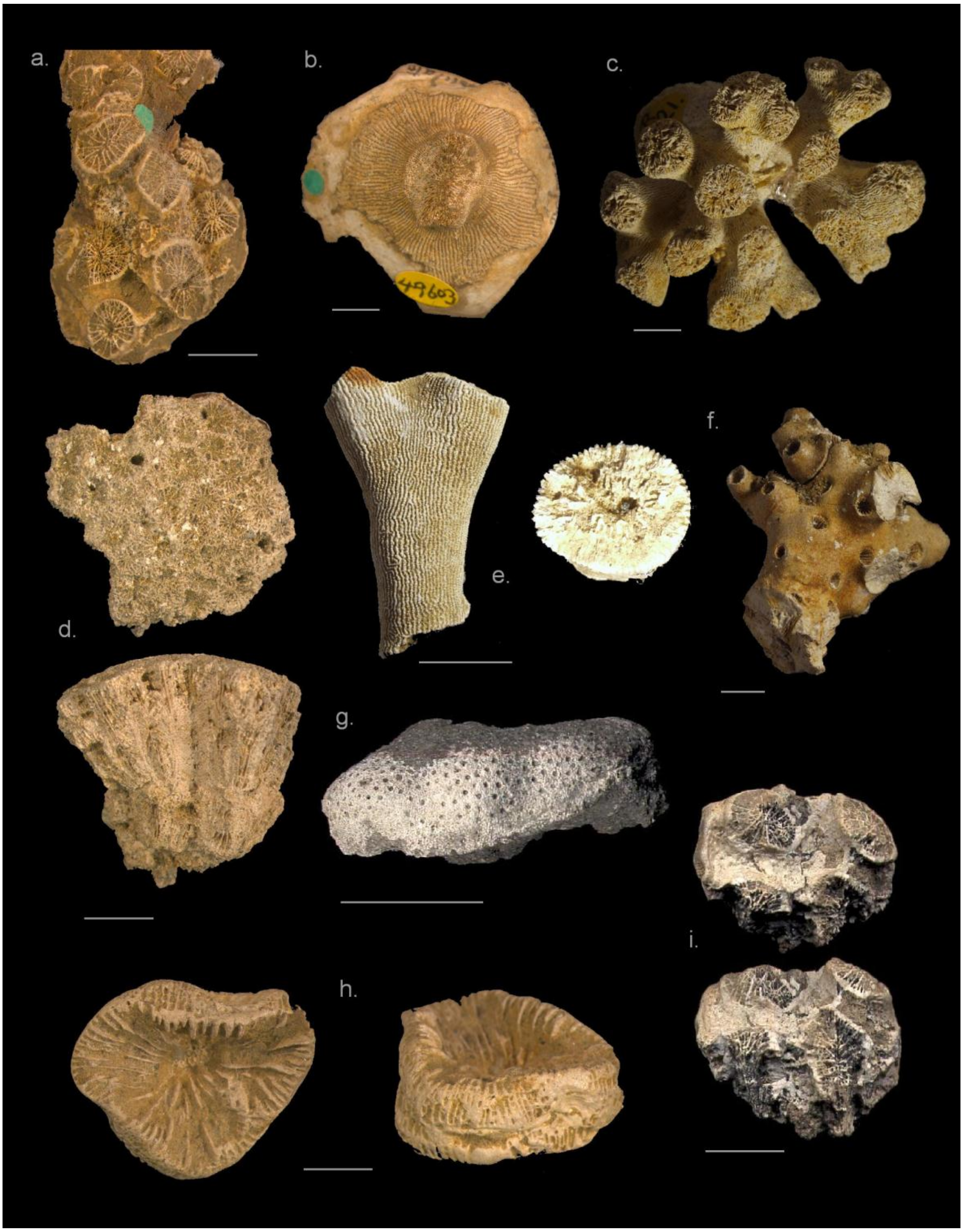


PLATE 11. Priabonian Corals, Hampshire Basin

a. NHM 49627*Solenastraea beyrichi*, b. NHM 49603 *Balanophyllia granulata*, c. NHM R35321 *Lobopsammia cariosa*, d. NHM R18219, *Goniopora brockenhursti*, e. NHM R52246 *Lobopsammia cariosa*,f. NHM R18223, g. PC AM *Axopora michelini,* h. NHM R18222 *Paracyathus sp*., i. PC AM *Solenastrea cf*. *beyrichi* (Scale 1cm)

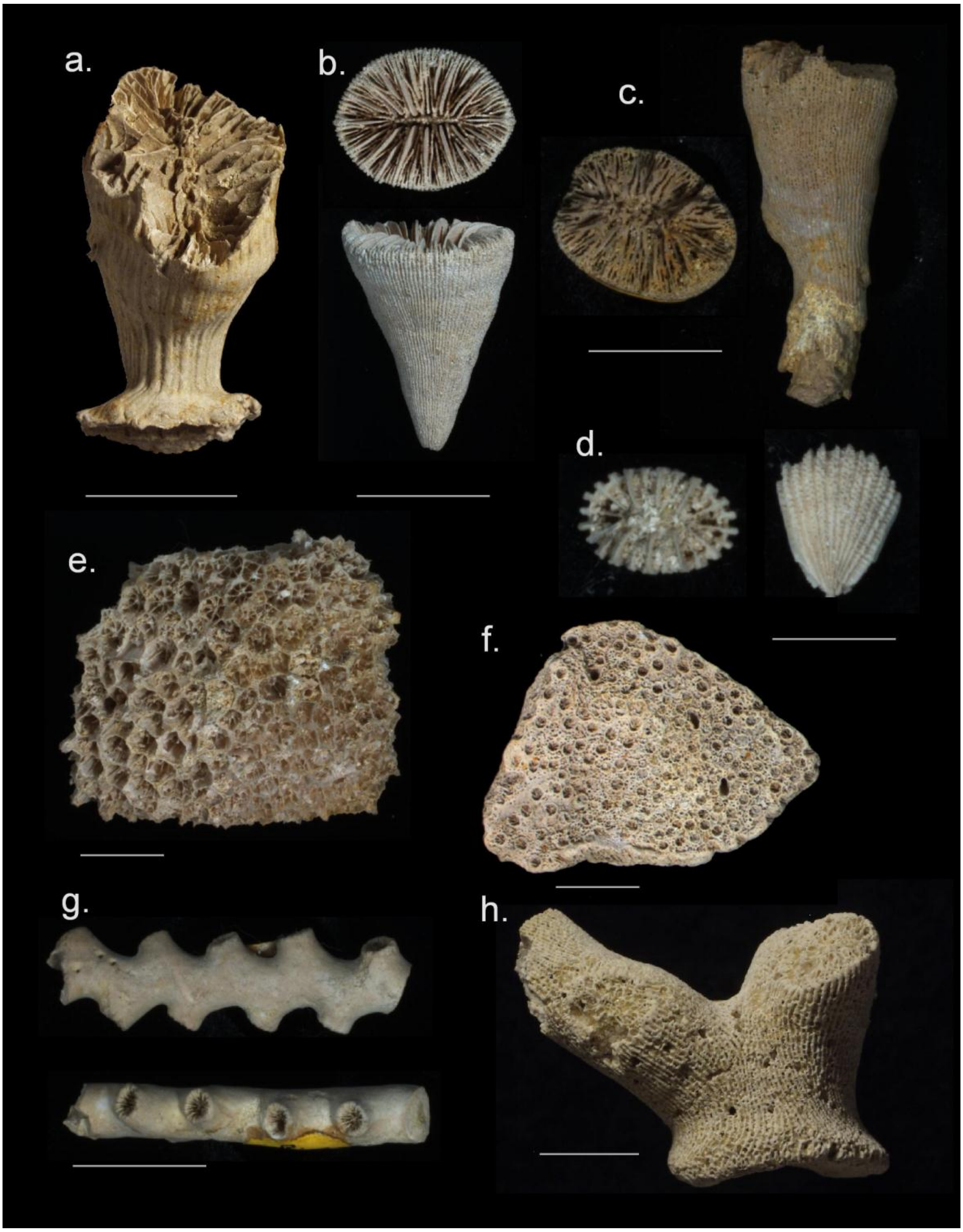


PLATE 12. Lutetian Corals, Paris Basin, France

a. NHM R958 *Parasmilia altavillensis,* b. NHM R40940 *Eupsammia sp*., c. NHM 55684 *Balanophyllia granulate,* d. NHM R54888 *Sphenotrochus sp*., e. NHM 65674 *Stylocoenia sp*. f. NHM 3593 *Astreopora panicea*, g. NHM R29109 *Diplohelia* sp. h. NHM R52056 *Lobopsammia cariosa* (Scale-1cm).

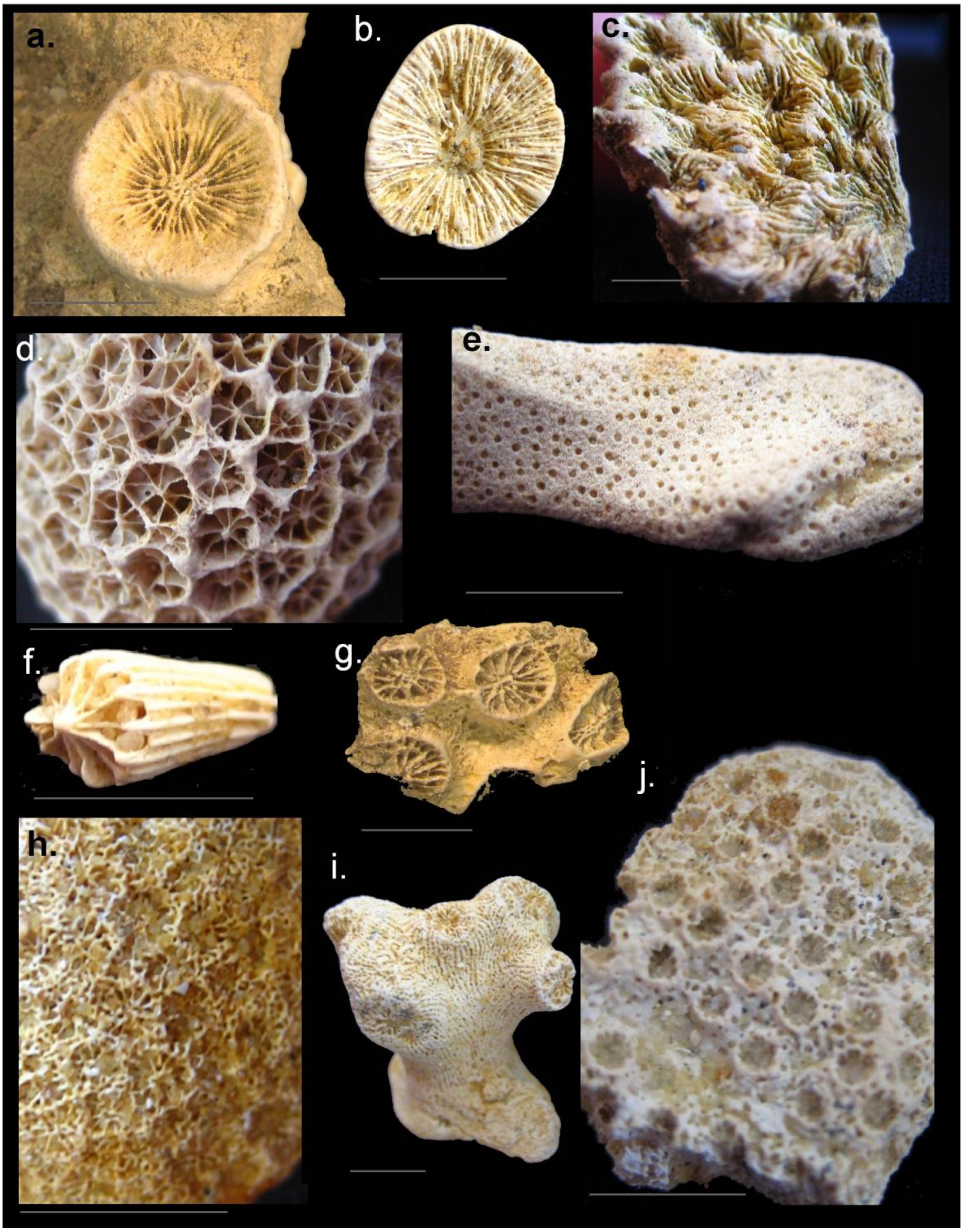


PLATE 13. Bartonian Corals, Paris Basin, France

a. FW P1A58 *Circophyllia* sp., b. FW P1A19 *Trochoseris* sp., c. FW P1A17 *Baroniseris* sp., d. FW P1A66 *Stylocoenia* sp., e. FW P1A36 *Axopora michelini,* f. FW P1A41 *Turbinolia sp*., g. FW P1A40 *Phyllocoenia irregularis*., h. FW P1A18 Goniopora sp. , i. FW P1A14 *Lobopsammia cariosa*, j. FW P1A37 *Astreopora asperrima* (Scale-1cm).

CHAPTER 6. PALAEOENVIRONMENTAL CONTEXT OF *ACROPORA* IN THE PALEOGENE OF NW EUROPE: STRATIGRAPHY AND BASIN ASSEMBLAGES

CONTENT

This chapter aims to summarise the palaeoenvironmental setting of *Acropora* in these high latitudinal Eocene occurrences of southern England and northern France. Multiple approaches were used. Firstly as thorough literature review provided information about the global, regional and local palaeoenvironmental context. Secondly fieldwork at selected localities provided detailed sedimentological and palaeoenvironmental data. Additionally, museum-based work on collections from the Hampshire and Paris basins. Finally, a taphonomic and diversity study of corals independently aided palaeoenvironmental interpretations.

6.1 INTRODUCTION: GEOLOGICAL AND PALAEOGEOGRAPHICAL SETTING

The localities in the Hampshire and Paris basins represent the most northerly latitudinal extent (~48ºN) of *Acropora* in its entire history. These high latitudinal occurrences coincided with a period of global warming in the Middle Eocene (Zachos, 2001; see Chapter 2 and 3). 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 (Fig. 6.1; Curry, 1992). The basins existed as two interconnected, shallow-marine, paralic embayments, connected to the Atlantic and with an intermittent connection to the North Sea.

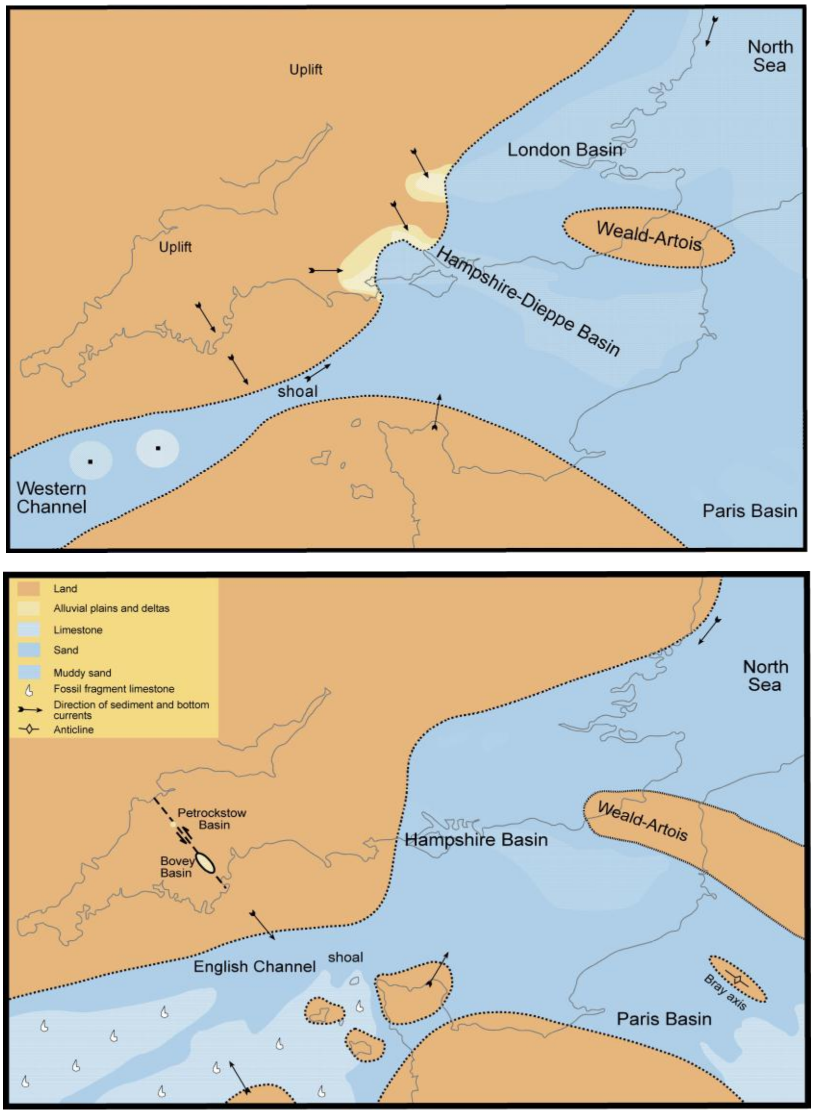


Figure 6.1. Palaeoenvironmental setting of the Hampshire and Paris basins in the a. Early and b. Middle Eocene (Lutetian) (Adapted from Cope, 1992, and Gale et al., *2006).*

Cenozoic tectonic activity within the two basins included monoclinal 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 by regional and local tectonic and climatic factors.

This chapter aims to summarise the palaeoenviromental setting of *Acropora* in these high latitudinal Eocene occurrences of southern England and northern France. Multiple approaches were used. Firstly a thorough literature review provided information about the global, regional and local palaeoenvironmental context. Secondly fieldwork at selected localities provided detailed sedimentological and palaeoenviromental data. Additionally, museum-based work on collections from the Hampshire and Paris basins. Finally a taphonomic and diversity study of corals independently aided palaeoenviromental interpretations.

6.2 MATERIALS AND METHODS

6.2.1 Fieldwork

Fieldwork was conducted at fossil localities in the Hampshire (Tab. 6.1) and Paris (Tab. 6.2) basins. The sedimentological contexts of the assemblages were examined and *Acropora* specimens were collected, and other specimens from the coral assemblage were listed and examples collected. Bulk samples of each *Acropora*-bearing lithologies were collected with additional samples from other areas within a section and of the same age from elsewhere within the basins.

LOCALITY	LAT-LONG	DESCRIPTION	ACCESS	AGE	STRATIGRAPHY	LITHOLOGY	EXPOSURE AND PRESERVATION	ACROPORA	CORAL
Whitecliff Bay, Isle of Wight	50'40'00N, 1'06'00W	Cliff and limited foreshore dependant on tides	v	Priabonian*	Headon Hill Formation	Sands and clays	Vertical and sub-vertical beds within cliff face and foreshore	v	v
Alum Bay, Isle of Wight	50'39'50N, 1'33'57W	Cliff faces and isolated chalk stacks	v	Ypresian-Bartonian	London Clay, Bracklesham Group & Barton Clay	Multicoloured sands and clays	Vertically orientated, steep beds, with well preserved molluscs	X	X
Lyndhurst, Brockenhurst	50'52'24N, 1'34'34W	River beds and banks	v**	Priabonian	Colwell Bay Member	Clays and sands	Stream beds and woodland where exposures ar often weathered and unfossiliferous at the surface	v	v
Barton Cliffs, Barton-on-sea	50'44'16N, 1'40'33W	Cliffs and foreshore	v	Bartonian	Barton Clay	Sandy-clays, clays and sands	Cliffs with a series of terraces	X	v
Brackelsham Bay	50'45'51N, 0'51'28W	Foreshore dependant on tides with pedestals	v	Lutetian	Bracklesham Group	Glauconitic clayey sands	Exposure of the solid geology depends on the state of the tide and the shifting beach sands and shingle.	X	v

Table 6.1. Summary of details of localities targeted during fieldwork in the Hampshire Basin, UK.

LOCALITY	LAT-LONG	DESCRIPTION	ACCESS	AGE	STRATIGRAPHY	LITHOLOGY	EXPOSURE AND PRESERVATION	ACROPORA	CORAL
Fleury-la-Riviere	49'06'13N, 3'50'50E	Series of pits, some recently dug, on the edge of forest	√	Lutetian	Sable calcaire	Grey-white calcareous sands	Various faces and pits with good ecposure and preservation	X	X
Chalons-sur-Vesle	49'17'263N, 3'55'430E	Large old quarry/sand pit in park area	√	Thanetian	Sables de Chalons-sur-Vesle	Thin lenses in yellow calcareous, fine sands	Limited lenses of molluscs with very small, fragile and difficult to remove fossils	X	X
Cauroy-les-Hermonville	49'20'55N, 3'55'31E	Large recent quarry with multiple exposures	√	Thanetian		Multiple lithologies with large lenses of molluscs		X	X
Vendrest	49'02'48N, 3'05'34E	Roadside small quarry, time limited access	√-X*	Bartonian		Fine grained white-grey calcareous sands with abundant, well preserved fauna	Well preserved mollusc and coral assembledge	?√**	√
Les Guepelle (La Chapelle-en-Serval)	49'05'067N, 2'32'243E	Large sand quarry closed to public	X	Lutetian-Bartonian	Sables du Guepelle	X		√	√
Auvers-sur-Oise	49'04'16N, 2'10'38E	Forest locality with old excavations realted to quarry area	√	Bartonian	Sables Auvers	2 lithologies: a) reworked spoil beds with fine, grey sands, abundant in mulluscs; b) Orange, trangressive beds, grain supported with disarticulated fragmented molluscs, also some larger intact		√	√
Vigny	49'04'17N, 1'54'55E	Area of outstanding natural beauty, protected area with huge quarry area	X	??		X		X	X
Fercourt	49'18'975N, 2'15'133E	Recently dug pits, excavations, on either side of the road in woodland	√	Lutetian	Clacaire grossier	Small molluscs in spoil and larger from further digging. Associated shallow marine fauna with forams, echinoid spines, sea cucumbers	Exceptional mollusc preservation	X	√
St.Vaast-Les-Mello	49'16'00N, 2'23'21E	Bike track entry to huge disused quarry	X	Lutetian		X		X	X
Cuise-la-Motte	49'23'08N, 3'00'35E	Quarry outcrop	√	Cuisien, U.Ypresian	Sables de Cuise	Brackish mullusc assembledge		X	X

Table 6.2. Summary of details of localities targeted during fieldwork in the Paris Basin, France

6.2.2 Museum collections

Many of the specimens within museum collections are listed as collected during the 19th Century from localities such as pits or railway cuttings which are now inaccessible. This makes the museum and private collections paramount to this research. For this thesis, visits were made to a selection of institutes as well as faunal lists been requested from institutes. Attempts were made to newly relocate and study fossil types.

Natural History Museum, London

The Natural History Museum, London, (NHM), Department of Zoology, houses a large amount of extant *Acropora* types at the off-site storage facility (Wandsworth, UK) which were used for taxonomic training and as a comparison with the fossil material. In the literature, the museum is often cited as the British Museum (Natural History), this being its older name. The Cenozoic coral collections in the Department of Palaeontology house many specimens of *Acropora* with a worldwide distribution. From the Paris and Hampshire basins, *Acropora* specimens within these collections are largely collected in the mid-nineteenth to late-twentieth centuries. No fossil types were housed here, apart from those newly assigned as part of this thesis. In addition to *Acropora* specimens being studied from European basins, coral faunal lists were made from the collection. An important recent addition to the fossil coral collections, was the Curry collection, reviewed as part of this thesis, but as of yet not formally registered.

British Geological Survey, Nottingham

An important step in work on the taxonomy of fossil *Acropora* (see Chapter 5) was the rediscovery of the Duncan (1866) type specimens of two species from the Hampshire Basin, now stored at the British Geological Survey (BGS), Nottingham. Previously these specimens had been housed at The Museum of Practical Geology, London, before the collection was distributed between the Natural History Museum (NHM), London, and the BGS in 1935. These type specimens had previously been thought lost. In addition, another type specimen from the Brockenhurst Bed, *Solenstraea koeneni*, was relocated here along with other corals from Brockenhurst and Whitecliff Bay.

Hampshire Museum, Winchester

Faunal lists were obtained from the curators of the coral collections. All corals were from the Hampshire Basin with no *Acropora* specimens identified.

Sedgwick Museum of Earth Sciences, University of Cambridge

The Sedgwick Museum houses a small collection of coral specimens from the Hampshire Basin. Included within this are nine *Acropora* specimens (*Acropora anglica* and *A. roemeri*) re-examined as part of this thesis (Chapter 4 and 5). Following this work, one fossil morphotype has been proposed within this collection.

Oxford University Museum of Natural History

A collection of coral specimens from the Lutetian Bracklesham Beds, Hampshire, and Calcaire Grossier, Fresville and Grignon, France, were studied at the Oxford University Museum along with a single *Acropora* specimen newly identified from Fresville.

Muséum National d'Histoire Naturelle

Faunal lists were obtained from the curators of the coral collections. Chevalier's collection (Chevalier, 1962) is housed here which includes many well preserved specimens from the Aquitaine Basin. Michelin's collection (Michelin, 1843) contains specimens, *Acropora [Madrepora] exarata,* from the Miocene, Bordeaux. No *Acropora* specimens were found from the Hampshire Basin within these collections. Wallace (1999) observed that many extant *Acropora* specimens within the museum's collections, due to handling, had led to the loss, or the dubious application, of some labels, and through communication with curators it is apparent this also applies to the fossil material. Multiple numbering systems exist and the collection appears scattered and has a lack of active and consistent curation protocol established.

Private collections

Private collections were studied from both the Hampshire and Paris basins. The collection of Steve Tracey (Natural History Museum, London) includes *Acropora* specimens and other corals from the Paris Basin. *Acropora* and *Lobopsammia* were identified within skeletal remnants collected by Andy Gale (University of Portsmouth) and Euan Lawrie now housed at the Natural History Museum, London, however remains unregistered. Alan Morton's (Imperial College) collection is solely of specimens from the Hampshire Basin and includes *Acropora* specimens from the Brockenhurst Beds.

Isle of Wight Museum

During fieldwork, an attempt was made to visit the Museum of Isle of Wight Geology, formerly based in Sandown. However, it appears that this museum no longer exists. This museum was originally founded by the Isle of Wight Philosophical Society in Newport in 1819 (*pers. comm.* Martin Munt). In 1913, the Society's geological specimens were transferred to Sandown Free Library, and were arranged to form a museum, which opened to the public in 1923, becoming known as the Museum of Isle of Wight Geology.

In 1974, the Geology Collections came into the care of the Isle of Wight County Council. The Museum of Isle of Wight Geology relocated its collections for display to the new Dinosaur Isle museum in 2001. However on contacting the Dinosaur Isle museum, collections do not appear to house any coral specimens and therefore further investigation would be needed to relocate these specimens.

6.2.3 Preparation of samples from fieldwork

Corals and skeletal debris were recovered by hand-retrieval and from sieved samples from Paris and Hampshire Basin localities. The bulk samples were dried (overnight at 40ºC), washed and wet-sieved through a 1 mm mesh and were picked for skeletal remains. From the mollusc material, apical fragments were identified to genera using collections at the Natural History Museum, London, and standard guides.

Thin sections were prepared of *Acropora*-bearing lithologies collected during fieldwork. A detailed guide for thin section preparation is given by Miller in Tucker (1988). Petrological microscope work and photomicrography were combined to identify and record features of samples. Regions of interest were imaged using a PixeLINK PL-A623 digital camera, mounted on a Nikon "Eclipse, E600 POL" polarizing microscope.

6.2.4 Coral diversity

Coral occurrences are recorded from Hampshire and Paris Basin fossil localities to determine how biodiversity has changed within the region over the middle-late Eocene. From both museum and private catalogues, and fieldwork, the coral content was recorded. The taxonomic updating and descriptions of specimens studied can be found in Chapter 4 and 5. For each record, genus and species name were recorded in addition to inferred symbiotic status (zooxanthellate and azooxanthellate; see Chapter 2; summarised in Appendix 8). Symbiotic status was largely based on the Treatise on

Invertebrate Paleontology (Scleractinia, Part F, Wells, 1956) updated where necessary with more recent generic revisions, for example the azooxanthellate dendrophylliid genera *Lobopsammia* reviewed by Cairns (2001). Two morphologically-based growth forms were also distinguished: *solitary* and *colonial* (*sensu* Brickner at al., 2006). Corals classified as colonial are further sub dived principally into the mode of colony formation (including reptoid, plocoid, dendroid, phaceloid, cerioid and flabellate, see Appendix 9). Where symbiotic or morphological characters are unclear, specimens are characterised as ‘unknown’. Detailed records for each horizon and basin are given in section 6.3.

6.3 RESULTS

The localities in the Hampshire and Paris basins represent the most northerly known latitudinal extent (~48ºN) of *Acropora* in its entire history (for global patterns, see Chapter 3). Regionally, the earliest known *Acropora* occurrences come from the Lutetian, middle Eocene of the Paris Basin (Fig. 6.2).

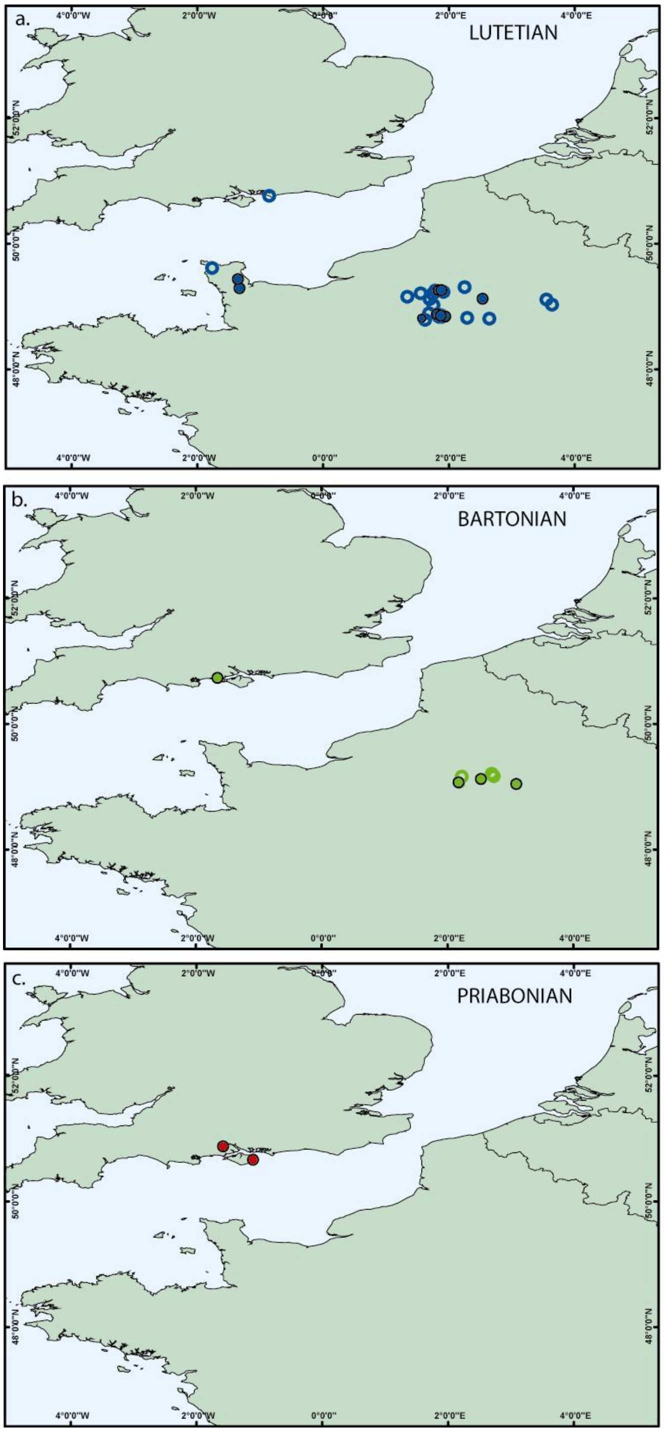


Figure 6.2. *<u>Acropora</u> and coral-bearing localities, Lutetian-Priabonian, Paris and Hampshire basins (● <u>Acropora</u>-bearing locality, ○ Coral-bearing locality, no <u>Acropora</u>)*

No *Acropora* records were found in the Hampshire Basin at this time, although other coral taxa are recorded in the Bracklesham Group, Bracklesham Bay. In the Paris Basin, Lutetian coral deposits are widespread, including *Acropora* recorded from the Cotentin Peninsula region. *Acropora,* and other coral occurrences, are geographically restricted within the Bartonian to a single locality in the Barton on Sea, Hampshire Basin, and in the Paris Basin localities restricted to the Ile-de-France region. During the Priabonian (Late Eocene), no corals are recorded in the Paris Basin and coral assemblages containing *Acropora* are restricted to two Priabonian sites in the Hampshire Basin (Whitecliff Bay and Brockenhurst).

6.3.1 Lutetian Deposits of the Paris Basin

Overview

The Lutetian was originally defined by De Lapparent (1883) as referring to the 'Calcaire Grossier' of the Paris Basin. The Lutetian deposits of the Paris area are now defined as being comprised of three units; the Calcaire Grossier (Abrard's Zones I and II) typified by the occurrence of *Nummulites laevigatus*, which unconformably overlies the Sables de Cuise; the Calcaire à milioles (Abrard Zone III); and the Marnes et Caillasses (Abrard Zone IV) (Aubry, 1986; Fig. 6.3). Middle Eocene *Acropora* specimens in museum collections are largely labelled as being from the *Upper Calcaire Grossier*. This may be taken as the upper part of the Calcaire Grossier outlined by Aubry (1986) (Abrard Zone II at the base of biozone NP15), but, on the basis of the historical stratigraphy of these deposits and the period when these specimens where collected (majority in the early-middle 20th century), these specimens are here considered to be largely from Abrard Zone IVa and in the middle to upper part of Biozone NP15.

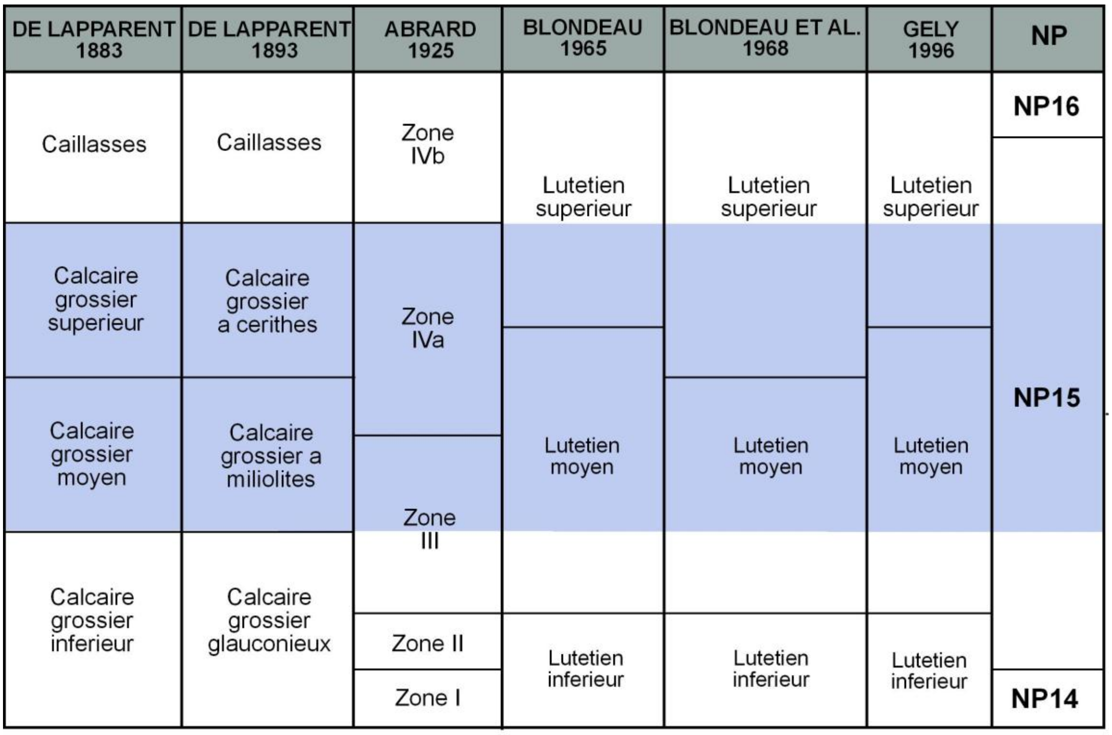


Figure 6.3. Historical stratigraphy of the Lutetian deposits of the Paris Basin (Modified from Gely, 1996, highlighted area shows Acropora *occurrence)*

Regionally, the Ypresian cycle ended with the deposition of continental sands and clays, although the sea did not retreat completely and in the west marine deposits are found passing up directly into those of the Lutetian cycle (Ager, 1980). Following this, the Lutetian sea then extended to the south and east, limited south of Paris by the Remarde anticline. During the Lutetian, the Paris Basin became a carbonate platform progressively more enclosed in response to uplift and short wavelength folding of the northern part of the basin (Guillocheau, 2000). Uplift of the Artois anticline resulted in separation of the sandy facies of Belgium and northernmost France, from the carbonate facies of the central Paris Basin area (Fig. 1). Sea grasses indicate a calm, tropical sea (Pomerol, 1982). Emergence in the Upper Lutetian resulted in lithification of limestone and development of karstic surfaces (Ager, 1980). Evaporitic and chemical sedimentation in the late Lutetian marks increasing isolation and periods of aridity (Pomerol, 1982). In this late Lutetian regressive phase, the retreating sea formed a sabkha zone and the first Cenozoic evaporate deposits of the Paris Basin appeared (Ager, 1980; Thiry, 1989).

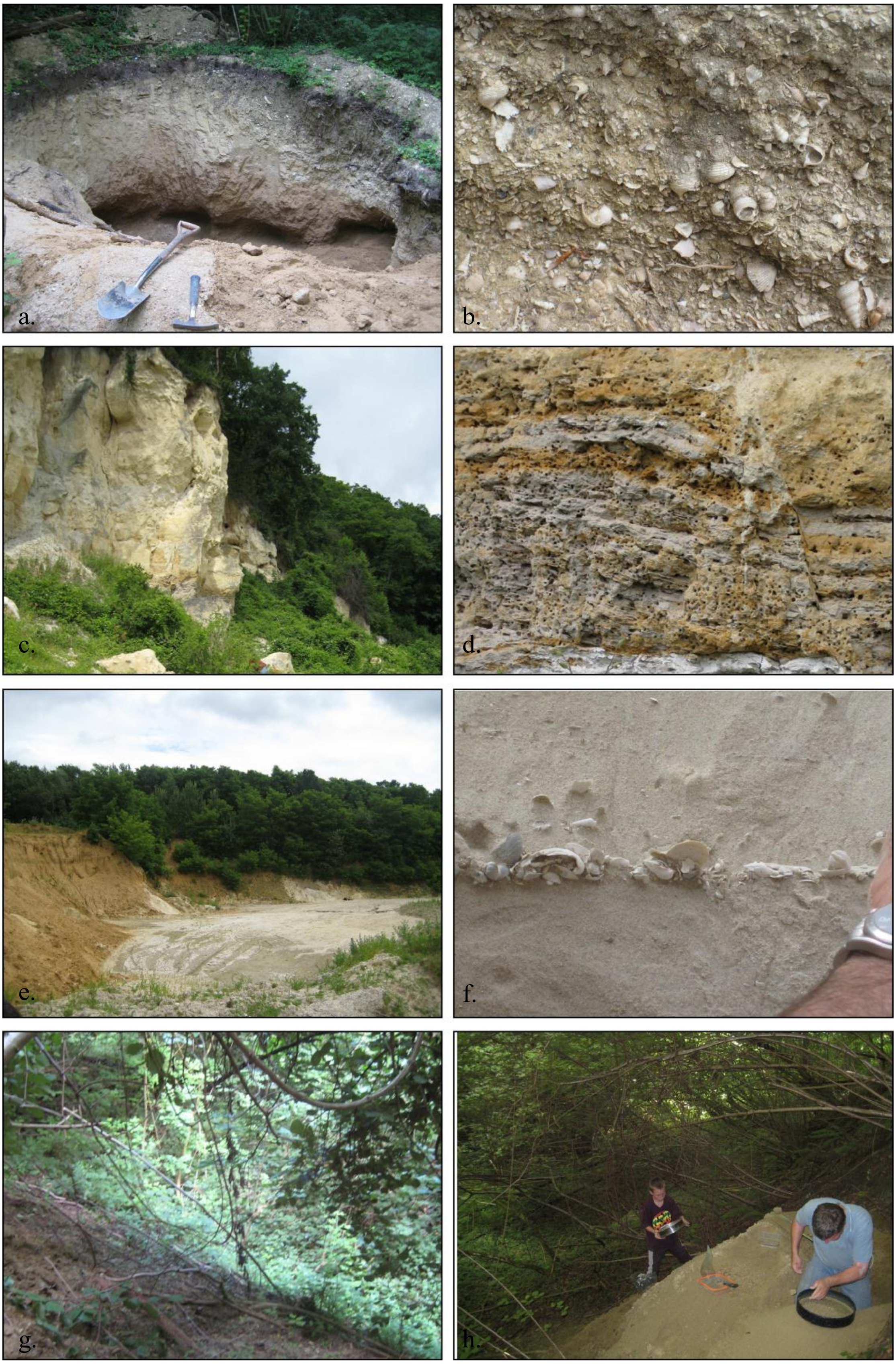


Figure 6.4. Examples of Thanetian and Lutetian sites studied during fieldwork in the Paris Basin, France; a-b. Fluery-la-Riviere (Lutetian), c-d. Chalons-sur-Vesle (Thanetian), e-f. Cauroy-les-Hemonville (Thanetian), g-h Saint Gobain (Lutetian).

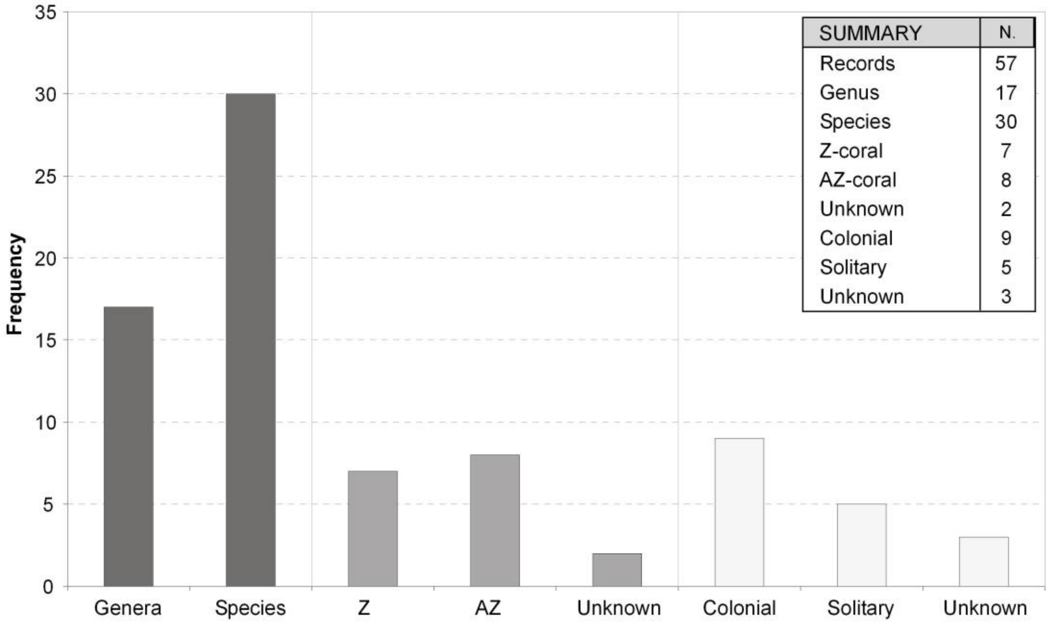
Description

Lutetian deposits of the Paris Basin were targeted during fieldwork. They are predominantly found in forest floors and pits, quarry excavations and river beds in the Yvelines and Ile de France regions, Paris (Fig. 6.4, Tab. 6.2). Due to their diverse, and exceptionally preserved, molluscan fauna, these deposits have been extensively collected from, although comparatively very little sedimentological work has been undertaken. Recently many of these localities have been warded to the MNHM, or remain privately owned, and therefore collecting and access is restricted. *Acropora*-bearing localities are included in these, reflecting their association with diverse marine molluscan faunas. Fieldwork was therefore undertaken at Lutetian sites, but although some were coral-bearing *Acropora* has not been recorded.

Throughout the central-Paris region of the basin, several sites contain the Lutetian deposits consisting of greenish-grey and buff, fine clastics with high carbonate content, including marls and sandy to clayey silts. Fine bioclasts are found within the porous micritic matrix with marine fauna including corals, crabs claws, rotalid foraminiferids, serpulid *Ditrupa* tubes, and the green algae order Dasycladales. Molluscan fauna include euryhaline brackish to shallow marine gastropods and bivalves with turritellids and venerids predominating.

Coral Diversity

A total of 30 species and 17 genera are recorded during this thesis, recorded in the literature, seen in museums, and collected during fieldwork, from the relatively moderately diverse *Acropora*-bearing lithologies of the Lutetian Paris Basin (Fig. 6.5). As summarised in section 6.2.4, for each record the inferred symbiotic status were recorded (as ‘zooxanthellate corals’ (or ‘z-corals’) or ‘azooxanthellate corals’ (or ‘az-corals’); Schuhmacher and Zibrowius, 1985; Rosen 2000). Symbiotic status was largely based on the Treatise on Invertebrate Paleontology (Scleractinia, Part F, Wells, 1956) updated where necessary with more recent generic revisions, for example the azooxanthellate dendrophylliid genera *Lobopsammia* reviewed by Cairns (2001).



SUMMARY	N.
Records	57
Genus	17
Species	30
Z-coral	7
AZ-coral	8
Unknown	2
Colonial	9
Solitary	5
Unknown	3

Figure 6.5. Histogram of coral occurrences in Acropora-bearing lithologies and coral assemblages from the Lutetian, Paris Basin

Zooxanthellate and azooxanthellate corals contribute almost equally (7 Z, 8 AZ), with colonial forms dominating (9 colonial, 5 solitary). These colonial forms display a variety of corallite integration, from simple branching forms (e.g. *Acropora, Oculina*), to cerioid (e.g. *Astrocoenia, Syloceonia*) corals (see Appendix 9). Branching and encrusting forms are fragmented, and massive, domal forms are small (<10cm). There is minor evidence of bioerosion with sparse molluscan borings.

Palaeoenvironment

On the basis of the distribution of modern zooxanthellate corals, the presence of *Acropora* in the Lutetian of the Paris Basin suggests tropical climate conditions during the Middle Eocene. This is supported by isotopic data in Chapter 7 and the presence of the rotalid foraminiferid *Nummulites*, which are here near the northernmost Eocene limit of this largely tropical genus (see Blondeau, 1972). From the distribution of the Lutetian limestones, and of *Acropora*-bearing lithologies (Fig. 6.2), in France, small relics of these deposits on the Cotenin Peninsula show that a small arm of the sea extended across this area during the Lutetian. *Acropora* specimens from the Cotenin area are distinct as they are the only occurrence of the species *Acropora lavandulina*, previously described in France from the Miocene of the Aquitaine Basin, SW France. This species appears native to the area, only being recorded elsewhere form the

Miocene of Italy, Portugal and Egypt, however it is not found in the Paris area or Hampshire Basin. Wallace (1999) suggested the fossil species is similar to the modern *Acropora aculeus*, from the *A. latistella* group, which presently occurs over a broad range of depths, often being found up to a depth of 20m on reef slopes and walls.

The combination of zooxanthellate and azooxanthellate corals in modern settings typifies marginal environments (pers. com. Rosen, 2010) and in the Lutetian assemblages corals show an equal contribution of both. It is difficult to ascertain the degree to which these communities preserved represent the original living community. Both biological and physical processes have altered the amount of ecological information eventually preserved in the fossil assemblage. However, the lack of reef rock, reef-building biota and sparse distribution of corals appears to indicate the absence of any reef in this area and the presence of a non-reefal community in sandy substrate. The exceptional preservation of coral specimens, with intact superficial morphological features, along with branches up to ~10cm in length, and articulated, complete molluscs, showing original colouration, is indicative of essentially in situ (i.e. autochthonous to parautochthonous) preservation. A combination of a low energy hydraulic regime, and high sedimentation rates, is thought to have resulted in the exceptional preservation of these specimens.

These corals in the Lutetian Paris Basin are found within predominantly carbonate-dominated beds and a mid-ramp environment is inferred. *Acropora* species from the Lutetian central Paris Basin area include *Acropora alverezi*, *A. wilsonae*, *A. proteacea* and *A. solanderi* showing arborescent and tabular growth forms. Tabular forms are found in modern settings on shallow reef fronts and reef tops (*A. hyacinthus* group, p. 62, Wallace, 1999).

6.3.2 Lutetian Deposits of the Hampshire Basin

Overview

The Earnley Sand is a middle Lutetian unit in the Bracklesham Group, Hampshire Basin, southern England (assigned to NP14 by Aubry, 1985). The Earnley Sand is a sandy clay with a high percentage of glauconite and varying marine faunas. It overlies the Marsh Farm formation, a primarily clay formation with lenses of sand. Both formations are uplifted with a heavily reworked contact (Gale *et al.*, 1999). Museum-based coral collections are largely labelled as from the E7 Bed (stratigraphy after Curry *et al.*, 1977), Earnley Formation, Bracklesham Group.

Description

During fieldwork the Bracklesham Beds, at Bracklesham Bay, were found outcropping along the coast from Chichester Harbour to Pagham Harbour and are periodically exposed in foreshore outcrops with tides and shifting beach deposits episodically covering deposits (Tab. 6.1). The section is ~100m thick with an abundant molluscan fauna, indicative of a high organic productivity. The section contains the E7 Bed characterised by green, glauconitic, poorly sorted, shelly muds and silts with abundant microspherical, large rotalid foraminiferids *Nummulites laevigatus*. The bed contains a variety of molluscs and corals.

Coral diversity

No *Acropora*-bearing lithologies have been found in the Lutetian of the Hampshire Basin. Coral occurrences are geographically restricted with a low diversity assemblage found in the E7 Bed of the Bracklesham Group, Bracklesham Bay. Eight coral genera have been identified from fieldwork and museum collections with 2 zooxanthellates and 6 azooxanthellates. In the field, *Goniopora* is abundant principally reflecting the genera's robust growth form and lack of taphonomic alteration. X-ray powder diffraction, over a 25° to 37˚ 2θ range, shows the main carbonate mineral peaks were four aragonite peaks (3.396Å, 3.273Å, 2.700Å, and 2.481Å) and an additional quartz peak (3.343Å) (Fig. 6.6a). This shows the pristine mineralogical preservation supporting rapid burial by high rates of sedimentation required to produce a geochemically enclosed system. Post-depositional modifications of the coral skeleton included entrapment of glauconitic sands with a degree of biological alteration having occurred with extensive boring and encrustation of the surfaces (Fig. 6.6).

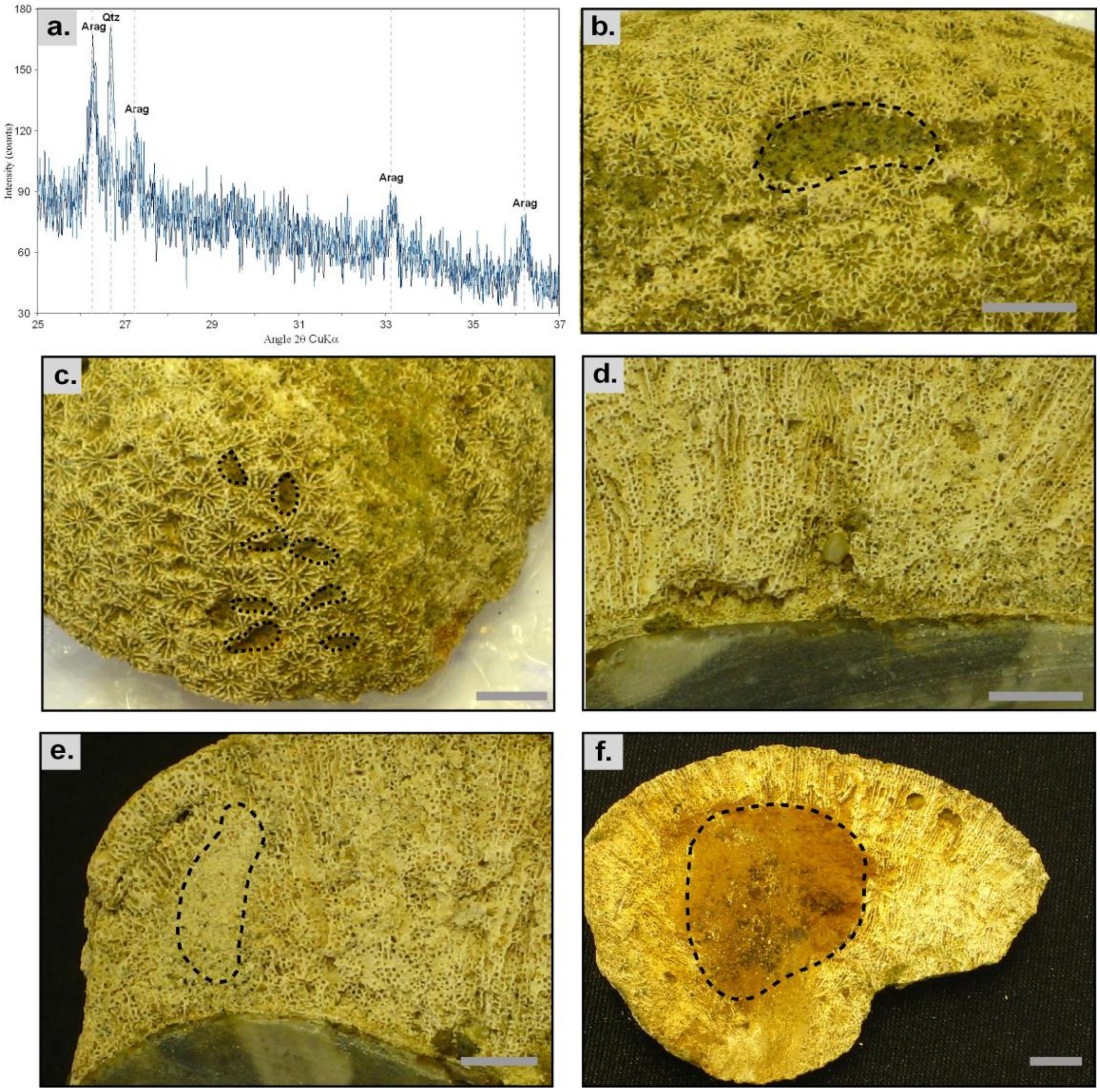


Figure 6.6. Preservational features of two <u>*Goniopora websteri*</u> *in hand specimen; H2B01 a. Diffractogram showing the main peaks of the carbonate minerals and quartz from samples scanned over 25-37 2θ (Arag-Aragonite, Qtz-Quartz), b. infilling of septal regions and larger surface voids with green glauconitic sands, c. surface borings, d. infilling by mm sized sediment grains within elongate septal voids and near areas of colonisation, e. concentrations of fine grained sediment and dissolution, H2B02 f. colony encrusting and surrounding degraded pebble (Scale: 1cm).*

Palaeoenvironment

These poorly sorted, shelly sublittoral sandy clays are characteristically green reflecting their glauconitic content. Glauconite is believed to be indicative of continental shelf marine depositional environments, tending to occur with slow rates of accumulation in some cases in association with marine flooding (transgressive) surfaces and condensed sections (see Amorosi, 1995). It is a reliable indicator of deposition in a shallow marine environment, although it can be reworked into deeper and shallower environments.

The low coral diversity and dominance of *Goniopora* provides clues about the palaeoecology. Restricted coral diversity and development has been shown to reflect environmental factors. Acevedo *et al*. (1989; Ponce Reef, Puerto Rico) demonstrated the influence of influxes of terrigenous sediment on reef environments where sedimentation reduced coral cover as well as the number of species. The Lutetian of the Paris Basin has been shown to be a time which was dry, with high aridity (Thiry, 1989), hence there was very little run-off and sediment supply, but in the Hampshire Basin Cope (1992) described large amounts of clastic input into the basin. A second influence on the diversity, and development, may be an increase in water nutrient content. This is supported at Bracklesham Bay by the presence of oysters, molluscan diversity and enhanced bioerosion (e.g. Hallock, 1988, Florida Keys) largely of the molluscan and coral fauna.

Additionally, the dominance of *Goniopora* can be explained by an environmental and evolutionary robustness, Rosen and Turnsek (1989) found that zooxanthellate corals were affected more severely than azooxanthellate corals during evolutionary perturbations. Rosen (2000) showed 11 z-like genera survived the K/T boundary, perhaps surviving in isolated refugia, one such genus being *Goniopora*. *Goniopora* has also shown to be more environmentally tolerant than other zooxanthellate genera (Wood, 1993). Morphologically, coral species with rapid growth rates, thinner tissue, and branching forms, (e.g., *Acropora*, *Stylophora*) tend to be environmentally sensitive, bleaching sooner, and more severely than slow-growing, massive corals with thicker-tissues (e.g. *Porites*, *Goniopora*) (Gates and Edmunds 1999; Loya *et al*. 2001).

Other fauna in the Earnley Sands include the gastropod mollusc *Turritella*. Recent turritellidae are found in modern settings in a wide range of environments, but prefer normal marine salinities (Allmon, 1988) and muddy environments (Taylor in McKerrow, 1978). They can be considered as indicators of high nutrient and productivity levels as well as the cooling of waters and associated with upwelling phenomena, but not necessarily precisely at the location of the upwelling area (Martinez and Rio, 2002). These suspension feeding, nutrient-loving gastropods are frequently found occurring alongside *Nummulites laevigatus* in the Bracklesham beds which are near the northernmost Eocene limit of this largely tropical genus (Blondeau, 1972).

6.3.3 Bartonian Deposits of the Paris Basin

Overview

In the Paris region, the Auversian Sables Moyen deposits are divided into the Sables d'Auvers and Sables de Beauchamp. These siliciclastic sands pass laterally and vertically into brackish and lacustrine calcareous deposits (Guillocheau *et al*., 2000).

Stratigraphically, *Acropora* specimens in collections are labelled as being from the Sables Moyen and Sables d'Auvers, which is part of the Sables Moyen. The Auversian belongs to the middle and upper nannoplankton zone NP16 (Aubry, 1986) and to the top of dinocyst zone W9 and to zone W10 (Chateauneuf and Gruas, 1978). The Auversian straddles the Lutetian/Bartonian boundary and hence is placed within the Middle to Upper Eocene. Considerable evidence for reworking of older deposits and associated fossils suggests the corals may be of Lutetian age reworked into Auversian (Bartonian) deposits.

The Lower Barton Beds belong to the base of the *Rhombodinium intermedium* and *Aerosphaeridium diktyoplokus* Zone characteristic of the Sables de Beauchamp in the late Auversian of the Paris Basin (Chateauneuf, 1980). The correspondence of the base of the Bartonian stratotype with the late Auversian is confirmed by the nannoplankton (Aubry, 1983) which places the Bartonian in the upper part of zone NP16 and zone NP17 and the assignment of the Sables d'Auvers to NP16 (Aubry, 1986). There is a scarce amount of calcareous nannofossils in the Sables de Beauchamp but Aubry (1986) assigned it to the upper part of NP16.

Emergence at the end of the Lutetian times led to the lithification of the limestones and to the development of a karstic surface over much of the Paris region. There were intermediate lagoonal deposits and then the deposition of sands and clays in the Bartonian seas that were less extensive than those of the Lutetian (Ager, 1980). The palaeoenvironment was dominated by beach sands with littoral barriers in a calm and shallow sea (Chavelier *et al*., 1980; Gely and Lorenz, 1991). Locally derived pebbles indicate that the Pays de Bray axis was a positive feature and the Artois anticline separated the Paris Basin from Belgium (Fig. 6.1). Lagoonal and beach deposits developed around the coastal margins of this early Bartonian sea.

Figure 6.7. Auvers-sur-Oise locality; a-b. Auversian deposits are found on the forest floor and within a series of shallow excavations, c-d. siliciclastic sands characterised by a yellow-orange rust colouration

Description

In the field, Bartonian deposits were studied from Auvers-sur-Oise, located about 40km north-north-west of Paris (Tab. 6.2), which is the stratotype for the regional stage of the Paris Basin, the Auversian (*sensu* Dollfus, 1880; Fig. 6.7). The forest floor and shallow pits exhibit good exposures and shallow excavation exposed new, fresh surfaces. The thickness of the coral layer varies between 2 and 3 metres. It can be followed laterally for several metres with no significant change in its faunal composition. These siliciclastic sands are characterised by a yellow-orange rust colouration, concentrated around bioclasts, indicative of oxidation with the formation of iron (III) oxides (Fig. 6.7). The fauna is dominated by a diverse assemblage of marine molluscs (e.g. bivalaves - *Cardita, Corbula, Cardium, Chama*, gastropods - *Potamides, Athleta, Cerithium*) and coelenterates. Other marine fauna include echinoids, bryozoa and calcareous algae (e.g. *Dactylopora*). There are multiple pebbles and fossils which are disarticulated, fragmented and indicative of being rolled and transported.

The coral branches, and molluscs, are more or less oriented in one direction, aligned parallel to bedding. Among the remarkably well preserved coral assemblage, a selection of the coral specimens is distinctive as being heavily worn and lacking superficial characteristics. The specimens are fragments of a branching genus, however the state of preservation makes further identification unachievable. These corals appear to suggest that these deposits were subjected to considerable reworking of older, Lutetian, deposits and their fossils (Barta-Calmus and Chevalier, 1980). There is no evidence for nearby presence of reef rock or coral framework.

Parallel bedding is evident at cm-scales with cyclic changes indicated by graded bedding and fining upward sequences (Fig. 6.7).

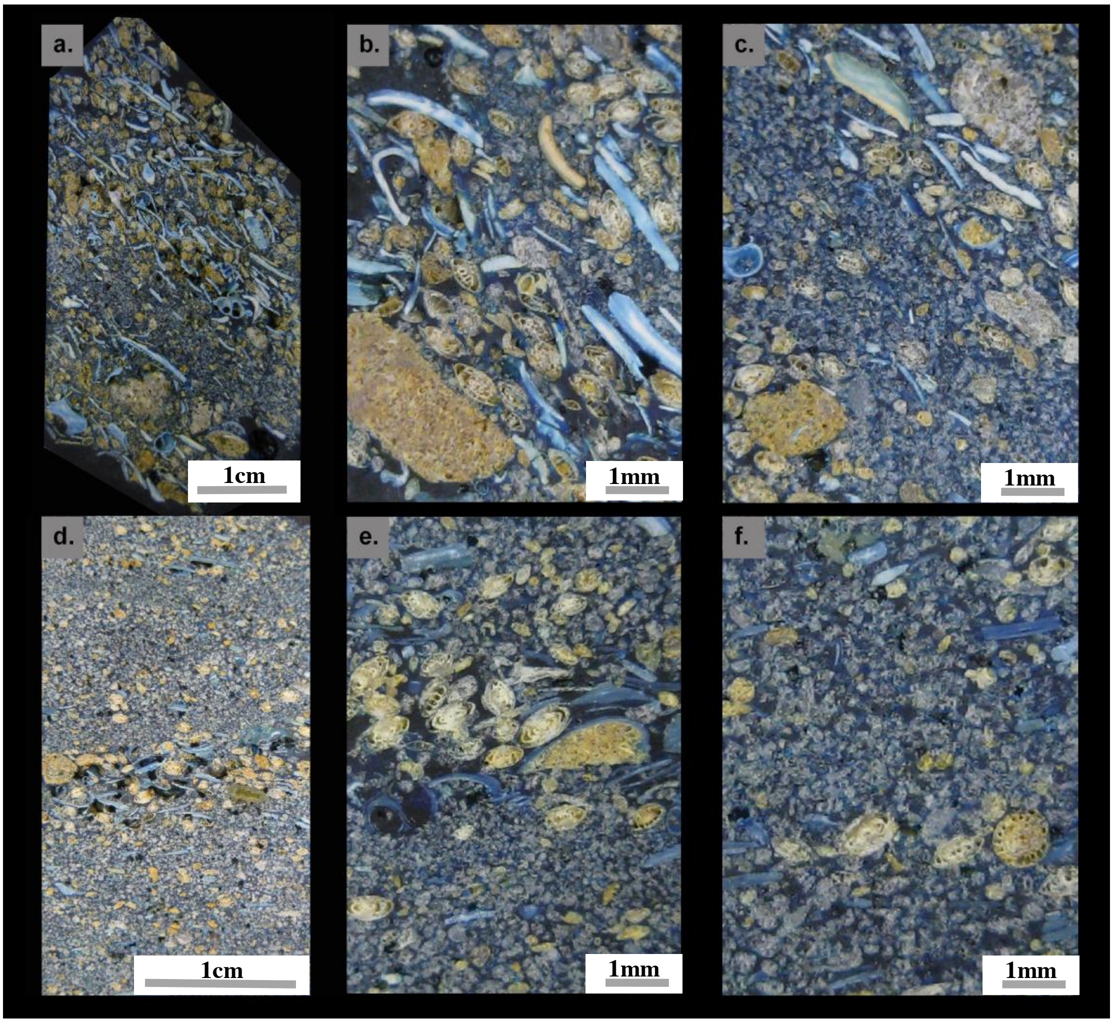


Figure 6.8. Sections of two block samples (a.-c. and d.-f., impregnated with blue resin to highlight porosity), a. Overview of sample from coarse bioclastic layer, b. layer dominated by molluscs and foraminifera (Nummulites, Endothyracid, Miliolids), lithic fragment, c. thin layer of quartz-dominated layer with rare, small foraminifera, d. Overview of sample from quartz-dominated layer, e. thin layer of coarser layers dominated bioclasts, f. sparse foraminifera within quartz-dominated layers.

Thin sections show evidence of cm-scale lamination with alternating quartz-dominated and bioclastic-dominated layers (Fig. 6.8). Quartz arenite layers are comprised of angular, monocrystalline quartz grains showing uniform and unit extinction and also polycrystalline quartz grains. Many quartz grains are coloured orange-brown principally due to high ferrous content (iron (III) oxide). Rare feldspar grains with evidence of simple (Carlsbad) twinning. Muscovite flakes show a blue colour with strong birefringence in crossed polars. Rock fragments include clasts of sedimentary origin, silty-shale with angular quartz grains and foraminifera. Heavy minerals include accessory minerals (zircon, apatite). Bioclasts are dominated by molluscs, gastropods, calcareous red algae, echinoid spines and foraminifera (*Endothyracid*, *Nummulites* and *Miliolids*) (Fig. 6.9).

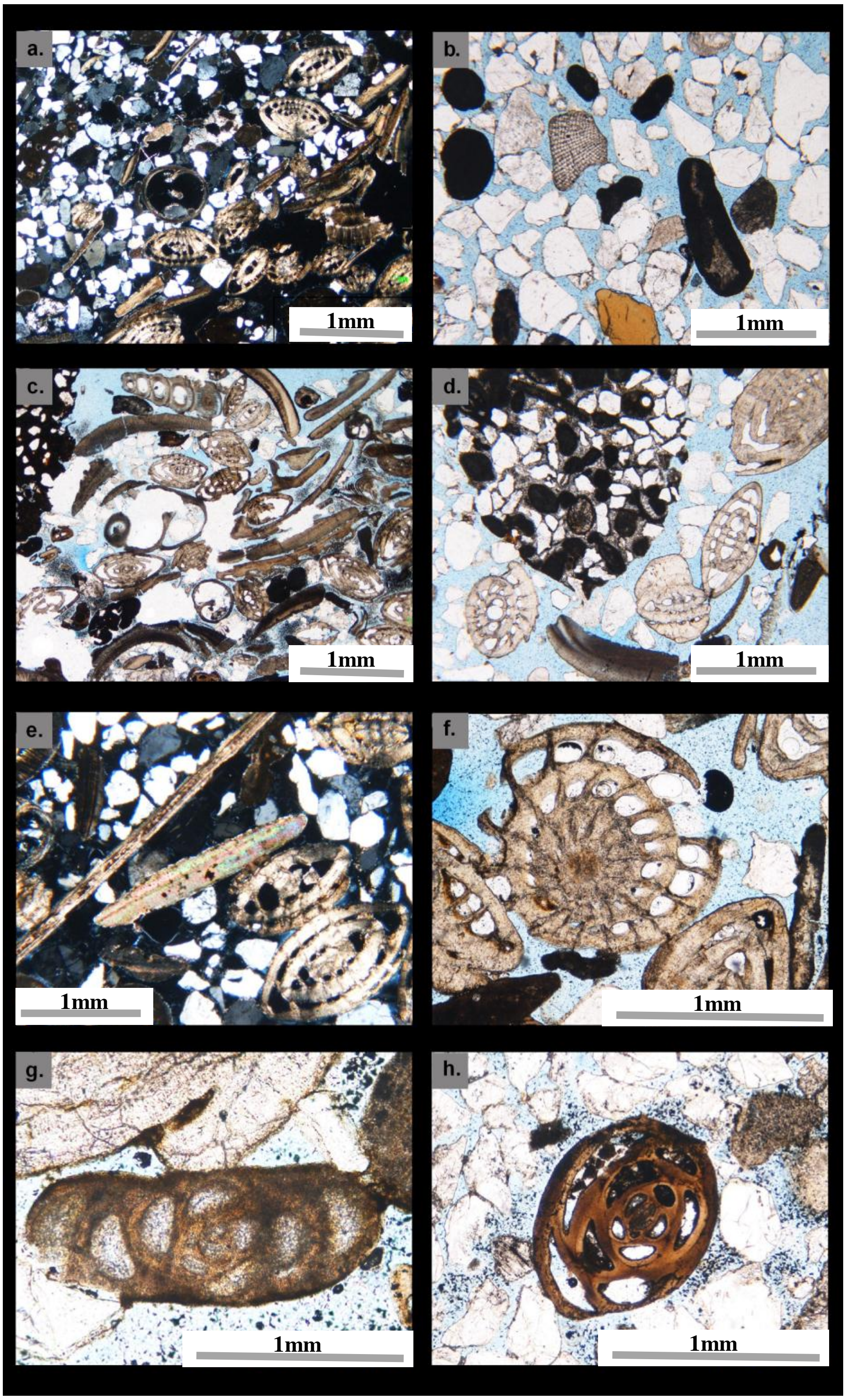


Figure 6.9. Auvers-sur-Oise a. Contact between a quartz- and bioclastic-dominated lamination (XPL), b. quartz-dominated layer - groundmass of angular, monocrystalline quartz, red calcareous algae fragment, c. bioclastic-dominated layer – bivalves, gastropods, foraminifera, d. lithic fragment e. echinoid spine (XPL), f. *Nummulites* *g.* *Endothyracid*, *and, h.* *Miliolid*

Coral Diversity

A total of 22 species and 14 genera are known from the moderately diverse Paris Basin Bartonian (Fig. 6.10).

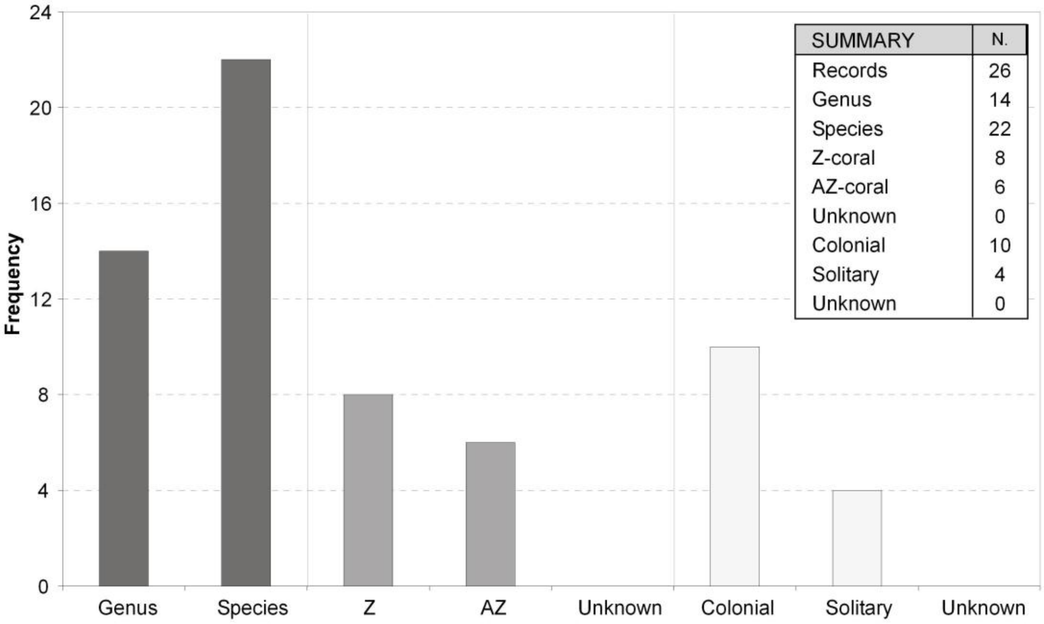


Figure 6.10. Histogram of <u>*Acropora*</u>*-bearing lithologies coral assemblage from the Bartonian, Paris Basin*

Zooxanthellate and azooxanthellate corals (8Z, 6AZ) contribute nearly equally with colonial growth forms dominating (10C, 4S). Colonial growth forms include ramose branching forms (e.g. *Acropora*) and phaceloid branching forms (e.g. *Dendrophyllia*) to more massive forms (e.g. *Goniopora, Porities, Stylocoenia*) and foliose forms (e.g. *Turbinaria*) (see Appendix 9). Faviid corals are generally small dome-shaped morphologies or encrusting forms.

These Bartonian *Acropora*-bearing localities have only 6 out of 14 coral genera in common with the Lutetian *Acropora*-bearing localities of the Paris Basin with 11 genera solely found from the Lutetian and 8 from the Bartonian.

Palaeoenvironment

The moderately diverse coral assemblage, similar contribution of zooxanthellate and azooxanthellate corals, and diverse assemblage of marine molluscs supports a tropical, marginal environment comparable to that seen in the Lutetian. Amongst the preserved coral assemblage, the small collection of heavily abraded specimens appears to support the interpretation that these deposits are the result of considerable reworking of older, Lutetian, deposits and their fossils (Barta-Calmus and Chevalier, 1980). The multiple pebbles and rolled fossils are indicative of a shoreface environment. Results suggest post-mortem parautochthonous to autochthonous deposition in a shoreface environment, with rapid burial creating a relatively enclosed geochemical system. The fragmentation of the branches point to at least occasional higher water movement. Nevertheless, the overall facies and coral growth forms suggest nearshore palaeoenvironment.

6.3.4 Bartonian Deposits of the Hampshire Basin

Overview

The localities 'Barton' and 'Barton Cliffs' described on the specimen label details is assumed to be the same and imply the sea cliffs extending from Highcliffe (50:44:00N, 1:45:32W) in the west to Milford-on-Sea (50:43:29N, 1:35:26W). Daley (1999) defined the locality of 'Barton Cliffs' as geographically including Highcliffe, Barton, Beacon and Hordle Cliffs. Three formations from the Barton Group are exposed in this section, the Barton Clay, the Chama Sand and the Becton Sand, and also above this the Headon Hill Formation (Fig. 6.11).

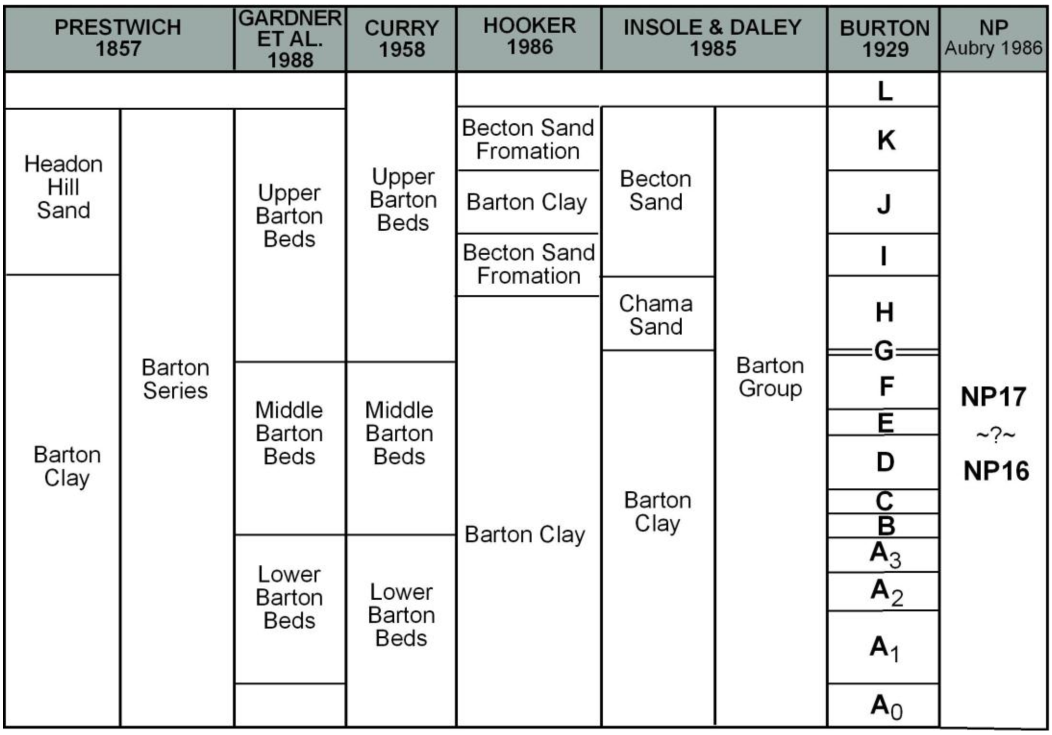


Figure 6.11. Historical stratigraphy of the Bartonian deposits of the Hampshire Basin (after Daley, 1999)

Four transgressive-regressive cycles have been identified by Hooker (1986) within the Barton Group, although the youngest is incomplete. The first two cycles are coarsening-upwards sequences with highly glauconitic muds passing up through non-glauconitic muds, sandy muds and into sands (Daley, 1999). Cycle 1, Beds A_0 to A_3, includes a basal pebble bed, transgressive lag, and Bed A3 contains abraded fossils, reworked as the regressive phase developed. There is no basal pebble bed in Cycle 2 (Beds B to I, Fig. 6.11) but a sharp burrowed junction instead and some rolled shells derived from Bed A_3. The trangressive phase is represented at the base by glauconitic silty clays. Bed I has been interpreted by Hooker (1986) as accumulating in middle to upper shoreface. Cycle 3 is comprised of Beds J, K and the Totland Bay Member of the Headon Hill Formation and shows a marked break at Bed J. In Bed K clean sands have been interpreted as reflecting the development of beach or barrier island conditions. In the remainder of Cycle 3 the trangressive phase is better represented. This part of the succession contains a variety of sediments and fossils representing brackish and freshwater conditions and comprising several minor transgressions and regression cycles and a major palaeochannel fill. Cycle 4 is incomplete, comprising the transgressive phase of the Colwell Bay Member, more fully developed on the Isle of Wight (Daley, 1999).

Acropora specimens in the NHM collection are labelled as being from the 'Barton Beds' (nomenclature used by Curry, 1965) which now is termed, after Insole and Daley (1985), the Barton Group and lowermost Solent Group and encompasses Burton's (1929) principal units (A-L) of the Barton Beds (Fig. 6.11). The lack of specific locality information in the label details led to the main aim of fieldwork to the area which was to obtain a more precise stratigraphic position of the coral-bearing horizons.

Description

This locality was visited during fieldwork. The section is dominated by a series of multicoloured sandy clays and sands outcropping as a series of slumped cliff and foreshore exposures (Fig. 6.12). Beds dip eastwards at very low angles with the oldest strata to the west. Burton's individual beds were hard to distinguish in the field, but the three units of Curry (1958), the Lower, Middle and Upper, were easily distinguished.

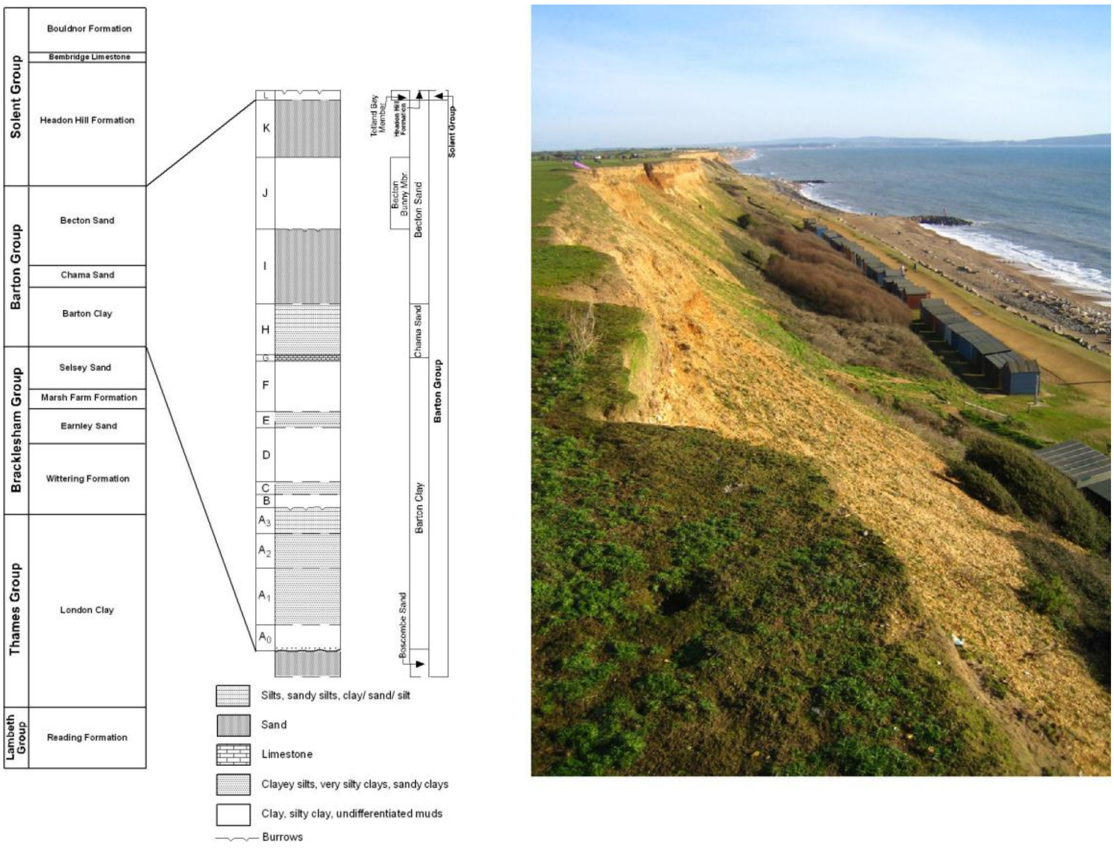
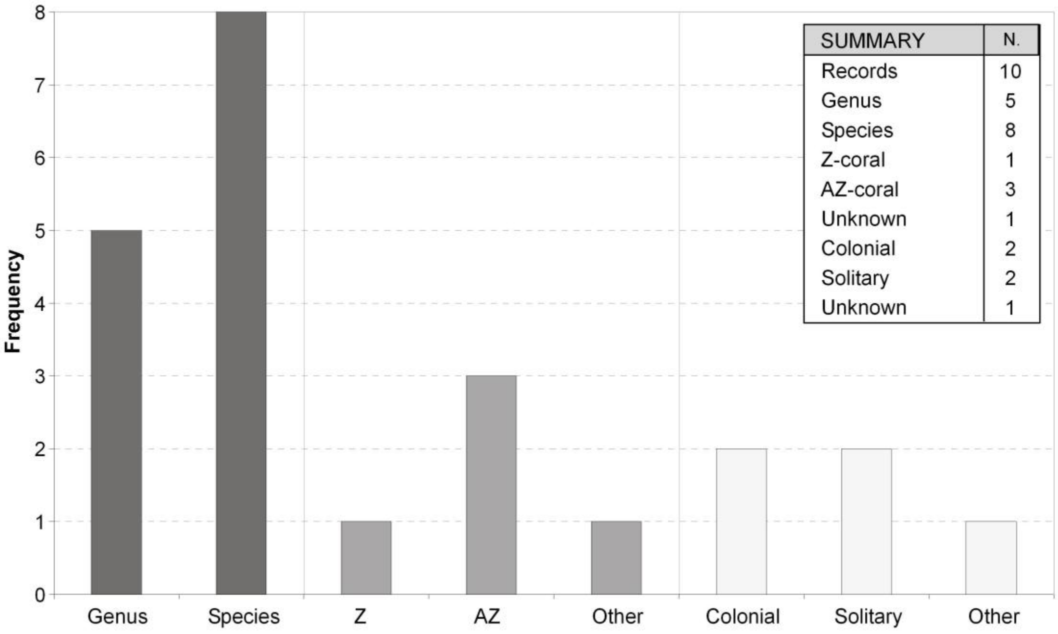


Figure 6.12. Generalised lithostratigraphic succession of the Barton Group, Barton (after Daley, 1999) and slumped cliff exposures of Barton section.

The Lower Barton consists of beds A1, A2, A3 and B and is mainly glauconitic clays. The Middle Barton consists of beds C, D, E and F and is mainly sandy clays and the Upper Barton consists of G, H, I, J and K and is more sandy (Fig. 6.12). Apart from *Turbinolia* found in the Middle Barton Beds, no coral horizons were identified (discussed below). Other marine fauna including sea urchins, crab claws, sharks teeth and *Nummulites* are found throughout the section and dominate the faunas of the Lower to Middle Barton Beds.

Coral Diversity

A total of 8 species and 5 genera are known from the low diversity Bartonian Hampshire Basin (Fig. 6.13).



SUMMARY	N.
Records	10
Genus	5
Species	8
Z-coral	1
AZ-coral	3
Unknown	1
Colonial	2
Solitary	2
Unknown	1

Figure 6.13. Histogram of Acropora-bearing lithologies coral assemblage from the Bartonian, Hampshire Basin

Primarily as a result of poor-resolution stratigraphic label information, combined with multiple periodic revisions of the stratigraphy at this locality, precise placement of corals within the section at Barton-on-Sea is problematic. During fieldwork, with the exception of stratigraphically widespread *Turbinolia*, no corals were found. In late twentieth century private collections corals are recorded from Burton's Lower Barton Bed A3 (*Dendrophyllia*), and Middle Barton Beds C (*Oculina*) and F (*Paracyathus)*. No further stratigraphic details exist for *Acropora* specimens.

From museum collections, the locality has low generic richness (5) with azooxanthellate corals dominating (1 Z, 3 AZ), and solitary and colonial forms contributing equally (2 colonial, 2 solitary). Colonial forms show ramose branching structures (e.g. *Acropora*) and phaceloid branching forms (e.g. *Dendrophyllia*) (see Appendix 9).

These Bartonian *Acropora*-bearing localities have 3 coral genera in common with the Bartonian *Acropora*-bearing localities of the Paris Basin with 11 genera solely found from the Bartonian of the Paris Basin and 2 from the Bartonian of the Hampshire Basin.

Palaeoenvironment

Low coral diversity in the Bartonian of the Hampshire Basin, and a lack of coral framework, raises the question as to whether this was a flourishing coral community or a disturbed/restricted state of development. Low coral diversity may be a reflection of either low abundances and/or poor preservation. However, in museum and private collections, the molluscan fauna is exceptionally preserved and therefore indicates that the coral assemblage indicates true low abundances and diversity. The highly diverse, often small and thin shelled molluscan assemblage implies a low hydraulic regime and high organic content.

A single *Acropora* species has been recorded from the locality and specimens only show evidence of hispidose forms, presently found confined to most sheltered leeward coasts, almost always subtidally (see Morton, 1974).

6.3.5 Priabonian Deposits of the Paris Basin

Overview

The Paris Basin Priabonian deposits are dominated by lacustrine and evaporitic sediments with brackish intercalations (Guillocheau *et al*., 2000).

Coral diversity

No *Acropora*-bearing lithologies or corals have been found in the Priabonian of the Paris Basin.

Palaeoenvironment

Regional synsedimentary tectonic movements (Blondeau *et al*., 1964, Pomerol, 1967, Chavelier and Pomerol, 1979, Lorenz, 1984) and global eustatic sea level fall (Zachos *et al*., 2001) undoubtedly combined resulting in the Paris Basin becoming progressively more isolated throughout the Eocene. This may have strongly influenced the conditions of sedimentation, and culminated in gypsum accumulation in the Paris area in the late Bartonian-Priabonian (e.g. Fontes and Létolle, 1976). The onset of non-marine conditions in the Late Eocene Paris Basin led to the loss of corals from the area.

6.3.6 Priabonian Deposits of the Hampshire Basin

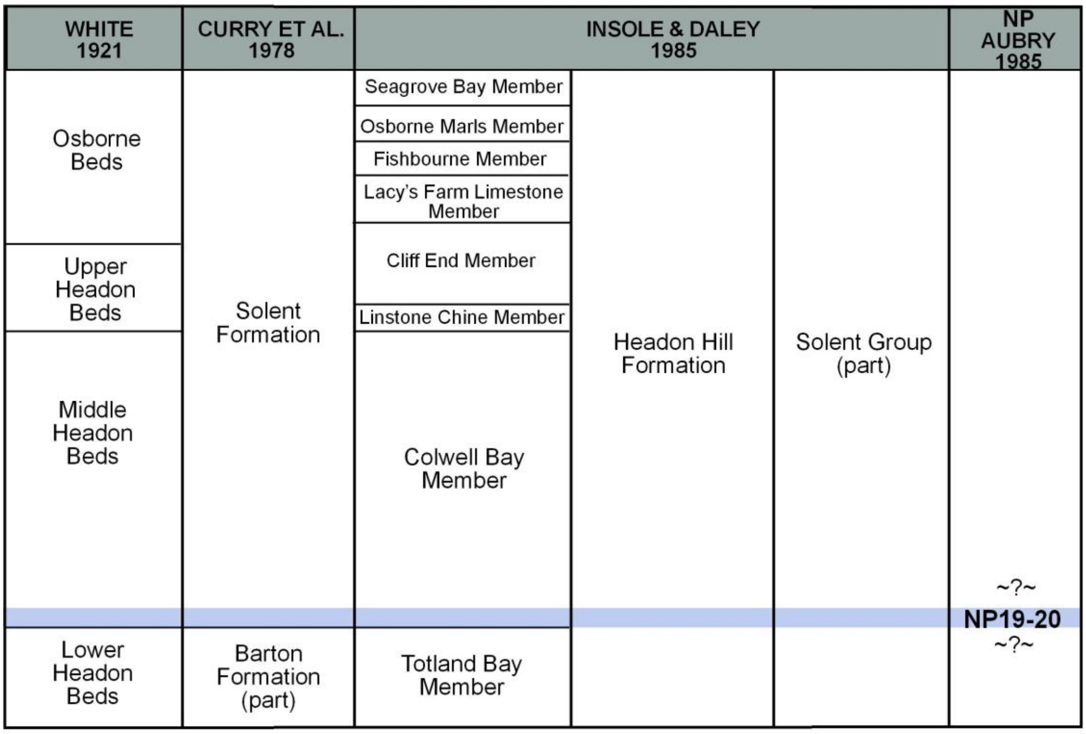
Overview

Acropora specimens have been recorded from two localities from the Priabonian of the Hampshire Basin; Brockenhurst, Hampshire, and Whitecliff Bay, Isle of Wight. Brockenhurst, Hampshire, lies within the National Park of the New Forest. This south-western area contains the uppermost Eocene strata of the Solent Group predominantly dominated by lacustrine or lagoonal deposits with high carbonate content, often described as marls. Within the Solent Group are the marine deposits of the Brockenhurst Bed, Headon Hill Formation. The Brockenhurst Bed in this region has been described as outcropping in a railway cutting between Brockenhurst and Sway (White, 1917) and tileyards (Davis, 1952).

Whitecliff Bay (50:40:19N, 1:06:17W) is located on the eastern coastline of the Isle of Wight and displays the most chronostratigraphically extensive and continuous Paleogene succession in Western Europe (Daley, 1999). The Paleogene cliffs consist of

~550m of strata ranging from Paleocene to early Oligocene which unconformably overlies the Cretaceous *Belemnitella mucronata* Zone of the Upper Chalk. In the most southern part of Whitecliff Bay, the Paleogene strata are vertical, reflecting the steep northern monoclinal limb of the Sandown anticline, but northwards, near the end of the cliff section at Black Rock Point, there is a northerly dip of about 5°. The predominantly clastic Paleogene strata at Whitecliff Bay comprise five lithostratigraphic units; the Lambeth Group, the Thames Group, the Bracklesham Group, the Barton Group and the Solent Group.

Acropora is found within the Brockenhurst Bed at the base of the Colwell Bay member of the Headon Hill Formation in the Solent Group. The Brockenhurst Bed is one of two purely marine horizons within the Headon Hill Formation of the Solent Group. This is demonstrated by its purely marine fauna with several genera of corals (Curry, 1992).



WHITE 1921	**CURRY ET AL. 1978**	**INSOLE & DALEY 1985**			**NP AUBRY 1985**
Osborne Beds	Solent Formation	Seagrove Bay Member	Headon Hill Formation	Solent Group (part)	
		Osborne Marls Member			
		Fishbourne Member			
		Lacy's Farm Limestone Member			
Upper Headon Beds		Cliff End Member			
		Linstone Chine Member			
Middle Headon Beds		Colwell Bay Member			~?~
					NP19-20
Lower Headon Beds	Barton Formation (part)	Totland Bay Member			~?~

Figure 6.14. Historical stratigraphy of the Priabonian deposits of the Hampshire Basin (after Daley, 1999, highlighted area shows <u>*Acropora*</u>*-occurrence-Brockenhurst Bed)*

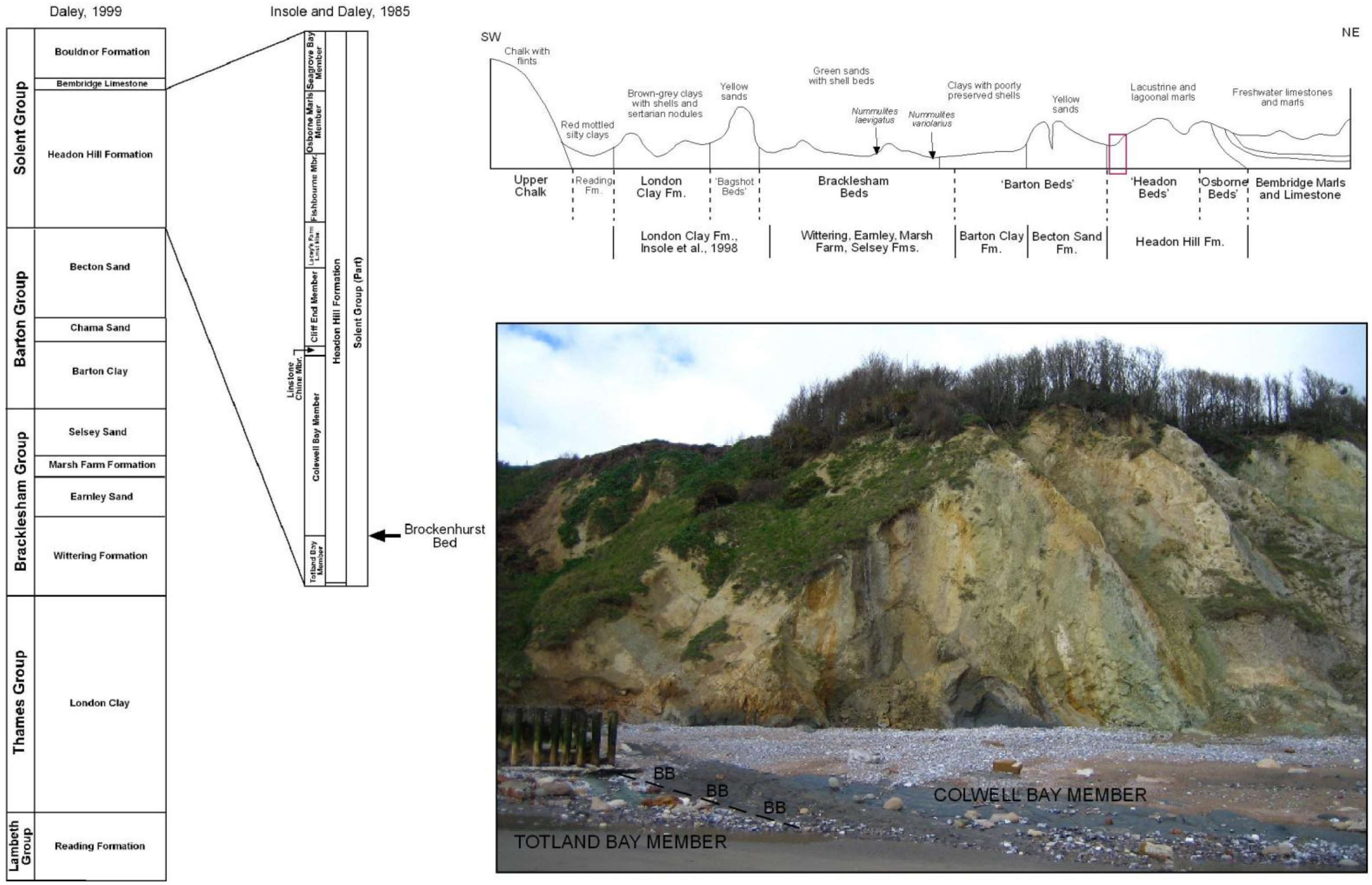


Figure 6.15. Generalised lithostratigraphic succession of the Headon Hill Formation, Solent Group (after Daley, 1999) and cliff, and foreshore, exposure of Whitecliff Bay section (BB-Brockenhurst Bed).

Description

From specimen label information, and the literature, two Priabonian localities were targeted during fieldwork; Brockenhurst in the Lyndhurst area, and Whitecliff Bay, Isle of Wight.

The mainland Brockenhurst locality was formerly exposed in local railway cuttings (Whitley Ridge) and tileyards (see details Davis, 1952). Most of the exposures had become overgrown or in-filled by the 1940s, but Davis (1952) arranged for some clearing to be made at the Victoria Tilery, Brockenhurst, and for two trial-holes to be sunk (*pers. comm.* Martin Munt). The railway cutting at Whitley Ridge is now inaccessible due to an electrified mainline. From fieldwork for this thesis, the Brockenhurst Bed is no longer exposed or accessible around the Brockenhurst area. The Victoria Tilery Cottage is still shown on modern Ordnance Survey maps but now is converted to a house. Nothing of the factory remains, but evidence of associated excavations can still be seen, including, a deep, disused pit that on the 1898 Ordnance Survey map is marked as a clay pit and another pit described as the ‘Old Clay Pit’ (White, 1917).

On the Isle of Wight, the Brockenhurst Bed was exposed during fieldwork in the cliff and foreshore at Whitecliff Bay. In the field the Totland Bay Member is seen to be composed of greenish clays with freshwater fossils (e.g. *Planorbis, Galba*). This is followed by the Colwell Bay Member which is capped by a *Thalassinoides*-burrowed omission surface marking a transgression surface. Overlying this is the 0.5m section of dark grey/brown, glauconitic and shelly sandy clay (Brockenhurst Bed) with a diverse marine fauna (e.g. molluscs, corals, ray teeth, echinoid spines; Fig. 6.16e.). Bivalves and gastropods are thick shelled and predominantly marine with some having an estuarine affinity (*Ostrea, Cardita, Cardium, Athleta, Venericor;* Fig. 6.16a.). The base is dominated by pebbles and degraded, rounded flints. Lignite is also present. Corals identified in the field are *Lobopsammia* and *Acropora*.

In thin section, the muds are composed predominantly of clay minerals, quartz and feldspar (Fig. 6.16a.). The clay mineral component is predominantly smectite. The heavy mineral rutile dominates thin sections, recognised by its extreme positive relief and yellowish-reddish brown colour in plane polarised light. Glauconite is a minor component, along with feldspars (orthoclase and microcline) and scattered, and fine grained, alteration (sericite), micas (Fig. 6.16a-f.).

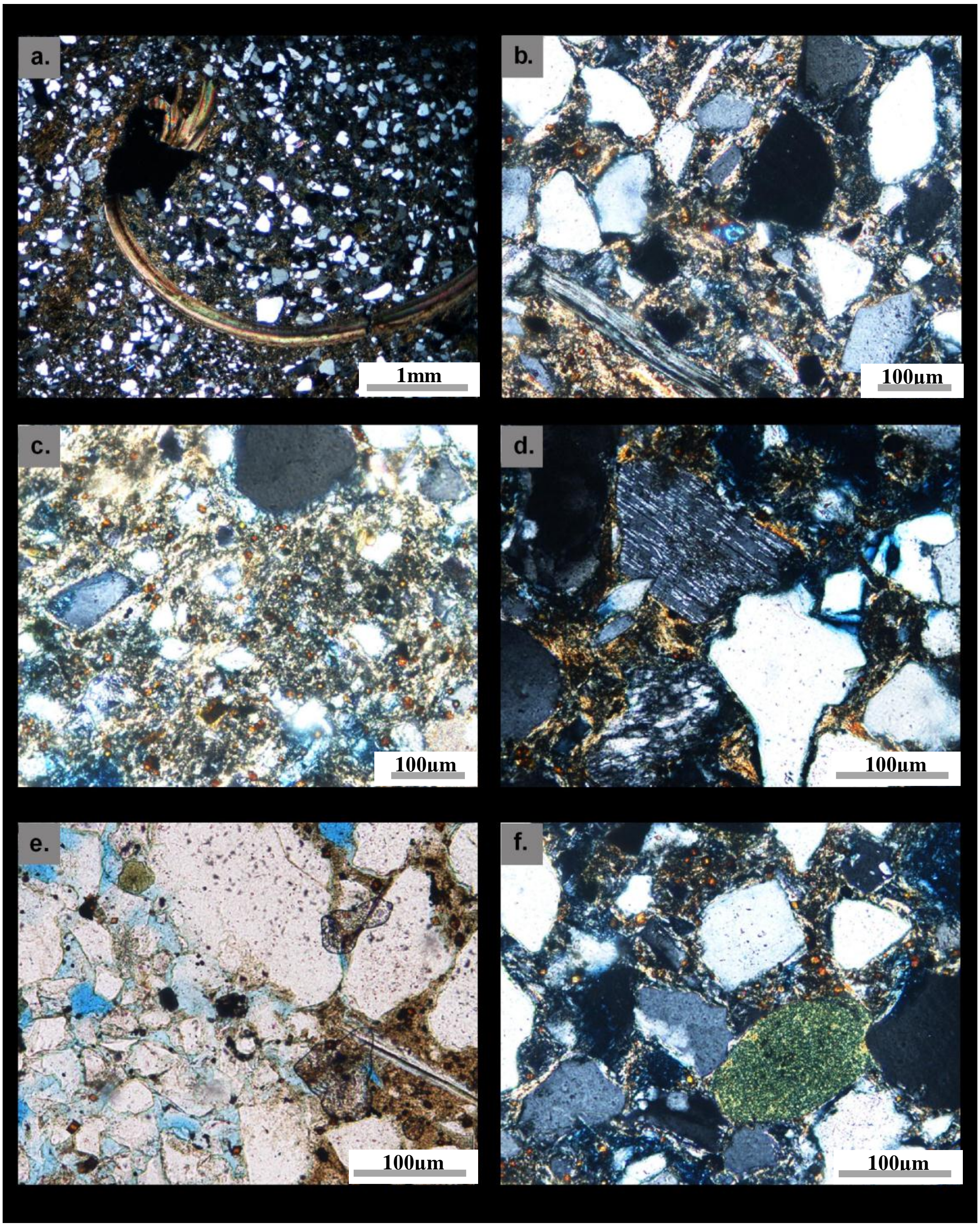
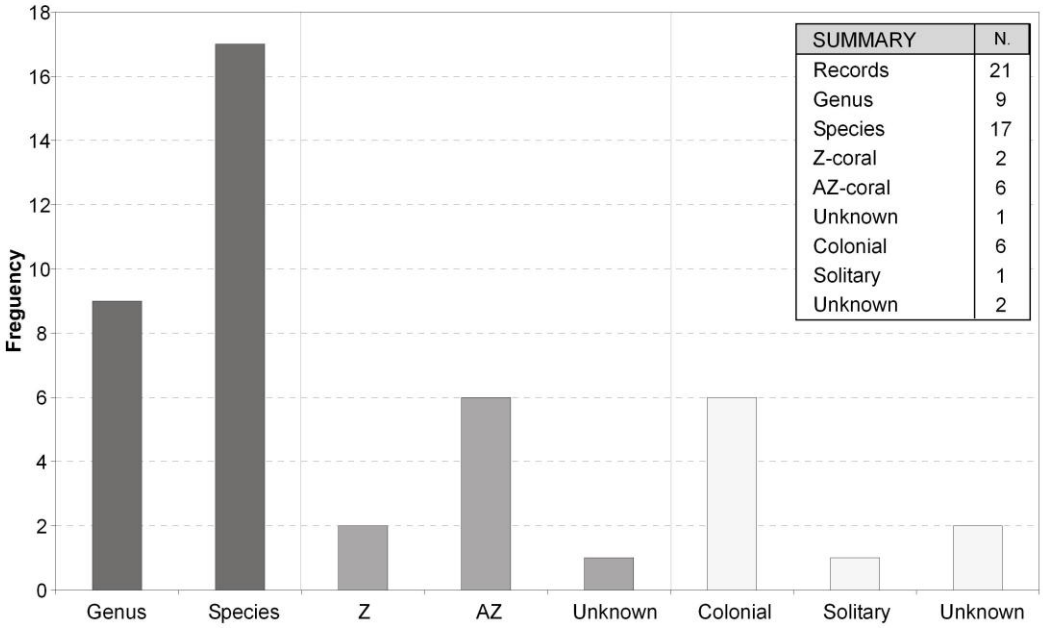


Figure 6.16. Brockenhurst Bed, Whitecliff Bay, Isle of Wight, a. bivalve in dark matrix of clay, silt-grade quartz and organic matter, b. clay matrix and absence of intergranular porosity, c. matrix dominated by heavy mineral rutile, d. feldspars showing evidence of overgrowths and sericite replacement and quartz grains (mostly monocrystalline with unit extinction), e. sponge spicule, f. glauconite pellet.

Coral diversity

A total of 17 species and 9 genera are known from the low diversity Priabonian of the Hampshire Basin, which is moderately diverse with respect to the Bartonian of the Hampshire Basin.



SUMMARY	N.
Records	21
Genus	9
Species	17
Z-coral	2
AZ-coral	6
Unknown	1
Colonial	6
Solitary	1
Unknown	2

Figure 6.17. Histogram of *Acropora*-*bearing lithologies coral assemblage from the Priabonian, Hampshire Basin*

Azooxanthellate (2Z, 6AZ) and colonial (6C, 1S) corals dominate (Fig. 6.17). Massive colony growth forms are exhibited (e.g. *Goniopora, Stylocoenia*) with ramose-branching and dendroid-branching forms also found (e.g. *Acropora, Dendrophyllia* respectively) (see Appendix 9). In the field, the assemblage is seen to be dominated by robust *Lobopsammia* specimens, probably reflecting a preservational bias but also possibly a true reflection of original abundances. *Acropora* specimens are difficult to extract, as although XRD shows exceptional preservation, specimens are soft and often fragment when removed from matrix.

These Priabonian *Acropora*-bearing localities have 2 coral genera in common with the Bartonian *Acropora*-bearing localities of the Hampshire Basin with 7 genera solely found from the Priabonian and 3 from the Bartonian of the Hampshire Basin.

Palaeoenvironment

The coral assemblage is dominated by azooxanthellate corals, mostly colonial. Modern coral colonies dominated by low-diverse azooxanthellate coral communities, dendroid growth forms, and evidence of colony breakdown by bioerosion as seen in the

Priabonian Hampshire Basin, are often associated with what are interpreted as colder and/or deep-water coral habitats (see Bernecker and Weidlich, 2006). Molluscs, sharks teeth and echinoid spines show evidence of fully marine conditions. These molluscs are thick-shelled, associated with this transgressive deposit.

This relatively high energy, marine debris lies on an eroded and *Thalassinoides*-burrowed surface. The rounded pebbles and degraded flints provide evidence that this is the result of a marine transgression and probably represents a transgressive, or shoreface lag into a lagoonal environment. Within the Priabonian the Brockenhurst Bed corals are found within siliciclastic beds in a relatively protected mid-shelf environment, below wave-base.

6.3.7 Coral taphonomy and preservation

As shown in Chapter 6 and 7, the coral specimens from these deposits are exceptionally preserved. The ramose, branching habit of *Acropora* renders the skeletal remains susceptible to fragmentation, through bioerosion, relatively high energy causing breakage, rolling and abrasion during transportation. However, the preservation of these fragments, up to 12cm in length, with intact morphological features, suggests relatively little transportation and reworking of the fossils. A morphological distinction between the specimens in each basin can be made on the basis of the maximum specimen length and branch thickness preserved (Fig. 6.18).

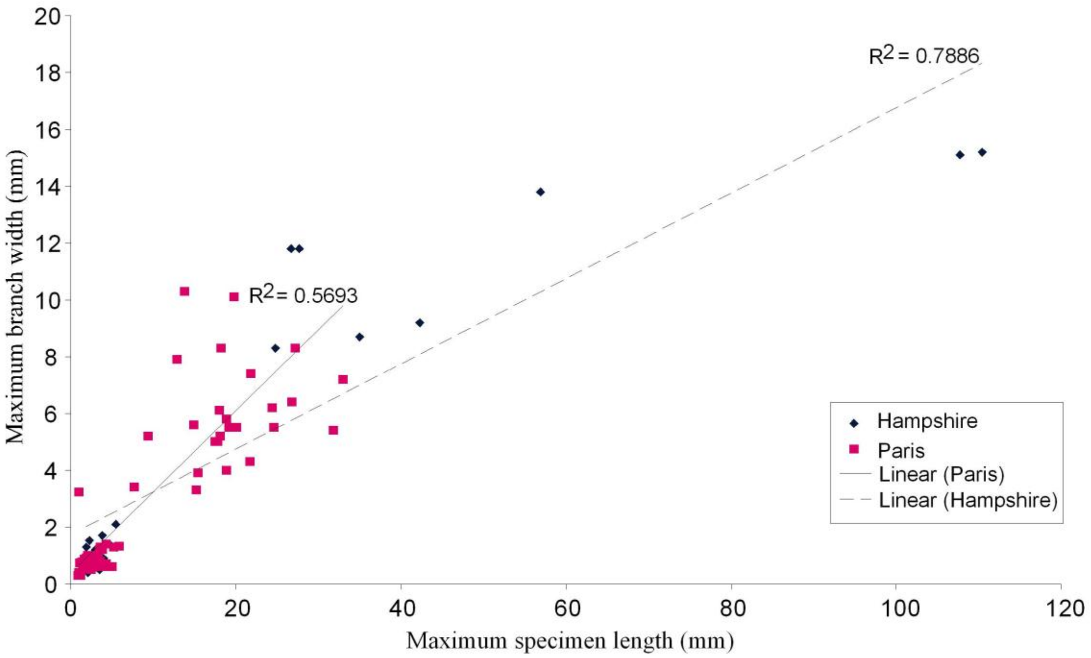


Figure 6.18. Comparison of maximum specimen length and branch width from the Hampshire and Paris basins.

The Paris Basin is dominated by specimens with a smaller maximum specimen length (mean 8.08, standard deviation 8.25, n. 72) in relation to maximum branch width (mean 2.73, standard deviation 3.28, n.72), compared with the Hampshire Basin (maximum length- mean 19.57, standard deviation 30.81, n. 24; maximum branch width mean 4.64, standard deviation 5.37, n. 24). Both morphological measurements reflect palaeoenvironmental factors. Maximum specimen length reflects both hydraulic regime and the degree of bioerosion taking place (often a function of nutrient levels), both leading to colony breakdown. Maximum branch width is a function of the individual species and hence the colony growth form, which in turn principally reflect environmental constrictions including hydraulic and sedimentation regime (see Wallace, 1999). Both measurements are also intrinsically linked with a larger maximum branch width allowing larger specimens to be preserved under higher hydraulic regimes, however narrower branches of larger specimens suggest lower hydraulic energy regimes. Additionally, palaeoenvironmental factors do not work exclusively. Overall the Hampshire Basin specimens show sturdier growth forms than those from the Paris Basin, however there is variation within in each basin reflected by different species and colony growth forms.

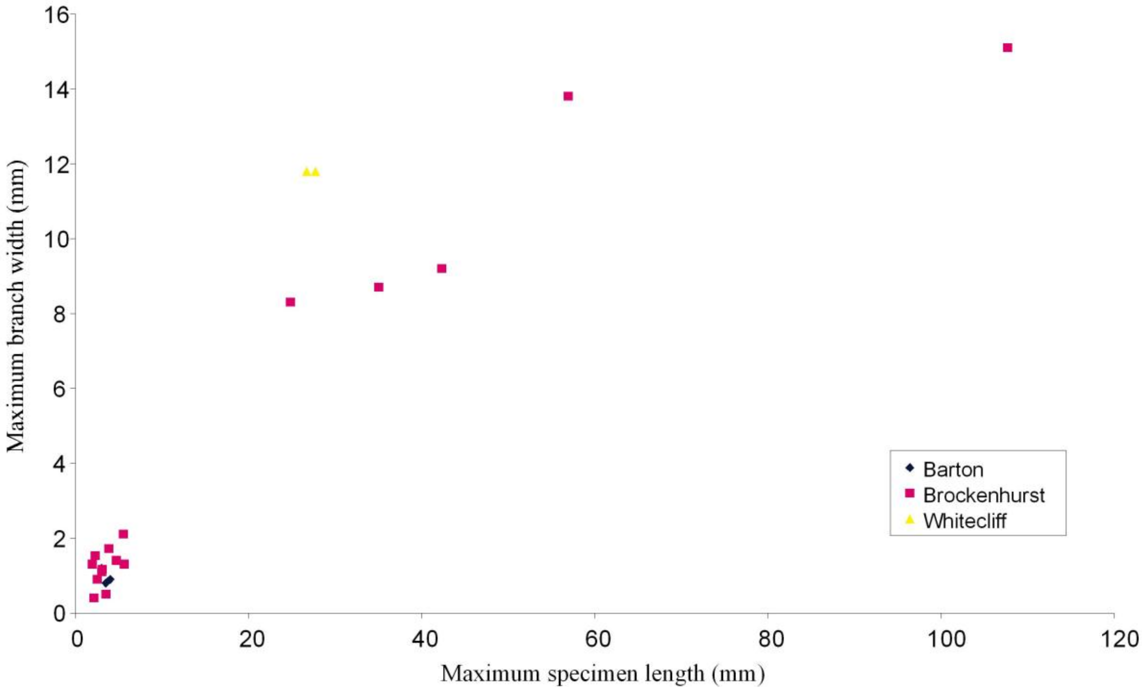


Figure 6.19. Localities from the Hampshire Basin. Comparison of maximum specimen length and branch width.

Specimens of *Acropora anglica*, *Morphotype 3*, and a single specimen of *Morphotype 1*, from the Hampshire Basin have a sturdier growth form than species from the Paris Basin. Comparison with modern *Acropora* species groups (see Chapter 5) shows the species are reminiscent of the modern *muricata* and *robusta*, presently associated with shallow high water-movement habitats such as the reef crest or edge, or patch reefs and shoals. These sturdier species all come from the Hampshire Basin Priabonian localities of Brockenhurst and Whitecliff Bay (Fig. 6.19). *Acropora* specimens from the Bartonian Barton-on-Sea locality only show evidence of the distinctly more fragile, hispidose forms, presently found confined to most sheltered leeward coasts, which are almost always subtidal (see Morton, 1974).

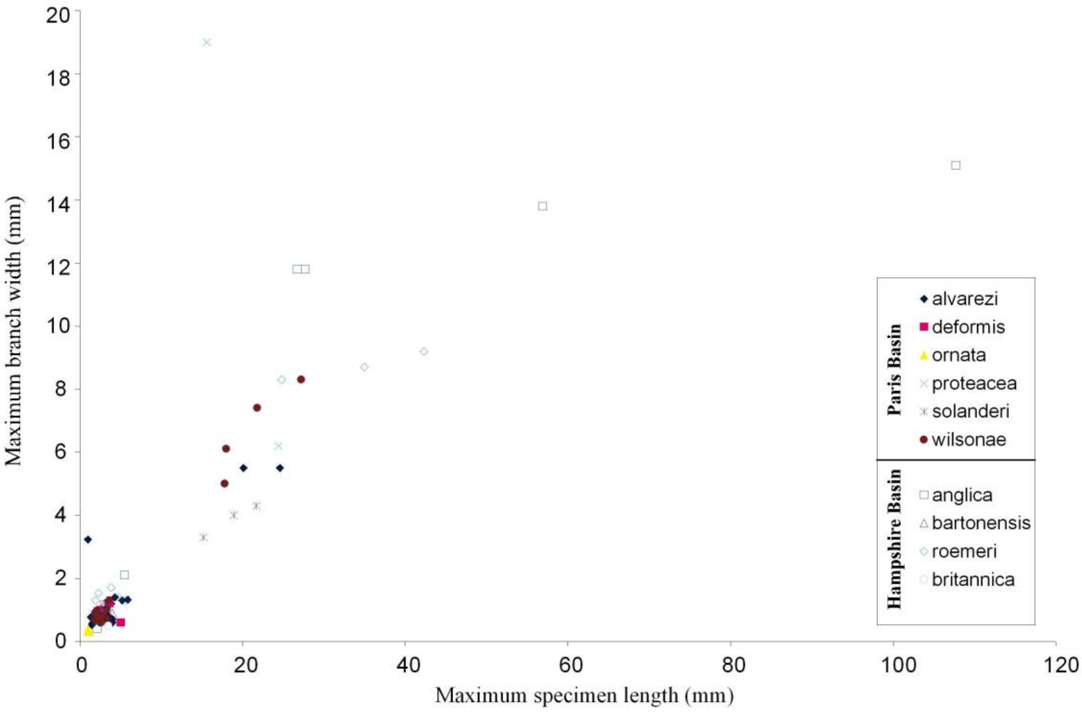


Figure 6.20. Species from the Hampshire and Paris basins. Comparison of maximum specimen length and branch width.

In the Paris Basin, overall more fragile forms are preserved with smaller specimen length and branch width (Fig. 6.21).

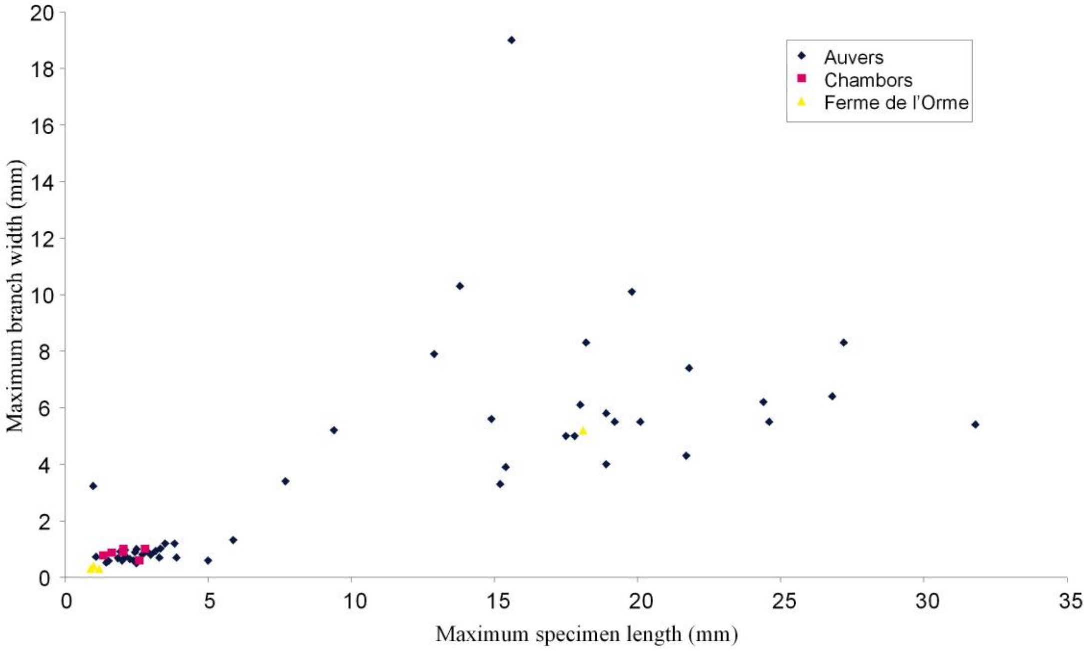


Figure 6.21. Localities from the Paris Basin. Comparison of maximum specimen length and branch width

The two Lutetian sites in France (Chambors and Ferme l'Orme) consistently have smaller specimen length and branch width than the Bartonian site (Auvers-sur-Oise), which displays large variation in both measurements. The slender species *Acropora ornata* is described solely from the Lutetian localities and is reminiscent of the modern species *Acropora russelli* associated today with calm, deep-water localities. Specimens from both the Lutetian and Bartonian Paris Basin sites are dominated by the species *Acropora alvarezi* and *A. wilsonae* and are largely responsible for the spread of branch width and length data, although again the more robust specimens are from the Bartonian of Auvers-sur-Oise. Slender branching species *Acropora deformis* and *A. solanderi* are only found in Bartonian deposits. For many of the species an element of the variation found in branch width is likely to be determined by growth variation across the colony structure, with stronger supporting branches below the lightly structured terminal branches. Additionally, intraspecies variation in colony form due to environmental forcing has been seen in the modern record, in the World Wide *Acropora* Collection at the Museum of Tropical Queensland.

6.4 DISCUSSION

The occurrence of *Acropora* in the Paris and Hampshire basins during the Eocene was largely controlled by global climatic controls and regional tectonics. The Eocene was a time of climatic cooling with tropical and subtropical faunas being lost from NW Europe to be replaced by temperate faunas (Fig. 6.22). This period of a general cooling trend was associated with falling sea levels, which ultimately led to the restriction of both basins. The distribution of *Acropora*, and other corals, within the two basins appears to be temporally offset with occurrences starting and disappearing from the Paris Basin before the Hampshire Basin.

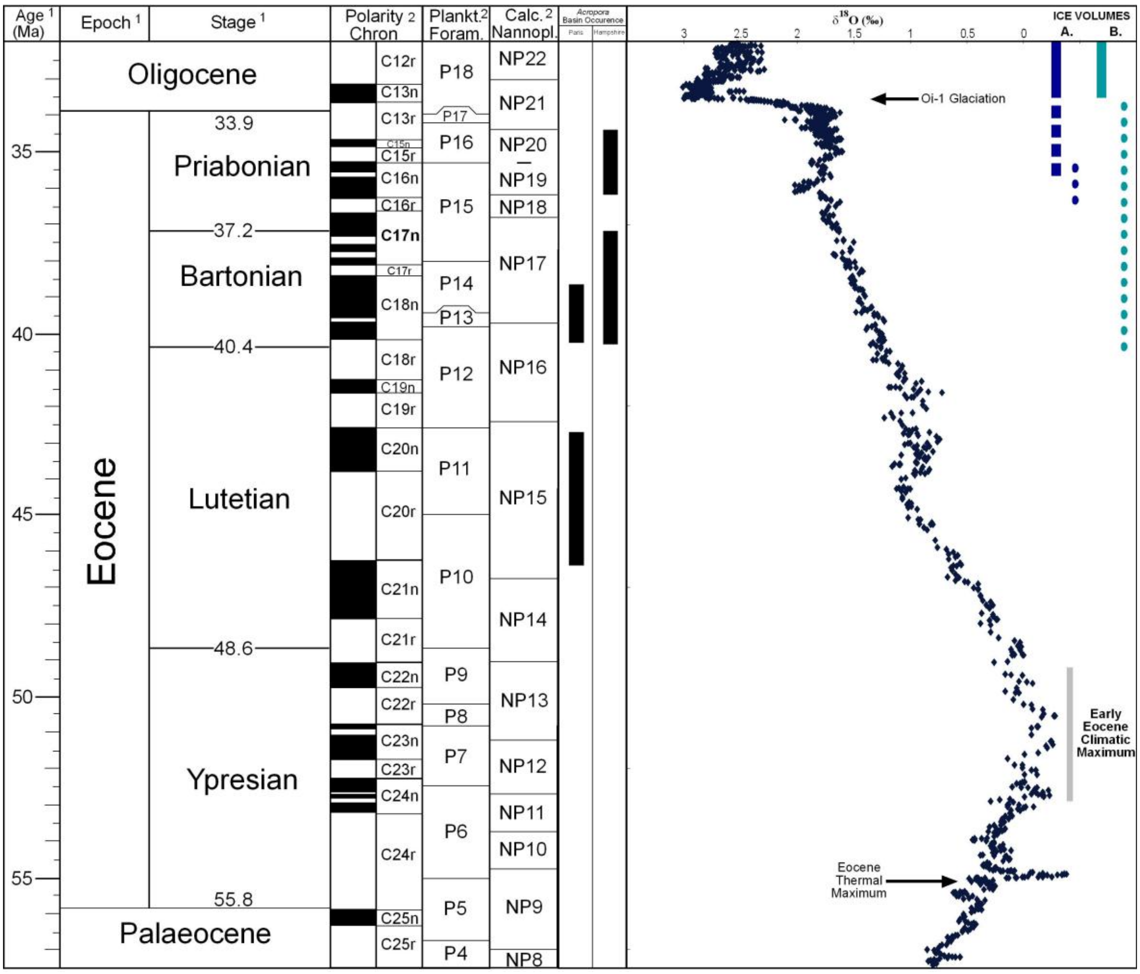


Figure 6.22. Summary time-scale from the late Paleocene to early Oligocene (1. Gradstein et al.*, 2004, Gradstein and Ogg, 2008, 2. Berggren* et al.*, 1995). Acropora occurrences and global deep-sea oxygen isotope records (data from Zachos* et al.*, 2001).*

In both basins of the Late Eocene there was a shift from marine and marginal marine to dominantly non-marine and coastal deposits. Regional tectonics including the uplift of the Weald-Artois anticline led to the isolation of these basins from the North Sea Basin. The Paris Basin became more isolated, leading to the onset of gypsum deposition, before the isolation of the Hampshire Basin and lacustrine conditions. The distribution of coral assemblages largely depends on; topography, hydrodynamics, light, temperature and, suspension load. Eocene tectonic activity persisted within both the Hampshire and Paris basins and effected the distribution of *Acropora* by creating shallow marine, sheltered areas as anticlinal islands were created. This increased availability of habitat, and substrate, was accompanied by varying sediment supply, affecting circulation patterns and varying nutrient supply.

No fragments of reef rock have been found in this study. This together with 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 energy hydraulic conditions would be needed to demolish evidence of this structure but to selectively preserve a limited number of pristine specimens. This is thought to be unlikely. The low to moderate coral diversity in both basins and the combination of zooxanthellate and azooxanthellate corals (Fig. 6.23), which in modern settings typifies marginal environments, and the lack of other reef-building biota, also supports the absence of any reef.

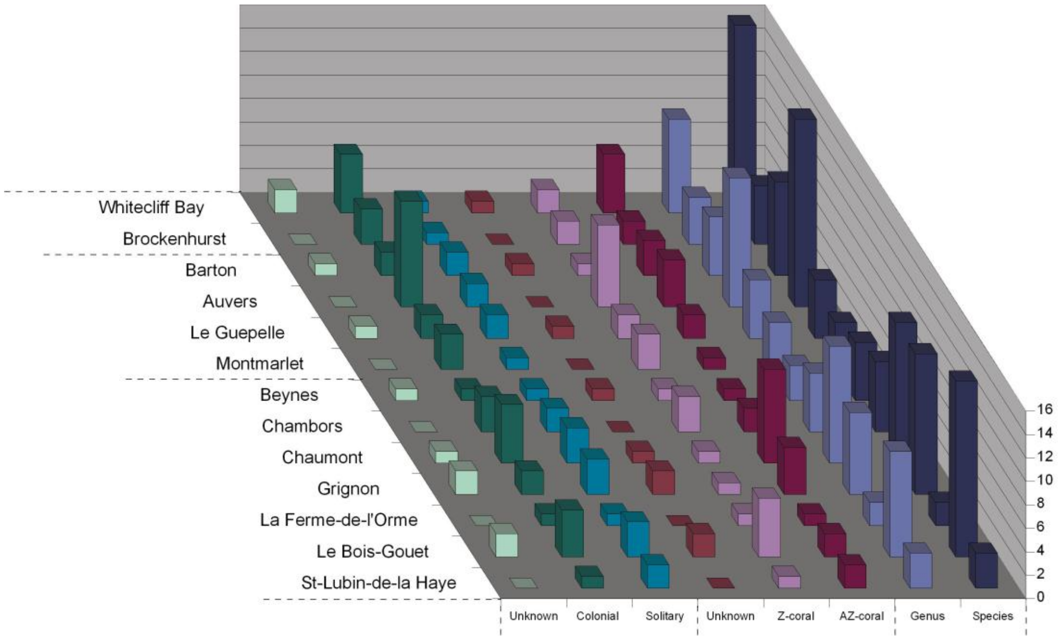


Figure 6.23. Summary of coral genera, species, symbiotic status and two morphologically based growth forms (solitary and colonial) from the Hampshire and Paris basins.

Other fauna, including molluscs, foraminifera, echinoids, sharks teeth, indicate marine conditions at least periodically, during the Eocene of these basins.

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 (Fig. 6.24).

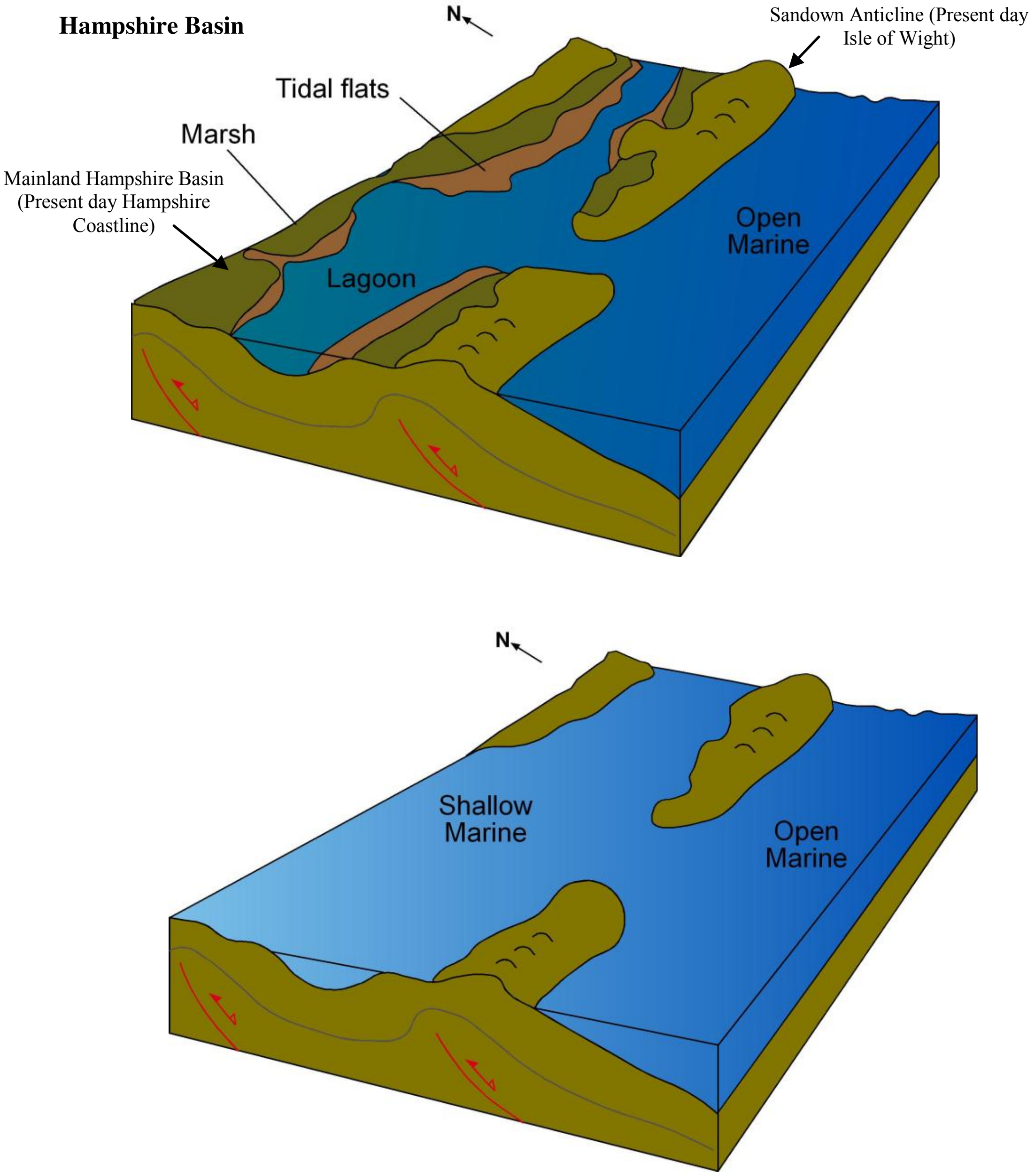


Figure 6.24. Summary cartoons of palaeoenvironmental setting of the Priabonian (Late Eocene) Hampshire Basin, a. deposition of the Colwell Bay Member, b. marine transgression of the Brockenhurst Bed (general setting adapted from Tucker, 2001, see Fig. 6.1 for general setting).

Corals in the Lutetian Paris Basin are found within predominantly carbonate-dominated beds and a mid-ramp environment is inferred (Fig. 6.25). In contrast, the Bartonian palaeoenvironment and palaeoecology of *Acropora*-bearing lithologies points to a high energy shoreface setting. The stratigraphy of the *Acropora*-bearing sections in both basins show alternating brackish and marine deposits, with marine incursions being short lived into largely non-marine environments.

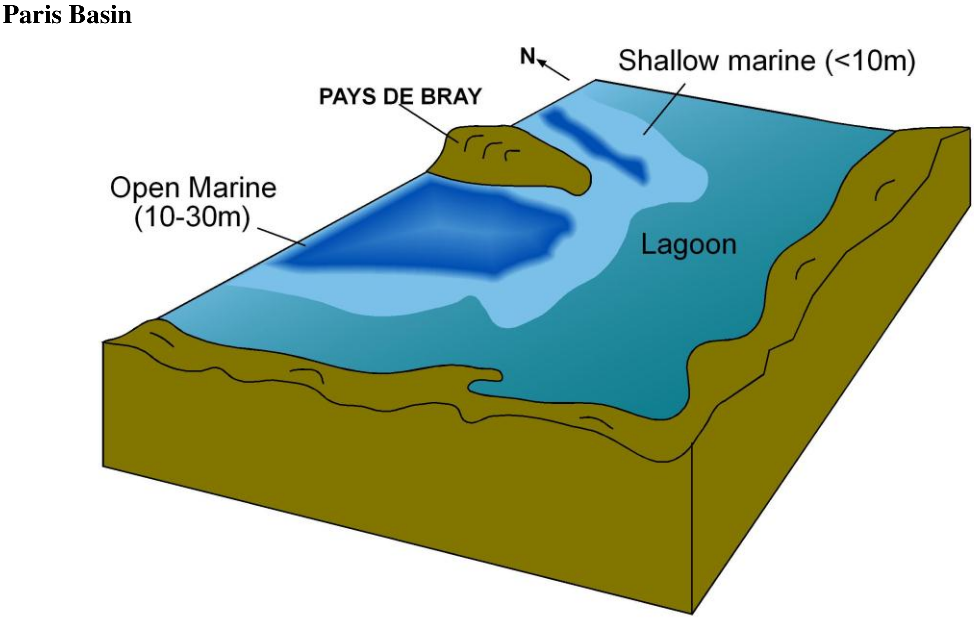


Figure 6.25. Summary cartoon of palaeoenvironmental setting of the Lutetian (Middle Eocene) Paris Basin.

Different colony morphologies tend to dominate in different environmental conditions (Geister, 1977; Done, 1983). Delicately branching and thin plate-like corals tend to be most common in low energy environments. Massive, encrusting, and robust branching corals tend to be more common in high-energy environments. Variations in colony morphology also influence a corals ability to harness available light, and effectively remove large amounts of sediment (see Chapter 2; Rosen, 1971). Platy or tabular corals can be more effective at collecting light while branching corals are more effective at removing sediment from their polyps. The ramose, branching habit of *Acropora* renders the skeleton subject to fragmentation, through bioerosion, hydraulic energy, and rolling and abrasion by transportation. However, the preservation of these fragments, up to 12cm 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 rapid burial near the life habit of the coral. Morphologically the sturdier growth forms come from the Hampshire Basin implying higher wave energy in this basin relative to the Paris Basin. Intrabasin morphological variation also shows temporal palaeoenvironmental variation with lower wave energy implied in the Hampshire Basin Bartonian relative to the Priabonian. These environments represent areas with calm, low hydrodynamic conditions and suggest that *Acropora*, which occurs today mainly in medium to high energy environments (McCall *et al*. 1994), has probably shifted its overall ecological adaption from low to higher energy environments through geological and evolutionary time.

The absence of reef rock as to whether this was a flourishing coral community or a disturbed/restricted state of development. More likely the corals occurred in thickets and possible more extensive coral carpets rather than in framework-related conditions. From the data in this thesis, the distribution of *Acropora* in the Hampshire and Paris basins during the Eocene was at, or very close to, it's northern limit. *Acropora* became extinct in these basins in the Late Eocene, existed for a geologically short period in each, and its northern limits subsequently retracted southwards. This also suggests that these basins were marginal settings (see Chapter 3). 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).

CHAPTER 7. ESTIMATES OF PALAEOTEMPERATURES IN NW EUROPEAN CENOZOIC BASINS FROM TAXONOMIC RICHNESS AND STABLE ISOTOPES

CONTENT

This chapter aims to overview the availability and suitability of the specimens used as part of this research to infer palaeoenvironmental information and from this, to make conclusions about the Eocene-Miocene palaeoenvironmental setting of Northwest Europe.

7.1 INTRODUCTION

This chapter combines a two fold methodology (Fig. 7.1). Firstly, a thorough assessment of the coral diversity of *Acropora*-bearing lithologies from the Eocene of the Hampshire and Paris basins, and of the Oligocene and Miocene of the Aquitaine Basin was conducted. This allowed an evaluation of zooxanthellate coral generic richness values from a selection of these localities as a proxy for relative palaeotemperatures by using the quantitative relationship between present-day coral taxonomic richness and prevailing sea-water temperature, underlined by the so-called "energy hypothesis" (*sensu* Rosen, 1999). Secondly, an assessment of the preservation and diagenesis of the coral and mollusc specimens allowed inferences to be made directly about the palaeoenvironmental setting. Additionally this assessment led to the identification of original skeletal carbonate, with original isotopic values, allowing palaeotemperatures to be established. Therefore by combining an assessment of preservation and diagenesis, and stable isotope work further inferences can be made about the palaeoenvironmental setting.

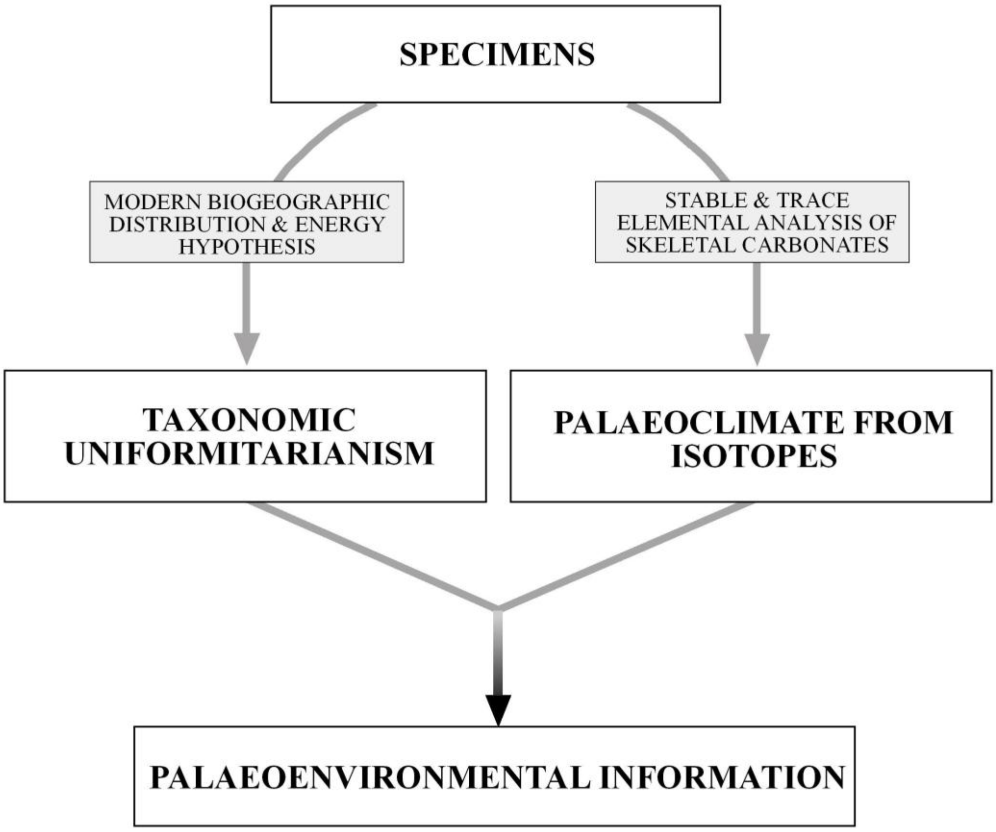


Figure 7.1. Summary of two-fold methodology used in this research

These two methods encompass two categories of information. Firstly, information based on taxonomic uniformitarianism which relates the environmental requirements of fossils to those of their taxonomically nearest living relatives. This includes the assumption that a genus, such as *Acropora,* that are zooxanthellate today, were also zooxanthellate in the past. From this, inferences can be made about the palaeoenvironmental and ecological restrictive factors. In the case of zooxanthellate corals the primary factor being water depth due to the presence of symbiotic algae, resultantly being restricted to the photic zone. A drawback of this method is that the ecological requirements of individuals may have evolved and changed.

The second category of information comes from isotopic indicators of environmental conditions, which are independent of taxonomic uniformitarianism. Keeping these two types of information separate allows authentication of information inferred from each.

This chapter aims to overview the availability and suitability of the specimens used as part of this research to infer palaeoenvironmental information and from this, to make conclusions about the Eocene-Miocene palaeoenvironmental setting of Northwest Europe.

7.2 PALAEOCLIMATE FROM CORALS

Scleractinian corals, and the reefs they form, are largely restricted to a latitudinal belt 30°N and 30°S. This pattern is related to decreasing temperatures with increasing latitude (Veron, 1995; Spalding *et al*., 2001). In addition to this a suite of limiting factors including salinity, sediments, nutrients and ocean circulation control the development of these shallow, marine ecosystems (see Chapter 2).

By using the quantitative relationship between present-day coral taxonomic richness and existing sea-water temperature, underlined by the so-called “energy hypothesis”, the zooxanthellate-coral generic richness values are used from a selection of 102 Oligocene–Miocene localities of the Hampshire, Paris and Aquitaine regions as a proxy for relative palaeotemperatures. In the Mediterranean region Chevalier (1962) was the first to use coral richness as a way to support cooler conditions during the Miocene. Rosen (1999) used the ‘energy hypothesis’ to provide a working model of the global relationship between taxonomic richness to prevailing temperatures, and to infer minimum palaeotemperatures for Mediterranean waters during the Miocene. Bosellini and Perrin (2008) have most recently used the ‘energy hypothesis’ to test zooxanthellate-coral generic richness values from a selection of 23 Eocene-Miocene localities of the Mediterranean region as a proxy for relative palaeotemperatures.

Corals are potentially a powerful retrospective tool for the reconstruction of long-term and seasonal variations of certain climate variables. For both palaeontologists and sedimentologists there is a need for precise palaeoclimatic information to model, interpret and understand past palaeoenvironments. Within these palaeoenvironments the primary representation of the state of the climate system is temperature. Temperature fundamentally determines the biogeographical range of an organism as most metabolic processes are temperature dependant. Thus climate determines the geographic range of species and plays a major role in determining the composition and diversity of biogeographical provinces. A suite of isotopic and elemental proxies, preserved in marine sediments, provides a long, continuous record of past climates, the most commonly produced geochemical records of these are the stable oxygen and carbon isotopic compositions of fossil carbonate material, particularly foraminiferids.

This source of quantitative analytical information, although often distorted and complicated, forms the basis of numerous efforts to precisely reconstruct climatic conditions through time. This independent approach overcomes past reliance on taxonomic uniformitarianism, the main problem, as outlined above, is that organisms may have evolved through time. Palaeotemperature research has remained at the forefront of geological research since the development of new techniques by the work of Harold Urey, in the 1950s. Urey first established a method for determining palaeotemperatures based on recorded temperature-dependant fractionation of oxygen isotopes by marine organisms in the present-day oceans. This was further elaborated by Epstein *et al*. (1951) who confirmed the basic relationship between temperature and relative ^{18}O abundance in recent marine shell material and produced an isotopic temperature equation and scale allowing ambient seawater temperature to be determined. Urey *et al*. (1951) then applied the method to fossil material from the Late Cretaceous of Europe and the south-eastern United States. This was followed by work by Shackleton *et al*. (1973) on forminifera improving the precision of the palaeotemperature scale. Continued interest in oxygen and carbon isotope palaeothermometry has lead to a plethora of reviews since its inception contributing to an understanding of the procedures, limitations and major features of Earths climatic history (e.g. Swart, 1983; McConnaughey, 1989; Zeebe and Wolf-Gladrow, 2001).

Interest in isotopic studies of corals was initially not pursued due to apparent disparities between the $\delta^{18}O$ values of coral skeletons and that of molluscs and other marine organisms. Lowenstam and Epstein (1954, 1957) declared corals unsuitable for isotopic palaeotemperature analysis due to the oxygen isotopic composition being invariably depleted relative to equilibrium (presently thought to result from their different biochemical mechanisms as well as the influence of symbiotic zooxanthellae). However, by the late 1960s interest reignited in obtaining climatic records from coral skeletons with further investigation into the 'centre of calcification', a term first coined by Ogilvie (1896), later termed under the broader heading the 'vital effect'. Weber and Woodhead (1972) showed that despite the offset in $^{18}O/^{16}O$ ratios in corals this was still a function of temperature and a simultaneous revolution in the use of trace elements and stable isotopes in corals led to the discovery of annual bands in corals. Swart (1983) further reviewed the phenomenon of growth banding, with alternating dense and less dense aragonite displaying an annual signal, and made a distinction in the signal from hermatypic (z-corals) and ahermatypic corals (az-corals). Recent research into isotopic features of corals (de Villiers *et al.*, 1995; Reynaud *et al.*, 2004) has led to the establishment of relationships between a series of proxy indicators and climate variables allowing past climate conditions to be estimated. Corals are potentially a powerful and high resolution tool for the reconstruction of long-term and seasonal variations of climate variables throughout the Cenozoic. The biogenic calcium carbonate skeletal minerals reflect both the composition and temperature within which an organism lived. Various elements incorporated from the seawater are taken up and transported by various mechanisms into the carbonate lattice of their skeletons (see McConnaughey, 1989). Several geochemical tracers in coral skeletons (Sr/Ca, Mg/Ca, U/Ca) have been proposed as proxies for sea surface temperature. Both Mg and Sr have long residence times in seawater and their ratios to Ca in coral skeletons have been shown to be temperature dependant (Broecker and Peng, 1982). As Sr content in corals is relatively high, the Sr/Ca ratios have been studied in greatest detail and used to reconstruct palaeotemperature (Beck *et al.*, 1992). Problems with this method relate to uncertainties regarding the age of corals and subsequent susceptibility to diagenetic alteration. However, notwithstanding these difficulties, the environmental information stored in coral skeletons can be a unique record of information which resolves to seasonal and interannual climate change. Exceptionally well preserved corals (*Porites*) from the Late Miocene of Crete (eastern Mediterranean, Greece) showed evidence of seasonal changes in sea surface temperatures and symbiotic autotrophy (Brachert *et al.*, 2006)

In the Hampshire and Paris basins, Murray and Wright (1974) first assessed Paleogene foraminifera and palaeoecology. In the Hampshire Basin, Purton and Brasier (1999) used high-resolution drilling techniques in *Nummulites*, to show that both *N. laevigatus* and coeval bivalve *Venericardia planicosta* from the Lutetian of Hampshire, United Kingdom (ca. 50–42.5 Ma), underwent strong, annual alternations in carbon and oxygen isotopes, possibly reflecting tolerance of broad environmental variation. Grimes *et al.* (2005) reported the first oxygen isotope–derived summer palaeotemperatures for continental freshwater in the Northern Hemisphere (Late Eocene-Early Oligocene, Hampshire Basin, Isle of Wight, UK) leading up to and across the Oi-1 glaciation event. These palaeotemperatures are derived from multiple palaeoproxies (rodent tooth enamel, gastropod shells, charophyte gyrogonites, and fish otoliths) and are independent of freshwater evaporation effects and changes in ice volume.

In the Paris Basin, Andreasson and Schmitz (1996) examined intra-annual temperature variations in the warm early Cenozoic, using stable oxygen and carbon isotopes along the transect of growth on excellently preserved specimens of the gastropod *Turritella imbricataria* and the bivalve *Venericardia imbricata* from sedimentary rocks of early Middle Eocene age (ca. 46 Ma). The oxygen isotope profiles indicate winter temperatures of about 14°C and summer temperatures of up to 28°C, i.e. seasonality indistinguishable from the present situation but an annual temperature some 10°C higher. Schmitz and Andreasson (2001) also detailed isotopic ($\delta^{18}O$, $\delta^{13}C$, $^{87}Sr/^{86}Sr$) analyses performed on aragonitic fresh-water, brackish-water, and marine gastropod shells of latest Paleocene–earliest Eocene age from north-western Europe to reconstruct the development of subtropical highs and Hadley cell circulation in the past.

7.3 THE 'ENERGY HYPOTHESIS' METHOD

It is widely accepted that coral species richness is limited by sea surface temperatures (Sanders, 1968; Stelhi and Wells, 1971; Veron, 1995) and that with increasing sea surface temperature results in increased coral richness.

Variance in species richness of terrestrial organisms has been largely related to levels of available energy (the species richness-energy hypothesis; Brown 1981; Wright 1983). In contrast, the global patterns of coral diversity have been hypothesised to depend mainly on disturbance and historical factors. Fraser and Currie (1996) suggested the best environmental predictors of diversity are mean annual ocean temperature and an estimate of regional coral biomass, which suggests that available energy limits regional generic richness.

Rosen (1999) deduced palaeotemperatures from richness values of a given coral fauna at a given places in the fossil record. Data presented tested the approach by using richness data from 15 Miocene localities of the Mediterranean area and showed that most coral reefs occur in this region during three major high sea-level phases, the Early (Aquitanian), Middle (Langhian-Serravalian) and Late Miocene (Tortonian-early Messinian).

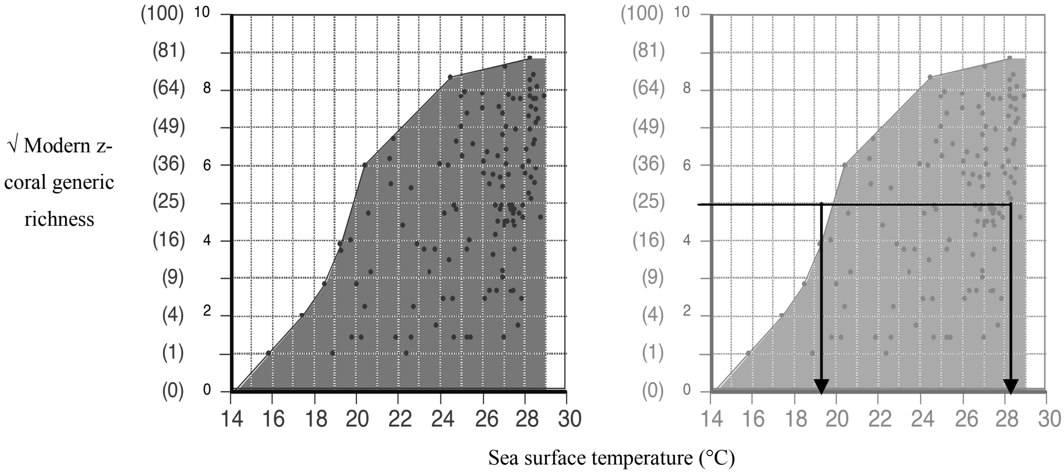


Figure 7.2 a. The variation in the square root of modern generic richness in 130 sites worldwide, expressed as a function of mean annual ocean surface temperature (°C) at each site. The original plot of Fraser and Currie (1996) has been modified by Rosen (1999), with the integration of the envelope curve of maximum richness values (from Rosen, 1999), b. maximum and minimum past sea surface temperatures from an example of palaeodiversity values of z-corals using the modern diversity-temperature curve.

For a detailed explanation of the method see Rosen (1999). Firstly the square root of z-coral richness is taken for each locality and the minimum possible temperature can be read using the envelope curve of maximum richness values (see Fig. 7.2)

7.3.1 Dataset

Here, palaeotemperatures are estimated using the ‘energy hypothesis’, derived from the richness values of z-corals from the Eocene of the Hampshire and Paris basins, and from the Miocene of the Aquitaine Basin.

Richness data was recorded as part of the *Acropora* database from a large literature search and studies of coral collections with a need for periodic taxonomic and stratigraphic review. Individual *Acropora* and non-*Acropora* bearing localities were listed for each stage as well as the three general regions of the Hampshire, Paris and Aquitaine basins.

In Table 7.1 the category of 'Genera (Z)' includes both, a) z-corals *sensu* Wilson and Rosen (1998: extant genera which are known to be zooxanthellate) and, b) z-like (extinct genera with features which resemble characters of living z-corals). As a comparison the total number of genera 'Genera (Z + AZ)', including az-coral, az-like corals (*sensu* Wilson and Rosen, 1998) and unknown corals, is provided.

Locality	Age	Genera (Z)	Genera (Z+AZ)	T (°C, Z)	Primary references
Paris region (France)	Lutetian	9	24	18.7	New, private and museum collections
Chambors, Paris (France)	Lutetian	3	5	17	Private and museum collections
Chaumont en Vexin, Paris (France)	Lutetian	1	12	15.8	Private and museum collections
Grignon, Paris (France)	Lutetian	3	8	17	New collections
Ferme de l'Orme, Paris (France)	Lutetian	1	2	15.8	Private and museum collections
Le Bois-Gouet, Paris (France)	Lutetian	6	9	18	Private and museum collections
Paris region (France)	Bartonian	9	17	18.7	New, private and museum collections
Auvers, Paris (France)	Bartonian	7	11	18.3	New collections
Le Guepelle, Paris (France)	Bartonian	3	5	17	Private and museum collections
Hampshire region (UK)	Bartonian	1	5	15.8	New collections
Barton, Hampshire (UK)	Bartonian	1	5	15.8	New collections
Hampshire region (UK)	Priabonian	3	9	17	New collections
Whitecliff Bay, Hampshire (UK)	Priabonian	2	4	16.5	New collections
Brockenhurst, Hampshire (UK)	Priabonian	3	8	17	Private and museum collections
Gass, Aquitaine (France)	Rupelian	11	13	18.90	Chevalier (1956)
Landes, Aquitaine (France)	Chattian	11	17	18.90	Chaix & Cahuzac (2001)
Aquitaine region (France)	Chattian	45	73	21.70	Chaix & Cahuzac (1993, 1996)
Aquitaine region (France)	Aquitanian	28	37	20.10	Chaix & Cahuzac (1993, 1996)
Gironde, Aquitaine (France)	Aquitanian	15	18	19.30	Chevalier (1962)
Aquitaine region (France)	Aquitanian-Burdigalian	16	18	19.40	Oosterban (1988)
Aquitaine region (France)	Burdigalian	33	45	20.30	Chaix & Cahuzac (1993, 1996)
Gironde, Aquitaine (France)	Burdigalian	22	24	19.75	Chevalier (1962)
Dax, Aquitaine (France)	Burdigalian	24	27	19.90	Chevalier (1962)

Table 7.1. List of Acropora-bearing localities and coral-bearing regions from the Lutetian-Bartonian Paris Basin, numbers of z and az genera and calculated palaeotemperature

7.3.2 Potential bias

There are many potential biases that interfere with the ‘energy hypothesis’ method. Estimates of z-coral richness are affected by potential biases which influence the stratigraphical range of any z-coral site, the collection of data, the taxonomic identification, and the attribution of the symbiotic status of any scleractinian genus (see Bosellini and Perrin, 2008, for details). A variety of examples of these biases are in the data presented here. Within the data, the stratigraphic resolution of localities is highly variable, and often affected by the allochthonous nature of coral components within a locality. The collection of data is influenced by the level, and amount, of investigation in an area, along with the motivation behind collecting material (see Chapter 4). Furthermore, the availability of material is intrinsically linked to the preservation and diagenesis of material (see section 7.4). The degree of skeletal preservation introduces a degree of taxonomic subjectivity. There are vast amounts of morphological variability leading to difficulties in identifying characters to make species- or even genus-level identifications. Additionally changing taxonomic protocol through time, such as that shown within the genus *Acropora*, can lead to misidentifications introducing bias. Finally, the attribution of a symbiotic status can be problematical with assumptions being made by comparing with living counterparts which belong to the same genus or family. This assumes that symbiotic status has remained stable through time and that it is strongly reliant on its taxonomic identification.

Additionally to these bias affecting estimates of the z-coral richness, various biases affect the relationship between z-coral richness and sea-surface temperature. Environmental factors can act on a local scale, including factors such as turbidity which can limit taxonomic richness (Acevedo *et al*. 1989). On a regional and local scale, historical biogeographic patterns can shape diversity patterns with tectonic variation influencing habitat availability (Wilson and Rosen, 1998).

7.3.4 Results

Coral diversity patterns

From the Middle Eocene-Middle Miocene Hampshire, Paris and Aquitaine basins 257 z-coral occurrences and 23 localities were recorded (Tab. 7.1). The total number of coral genera recorded from this period is 101, 3 of which have unknown symbiotic status. 11 genera are common to the Eocene, Oligocene and the Miocene (5 z-coral, 6 az-coral). 33 genera occur in the Miocene and Oligocene, 3 common to the Eocene and Oligocene, with no common genera between the Eocene and Miocene. 19 genera are exclusively known from Eocene localities, 27 from Oligocene localities and 8 occur only in the Miocene. The highest stage-level generic diversity for the whole region is recorded during the Chattian, and is followed by a marked decrease in the Aquitanian (Fig. 7.3).

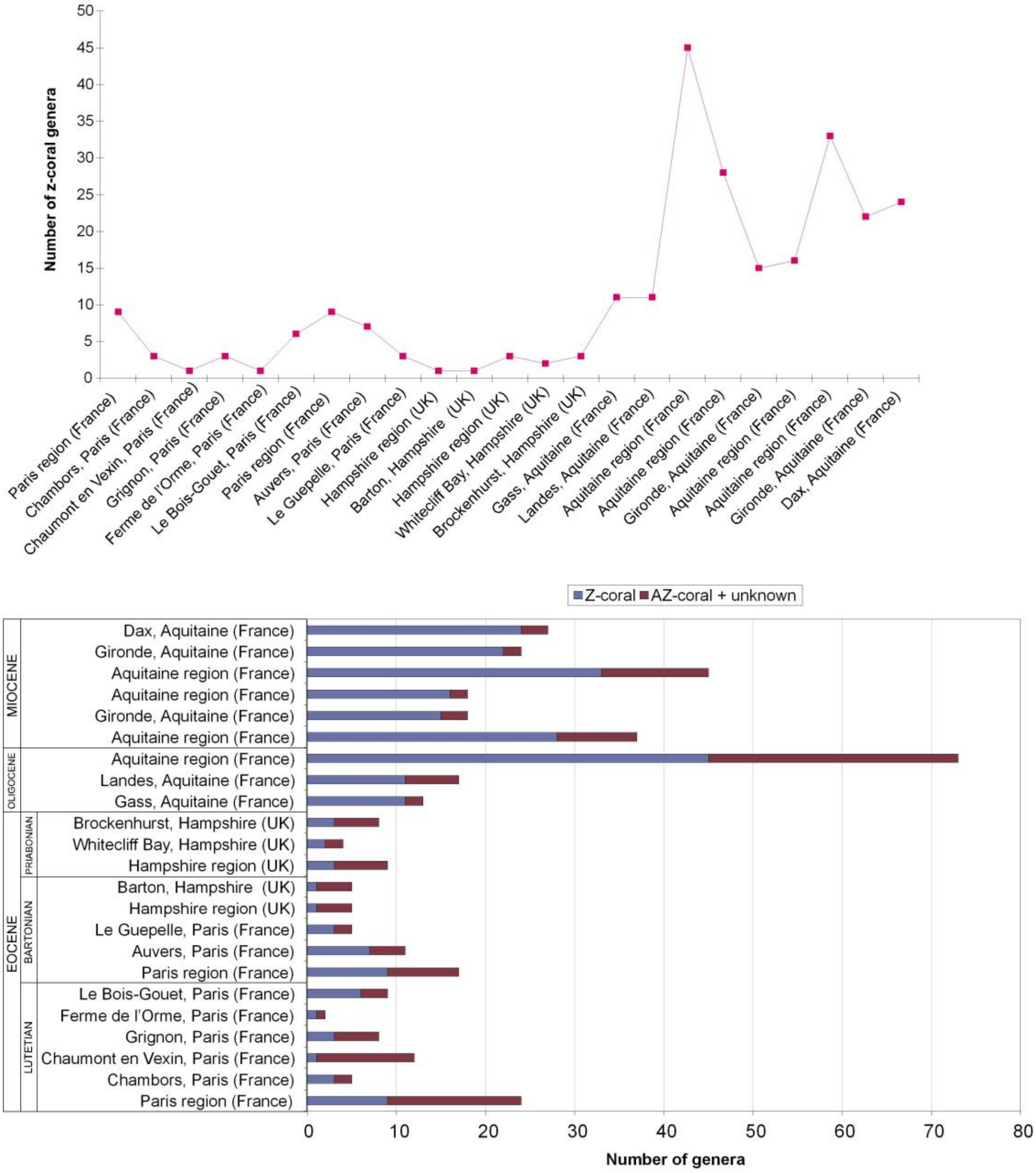


Figure 7.3a. Number of z-coral genera for each <u>*Acropora*</u>*-bearing locality in the Hampshire, Paris and Aquitaine basins, b. Occurrences of z-, az- and unknown coral genera plotted stratigraphically.*

Overall the generic richness is higher in the Paris region than in the Hampshire region. Comparatively, the Hampshire and Paris regions both have lower generic diversity than in the Aquitaine region. The Aquitaine region is characterized by relatively high values of generic richness. Within this region there is a decrease from the Oligocene into the early Miocene. Undoubtedly, taxonomic biases are acting particularly in the Aquitaine region where anomalous values in generic richness are certainly related to excessive taxonomic splitting (Bosellini and Perrin, 2008).

Inferred palaeotemperatures

From the coral diversity patterns inferred temperatures have been calculated (Tab. 7.1). Figure 4 shows the range of palaeotemperatures inferred from the number of z-coral genera at each locality by using the energy hypothesis of Fraser and Currie (1996) and Rosen (1999).

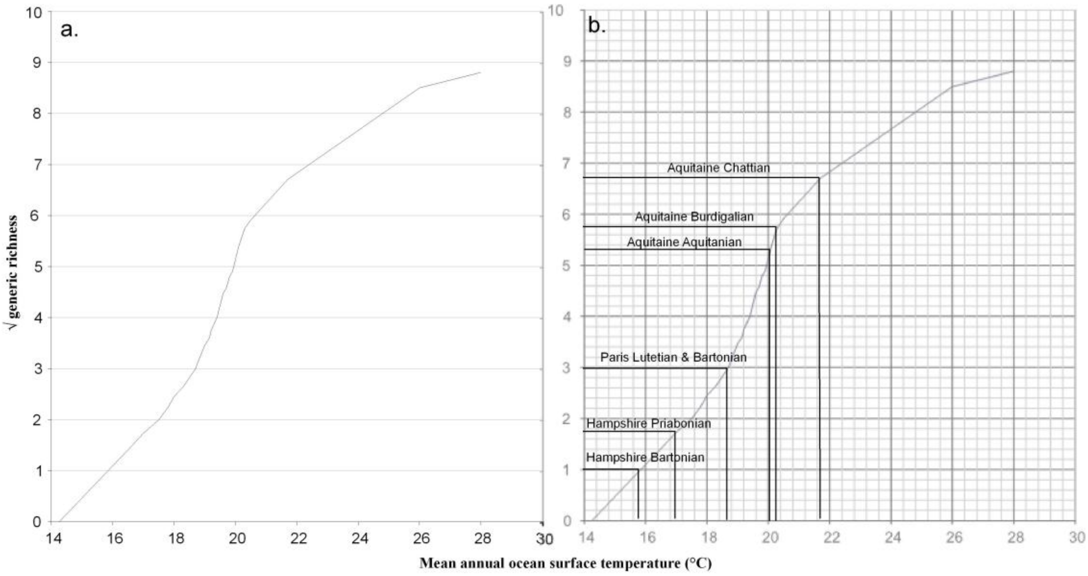


Figure 7.4. Palaeotemperatures inferred from the number of z-coral genera of all localities, a. curve of maximum richness values (from Rosen, 1999), b. minimum past sea surface temperatures from palaeodiversity values of z-corals using the modern diversity-temperature curve.

Inferred minimum sea surface palaeotemperatures of all localities range from a maximum of 21.7°C to a minimum of 15.8°C (Tab. 7.2).

Basin*	Age	Inferred Temperatures (°C)		Mean	Standard Deviation
		MAXIMUM	MINIMUM		
All localities	Eocene-Miocene	21.7	15.8	18.12	1.69
Hampshire	Eocene	17.0	15.8	16.43	0.60
Paris	Eocene	18.7	15.8	16.99	0.96
Aquitaine	Oligocene	18.9	18.9	18.90	0.00
Aquitaine	Miocene	19.9	19.3	19.65	0.31

Table 7.2. Inferred maximum and minimum palaeotemperatures for the Eocene-Miocene, Hampshire, Paris and Aquitaine basins.

Figure 7.5 shows the distribution of the number of z-coral genera against palaeolatitude. The general relationship shows the number of z-coral genera increases as the palaeolatitude decreases. The equivalent minimum past sea surface temperatures from the palaeodiversity values of z-corals using the modern diversity-temperature curve show an inverse relationship between palaeolatitude and inferred palaeotemperature. In summary, the fossil record shows a relationship with sea-surface temperature similar to that of their modern equivalents with a distinct attenuation of taxonomic richness with increasing latitude and decreasing temperature.

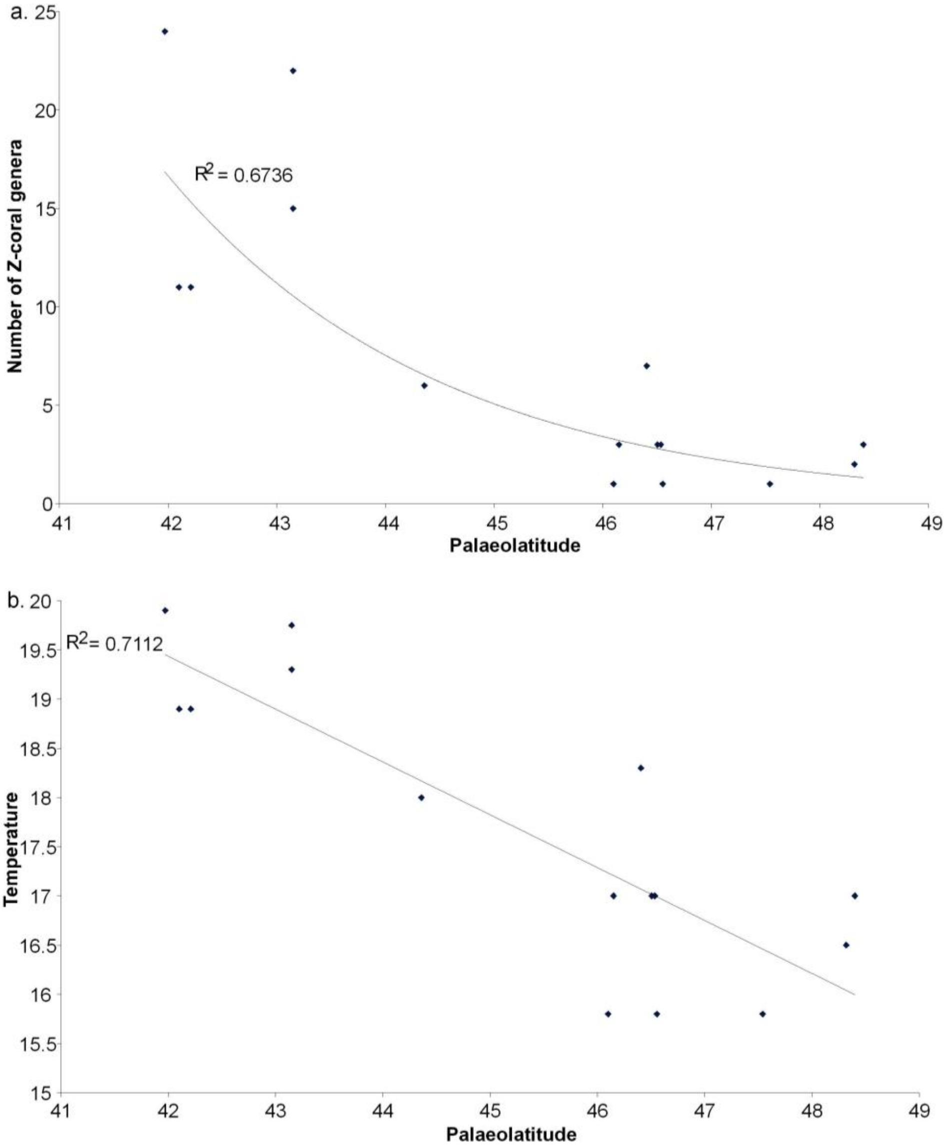


Figure 7.5a. Palaeolatitudinal distribution of z-corals from all basins against coral richness, b. palaeolatitudinal distribution of all corals against palaeotemperature.

Palaeotemperatures inferred from generic richness at each locality probably reflect the gradual adaptation of the Mediterranean z-coral fauna to a larger range of sea-surface temperatures as the regional cooling was progressively occurring (shown previously by Bosellini and Perrin, 2008). Overall, the relatively low temperatures estimated for these localities, particularly the Eocene of the Paris and Hampshire basins, show values below the common threshold of 18°C annual average for coral reef growth. However, zooxanthellate corals can tolerate temperatures below 14°C and although rare, these records are taxonomically and geographically widespread (Veron, 1995; Wood, 1999). As we are dealing here with occurrence of z-corals and not with coral reefs, these values are consistent with present-day z-corals living for example around Japan where 22.5% of all species tolerate a minimum SST of 10.4°C, 27% tolerate 13.2°C and 48% tolerate 14.1°C (Veron and Minchin, 1992).

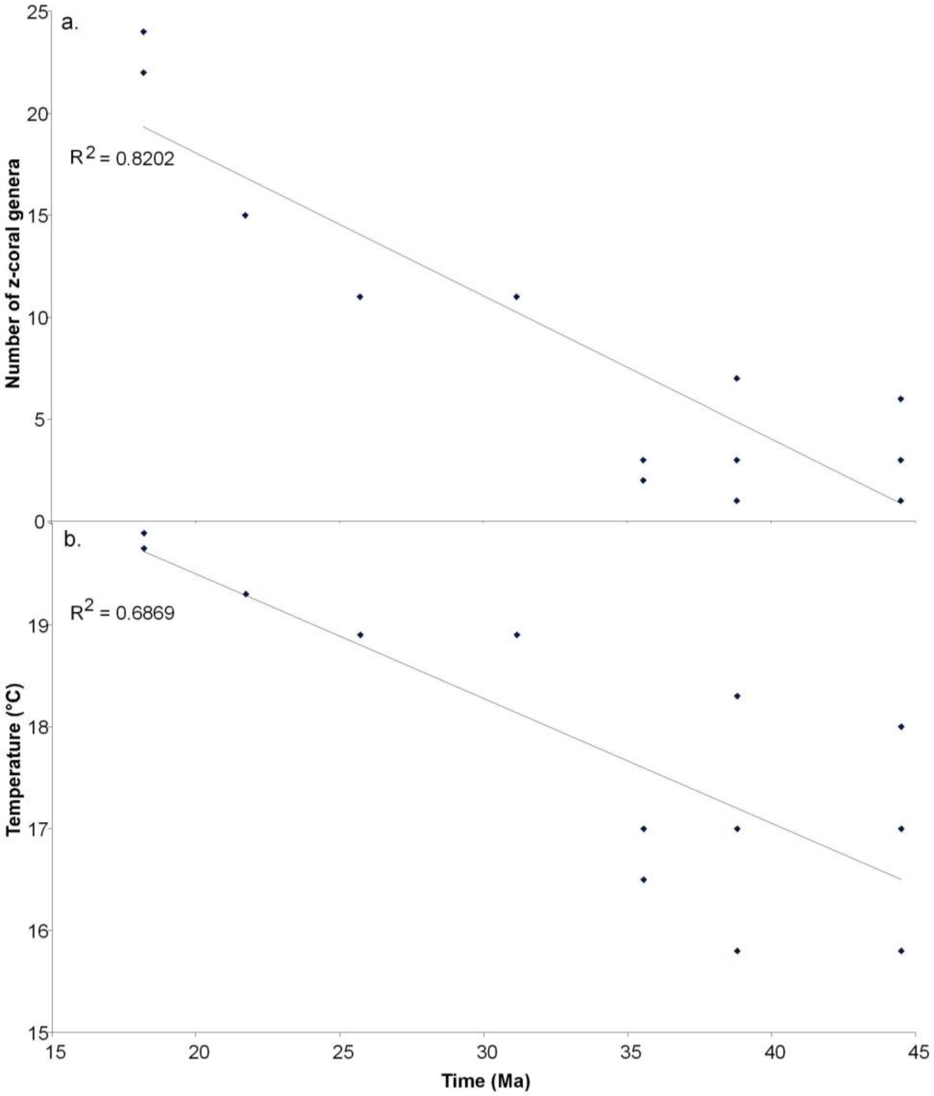


Figure 7.6. Changes in the number of z-corals and inferred temperature with time

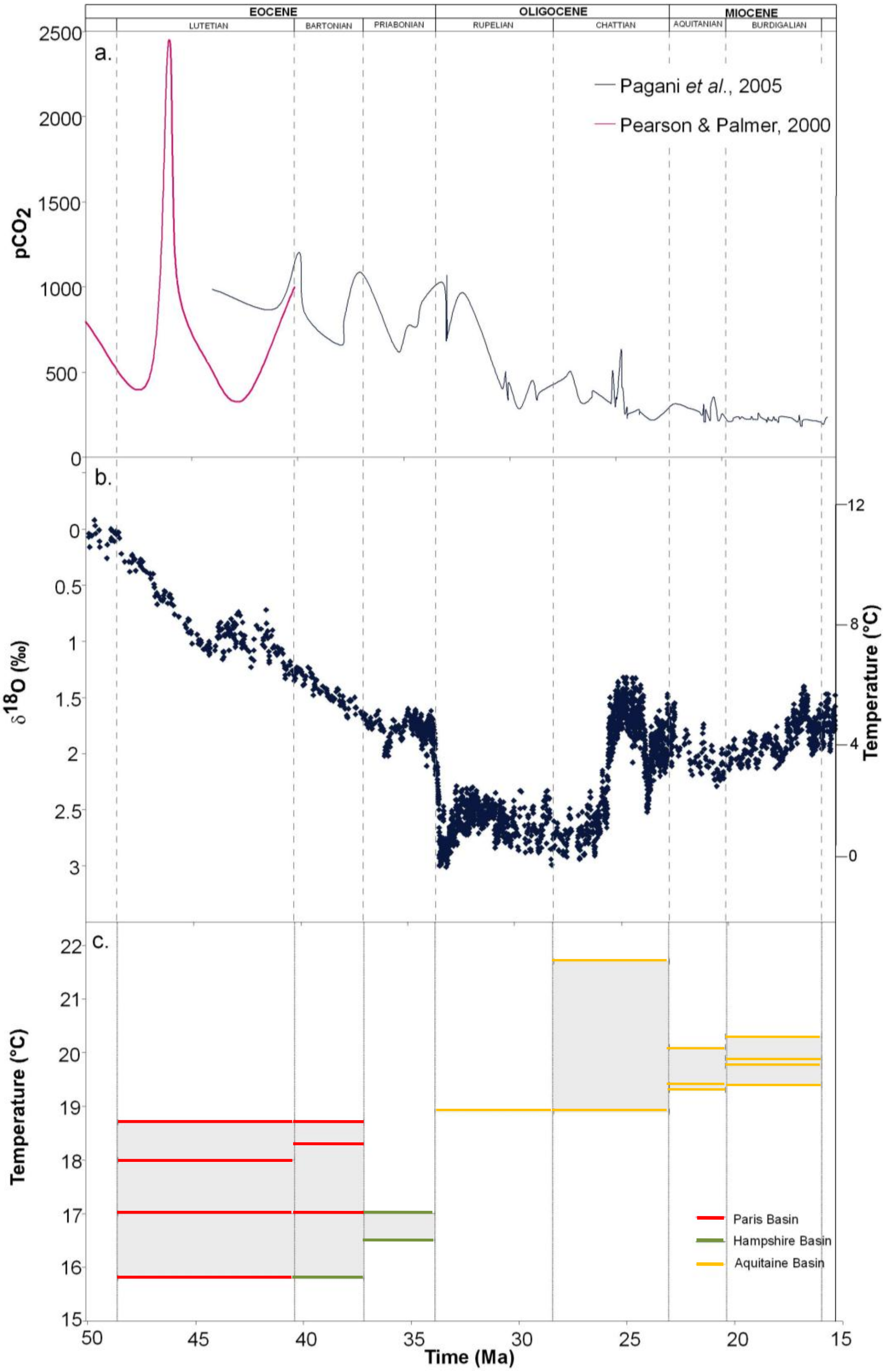


Figure 7.7. a. Reconstructed atmospheric carbon dioxide concentrations (data from Pearson and Palmer, 2000; Pagani et al., *2005). Time-scale of Gradstein and Ogg (2009). b. Global deep-sea oxygen record based on data compiled from more than 40 DSDP and ODP sites (from Zachos et al., 2001, modified). c. Palaeotemperatures inferred from generic richness at each locality.*

When compared with the global Cenozoic setting the diversity patterns appear to be strongly controlled by climate variability and changes in sea-surface water temperature, along with historical biogeography both at global and regional scales (Fig. 7.7). The global climatic deterioration (Fig. 7.7b) and associated sea level variation resulted in the latitudinal restriction of the genus. Associated with this the minimum inferred temperatures for the genus increased through time as *Acropora* was lost from the Hampshire and Paris basins (palaeolatitude ~49°N) to the Aquitaine Basin (palaeolatitude ~43°N). Cahuzac and Chaix (1996) previously described the high coral diversity of the Early Miocene Mediterranean reefs seen here in the Aquitaine Basin. By the Late Miocene, Messinian, *Porites* and *Tarbellastraea* were dominating (Pomar *et al*., 1996). This work corroborates the range of palaeotemperature estimates of Bossellini and Perin (2008) from Oligocene–Miocene localities of the Mediterranean region, expanding it into the non-reefal Eocene deposits of the NW European region.

7.3.5 Discussion

The ‘energy hypothesis’ here has been used to derive palaeotemperatures from richness values of z-corals in the Hampshire, Paris and Aquitaine basins. Derived temperatures show a minimum estimate of 15.8°C which is consistent with temperatures associated with modern, high latitude non-reefal coral assemblages. Biases acting on these estimates may have resulted in underestimations and overestimates particularly due to the allocthonous nature of coral components within a locality, the level and amount of investigation in an area, along with the motivation behind collecting material. These often being the availability of material, intrinsically linked to the preservation and diagenesis of the fossil material. Equally, overestimates may have been created by taxonomic over splitting leading to a misjudgement of richness values (i.e. the Aquitaine Basin).

The Cenozoic is characterised climatically by a general cooling trend, punctuated by brief, and often dramatic, periods of warming (Fig. 7.7). One of these is the Eocene when *Acropora* is found at its most northerly limit in the Hampshire and Paris basins. Many of the *Acropora*-bearing lithologies of both basins have comparatively low z-coral richness values, hence low derived temperatures, with a large contribution of az-corals. Palaeogeographic restriction of these latitudinally northerly basins led to the loss of z- coral communities from these areas and the diversification of these communities allowed them to thrive and adapt to a wider temperature range, being found in the Aquitaine Basin.

This method, in collaboration with isotopic data, provides a powerful tool to estimate and quantify temperatures from the Cenozoic of this region.

7.4 STABLE ISOTOPES

7.4.1 Introduction

This section introduces the research methodology and main results involved in acquiring palaeoenvironmental information directly from fossil coral, and associated carbonate material, following selection of suitable specimens after taphonomic and geochemical analysis. The methodology is presented below in two sections. Firstly, a variety of quantitative and qualitative techniques (thin section, XRD, cathodoluminescence and SEM) allowed an assessment of preservation and diagenesis, which can independently impart information about palaeoenvironmental setting. Secondly, selected material can be used in combination with stable isotope analysis, allowing further quantitative palaeoenvironmental information to be attained.

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 and thin section microscopy, x-ray diffraction, cathodoluminescence, scanning electron microscopy (SEM) and stable C and O isotope, and trace element analysis), allowed an assessment of preservation and diagenesis, which independently aided the palaeoenvironmental interpretation. Fossil aragonitic corals, and molluscs, 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 and stable isotopes of the sample leading to erroneous estimates of past climate. Petrographic and XRD enabled selection of pristine unaltered skeletal aragonite for stable isotope work.

The localities in the Hampshire and Paris basins represent the most northerly latitudinal extent (~48ºN) of *Acropora* in its entire history. These high latitudinal occurrences coincide with a period of global warming in the Middle Eocene (Zachos *et al*., 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). The basins existed as two interconnected, shallow-marine, paralic embayments, connected to the Atlantic and with intermittent connections to the North Sea. Cenozoic tectonic activity within the two basins included monoclinal 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.

7.4.2 Materials and Methods

Stable isotope and trace element profiles of corals, marine bivalves and gastropods have been widely used for palaeonvironmental studies as reviewed above (section 7.2). Previously data from oxygen and carbon isotope analyses of *Acropora* specimens from the pilot study of White (2006) were re-corrected and newly calibrated here and compared with other corals and molluscs from *Acropora*-bearing lithologies of the Paris and Hampshire basins with additional elemental/Ca analyses conducted here. The techniques outlined above were used on corals (*Lobopsammia, Goniopora, Trochoseris*), gastropods (*Turritella imbricataria*) and bivalves (*Venericardia imbricata, Cubitostrea plicata* and *Ostrea velata*) from the Bartonian and Priabonian (Late Eocene), Hampshire Basin, and Lutetian and Bartonian (Middle Eocene), Paris Basin (Tab. 7.3).

Additionally a single, modern specimen of *Acropora abrotanoides* collected from the Chesterfield Atoll, Queensland, Australia was studied.

Specimen	Identification on NHM label	New Identification (see Chapter 4)	Location on NHM label	Country	Age on NHM label
AZ2902	*Acropora sp*.	*Acropora wilsonae* (Wallace)	Auvers (Oise)	France	Middle Eocene, Late Lutetian, Sables d'Auvers
AZ2903	*Acropora sp*.	*Acropora wilsonae* (Wallace)	Auvers (Oise)	France	Middle Eocene, Late Lutetian, Sables d'Auvers
R.40833	*Acropora solanderi* (Defrance)	*Acropora wilsonae* (Wallace)	Auvers	France	Eocene, Bartonian, Sables Moyen
46824a	*Madrepora solanderi* (Defrance)	*Acropora wilsonae* (Wallace)	Auvers	France	Eocene
46824b	*Madrepora solanderi* (Defrance)	*Acropora wilsonae* (Wallace)	Auvers	France	Eocene
49583	*Madrepora sp*.	*Acropora roemeri* (Duncan)	Brockenhurst, Hampshire	England	Eocene, Middle Headon Beds
50236c	*Madrepora solanderi* (Defrance)	*Acropora alvarezi* (Wallace)	Auvers	France	Eocene, Jarisien B2
50236d	*Madrepora solanderi* (Defrance)	*Acropora wilsonae* (Wallace)	Auvers	France	Eocene, Jarisien B2
R.52048	*Acropora sp*.	*Acropora proteacea* (Wallace)	Chambors	France	Eocene, Upper Calcaire Grossier
R.52050	*Acropora sp*.	*Acropora proteacea* (Wallace)	Chambors	France	Eocene, Upper Calcaire Grossier
55687a	*Acropora solanderi* (Defrance)	*Acropora alvarezi* (Wallace)	Auvers	France	Middle Eocene
50596	*Lobopsammia cariosa*	*Lobopsammia cariosa* (Goldfuss)	Auvers	France	Mid Eocene
AZ2901	*Lobopsammia cariosa*	*Lobopsammia cariosa* (Goldfuss)	Auvers (Oise)	France	Middle Eocene, Late Lutetian, Sables d'Auvers
R.14518	*Lobopsammia sp*.	*Lobopsammia cariosa* (Goldfuss)	Brockenhurst, Hampshire	England	Eocene, Headon Beds
R.40672	*Lobopsammia cariosa* (Goldfuss)	*Lobopsammia cariosa* (Goldfuss)	Whitecliff Bay, Isle of Wight	England	Eocene, Brockenhurst Bed
R.52055	*Lobopsammia cariosa* (Goldfuss, 1826)	*Lobopsammia cariosa* (Goldfuss)	Chambors	France	Eocene, Upper Calcaire Grossier
R.52061	*Lobopsammia cariosa* (Goldfuss, 1826)	*Lobopsammia cariosa* (Goldfuss)	Chambors	France	Eocene, Upper Calcaire Grossier
55685b	*Lobopsammia cariosa*	*Lobopsammia cariosa* (Goldfuss)	Auvers	France	Mid Eocene
FWP1018*	-	*Trochoseris* (Milne-Edwards &Haime)	Auvers	France	Eocene, Bartonian, Sables Moyen
FWP1019*	-	*Goniopora* (Blainville)	Auvers	France	Eocene, Bartonian, Sables Moyen
T1*	-	*Turritella imbricataria* (Lamarck)	Fercourt	France	Eocene, Upper Calcaire Grossier
V1*	-	*Venericardia imbricate* (Lamarck)	Fleury La Riviere	France	Eocene, Upper Calcaire Grossier
C1*	-	*Cubitostrea plicata* (Solander)	Whitecliff Bay, Isle of Wight	England	Eocene, Brockenhurst Bed
O1*	-	*Ostrea velata* (Linnaeus)	Whitecliff Bay, Isle of Wight	England	Eocene, Brockenhurst Bed

Table 7.3. Details of specimens used for geochemical analysis and comparison during this research (Collected during fieldwork)*

Eocene Corals, England and Paris

One hundred and eight fossil *Acropora* fragments were studied for this thesis (Chapter 4), of these specimens eleven were selected for geochemical analysis (Natural History Museum, London (NHM) AZ2902, AZ2903, R40833, 46824a, 46824b, 49583, 50236c, 50236d, R52048, R52050, 55687a) in White (2006). Here an additional seven of the genus *Lobopsammia* (NHM 50596, AZ2901, R14818, R40672, R52055, R52061, 55685b) and a single *Goniopora* (FWP1018) and *Trochoseris* (FWP1019) specimen were selected from *Acropora*-bearing lithologies (Tab. 7.3). Five of the *Acropora* specimens were labelled as *Madrepora*, the generic synonym extensively used by nineteenth century authors (e.g. 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 *Lobopsammia* specimens were identified as the fossil species *Lobopsammia cariosa* (Goldfuss), with two identified as non-specific *Lobopsammia*. All *Acropora* specimens were re-identified for this study on the basis of the taxonomic review of fossil *Acropora* (Chapter 4). From the Hampshire Basin localities three species were identified (*Acropora anglica* (Duncan), *A. bartonensis* (Wallace), *A. roemeri* (Duncan)) and from the Paris Basin six species were identified (*Acropora alverezi* (Wallace), *A. deformis* (Michelin), *A. ornata* (Defrance), *A. proteacea* (Wallace), *A. solanderi* (Defrance), *A. wilsonae* (Wallace)). The two other coral specimens (FWP1018, FWP1019) were collected and identified to genus-level during fieldwork.

Specimens came from six localities identified by Wallace and Rosen (2006): 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). Pristine coral and molluscan specimens were identified for geochemical analysis from three 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 7.4.

Locality	Palaeolatitude[1]	Age (Ma)[2]	Stratigraphic age[2]	Calcareous Nannoplankton Zone[2]	Lithostratigraphy[3]	Position within stratigraphy[3,4]	Lithology[4,5]
Brockenhurst, Hampshire, England	48.4ºN	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	48.3ºN	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	47.5ºN	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	46.9ºN	43.4-40.4	Bartonian, Late Eocene	NP 16	Sables d'Auvers	Base of the Sables Moyen, Auversian	Sands of variable character
Chambors, France	46.5ºN	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	46.1ºN	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
Fercourt, France	46.8ºN	47.3-43.4	Lutetian, Middle Eocene	NP 15	Calcaire Grossier (Upper)	Upper Middle to Upper Lutetian deposits, Abrard Zone upper Zone III to lower Zone IV	Fine sands
Fleury La Riviere, France	46.4ºN	47.3-43.4	Lutetian, Middle Eocene	NP 15	Calcaire Grossier (Upper)	Upper Middle to Upper Lutetian deposits, Abrard Zone IVa	Fine sands

Table 7.4. Summary of stratigraphic and geographic setting of specimens from the Eocene, Hampshire and Paris basins.

Priabonian Molluscs, England

One specimen of *Cubitostrea plicata* (C1) and one of *Ostrea velata* (O1) were chosen for isotopic analyses. The specimens were collected during fieldwork as part of this thesis. Geographically, C1 and O1 are from Whitecliff Bay, Isle of Wight (50:40:20N, 1:06:17W), Hampshire Basin. Specimens are stratigraphically from the Brockenhurst Bed, Colwell Bay Member, Headon Hill Formation (Insole and Daley, 1985), and global calcareous nannoplankton zone NP19-20 (Martini, 1970, and confirmed by the presence of *Discoaster saipanensis* and *Ismolithus recurvus*).

The state of preservation of the specimens was confirmed by thin section and scanning electron microscope studies, and X-ray diffraction analysis. The shells were cleaned ultrasonically in distilled water to remove coating and infilling sediment, and adhered $CaCO_3$.

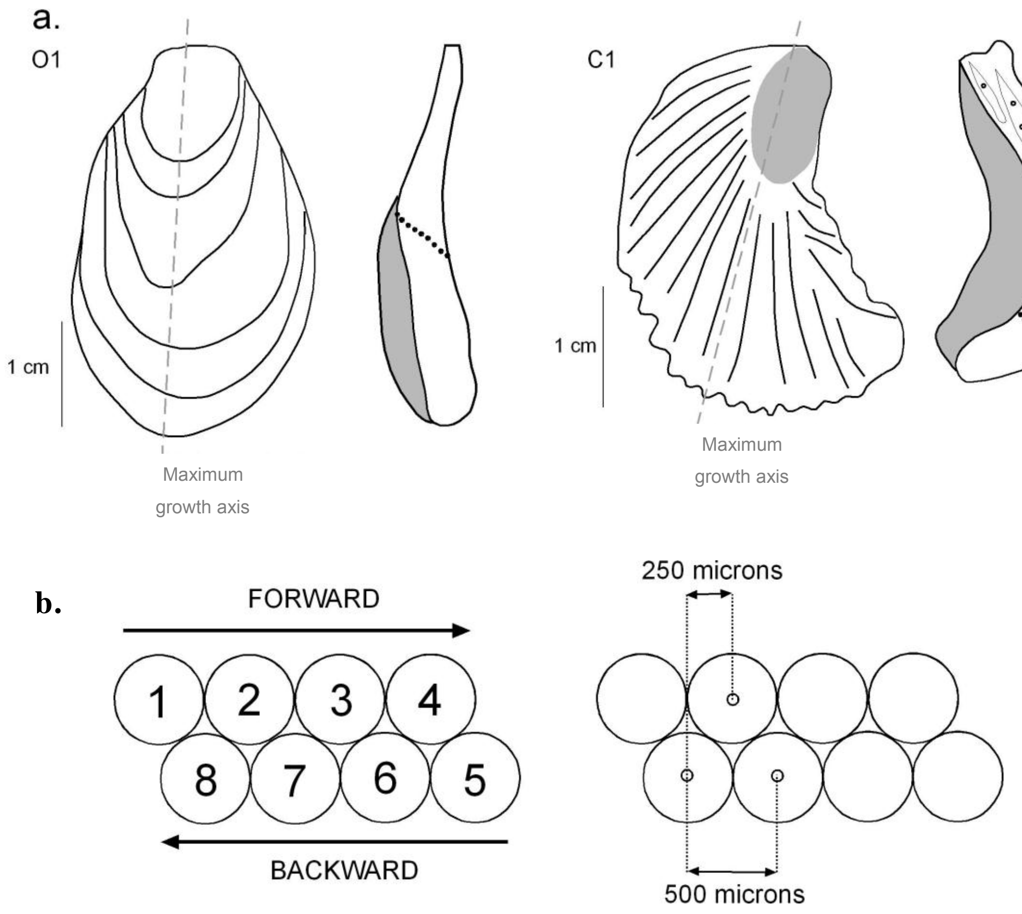


Figure 7.8 a. Sampling strategy of O1 and C1 showing pathway of laser runs, b. forward and reverse laser runs

Lutetian Molluscs, France

One specimen of *Turritella imbricataria* (T1) and one of *Venericardia imbricata* (V1) were chosen for isotopic analyses. The specimens were collected during fieldwork as part of this thesis. Geographically T1 is from Fercourt (49:18:32N, 2:14:38E) and V1 is from Fleury La Riviere (49:05:53N, 3:53:01E), Paris Basin. Specimens are stratigraphically from regional upper Zone III to lower Zone IV (Abrard, 1925), and global calcareous nannoplankton zone NP15 (Aubry, 1986).

The state of preservation of the specimens was confirmed by thin section and scanning electron microscope studies, and X-ray diffraction analysis. The shells were cleaned ultrasonically in distilled water to remove coating and infilling sediment, and adhered $CaCO_3$. Samples of 35 to 55 μg were collected using a 1.0mm drill bit. For both specimens, samples were collected along the growth transect.

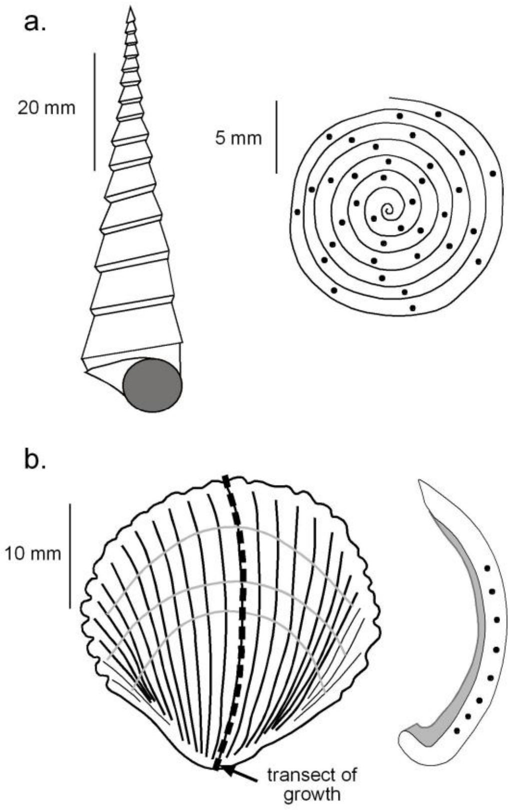


Figure 7.9. Sampling strategy of: a. T1 as shown looking down from the apex and, b. V1 section along maximum growth transect. Dots show sampling locations on shell.

7.4.3 Specimen selection and handling

For specimen curation, selection, handling and databasing see Appendix 10. All samples were separated from the host matrix and washed in an ultrasonic bath containing distilled water before being air-dried and examined under a binocular microscope to ensure no host matrix remained. Specimens were selected from the MTQ database as the most appropriate modern analogue to the fossil material. All specimens were cut along the maximum growth axis, through the axial corallite.

7.4.5 Assessment of Preservation and Diagenesis

Palaeoenvironmental interpretations can be made from two aspects of the direct study of the coral specimens. Firstly, taphonomic information can be gained from the state of preservation of the specimens and secondly through palaeotemperature estimates based on oxygen/carbon isotope studies of the fossil coral material. Fossil corals often undergo post-depositional diagenesis during which secondary minerals and/or cements are deposited. The inclusion of these in any palaeoclimatic analysis may significantly affect the bulk coral trace element geochemistry of the sample leading to erroneous estimates of past climate. Therefore, through petrographic and analytical analysis of the fossil samples, it is essential to assess the levels of preservation and diagenesis before any palaeoclimatic analysis can be undertaken. Further details of these methods are given in Appendix 10 and are summarised here:

- **Hand specimen and thin sections**-the fossils were examined, using a binocular microscope with an eyepiece graticule, to identify the presence of diagnostic coral and in particular *Acropora* features (see Wallace, 1999; Wolstenholme *et al.,* 2003). An assessment of the fossils preservation was also made looking for pristine micro-morphological features and evidence of diagenetic overgrowths and recrystallisations. Thin sections exposed the main morphological features, allowed an assessment of preservation and exposed the area on the opposite half of the specimen needed for geochemical analysis. Petrological microscope work and photomicrography were combined to identify and record features of the specimens.
- **Scanning Electron Microscopy (SEM)-**the LEO 1455VP Scanning Electron Microscope, Natural History Museum, London, was used to produce high resolution images in low vacuum mode (15 Pa). Examples of morphological characters were photographed of uncoated modern *Acropora* samples.
- **EDX**-EDX across the surface was undertaken using VP-SEM for non-destructive qualitative X-ray analysis of uncoated specimens in low vacuum mode.

- **Cathodoluminescence (CL)-**a CITL CCL 8200 MkIV cold cathode chamber and control unit mounted on a Leica DM LM optical microscope, Natural History Museum, London, was used to identify geochemical and diagenetic variations of coral specimens.
- **X-ray powder diffraction (XRD)-**performed using a Philips Analytical X-Ray BV PW 3710 machine, with a copper anode. The samples were scanned from 25° to 37° 2θ in order to cover the main $CaCO_3$ minerals peak intensities of aragonite and calcite. The main peaks were identified and the angle (2θ) of each noted (Fig. 7.10a).

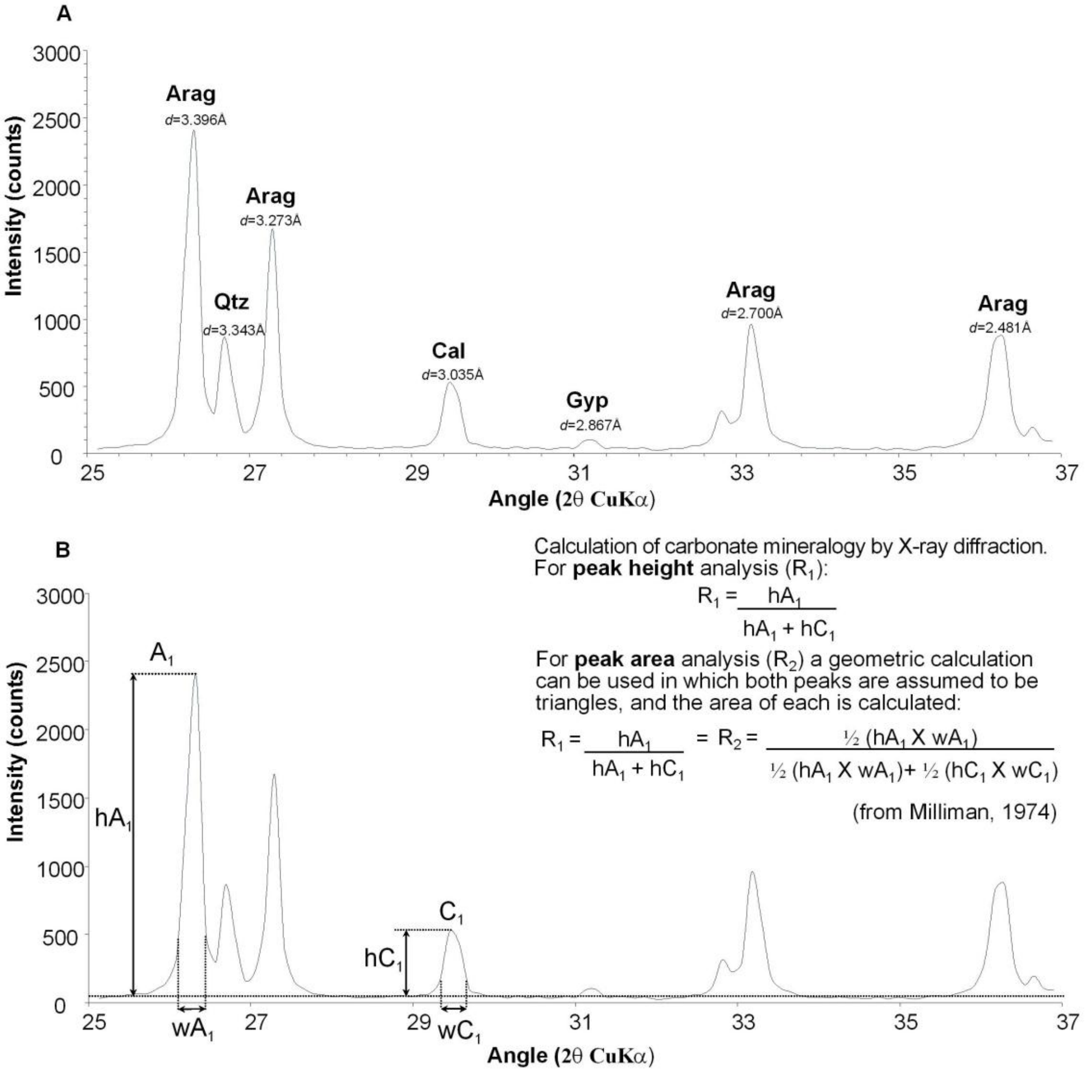


Figure 7.10. A. Diffractogram showing the main peaks of the carbonate minerals and quartz from samples scanned over 25-37 2θ, with d-values from Milliman (1974) (Arag-Aragonite, Qtz-Quartz, Cal-Calcite, Gyp-Gypsum). B. Peak height (R_1) and peak area (R_2) for the relative amounts of aragonite were calculated and compared with a standard curve to give relative percentages of aragonite.

These angles were converted to lattice spacing (*d*) (in angstroms, Å). Comparing the unique X-ray diffraction pattern of each sample with a set of standard patterns allowed the assignment of peaks to mineral phases. The relative amounts of aragonite were calculated using the peak area method after Milliman (1974) (Fig. 7.10b). Using peak areas and a standard curve with an accuracy of +3% (Milliman, 1974), the ratio of aragonite to total calcite (calcite plus magnesium calcite) was calculated for each sample.

As previously stated, petrographic and analytical analysis of the fossil samples allowed the essential assessment of the levels of preservation and diagenesis prior to stable oxygen isotopic, and the trace and minor element composition, analysis (methods follow those outlined for previous geochemical studies of fossils from the Eocene and Miocene; Grimes *et al*., 2005; Brachert *et al*., 2006; Gale, A *pers comm*, 2006). The combination of all methods outlined above allowed for detailed mapping (principally through detailed thin section and SEM images, followed by cathodoluminescence and XRD of well-preserved areas) and planning of sampling protocol for all specimens. In particular analysis showed that secondary calcite cement and infilling by sediment was concentrated around void areas particularly widespread within the coral structures. Therefore for *Acropora* specimens, geochemical sampling was concentrated

The results outlined below (section 7.4.6) not only provided independent palaeoenvironmental information but fundamentally shaped specimen selection and sampling areas.

7.4.6 Results

Preservation of Corals

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. 7.11a and b). All specimens show axial corallite apices with some distinguishable radiating septa. Radial corallites are identifiable with variations in costate or reticulate coenosteum (Fig. 7.11c and d). Selected specimens show radial corallites abraded flat against the main wall structure (Fig. 7.11b). In thin section multiple pristine microstructures were identified (Fig. 7.11a). Primarily, the aragonite composition is shown by the brown colouration of the skeleton with preserved original fanning and 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.

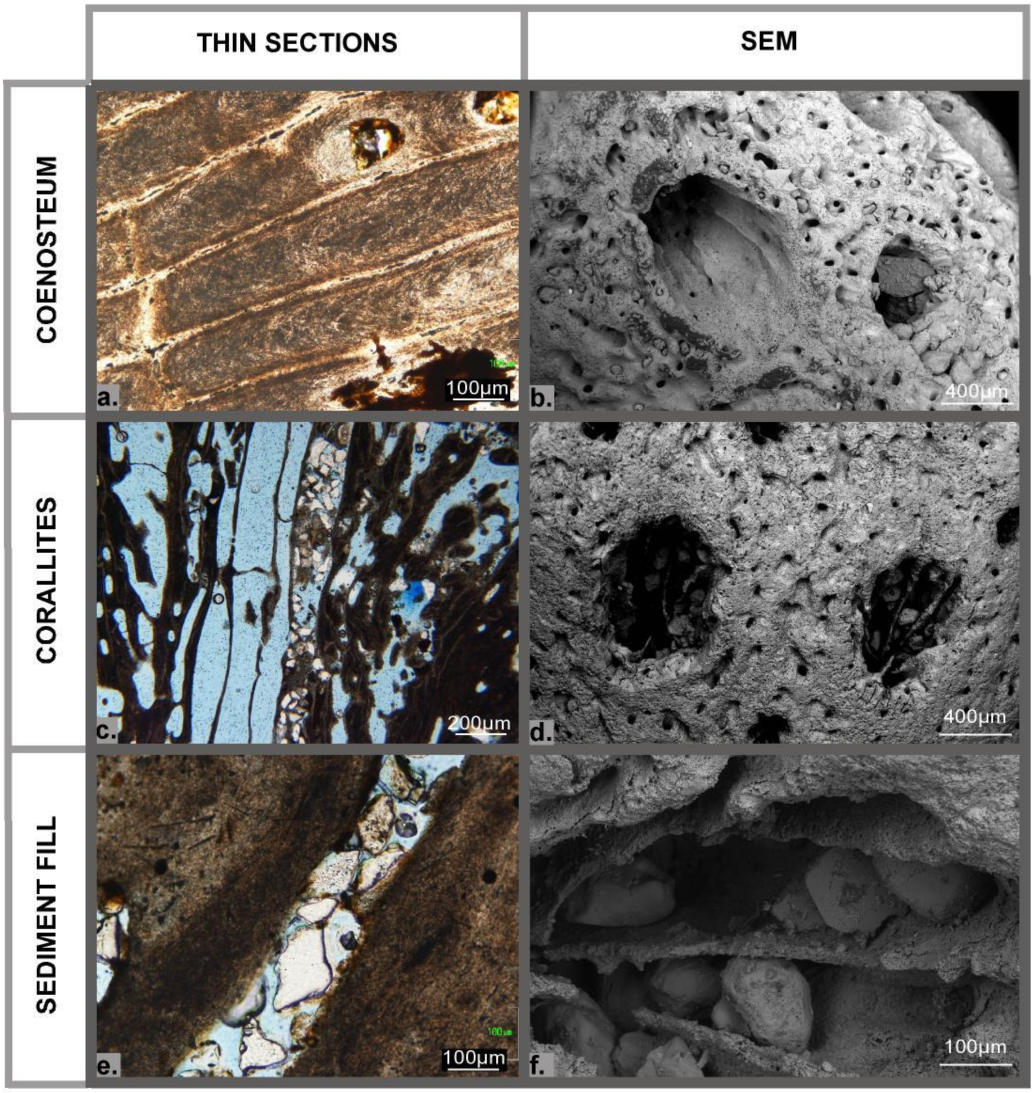


Figure 7.11. Summary of preservation features identified using thin sections and SEM. a. Characteristic trabecular structure of skeletal aragonite. b. Highly porous coenosteum with sediment infilling radial corallites. c. Axial corallite identified by elongate septal remnants and void areas. Fine grained sediment infilling corallite, mostly subangular-angular monocrystalline quartz. d. Abraded radial corallites with remnant septal structure and sediment infilling. e. Fine grained sediment infilling void areas. f. Sediment fill between septa 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. There is a morphological distinction between the specimens in each basin in 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. 7.12).

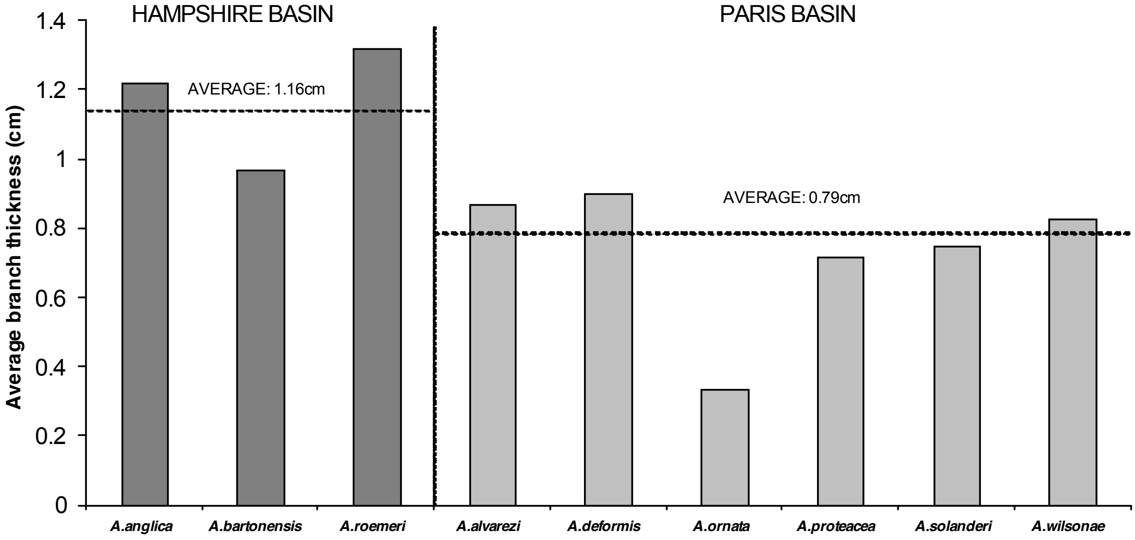


Figure 7.12. Variation in branch thickness shown between each species, and average thickness values between the two basins (n=71)

Another significant difference is the larger amount of infilling sediment in the Hampshire Basin specimens probably reflecting the finer grained nature of the encompassing lithology and the larger void structures produced by the larger, coarser skeletal structures in specimens.

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 (see Appendix 10), the majority of samples recorded seven main peak intensities (Fig. 7.13). 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).

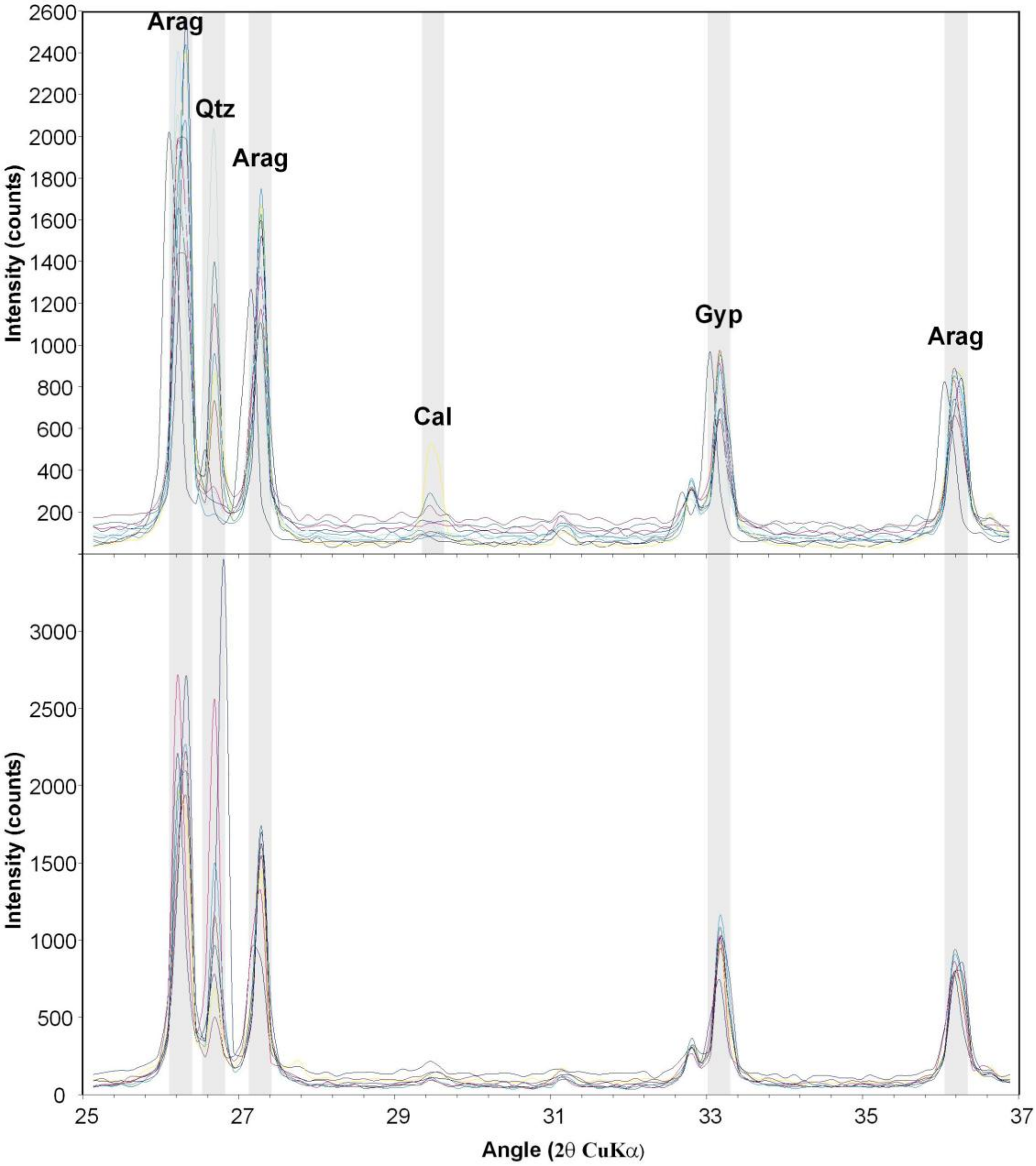


Figure 7.13. X-ray diffractogram of all coral specimens studied here from the Hampshire and Paris basins.

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 was used to convert these values to percentage aragonite with respect to calcite. For *Acropora* specimens the percentage aragonite ranged from 92.55%±1.8 to 100%.±2.2, and for the *Lobopsammia* specimens from 98.88%±2.1 to 100%±2.2, and can be regarded as 100% aragonite with respect to their carbonate mineralogy.

The additional peaks seen in XRD across the 25° to 37˚ 2θ range, representing quartz and gypsum, are from infilling sediment or surface weathering of calcium carbonate and iron pyrites (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. 11e and f). The grains are subangular to subrounded and infilling corallites trapped particularly by intact septal structures and are consistent with the matrix enclosing the corals.

All the coral 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 early aragonite cement and later calcite cement precipitation, infilling and lining porous areas (Fig. 7.14). Bioerosion is minor corals showing boring molluscs identified by their foliated internal structure.

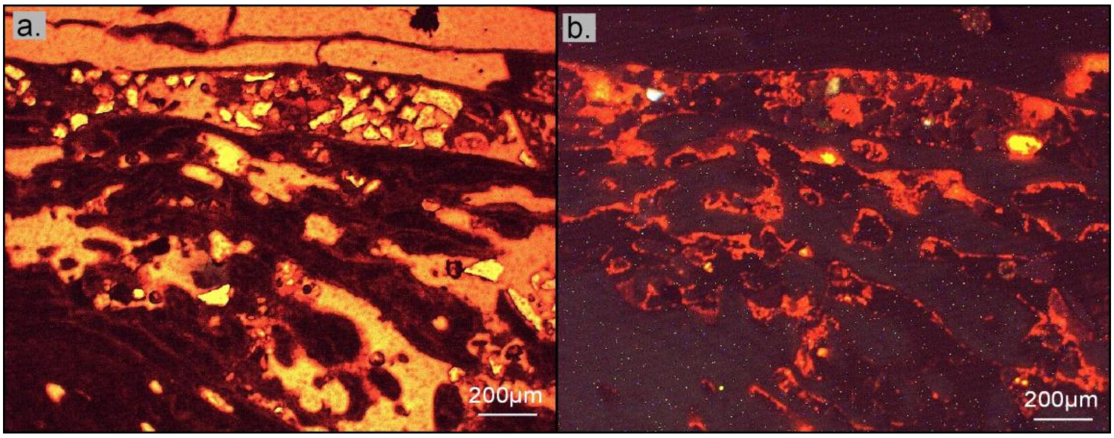


Figure 7.14a. Plane polarised and, b. CL image showing example of calcitic areas (bright yellow) within mainly aragonitic (brown) skeletal area.

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.

Preservation of Molluscs

Morphology and taphonomy

Like the corals from the Paris and Hampshire basins the molluscs also show exceptional preservation for Eocene specimens. In hand specimen the samples are complete with intact surface features including prominent diagnostic umbo and hinges. Thin section and scanning electron microscopy of fossil specimens identified intact internal morphological features including clear growth banding structures represented by a foliated structure. Within the Hampshire Basin specimens (*Cubitostrea plicata* C1; *Ostrea velata* O1) show characteristic thick sheets (folia) formed of subparallel calcite laths joined laterally (Fig. 7.15a and c). In thin section pockets of an earlier cement phase represented by micrite cement and isopachous calcite cement are identified. These areas of alteration are generally restricted to lenses along the outer margin of the mollusc.

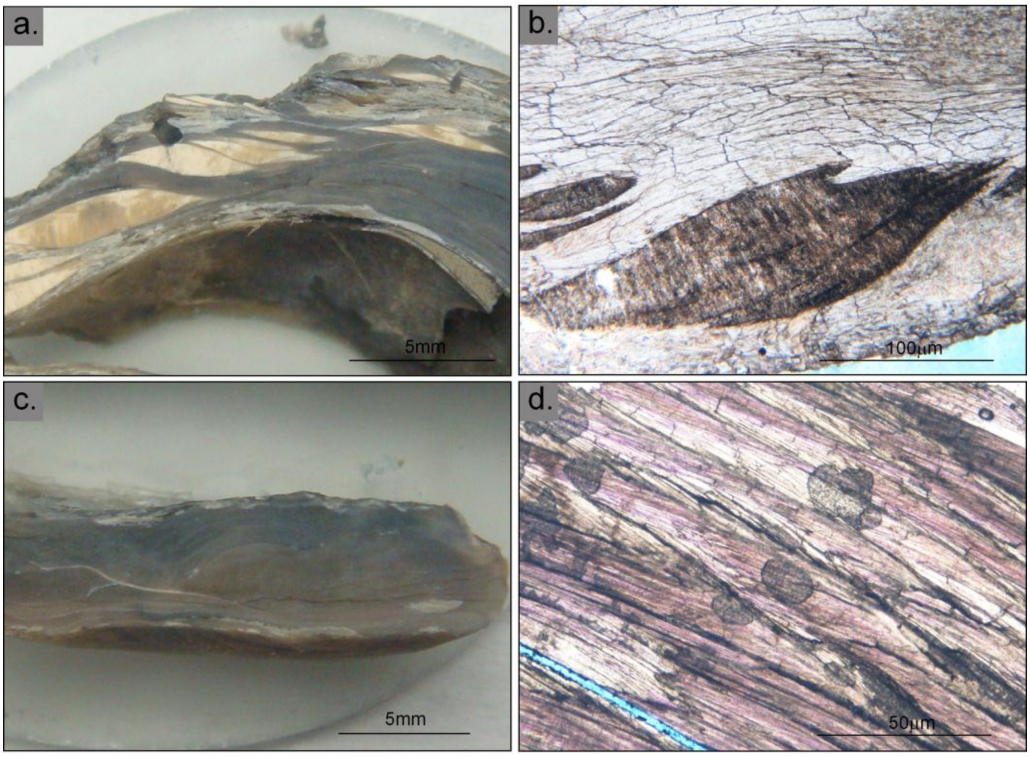


Figure 7.15. a-b. Cubitostrea plicata C1, c-d. Ostrea velata O1 – a. calcite lenses shown by cream colouration, b. pyrite lenses, c. thin calcitic veins, d. foliated structure.

Some of these lenses appear to be related to fragmentation of specimens resulting in dense pyrite inclusions, replacement of originally aragonite mollusc shells by pyrite commonly occurs in the Lower Oxford Clay (Fisher, 1986). These may be associated with a greater availability of iron as the sediment becomes more reducing with burial (Fig. 7.15b).

The Paris Basin specimens show exceptional preservation with original colour patterns and lustre preserved in selective areas of some specimens. This is thought to be due to their preservation in fine-grained, marl of the surrounding lithology. The *Turritella imbricataria* (T1) shows evidence of early pyritisation, confined to the surface around the edges of spires.

Skeletal mineralogy; preservation, diagenesis and infilling

Using X-ray powder diffraction, over a 25° to 37˚ 2θ range, the majority of samples recorded six 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) was recorded.

The two Brockenhurst Bed specimens (C1, O1) show no peaks for aragonite (below 1% detection limit) and can be regarded as 100% calcite with respect to their carbonate mineralogy (Fig. 7.16). This is consistent with both genera belonging to the calcitic oyster family. The additional peaks seen in XRD across the 25° to 37˚ 2θ range, representing quartz, are from infilling sediment and are seen in thin section to be a minor component coating specimens and infilling sub-surface cracks.

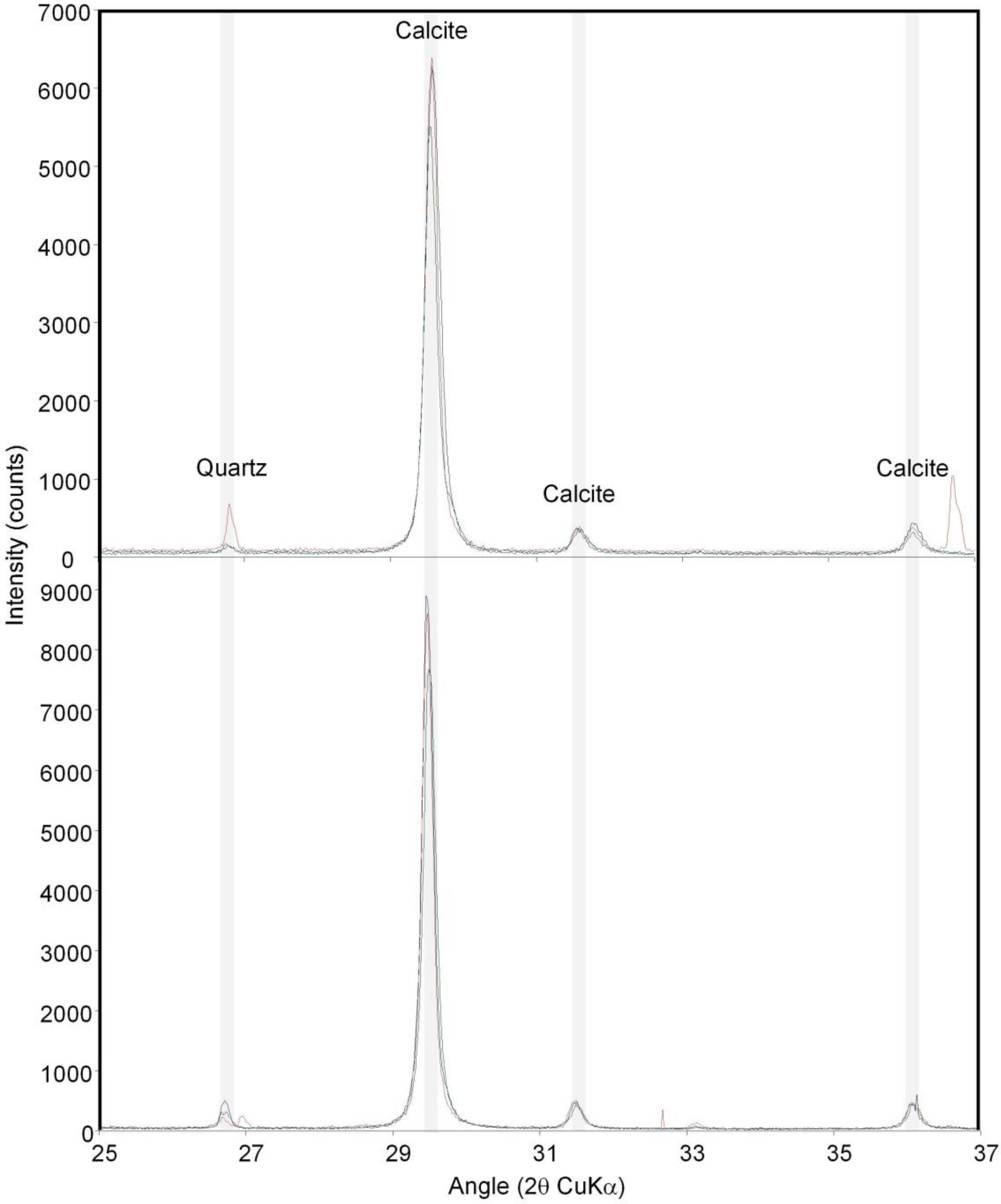


Figure 7.16. X-ray Diffractogram of <u>Cubitostrea plicata</u> C1 and <u>Ostrea velata</u> O1

For the two Paris Basin specimens, peak height analysis allowed the ratio for aragonite peak intensity to be determined. For *Turritella imbricataria* (T1) this is 0.8299±0.04 and for *Venericardia imbricata* (V1) this is 0.9770±0.05. From this, the Milliman (1974) calibration curve allowed these values to be converted to percentage aragonite with respect to calcite. For the *Turritella imbricataria* (T1) percentage aragonite is 92.55%±1.8 and for *Venericardia imbricata* (V1) is 98.88%±2.1. 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 summary, post-depositional modifications of the mollusc skeletons include entrapment of fine grained sands and the precipitation calcite cements and pyrite within and near the edges of shells.

7.4.7 Palaeoenvironmental information from stable isotope analysis

The most commonly used climate proxies in corals are the stable oxygen isotopic composition of the skeleton, and the trace and minor element composition. This work focuses on the oxygen isotopic composition ($\delta^{18}O$) and Sr/Ca ratios of coral skeletal aragonite, which are proxies for SST/hydrology and SST, respectively. Skeletal Mg/Ca and U/Ca have also been proposed as SST proxies, but significant uncertainties still surround the true environmental significance of these elements. Other trace and minor elements and isotopes are potentially useful for reconstructing terrestrial inputs (e.g. Ba/Ca), upwelling (e.g. Ba/Ca), ocean circulation (e.g. ^{14}C), and pH (e.g. boron isotopes). Sources of uncertainty in δ18O and Sr/Ca-based palaeotemperature reconstructions are summarised in Appendix 10.

7.4.8 Methods

Continuous Flow-Mass Spectrometry: Acid digestion

For the coral specimens, powdered carbonate samples were generated using a computer controlled micromill from the counterpart of the specimen which was left after thin sectioning. Due to the porous nature of some coral specimens within these samples trenches were drilled instead of spots. Spots led to material being displaced downwards making it impossible to collect. Instead 3mm trenches were drilled displacing the material forward onto the sample surface. Each trench was scanned 4 times at a depth of 210μm. For each sample at least 3 linear trenches, and if possible 4 trenches, were micromilled parallel to the axial corallite. Due to the greater robustness of molluscs these were hand-drilled using fine dental drill and a stabilized drilling apparatus.

Analysis of the carbonate component of both corals and molluscs were conducted using an acid digestion technique with a continuous helium flow Micromass Isoprime multiflow Mass-spec. For the analysis of these samples 500g of was weighed into individual, septum sealed, vials and placed in a hot plate maintained at 90°C. Each vial was automatically flushed with helium before excess H_3PO_4 was added. After approximately an hour of equilibration time the CO_2 was analyzed by continuous flow Mass Spectrometry. For the analysis of the oxygen component of the carbonate palaeoproxies the run NBS-19 standard gave a ^{18}O value of -2.26±0.05‰ (VPDB) (n9) and a ^{13}C value of 1.96±0.04‰ (VPDB) (n9). The internal lab carbonate standard (RHBNC) gave a ^{18}O value of -10.74±0.04‰ (VPDB) (n9) and a ^{13}C value of 3.25±0.05‰ (VPDB) (n.9). All the carbonate palaeoproxy samples were calibrated to the NBS-19 standard. The error on the individual carbonate analyses was taken to be the same as that on the NBS-19 standard (0.05‰).

Dual inlet mass spectrometer: Optima

Specimens were sectioned along the maximum growth axis and mounted on a 40mm glass circular slide. The Dual inlet mass spectrometer allows fully automated system of micro-analysis of δ^{18}O under vacuum using a SYNRAD CO2 laser for combustion and under a BrF5 reagent atmosphere. The oxygen extraction section is online to a dual-inlet Optima mass spectrometer that measures O_2 directly allowing δ^{18}O and δ^{16}O ratios to be measured. Forward and reverse profiling was carried out with 500µm in one direction then an offset of half a step to the right and repeats on the reverse every 500µm. Due to the offset the end result is a spot being lasered every 250µm, hence allowing a doubling of the resolution. For the analysis of the oxygen component of the carbonate palaeoproxies the run Carrara marble standard gave a δ^{18}O value of -3.79±0.05‰ (VPDB) (n47) and a δ^{13}C value of 1.94±0.04‰ (VPDB) (n47).

Laser Ablation Inductively Coupled Plasma-Mass Spectrometry: LA-ICP-MS

Standard ICP-MS, uses an argon plasma source that dissociates and ionises a gas-phase or nebulized solution sample into its constituent ions (Muller *et al.*, 2009). The ions are separated from the plasma by a series of apertures or cones, filtered by their mass: charge ratio, and then detected with a quadrupole or multi-collector mass spectrometer. The amount of each elemental isotope in the sample is proportional to its peak intensity.

LA-ICP-MS is used here to determine quantitatively trace multi-element and isotopic ratio compositions of carbonate samples. It combines the µm-scale resolution of a pulsed, 193 nm ArF laser probe to ablate nm-sized aerosol particles from surfaces, with the speed, sensitivity and multi-element and isotopic analytical capability of ICP-MS. This LA system is coupled to a Multi Collector (MC)-ICP-MS (IsoProbe) for high-precision isotope ratio analysis (for further details see Muller *et al.*, 2009).

Calculation of palaeotemperature

Geochemical analyses of coral skeletons are widely being used to estimate past sea surface temperatures (Swart, 1983; Beck *et al*., 1992; de Villiers *et al*., 1995, Reynaud *et al*., 2007). There is a plethora of research showing differences in the slopes and intercepts of calibrations from different geographical areas or for different coral genera. It is essential to study isotope ($\delta^{18}O$) and elemental ratio (Sr/Ca, Mg/Ca) records in modern corals and their relationships with instrumental SST over coral reef areas worldwide and over different genera. Advice was sort for the selection of calibrations outlined below and was largely based on calibrations derived from similar modern settings as that interpreted for the palaeoenvironment of the Hampshire and Paris basins (Swart, P. *pers comm*., November 2006; Reynaud, S. *pers comm*., March 2007).

The isotopic values are reported in conventional 'δ' notation as 'parts per thousand' difference between an isotopic ratio of a specimen compared to the same ratio in an international standard, the Vienna Peedee Belemnite (VPDB) or Standard Mean Ocean Water (SMOW).

For Corals and Aragonitic Molluscs:

Temperatures were calculated from the oxygen isotope ratios of the specimens ($\delta^{18}O_{aragonite}$) using the modified Grossman and Ku (1986) function, from Schone *et al*. (2005):

$$T\delta^{18}O(^{\circ}C)=20.6-4.34[_{aragonite}-(\delta_{ocean}-0.2)]$$

where T is the isotopic temperature estimate; $\delta_{aragonite}$ is the $\delta^{18}O$ of the aragonitic specimen; δ_{ocean} is the $\delta^{18}O$ of the surface waters.

For corals, additionally vital effect corrections were applied from 0 to -6‰. Arthur and Anderson (1983) identified the correction, for scleractinian z-corals, as lying between -3 to -6‰.

For Calcitic Molluscs:

Temperatures were calculated from the oxygen isotopes ratios of the specimens using the method of Shackleton (1974) based on O'Neil *et al*. (1969):

$$T\delta^{18}O(^{\circ}C)=16.0-4.38(\delta_{calcite}-\delta_{ocean}) + 0.1(\delta_{calcite}-\delta_{ocean})^2$$

where T is the isotopic temperature estimate; $\delta_{calcite,}$ is the $\delta^{18}O$ of the calcite mollusc; δ_{ocean} is the $\delta^{18}O$ of the surface waters.

7.4.9 Results

This section summarises results from the various methods of isotopic and trace element studies outlined above and detailed in Appendix 10. Firstly results are summarised from a single modern *Acropora* specimen from the Chesterfield Atoll, Queensland, Australia.

Modern Acropora, Australia

Elemental concentrations have been simultaneously determined including major trace elements in corals (Mg, Ca, Sr, Ba, and U) and minor trace elements (Al, P, Fe, Zn, Pb) using LA-ICP-MS from a single modern *Acropora* specimen (Fig. 7.17).

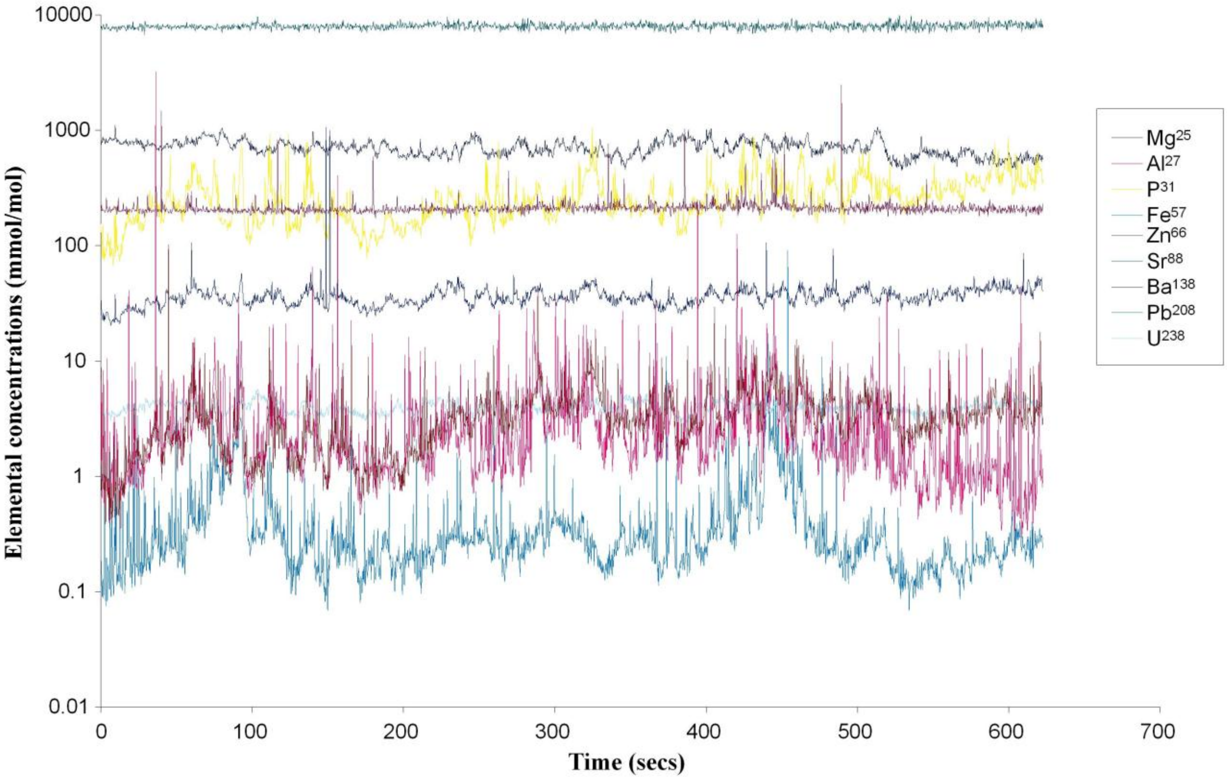


Figure 7.17. Summary of all major elements and minor trace elements

Biocarbonates consist of carbonate ($CaCO_3$) within which minor and trace elements are incorporated in reflecting environmental setting. The relative concentration of each of these elements (i.e. element/Ca ratio) is used here to reconstruct past environmental conditions. Sr/Ca (Swart, 1981; Beck *et al.*, 1992) and Mg/Ca (Weber, 1973) ratios of coral skeletons have widely been used as proxies for past changes in sea surface temperature of tropical and subtropical oceans (Weber, 1973; Beck *et al.*, 1992). Ba/Ca and U/Ca ratios have also been determined with U/Ca ratio shows a positive correlation with Sr/Ca ratio (Fig. 7.18).

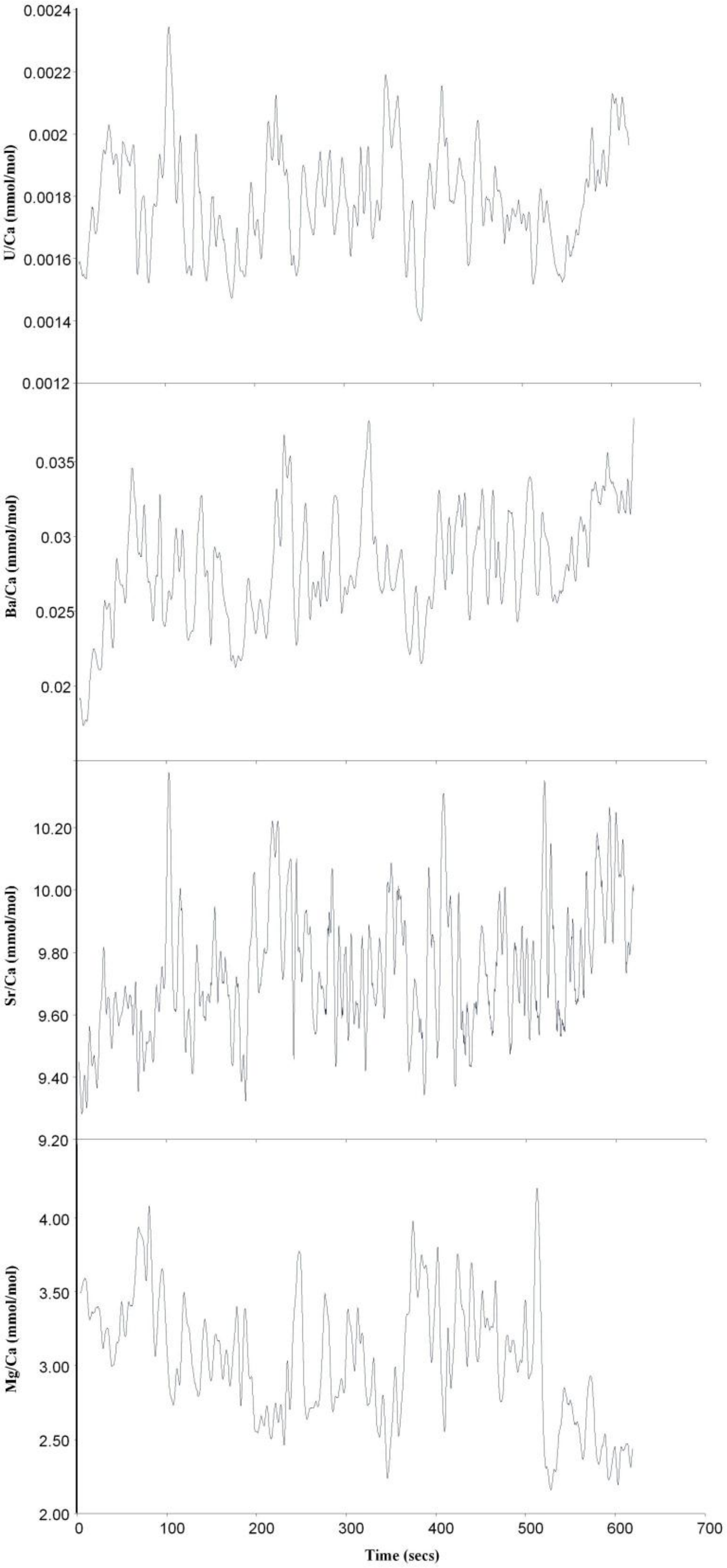


Figure 7.18. Comparison of U/Ca, Sr/Ca and Mg/Ca from modern Acropora specimen

The element/Ca ratios do not appear to show the classic sigmoidal seasonal patterns often associated with corals, shown here by a specimen of *Siderastrea* from the Miocene, Venezuela (Fig. 7.19).

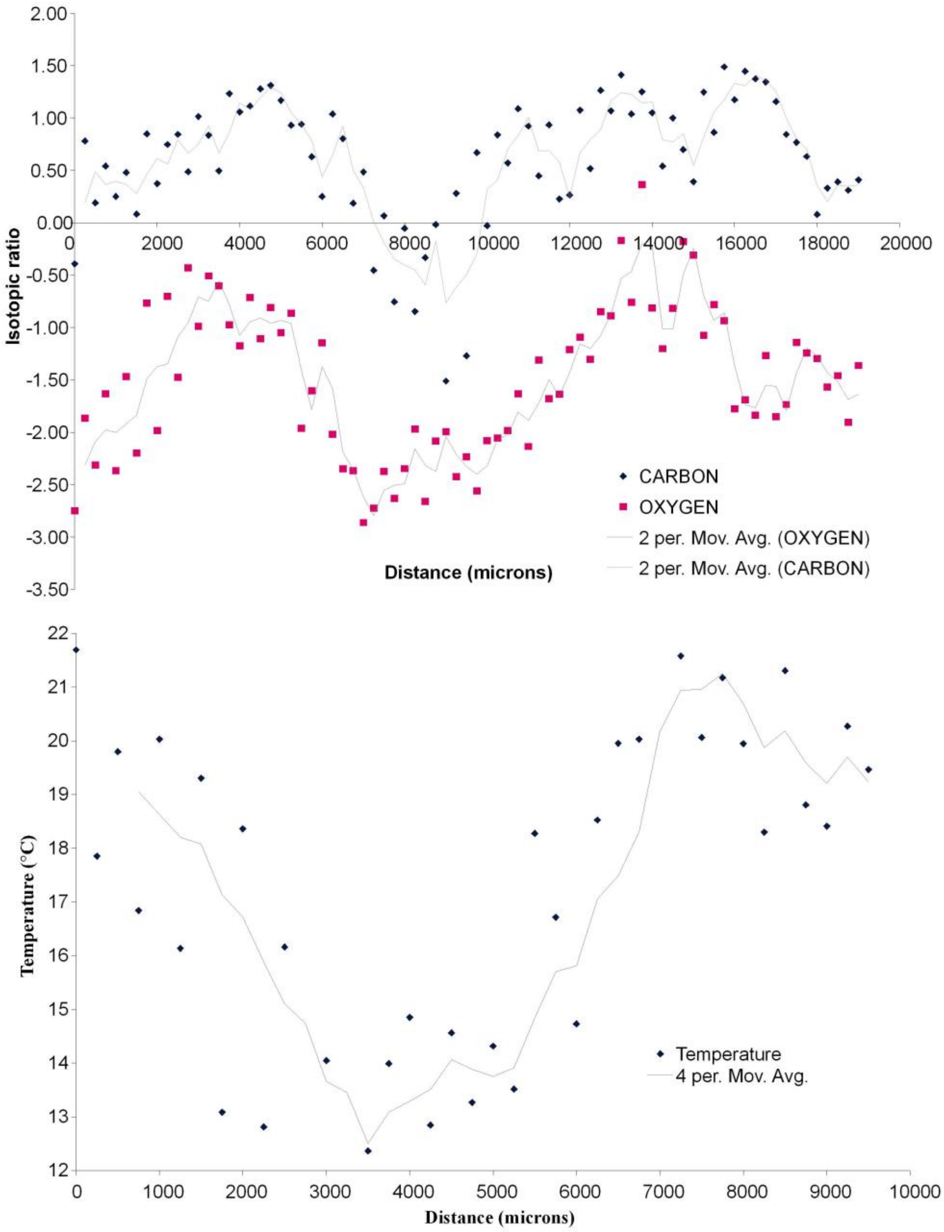


Figure 7.19. Classic sigmoidal seasonality shown by a single specimen of ***Siderastrea conferta*** *(unregistered, NHM) from the early Miocene Cantaura Formation outcropping in the central part of the Paraguana Peninsula in the Falcon State, near San Jose de Crocodite, Venezuela. Ahmed, 2008 (unpublished) studied the preservation of the specimen and the isotopic data was corrected and temperature derived for this thesis.*

The growth rates of *Acropora* are very high (5-20cm/year) , because a distance of only a few centimetres has been studied here, this may only represent a section within a single season and variation in the signal probably reflects sub-annual variation.

The relationship between Sr/Ca, Mg/Ca, Ba/Ca, U/Ca and SST is still not widely understood and resultantly new calibrations are regularly being described. This is largely the result of disparities between coral-based estimates of SST and in situ measurements of SST. Variables such as growth rates and between different coral species (so-called 'vital effects') could significantly affect coralline element/Ca ratios. Tables 7.5 and 7.6 show a literature survey of Sr/Ca and Mg/Ca calibrations against SST, respectively, with details of sample site/region and methodology where found.

Reference	**Species**	**Locality**	**B**	**A**	**Method**
Smith *et al.* (1979)	*Montipora verrucosa*		-0.089	11.64	
	Porites sp.		-0.070	10.94	
	Pocillopora damicornis		-0.071	11.01	
Beck, *et al.* (1992); Beck *et al.* (1994)	*Porites lobata*	New Caledonia	-0.062	10.48	TIMS
de Villiers *et al.* (1994)	*Porites lobata*	Hawaii	-0.080	10.96	TIMS
	Pocillopora eydouxi	Hawaii	-0.076	11.00	TIMS
	Pavona clavus	Hawaii	-0.067	10.65	TIMS
Alibert *et al.* (1994)	*Porites mayeri*		-0.075	10.80	
de Villiers *et al.* (1995)	*Pavona clavus* (6mm y^{-1})		-0.042	10.25	
	Pavona clavus (12mm y^{-1})		-0.039	10.11	
	Pavona clavus (14mm y^{-1})		-0.033	9.92	
Mitsuguchi *et al.* (1996)	*Porites lutea*		-0.061	10.50	
Shen *et al.* (1996)	*Porites lobata, P.lutea*	Taiwan	-0.05	10.29	TIMS
Cardinal (1996)	*Diplora labyrinthiformis*		-0.045	10.10	
Alibert and McCulloch (1997)	*Porites sp.*	Great Barrier Reef	-0.062	10.48	TIMS
Boiseau *et al.* (1997)	*Acropora nobilis*		-0.33	18.20	
Heiss *et al.* (1997)	*Porites lutea*		-0.061	10.58	
Gagan *et al.* (1998)	*Porites lutea*		-0.066	10.78	
McCulloch *et al.* (1994)	*Porites sp.*		-0.062	10.70	
Fallon *et al.* (1999)	*Porites lobata*		-0.063	10.76	
Swart *et al.* (2002)	*Montastraea annularis*		-0.038	9.99	
Fallon *et al.* (2003)	*Porites sp.*		-0.058	10.41	
Marshall and McCulloch (2002)	*Porites sp.*	Great Barrier Reef	-0.059	10.40	
Linsley *et al.* (2004)	*Porites lutea*	Fiji	-0.053	10.65	ICP-AES
Linsley, Wellington, and Schrag (2000)	*Porites lutea*	Rarotonga	-0.065	11.12	ICP-AES

Table 7.5. Summary of several published calibrations of the Sr/Ca-Temperature proxy (Sr/Ca (mmol/mol)= b x T(°C) + a

Reference	Species	B	A
Mitsuguchi *et al*. (1996)	*Porites sp*.	0.129	1.15
Fallon *et al*. (1999)	*Porites lobata*	0.088	1.38
Wei *et al*. (2000)	*Porites sp*.	0.113	1.60
Fallon *et al*. (2003)	*Porites sp*.	0.098	1.54
Reynaud *et al*. (2007)	*Acropora sp*.	0.138	0.90

Table 7.6. Summary of several published calibrations of the Mg/Ca-Temperature proxy (Mg/Ca (mmol/mol)= b x T(°C) + a

In addition to common identified problems in this type of research (i.e. diagenetic alteration; Fig. 7.20) this literature review clearly shows other common sources of variation including sampling protocol, species/genus-related variation and local geographic variation.

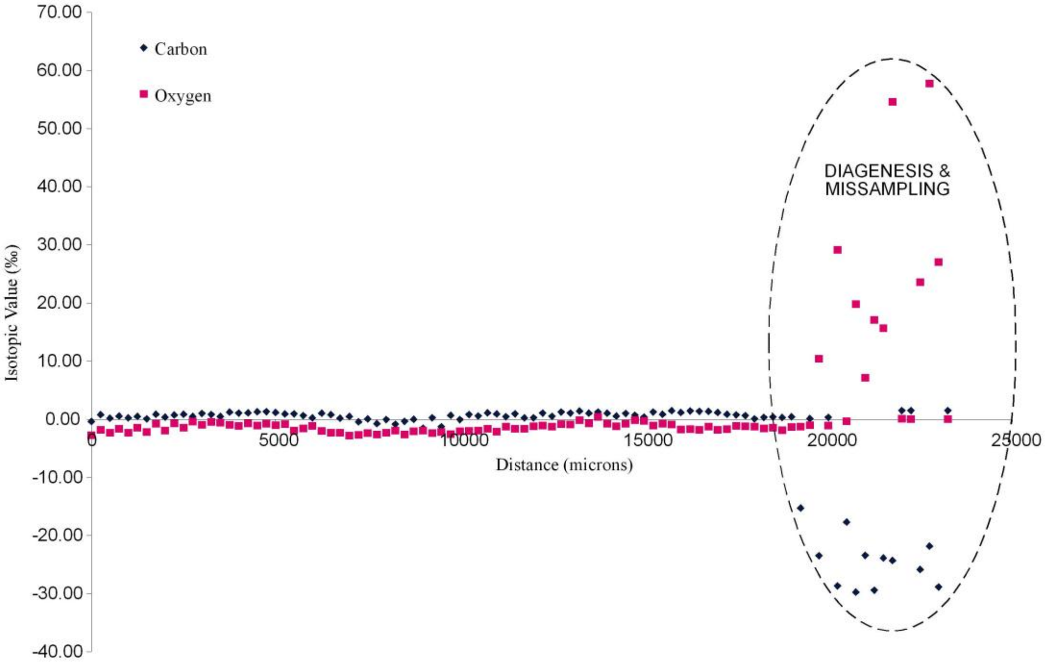


Figure 7.20. Anomalous results caused by sampling of diagenetic regions, pore spaces and the sample mounting rather than carbonate material (Specimen: Siderastrea conferta (unregistered, NHM) from the Early Miocene Cantaura Formation, Venezuela)

These show that at higher resolutions there are many factors which may affect elemental ratios in skeletal calcium carbonate. However recent studies, such as those by Reynaud *et al*. (2007), show that there is a strong first-order correlation between both Sr/Ca and Mg/Ca ratios and water temperature.

Element/ Ca Ratio	Calibration	Derived Palaeo-SST (°C)			
		Max	Min	Mean	Standard Deviation
Sr/Ca	Linsley *et al*., 2004	25.83	5.15	17.13	3.93
Mg/Ca	Reynaud *et al*., 2007	23.92	9.12	15.43	3.01

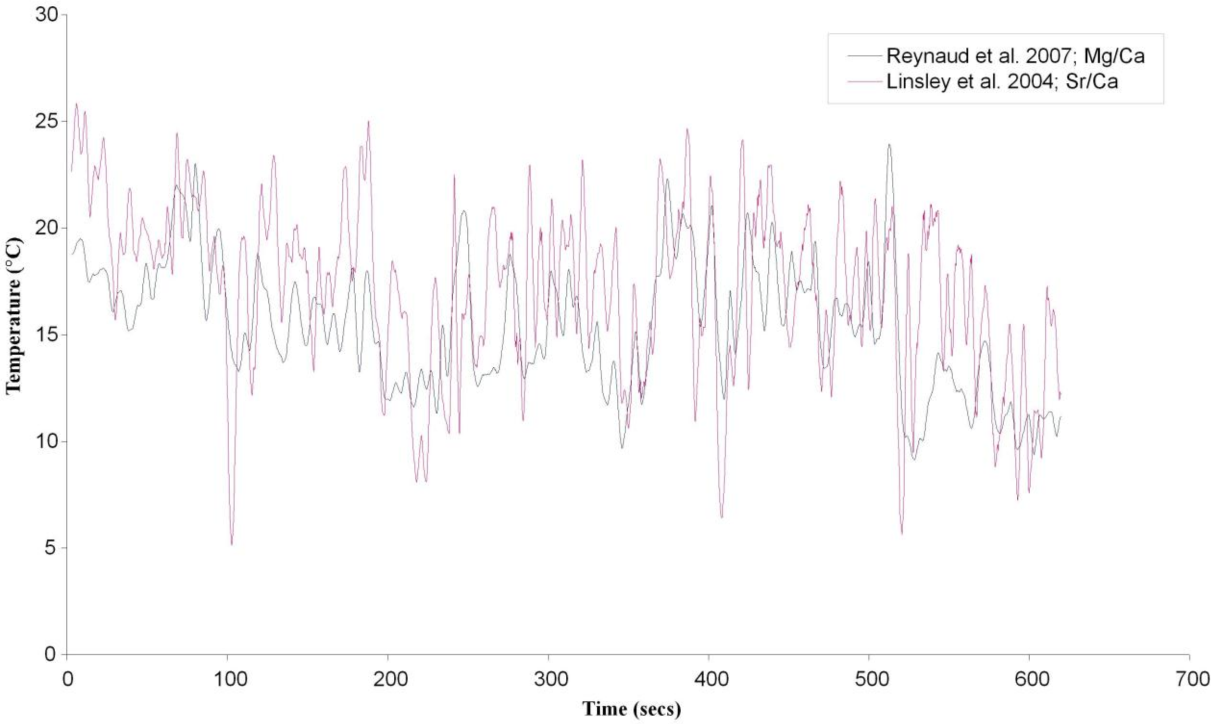


Figure 7.21. Derived SST from Sr/Ca and Mg/Ca ratios using two calibrations of the element/Ca palaeo-SST proxy, from Linsley et al. *(2004) (Sr/Ca) and Reynaud* et al. *(2007) (Mg/Ca).*

Using two calibrations for Mg/Ca and Sr/Ca (Reynaud *et al*., 2007 and Linsley *et al*., 2004) it is possible to estimate SST from the analysis of the modern *Acropora* specimen. Sr/Ca ratios estimate a variation in SST of between 17.13°C and 25.83°C. Mg/Ca ratios estimate a SST variation of between 15.43°C and 23.92°C.

The maximum estimate of SST from both Sr/Ca and Mg/Ca ratios is consistent with instrumental data from the Bureau of Meteorology, Australia (fig. 7.22).

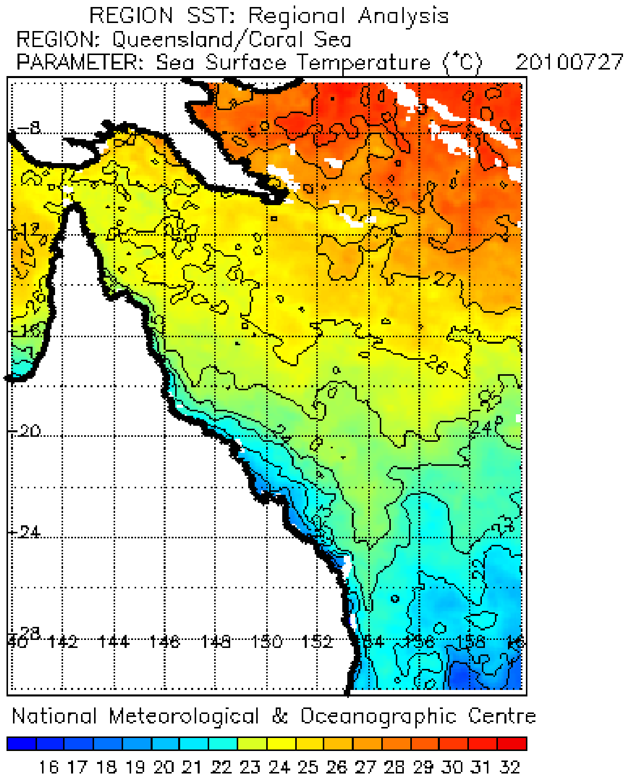


Figure 7.22. Regional SST from the Bureau of Meteorology, Australia

Eocene Corals, England and Paris

All corals from these two basins show a δ^{18}O variation of between -4.61‰ to -7.64‰ (mean -5.56, standard deviation 0.61, n62) (Fig. 7.23). For Lutetian corals the δ^{18}O values show a maximum of -4.67‰ and a minimum of -6.43‰ (n9). For all *Acropora* specimens, mean interpreted temperature is 32.4°C (standard deviation 1.93, n6). For all *Lobopsammia* specimens, mean interpreted temperature is 30.1°C (standard deviation 2.76, n3).

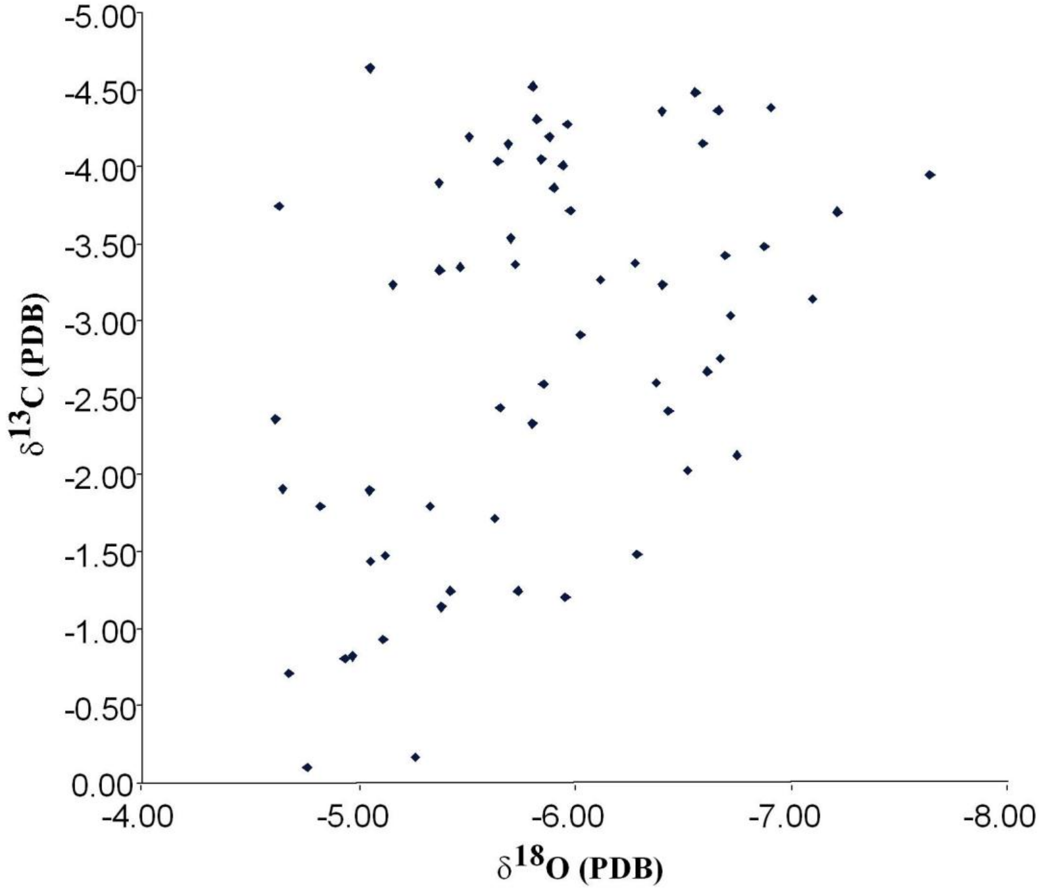


Figure 7.23. Plot of δ^{18}O versus δ^{13}C values for all corals from the Hampshire and Paris basins

For Bartonian corals the δ^{18}O values show a maximum of -4.61‰ and a minimum of -7.64‰ (mean -5.99, standard deviation 0.74, n43). For all *Acropora* specimens, mean interpreted temperature is 33.2°C (standard deviation 4.04, n29). For all *Lobopsammia* specimens, mean interpreted temperature is 31.0°C (standard deviation 3.53, n9). For all *Goniopora* specimens, mean interpreted temperature is 31.0°C (standard deviation

1.84, n3). For all *Trochoseris* specimens, mean interpreted temperature is 31.0°C (standard deviation 1.84, n3).

For Bartonian corals the $\delta^{18}O$ values show a maximum of -4.63‰ and a minimum of -6.4‰ (mean -5.45, standard deviation 0.51, n10). For all *Acropora* specimens, mean interpreted temperature is 32.5°C (standard deviation 1.35, n3). For all *Lobopsammia* specimens, mean interpreted temperature is 28.9°C (standard deviation 1.23, n6).

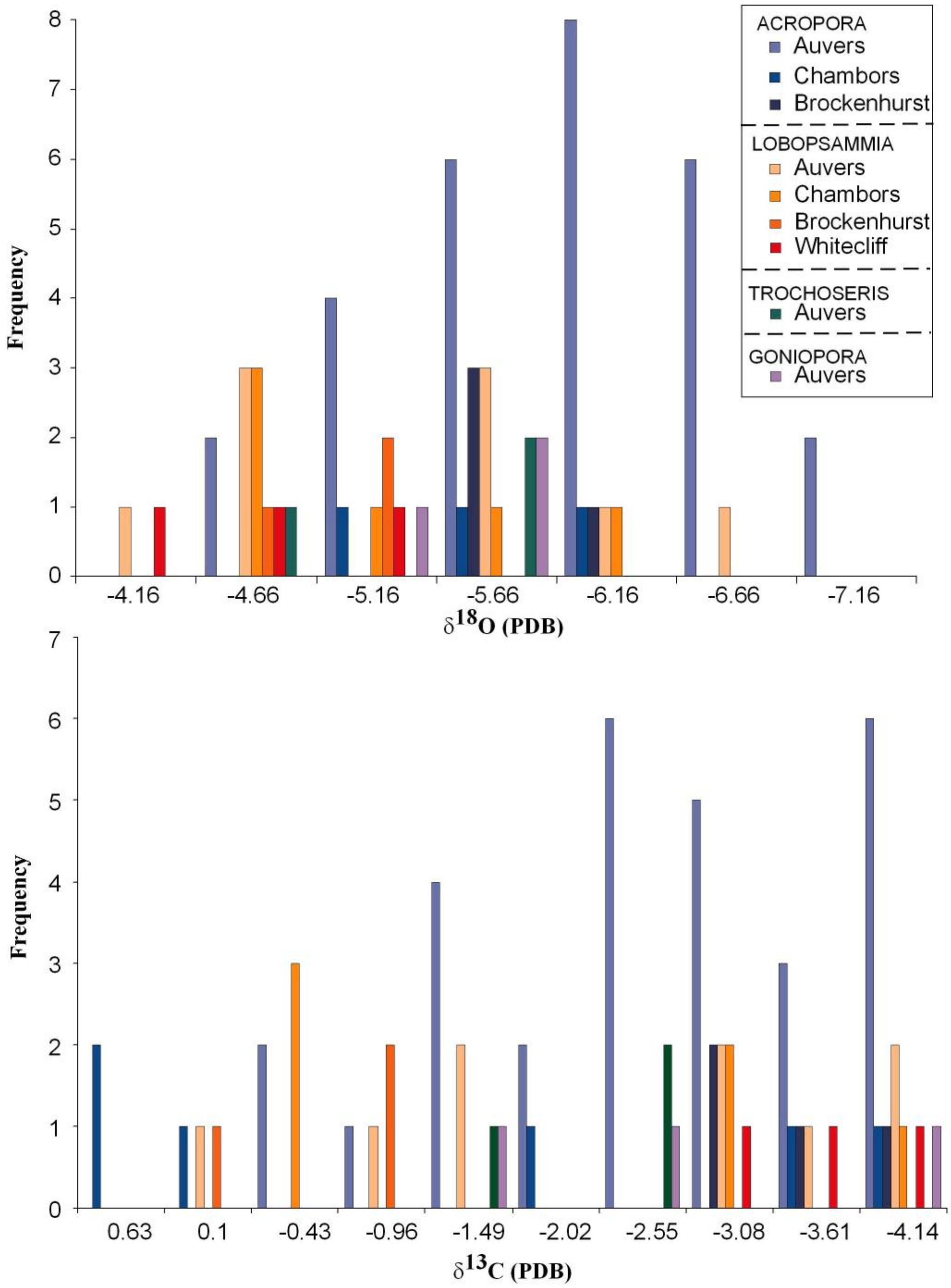


Figure 7.24. Summary of $\delta^{18}O$ and $\delta^{13}C$ values for all localities from the Hampshire and Paris basins

For all localities from these two basins the δ^{13}C shows a variation of between -4.61‰ to -7.64‰ (mean -5.56, standard deviation 0.61, n62; Fig. 7.24). This large amount of variation probably reflects the influence of nearshore setting predominantly found within mud-rich deposits.

For all localities from these basins the Sr/Ca from *Acropora* specimens show a variation of between 7.83‰ to 11.86‰ (mean 9.63‰, standard deviation 0.44, n4584). Interpreted temperatures show a minimum of 11.4°C and maximum of 30.9°C (mean 19.4°C, standard deviation 3.24, n4584; Fig. 7.25).

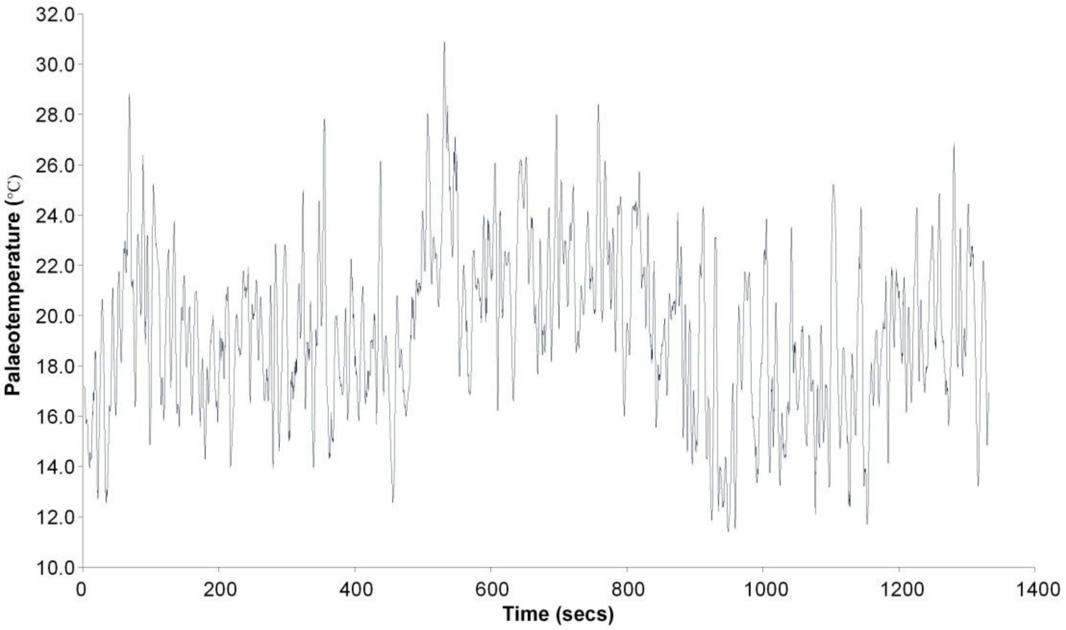


Figure 7.25. Inferred palaeotemperatures from Sr/Ca ratios from Acropora specimens from the Eocene Hampshire and Paris basins (calibration from Linsley at al., 2004).

Other elemental ratios show similar profiles with corresponding peaks (Fig. 7.26) and probably reflect pulsed amplification of elements during periods of elevated sedimentation. Due to the fast growth rate of *Acropora* these pulses do not reflect seasonal variations, however may reflect interannual variability of sedimentation, closely linked to precipitation.

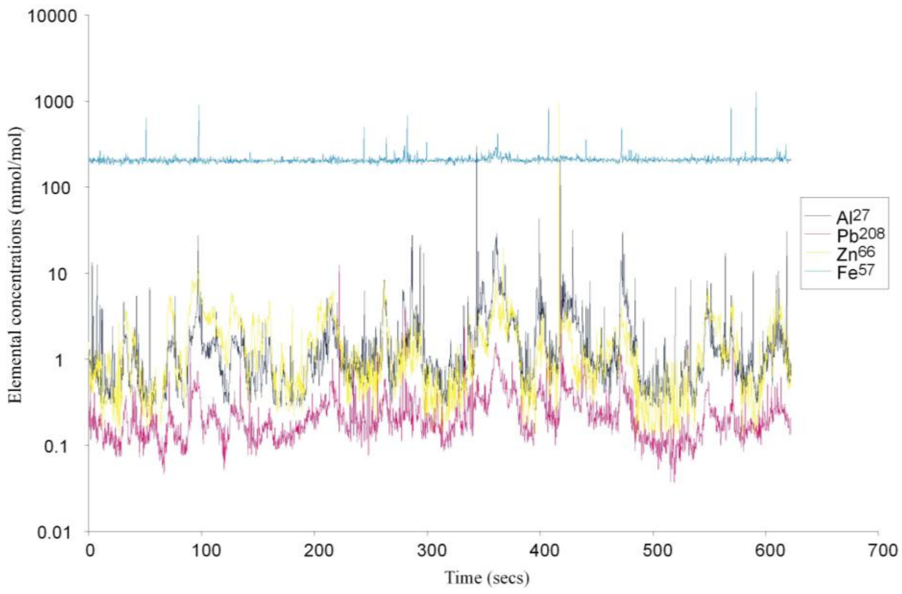


Figure 7.26. Minor trace elements (Al, Fe, Zn, Pb) variations

Ba/Ca ratios in corals can provide records of suspended sediment loads and hence in the nutrients entering reef areas as a result of river floods (McCulloch *et al*., 2003). Records from the Tertiary basins show periods of pulsed elevation (Fig. 7.27), however larger specimens that might provide longer growth transects would be needed to confirm the frequency of these and the long-term regional palaeoenvironmental implications.

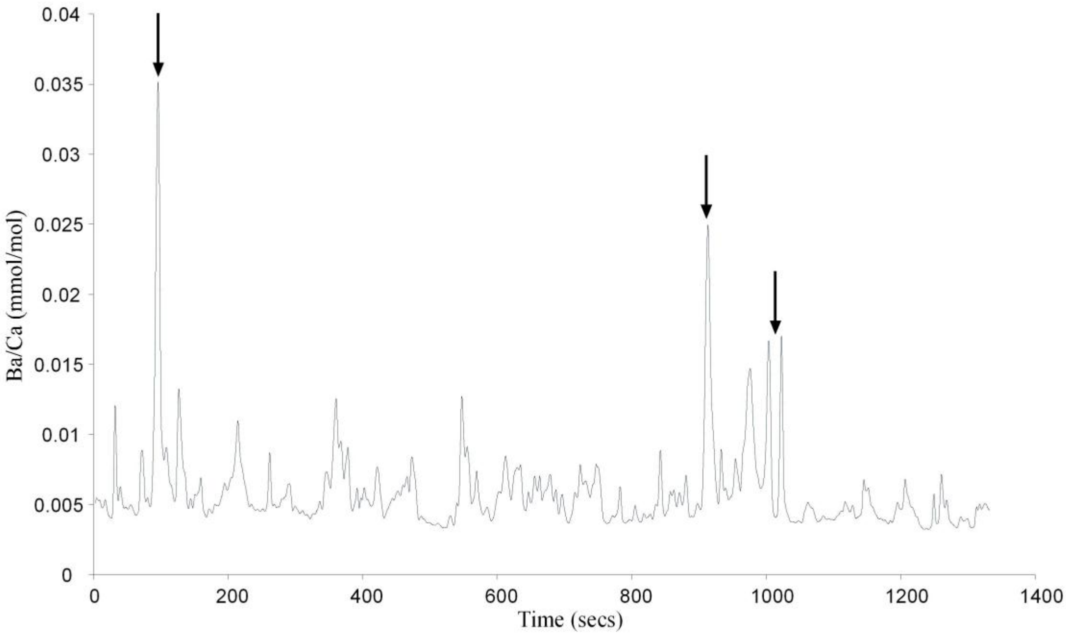


Figure 7.27. Ba/Ca ratios showing periods of pulsed elevation (arrows).

Priabonian Molluscs (C1, O1)

Oxygen and carbon isotopes were analysed from unaltered areas of the specimen *Cubitostrea plicata* (C1) as well as three spot analyses in the diagenetic calcitic veins which are confined to the outer fractured subsurface, in the hinge areas of the specimen (see preservation section for details; Fig. 7.28). These samples show a striking offset in the δ^{13}C values (mean -12.78‰, standard deviation 1.10; Fig. 7.28).

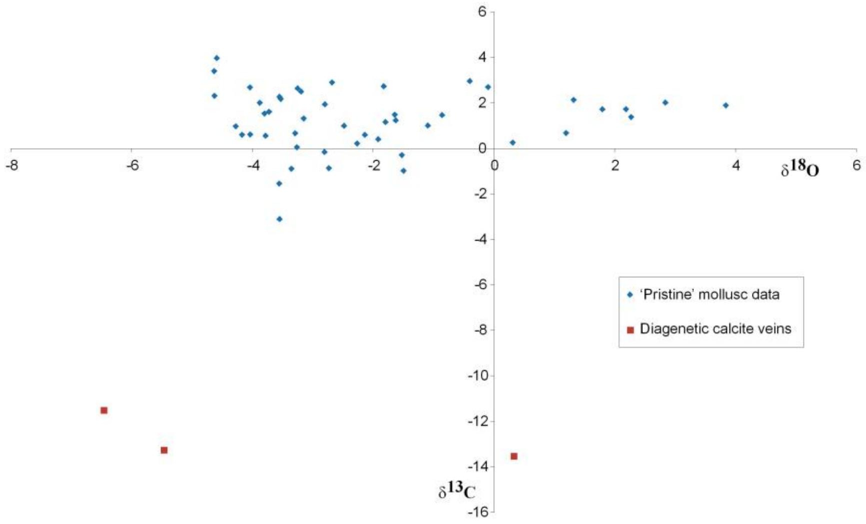


Figure 7.28. All oxygen and carbon data from <u>*Cubitostrea plicata*</u> *(C1) showing the range of data and the effect of sampling diagenetically altered areas*

Samples from two runs on unaltered areas recorded δ^{18}O values between -1.10‰ and -4.63‰ (mean -2.96‰, standard deviation 0.94, n23; Fig. 7.29). From these δ^{18}O values the mean interpreted temperature is 27.1°C (standard deviation 4.47, n23). δ^{13}C values range between 3.40‰ and -3.11‰ (mean 0.58‰, standard deviation 1.50, n23).

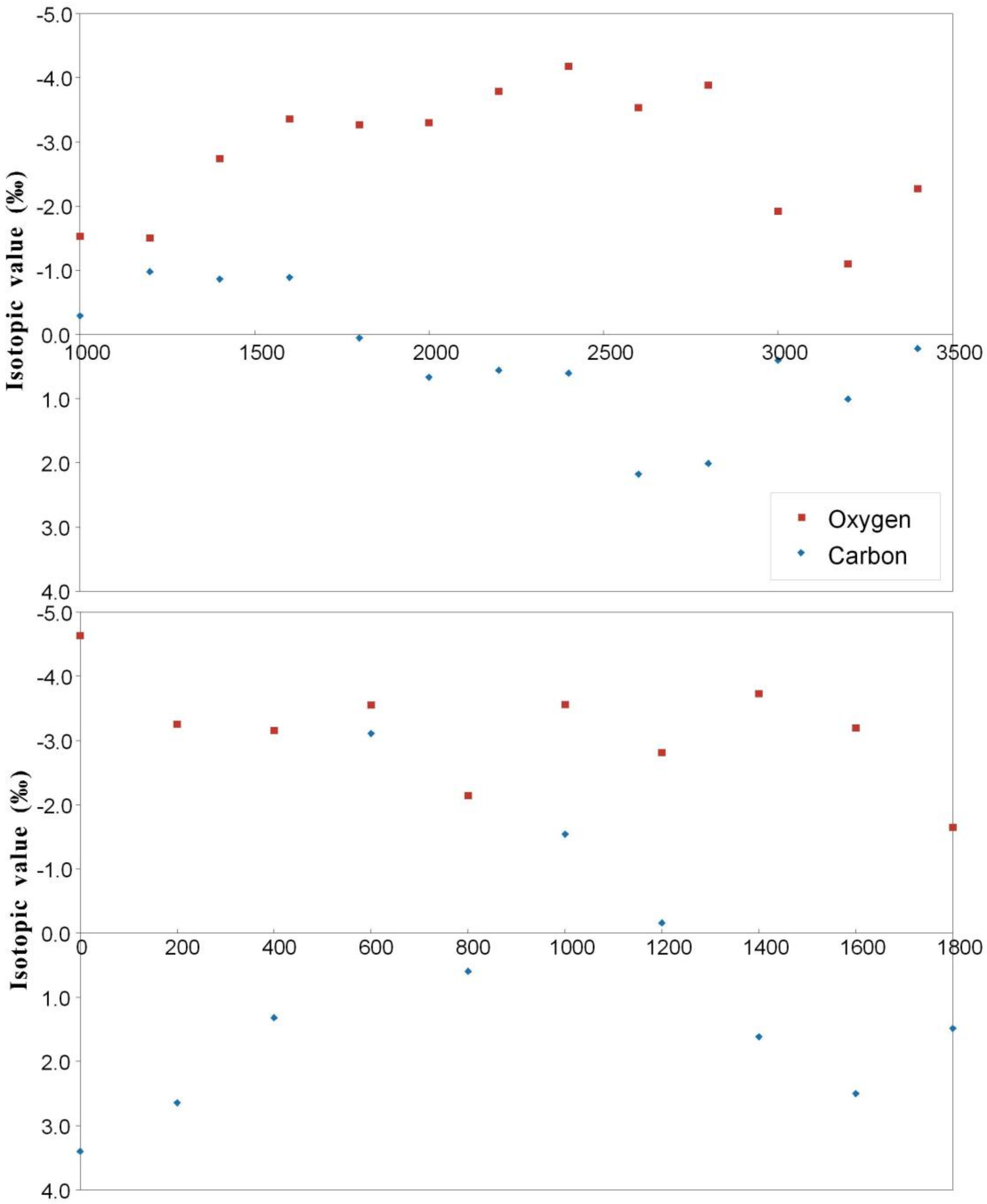


Figure 7.29. Stable isotope profiles <u>Cubitostrea plicata</u> (C1) of two transects from the hinge area to the umbro (left-right)

Samples from *Ostrea velata* (O1) unaltered areas recorded δ^{18}O values between -0.86‰ and -4.28‰ (mean -2.72‰, standard deviation 1.22, n8; Fig. 7.30). From these δ^{18}O values the mean interpreted temperature is 26.0°C (standard deviation 5.76, n8). δ^{13}C values range between 2.91‰ and 0.97‰ (mean 1.81‰, standard deviation 0.83, n8).

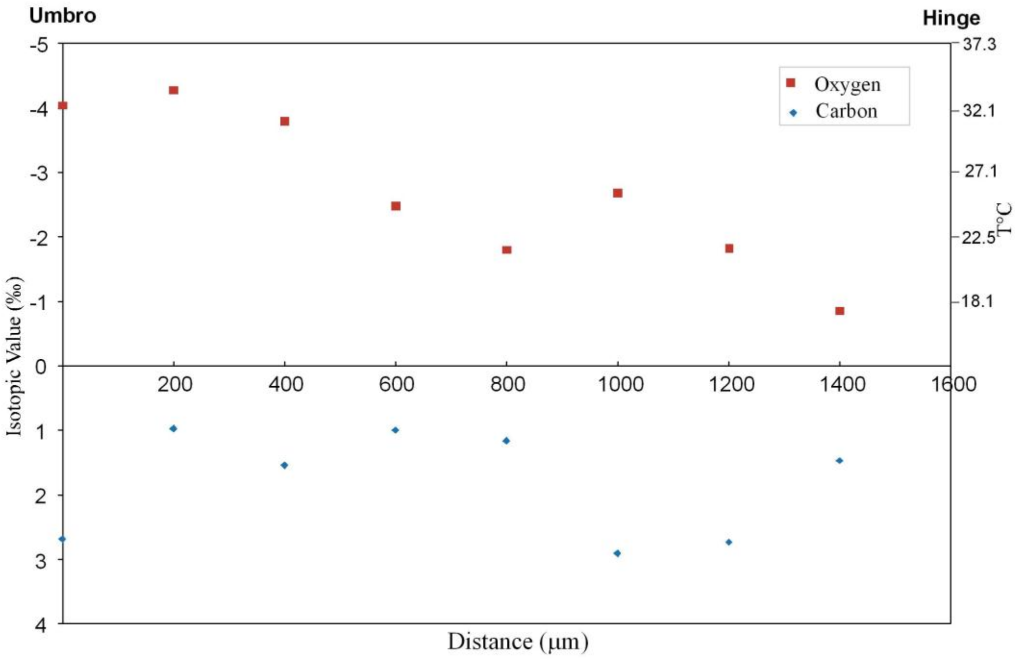


Figure 7.30. Stable isotope profile of *<u>Ostrea velata</u>* *(O1) of a single transect µm*

Lutetian Molluscs (T1, V1)

Oxygen and carbon isotopes were analysed from unaltered areas of the specimen *Cubitostrea plicata* (C1, Fig. 7.31)

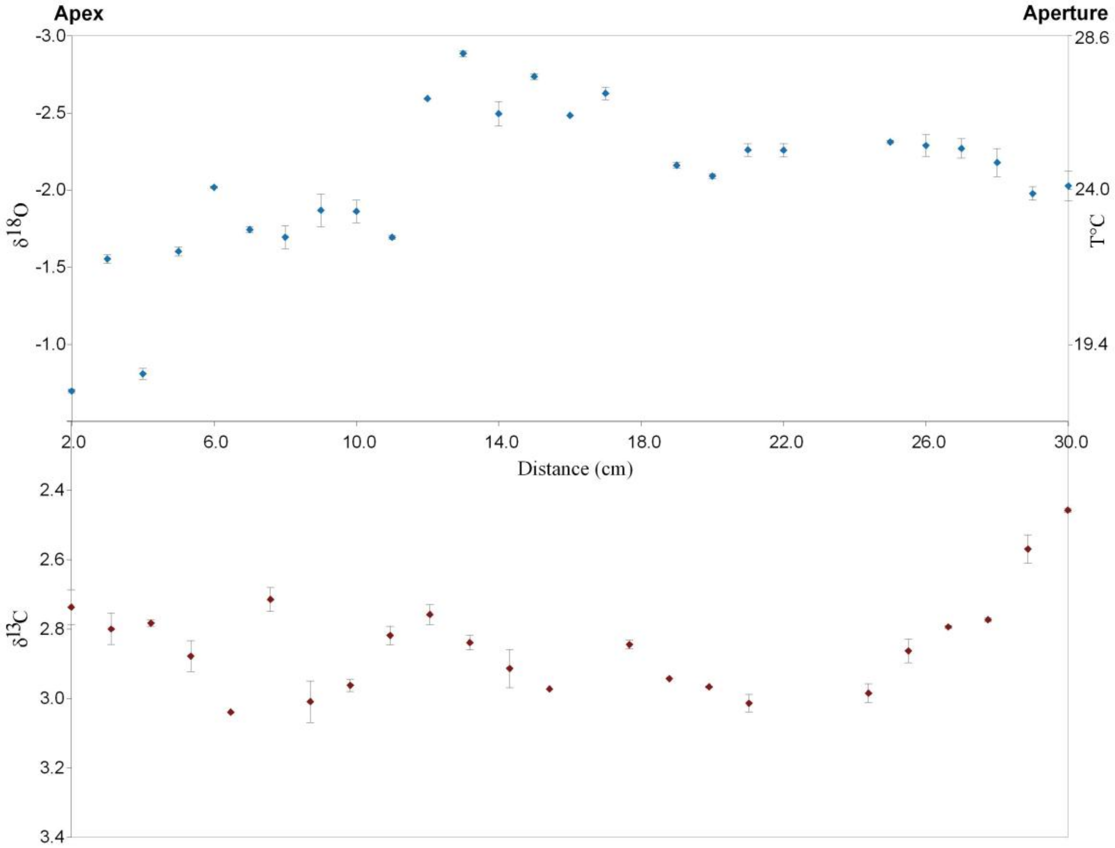


Figure 7.31. Stable isotope profile of *<u>Turritella imbricataria</u>* *(T1)*

Samples recorded δ^{18}O values between 1.60‰ and -2.89‰ (mean -2.19‰, standard deviation 0.36, n21). From these δ^{18}O values the mean interpreted temperature is 24.9°C (standard deviation 1.65, n19). δ^{13}C values range between 3.04‰ and 2.46‰ (mean 2.84‰, standard deviation 0.14, n21).

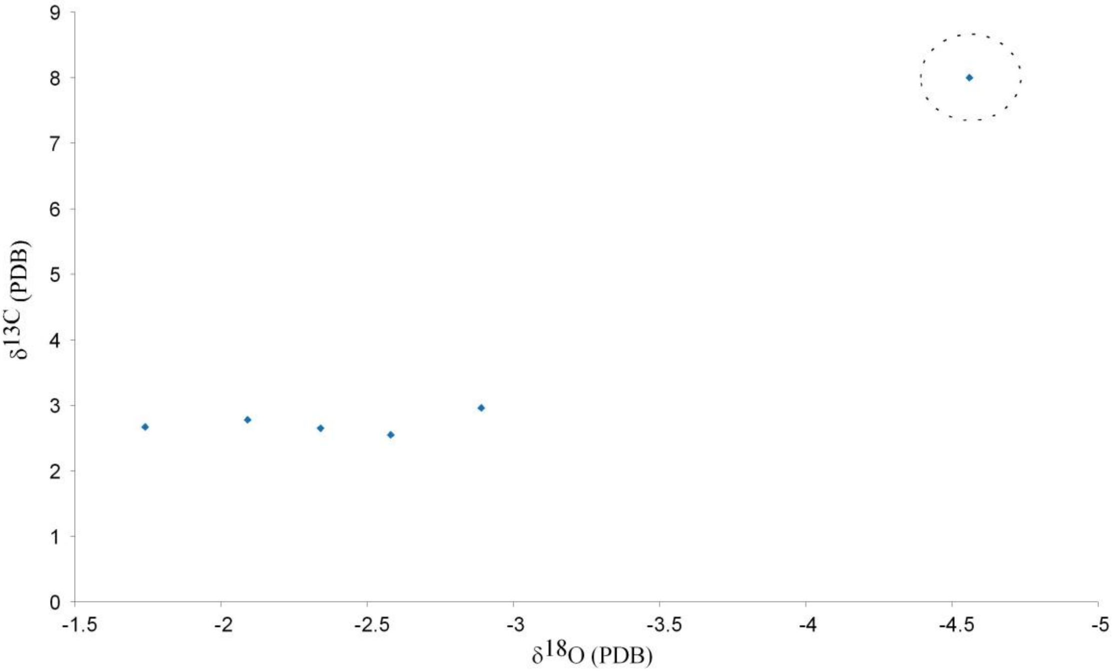


Figure 7.32. Stable isotope profile of *Venericardia imbricata* *(V1)*

Oxygen and carbon isotopes were analysed from unaltered areas of the specimen *Venericardia imbricata* (V1, Fig. 7.32). Samples recorded δ^{18}O values between -1.74‰ and -2.89‰ (mean -2.33‰, standard deviation 0.44, n5). From these δ^{18}O values the mean interpreted temperature is 25.5°C (standard deviation 2.02, n5). δ^{13}C values range between 2.95‰ and 2.65‰ (mean 2.72‰, standard deviation 0.16, n5). An additional result appears anomalous with a δ^{18}O value of -4.56‰ and a δ^{13}C value of 8.01‰.

7.4.10 Discussion

The long term trend of the Cenozoic is of an evolution from a 'greenhouse', ice-free world in the Cretaceous, with low latitudinal temperature gradients, to the 'icehouse', glacially dominated world characterising the Oligocene through to present, with steep latitudinal temperature gradients (Crowley and North, 1991; Frakes *et al*., 1992). Studies have concluded that tropical sea surface temperatures cooled gradually throughout the Eocene, however most climate proxy records support warm and stable tropical sea surface temperatures throughout the Eocene, with small cooling steps at 48, 45 and 42 Ma (Zachos *et al*., 2000; Tripati *et al*., 2005). The distribution of *Acropora* in the Hampshire and Paris basins during the Eocene is believed to have been at its maximum northern Cenozoic limit and support a poleward migration of tropical faunas. Mega-thermal vegetation distributions, including rainforests and mangroves, showed their maximum poleward extent with polar broad-leaved deciduous forests at the poles (Collinson, 2000), and rich tropical fauna extending 10-15° poleward of their present position today (Crowley and North, 1991).

Various biocarbonates have been analysed for stable oxygen and carbon isotopes, and Sr/Ca ratios, along the transect of growth, on excellently preserved specimens from the Hampshire and Paris basins.

CARBONATE	AGE	TAXA	TEMPERATURE (°C) MAX	MIN	MEAN	STANDARD DEVIATION
Corals	Lutetian	*Acropora*	34.6	31.2	**32.4**	1.93
		Lobopsammia	33.9	27.0	**30.1**	2.76
	Bartonian	*Acropora*	39.9	27.0	**33.2**	4.04
		Lobopsammia	36.5	26.9	**31.0**	3.52
		Goniopora	32.3	28.9	**31.0**	1.84
		Trochoseris	31.2	26.7	**29.4**	2.37
	Priabonian	*Acropora*	34.5	31.5	**32.5**	1.35
		Lobopsammia	30.1	26.7	**28.9**	1.23
	Eocene	*Acropora*	30.9	11.4	**19.4**	3.24
Molluscs	Lutetian	*Turritella*	28.1	22.2	**24.9**	1.65
		Venericardia	28.1	22.8	**25.5**	2.02
Molluscs	Priabonian	*Cubitostrea*	35.3	18.5	**27.1**	4.47
		Ostrea	33.5	17.5	**26.0**	5.77

Table 7.7. Summary of palaeotemperatures derived from various biocarbonates of the Eocene of the Hampshire and Paris basins

Detailed isotopic analyses have been performed on aragonitic corals and marine molluscs, and calcitic marine mollusc shells of Middle to Late Eocene age. Overall the mean inferred temperatures show a minimum of 24.2°C and a maximum of 33.2°C (mean 29.2°C, standard deviation 3.06; Tab. 7.7). The mean Lutetian palaeotemperature is 27.9°C. For the Bartonian the mean palaeotemperature is 31.1°C. Finally, the mean Priabonian palaeotemperature is 28.6°C. Specimens from both basins indicate subtropical to tropical palaeoenvironments.

This is supported by Early to Middle Eocene, middle to high latitude, tropical to subtropical indicators. Sedimentological indices included laterite soils, which are indicative of warm climates with seasonal rainfall, extending up to 45° in both hemispheres (Crowley and North, 1991). Pacific sediments showed a dramatic decrease in aeolian grain size which reflects a reduction in wind velocities. The Eocene mammalian fauna of Ellesmere Island, Greenland, includes flying lemurs, alligator-like crocodilians, rodents and turtles (McKenna, 1980). Associated with the rise in sea-level during the Middle Eocene was the isolation of Western Europe. The Northern Atlantic corridor was severed and warm, tropical waters expanded northwards dividing Europe into an archipelago of islands in a shallow tropical sea (Prothero, 1994).

On the basis of taxonomic uniformitarianism, the presence of z-corals in both basins reflects tropical conditions which are supported by the oxygen isotope ratios (Tab. 7.8).

TIME	METHOD	BASIN	INFERRED TEMPERATURE (°C)
Lutetian	Isotopes	Paris	27.9
	Energy hypothesis	Paris	18.7
Bartonian	Isotopes	Paris	31.1
	Energy hypothesis	Paris	18.7
	Energy hypothesis	Hampshire	15.8
Priabonian	Isotopes	Hampshire	28.6
	Energy hypothesis	Hampshire	17.0
Eocene	Isotopes	Hampshire and Paris	19.4
Chattian	Energy hypothesis	Aquitaine	21.7
Aquitanian	Energy hypothesis	Aquitaine	20.1
Burdigalian	Energy hypothesis	Aquitaine	20.3

Table 7.8. Comparison of average inferred palaeotemperatures from both methods

Derived temperature estimates based on the ‘energy hypothesis’ show a minimum mean estimate of 15.8°C which is consistent with temperatures associated with modern, high latitude non-reefal coral assemblages (e.g. Japan, see Halfer *et al.*, 2005). Disparities between the minimum isotope-based estimates and the ‘energy hypothesis’ probably reflect underestimates of generic z-coral diversity resulting in lower minimum mean temperature estimates.

Results of previous reconstructions for this time interval support the seawater temperature estimates here with early middle Eocene water temperature estimates from Andreasson and Schmitz (1996) between ~14 and ~28°C, with a mean annual temperature (MAT) of ~21°C. Whilst other work argues against these seawater temperatures, for example this MAT estimate is significantly warmer (~9°C) than that of Zachos *et al*. (1994). Murray and Wright (1974) indicate Middle Eocene summer temperatures of ~22°C and thermophilic fauna and flora in Germany indicate MAT >20°C and cold month mean (CMM) >10°C during the early and middle Eocene (Schaal and Ziegler, 1992). Late Eocene Summer temperatures are estimated at 16-18°C (Murray and Wright, 1974).

Such a large temperature difference between these localities and other open ocean estimates require an unrealistically high temperature gradient. The stratigraphy of the section in both basins suggests that the seawater could have been diluted by fresh water, which would give rise to erroneously high ^{18}O estimates of palaeotemperature. At the Lutetian localities, according to Aubry (1986), Abrard’s Zone IV consists of alternating brackish and marine deposits, which suggests that the ambient waters may have been diluted at least episodically. In the Priabonian Hampshire Basin, the Headon Hill Formation (Solent Group) is dominantly a freshwater and brackish water section with a short-lived marine incursion (Daley, 1999). The molluscan fauna are most frequently small, white and thin-shelled indicative of quieter water conditions. Most of them lived in lacustrine conditions or brackish, lagoonal water with pond snails such as *Galba* or *Viviparus* common in the freshwater strata. Locally derived fresh water may have been considerable even in a semiarid environment of the Paris Basin.

Temperature seasonality, the difference between summer and winter temperature, is another important element of the Eocene climate. Intrashell stable isotope profiles from shallow-water gastropods and bivalves from the Middle to Late Eocene were studied here in order to determine the seasonality of sea surface temperature. Oxygen isotope profiles of shells from the Middle Eocene Paris Basin suggest a seasonality of ~6°C, with a winter temperature of ~22°C and a summer temperature of ~28°C. Relative to the present temperatures in the area, the Eocene summer temperature was similar, whereas the winter temperature was higher with resultant mean temperatures being higher than Eocene times. Isotope profiles of shells from southern England indicate during the Late Eocene the mean temperature was 8–10°C higher in Eocene time.

By the Late Eocene, the floral assemblages in Europe showed subtle evidence of the cooling, due to the cooling and drying being balanced by the tropical seas and island humidity. This was represented by a decline in the diversity of tropical and subtropical plants and an increase in fresh water plants (Collinson and Hooker, 1987). Flora altered from the evergreen subtropical to tropical forest belts prevailing in the early Eocene to dominantly deciduous or semi-evergreen assemblages at the end of the Eocene (Collinson, 2000). Coincidental to this, *Acropora* was progressively lost from NW Europe, first from the Paris Basin, followed by the final occurrences of the genus, and z-corals, in the Priabonian Hampshire Basin deposits. All the tropical characteristics of the early Eocene had disappeared and the majority of the floral assemblage of Europe, and specifically England, were reed marshes, pondweeds, walnuts, Papaver poppies, buttercups, raspberries and blackberries (Prothero, 1994).

Work here has supported the opinion that the application of ^{18}O palaeothermometry to calcareous skeletons from marginal marine settings has the tendency to overestimate palaeotemperatures as the result of fresh-water mixing. Multi-proxy climate reconstruction attempts using Mg/Ca and Sr/Ca ratios may help in these environments. Sr/Ca ratios appear to confirm the palaeotemperature results from the oxygen isotope ratios although uncertainties and continued research into new calibrations make this technique in the fossil record highly speculative. Mg/Ca ratios have been regularly used to isolate the temperature record from that of the $\delta^{18}O_{seawater}$ in oxygen isotope ratios and could be utilised here. Fundamentally the signal from these specimens is highly complex due to their nearshore, shallow marine settings.

The combination of the two methods, the 'energy hypothesis' and geochemical analysis, are both riddled with uncertainties. However, where these can be minimised, the two methods can be used in conjunction for palaeotemperature reconstructions from carbonates in the shallow marine setting. A comparison between the average estimated palaeotemperatures from both the energy hypothesis and isotopes shows a range. Palaeotemperatures inferred from the number of z-coral genera of all localities (the energy hypothesis) estimates the minimum past sea surface temperatures, however the geochemical results show an average of both the minimum and maximum estimated palaeotemperatures.

7.5 CONCLUSIONS

- *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, and is commonly regarded as a genus of fast growing corals. The fossil record shows that *Acropora* existed up to ~48°N during the Eocene in the Hampshire and Paris basins (Chapter 7).
- 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 rapid rates of sedimentation 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.
- *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 12cm 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.
- On the basis of modern distribution of zooxanthellate corals, the presence of *Acropora* within the two basins suggests tropical climatic 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 here by oxygen stable isotope values and strontium/calcium ratios on specimens from both basins indicating subtropical to tropical

palaeoenvironments and the higher variation in carbon values reflecting the paralic environment in both basins.

- Additional elements and elemental ratios (Fe, Zn, Pb, Ba/Ca) indicate episodic elevated levels of sediment input, and nutrients, on an interannual range.
- In summary, 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.

CHAPTER 8. DISCUSSION

CONTENT

8.1 OVERVIEW

This thesis aimed to establish the stratigraphic, evolutionary, and biogeographical history of the genus *Acropora* and compare this with known patterns of climate change and palaeogeographical reconstructions of availability of suitable habitat through the Cenozoic. This has been treated in a series of steps as follows:

1. A database was compiled of existing fossil *Acropora* records, revised as necessary to bring the names and stratigraphy into line with current classifications (Chapter 3).

2. Training in coral taxonomy allowed species-level identifications of fossil *Acropora* and the development of a working taxonomy for fossil *Acropora* based on how the surface characters used for modern species recognition correspond (or not) to characters seen in sectional preparations of fossil specimens (Chapter 4 and 5).

3. Field work in high palaeolatitudinal settings of selected areas in France and England to improve the distributional data of *Acropora* and gain an understanding of *Acropora* taphonomy and palaeoecology (Chapter 6).

4. Fossil specimens were assessed for diagenetic alteration followed by stable isotope work on selected pristine aragonitic specimens, for palaeoenvironmental information (Chapter 7).

5. This was supported by the palaeoenvironmental context of the databased records, using (a) stratigraphical, taphonomic, palaeoecological and sedimentological information, (b) stable isotope work on the *Acropora* specimens, and (c) published regional and global palaeoclimate models for the Cenozoic (Chapter 6 and 7).

The results of each of these lines of investigation are discussed below in relation to the findings in this thesis and previously published work in this field.

8.2 CENOZOIC HISTORY OF THE GENUS, *ACROPORA*

The database of 308 existing species-level fossil records in Chapter 3 documents the history of one individual taxon, *Acropora*, to demonstrate how one of today's particularly important reef coral genera has responded to global change through its geological time-span. A complementary stratigraphic approach has been used to generate spatio-temporal plots ('Boucotgrams', named for Art Boucot) of the fossil record of *Acropora,* to identify its past distributions and hence the changing patterns of its distribution through the Cenozoic from its earliest Paleocene records. This genus was chosen as an exemplar for zooxanthellate corals in general because it is the most diverse, widespread and abundant of modern tropical reef corals, with its centre of diversity in the 'Coral Triangle' of the Indo-West Pacific.

From the distribution data a series of patterns have been generated (Chapter 3). These patterns are abstractions of raw data and it is sometimes possible to infer different patterns from the same data, depending on methods used. These patterns reflect not only a palaeoenviromental control but also an artefactual component. It has been widely recognised that different geological periods yield different numbers of fossils principally due to the different amounts and types of sedimentary rock being formed. Additionally, a palaeolatitudinal sampling bias of these fossils is affected by a skew of onshore rocks being preserved in the northern hemisphere affecting the collecting opportunity. Other issues include historical, political and economic factors which have also produced a bias towards collecting from the northern hemisphere, in particular to records from western Europe and northern America, where fossil collecting has been much more extensive and for longer. Throughout this work, collections have shown that regions such as Southeast Asia are under-sampled, and have preservational issues, and a lack of recent work on collections and publications. Furthermore, publications relating to the fossil content of this area are often in a variety of languages, in local publications that date well back into the nineteenth century. In relation to the wealth of databases outlined above, many of these are worked on by multiple authors which can produce a lack of clarity in standardisation, particularly with respect to taxonomy and stratigraphy. In relation to taxonomy, the 'monographic effect' (Raup and Boyajian, 1988) also causes problems due to the effect of periodic taxonomic revision. Another problem is that these records are often based on both specimen and literature based records with no transparency or distinction between the two.

Although some of the patterns identified in this thesis may be due to sampling bias (as above), they indicate that *Acropora* (along with numerous other reef coral taxa) did not occur in SE Asia during the early Cenozoic, but was common during the Paleogene to early Neogene in Europe. The fossil record of *Acropora* indicates that its earliest records, and therefore likely origin, were in a North African-Mediterranean region (Chapter 3) and that the genus diversified (Chapter 4 and 5) in this region (Wallace and Rosen, 2006; White *et al*., 2006; Wallace, 2008). The oldest records are from the late Paleocene of Italy (Moussavian and Vecsei, 1995), Austria (Tragelehn, 1996) and Somalia (Carbone *et al*., 1994). The Middle-Late Eocene localities in the Hampshire and Paris basins represent the most northerly latitudinal extent (~48ºN) of *Acropora* in its entire history. These high latitudinal occurrences coincide with a period of global warming in the Middle Eocene (Zachos *et al*., 2001) as documented in Chapters 3 and 6.

Acropora often occurs today as an ecologically dominant coral within many z-coral reefal assemblages. However, from the earliest occurrences of the Paleocene to the Middle Oligocene there seems to be an absence of *Acropora*-dominated assemblages until those of the Late Oligocene in shallow sublittoral environments of the Mesohellenic Basin of Northwest Greece and the Early Miocene lagoonal deposits of Egypt (Schuster, 2000). Nevertheless, *Acropora* is common in the Late Eocene coral assemblages of the Hampshire and Paris basins (Chapter 6), and in coral patches and small patch reefs within the lagoonal deposits of Mallorca (Alvarez, 1993). In the Oligocene, *Acropora*-bearing coral assemblages are described from Italy (Pfister, 1980 and 1985) and in coral layers of southern France (Chevalier, 1961; McCall *et al*., 1994; Monleau *et al*., 1994). The dominant genera of the different coral associations described by Pfister (1985) are *Goniopora*, *Actinacis*, and *Astreopora*. The coral occurrences of southern France (Carry-le-Rouet, Provence; Monleau *et al*., 1994) are mainly composed of allochthonous layers formed by branches of *Porites* and *Acropora* and authochthonous isolated, massive colonies (Chevalier, 1961; Monleau *et al*., 1994). By the early Miocene, in the Aquitanian, *Acropora* is found within the coral assemblages of southern Portugal, however by the Tortonian, coral reefs had disappeared on the Atlantic side of France and yet were described as flourishing on the Mediterranean side (Chevalier, 1961; Cahuzac and Chaix, 1996). This suggested that the Mediterranean area was a "refuge" during the Late Miocene (Esteban, 1978). Other Early Miocene occurrences of *Acropora* are described from European localities of SW

France (Chevalier, 1961), Italy (Chevalier, 1962), Cyprus (Follows, 1992; Follows *et al.*, 1996), Turkey (Hakyemez, 1989), and on the Arabian peninsular in Iran (Schuster, 2002) and in Pakistan (Duncan, 1880). In the periods of re-establishment of marine conditions during the Messinian the dominant reef builder in Spain was *Porites,* and within more protected areas, *Sidereastrea* and *Montastrea* occurred (Esteban, 1978). Nevertheless *Acropora* is described by Barrier *et al.* (1991) from the Breches Rouges de Carboneras Formation, La Atalaya Mazarron section, of SE Spain, which appears to be the latest occurrence of *Acropora* in the Mediterranean region, following an absence of occurrences in the Langhian-Serravalian. By the latest Miocene, *Acropora* was no longer in the Mediterranean region, however it had become established in both the modern realms of the Atlantic-Caribbean and Indo-Pacific. In summary, *Acropora* appears to have become extinct in Europe during the latest Miocene, but emerged relatively recently in the SE Asia region. This suggests (1) a ‘hotspot shift’ (‘hotspots’ are areas of exceptionally high biodiversity and rates of endemism; Mittermeier *et al.*, 1998, Hughes *et al.*, 2002) from Europe and adjacent regions to SE Asia during the Oligocene-Miocene and (2) that at least part of the taxonomic structure of the modern SE Asia hotspot consists of taxa accumulated from Europe and elsewhere (cf. Centre of Accumulation; *sensu* Bellwood *et al.*, *in press*).

These stratigraphic patterns of the genus were compared with global climatic reconstructions to identify how closely these patterns seemed to match (or not) climatic patterns. Although, global climatic deterioration led to the retraction of the maximum northerly limit of the genus in the late Eocene, the continued sub-tropical conditions and availability of habitat through the archipelago of the proto-Mediterranean area led to the continuation of *Acropora* in the area. The progressive restriction of the northerly latitudinal extent of the genus fits with the overall global cooling trend of the Cenozoic. This climatic trend was interrupted by geological short periods of climatic warming in the Eocene, coincidental with this *Acropora* extended into its most northerly latitudinal extent of its Cenozoic history. Following this, as the global climate continued to progress from the Cretaceous greenhouse to the Neogene icehouse conditions, the northerly latitudinal extent continued to contract.

The maximum southerly latitudinal pattern does not appear to follow global climatic reconstructions and although potentially does correlate with climatic patterns this is probably masked by the sampling biases outlined above. The palaeolongitude pattern shows a similarly restricted extent during the earliest records of *Acropora*, with records only from the North African-Mediterranean area. This was followed by the palaeolongitudinal expansion of occurrences at the Paleogene/Neogene boundary. The palaeolongitudinal distribution pattern of the genus is partly explained by global climatic patterns, although additionally the availability of habitat, particularly in Southeast Asia region. *Acropora's* distribution was persuasively disrupted by a series of plate tectonic events throughout the Cenozoic. The Tethys Sea remained open with an east-west connection between the present-day Pacific and Atlantic Oceans via the Mediterranean. This Tethys seaway is hypothesised to have flowed in a westerly direction including a passage north of the Indian continent and through the Mediterranean region, and may have resulted in the Indian Ocean corals playing an important role in seeding the European reefs. Rosen (1988) suggested that there were several closures of the pan-tropical seaway in the Late Oligocene-Early Miocene, with the latest possible date of contact between the Caribbean and Indo-Pacific taxa via the Middle East and final closure of the Tethys in the mid-Miocene (~12 Ma; Rogl and Steiniger, 1984). The net affect of these Cenozoic plate tectonic events on the genus was the establishment of two diversity highs in the Atlantic-Caribbean and the Indo-West Pacific. Like other marine biota (Knowlton *et al*., 1993) the differentiation of *Acropora* species on both sides of the Isthmus of Panama preceded the closure of the Tethys seaway in the Middle East. The Neogene saw a global shift to shallow marine, low latitude coral reefs (Kiessling *et al*., 2004) which paralleled global cooling, the diversification of z-corals and the occurrence of *Acropora* becoming ecologically dominant in low latitude coral reefs.

This thesis has demonstrated that it is possible to extract global and regional ancient climate responses from the fossil records of one coral genera but there are limitations and these may be overcome by using several genera, as discussed below.

8.3 CENOZOIC *ACROPORA* DIVERSITY, COMPARISON WITH THE REST OF THE FAMILY AND OTHER CORALS

An Eocene appearance date (54 Myr) for *Acropora* has been used as a molecular clock calibration (Fukami *et al*. 2000) (though as confirmed here in Chapter 3, the oldest records of *Acropora* are Paleocene), but potentially the fossil record provides much more information about the relationship between past and present taxonomic composition (Stehli and Wells 1971; Potts 1985; Veron 1995; Fukami *et al*. 2000). It is commonly assumed that the species composition of extant reef corals, including *Acropora*, has been most strongly influenced by Neogene evolutionary events, particularly the Panama closure and Plio-Pleistocene sea level fluctuations of the last two million years (Fukami *et al*., 2000).

The fossil *Acropora* specimens studied in this thesis came from the Eocene of the Hampshire and Paris basins, and from the Miocene of the Aquitaine Basin. In total 78 specimens were studied. This material fell into 15 morphological groups whose characters were consistent with separate species (Chapter 5). Of these groups, twelve correspond to previously described fossil species: *Acropora alverezi, A. anglica, A. bartonensis, A. deformis, A. britannica, A. exarata, A. lavandulina, A. ornata, A. proteacea, A. roemeri, A. solanderi* and *A. wilsonae*. The remaining material is interpreted as representing three new morphospecies, two from the English deposits: from the Bartonian and Priabonian of the Hampshire Basin (morphotype 1 and 3) and one from the Bartonian of the Paris Basin, France (morphotype 2). This thesis used well-established morphological characters of skeletal surfaces as used by Recent coral taxonomists in general and by Wallace (1999) in particular for *Acropora*. In addition, this thesis has pioneered the use of internal detail for *Acropora*, by routinely using standard thin section methods, but also developing a micro-CT-based approach. These methods are largely non-quantitative and broadly follow the approach of Wallace (2008) when tackling the fossil record. Specimens of all 15 species in general exhibit remarkable morphological variation, including at least six colony shapes, both determinate and indeterminate growth (*sensu* Wallace, 1999, p. 50–51), at least four types of radial corallite, four types of coenosteum and variations of other *Acropora* characters. Some characters were identified as to be simply part of the spectrum of intra-specific variation for a particular species, and others were characters (i.e. ‘conservative characters’) which were species-diagnostic. In the fossil record this distinction has largely been done by quantitative/statistical methods for morphospecies (e.g. Budd *et al*., 1994; Johnson and Budd, 1994), but here, as with Wallace (2008), non-quantitative methods have been used. This leads naturally to the possibility of reservations or problems about deciding on species limits. Although specimens of branches up to 12cm were found from the Eocene of the Hampshire and Paris basins showing clear colony form, many are only on a centimetre scale and therefore only represent a small area of the colony form, making their species designation more subjective.

These descriptions (Chapter 5) support the hypothesis that the genus diversified rapidly in North Africa-Mediterranean, with 20 species (out of 40 described and recorded here from the fossil record; Fig. 8.1) described from the North African-Mediterranean region after its first appearance in the fossil record in the Late Paleocene of Somalia, Austria and Italy.

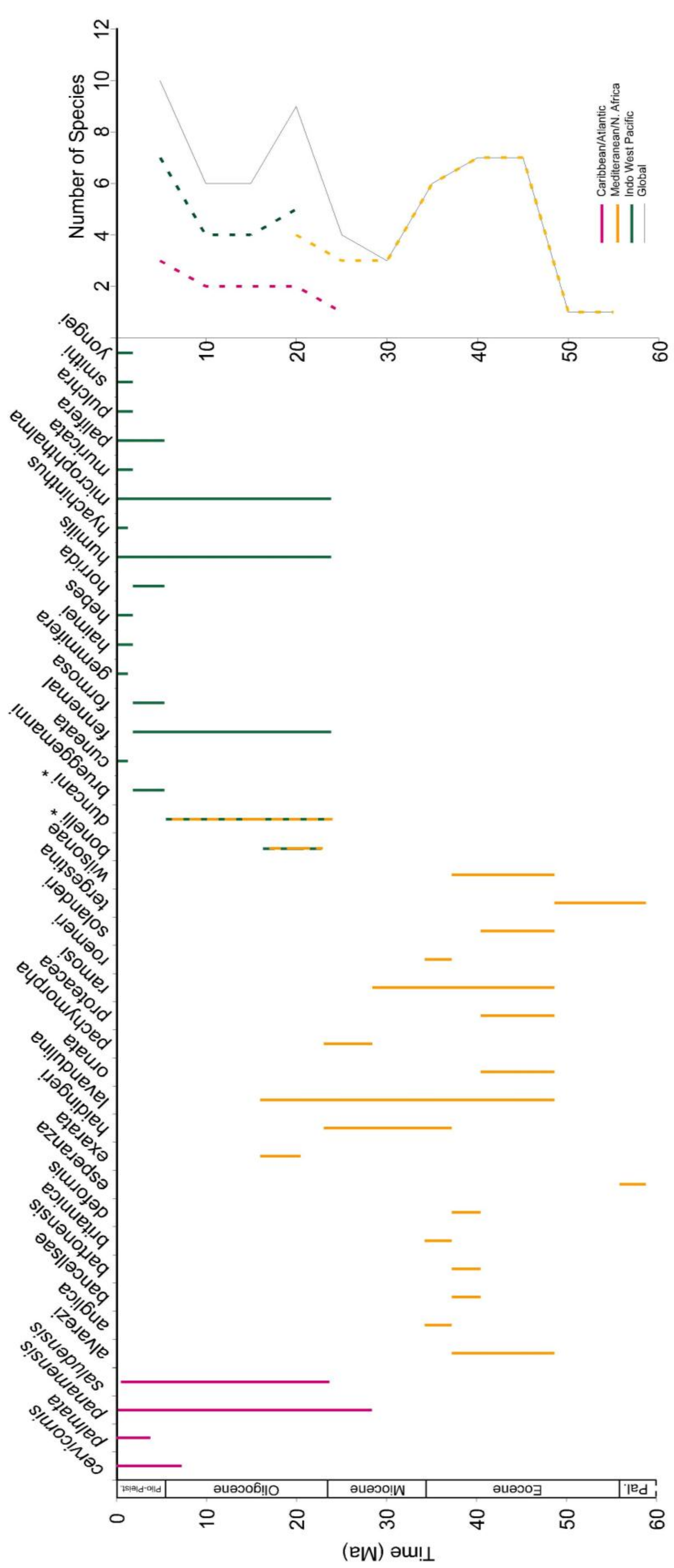


Figure 8.1. Cenozoic worldwide distribution of Acropora species recorded in this thesis

Figure 8.1 also demonstrates the problem of how low the late Cenozoic diversities appear in relation to modern diversity and distribution of *Acropora*. The view of the lineage of *Acropora* is skewed by the limitation of knowledge about recent records that have existed, thus subjecting us to the 'pull of the recent' (*sensu* Raup 1972). The latest Cenozoic curve falls short of known Recent *Acropora* species principally because species with only a very recent geological record have been omitted, these are clearly beyond the present scope of this investigation. Therefore, although they do not have a long fossil record, these records may be out there waiting to be discovered if they have not been omitted as a result of taphonomic problems. An additional feature of this plot (Fig. 8.1) is that all the species (with the exception of *Acropora duncani* and *A. bonelli*) seem to stay in their respective geographic regions. If, as the taxonomic record and diversity appear to imply, the older European (etc.) forms 'seed' the SE Asian region, then this would apparently be contradictory. Species from the older European region should appear in the SE Asian region. This is proposed here to be a problem with a lack of continuity and taxonomic protocol on work done across basins. Workers are often geographically restricted in their careers and in availability of material to study and hence there is very little comparison across regions. This would benefit from future, taxonomically consistent work across regions within the geological history of the genus. With this comes a reliance on the state of preservation of specimens in the fossil record. As part of this thesis, specimens were also studied from regions other than those primarily identified to be included in the database, but these specimens, from the Neogene of the SE Asian region, were often poorly preserved, recrystallised and lacked supraficial features making it difficult for species-level identification.

The robustness of this inferred radiation could be questioned here as being an artefactual pattern. Previously within this thesis (Chapter 3) the 'monographic effects' were discussed and this study maybe a case in point. Future taxonomic work on other assemblages from other areas within the North African-Mediterranean region would test this. The radiation of the genus inferred from species patterns (as above) is further supported by consideration of 'species groups' (*sensu* Wallace, 1999), as based on Recent species. At least some of these can be identified in the fossil record and all material studied in this thesis appears to fit within these species groups. At least half of the currently recognised *Acropora* species groups already existed in the Eocene of England and France and spread into new habitats in the Indo-West Pacific following the collision of Australia with Southeast Asia (~25Ma) when the Tethyan seaways were still open in the Middle East (Fig 8.2).

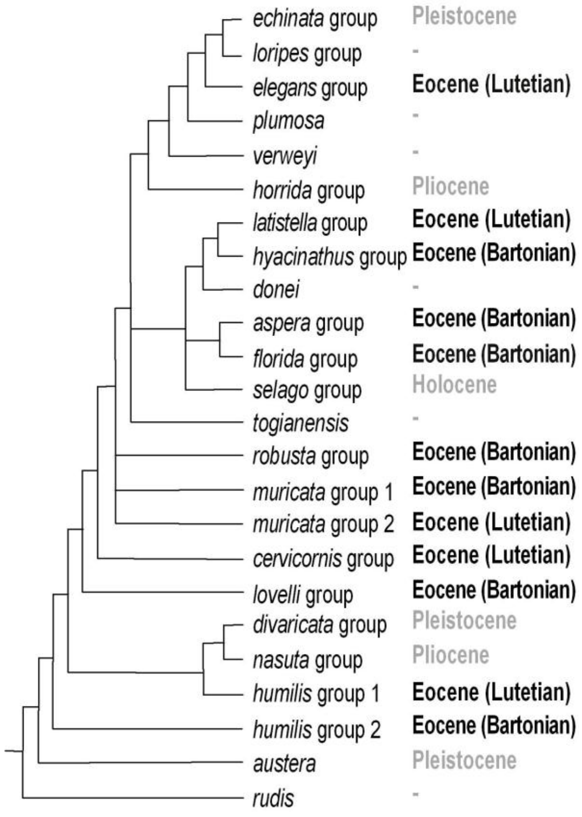


Figure 8.2. Morphology-based cladogram of species group relationships within genus Acropora from Wallace (1999), indicating earliest fossil occurrences Wallace and Rosen (2006) and updated with new species groups described in this thesis (see Chapter 5).

Molecular work on the genus appears to generate another set of groups (clades) which do not match the morphological-based species groups of Wallace (1999), hence, recent molecular data (van Oppen, 2001) are inconsistent with both cladistic phylogenies based on skeletal morphology (Wallace, 1999) and are also at odds with the fossil record. Wells (1964) recorded two species (*Acropora humilis* and *Acropora microphthalma*) from the Miocene and, van Oppen *et al*. (2001) noted that these species would both be expected to have a basal position in the phylogenetic trees, but members of the *A. humilis* group, as well as *A. microphthalma,* are scattered through different subgroups of the derived clades III and IV (see Chapter 5 for details).

Today, corals (both zooxanthellate and azooxanthellate), together with numerous other organisms such as fish and mangroves, show their highest taxonomic richness today in SE Asia and adjacent regions (‘The Coral Triangle’) (Fig. 8.2, for further details see Chapter 2).

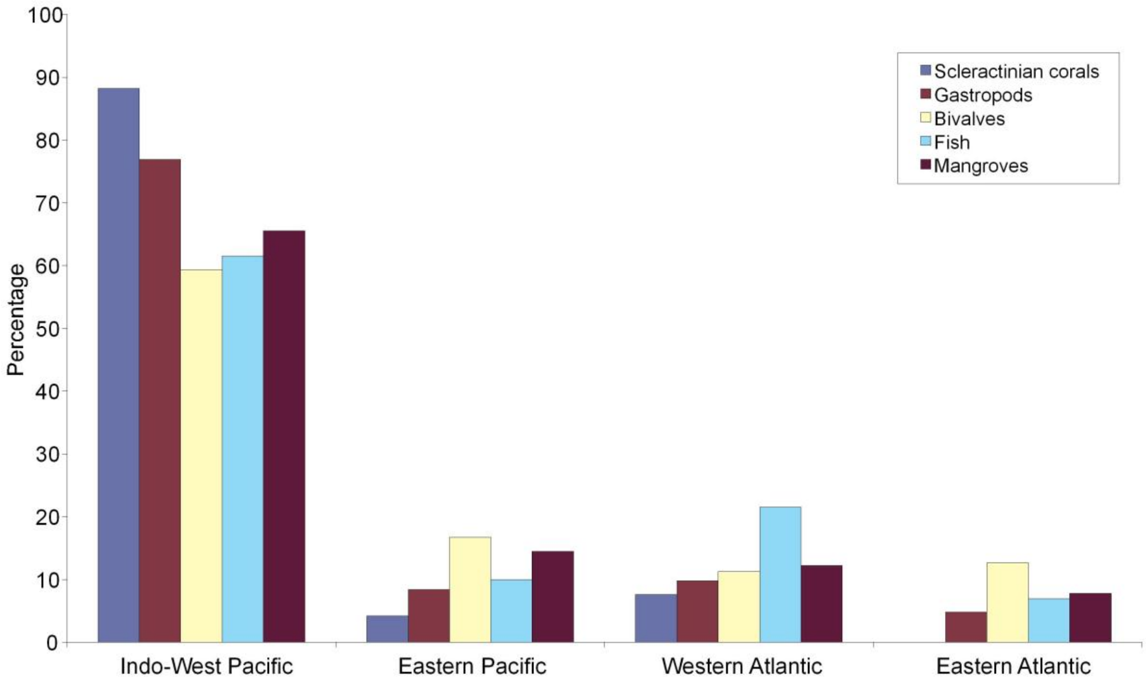


Figure 8.3. Regional patterns of species diversity in modern coral reefs and related ecosystems (data from Spalding, 2001).

The modern diversity of *Acropora* corresponds to this pattern (Fig. 8.3). *Acropora* has more than 120 valid species worldwide with at least 84 of these occurring in the Indian Ocean (Fig 8.4). Three species occur exclusively in the Atlantic Ocean (*A. cervicornis, A. palmata* and *A. prolifera*) and the remainder in the Indo-Pacific. The highest *Acropora* biodiversity is recorded from the Indonesian archipelago with the main component of this region being the ‘coral triangle’.

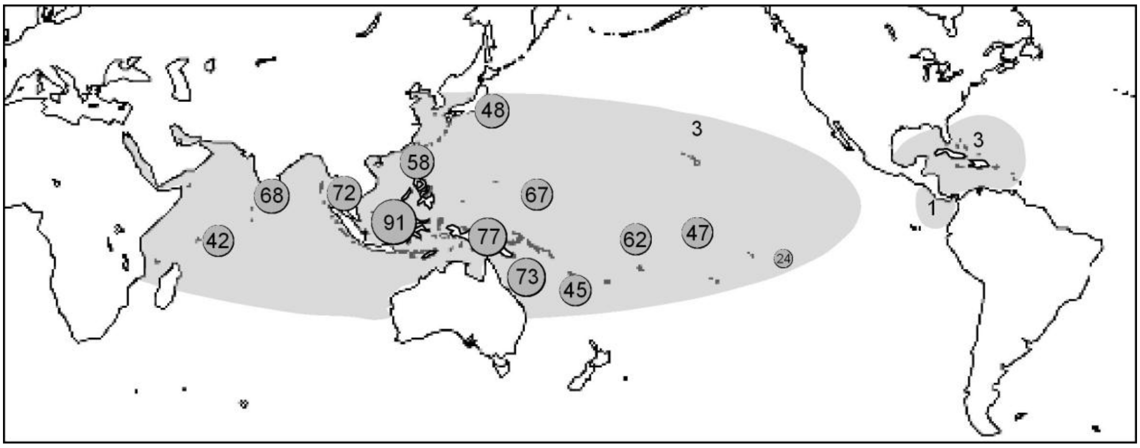


Figure 8.4. Worldwide distribution of Acropora and species numbers in each oceanic area (adapted from Wallace and Muir, 2005; data from Wallace, 1999).

Previously, hypotheses have been proposed to explain the high diversity pattern of the Coral Triangle including ''Centre of Origin'' theories hypothesising that speciation rates are unusually high within the region, and that this is responsible for high biodiversity in this region (Chapter 2). However, this work is consistent with the hypothesis that before the isolation of the Indo-Pacific there was pre-existing diversity of the genus which spread into the Indo-Pacific and subsequently contributed to rapid Indo-Pacific speciation and dispersal in this dominant genus during the Neogene, culminating in its extraordinary dominance of modern Indo-Pacific reefs. Whereas there were already quite a few z-coral taxa in the Indo-Pacific in the pre-Neogene (e.g. Wilson and Rosen 1998), this did not seem (from this work, and confirming earlier work) to include *Acropora*. Therefore in this respect, as a possible exemplar genus, its pattern seems to be different from that of some of the other modern z-corals. Following the closure of the Tethyan seaway in the early-mid Miocene, new species groups and species evolved in the Indo-Pacific. This suggests that at least part of the taxonomic structure of the modern SE Asia hotspot, the Coral Triangle, derives from taxa accumulated from Europe and elsewhere (cf. Centre of Accumulation; Bellwood *et al.*, in press). As shown above, many of the species-groups are the same today as entered the SE Asia region in the Miocene, however at species-level, no extant species have records outside the SE Asia region and this infers that they are derived from the evolution of taxa which entered the region. Many of the hypotheses proposed for the origin of this high diversity centre are based entirely on analysis of data from living taxa. However, there are also 'lost' (extinct) distributions beyond the modern areas sampled, as in the case of fossil *Acropora* studied here. This pre-determines the kind of hypotheses generated from such results, because they ignore, *a priori*, the possible biogeographical and evolutionary significance of these 'lost' distributions. Only by studying the fossil record can one uncover such patterns and hence investigate their implications for the origin of the modern high diversity centre of SE Asia. Contrary to the still popular notion of an Indo-Pacific Centre of Origin for z-corals, the Cenozoic history of *Acropora*, implies that important clues about the history of the modern 'Coral Triangle' are to be found in these 'lost' distributions outside both this area, and the entire modern z-coral belt altogether. In particular, there was an important contribution from the now extinct z-coral biota of what is now Europe and the Mediterranean.

8.3.1 Is the palaeogeographic history of *Acropora* unique?

High latitude occurrences of *Acropora* coincided with global climatic warming events of the Early-Middle Eocene (Chapter 7). This is mimicked by other warm climate indicator-organisms which showed expansion into high palaeolatitudes during this time interval, including the early Eocene London Clay Flora of southern England and the *Nypa*-dominated mangroves which extended to ~55-65° N and S during the Eocene thermal maximum (Fig 8.5; Chapter 2).

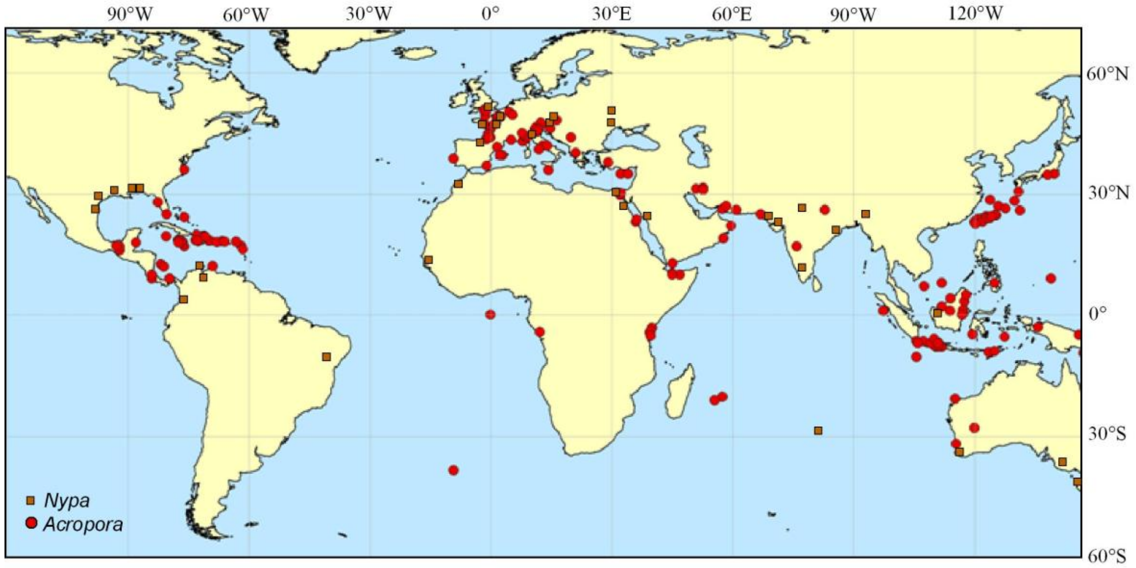


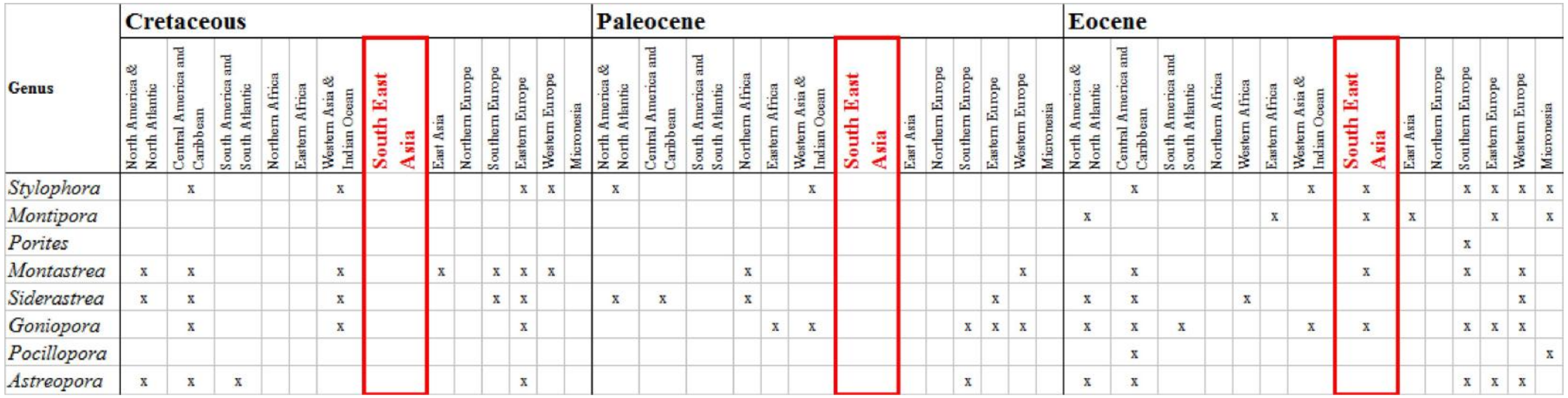
Figure 8.5. Distribution of fossil Acropora and Nypa mangroves throughout the Cenozoic (Acropora data from Chapter 3 and Nypa data from Collinson and Cleal, 2001)

During the Paleocene, new coral genera were apparently concentrated in low latitudes, suggesting that the tropics formed a source of evolutionary novelty in the recovery phase following the K/T extinction event (Kiessling, 2004). However, the very first occurrence of *Acropora* appears to have been in the low (Paleocene, Somalia; Carbone at al., 1993) and mid to high latitudes (Paleocene, Italy, Vecsei and Moussavian, 1997; Paleocene, Austria, Tragelehn, 1996). Like *Acropora*, the first appearance of another Acroporidae family member, *Dendracis*, was in the Late Paleocene of Somalia (Berbera-Sheikh area; Carbone *et al*., 1993). Unlike *Acropora*, *Dendracis* is now believed to be extinct with its last occurrence in the Miocene of South Africa

(Bessalampy, Madagascar, Colligon and Cottreau, 1927). A tentative explanation advanced here is its lack of a leading axial corallite, and consequent corallite dimorphism, restricted its potential for the much wider range of morphological variation seen in across the entire genus of *Acropora*. The genus was described by Wells (1955) as '*the protean coral genus'*, after the Greek sea-god Proteus who constantly changed his form, referring to vast within-species variability and the high degree of between-species similarity. Colony form is the morphological characteristic which is highly diverse within *Acropora* as a whole, compared with many other coral genera. This is a speculative idea put forward on the basis of information about *Dendracis* only from small pieces, and therefore is not easy to test. However morphological diversity within species from the Hampshire and Paris basins and designation to morpho-groups has been discussed in Chapter 5. However the almost similarly non-diverse, branching coral *Stylophora* has survived to the present day, although first occurrences appear different with a single European record from the Cretaceous of Ukraine (Felix, 1906) and other early records from the Indo-West Pacific. It also has a long record in the Caribbean with a first occurrence in the Eocene of Saint-Barthelemy Island, Lesser Antilles (Vaughan, 1919), but then became extinct from this area in the Miocene. Fungiid corals, which show their richest diversity at the present day in the Indo West-Pacific centre, show a similar pattern to *Acropora* with the oldest records of *Cycloseris* in the Paleocene of Somalia (Carbone *et al*., 1993) and western Pakistan (Duncan, 1880), but having occurrences in the Eocene of Europe (Germany, Draga, 1992; Italy, Maddaleni *et al*., 1997), and the Miocene of SE Asia (Kalimantan, Indonesia, Wilson and Lokier, 2002; Wilson and Rosen 1998).

Molluscan faunas display their Oligocene centre of diversity in the western part of the Western Tethys (e.g. France, Italy, see Harzhauser *et al*. 2002). The ''go-east'' scenario proposed by Harzhauser *et al*. (2002) of the molluscs fits well with the history of *Acropora* and is consistent with the interpretation of the Western Tethys as Paleogene centre of origination and diversity (Wallace and Rosen, 2006; White *et al*., 2006, this thesis). From molecular data of scleractinian corals, a relatively high proportion of Western Tethyan corals exhibit a relatively great genetic distance between many modern forms of the Indo-West Pacific and those of the Atlantic (Fukami *et al*. 2004). This, therefore supports the view (above) that important clues about the history of the modern 'Coral Triangle' are to be found in these 'lost' distributions outside both this area, and the entire modern z-coral belt.

In summary, there was the prediction in the Introduction of this thesis that *Acropora* is an ‘exemplar’ genus for a study such as this (after Wallace and Rosen, 2006; White *et al*., 2006). However, while it is an important genus to study as a potential exemplar, it may not be an exemplar for **all** z-corals. This in turn points to there being more than one kind of historical biogeographical pattern amongst Cenozoic z-corals. Further studies similar to the approach in this thesis, but on other genera, would be useful in order to discover whether the historical-biogeographical patterns shown by individual Cenozoic z-coral genera are just all randomly heterogeneous, or whether Cenozoic z-corals fall into a restricted number of patterns, and what these indicate, e.g. is the ‘go east’ or ‘hopping hotspot’ model generally applicable to most z-corals, or is it just applicable to *Acropora* and a subset of other genera. A brief summary of the Cretaceous - Cenozoic distribution of 8 z-coral genera is shown in table 8.1 for which all first occurrences are outside of the Southeast Asia area, with the earliest records of any of these being found in the region in the Eocene for 4 of the genera, with the rest having Oligo-Miocene first occurrences in the Southeast Asian region. These data support the view that important clues about the history of the modern ‘Coral Triangle’ are to be found in ‘lost’ distributions outside both this area, and the entire modern z-coral belt, with first occurrences for all 8 genera being spread throughout other Cenozoic oceanic realms.



Genus	Cretaceous												
	North America & North Atlantic	Central America and Caribbean	South America and South Atlantic	Northern Africa	Eastern Africa	Western Asia & Indian Ocean	**South East Asia**	East Asia	Northern Europe	Southern Europe	Eastern Europe	Western Europe	Micronesia
Stylophora		x				x					x	x	
Montipora													
Porites													
Montastrea	x	x				x		x		x	x	x	
Siderastrea	x	x				x				x	x		
Goniopora		x				x					x		
Pocillopora													
Astreopora	x	x	x								x		

Genus	Paleocene												
	North America & North Atlantic	Central America and Caribbean	South America and South Atlantic	Northern Africa	Eastern Africa	Western Asia & Indian Ocean	**South East Asia**	East Asia	Northern Europe	Southern Europe	Eastern Europe	Western Europe	Micronesia
Stylophora	x					x							
Montipora													
Porites													
Montastrea				x								x	
Siderastrea	x	x		x							x		
Goniopora					x	x				x	x	x	
Pocillopora													
Astreopora										x			

Genus	Eocene													
	North America & North Atlantic	Central America and Caribbean	South America and South Atlantic	Northern Africa	Western Africa	Eastern Africa	Western Asia & Indian Ocean	**South East Asia**	East Asia	Northern Europe	Southern Europe	Eastern Europe	Western Europe	Micronesia
Stylophora		x					x	x			x	x	x	x
Montipora	x					x		x	x			x		x
Porites											x			
Montastrea		x						x			x		x	
Siderastrea	x	x			x								x	
Goniopora	x	x	x				x	x			x	x	x	
Pocillopora		x												x
Astreopora	x	x									x	x	x	

Table 8.1. Comparison of the distribution of Cenozoic z-coral genera other than <u>Acropora</u> showing many have first sciences outside of Southeast Asia (highlighted by red box) and do not show occurrences in this region until the Eocene.

8.4 PALAEOENVIRONMENTAL SETTING OF ACROPORA: A TROPICAL TO SUB-TROPICAL, MARGINAL, NON-REEFAL ENVIRONMENT?

Acropora is presently found within the limits of z-coral and coral reef, in all three major oceans of the world (Chapter 2), with a modern latitudinal limit of ~30°N and 30°S. The genus exists in a wide range of depths, reef zones and hydraulic regimes, and is commonly known as a genus of fast growing corals (up to ~20cm/year). In contrast, the fossil record shows that *Acropora* existed up to ~48°N palaeolatitude during the Eocene in the Hampshire and Paris basins (Chapter 6). 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. Coral reefs have not been reported. *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 12cm in length, with intact morphological features, suggests that there was relatively little transportation and reworking of the fossils (Chapter 6). Morphologically the sturdier growth forms come from the Hampshire Basin implying relatively 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 the interpretation of rapid burial following fragmentation of the coral branches. This points to sufficiently rapid rates of sedimentation to produce a geochemically enclosed system to preserve the aragonitic fossil *Acropora* and sufficient burial to prevent bioerosion by benthic organisms. Post-depositional modifications of the coral skeleton included entrapment of glauconitic sands, in the interstices of the coral skeleton, and the precipitation of early aragonite and later calcite cement within the porous skeletal structure. Overall, relatively calm conditions prevailed within the two basins during the mid-late Eocene, although the morphology of specimens implies that the conditions were relatively higher energy in the Hampshire Basin compared to those in the Paris Basin. This may have reflected the Hampshire Basin being palaeogeographically more open to the oceanic influences of the Atlantic and North Sea, compared to Paris Basin localities. These lay set to the south of the large embayment protected by a series of anticlinal highs in the north of the embayment. These conditions would have been interrupted by a short lived period of high hydraulic energy in order to cause fragmentation of the specimens with high sedimentation rates for rapid burial.

8.4.1 Tropical to sub-tropical?

On the basis of modern distribution of zooxanthellate corals, the presence of *Acropora* within the two basins suggests tropical to sub-tropical climatic conditions persisted in Northern Europe during the Middle to early Late Eocene (Chapter 6). This is confirmed by oxygen stable isotope values and strontium/calcium ratios from aragonitic coral and molluscan specimens from both basins. Also higher variation in carbon values reflect the influence of both freshwater input and evaporitic processes within both basins (Chapter 7). This is consistent with other palaeoclimatic indicators such as palaeobotanical studies (Collinson and Cleal, 2001; Chapter 2). Additional elements and elemental ratios (Fe, Zn, Pb, Ba/Ca) indicate episodically elevated levels of sediment input, and nutrients, on an interannual scale.

8.4.2 Marginal?

‘Marginal’ coral reefs are defined as regions where steady-state or long-term average environmental limitations are reflected by the state of coral reefs or communities (Guinotte *et al*., 2003; Perry and Larcombe, 2003; Tab. 8.2). In the Hampshire and Paris basins, the evidence presented here is that in both basins *Acropora* occurred within isolated thickets/colonies, possibly forming more laterally extensive veneers, such as those seen today in the marginal settings of Broward County, on the Atlantic side of Florida (26°N; Perry and Larcombe, 2003) and Moreton Bay, Australia (27°S; Wallace *et al*., 2009). Moreton Bay is an example of a modern sub-tropical, high-latitude, marginal, non-reefal environment, where there is a total of 143 species representing 40 genera including both colonial and solitary, and zooxanthellate and azooxanthellate forms (Wallace *et al*., 2009). These coral communities are regarded by Pandolfi *et al*. (2003) as close to environmental extinction, but they have persisted as a result of a naturally dynamic system in which intermittent loss of species due to severe natural impacts such as episodic freshwater flooding is mitigated by recruitment from outside the bay. Like the Eocene of the Hampshire and Paris basins, the Moreton Bay corals show evidence of diminished coral groups occurring in thickets or small patches. However, the coral assemblage from Moreton Bay is relatively more diverse than the faunas seen in both these ancient basins, though they are not at the latitudinal limit of reefal development. Iki Island, Japan, is believed to be the most northern site supporting reef formation and this is reflected in coral diversity being low with only 22 genera. Only 4 species of *Acropora* have been identified, comparable to the number of species found in the Hampshire Basin. The distribution of *Acropora* in the Hampshire and Paris basins during the Eocene seems to have been at its northern limit, with corals potentially close to ecological extinction. Other modern marginal coral assemblages include the coral communities of Hong Kong which are near the northern limit of climatic conditions suitable for z-corals. Winter temperatures often drop below 15°C and summer temperatures can exceed 30°C at the surface in the summer (Scott, 1984). These temperatures are well outside those conditions often regarded as optimal for z-coral assemblages, but comparable to the ranges apparently experienced by Eocene corals and molluscs in both NW European basins. Other conditions, such as the south-east monsoons and associated rains which reduce salinity and smother the corals with silt, contribute to the marginal conditions of the Hong Kong area, forcing corals into shallower water and resulting in corals being unable to flourish into large reefal developments. Hong Kong is an example of a marginal environment where there is a contribution from both azooxanthellate and zooxanthellate corals including the occurrence of azooxanthellate dendrophyllids co-occurring at shallow water depths with the zooxanthellate corals. Normally they would have been pushed out to greater depths by the more competitive zooxanthellate corals (Scott, 1984). This setting also shows sedimentological similarities to the Hampshire Basin in particular as it is a mud-dominated mid-shelf environment with high sedimentation rates. Coral diversity is low with only 3 species of *Acropora* recorded (*Acropora tumida*, *A. pruinosa* and *A. candelabrum*; 2 arborescent and 1 tabular; Scott, 1984).

The combination of zooxanthellate and azooxanthellate corals in modern settings typifies marginal environments in the Hampshire and Paris basins, and the lack of other reef-building biota corresponds to the apparent absence of any reefs. The combined evidence that *Acropora* became extinct in these basins in the Late Eocene, existed for a geologically short period in each and that subsequently its northern limits retracted southwards, is all consistent with a marginal setting (see Chapter 3).

MAIN ENVIRONMENTAL LIMITS OF Z-CORALS	FOSSIL MARGINAL ENVIRONMENTS		MODERN MARGINAL ENVIRONMENTS		LATITUDINAL REEF LIMIT	
					NORTHERN	SOUTHERN
	PARIS BASIN	HAMPSHIRE BASIN	MORETON BAY	HONG KONG	IKI ISLAND	LORD HOWE
Latitude	47°N*	49°N*	27°S	22°N	34°N	32°S
Temperature	**Middle Eocene**: Summer temperatures >22˚C (Murray and Wright, 1974). MAT >20°C and CMM >10°C during the early and middle Eocene (Schaal and Ziegler, 1992).Semi- or seasonably-arid climate with rainfall less than 400mm per year (Ager, 1980) **Mid-Late Eocene:** Tendency to aridity with rainfall less than 250 m/yr (Thiry, 1989)	Late Eocene: Summer temperatures 16-18˚C (Murray and Wright, 1974)	16 °C -26 °C (Ryan, 1998)	Winter temperatures often drop below 15°C and summer temperatures can exceed 30°C at the surface in the summer (Scott, 1984). In Winter large beds of the seaweed *Sargassum* a temperate water indicator, reduced to stubs in the warm summer months	Mean annual sst ~20°C, near-shore Kurosaki 13.3°C-26.2°C (Natsukari and Takita, 1972)	18-23°C
Depth	Isolated, shallow sea	Shallow marine (<30m) (Gale, 1999)	Shallow marine, average depth 6.8m	Shallow marine, few corals exist below -10 C.D. although many of the same species thrive at -30 to -40 m C.D. in the South Pacific (Scott, 1984)	Shallow marine	Shallow marine (<20 m depth; Harriott *et al.*, 1995)
Salinity	36-40‰ (Murray and Wright, 1974)	Fully marine ≈ 36ppm (Murray and Wright, 1974, Gale, 2006)	Outflow from several river estuaries, whose occasional intense flooding may significantly reduce salinity and enhance sediment input (Wallace *et al.*, 2009)	The Pearl River Estuary with its lowered salinity and increased turbidity, influences the western waters of Hong Kong, especially in summer, on eastern shores oceanic waters prevail (Morton, 1982)	Open marine	Open marine
Substrate	Elongate anticlinal islands	Low east-west islands, formed of London Clay and Bracklesham Group sediments, created by a minimum of 500m uplift (Gale, 1999)	Unconsolidated Holocene carbonate deposits	Embayments of shale beds and artificial dollos (emplaced in 1974 to break the force of storm waves to protect the exposed dam wall)		
Water movement	Progressive isolation of the basin limited water movement. Seagrasses indicative of calm, tropical sea (Pomerol, 1982).	Protection from Atlantic storms by low east-west islands (Gale, 1999)	Lagoonal with the existence of a series of off-shore barrier islands that restrict the flow of oceanic water (Dennison and Eva, 1999)	Monsoonal climate brings water from the North China coast during the winter and warm South China Sea in the summer	High energy	High-energy conditions dominated the reef with robust branching corals dominating the developing reef (Kennedy and Woodruffe, 2000). South flowing East Australia current brings warm water and new larval recruits (Woodroffe *et al.*, 2005)
Light	**Middle Eocene**: Uplift and short wavelength folding in the northern part of basin (Guillocheau *et al.*, 2000). Eocene tectonic stability favoured prolonged pedological processes (calcretes and silicates) restricting erosion and clastic input (Thiry, 1989). **Late Eocene**: Locally derived pebbles with the Aversian deposits are indicative of the Pays de Bray axis being a positive feature and the Paris Basin was separated from the Belgium Basin by the Artois anticline (Ager, 1980).	Sediment supply from marine erosion during inversion of the Sandown Pericline and contemporaneous movement on other structures in southern England (Gale, 1999)	Enhanced sediment input from outflow from rivers (Wallace *et al.*, 2009). Additionally bottom trawling and coral mining results in the scraping and ploughing of the substrate, sediment resuspension, destruction of benthos, and dumping of processing waste	Richest coral communities occur in the unspoiled areas close to the low density population and clean water in the northeast. West is subject to influence from the Pearl River and run off of silted waters, so only small isolated colonies	Clear waters	Clear waters
Coral diversity	**Lutetian:** 30 species and 17 genera, zooxanthellate and azooxanthellate corals contribute almost equally (7 AZ, 8 Z), with colonial forms dominating (9 colonial, 5 solitary); **Bartonian:** 22 species and 14 genera, zooxanthellate and azooxanthellate corals (8Z, 6AZ) contribute nearly equally with colonial growth forms dominating (10C, 4S).	**Bartonian:** 8 species and 5 genera, azooxanthellate corals dominating, and solitary and colonial forms contributing equally, **Priabonian:** 17 species and 9 genera, azooxanthellate and colonial corals dominate	143 species from 40 genera (7 species *Acropora)*	28 genera, 44 species (3 species *Acropora*). One group which is conspicuous by its absence is *Fungia*, a free-living solitary coral living on the sandy bottom in large concentrations in the Philippines, Thailand and other SEA countries. Many of 8 species of branching *Acropora* missing, as are those of ramose Pocilloporidae. Many coral species uncommon on GBR or in different environments are found (i.e. *Pavona,* more common than in Australia)	22 genera, 39 species (4 species Acropora)	83 species (13 species of *Acropora);* coral communities contain a unique association of tropical species at their southern limits of distribution, and subtropical species which are rare or absent from the Great Barrier Reef.
Coral colony form	Coral thickets	Coral thickets	Coral thickets. Veneer on unconsolidated Holocene carbonate deposits	Fringing reefs or thickets, slow growth rates, virtually no intertidal corals apart from intertidal rock pools.	Fringing reef	Discontinuous fringing reef flanks the western side of the island (Kennedy and Woodruffe, 2000). Cover of hard coral was comparable with coral cover on some tropical reefs, ranging from less than 10% at some reef flat sites to greater than 40% cover at two seaward beach sites.
Summary of Palaeoenvironment	**Middle Eocene:** Carbonate platform becoming progressively more isolated (Guillocheau *et al.*, 2000) Wide shallow embayment, bordered by a flat hinterland (Thiry *et al.*, 2003) **Late Eocene:** Siliciclastic marine platform with development of a semi-enclosed sea open to the English Channel (Guillocheau *et al.*, 2000)	Low energy, low gradient estuarine system (Armentos at al., 1997)				

Table 8.2. Comparison of Eocene Hampshire and Paris Basin localities, examples of modern marginal settings (Hong Kong and Moreton Bay) and the latitudinal limits of z-coral reef formation (Iki Island and Lord Howe).

8.4.3 Non-Reefal?

The relatively sparse distribution of specimens, and their preservation as broken fragments in fine-grained sediments of the Hampshire and Paris basins, indicates that active reef accretion or reefal build-ups were unlikely to have occurred in either basin. In any case there is no independent evidence for build ups and framework facies. If these specimens were derived from reefal structures then unusually high energy conditions would be needed to destroy completely all evidence of such structures yet selectively preserve a limited number of pristine specimens. The existence of thickets and possible coral carpets rather than reefs raises the question as to whether this was a flourishing coral community or a disturbed/restricted state of development as seen today at Moreton Bay, Australia (Wallace *et al*., 2009).

Duncan (1866) originally suggested the presence of a reef in the Hampshire Basin saying '*now the Brockenhurst beds must be admitted amongst the strata whose remains indicate the former existence of coral reefs exposed to a furious surf and the wash of a great ocean'*. Although evidence from the present work appears to imply there was no reef within either basin it is conceded that there may have been reefal development outside, and close by, within the English Channel area. Although they do not appear to have been observed (e.g. Hamblin *et al.,* 1992), seismic profiles across the English Channel may give us future clues about this. Interestingly the presence of the fossil species, *Acropora lavandulina*, in the Cotentin area of northern France, appears anomalous since this species is not found in either of the main basins, perhaps this area was influenced by other environmental conditions connected with reef development in the English Channel area. *Acropora lavandulina* is one of two species previously identified (see Chapter 5) from the Miocene (Aquitanian-Burdigalian) reefal assemblages of Southwest France, and also from other Miocene (Burdigalian) deposits including the upper part of the Okheider section in a small patch reef, Egypt (Schuster, 2002), and the Torino Hill section, Piedmont (Chevalier, 1961). The fossil species is most similar to the modern *Acropora aculeus*, from the *A. latistella* Group.

In summary, the primary control on the spatial and temporal distribution of *Acropora*, and other coral genera, within the Hampshire and Paris basins, appears to have been 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 eventually resulted in the loss of *Acropora*, and other corals, from the two basins by the end of the Late Eocene.

8.5 FUTURE PREDICTIONS FOR CORAL REEFS

A principal aim of this project was to use the fossil record to demonstrate how one particular important reef coral genus has responded to global change throughout its geological time-span. This was to provide insights to help predict the fate of modern coral reefs complimentary to predictions based on living corals and reefs.

Regional anthropogenic processes such as pollution, dredging, and overfishing on coral reefs currently threaten the biodiversity of corals and their ecosystems (Chapter 2). Global climate change and anthropogenic processes will undoubtedly combine to add to the impact on these systems. In order to predict these changes, it is necessary to understand the magnitude and causes of variation in scleractinian coral diversity throughout its entire geological history. The fossil record documents long periods of background speciation and radiation in corals, interrupted repeatedly by various scales of extinction. Some of these events relate clearly to changes in global climate. Additionally, evidence supports the theory that relative habitat area and changing patterns of oceanic circulation and connectivity are mainly responsible for the two observed centres of recent coral diversity of the Atlantic and Pacific oceans. The Cenozoic pattern of *Acropora* as studied here corresponds to these global events, including the last mass extinction at the end of the Cretaceous, the fragmentation of the once pan-tropical Tethys Sea and its z-coral biotas into two major biogeographical provinces, and periods of glaciation causing major changes in sea level and temperature. As global climate change drives the demise of present-day tropical reef ecosystems, attention is turning to the suitability of refuge habitats. Non-framework building, high latitude coral assemblages have recently received increased attention as a potential refuge during global change, as a proxy for these changes and for testing the tolerances of these coral species (northern Gulf of California, Mexico, 29°N; Halfar *et al.*, 2005). The fossil record of *Acropora* shows that during previous globally warm periods, the genus has survived in higher latitudinal positions than seen today in marginal environments, suggesting that this genus at least may have the potential to adapt and acclimatise to globally warm conditions deemed more environmentally marginal than those seen today. The fossil record appears to imply that warmer climates ameliorate pre-existing marginal and unfavourable environments (for z corals) by making them more suited to z-corals. Potentially, the hotspot shift from an oceanic realm which is not seen today could be seen again with a latitudinal shift into more northerly latitudes.

However, something that the Cenozoic fossil record cannot shed direct light on is regional anthropogenic impacts, which are effectively superimposed on global consequences of climate change. Centres of high reef coral diversity coincide with high-density human population centres in SE Asia and the Caribbean, and thus the greatest potential for species loss lies in these geographical areas. Additionally another important factor is the potential impact of anthropogenic ocean acidification (Hoegh-Guldberg *et al*., 2007), probably not restricted to areas of high population. Global climatic warming and ocean acidification will compromise carbonate accretion, leading Hoegh-Guldberg *et al*. (2007) to predict that corals would become increasingly rare in reef systems. Resulting from this will be less diverse reef communities and carbonate reef structures that fail to be maintained. Climate change also exacerbates local stresses from declining water quality and over-exploitation of key species, driving reefs increasingly toward the tipping point for functional collapse.

Hence, data on the past response of marine ecosystems to climate change have become increasingly relevant. The major difference at present and for future predictions is the unprecedented affect of human activity on these ecosystems. However, understanding a coral’s ecological response to global climate change in the geological record will undoubtedly help to understand the future of coral reefs.

CHAPTER 9. CONCLUSIONS AND FUTURE WORK

CONTENTS

This chapter summarises the important conclusions of this thesis and makes suggestions for future work.

9.1 SUMMARY OF CONCLUSIONS

The most important conclusions that have resulted from this study are summarised below.

CHAPTER 2.

- Coral reefs are widely documented as offering both substantial economic and scientific value which explains the concern about the widespread deterioration and the view that reefs are in 'crisis'.
- The coral genus '*Acropora*' is considered a modern environmental indicator genus, vulnerable to anthropogenic and natural induced stress.
- Some of the future climatic changes that are predicted to occur, have occurred repeatedly in the geological past. Coral ecosystems have diminished in response to these changes but have often rebounded offering us hope for worldwide coral reefs.
- Understanding the ecological response of z-corals, and their communities, to global climate change in the geological record will undoubtedly help to understand the future of coral reefs.

CHAPTER 3.

- This is the first study that attempts to compile the stratigraphic history of a single z-coral genus which is widespread, diverse and ecologically important today.
- *Acropora's* fossil record indicates that it originated in a North Africa-Mediterranean region.
- The maximum latitudinal extent of the genus was in the Middle Eocene coincidental with a period of global warming in the Middle Eocene.
- *Acropora* became extinct in the Miocene of Europe and emerged in Southeast Asia during the Oligo-Miocene.
- This suggests a shift in centre of diversity from Europe and adjacent regions to Southeast Asia during the Oligo-Miocene and that at least part of the taxonomic structure of the modern Southeast Asia hotspot consists of taxa accumulated from Europe and elsewhere.

CHAPTER 4.

- In addition to the well established morphological characters of skeletal surfaces used in Chapter 4, this thesis has pioneered the use of the internal detail of *Acropora* specimens by routinely using thin section methods, but also developing a micro-CT approach.
- Surficial diagnostic characters are preserved internally and hence assist identification of fossil coral fragments at genus- and species-level.
- These methods can also be used to aid assessments of preservation and diagenesis of fossil specimens.

CHAPTER 5.

- *Acropora* specimens from the Eocene of the Hampshire and Paris basins, and from the Miocene of the Aquitaine Basin, fall into fifteen groups whose characters were found to be consistent with separate species. Twelve existing fossil species were identified and an additional three new potential species are described.
- These specimens are a unique collection showing abundant morphological diversity including three colony shapes, four types of radial corallites, four types of coenosteum and variation in other *Acropora* characters.
- Species groups have been identified suggesting *Acropora* not only originated, but additionally, diversified in the Eocene of NW Europe.
- Within each basin two other members of the Acroporidae family have been recorded; *Astreopora* and *Dendracis*.

CHAPTER 6.

- *Acropora* occurred in the Lutetian-Bartonian of the Paris Basin and in the Bartonian-Priabonian of the Hampshire Basin. The basins existed as two interconnected, shallow-marine, paralic embayments, connected to the Atlantic and with an intermittent connection to the North Sea.
- The palaeonvironmental settings are different within two basins. In the Hampshire Basin, corals are found within siliciclastic storm beds in a relatively protected mid-shelf environment, below wave base. Corals from the Lutetian Paris Basin are found within predominantly carbonate-dominated beds and a

mid-ramp environment is inferred. During the Bartonian of the Paris Basin, results suggest deposition in a shoreface environment. Rapid burial is inferred in both basins creating a relatively enclosed geochemical system.

- Overall calm conditions in both basins were interrupted by brief periods of high energy to fragment the branches. Relatively, more robust growth forms of the *Acropora* species from the Priabonian of the Hampshire Basin imply higher energy than in the Paris Basin.
- The low to moderate coral diversity in both basins and the combination of zooxanthellate and azooxanthellate corals seen in modern marginal environments, and the lack of other reef-biota, typifies marginal environments.
- Corals are likely to have occurred in thickets rather than framework-related conditions. The absence of reef rock raises the question as to whether this was a flourishing community or a disturbed/restricted state of development.
- 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.

CHAPTER 7.

- The distribution of *Acropora* in the Hampshire and Paris basins during the Eocene is believed to have been at its maximum northern Cenozoic limit and support a poleward migration of tropical faunas.
- The pristine morphological and mineralogical preservation of coral and mollusc specimens, and lack of bioerosion, from both basins supports rapid burial following fragmentation of the coral branches. This infers rapid rates of sedimentation 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.
- Detailed isotopic analyses have been performed on aragonitic corals and marine molluscs, and calcitic marine mollusc shells of middle to late Eocene age. Overall the mean inferred temperatures show a minimum of 24.2°C and a maximum of 33.2°C (mean 29.2°C, standard deviation 3.06). The mean Lutetian palaeotemperature is 27.9°C. For the Bartonian the mean palaeotemperature is 31.1°C. Finally, the mean Priabonian palaeotemperature is 28.6°C.

- Specimens from both basins indicate sub-tropical to tropical palaeoenvironments.
- Derived temperature estimates based on the 'energy hypothesis' show a minimum mean estimate of 15.8°C which is consistent with temperatures associated with modern, high latitude non-reefal coral assemblages (e.g. Japan).
- Disparities between the minimum isotope-based estimates and the 'energy hypothesis' probably reflect underestimates of generic z-coral diversity resulting in lower minimum mean temperature estimates.

CHAPTER 8.

- In summary the depositional environment of *Acropora* in the Eocene of the Hampshire and Paris basins is marginal, high latitude, tropical to subtropical setting, showing similarities to modern analogues of high latitude, marginal settings.
- 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.
- Data on the past response of marine ecosystems to climate change have become increasingly relevant. The major difference at present and for future predictions is the unprecedented affect of human activity on these ecosystems.
- Potentially, high-latitude, marginal settings may provide a refuge from future predicted global environmental change.

9.2 FUTURE WORK

As described in Chapter 4 many of the early descriptions of *Acropora* species were mostly named *Madrepora*, or were classified as different names, therefore there are potentially many fossil species of the genus waiting to be identified and it still remains unclear how many of these species are true *Acropora* and which are not. Future taxonomic reviews of the literature and studies of museum specimens, in particular fossil type specimens, may identify the validity of these early descriptions. The Cenozoic distribution and taxonomic descriptions of another member of the Acroporidae family, *Dendracis,* have shown that counterintuitive to *Acropora* dominance in reefal communities becoming the most widespread and abundant z-coral today, *Dendracis* became extinct in Miocene This is believed to be the result of a morphological control, future work on the taxonomy and distribution of the genus will help to test this hypothesis.

This work has pioneered the use of internal detail for *Acropora*, by routinely using standard thin section methods, but also developing a micro-CT-based approach. Future work, particularly on quantifying results from using these methods may improve this approach and additionally further identifications of how internal manifestation of surficial characters used by Wallace (1999) for species designation.

As described in Chapter 8 this genus may not be an exemplar for all z-coral genera and hence reconstructions of the Cenozoic biogeographic history of other genera may clarify this. Further fieldwork at global fossil localities will improve distributional data of *Acropora* and understanding of *Acropora* taphonomy, palaeoecology and sedimentological information in other settings. Palaeonvironmental context will be added to specimen-based records through stable isotope and trace element analysis of the coral specimens and associated fauna following the methodology used in this thesis.

CHAPTER 9. CONCLUSIONS AND FUTURE WORK

CONTENTS

This chapter summarises the important conclusions of this thesis and makes suggestions for future work.

9.1 SUMMARY OF CONCLUSIONS

The most important conclusions that have resulted from this study are summarised below.

CHAPTER 2.

- Coral reefs are widely documented as offering both substantial economic and scientific value which explains the concern about the widespread deterioration and the view that reefs are in 'crisis'.
- The coral genus '*Acropora*' is considered a modern environmental indicator genus, vulnerable to anthropogenic and natural induced stress.
- Some of the future climatic changes that are predicted to occur, have occurred repeatedly in the geological past. Coral ecosystems have diminished in response to these changes but have often rebounded offering us hope for worldwide coral reefs.
- Understanding the ecological response of z-corals, and their communities, to global climate change in the geological record will undoubtedly help to understand the future of coral reefs.

CHAPTER 3.

- This is the first study that attempts to compile the stratigraphic history of a single z-coral genus which is widespread, diverse and ecologically important today.
- *Acropora's* fossil record indicates that it originated in a North Africa-Mediterranean region.
- The maximum latitudinal extent of the genus was in the Middle Eocene coincidental with a period of global warming in the Middle Eocene.
- *Acropora* became extinct in the Miocene of Europe and emerged in Southeast Asia during the Oligo-Miocene.
- This suggests a shift in centre of diversity from Europe and adjacent regions to Southeast Asia during the Oligo-Miocene and that at least part of the taxonomic structure of the modern Southeast Asia hotspot consists of taxa accumulated from Europe and elsewhere.

CHAPTER 4.

- In addition to the well established morphological characters of skeletal surfaces used in Chapter 4, this thesis has pioneered the use of the internal detail of *Acropora* specimens by routinely using thin section methods, but also developing a micro-CT approach.
- Surficial diagnostic characters are preserved internally and hence assist identification of fossil coral fragments at genus- and species-level.
- These methods can also be used to aid assessments of preservation and diagenesis of fossil specimens.

CHAPTER 5.

- *Acropora* specimens from the Eocene of the Hampshire and Paris basins, and from the Miocene of the Aquitaine Basin, fall into fifteen groups whose characters were found to be consistent with separate species. Twelve existing fossil species were identified and an additional three new potential species are described.
- These specimens are a unique collection showing abundant morphological diversity including three colony shapes, four types of radial corallites, four types of coenosteum and variation in other *Acropora* characters.
- Species groups have been identified suggesting *Acropora* not only originated, but additionally, diversified in the Eocene of NW Europe.
- Within each basin two other members of the Acroporidae family have been recorded; *Astreopora* and *Dendracis*.

CHAPTER 6.

- *Acropora* occurred in the Lutetian-Bartonian of the Paris Basin and in the Bartonian-Priabonian of the Hampshire Basin. The basins existed as two interconnected, shallow-marine, paralic embayments, connected to the Atlantic and with an intermittent connection to the North Sea.
- The palaeonvironmental settings are different within two basins. In the Hampshire Basin, corals are found within siliciclastic storm beds in a relatively protected mid-shelf environment, below wave base. Corals from the Lutetian Paris Basin are found within predominantly carbonate-dominated beds and a

mid-ramp environment is inferred. During the Bartonian of the Paris Basin, results suggest deposition in a shoreface environment. Rapid burial is inferred in both basins creating a relatively enclosed geochemical system.

- Overall calm conditions in both basins were interrupted by brief periods of high energy to fragment the branches. Relatively, more robust growth forms of the *Acropora* species from the Priabonian of the Hampshire Basin imply higher energy than in the Paris Basin.
- The low to moderate coral diversity in both basins and the combination of zooxanthellate and azooxanthellate corals seen in modern marginal environments, and the lack of other reef-biota, typifies marginal environments.
- Corals are likely to have occurred in thickets rather than framework-related conditions. The absence of reef rock raises the question as to whether this was a flourishing community or a disturbed/restricted state of development.
- 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.

CHAPTER 7.

- The distribution of *Acropora* in the Hampshire and Paris basins during the Eocene is believed to have been at its maximum northern Cenozoic limit and support a poleward migration of tropical faunas.
- The pristine morphological and mineralogical preservation of coral and mollusc specimens, and lack of bioerosion, from both basins supports rapid burial following fragmentation of the coral branches. This infers rapid rates of sedimentation 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.
- Detailed isotopic analyses have been performed on aragonitic corals and marine molluscs, and calcitic marine mollusc shells of middle to late Eocene age. Overall the mean inferred temperatures show a minimum of 24.2°C and a maximum of 33.2°C (mean 29.2°C, standard deviation 3.06). The mean Lutetian palaeotemperature is 27.9°C. For the Bartonian the mean palaeotemperature is 31.1°C. Finally, the mean Priabonian palaeotemperature is 28.6°C.

- Specimens from both basins indicate sub-tropical to tropical palaeoenvironments.
- Derived temperature estimates based on the ‘energy hypothesis’ show a minimum mean estimate of 15.8°C which is consistent with temperatures associated with modern, high latitude non-reefal coral assemblages (e.g. Japan).
- Disparities between the minimum isotope-based estimates and the ‘energy hypothesis’ probably reflect underestimates of generic z-coral diversity resulting in lower minimum mean temperature estimates.

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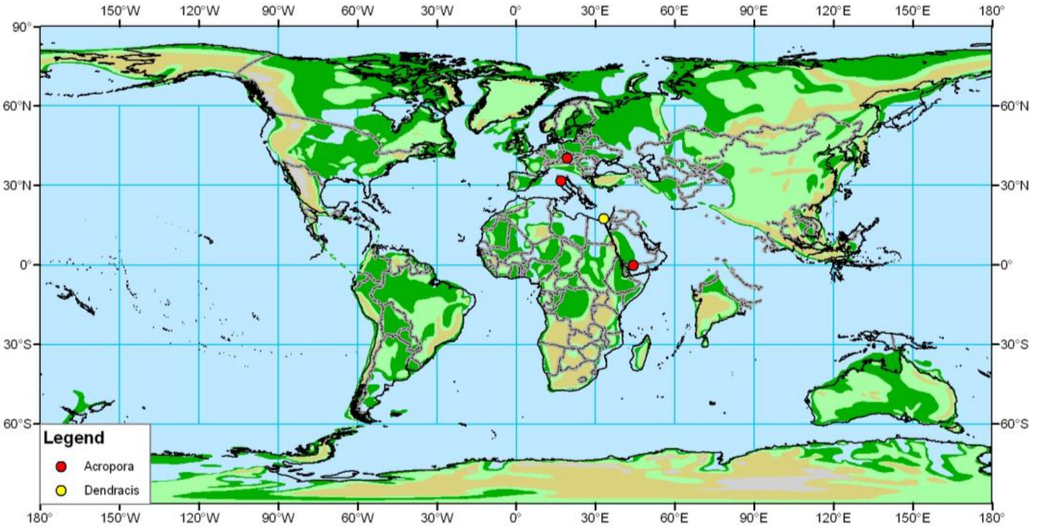
APPENDICES

APPENDIX 1. *ACROPORA* DATABASE (CD)

APPENDIX 2. GLOBAL CENOZOIC DISTRIBUTION OF *DENDRACIS*

Late Paleocene



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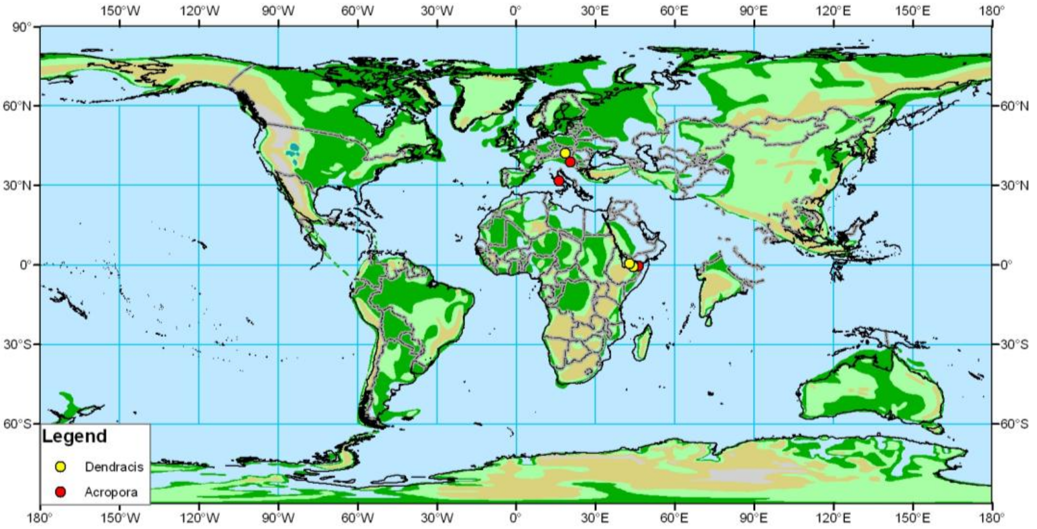

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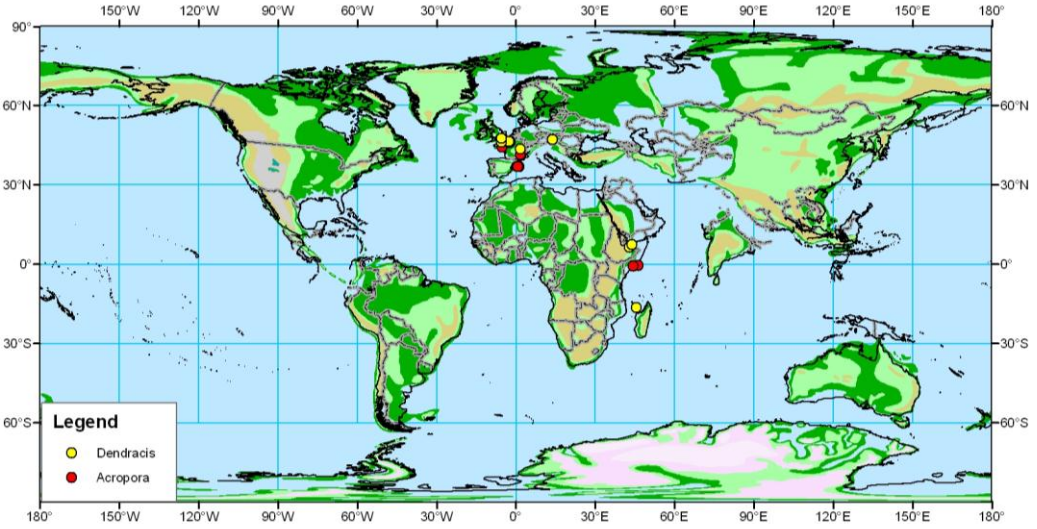

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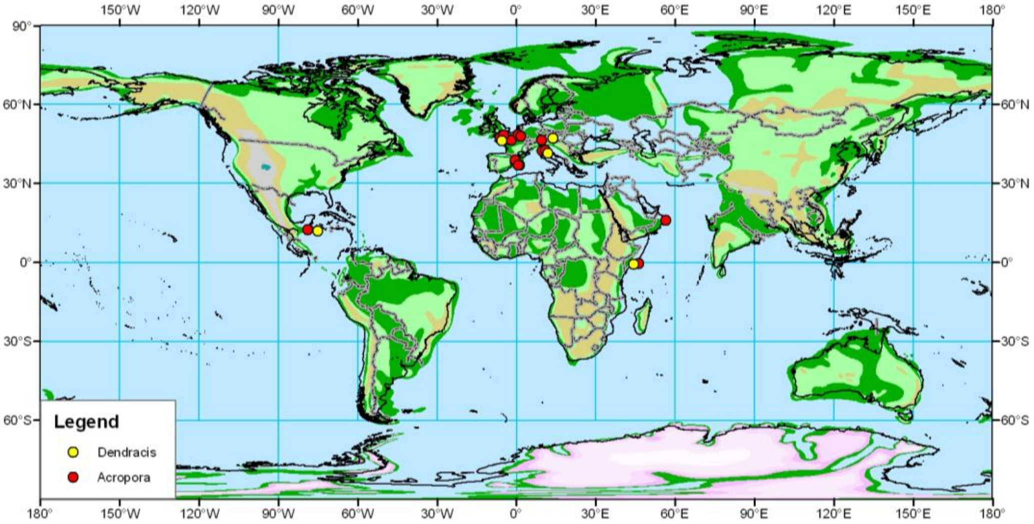

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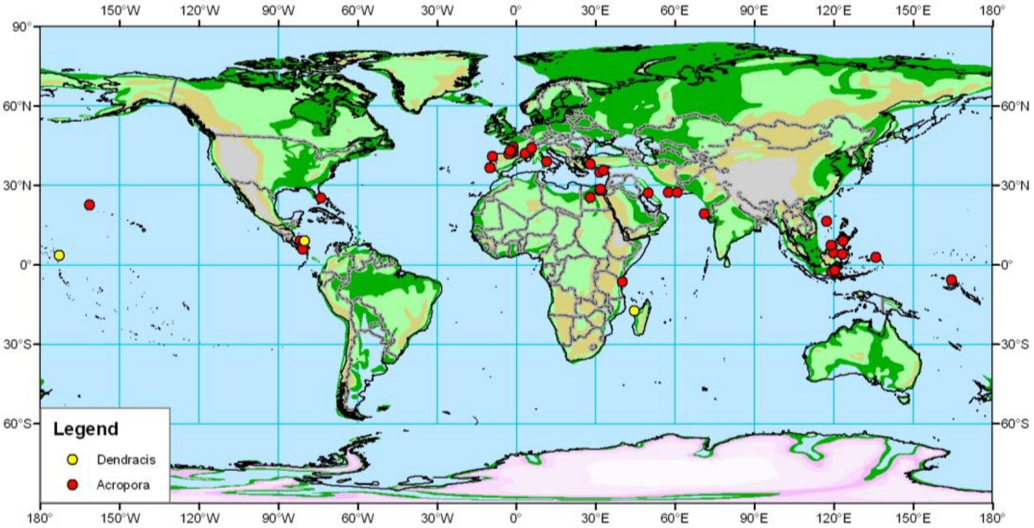

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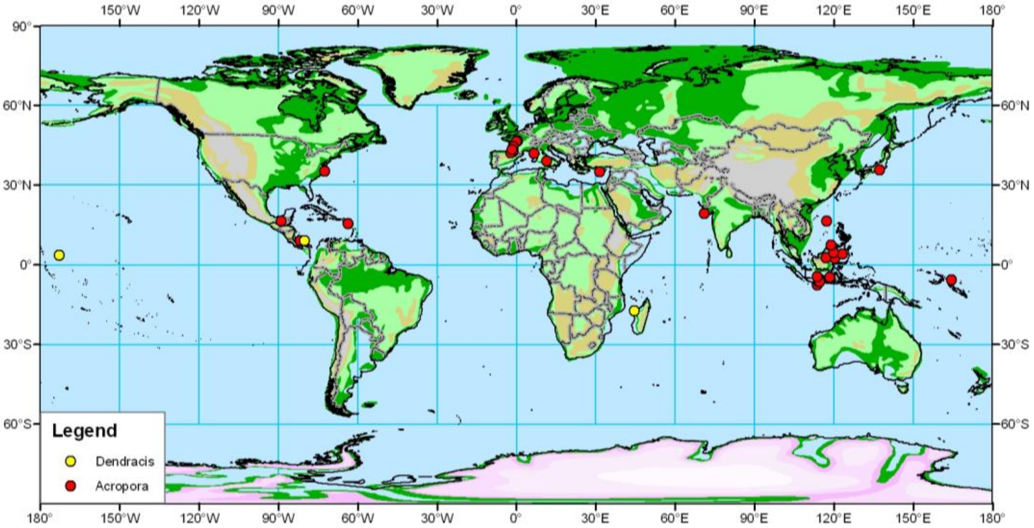
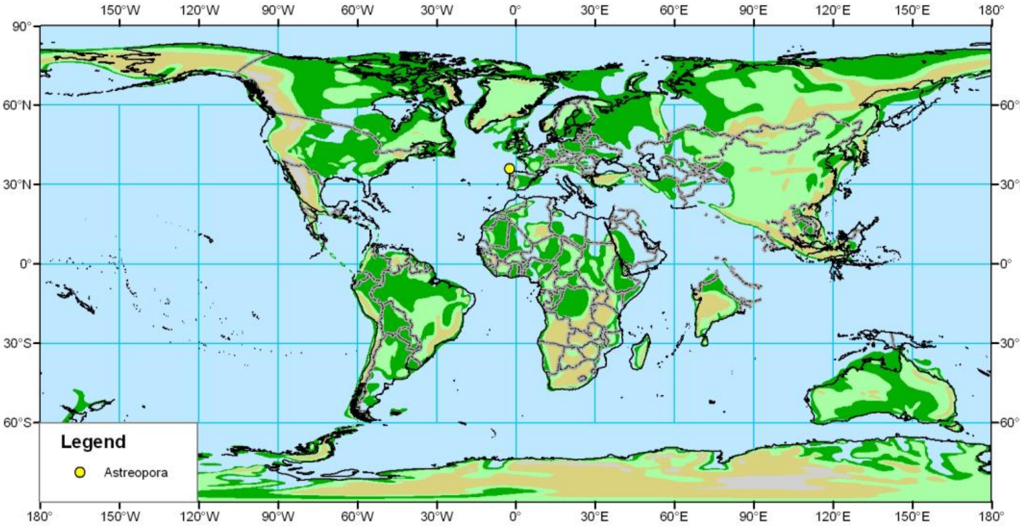


Appendix 3. Global Cenozoic distribution of *Astreopora*

Middle Paleocene



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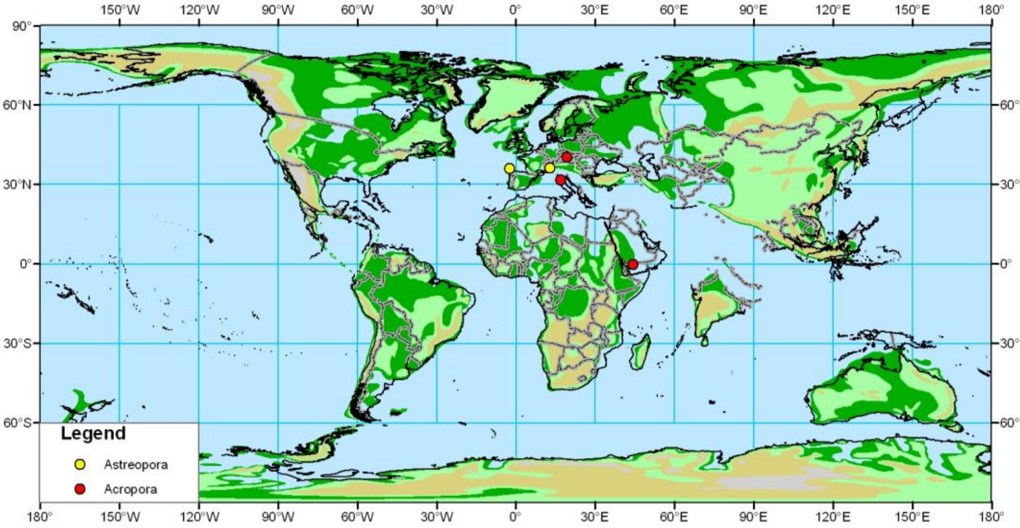

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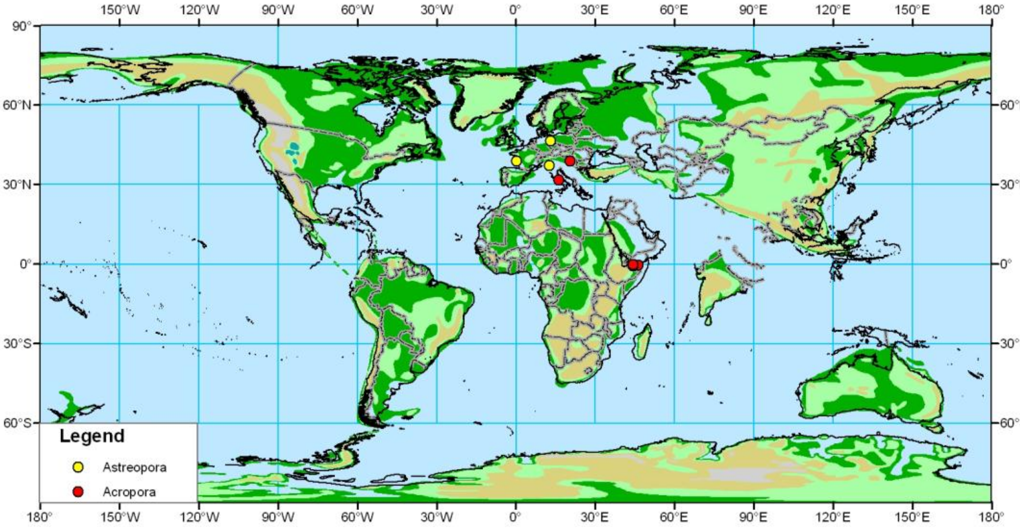

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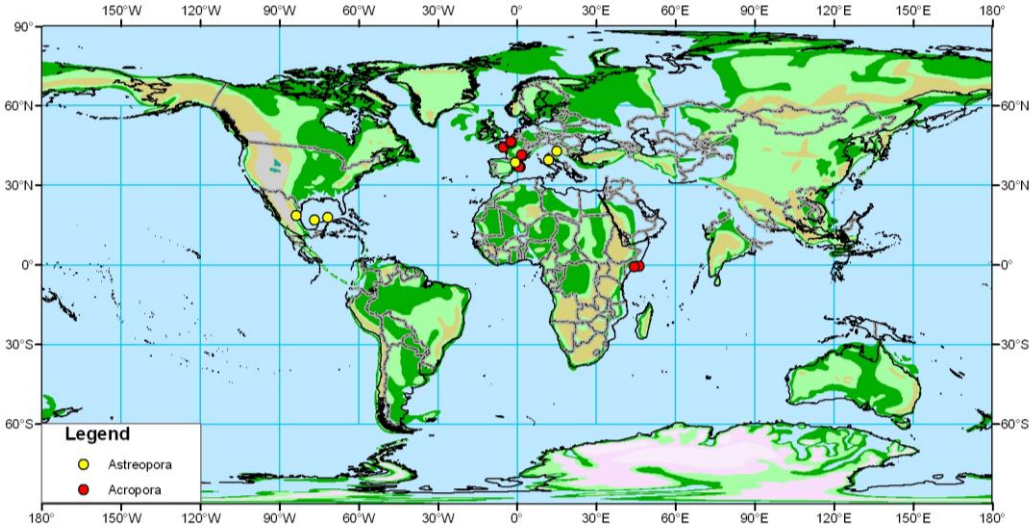

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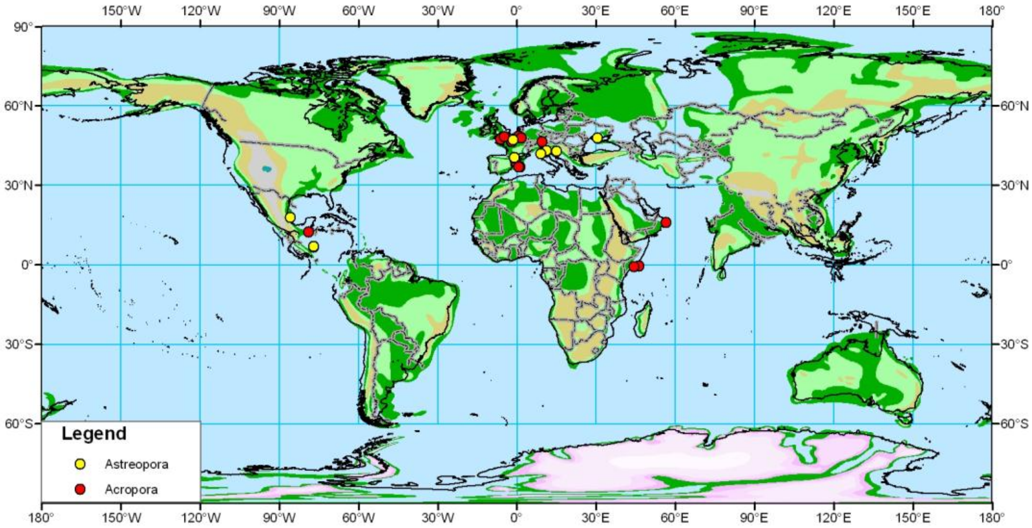
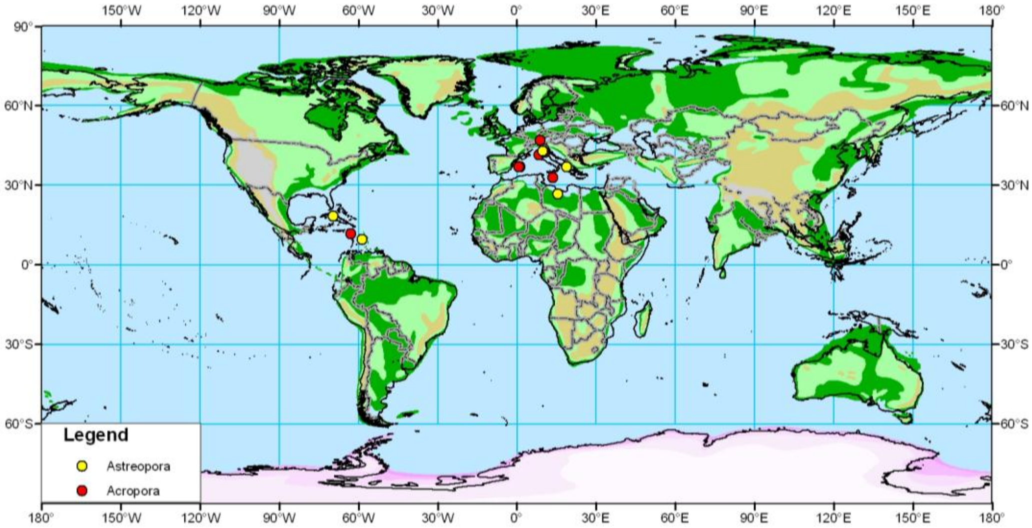


Early Oligocene



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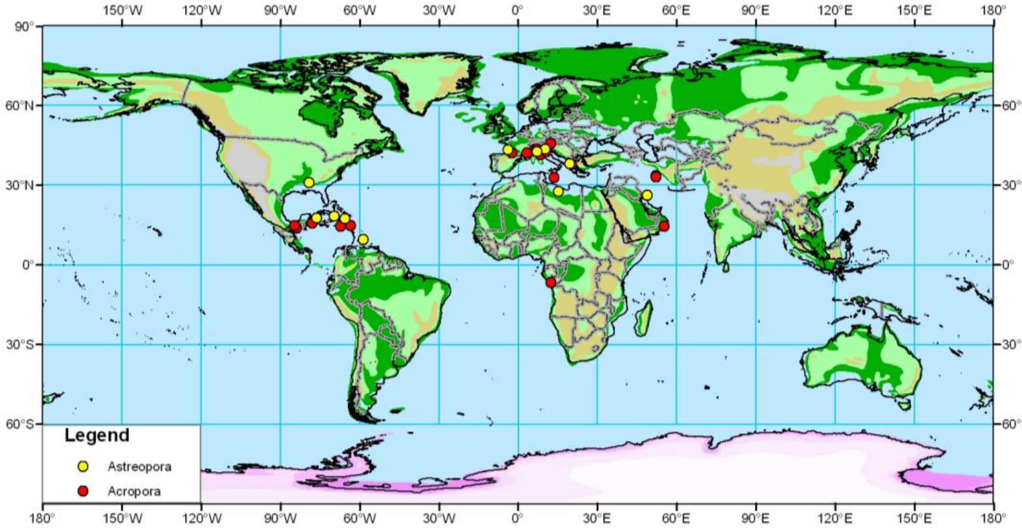

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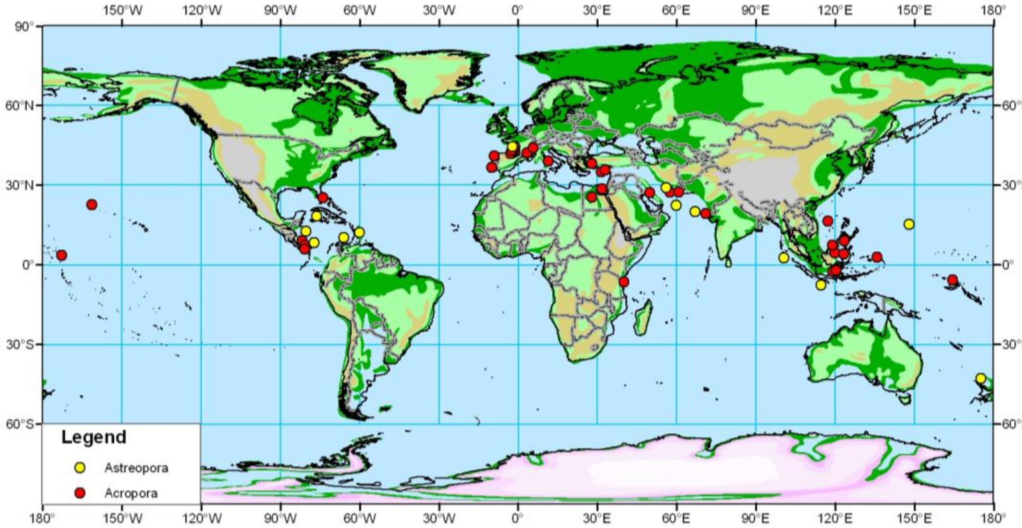

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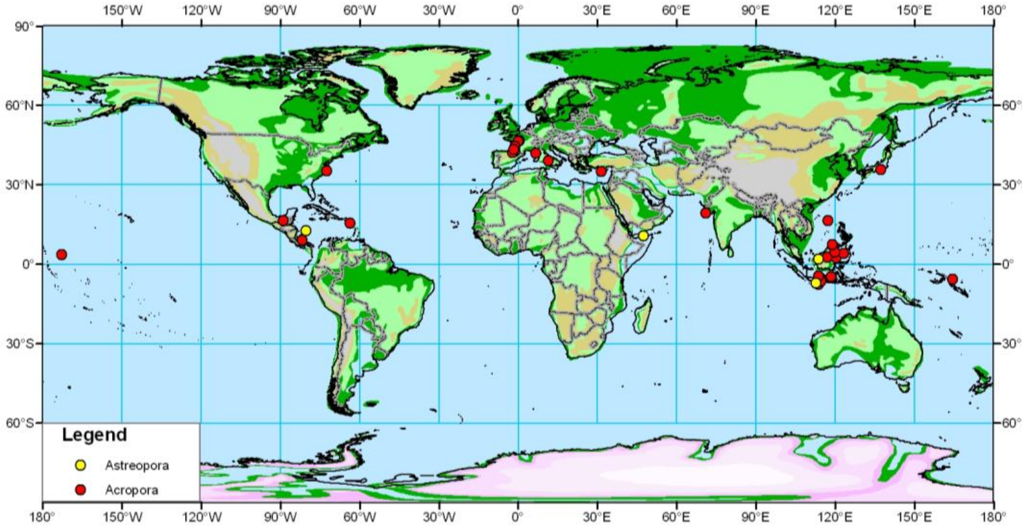

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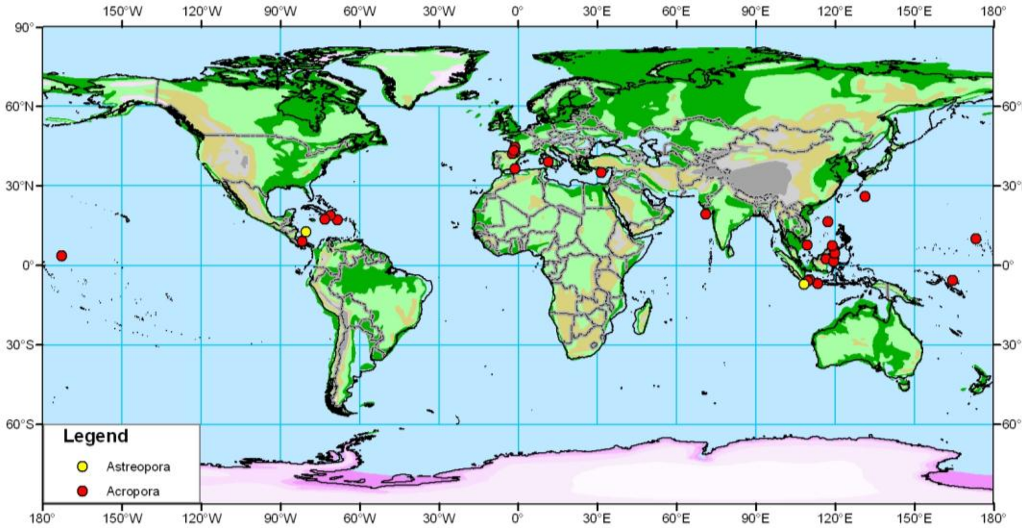

APPENDIX 4. *ACROPORA* FOSSIL SPECIMENS

Specimen no.	Holding	Label description					
		Locality	Country	Age	Lithology	Original identification	Collector
R2209b	NHM	Auvers	France	Eocene	Sables Moyen	Madrepora solanderi (Defrance)	No label details
R2209a	NHM	Auvers	France	Eocene	Sables Moyen	Madrepora solanderi (Defrance)	No label details
R54843	NHM	No label details	France	Middle Eocene	No label details	No label details	No label details
R54910	NHM	No label details	France	Eocene	No label details	Acropora sp.	No label details
R54912	NHM	Brockenhurst	UK	No label details	No label details	No label details	No label details
R40382	NHM	La Ferme de l'Orme	France	Eocene	No label details	Acropora ornata (Defrance)	A. Chavan Exchange (1948)
R40383	NHM	La Ferme de l'Orme	France	Eocene	No label details	Acropora ornata (Defrance)	A. Chavan Exchange (1948)
R40384	NHM	La Ferme de l'Orme	France	Eocene	No label details	Acropora ornata (Defrance)	A. Chavan Exchange (1948)
R40385	NHM	La Ferme de l'Orme	France	Eocene	No label details	Acropora ornata (Defrance)	A. Chavan Exchange (1948)
R18266	NHM	Auvers	France	Eocene	Lower Bartonian Sables Moyen	Acropora solanderi (Defrance)	No label details
R54911	NHM	No label details	France	Eocene	No label details	Acropora sp.	No label details
R55689	NHM	Auvers	France	Middle Eocene	No label details	Acropora deformis (Michelin)	No label details
R35320	NHM	No label details	France	Eocene	No label details	Acropora solanderi (Defrance)	No label details
R45675	NHM	Auvers-sur-Oise	France	Eocene	No label details	Acropora solanderi (Defrance)	L.J.Pitt Colln. (1964)
R45676	NHM	Auvers-sur-Oise	France	Eocene	No label details	Acropora solanderi (Defrance)	L.J.Pitt Colln. (1964)
R45677	NHM	Auvers-sur-Oise	France	Eocene	No label details	Acropora solanderi (Defrance)	No label details
R45679	NHM	Auvers-sur-Oise	France	Eocene	No label details	Acropora solanderi (Defrance)	L.J.Pitt Colln. (1964)
R52067	NHM	Chambors	France	Eocene	Upper Calcaire Grossier	Acropora sp.	A.G.Davis Colln. (purch. 1957)
R54831	NHM	Paris Basin	France	Eocene	No label details	Acropora solanderi (Defrance)	F.L.Fletcher Colln.
R54832	NHM	Paris Basin	France	Eocene	No label details	Acropora solanderi (Defrance)	No label details
R54833	NHM	Paris Basin	France	Eocene	No label details	Acropora solanderi (Defrance)	F.L.Fletcher Colln.
R54838	NHM	Paris	France	Eocene	No label details	Madrepora solanderi (Defrance)	No label details
R54849	NHM	Paris Basin	France	Middle Eocene	No label details	Acropora solanderi (Defrance)	No label details
R54861	NHM	Auvers	France	Eocene	Sables Moyen	Acropora solanderi (Defrance)	No label details
R52065	NHM	Chambors	France	Eocene	Upper Calcaire Grossier	Acropora sp.	A.G.Davis Colln. (purch. 1957)
49583	NHM	Brockenhurst	UK	Eocene	Mid-Headon Beds	Madrepora sp.	F.E.Edwards Colln.

R18216	NHM	Brockenhurst	UK	Eocene	Mid-Headon Beds	Madrepora solanderi (Defrance)	R.F.Tomes Colln. (purch. 1905)
R18217	NHM	Brockenhurst	UK	Eocene	Mid-Headon Beds	Madrepora solanderi (Defrance)	R.F.Tomes Colln. (purch. 1905)
R14571	NHM	Barton	UK	Eocene	Barton Beds	Dendrophyllia sp.	No label details
R19125	NHM	Barton	UK	Eocene	Barton Beds	Dendrophyllia dendrophylloides (Milne-Edwards & Haime)	H.E.Walton (1916)
R29687	NHM	Barton	UK	Eocene	Barton Beds	Acropora (Madrepora) solanderi (Defrance)	E.St.J. Burton (pres. 1912)
R54837	NHM	Paris	France	Eocene	No label details	Madrepora solanderi (Defrance)	No label details
R54838	NHM	Paris	France	Eocene	No label details	Madrepora solanderi (Defrance)	M.Milne-Edwards pres.
R54839	NHM	Paris	France	Eocene	No label details	Madrepora solanderi (Defrance)	M.Milne-Edwards pres.
R54913	NHM	Brockenhurst	UK	Oligocene	No label details	Madrepora sp.	No label details
R54914	NHM	Brockenhurst	UK	Oligocene	No label details	Madrepora sp.	No label details
49583a	NHM	Brockenhurst	UK	Eocene	Mid-Headon Beds	Madrepora sp.	F.E.Edwards Colln.
49583b	NHM	Brockenhurst	UK	Eocene	Mid-Headon Beds	Madrepora sp.	F.E.Edwards Colln.
R2339	NHM	Brockenhurst	UK	Eocene	No label details	Madrepora sp.	Executors H.S.Beckles (1891)
R45678	NHM	Auvers-sur-Oise	France	Eocene	No label details	Acropora solanderi (Defrance)	No label details
R.54847	NHM	Paris Basin	France	Middle Eocene	No label details	No label details	No label details
R2209c	NHM	Auvers	France	Eocene	Sables Moyen	Madrepora solanderi (Defrance)	No label details
R18265	NHM	Auvers	France	Eocene	Lower Bartonian Sables Moyen	Acropora solanderi (Defrance)	R.F.Tomes Colln. (purch. 1905)
R54842	NHM	No label details	France	Middle Eocene	No label details	Acropora solanderi (Defrance)	No label details
R54844	NHM	No label details	France	Middle Eocene	No label details	Acropora solanderi (Defrance)	No label details
R52067	NHM	Chambors	France	Eocene	Upper Calcaire Grossier	Acropora sp.	No label details
R52051	NHM	Chambors	France	Eocene	Upper Calcaire Grossier	Acropora sp.	A.G.Davis Colln. (purch. 1957)
R40833	NHM	Auvers	France	Eocene, Bartonian	Sables Moyen	Acropora solanderi (Defrance)	A.Wrigley Esq. Colln. (purch 1953)
50236c	NHM	Auvers	France	Eocene	Jarisien B2	Madrepora solanderi (Defrance)	No label details
AZ2902	NHM	Auvers (Oise)	France	Middle Eocene, Late Lutetian	Sables d'Auvers	Acropora sp.	Steve Tracey Colln. (pres. 2005)
AZ2903	NHM	Auvers (Osie)	France	Middle Eocene, Late Lutetian	Sables d'Auvers	Acropora sp.	Steve Tracey Colln. (pres. 2005)
55687a	NHM	Auvers	France	Middle Eocene	No label details	Acropora solanderi (Defrance)	No label details
46824b	NHM	Auvers	France	Eocene	No label details	Madrepora solanderi (Defrance)	No label details
46824a	NHM	Auvers	France	Eocene		Madrepora solanderi (Defrance)	No label details
50236d	NHM	Auvers	France	Eocene	Jarisien B2	Madrepora solanderi (Defrance)	No label details
49583c	NHM	Brockenhurst	UK	Eocene	Mid-Headon Beds	Madrepora sp.	F.E.Edwards Colln.

R52048	NHM	Chambors	France	Eocene	Upper Calcaire Grossier	Acropora sp.	A.G.Davis Colln. (purch. 1957)
R52050	NHM	Chambors	France	Eocene	Upper Calcaire Grossier	Acropora sp.	A.G.Davis Colln. (purch. 1957)
49583a	NHM	Brockenhurst	UK	Eocene	Middle Headon Beds	Madrepora sp.	F.E.Edwards Colln.
49583b	NHM	Brockenhurst	UK	Eocene	Middle Headon Beds	Madrepora sp.	F.E.Edwards Colln.
49583c	NHM	Brockenhurst	UK	Eocene	Middle Headon Beds	Madrepora sp.	F.E.Edwards Colln.
R.52052	NHM	Chambors	France	Eocene	Upper Calcaire Grossier	Acropora sp.	A.G.Davis Colln. (purch. 1957)
50236b	NHM	Auvers	France	Eocene	Jarisien B2	Madrepora solanderi (Defrance)	No label details
50236a	NHM	Auvers	France	Eocene	Jarisien B2	Madrepora solanderi (Defrance)	No label details
R40831	NHM	Auvers	France	Eocene, Bartonian	Sables Moyen	Acropora solanderi (Defrance)	A.Wrigley Esq. Colln. (purch 1953)
R52049	NHM	Chambors	France	Eocene	Upper Calcaire Grossier	Acropora sp.	A.G.Davis Colln. (purch. 1957)
55687c	NHM	Auvers	France	Middle Eocene	No label information	Acropora solanderi (Defrance)	No label details
R40830	NHM	Auvers	France	Eocene, Bartonian	Sables Moyen	Acropora solanderi (Defrance)	A.Wrigley Esq. Colln. (purch 1953)
AZ2904	NHM	Auvers (Oise)	France	Middle Eocene (Late Lutetian)	Sables d'Auvers	Acropora sp.	Steve Tracey Colln. (pres. 2005)
55687b	NHM	Auvers	France	Middle Eocene	No label information	Acropora solanderi (Defrance)	No label details
R40832	NHM	Auvers	France	Eocene, Bartonian	Sables Moyen	Acropora solanderi (Defrance)	A.Wrigley Esq. Colln. (purch 1953)
R35593	NHM	Gaas	SW France	Miocene	No label details	No previous	No label details
R35594	NHM	Gaas	SW France	Miocene	No label details	No previous	No label details
R35595	NHM	Gaas	SW France	Miocene	No label details	No previous	No label details
R46822	NHM	Gaas	SW France	Miocene	No label details	No previous	No label details
R18276	NHM	Aquitaine, Bordeaux	France	Miocene	No label information	No previous	No label details
P1A01	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.08
P1A02	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.09
P1A03	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.10
P1A04	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.11
P1A05	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.12
P1A06	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.13
P1A07	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.14
P1A08	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.15
P1A09	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.16

P1A10	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.17
P1A11	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.18
P1A12	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.19
P1A13	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.20
P1A21	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.21
P1A22	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.22
P1A23	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.23
P1A24	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.24
P1A25	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.25
P1A26	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.26
P1A27	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.27
P1A28	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.28
P1A29	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.29
P1A30	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.30
P1A31	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.31
P1A32	Fieldwork	Auvers-sur-Oise	France	Bartonian, France	Sables d'Auvers	No previous	C. H. White, 06.32
C 25746	Sedgewick	Brockenhurst	UK	No label details	Brockenhurst Bed	Madrepora anglica, Duncan	Keeping and Tawney, 1881
C 25799	Sedgewick	Brockenhurst	UK	No label details	Brockenhurst Bed	Madrepora anglica, Duncan	Keeping and Tawney, 1881
C 25911	Sedgewick	Brockenhurst	UK	No label details	Brockenhurst Bed	Madrepora anglica, Duncan	Fisher Collection
C 29419	Sedgewick	Whitecliff Bay, Isle of Wight	UK	lowest 2' of Mid Headon Beds	Middle Headon Bed (lowest 2 feet)	Madrepora anglica, Duncan	Keeping and Tawney, 1881
C 29420	Sedgewick	Whitecliff Bay, Isle of Wight	UK	lowest 2' of Mid Headon Beds	Middle Headon Bed (lowest 2 feet)	Madrepora anglica, Duncan	Keeping and Tawney, 1881
C 26189	Sedgewick	Brockenhurst	UK	No label details	Brockenhurst Bed	Coral	J. F. Walker Collection, 1908
EL_2002_Brock_White_1	Ewan Laurie Fieldwork 2002	Isle of Wight	UK	Upper Eocene	Brockenhurst Bed	No previous	Ewan Laurie August 2002
EL_2002_Brock_White_2	Ewan Laurie Fieldwork 2002	Isle of Wight	UK	Upper Eocene	Brockenhurst Bed	No previous	Ewan Laurie August 2002
AG_2002_Brock_White_1	Andy Gale Fieldwork 2002	Isle of Wight	UK	No label details	Brockenhurst Bed	No previous	A. Gale 11.02.02
MIWG2611	Alan Morton	Whitecliff Bay, Isle of Wight	UK	Priabonian	Brockenhurst Bed	No previous	Alan Morton
BGS X/X 2/19	BGS	Brockenhurst	UK	Priabonian (Eocene)	Mid Headon	Madrepora roemeri	Duncan, 1866
BGS X/X 3/20	BGS	Brockenhurst	UK	Priabonian (Eocene)	Mid Headon	Madrepora anglica	Duncan, 1866

C1D101	OM	Fresville, Basse-Normandie	France	Middle Eocene	No label information	No previous	No label details
R50912	NHM	Bordeaux, Graviere de Cante, Saucats	France	Burdigalian, Miocene	No label information	No previous	No label details

APPENDIX 5. GLOSSARY OF MORPHOLOGICAL TERMS (FROM WELLS, 1956 & WALLACE, 1999)

Arborescent	Growth form in which branches are equal-sized and at wide angles to each other
Axial corallite	The skeleton of the polyp that runs through the centre of an *Acropora* branch, opening at the tip of the branch
Calice	The opening of the corallite
Cochleariform	A radial corallite shape in which the lower wall is expanded outwards and the upper wall is reduced. So named because the shape appears like an ear
Coenenchyme	System of interconnecting canals which make up the gastrovascular system of an *Acropora* colony
Coenosteum	The skeletal structures between corallites, also used in *Acropora* to describe corallite wall structure
Corallite	The skeleton of an individual coral polyp
Corymbose	Shape of an *Acropora* colony in which the branches originate more or less from a central growing point and end in the same place
Costate	Foem of coenosteum consisting of ridges
Hispidose	Growth form in which small branchlets are given off around the main, usually arborescent, branches
Labellate	Shaped like a lip (of radial corallites)
Nariform	A character state of a radial corallite in which it is shaped like an inverted nose
Radial corallites	The skeletons of polyps that are budded off around the outside of the axial corallite on an *Acropora* branch
Reticulate	Having the appearance of a network, divided into mesh-like compartments (used for coenosteum)
Septum/septa	The radiallly arranged skeletal divisions of the corallite
Synapticulae	Rods or bars connecting opposed faces of adjacent septa and perforating the mesenteries between them
Trabeculae	The spines of crystal aragonite that form the septa and other processes that make up the skeleton of the polyp

APPENDIX 6. ABBREVIATIONS

AIMS	Australian Institute of Marine Science, Australia
BGS	British Geological Survey, Nottingham, England
CITES	Department of Conservation and Land Management, Western Australia
FW	Fieldwork specimens
GBR	Great Barrier Reef, Queensland, Australia
HM	Hampshire Museum, England
MNHM	Muséum National d'Histoire Naturelle, Paris, France
MTQ	Museum of Tropical Queensland, Townsville, Australia
NHM	Natural History Museum, London, England
OM	Oxford University Museum of Natural History, England
PC	Private collection
SGW	Sedgewick Museum, Cambridge, England
sp.	species

APPENDIX 7. MICRO-CT SCAN DETAILS

CT SCAN RUNS

Date	File	Run (day)	Specimen		Voltage	Current	Projections
1.4.08	Coral49583A	1	R49583a	Fossil	80	100	720
1.4.08	CoralAZ2904A	2	AZ2904a	Fossil	80	100	720
1.4.08	CoralR40832A	3	R40832a	Fossil	80	100	720
9.4.08	Coral1A	1	G37359	Modern	80	150	720
9.4.08	Coral1A	1	G37359	Modern	80	150	720
9.4.08	Coral1A	1	G37359	Modern	80	150	720
9.4.08	Coral1A	1	G37359	Modern	80	150	720
9.4.08	Coral1A	1	G33190	Modern	80	150	720
9.4.08	Coral1A	1	G33190	Modern	80	150	720
9.4.08	Coral1A	1	G33190	Modern	80	150	720
9.4.08	Coral1A	1	G37361	Modern	80	150	720
9.4.08	Coral1A	1	G37361	Modern	80	150	720
9.4.08	Coral2A	2	G27687	Modern	85	190	720
9.4.08	Coral2A	2	G51492	Modern	85	190	720
9.4.08	Coral2A	2	G51489	Modern	85	190	720
9.4.08	Coral2A	2	G46845	Modern	85	190	720
9.4.08	Coral2A	2	G46845	Modern	85	190	720
9.4.08	Coral2A	2	G46845	Modern	85	190	720
9.4.08	Coral2A	2	G46845	Modern	85	190	720
9.4.08	Coral2A	2	G46845	Modern	85	190	720
9.4.08	Coral3A	3	A46844	Modern	85	190	720
9.4.08	Coral3A	3	A46844	Modern	85	190	720
9.4.08	Coral3A	3	A46844	Modern	85	190	720
9.4.08	Coral3A	3	A46844	Modern	85	190	720
9.4.08	Coral3A	3	A46844	Modern	85	190	720
9.4.08	Coral3A	3	A46844	Modern	85	190	720
9.4.08	Coral3A	3	A46844	Modern	85	190	720
9.4.08	Coral3A	3	G54474	Modern	85	190	720
9.4.08	Coral3A	3	G54474	Modern	85	190	720
9.4.08	Coral3A	3	G37371	Modern	85	190	720
9.4.08	Coral3A	3	G37371	Modern	85	190	720
9.4.08	Coral3A	3	G37371	Modern	85	190	720
9.4.08	Coral3A	3	G37371	Modern	85	190	720
9.4.08	Coral4A	4	G35057	Modern	175	150	720
9.4.08	Coral4A	4	G35057	Modern	175	150	720
9.4.08	Coral4A	4	G35057	Modern	175	150	720
9.4.08	Coral4A	4	G30507	Modern	175	150	720
9.4.08	Coral4A	4	G30507	Modern	175	150	720
9.4.08	Coral4A	4	G30410	Modern	175	150	720
9.4.08	Coral4A	4	G51491	Modern	175	150	720
9.4.08	Coral4B	5	G35057	Modern	97	125	720
9.4.08	Coral4B	5	G35057	Modern	97	125	720
9.4.08	Coral4B	5	G35057	Modern	97	125	720
9.4.08	Coral4B	5	G30507	Modern	97	125	720
9.4.08	Coral4B	5	G30507	Modern	97	125	720

9.4.08	Coral4B	5	G30410	Modern	97	125	720
9.4.08	Coral4B	5	G51491	Modern	97	125	720
9.4.08	Coral5A	6	G48739	Modern	82	200	720
9.4.08	Coral5A	6	G48739	Modern	82	200	720
9.4.08	Coral5A	6	G48378	Modern	82	200	720
9.4.08	Coral5A	6	G48378	Modern	82	200	720
9.4.08	Coral5A	6	G48378	Modern	82	200	720
9.4.08	Coral5A	6	G48378	Modern	82	200	720
18.11.08	Scan 5a	1	C25799	Fossil	180	190	3145
18.11.08	Scan 6a	2	GSM 120392	Fossil	180	190	3145
18.11.08	Scan 7a	3	R18276	Fossil	180	190	3145
18.11.08	Scan 7a	3	55688	Fossil	180	190	3145
18.11.08	Scan 7a	3	Dendracis	Fossil	180	190	3145
18.11.08	Scan 7a	3	R2416	Fossil	180	190	3145
18.11.08	Scan 7a	3	Lavandulina	Fossil	180	190	3145
18.11.08	Scan 7a	3	54882	Fossil	180	190	3145
18.11.08	Scan 8a	4	R18217	Fossil	180	190	3145
18.11.08	Scan 8a	4	R40382	Fossil	180	190	3145
18.11.08	Scan 8a	4	R18265	Fossil	180	190	3145
18.11.08	Scan 8a	4	R54847	Fossil	180	190	3145
18.11.08	Scan 8a	4	R19125	Fossil	180	190	3145
18.11.08	Scan 8a	4	R54838	Fossil	180	190	3145
18.11.08	Scan 9a	5	R2339	Fossil	180	190	3145
18.11.08	Scan 9a	5	R18266	Fossil	180	190	3145
18.11.08	Scan 9a	5	R54844	Fossil	180	190	3145
18.11.08	Scan 9a	5	R54837	Fossil	180	190	3145
18.11.08	Scan 9a	5	R54849	Fossil	180	190	3145
18.11.08	Scan 9a	5	55689	Fossil	180	190	3145

APPENDIX 8. CORAL DISTRIBUTION – SYMBIOTIC STATUS

Genus	Symbiotic status	Lutetian France						Lutetian England						Bartonian France						Bartonian England						Priabonian England						Aquitanian France			Burdigalian France			Chattian France		
		ALL			with *Acropora*			ALL			with *Acropora*			ALL			with *Acropora*			ALL			with *Acropora*			ALL			with *Acropora*			ALL			ALL			ALL		
		Z-coral	AZ-coral	Unknown	Z-coral	AZ-coral	Unknown	Z-coral	AZ-coral	Unknown	Z-coral	AZ-coral	Unknown	Z-coral	AZ-coral	Unknown	Z-coral	AZ-coral	Unknown	Z-coral	AZ-coral	Unknown	Z-coral	AZ-coral	Unknown	Z-coral	AZ-coral	Unknown	Z-coral	AZ-coral	Unknown	Z-coral	AZ-coral	Unknown	Z-coral	AZ-coral	Unknown	Z-coral	AZ-coral	Unknown
Acropora	Z	1			1									1			1			1			1			1			1			1			1			1		
Agaricia	Z																																					1		
Alveolites	U			1			1																																	
Alveopora	Z																															1			1			1		
Amphihelia	AZ																																						1	
Antiguastraea	Z																															1			1			1		
Antillophyllia	Z																																					1		
Aphrastraea	Z																															1			1			1		
Astrangia	AZ																																1			1			1	
Astreopora	Z	1			1									1			1															1			1			1		
Astrohelia	AZ																																			1				
Astroria	Z																															1			1			1		
Axopora	AZ																										1			1										
Astreocoenia	Z	1			1																																	1		
Balanophyllia	AZ																										1			1									1	
Baroniseria	Z													1																										
Caryophyllia	AZ		1												1			1																					1	
Caulastrea	Z																															1			1			1		
Ceratotrochus	AZ																																			1			1	
Chaelites	U			1			1																																	
Circophyllia	Z	1			1																																			
Cladangia	AZ																																1			1			1	
Cladocora	Z																															1						1		
Clonosmilia	Z																																					1		
Coelocyathus	AZ																																						1	
Colpophyllia	Z																																					1		
Conocyathus	AZ																																						1	
Cryptangia	AZ																																1						1	
Cyathoceras	AZ																																			1			1	
Cyathoseris	Z																																					1		
Cylindrophyllia	AZ																																			1				
Culicia	AZ																																1			1			1	
Dandromilia	U															1																								
Deltocyathus	AZ																																						1	
Dendracis	Z	1																																						
Dendrophyllia	AZ		1						1						1			1			1			1			1			1			1			1			1	
Dendrosmilia	AZ																																						1	
Desmophyllum	AZ																																						1	
Diploastraea	Z																																					1		
Diplohelia	AZ		1			1			1																		1			1						1			1	
Distichopora	AZ		1			1																																		
Dyctioastraea	Z																																		1					
Echinophyllia	Z																																					1		
Ellasmoastraea	Z																															1			1			1		
Eupsammia	AZ		1			1																																		
Eusmilia	Z																																					1		
Favia	Z																															1			1			1		
Favites	Z																															1			1			1		
Fiabellum	AZ		1																														1						1	
Glyphastraea	Z																															1						1		
Goniastrea	Z																															1			1					
Goniopora	Z							1						1			1									1			1						1			1		
Graphularia	AZ		1			1			1												1			1																
Heliastraea (Aquitanastraea)	Z																															1			1			1		
Heliastraea (Heliastraea)	Z																															1			1			1		
Hexastraea	Z																																		1					
Leptomussa	Z																																					1		
Lithodendron	Z	1																																						
Lithophyllia	Z																															1			1			1		
Lobophyllia	Z																																					1		
Lobopsammia	AZ		1			1									1			1									1			1										
Madracis	Z																																					1		
Meandrina	Z													1			1																					1		
Miophora	Z																																					1		
Montastrea	Z																															1			1					
Mussismilia	Z																																					1		
Nerthastraea	Z																															1			1			1		
Oculina	AZ		1			1			1																		1			1										
Oulangia	AZ																																			1			1	
Oxypora	Z																																					1		
Pachyseris	Z																																		1			1		
Paleoastroides	AZ																																1			1			1	
Paracyathus	AZ								1												1			1																
Palmipora	AZ		1												1			1																						
Parasmilia	AZ		1												1			1															1						1	
Pavona	Z																																		1			1		
Phyllangia	AZ																																1							
Platycoenia	Z																															1			1			1		
Plerogyra	Z																																					1		
Plesiastraea	Z																															1			1			1		
Pocillopora	Z																															1			1			1		
Porites	Z	1												1			1															1			1			1		
Ruessopsammia	AZ																																						1	
Rhizangia	AZ																																1						1	
Scolymia	Z																																					1		
Seriatopora	Z																																					1		
Siderastraea	Z																															1			1			1		
Smilotrochus	AZ																																						1	
Solenastrea	Z																									1			1											
Sphenotrochus	AZ		1			1																														1			1	
Stephanocoenia	Z																																					1		
Stephanophyllia	AZ																																			1			1	
Stylocoenia	Z	1			1			1						1			1																							
Stylophora	Z	1			1																											1			1			1		
Syzygophyllia	Z																															1			1			1		
Tarbellastraea	Z																															1			1					
Thegioastraea	Z																															1			1			1		
Trochocyathus	AZ																																						1	
Trochoseris	Z	1			1									1			1																							
Turbinaria	Z													1			1															1			1			1		
Turbinola	AZ		1			1			1						1			1			1			1																
TOTAL		**10**	**13**	**2**	**7**	**8**	**2**	**2**	**6**	**0**	**0**	**0**	**0**	**9**	**6**	**1**	**8**	**6**	**0**	**1**	**4**	**0**	**1**	**4**	**0**	**3**	**6**	**0**	**3**	**6**	**0**	**28**	**10**	**0**	**31**	**13**	**0**	**48**	**26**	**0**
ALL CORAL (Z+AZ+Unknown)				25			17			8			0			16			14			5			5			9			9			38			44			74
GENERIC RATIO OF Z-CORAL				0.77			0.88			0.33			0.00			1.50			1.33			0.25			0.25			0.50			0.50			2.80			2.38			1.85

APPENDIX 9. CORAL DISTRIBUTION – GROWTH FORM

Genus	Growth Form	Colony form	Lutetian France						Lutetian England						Bartonian France						Bartonian England						Priabonian England						Aquitaine France			Burdigalian France			Chattian France		
			ALL			with Acropora			ALL			with Acropora			ALL			with Acropora			ALL			with Acropora			ALL			with Acropora			ALL			ALL			All		
			Colonial	Solitary	Unknown	Colonial	Solitary	Unknown	Colonial	Solitary	Unknown	Colonial	Solitary	Unknown	Colonial	Solitary	Unknown	Colonial	Solitary	Unknown	Colonial	Solitary	Unknown	Colonial	Solitary	Unknown	Colonial	Solitary	Unknown	Colonial	Solitary	Unknown	Colonial	Solitary	Unknown	Colonial	Solitary	Unknown	Colonial	Solitary	Unknown
Acropora	C	Ramose, rarely massive or incrusting	1			1									1			1			1			1			1			1			1			1			1		
Agaricia	C	Foliaceous unifacial or bifacial fronds or submassive coralla																																					1		
Alveolites	U				1			1																																	
Alveopora	C	Massive or ramose																															1			1			1		
Amphihelia	C	Dendroid																																					1		
Antiguastraea	C	Massive, incrusting, or subfoliaceous, subcerioid colonies																															1			1			1		
Antillophyllia	S																																							1	
Aphrastraea	C	Cerioid																															1			1			1		
Astrangia	C	Incrusting, subplocoid																															1			1			1		
Astreopora	C	Massive or subramose	1			1									1			1															1			1			1		
Astrohelia	C	Subramose																																		1					
Astroria	C	Meandroid																															1			1			1		
Axopora	C	Incrusting forming lumpy protuberances or arborescent																									1			1											
Astreocoenia	C	Cerioid; ramose, masive or incrusting	1			1																																	1		
Balanophyllia	S																											1			1									1	
Baroniseria	C	Unknown													1																										
Caryophyllia	S			1												1			1																					1	
Caulastrea	C	Phaceloid																															1			1			1		
Ceratotrochus	S																																				1			1	
Chaelites	U				1			1																																	
Circophyllia	S			1			1																																		
Cladangia	C	Massive or subramose, plocoid																															1			1			1		
Cladocora	C	Phaceloid																															1						1		
Clonosmilia	C	Unknown																																					1		
Coelocyathus	S																																							1	
Colpophyllia	C	Meandroid																																					1		
Conocyathus	S																																							1	
Cryptangia	C	Subtrochoid corallites																															1						1		
Cyathoceras	S																																				1			1	
Cyathoseris	C	Massive																																					1		
Cylindrophyllia	S																																				1				
Culicia	C	Tympanoid, reptoid																															1			1			1		
Dandromilia	U																1																								
Deltocyathus	S																																							1	
Dendracis	C	Ramose, rarely massive or incrusting	1																																						
Dendrophyllia	C	Dendroid	1						1						1			1			1			1			1			1			1			1			1		
Dendrosmilia	C	Dendroid or subphaceloid																																					1		
Desmophyllum	S																																							1	
Diploastraea	C	Plocoid																																					1		
Diplohelia	C	Dendroid	1			1			1																		1			1						1			1		
Distichopora	C	Flabelliform	1			1																																			
Dyctioastraea	C	Plocoid, massive, foliaceous, or incrusting																																		1					
Echinophyllia	C	Foliated																																					1		
Ellasmoastraea	C	Cerioid																															1			1			1		
Eupsammia	S			1			1																																		
Eusmilia	C	Phaceloflabellate																																					1		
Favia	C	Plocoid, massive, foliaceous, or incrusting																															1			1			1		
Favites	C	Cerioid																															1			1			1		
Flabellum	S			1																														1						1	
Glyphastraea	C	Ramose																															1						1		
Goniastrea	C	Cerioid or submeandroid																															1			1					
Goniopora	C	Massive, columniform, or ramose, rarely encrusting							1						1			1									1			1						1			1		
Graphularia	U			1				1			1												1			1															
Heliastraea (Aquitanastraea)	C	Plocoid																															1			1			1		
Heliastraea (Heliastraea)	C	Plocoid																															1			1			1		
Hexastraea	C	Ramose																																		1					
Leptomussa	S																																							1	
Lithodendron	C	Meandroid-phaceloid clumps	1																																						
Lithophyllia	C	Meandroid-phaceloid clumps																															1			1			1		
Lobophyllia	C	Meandroid-phaceloid clumps																																					1		
Lobopsammia	C	Dendriod	1			1									1			1									1			1											
Madracis	C	Ramose or submassive																																					1		
Meandrina	C	Meandroid													1			1																					1		
Miophora	C	Unknown																																					1		
Montastrea	C	Massive, incrusting, or subfoliaceous, plocoid																															1			1					
Mussismilia	C	Phaceloid																																					1		
Nerthastraea	U																																		1			1			1
Oculina	C	Ramose	1			1			1																		1			1											
Oulangia	C	Reptoid																																		1			1		
Oxypora	C	Foliaceous																																					1		
Pachyseris	C	Foliaceous, unifacial or bifacial																																		1			1		
Paleoastroides	C	Unknown																															1			1			1		
Paracyathus	S									1												1			1																
Palmipora	C	Arborescent	1												1			1																							
Parasmilia	S			1												1			1															1						1	
Pavona	C	Massive to foliaceous																																		1			1		
Phyllangia	C	Reptoid, encrusting																															1								
Platycoenia	C	Plocoid																															1			1			1		
Plerogyra	C	Phaceloflabellate																																					1		
Plesiastraea	C	Plocoid																															1			1			1		
Pocillopora	C	Ramose, rarely massive or incrusting																															1			1			1		
Porites	C	Massive, ramose or encrusting	1												1			1															1			1			1		
Ruessopsammia	U																																								1
Rhizangia	C	Tympanoid, reptoid																															1						1		
Scolymia	C	Meandroid-phaceloid clumps																																					1		
Seriatopora	C	Ramose or submassive																																					1		
Siderastraea	C	Massive, ramose or encrusting, cerioid																															1			1			1		
Smilotrochus	S																																							1	
Solenastrea	C	Unknown																									1			1											
Sphenotrochus	S			1			1																														1			1	
Stephanocoenia	C	Plocoid to subcerioid, massive																																					1		
Stephanophyllia	S																																				1			1	
Stylocoenia	C	Cerioid; ramose, massive, or encrusting	1			1			1						1			1																							
Stylophora	C	Plocoid; massive or ramose	1			1																											1			1			1		
Syzygophyllia	S																																	1			1			1	
Tarbellastraea	C	Plocoid; massive, incrusting, or subfoliaceous																															1			1					
Thegioastraea	C	Plocoid																															1			1			1		
Trochocyathus	S																																							1	
Trochoseris	S			1			1									1			1																						
Turbinaria	C	Contorted foliaceous													1			1															1			1			1		
Turbinola	S			1			1			1						1			1			1			1																
		Total:	**14**	**9**	**2**	**9**	**5**	**3**	**5**	**2**	**1**	**0**	**0**	**0**	**11**	**4**	**1**	**10**	**4**	**0**	**2**	**2**	**1**	**2**	**2**	**1**	**8**	**1**	**0**	**8**	**1**	**0**	**34**	**3**	**1**	**37**	**6**	**1**	**55**	**17**	**2**

APPENDIX 10. METHODS

SPECIMEN SELECTION AND HANDLING

Curation Training

Training was undertaken in basic curration techniques from fundamental collection documentation and research to preventive conservation or storage conservation.

Specimen Selection

The collection of *Acropora* specimens and associated corals, along with contemporaneously collected molluscs, were documented and databased. All specimens were selected primarily on their suitability for geochemical analysis but also on the basis of adequate label details such as locality and age. After selection, each specimen was photographed to produce a digital record due to the destructive nature of some of the analytical techniques used in this research.

Databasing

Databases were created in Excel documenting all label information. Additions were made to these as geochemical analysis provided more information about each specimen.

Specimen cleaning and preparation

All samples were separated from the host matrix and washed in an ultrasonic bath containing distilled water before being air-dried and examined under a binocular microscope to ensure no host matrix remained. For Modern specimens, the removal of organic material from the specimens was carried out at Museum of Tropical Queensland (MTQ). Organic material was removed from the coral samples by being placed in 30% hydrogen peroxide in plastic vials and sonicated for 60 minutes. This was repeated until no additional whitening of the specimens was observed. Specimens were selected from the MTQ database as the most appropriate modern analogue to the fossil material. All specimens were cut along the maximum growth axis, through the axial corallite.

ASSESSMENT OF PRESERVATION AND DIAGENESIS

Palaeoenvironmental interpretations can be made from two aspects of the direct study of the coral and molluscan specimens. Firstly, taphonomic information can be gained from the state of preservation of the specimens and secondly through palaeotemperature estimates based on $\delta^{18}O$ and Sr/Ca-based paleotemperature reconstructions of the fossil material. Fossil corals often undergo post-depositional diagenesis during which secondary minerals and/or cements are deposited. The inclusion of these in any palaeoclimatic analysis may significantly affect the bulk coral trace element geochemistry of the sample leading to erroneous estimates of past climate. Therefore, through petrographic and analytical analysis of the fossil samples, it is essential to assess the levels of preservation and diagenesis before any palaeoclimatic analysis can be undertaken.

Hand Specimen and Thin Sections

The fossils were examined, using a binocular microscope with an eyepiece graticule, to identify the presence of diagnostic coral and in particular *Acropora* features (see Wallace, 1999; Wolstenholme *et al.*, 2003). An assessment of the fossils preservation was also made looking for pristine micro-morphological features and evidence of diagenetic overgrowths and recrystallisations.

Thin sections were made, using a diamond saw with a water lubricant, by slicing specimens down the centre of the axial corallite and mounting them on a glass slide. This exposed the main morphological features, allowed an assessment of preservation and exposed the area on the opposite half of the specimen needed for geochemical analysis. Thin sections were impregnated with blue-dyed resin to stop the porous specimens from breaking during thin section preparation and also allowed identification and evaluation of the porous nature of the samples. Thin sections were left uncovered to allow the possibility of further treatment such as staining, cathodoluminescence and microprobe work. Petrological microscope work and photomicrography were combined to identify and record features of the specimens.

Scanning Electron Microscopy (SEM)

The LEO 1455VP Scanning Electron Microscope, Natural History Museum, London, was used to produce high resolution images in low vacuum mode (15 Pa). Examples of morphological characters were photographed of uncoated modern *Acropora* samples. Images of uncoated modern and fossil *Acropora* specimens allowed a comparative assessment of the taphonomic features of the fossil material.

EDX

EDX across the surface was undertaken using VP-SEM for non-destructive qualitative X-ray analysis of uncoated specimens in low vacuum mode. Detection limits are in the order of 0.2%. Point analysis was used to produces a series of EDX X-ray spectra.

Cathodoluminescence (CL)

A CITL CCL 8200 MkIV cold cathode chamber and control unit mounted on a Leica DM LM optical microscope, Natural History Museum, London, was used to identify geochemical and diagenetic variations of coral specimens. These specimens were selected on the basis of having the least and greatest aragonite percentage as identified by x-ray powder diffraction. Cathodoluminescence was used to verify and compare with XRD results and identify distribution of minerals within the specimens. Images were created of primary skeletal compositions and secondary cements, replacement and dissolution, using a Lecki 2000 mounted camera.

X-ray powder diffraction (XRD)

X-ray diffraction analysis (XRD) was performed using a Philips Analytical X-Ray BV PW 3710 machine, with a copper anode. Samples were hand ground using an agate mortar to form a powder, combined with water and smeared onto a glass slide. The grinding time of around 4 minutes has been documented as that required to provide optimal peak intensity for X-ray diffraction (XRD) analysis (Milliman, 1974). These slides were dried in a warm oven (~45˚C). The samples were scanned from 25° to 37˚ 2θ in order to cover the main $CaCO_3$ minerals peak intensities of aragonite and calcite.

XRD spectra points were saved as text files and imported into Excel allowing high quality, annotated plots to be generated. The main peaks were identified and the angle (2θ) of each noted. These angles were converted to lattice spacing (*d*) (in angstroms (Å)) using the conversion charts for copper radiations. Comparing the unique X-ray diffraction pattern of each sample with a set of standard patterns allowed the assignment of peaks to mineral phases. These standard patterns have been compiled by an international organisation called the Joint Committee on Powder Diffraction Standards (JCPDS), which collects and updates diffraction data, and using the JCPDS Powder Diffraction Index for Minerals allowed the identification of different minerals (*Table A10.1*).

GYPSUM	*d*(Å)	7.56	3.059	4.27	2.679	2.867	3.79
	I/I_1	100	55	50	28	25	20
	hkl	020	141	121	022	022	031
	$2\theta_{Cu}$	11.70	29.19	20.80	33.44	31.20	23.47
ARAGONITE	*d*(Å)	3.396	1.977	3.273	2.700	2.372	2.481
	I/I_1	100	65	52	46	38	33
	hkl	111	221	021	012	112	200
	$2\theta_{Cu}$	26.24	45.90	27.25	33.18	37.93	36.21
QUARTZ	*d*(Å)	3.343	4.26	1.817	1.541	2.458	2.282
	I/I_1	100	35	17	15	12	12
	hkl	101	100	112	211	110	102
	$2\theta_{Cu}$	26.67	20.85	50.21	60.03	36.56	39.49
CALCITE	*d*(Å)	3.035	2.285	2.095	1.913	1.875	2.495
	I/I_1	100	18	18	17	17	14
	hkl	104	113	202	108	116	110
	$2\theta_{Cu}$	29.43	39.43	43.18	47.53	48.55	36.00

Table A10.1. Summary of main minerals identified in specimens using XRD (highlighted values are the main peaks identified)

The relative amounts of aragonite were calculated using the peak area method after Milliman (1974). Using peak areas and a standard curve with an accuracy of +3%

(Milliman, 1974), the ratio of aragonite to total calcite (calcite plus magnesian calcite) was calculated for each sample (Fig. A10.1).

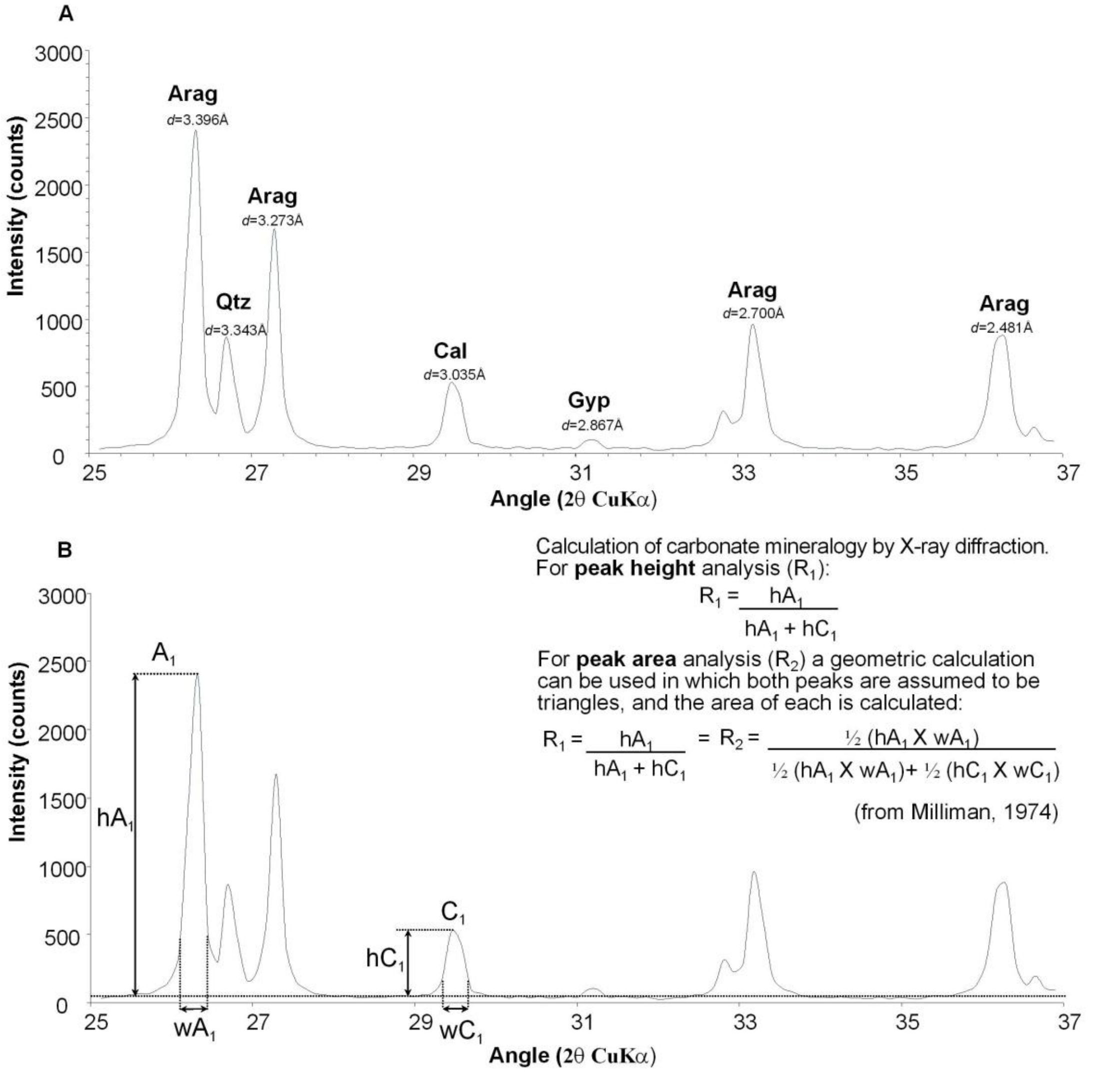

Figure A10.1. A. Diffractogram showing the main peaks of the carbonate minerals and quartz from samples scanned over 25-37 2θ, with d-values from Milliman (1974) (Arag-Aragonite, Qtz-Quartz, Cal-Calcite, Gyp-Gypsum). B. Peak height (R_1) and peak area (R_2) for the relative amounts of aragonite were calculated and compared with a standard curve to give relative percentages of aragonite.

It should be noted that mixtures do pose a problem. XRD allows measurements down to 5% so minerals can only be identified in a sample if it makes up 5% or more of the sample. Hence it is important to combine this technique with detailed thin section work in order to identify diagenetic minerals and cements.

Sources of uncertainty in δ18O and Sr/Ca-based paleotemperature reconstructions

Coralline aragonite $\delta^{18}O$ reflects sea water temperature, seawater $\delta^{18}O$ and a biological offset, the 'vital affect'. Sea surface temperature estimates from stable isotope analysis may produce erroneous results due to a series of factors including: changes in $^{18}O/^{16}O$ ratio of the ocean (δ^{18}Oocean) over time; changes global ice-volumes in over time; and uncertainties about the biological offset. Erroneous results may also be affected by diagenetic effects on skeletal material in both $\delta^{18}O$ and Sr/Ca-based palaeotemperature reconstructions.

Oceanic $^{18}O/^{16}O$ ratio and Global Ice Volume and Temperature Reconstructions

The exact value of past seawater $\delta^{18}O$ still remains unclear. It is presently believed that there was a smaller ice volume during the middle to late Eocene and therefore the ocean was isotopically lighter than it is now. Generally it is accepted that during the middle to late Eocene a value of -0.5‰ is suitable (Paul Pearson, Cardiff University, pers. com.). Using the Grossman and Ku (1986) equation outlined in Chapter 6 a δ^{18}Oocean value of -0.5‰ was applied. A value of -0.7‰ was also applied to take into account the near-shore setting of these specimens and the possible affect additional freshwater input would have in this environment.

There are still relatively few long records of coral skeleton Sr/Ca from which to derive SST reconstructions and hence coral-based temperature reconstructions are based largely on skeletal $\delta^{18}O$. Sea surface temperature uncertainties from coral $\delta^{18}O$ are related to potential changes in seawater $\delta^{18}O$ composition, such as changing global ice volume and regional freshwater inputs. 'Local' calibration and verification of coral skeletal $\delta^{18}O$ against instrumental-based records of SST can provide a way to address the problem, but has some significant drawbacks. However in these 'local' environments, 'local' specific conditions include rainfall amount, ocean mixing and advection may be more important. Therefore it appears impossible to reconstruct the magnitude of SST trends from coral $\delta^{18}O$ alone, given the large errors associated with trends in the instrumental SST databases particularly within the fossil where temperature reconstructions based on the modern record.

Analytical uncertainty

The 2-sigma instrumental uncertainty on a single δ^{18}O analysis is less than 0.1 ‰, i.e. less than 0.5° C equivalent (Cobb et al., 2008). The analytical uncertainty in a single Sr/Ca measurement is generally less than 0.5°C equivalent. Multiple measurements through the replication of analysis of the same sample can result in this analytical uncertainty being reduced. Analytical uncertainty is therefore not considered as a limiting factor for coral-based palaeotemperature reconstructions.

Between-coral offsets

For reasons that remain poorly understood, the absolute δ^{18}O composition of coral colonies from the same island has been found to differ by up to about 0.3‰, far larger than can be explained by the relatively small differences in either water δ^{18}O composition and/or temperature that generally exist in open ocean reef settings (Cobb *et al*., 2008). This is equivalent to a temperature uncertainty of about 1.5°C. Coral's oxygen isotopic composition are invariably depleted relative to equilibrium believed to be due to a combination of varying biochemical mechanisms of precipitation and also the influence of symbiotic zoothanthellae (McConnaughey, 1989). Arthur and Anderson (1983) outlined the oxygen and carbon isotope offsets of selected organisms due to the vital effect (Fig. A10.2).

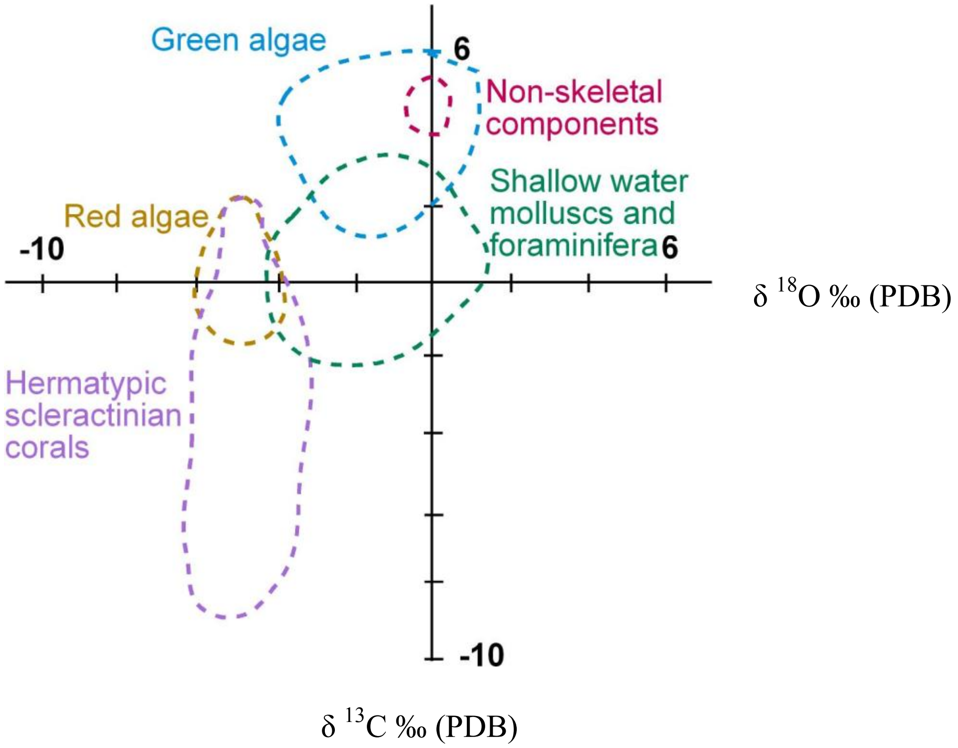

Figure A10.2. Oxygen and carbon isotope offsets (after Arthur and Anderson, 1983)

Post-depositional alteration of the skeleton

Carbon and oxygen isotope ratios of biogenic carbonate can be changed by two diagenetic processes: addition of new carbonate by cementation and dissolution of unstable carbonate and reprecipitation of a stable mineral. The methodology outlined in Chapter 6 attempts to identify any sources of error produced by these diagentic processes. Diagenesis can alter the bulk skeletal $\delta^{18}O$ and Sr/Ca by adding phases, often of secondary aragonite or calcite cements, with a different isotopic and Sr/Ca composition (McConnaughey, 1989; de Villiers *et al*., 1995; Cobb *et al*., 2008). Diagenesis has been documented in living coral colonies but is far more common in fossil corals. In extreme cases, diagenesis can result in values equivalent to well over 1°C (Weber and Woodhead, 1970).