BENTHIC CALCAREOUS ALGAE AS JURASSIC MARINE TEMPERATURE INDICATORS IN WESTERN EUROPE

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By

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Abstract

The determination of calcareous chlorophyte distributional limits is via temperatures – namely isocrymal limits, because the green algae are very susceptible to cold temperatures.

The calcareous green algae are today and were in the past, one of the most sensitive and useful environmental indicators. As well as being useful in distribution analysis, they are a useful part of biotic analysis in general. Calcareous green algae are mostly, but not wholly tropical in nature – they are found in shallow marine environments up to their range extent of just into temperate water masses (12°C isocrymal).

The Dasycladales were the dominant form of calcareous alga in the Jurassic (today their role has been largely taken over by the Halimedaceae). It can be seen that in the Upper Jurassic (where there are enough datapoints to form a reasonable limit, as opposed to the Lower or Mid Jurassic) that the Halimedaceae appeared to terminate at a line slightly southwards of the Dasycladales (this compares with the modern situation of a shared termination limit).

Modern calcareous Chlorophyta distributions can delimit the 12°C isocrymal water temperature boundary, and this limit can be imposed on the Jurassic Chlorophyta distribution dataset for palaeothermometry purposes. Together with selected isotope values, it is possible to estimate Jurassic isocrymes across Western Europe. This suggests the possibility of creatures such as belemnites (which are used for isotopically derived palaeotemperatures) having recorded summer temperatures in their isotopes rather than annual average. Modern algal temperature value differences (isocrymal versus summer maximum) is by ~10°C and this change in values for the Jurassic Chlorophyta produces temperature figures equivalent to a majority of the isotopically derived temperature values.
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I would also like to thank all of the people with whom I have shared an office for putting up with me!

"It has been justly said that palaeontologists have been in the habit of referring to algae such impressions or markings on rocks as cannot well be included in any other group. ‘A fossil alga’ has often been the dernier ressort of the doubtful student”

A.C. Seward
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Chapter 1 Introduction

1.1 Aim

This thesis is designed to test the hypothesis that:

"Jurassic marine temperatures can be inferred throughout northwestern Tethys from the distribution of calcified algae."

This requires comparative analysis based on documenting the affinities and distribution of calcified marine algae in the Jurassic of western Europe and the temperature distribution of similar present-day algae.

Algae are arguably the most sensitive and yet abundant indicators of water temperature (more so than corals for example) and are widely distributed in oceanic surface waters. Modern calcified marine algae have only so far been crudely used to help indicate differences in water temperature: - calcified greens, e.g. Dasycladales and Halimedaceae, are used to characterise tropical water, while coralline reds indicate the cooler waters (Wray, 1977).

The aim can be achieved through the refining of temperature-related assemblages and their application to palaeoclimate interpretation; via:

- Recognition of stages of tropical to temperate changes in sequences;
- Location of palaeoclimatic boundaries spatially within Jurassic time slices.

The following approach has been used:

- Interpret palaeoclimatic affinities of Jurassic algae from modern-day algal distributions and morphological adaptations.
- Differentiate between the influences of latitudinal change and differential local effects.
- Sample Jurassic algae from different relevant palaeolatitudinal positions for distribution analysis.
1.2 Jurassic

The Jurassic time period was selected in western Europe out of the three Mesozoic periods due to its lithological appropriateness; the Jurassic has widely distributed fossiliferous shallow marine limestones containing calcareous algae that can, on the whole, be compared with extant relatives.

In contrast in the Mesozoic, the Triassic period North of the Alps is mostly represented by non-marine deposits while the Cretaceous period contains many lithologies pertaining to deep-water environments, or conversely, non-marine sequences (e.g. the Wealden).

Of all the Mesozoic sequences, only the Jurassic time period has sufficient outcrops of shallow-water limestones in the general latitudinal range of interest to this study (in modern geographical terms, the European area).

The Jurassic setting of Western Europe was dominated by its location in the northwestern Tethyan Ocean. Tethys was first so-called by Suess (1893) when he referred to the “Central Mediterranean” great equatorial sea of Jurassic age stretching from Mexico to the Himalayas, described by Neumayr (1885). The origin of the name “Tethys” (which was also assigned to the 5th largest moon of Saturn [diameter 650 miles] in 1684 by the Italian astronomer G.D. Cassini [1625-1712] (Readers Digest 1994) [there are also two sub-orbital satellites around Tethys – Tethys B and Tethys C] (Asimov 1987)) is uncertain, it could refer to either:

**Tethys (Τῆθος)** – A Titaness and sea Goddess who was the wife / “sister and consort” of Oceanus,

Or, possibly but less likely;

**Thetis (Θετις)** – A Nereid, wife of Peleus, the mother of Achilles.

(Sylvester- Bradley 1967)

The Jurassic setting of Europe was different to that found today, located at slightly lower latitudes, the area was a shallow marine setting. The plate configurations were different in that the Iberian peninsula and the Italian and Greek /
Yugoslavian areas were all separate at this point – colliding and therefore joining later on in the Cretaceous. This setting was one of rising sealevels from Early Jurassic times into the Cretaceous (Stanley, 1986).

1.3 Palaeobiogeography of marine environments

Modern oceanic surface waters can be sub-divided into zones which are approximate to latitudinal climatic belts but are by no means always parallel to them (Craig 1961). See Table 1.1:

<table>
<thead>
<tr>
<th>Name</th>
<th>Temperature range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Polar</td>
<td>1.9-5°C</td>
</tr>
<tr>
<td>Subpolar</td>
<td>5-10°C</td>
</tr>
<tr>
<td>Temperate</td>
<td>10-25°C</td>
</tr>
<tr>
<td>Subtropical</td>
<td>15-33°C</td>
</tr>
<tr>
<td>Tropical</td>
<td>25-36°C</td>
</tr>
</tbody>
</table>

Table 1.1 Modern-day oceanic surface temperature zonation (after Milliman 1974). (N.B. On the shore and in shallow waters, limits may be exceeded.)

There are problems with different authors understanding of temperature related terminology:

Tropic – 1. either of two parallels of latitude 23°27’ North and South of the equator, being the Tropic of Cancer and the Tropic of Capricorn. 2. (the tropics) the region bounded by these latitudes, corresponding to the Torrid Zone (Morris, 1992).

Tropical – relating to, characteristic of, inhabiting, or occurring in the tropics (Morris, 1992).

Tropical seas – biological context: warm seas with small temperature fluctuations and biotic reefs (Michanek, 1979).

Subtropics – either of two latitudinal belts between the tropics and the temperate regions, roughly between 35° and 40° in latitude but varying in width according to continental influences (Morris, 1992).

Subtropical - biological context: equivalent to ‘warm temperate’ but has been used for the outer part of the tropics (Michanek, 1979).

Subtropical convergence – the boundary zones between warm subtropical and cold subpolar waters where some ocean currents tend to converge; the term generally refers to the well-defined southern convergence zone around 40°S,
but it may also refer to the ill-defined northern zone between 20ºN and 28ºN (Morris, 1992).

Temperate – sea area between 5 and 18ºC mean annual surface isotherms with surface water seasonal temperature changes. The colder part of the temperate region (5-10ºC) is called the Boreal zone in the northern hemisphere and the Antiboreal zone in the southern hemisphere (Tait, 1981).

Temperate belt – either of two broad belts around the earth, between the hot belt and the cold caps, within which the mean annual temperature is less than 20ºC and the mean temperature of the warmest month is above 10ºC (Morris, 1992).

Temperate zone – either of the two latitudinal zones on the earth’s surface which lie between 23º27’ and 66º32’ N and S (the North Temperate Zone and South Temperate Zone, respectively) (Parker, 1994).

Non-tropical shelf carbonates – those in higher latitude than development of hermatypic coral reefs, or in areas of less than 20ºC mean annual surface temperature which is near 30º latitude (displaceable by currents by 5-10º) (Nelson, 1988).

While James and Kendall (1997) state “A water temperature of about 20ºC partitions carbonates in modern shallow seas into a warm water, low-latitude realm and a cool-to cold-water mid-to high latitude realm”, Milliman (1974) separated the areas thus:

Tropical – >25ºC
Subtropical – 15-30ºC
Temperate – 10-25ºC

Therefore it can be seen that confusion over distribution can occur when non-quantitative terminology is used, as there are no standard terms used governing latitudinal areas and their environmental parameters. In this work, ‘tropical’ has been taken by me to mean warm water relating to the tropical areas of the globe (between the two tropics); this can be associated with the sea surface isocryme of 18ºC or higher. This definition ties in with Tait (1981) and his approximation of the temperate realm (see above).
The temperature gradient through the subdivisions varies gradually but recognisably and is the primary influence on the geographical distribution of marine organisms (Craig 1961), as well as restricting the diversity from tropics to poles (Fischer A.G. 1961). See Figure 1.1.

<table>
<thead>
<tr>
<th>LATITUDE</th>
<th>Tropical</th>
<th>Subtropical</th>
<th>Temperate</th>
<th>Subarctic</th>
<th>Arctic</th>
</tr>
</thead>
<tbody>
<tr>
<td>°C</td>
<td>25-36°C</td>
<td>15-33°C</td>
<td>10-25°C</td>
<td>5-10°C</td>
<td>1.9-5°C</td>
</tr>
<tr>
<td></td>
<td>Warm-water</td>
<td>20°C</td>
<td>Cool-water</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

![Diagram of modern calcareous algal distribution in oceanic surface-waters](image)

Fig. 1.1 Generalized diagram of modern calcareous algal distribution in oceanic surface-waters (after Wray, 1977, Milliman, 1974 and James & Kendall, 1997).

There is some evidence proposed of temperature control of at least fauna in the Jurassic Tethyan area of Europe – namely a northward decrease in diversity from the Tethyan to Boreal realm which possesses a similarity to the climatic zonation of the modern day Northern Hemisphere as well as a matching decline in the limestone abundance northwards from Southern Europe (Hallam 1969, 1975). The Tethyan realm, a faunal province based in the area of the Tethys, is characterised by a tropical to subtropical biota. It is opposed to the cooler more northerly Boreal realm (Arkell, 1956 and Hallam, 1975) which appeared to possess a lesser diversity of organisms (Hallam, 1975). The boundary between the Boreal and the Tethyan realms was gradational in nature and therefore has no precise (palaec) geographical location and is further complicated due to it fluctuating over time (Hallam, 1975). It appears that there was little / no differentiation between these realms in the Lias but this changed throughout the Jurassic until the Upper Jurassic when the two realms were clearly differentiated (Arkell, 1956).

The study of palaeobiogeographical raw data allows the recognition of palaeobiogeographic patterns and delimitation of provinces as well as the inference of
palaeobiogeographical processes and, in some cases, palaeogeographical (geological) processes (Cecca 1999). This basic premise is the central axial principle of palaeobiogeographical analysis; however, it is met with an opposite view, such as that stated by Valentine (1967) which say that estimates of the actual distribution of ancient organisms, whether spatially or temporally, lack precision due to the incompleteness of the fossil record, uncertainties in correlation, and bias in the treatment of fossils by palaeontologists.

The trouble with palaeobiogeography is that much of it is subjective and can dwell too much on subsidiary issues such as ecology and climatology (Rosen 1992). The theoretical aspects of (palaeo) biogeography framework is itself difficult in so much as it requires much generality. However, as with so much, the best approach to understanding can be achieved via perception of the basic aims of the subject:

1. To document the geographical distributions of organisms;
2. To analyse and derive patterns from this documentation;
3. To use these patterns to understand biogeographical processes.

(after Rosen 1992)

That is to say, in palaeobiogeography, the main basic emphasis is to delimit provinces and realms and to find the determinants of provinciality.

Rosen (1992) states a number (12 in total) of biogeographical and palaeobiogeographical rationales (from basic premises to complex expositions involving what he refers to as the ‘black box’ which covers the conjectural processes) which outline the routes taken by people in researching (palaeo) biogeography. Of these rationales, the suitable one for a study such as is undertaken in this thesis is that which covers the biogeographical consequences of such subjects as climate change, eustacy and geotectonics as well as the basic aims stated above. This rationale can be summarized as:

\[(\text{palaeo) biogeographical raw data } \rightarrow (\text{palaeo) biogeographical pattern } \rightarrow \text{biogeographical process } \rightarrow \text{relevant geological and related processes.}\]

This thesis will endeavour to derive a testable biogeographical hypothesis via three possible ways:
1. Bioclines patterns,
2. Inferred palaeolatitudinal patterns of fossil distributions, and
3. Synoptic comparison of fossil distributions over successive time intervals.

(Rosen 1992)

There are eight constraints on the use of fossil data in palaeobiogeographical analysis:
1. Taxonomic precision,
2. Sample size,
3. Incompleteness of the fossil record,
4. Stratigraphical correlation and resolution,
5. The hypothetical nature of palaeogeographical reconstructions,
6. Geotectonic setting,
7. Discontinuity of sample horizons,

(Rosen 1992)

Due to all these factors, fossil geographical patterns are more conjectural than modern ones. A further complication arises for fossils without extant counterparts (or close relatives) – (this problem is increased the further back in geological time you go; the value for understanding present distributions becomes more tenuous and the quality of distributional evidence decreases with increasing age (Myers and Giller 1988)). In such cases, mode of life must be deduced or assumed, which many people (e.g. Rosen 1992) state justifiably, will weaken the work – the more assumptions there are, the increased chance of mistake that can lead to erroneous conclusions.

There is one final niggle with fossil organism distribution analysis which is that the restricted distribution of geological systems makes the interpretation of palaeoclimatic zones based on geographical distribution of fossils complicated. Only part of the former marine life is preserved and procurable, and that part is generally to be found in the epicontinental and continental marginal deposits where faunas are notoriously variable (Craig, 1961).
1.4 Temperature from shallow marine carbonates

The staple idea of limestone deposition mostly revolved around a carbonate ‘factory’ (as defined by James and Kendal, 1992) in the tropics – conjuring images of warm shallow waters. Many examples of these kinds of carbonate environments can indeed be found in the fossil record. However, this core idea of carbonate production is incomplete – there are fossil limestone environments which cannot be fitted into such a tropical setting. In 1967, Chave showed that carbonates were forming today in areas outside of the ‘archetypal’ tropical setting – namely areas of high latitude, so-called “cold water” environs.

Such a possibility for the formation of limestones outside of the tropical regions led people to look at the recognisable differences between these types of calcareous sediment. The seminal paper on this being Lees and Buller (1972); which categorised the presence and associations of the two different types of carbonate related primarily to temperature differences (see Table 1.2):

<table>
<thead>
<tr>
<th>Lithofacies</th>
<th>Relative water temperature</th>
<th>Key elements</th>
<th>Other constituents</th>
</tr>
</thead>
<tbody>
<tr>
<td>Foramol</td>
<td>Temperate and warm</td>
<td>Benthic FORAminifera MOLLuscs</td>
<td>Calcareous red algae Ahermatypic corals Echinoids Bryozoans Barnacles Sponge spicules Worm tubes</td>
</tr>
<tr>
<td>Chlorozoan</td>
<td>Warm only</td>
<td>CHLOROphyta ZOANTharia</td>
<td>Ahermatypic corals Calcareous red algae Echinoids Sponge spicules Worm tubes</td>
</tr>
</tbody>
</table>

Table. 1.2 Carbonate temperature differences (after Lees and Buller 1972).

It should be noted that foramol and chlorozoan associations can be found together. It is the lack of any chlorozoan assemblage that must be used (the presence of foramol association characteristics does not necessarily mean the absence of a chlorozoan association, but conversely the absence of a chlorozoan assemblage does mean the presence of a foramol association in carbonate systems).

These two settings are separated by a zone of transition, which would be narrow in areal distribution and would appear more gradational if the skeletal
components were plotted at lower taxonomic divisions (Lees and Buller, 1972). The temperature boundaries in real life would be similar to latitudinal banding, but naturally disrupted from purely latitudinal by such factors as water currents, landmasses, localised salinity conditions etc.

There is a noted mutual compensating effect of temperature and salinity which can overprint the general regional normal (Lees, 1975). This salinity effect leads to an extension of the chlorozoan terminology:

<table>
<thead>
<tr>
<th>Lees &amp; Buller 1972</th>
<th>Lees 1975</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chlorozoan</td>
<td>chlorozoan – warm water, 31-40% salinity</td>
</tr>
<tr>
<td>(warm water)</td>
<td>chloralg – warm water, &gt;40% salinity</td>
</tr>
</tbody>
</table>

The possibility of using these temperature-dominated facies for palaeolatitudinal interpretation (which Lees [1975] says is both not the aim or possible) is first approached by Schlanger and Konishi (1975). They differentiated similar facies to Lees and Bullers’ chlorozoan and foramol, namely “coral-algal” and “bryozoan-algal” respectively. They show that the traditional warm-water “tropical” (chlorozoan; coral-algal) facies is a much more prolific generator of limestone than its temperate counterpart by up to an order of magnitude. This difference in the absolute rate of net CaCO₃ accumulation can be used as a palaeolatitudinal location marker (Schlanger and Konishi, 1975). Naturally, the occurrence / real (not preservational) absence of a ‘lithofacies’ indicator (e.g. Chlorophyta) could also be used as a facies extent locality marker.

One important factor to be taken into account first is the importance of scale influence, i.e. local topographic effects overprinting the regional latitude-linked climatic and oceanographic changes. Also important is the factor of depth which is also linked to temperature like latitude is (N.B. Chlorophyta are depth restricted to ‘shallow’ waters [normally c<20m] and so, again, are exemplar in this respect).

‘Cool-water carbonates’ (‘non-tropical shallow marine carbonates’; ‘cold water carbonates’; ‘temperate-region carbonates’; ‘mid and/or high-latitude carbonates’; ‘temperate latitude carbonates’; ‘foramol carbonates’; ‘temperate
carbonates’ are defined by Nelson (1988) as – those in higher latitude than
development of hermatypic coral reefs, or in areas of less than 20°C mean annual
surface temperature which is near 30° latitude (displaceable by currents by 5-10°).

The distinguishable and recordable differences between the ‘warm’ and ‘cool’
carbonate lithofacies can be seen in Table 1.3.

<table>
<thead>
<tr>
<th>ENVIRONMENTAL AND FACIES PARAMETERS</th>
<th>TROPICAL - SUBTROPICAL CARBONATES</th>
<th>TEMPERATE - POLAR CARBONATES</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude</td>
<td>30°N - 30°S</td>
<td>Beyond 30°N &amp; S</td>
</tr>
<tr>
<td>Depositional setting</td>
<td>Rimmed shelves or platforms</td>
<td>Open shelves or ramps</td>
</tr>
<tr>
<td>Terrigenous supply</td>
<td>Low</td>
<td>Low to high</td>
</tr>
<tr>
<td>Mean temperature</td>
<td>Above 23°C</td>
<td>Below 20°C</td>
</tr>
<tr>
<td>Minimum temperature</td>
<td>About 14°C</td>
<td>Below 12°C</td>
</tr>
<tr>
<td>Salinity</td>
<td>Normal to hypersaline</td>
<td>Normal (to reduced)</td>
</tr>
<tr>
<td>Carbonate saturation</td>
<td>Supersaturated to saturated</td>
<td>Saturated to undersaturated</td>
</tr>
<tr>
<td>Water circulation</td>
<td>Restricted to open</td>
<td>Open</td>
</tr>
<tr>
<td>Reefs</td>
<td>Abundant</td>
<td>Rare or absent</td>
</tr>
<tr>
<td>Algal mats and stromatolites</td>
<td>Common</td>
<td>Absent or not preserved</td>
</tr>
<tr>
<td>Carbonate content</td>
<td>Very high (&gt;90%)</td>
<td>Moderate to very high (50 – 100%)</td>
</tr>
<tr>
<td>Sedimentation rate</td>
<td>Relatively high (&gt;10cm / 1000y)</td>
<td>Relatively low (&lt;10cm / 1000y)</td>
</tr>
<tr>
<td>Ooids</td>
<td>Common</td>
<td>Absent</td>
</tr>
<tr>
<td>Flora components</td>
<td>Calcareous green algae</td>
<td>Calcareous red algae</td>
</tr>
<tr>
<td>Fauna components</td>
<td>Calcareous red algae</td>
<td>Coccolithophorids</td>
</tr>
<tr>
<td>Hermatypic corals</td>
<td>Bryozoans</td>
<td>Bivalve molluscs</td>
</tr>
<tr>
<td>Benthic foraminifers</td>
<td>Benthic foraminifers</td>
<td>Barnacles, Echinoderms</td>
</tr>
<tr>
<td>Molluscs</td>
<td>Serpulids, Brachiopods</td>
<td></td>
</tr>
<tr>
<td>Presence of carbonate mud</td>
<td>Common to abundant</td>
<td>Rare, locally common</td>
</tr>
<tr>
<td>Carbonate mineralogy</td>
<td>Aragonite dominant</td>
<td>Low- and / or high-Mg calcite dominant</td>
</tr>
<tr>
<td>Diagenetic regime</td>
<td>Constructive (grain preservation and chemical precipitation)</td>
<td>Destructive (grain dissolution and maceration, biodegradation)</td>
</tr>
<tr>
<td>Skeletal grain associations</td>
<td>Chlorozooan</td>
<td>Foramol</td>
</tr>
<tr>
<td></td>
<td>Chlororalgal</td>
<td>Bryomol</td>
</tr>
</tbody>
</table>

Table 1.3. Comparison of tropical and temperate carbonates (after Nelson 1988).

The attempt of physically locating such lithofacies and their boundaries was
first done with any success by Carannante et al (1988). Their work caused, as with the
workers before, the need for an expansion of Lees and Bullers terms; Carannante et al
split the foramol association into two sub-facies (see Table 1.4):
This provided an impression of the important, gradational zone of change which lies between the tropical / subtropical and cold temperate associations and marks the transition between them.

![Diagram of temperature-related zones and distribution of temperature controlled skeletal carbonate facies in <50m water depth.](image)

Their work also shows (in the case of Figure 1.2 on the SW Atlantic coast) how latitudinally linked, temperature dictated associations can be offset by other environmental factors (depth, upwelling, currents, river discharge etc.).

The transitional zone between the two end members of a global carbonate factory (warm and cool watermass associations) may be the most important facies in detailing the location of fossil lithofacies association occurrences. The best literature on this often rarely considered zone is that of Betzler et al (1997). This zone, which is the link between the tropical zooxanthellate coral reef-bearing province and the cold water realm (dominated by heterotrophic carbonate-producing organisms), is a zone
of gradual shifts in ecosystems and respective carbonate-producing assemblages (Betzler et al 1997). Some organisms can be used to try and delimit the boundaries (see Figures 1.3 and 1.4):

![Diagram of water mass temperature delimitation via organisms](image1)

**Fig. 1.3. Water mass temperature delimitation via organisms (after Betzler et al 1997).**

![Diagram of geographic boundaries from distribution of coastal macroscopic algae of the Atlantic](image2)

**Fig. 1.4 Geographic boundaries from distribution of coastal macroscopic algae of the Atlantic (after Round 1981).**

There is however, a problem when attempting to use this form of distribution analysis with the fossil record – namely preservational bias as is shown in Table 1.5:
<table>
<thead>
<tr>
<th>Tropical carbonates (e.g. Bahamas)</th>
<th>Warm temperate carbonates (e.g. Mediterranean)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calcified Chlorophyta well calcified.</td>
<td>Calcified Chlorophyta (e.g. Halimeda) show weaker calcification.</td>
</tr>
<tr>
<td>Water supersaturated in respect to aragonite, therefore, chances of rapid dissolution of heavily calcified algal skeletons – LOW.</td>
<td>Water undersaturated in respect to aragonite, therefore, chances of rapid dissolution of poorly calcified algal skeletons – HIGH.</td>
</tr>
<tr>
<td>Outlines of aragonitic skeletons preserved by micritic envelopes.</td>
<td>Occurrence of micritic envelopes is minor (in temperate carbonates).</td>
</tr>
</tbody>
</table>

Table 1.5. CaCO₃ differences in different temperatures (after Betzler et al 1997).

Therefore the chances of preservation of algal skeletons in the warm temperate facies of fossil carbonates is very poor compared to the tropical carbonate dwelling species. This can be misleading as to the position of the boundaries of fossil temperature-controlled carbonate facies.

Little work has actually been done on interpretation of the fossil locations of boundaries of these temperature-controlled carbonates. Elliott (1977) notes a Mid Jurassic Dasycladalean latitudinal distribution pattern (see Figure 1.5):

**Jurassic latitude**

| 50°N | Saline episodes - green algae but no Dasyclads |
| 40°N | Different and less common Dasyclads |
| 30°N | Characterised by *Selliporella* |

Fig. 1.5 Generalized Mid Jurassic Dasycladalean latitudinal banding (after Elliott 1977).

These three zones he distinguishes have not been connected to any temperature-related carbonates. Mu (1993) delineated the whole Cretaceous globe into three realms based on the presence and absence of aragonitic green algae (because they represent major groups and also have a widespread occurrence). His
phytogeographic realms are defined as "areas which have relatively homogeneous flora and are separated from others by floristic discontinuities", which appear to be a succinct distillation of the algal factors in the facies of Lees and Buller (1972) and their contemporaries.

The overall change in temperature-related carbonate terminology can be seen in Table 1.6 below:

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Chlorozoon (Coral-algal) [Photozoan]</td>
<td>Chlorozoon →</td>
<td>Chlorozoon</td>
<td>Tropical</td>
</tr>
<tr>
<td>Foramol (Bryozooan-algal) [Heterozooan]</td>
<td>Foramol →</td>
<td>Rhodalgal</td>
<td>Transitional</td>
</tr>
</tbody>
</table>

Table 1.6. Temperature related carbonate lithofacies terminology evolution and relationship.

The sedimentary nature of latitude-linked, temperature controlled limestones has already been stated. Modern-day tropical limestones extend up to the line of 20°C mean temperature of the coldest month; temperature is the prime control of the settings with associated latitude being only a crude proxy indicator of its extent (Schlager 2000). The transitional area between the tropical and cool-water carbonate factories is variable but tends to be >1000km wide in the modern day (Schlager 2000), although such environments are poorly studied (compared to the well understood tropical and the now better documented cool-water settings). Such an area of extensive, complete shelf area in the transitional zone in the modern day can be found at the SW part of Australia. Here, the transitional zone is broadly heterozooan (cool-water) but with some small warmer-water input. The green calcareous algae living in these areas are poorly calcified and do not form sediment like those in tropical waters. Also, this realm, like the cool-water realm, is dominantly calcitic in skeletal form (James et al 1999).

It is interesting to note that there is geological evidence which shows that cool-water carbonates (heterozooan assemblages) can, under specific conditions, occur in the midst of photozoan areas. The evidence for this comes from the late Carboniferous of the Austria-Italy border (Samankassou, 2002). The area was at the time at 5-10°S palaeolatitude and the sedimentary and palaeontological evidence
shows mostly a photozoan assemblage which is to be expected. However in one of the
cyclothsms found, in the midst of the photozoan environment, a bed displaying
heterozoan assemblages is to be found. This is explained by the alteration of local
conditions from the regional trend via a combination of an upwelling zone and
palaeoceanographic current activity. This shows that the difference between the
distribution of cool and warm water carbonates is (mostly but) not exclusively linked
to the latitude-related temperature banding of the oceanic surface waters.

1.5 Calcareous algae

Calcareous algae can be said to be: "Taxonomically diverse algae whose structure
Of these algae, those of interest are the ‘skeletal’ variety – i.e. possessing
morphologically differentiated calcareous hardparts (Flügel, 1982).

Of all the marine algae living at the present day only 8% of all algae of all
types are calcified (Wray, 1977, with 10% of green algal species being calcareous).

Calcareous algae are useful due to their increased fossilisation potential over
their non-mineralized counterparts. Algae in general are advantageous for
environmental analysis due to their inherent, environmentally-controlled,
physiological pre-conditioning. They can be used in phytogeographic investigation in
two ways:
1. Determination of the broad algal phytogeographic zones;
2. The geographic limits of individual taxa.

(Round, 1981)

Fossil algae, especially Dasycladales, produced large amounts of CaCO₃
which contributed significantly to lithologies at geological periods when they
flourished (Berger and Kaever 1992). Work on the palaeoenvironmental requirements
of Dasycladales appears to indicate that they did not occupy essentially different
habitats than at present, and that any changes are ‘lost’ the nearer to the present you
get (Berger and Kaever 1992). Elliott (1978) sees no real differences in the habitats of
fossil and modern Dasycladales from the Jurassic onwards.
Wray (1979), in his work on the use of benthic calcareous algae for palaeoenvironmental reconstruction, states in the introduction:

"Calcareous algae are potentially valuable fossils in the reconstruction of ancient depositional environments because they are abundant and widespread in carbonate shelf sediments. They provide a useful addition to other benthic organisms in delimiting marine biofacies. However, meaningful facies analysis may be difficult because of taxonomic problems and incomplete distributional data."

This echoes the hopes and encountered problems of all palaeoenvironmental workers – mainly:

1. The need for more and accurate distributional data,
2. Taxonomic problems due to uncertain affinities to extant forms leading to limitations and assumptions / guesswork on reconstructions,
3. The incompleteness of the environmental distribution of living taxa. (This is a problem more felt in the realm of calcareous algae than other palaeoenvironmentally used taxa.)

Benthic marine vegetation, occupying the edge of continents (in the shallow, well lit waters) are effectively restricted to about 2% of the marine surface (Prescott 1969). From the flora that inhabit this fringing environment, it can be seen that the correlation of their diversity and latitude is “one of the most imposing biogeographic features on Earth” (Fischer A.G. 1961). This link is the tool by which patterns can be wrought from the fossil record. In looking at this feature, it can be seen that regionally, temperature is the main factor of climatic control of marine plants (Fischer A.G. 1961, Berger and Kaever 1992, Wray 1977, and Craig 1961). The species comprising a population in an area can only exist within certain temperature zones, - most are confined within a 5°C banding, some are found across two such zones and a very few across three or even indiscriminately spread (Prescott 1969 and Fischer 1961)

The two main groupings of important calcareously coated algae today are the Halimedaceans and Dasycladales. They are both Chlorophyta which show temperature limited distribution in the modern ocean. There are differences between their environmental distributions:
1. Dasycladales are relatively inconspicuous in total marine algal flora, and much less evident than the calcareous Halimedaceans (also, fossil Halimedaceans tended to disaggregate into unidentifiable grains compared to the Dasycladales which were more prevalent in past times).

2. There are minor but important differences in tolerances to temperature, salinity and depth – Halimedaceae tolerate slightly more extremes in all factors.

   (after Wray 1977)

The importance of these algae will be shown in the modern algae distribution chapter.
Chapter 2 Methods

The following were the main methodologies used in the gathering of information for this study.

2.1 Fieldwork

Fieldwork was carried out at selected localities in W. Europe, and material was collected for further study. These areas were selected from Jurassic shallow marine carbonate outcrops likely or known to contain calcareous algae.

Field localities were:

**England** –
Cotswolds (Mid Jurassic) – 3 sites

**France** –
Normandy (Mid Jurassic) – 1 site
Ardennes (Mid Jurassic) – 7 sites
Lorraine (Upper Jurassic) – 7 sites
Jura (Upper Jurassic) – 4 sites
Ain (Upper Jurassic) – 10 sites
Languedoc (Upper Jurassic) – 11 sites

**Portugal** –
Lusitanian Basin (Upper Jurassic) – 5 sites

The details of these visits and the information gathered can be found in the fieldwork chapter (Chapter 3).

2.2 Thin Sections

A total of 165 standard 3 x 1 inch glass mounted thin sections of hand specimens obtained during fieldwork were made and studied under a binocular microscope in transmitted light. A few (seven) 3 x 5 inch glass mounted thin sections were made of some selected samples.
2.3 Literature Search / Databasing

Data obtained from extensive literature searches were used to establish present-day global occurrence of calcareous green algae and the distribution of Jurassic calcareous algae of all varieties throughout modern Europe. Personally obtained Jurassic data were compiled with the latter. These databases (which are to be found in the Appendices) are arranged taxonomically. The database of present-day algae (Appendix BII) is arranged into Dasycladales and Halimedaceae and further subdivided into genera and species (and in some cases subspecies, etc.). This database shows all relevant available data: species details, location, and any details of environment e.g. water temperature. The fossil database (Appendix C) is split into Dasycladales and other algae (including Microproblematica). This database lists genera and species alphabetically with pertinent details of stratigraphical age and location.

2.4 Maps and graphs

Maps of algal distributions constructed from the databases were used for graphical illustration and analysis, as follows.

Modern

Present day occurrences of calcareous Dasycladales and Halimedaceae genera were plotted on global maps. These distributions were compared with such factors as isocrymal plots, average isotherm plots, current and insolation data and various zonation plots.

Generic level cartography - The modern algal databases were constructed with as much detail as was possible – especially with regard to the elucidation of generic level to species, varietas and forma levels. However, when the distribution maps were drawn up, they were constructed at the generic level. This was for a number of reasons, as outlined in van den Hoek (1984):

- "... generic distribution patterns were thought to possibly reflect events and conditions in the geologic past better than species distributions..."
- "...more taxonomic tangles and uncertainties were expected on the species than on the genus level."
- "...if world-wide trends do exist on the generic level, they can be also expected on the species level (not necessarily the other way round)."

There is also the reverse scenario to be remembered, as stated by Lees and Buller (1972) with regards to the foramol and chlorozoan associations:
"In terms of areal distribution, the zone of transition from one association to the other is generally narrow. Naturally, if one were to plot the distribution of the skeletal components in terms of the lower taxonomic divisions (e.g. genera), then the change would appear less abrupt since it would be heralded by other changes."

**Fossil**

The database of Jurassic occurrences was used to plot distributions of the genera onto present day plate tectonic locations. These were then reconfigured to their positions for the relevant part of the Jurassic on palaeo reconstructions for the three series of the Jurassic: Lower (Lias), Mid (Dogger) and Upper (Malm). The maps were derived from the palaeo reconstruction program TIMETREKPRO (Timetrek, 1998) which produces animated continental fragment reconstructions. The maps from this program were chosen over other reconstructions (such as Smith et al, 1994) for ease of use and manipulation as well as the accuracy of reconstruction details which have been compiled from the latest information. From the reconstructed positions, the algae could be treated similarly to the modern day distribution plots. Palaeocurrent data could be used where available and comparisons made to other organisms, temperature sensitive deposits, isotopic data and Global Climate Model predictions.

Graphical representation of the data shown on the Jurassic distribution maps was made in order to display abundance variations of the algal groups and the position of areas of change as this is of interest to this study.

The quantitative temperature data from the modern distributions were then applied to the fossil counterparts and used to derive palaeotemperature interpretations.
3.1 Introduction

Fieldwork investigations were carried out throughout Western Europe, on a roughly North - South transect from England (Cotswolds) through France (Normandy, Ardennes, Lorraine, Jura, Ain and Languedoc) to southern Portugal (Lusitanian Basin) – see Figure 3.1, in areas of palaeoenvironmentally suitable Jurassic outcrops.

This fieldwork research was for the express purpose of finding calcareous algal material to provide supplementary data for distribution analysis and for systematic study.

The majority of the areas studied are of Upper Jurassic (Malm) strata, with the rest comprised of Mid Jurassic (Dogger) lithologies. The results of these two age series are separated so that a comparison can be made between them, in order to give an idea of the temporal phycological evolution of Western Europe between the Mid to Upper Jurassic.

In the case of the Upper Jurassic, each region is described below in turn and then the results of the individual studies are stated and collated. The results are discussed afterwards as a complete overall result, i.e. a discussion of the individual areas in the context of W. Europe as a whole as well as comparison between them.
3.2 Mid Jurassic

The fieldwork carried out in Northern Europe; the Cotswolds, Normandy and French Ardennes (see Figure 3.2) was in rocks of Mid Jurassic age (see Figure 3.3).

Fig. 3.2 Mid Jurassic field localities and Jurassic outcrop in Western Europe. Jurassic outcrops after Arkell (1956).

Fig. 3.3 Mid Jurassic time scale of localities. After Gradstein et al. 1994
These areas are all within Bathonian rocks, and have been studied previously with respect to calcareous algae.

The Cotswolds is the most northern of the Bathonian sites. During the time of its deposition, this limestone outcrop (found across Gloucestershire, England) was at a palaeolatitude and was of a sedimentary type which was expected to show algal material. The sparsity of phycological material from this area is discussed in a separate section (see Chapter 4).

The northern France Bathonian sites are situated on the flanks of the Paris Basin – Normandy to the northwest and Ardennes / Lorraine to the East. Both areas share the fate of being quarried for their stone – the lithologies being desired for construction works throughout France. This anthropogenic removal of outcrops has led to disappearance of the sites stated in previous works, and secondly an overall lack of remaining relevant outcrops being left. This presents the problems of the destruction of evidence of algal distribution during this time period.

3.2.1 Courtomer, Orne, Normandy

This mid Bathonian quarry site has been infilled since the data of Fily and Riout (1976) was obtained. This location, between Caen and Le Mans (c25km NE of Alencon) was found to have contained, within a pelmicrite layer, *Stichoporella cylindrica*, which is a characteristic Bathonian dasycladalean. This site is in fact only 30km North of the genotype locality for this alga (Mamers, Sarthe) (Fily and Riout, 1976).

3.2.2 French Ardennes

The NE France Bathonian outcrops (see Table 3.1) are part of a large carbonate shelf deposit of the Paris Basin abutting the Ardennes Rise landmass. The environment was one of shallow marine facies with a relatively high hydrodynamism. This has led to an invertebrate rich but phycologically poor site (see Table 3.2).
<table>
<thead>
<tr>
<th>Site</th>
<th>Sediment</th>
<th>Biota</th>
<th>Environmental interpretation</th>
<th>Thin section study</th>
</tr>
</thead>
<tbody>
<tr>
<td>Origny</td>
<td>Micritic limestone</td>
<td>-</td>
<td>Carbonate shelf slope</td>
<td>-</td>
</tr>
<tr>
<td>Martigny</td>
<td>Bedded limestone</td>
<td>-</td>
<td>Carbonate shelf slope</td>
<td>Cemented small oncoids and foraminifers</td>
</tr>
<tr>
<td>Leuze</td>
<td>Massive / bedded limestone and oncolite alterations</td>
<td>Bivalves Brachiopods</td>
<td>Shallower carbonate shelf slope</td>
<td>Foraminifers abundant, oncolidal, well cemented limestone</td>
</tr>
<tr>
<td>Chémeray</td>
<td>Oolitic limestone</td>
<td>Bivalves Brachiopods</td>
<td>Oolite</td>
<td>Mixed oolite and foraminifers with <em>Cay euxia?</em> in a light coloured cement</td>
</tr>
<tr>
<td>Signy l’Abbaye</td>
<td>Dipping bedded oolite</td>
<td>-</td>
<td>Oolite shoal</td>
<td>Well cemented ooids</td>
</tr>
</tbody>
</table>

Table 3.1 French Ardennes field sites

<table>
<thead>
<tr>
<th>Algal order</th>
<th>Taxon</th>
<th>Age</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhodophyta</td>
<td><em>Solenopora jurassica</em></td>
<td>Bathonian</td>
<td>Chémeray and Chesney</td>
</tr>
<tr>
<td>Dasycladales</td>
<td><em>Coniporella clavaeformis</em></td>
<td>Bathonian</td>
<td>Hirson</td>
</tr>
<tr>
<td>Dasycladales</td>
<td><em>Stichoporella stutterdi</em></td>
<td>Bathonian</td>
<td>Unknown</td>
</tr>
</tbody>
</table>

Table 3.2 French Ardennes calcareous algae previously reported.

Previous work

The Bathonian outcrops of the French Ardennes region were comprehensively documented by J.C. Fischer (1969). His interpretation of this area is still used as the main text on the subject and his lithologies can be seen in Table 3.3.

<table>
<thead>
<tr>
<th>Fichers terms</th>
<th>Time Periods</th>
<th>English equivalents</th>
</tr>
</thead>
<tbody>
<tr>
<td>calcaires marneux supérieurs</td>
<td>Callovian inférieurs</td>
<td>Upper Combrash</td>
</tr>
<tr>
<td>calcaires marneux inférieurs</td>
<td>Bathonian supérieurs</td>
<td>Upper Combrash</td>
</tr>
<tr>
<td>calcaires marno-crayeux supérieurs</td>
<td>Termes de Transition</td>
<td>Forest Marble</td>
</tr>
<tr>
<td>calcaires marno-crayeux inférieurs</td>
<td>Termes de Transition</td>
<td>Forest Marble</td>
</tr>
<tr>
<td>calcaires pseudo-oolithiques supérieurs</td>
<td>Bathonian Moyen</td>
<td>Marly beds &amp; “White 1st”</td>
</tr>
<tr>
<td>calcaires pseudo-oolithiques inférieurs</td>
<td>Bathonian Moyen</td>
<td>Marly beds &amp; “White 1st”</td>
</tr>
<tr>
<td>oolith miliaire</td>
<td>Bathonian inférieurs</td>
<td>Great oolite</td>
</tr>
<tr>
<td>marnes à <em>Pholadomyes</em> et marnes à <em>Ostrea acuminata</em></td>
<td>Bajocian supérieurs</td>
<td>Upper inferior oolite</td>
</tr>
</tbody>
</table>

Table 3.3 French Ardennes lithological explanation (after Fischer 1969)

Fischer's work suggests the environment to be shallow (<2m) warm (~20°C) supersaturated marine conditions with coral reefs and oolites.
Fischer reported the presence of:

- *Solenopora jurassica*
- *Coniporella clavaeformis*
- *Stichoporella stuterti*
- *Cayeuxia moldavica*

Also it has to be noted that since Fischer's work a lot of his sites no longer exist: they are either overgrown, quarried out or now are just part of the road system covering the countryside.

### 3.3 Middle Jurassic overall summation

Northern Europe was an area of apparently sparse phycological settlement during the Mid Jurassic. This lack of both amount and diversity of algal material could be due to:

- Algae originally present but not preserved;
- Algae originally scarce even though lithologies (shallow marine limestones) are suitable;
- Algae scarce because lithologies/environment unsuitable;
- A combination of the above.

The phycological sparsity is most likely due to a combination of the three factors stated. It is certainly true that many of the lithologies studied in the area show signs of preservational alteration; however, on the other hand, some of the other fossil organisms show good preservation.

Although these localities provide a very limited view of the Bathonian flora, the available literature (Elliott, 1975, 1983, 1985; Fischer, 1969; Fily and Rioult, 1976; and Bassoullet et al., 1978) does indicate that green calcareous algae in these areas are both scarce and of relatively low diversity.
3.4 Upper Jurassic

3.4.1 Jura / Ain

3.4.1.1 Introduction

The Jura mountains are a large chain of uplifted Jurassic and Cretaceous strata that run through mid eastern France and western Switzerland. The name Jura comes from the Celtic root *jur*, *juria* meaning forest and may be related to the Slavonic *gora* meaning mountain (Collet and Werenfels, 1927).

Most of the high Jura is covered by vast, thick evergreen forestry: the area in Ain is more agricultural (the trees now having been felled) and is dominated by the Rhône valley. It is from this area that the Jurassic time period was first correlated and named by von Humboldt in 1795.

The Jura mountains fan out northwards from the Alps and cover about 300 kilometres in length and 150km in width; their structure is the result of a tangential Alpine push through the Tertiary molasse syncline (Collet and Werenfels, 1927).

Most of the limestones in the area have been severely affected by the tectonic upheaval of the orogeny as well as by modern weathering (and biological actions) which have altered them chemically and physically.

3.4.1.2 Calcareous algae and their facies

There are many papers associated with the tectonic regime of the area and a reasonable geologic guide by Chauve (1975). Johnson et al. 1984 state “...The structural setting of the Jura has long been a classical example of a foreland fold-thrust belt...” However, this work is devoted to the algal assemblages of the area, and there is far less information in this regard.

P. Bernier has produced a number of papers on Jura algae and their stratigraphical correlation. The first on the subject was a comparison of a carbonate sequence in the S. Juras to the carbonate tidal flats of Andros Island (Bahamas) (Bernier 1979c). There was also a fossil algal conference in Paris, with a field trip to the Jura to display the areas algal assemblages and palaeoenvironments (Bernier and Gaillard 1979). The field excursion guide for that was similar to, due to it being based
on, a paper by these workers which was published a year later (Bernier and Gaillard 1980). This paper is a useful guide to localities and algal assemblages in the French Jura region as well as being of stratigraphical use. All the work was accumulated and expanded in his later work (Bernier 1984).

Of the other work on the area, one of the most useful is that of Strohmenger et al. (1991) which is concerned with eustatic effects on the limestones of the Jura and Dinarides, and attempts to correlate between the two platforms in terms of overall effects of sea-levels as well as the floristic similarities.

K. Dahanayake (1978) has published a paper on the environmentally interpretive use of oncocoids, based on those found in the Upper Jurassic French Jura (more specifically in the department of Ain). He defines four types (see Table 3.4):

<table>
<thead>
<tr>
<th>Oncoid type</th>
<th>Description</th>
<th>Environmental significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>Generally round, up to 10mm diameter, micritic / organic laminations around an intraclast or bioclast.</td>
<td>High energy depositional milieu. Constant flooding – winnow away mud. Subtidal zone of tidal flat.</td>
</tr>
<tr>
<td>II</td>
<td>Mostly elliptical with long diameter of 0.5 to 3cm. Interlayers of micrite, grumose and organic laminations around bioclast, intraclast, entire organism or smaller oncocid.</td>
<td>Dry conditions e.g. upper intertidal zones or supratidal of tidal flat. Shallow / mild energy.</td>
</tr>
<tr>
<td>III</td>
<td>Spherical 1 to 3cm diameter interlayers of micrite and organism bearing laminations around a bioclast, intraclast, entire organism or smaller oncocid.</td>
<td>Depressions of supratidal milieu?</td>
</tr>
<tr>
<td>IV S (simple)</td>
<td>Algal mesh encrusting entire organisms and debris. Amoeboid form – long diameter of 1mm to 4cm. No laminations.</td>
<td>Low depositional energy – upper supratidal zone of tidal flats. Rounding due to storm currents.</td>
</tr>
<tr>
<td>IV C (compound)</td>
<td>Algal mesh like IV S + encrusted oncocoids. Amoeboid form – long diameter of 1 to 3cm.</td>
<td>Type III environment – flooding brings in types I and II and calmer period binds in algal mesh forming IV C.</td>
</tr>
</tbody>
</table>

Table 3.4 Oncoid differentiation. (Information modified from Dahanayake, 1978)

Dahanayake summarized the composition of the Jura oncocoids as:

1. Micritic laminations.
2. Grumose laminations.
4. Algal mesh of *Bacinella irregularis*. 

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Another palaeoenvironmental setting indicator is that of temorary and/or episodic emersion – this has been noted by Bernier and Enay (1972) in Grand-Colombier (an elevation containing the site in this work referred to as Virieu-Martin). These emersion features include evaporite evidence (in the guise of Gypsum pseudomorphs) and also the presence of star shaped dessication cracks within the upper surfaces of limestone beds. Further support for emergence comes from nearby Mortveau (France) where upper Portlandian beds with brackish fauna are found, demonstrating the change into Purbeckian fresh-water deposits (Collet and Werenfels, 1927).

More evidence for this repeated emersion can be found in the Upper Kimmeridgian lithographic, lagoonal limestone of the Cerin site. Gall et al (1985) show indications of an algal film (possibly cyanobacterian) on the carbonate mud surface.

It is considered by some (Bernier and Courtinat 1979), that the Upper Kimmeridgian deposits of the French Southern Jura region are representative of a confined lagoon setting composed of several small independent basins. This idea coming from the microplankton and other organic debris to be found in the limestones of the area.

An additional factor to be noted in this study is that of diagenetic alteration – this tectonically upheaved area will have been subjected to some diagenetic alteration of the limestone strata: - work done by Johnson et al (1984) points to the difference in diagenetic and non-diagenetic limestone in the region being identifiable by:

- Diagenetically altered – limestone is tan coloured – due to goethite interaction on the limestone in the Tertiary.
- Non-diagenetically altered – limestone is blue-grey coloured – natural colouring for this limestone.

3.4.1.3 Results

My algal studies in the Jura have shown the following occurrences (see sites maps Figures 3.4 and 3.5, outcrop map Figure 3.6 and algal table Table 3.5):
Fig 3.4 Map of Jura site locations
Fig. 3.6 Geological map of the French Jura and Ain regions with upper Malm outcrop shown in green.
<table>
<thead>
<tr>
<th>Site</th>
<th>Algae present</th>
</tr>
</thead>
</table>
| Cluse de la Balme | Salpingoporella pygmaea?  
                        Campbelliella striata  
                        Cayeuxia sp.?  
                        Baccinella irregularis  |
| St. Didier    | Salpingoporella pygmaea?                           |
| Le Rocheret   | Salpingoporella annulata?                         |
| Cerin         | Clypeina jurassica  
                        Salpingoporella annulata  
                        Campbelliella striata  
                        Cayeuxia  
                        Pseudoepimastopora?     |
| Armix         | Cayeuxia  
                        Varioparietes?           |
| Landaize      | Clypeina jurassica  
                        Campbelliella striata  
                        Either Salpingoporella sp. or Cylindroporella sp.   |
| Virieu – Martin | Clypeina jurassica  
                         Campbelliella striata  
                         Macroporella sp.?  
                         Lithocodium / Baccinella?  |
| Echallon      | Campbelliella striata                             |
| Oyonnax       | Clypeina jurassica                                |
| Molinges      | Salpingoporella annulata  
                        Macroporella sp.  
                        Cayeuxia sp.  
                        Pseudoepimastopora?     |
| Pont de Lemme | Clypeina jurassica  
                        Salpingoporella annulata?  
                        Likanella bartheli  
                        Cayeuxia           |
| Pont de la Chaux | Cayeuxia  
                         Halimedacean?                   |

Table 3.5 Algae found at Jura localities.

This fits into the overall algal scheme of the area, according to other published sources, as can be seen in Table 3.6:
<table>
<thead>
<tr>
<th>ALGAE</th>
<th>CEB</th>
<th>ETC</th>
<th>LE-ROC</th>
<th>CEH</th>
<th>ARM</th>
<th>LAND</th>
<th>V-M</th>
<th>MQ</th>
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<th>V-DAM</th>
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</table>

Table 3.6 Algae found at Jura localities by myself and other authors.

**Sites**: CDB = Cluse de la Balme; STD = St. Didier; LE ROC = Le Rocheret; CER = Cerin; ARM = Armill; LAND = Landaise; V-M = Virieu-Martin; MQ = Mares Quarry; ECH = Echallon; OY = Oyonnax; MOL = Molenge; V DAM = Vouglans Dam; PDL = Pont de Lemme; PDL = Pont de la Chaux.

**Algæ**: Cj = Clypeina jurassica; Cas = Clypeina aff.solkani; Ss = Salpingoporella sp.; Sj = Salpingoporella jurassica; Sa = Salpingoporella annulata; Sp = Salpingoporella pygmaea; Cs = Campbelliella striata; Mf = Montenegroella florifera; Lb = Likanella bartheli; As = Acicularia sp.; Ae = Acicularia elongata; An = Acicularia americana; Pb = Petrascula burstiformis; Pg = Petrascula guembeli; Pp = Petrascula piai; Pa = Petrascula annulata; Pt = Petrascula bugesiaca; Cm = Cladocoropsis mirabilis; Gs = Gyroporella sp.; Ms = Macroporella sp.; Cys = Cylindroporella sp.; Cyl = Cylindroporella lemenstis; Cysu = Cylindroporella sudeni; Tc = Terquemella concava; Vs = Vaginella striata; Pj = Parachaetes jurassica; Sej = Solenopora jurassica; Casp = Cayeuica sp.; Cas = Cayeuica piae; Cam = Cayeuica moldavica; La = Lithocodium aggregatum; Tp = Thaumatoporella parvovesculifera; Bi = Bacinella irregularis; Lb = Lithocodium - Bacinella; P = Pseudoepimastopora; Vs = Varioarietes sp.; UC = Unknown Codiacous type thing.

<table>
<thead>
<tr>
<th>Legend</th>
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<tbody>
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<tr>
<td>X</td>
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<tr>
<td>?</td>
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<tr>
<td>Never found at this site</td>
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</table>

Also found at the sites visited were the following types of fauna (see Table 3.7):
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<tr>
<th>Site</th>
<th>Macrofossils</th>
<th>Microfossils</th>
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<tbody>
<tr>
<td>Cluse de la Balme</td>
<td>Bivalve fragments</td>
<td>Eggerella cf. meentzeni</td>
</tr>
<tr>
<td></td>
<td>Gastropod fragments</td>
<td>Very abundant Milioids?</td>
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<tr>
<td></td>
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<td>Trocholina elongata</td>
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<td>Stomatostaecha sp.?</td>
</tr>
</tbody>
</table>

Table 3.7 Other fossils found at Jura localities.
From the above biota, and the lithologies found, it can be seen that the palaeoenvironment of the area in the latest Jurassic was a relatively warm shallow marine carbonate setting with some reefs present. A "typical" Upper Jurassic carbonate shelf/ramp setting on the N. Tethyan margin.

There are a great number of similarities between the algae found in the latest Jurassic strata of the Jura and also of the reefal setting of Languedoc and of the Dinaric Platform – indicating similar conditions (see Section 3.4.4 and Figure 3.7 and Table 3.8):

![Jura comparative location map](image)

Flügel (1982) states that the fossil assemblage of *Clypeina jurassica*,
*Campbelliella striata* and *Salpingoporella annulata* has a true stratigraphic value and
is indicative of Upper Malm strata.

### 3.4.1.4 Conclusions

This area of Europe on the Swiss – French border is the location of algally abundant Upper Jurassic limestones which were originally deposited on the northern Tethyan margin in lagoonal environments.

This environment and, the algal species found here are very similar to those found further to the South in Languedoc and to the East in the Dinarides. This would seem to indicate a regional banding trend to the environmental conditions prevalent at the time, at these localities.

The French Jura mountains are an important area in the algal latitudinal distribution scheme, for they indicate that this latitudinal locality was still in the sphere of influence of the area to the South – the conditions of preferred algal growth, as compared to the relatively algally sparse areas to the North.
3.4.2 Languedoc

3.4.2.1 Introduction

The province of Languedoc in southern France covers a number of geologically and historically interesting areas. This report is concerned with the upper Jurassic outcrops in the Cévennes region, namely those in the L’Hérault area.

The terrain is one of pseudo-karstic Jurassic limestone mountains, with a number of cave systems within them, and Tertiary infilled grabens separating the small scale ranges. The limestone is of the last parts of the Jurassic - mainly Tithonian in age (with, in some areas, some Kimmeridgian) and varies in composition and construction from area to area due to the nature of the various depositional regimes operating at the time (see Bernier, 1967, 1968; Bodeur, 1980) (see Figures 3.8 and 3.9 for geological map and localized facies map).

There was a large reefal complex stretching latitudinally across the S.E. of France (Séguret et al, 1997) in what was at the time a carbonate basin. This basin was sinking at a fairly fast rate and this was matched by copious limestone production which gives up to c500-600m of backreef limestone facies rocks in some areas.

The L’Hérault area was to the extreme West of the reefal chain, but is characteristic of the facies as a whole, and is the best exposed. The area is uplifted and faulted partly due to the Pyrenean orogeny as well as the Tethyan closure event (Alpine orogeny).

This area will potentially provide good information on Jurassic carbonate reef algae and their environments. Logs and site maps are shown in Figures 3.10 and 3.11.

3.4.2.2 Previous work on area

As with any part of France, the geology of the area is summarised in the regional geology guide (Gèze, 1995) with traverses / routes through the area. More detail is provided by papers on specific aspects of the area.

The area is part of a carbonate ramp extending across SE France during the relevant time of Tethyan existence (Séguret et al.,1997a & b). This well preserved carbonate system enables us to distinguish the zones present in the reefal structure; and
Fig. 3.8 Languedoc geological map, after 1967 version of Carte Géologiques Français.
Fig. 3.9 Localized site and palaeofacies map, after Seguret et al (1997)
Fig. 3.11 Languedoc sites

- **Montagne de la Serrane / Rocher de la Barre**
  - La Table
  - Mont-Maury
  - Tab 1-3
  - 500m
  - Cazilhac (Le Haut)
  - Rdb 1-4
  - 872
  - Le Roc Blanc
  - Roc Blanc
  - L’Escarrelt
  - Mse 5-4
  - Mse 1-2
  - Mse 3-4
  - Montagne de la Serrane
  - 914 Ridge line
  - 500m
  - 939
  - Roc de la Barre
  - Les Prats / Maline
  - Les Prats
  - 170
  - St. Jean-de-Bueges
  - 396
  - La Maline
  - 557
  - Les Prats
  - 821
  - Le Roc Blanc
  - 821
  - Rdb 1-4

- **Les Oliviers**
  - La Cadière
  - Le Vigan
  - Oli 2-1
  - 575
  - Ganges
  - Montpellier
  - St. Hippolyte du Fort
  - D999
  - 500m
  - St. Martin-de-Londres
  - Arg 1-25
  - D986
  - D107e
  - 500m
  - Farm 1
  - Farm 2
  - Fliv 4-6
  - Fliv 1-3
  - Ferriére-les-Verreries
  - D107e
  - 500m
  - Claret
  - D181
  - St. Martin-de-Londres

- **La Cadière**
  - St. Hippolyte du Fort
  - D999
  - 500m
  - 252
  - Carconne
  - 149
  - Quissac
  - 149
  - Cremal
  - 149
  - Pomponnan
  - 149
  - Claret
  - 149
  - D181

- **Rieutord**
  - Disused railway line
  - 252
  - Carconne
  - 149
  - Quissac
  - 149
  - Cremal
  - 149
  - Pomponnan
  - 149
  - Claret
  - 149
  - D181

- **Coupe du Coutah / Pont du Hasard**
  - Pont du Hasard
  - 302
  - 270
  - 149
  - Quissac
  - 149
  - Cremal
  - 149
  - Pomponnan
  - 149
  - Claret
  - 149
  - D181

- **Argillers**
  - Puechabon
  - D27c
  - Argillers
  - D27c
  - St. Martin-de-Londres

- **Rocher de la Barre**
  - Le Prats
  - 170
  - St. Jean-de-Bueges
  - 396
  - Les Prats
  - 821
  - Le Roc Blanc
  - 821
  - Rdb 1-4

- **Montagne de la Serrane**
  - La Table
  - Mont-Maury
  - Tab 1-3
  - 500m
  - Cazilhac (Le Haut)
  - Rdb 1-4
  - 872
  - Le Roc Blanc
  - Roc Blanc
  - L’Escarrelt
  - Mse 5-4
  - Mse 1-2
  - Mse 3-4
  - Montagne de la Serrane
  - 914 Ridge line
  - 500m
  - 939
  - Roc de la Barre
  - Les Prats / Maline
  - Les Prats
  - 170
  - St. Jean-de-Bueges
  - 396
  - La Maline
  - 557
  - Les Prats
  - 821
  - Le Roc Blanc
  - 821
  - Rdb 1-4

**Legend**
- Spot height (m)
- Sample location
also preserved are the organisms inhabiting / constructing this framework. The western end of the reefal “chain” is well studied in terms of both lithology and (micro) palaeontology, with particular emphasis on Upper Jurassic and Cretaceous deposits, as these are the most important and prevalent constituents present.

Algal specialists were shown the important sites as part of the 1979 algal symposium (Jaffrezo, 1979). These sites, the knowledge of the algae present and the geological settings were all based upon the thesis of Bernier (1979). In this work he details the phycological finds of the area. Following this, other workers have published algal work on the area and the palaeogeographical / palaeoecological interpretations from this information (e.g. Lébouché and Lemoine, 1963, Bodeur, 1980 and 1995). This has given us a reasonably good understanding of the area at the time and this information can be used to interpret Languedoc standing relevant to other sites as well as giving us the opportunity to use the information of the inhabiting flora in a wider context.

### 3.4.2.3 General Area Relevant To Sites

The Tithonian of this region is made up of massive reef limestone, which can be distinguished by the limestone type and biota present (see Table 3.9 and Figure 3.12).

<table>
<thead>
<tr>
<th>Facies</th>
<th>Localities</th>
<th>Lithology</th>
<th>Fossils</th>
</tr>
</thead>
<tbody>
<tr>
<td>External</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Platform (Basin)</td>
<td>Les Oliviers</td>
<td>Pelagic, stratified thin beds, 100-250m thick, beige micrite.</td>
<td>Ammonites, Radiolaria and</td>
</tr>
<tr>
<td></td>
<td>La Cadière</td>
<td></td>
<td>Globochaete</td>
</tr>
<tr>
<td></td>
<td>Coupe du Couthah</td>
<td></td>
<td></td>
</tr>
<tr>
<td>External</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reef Slope (Forereef)</td>
<td>Rieutord</td>
<td>Hemi-pelagic, 200-400m thick, purer limestone, more massive and very</td>
<td>Dasycladales, Diceratids</td>
</tr>
<tr>
<td>Barrier</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>La Table</td>
<td>Reefal, white bioclastic, massive limestone, up to 500m thick.</td>
<td>Corals, Diceratids,</td>
</tr>
<tr>
<td></td>
<td>Roc Blanc</td>
<td></td>
<td>Dasycladales, Echinoid</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>debris, Gastropods,</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Hydrozoans, Bryzoans,</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Foraminifers and rare</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Ammonites.</td>
</tr>
<tr>
<td>Internal</td>
<td></td>
<td></td>
<td>Diceratids, Foraminifers,</td>
</tr>
<tr>
<td>Platform (Lagoon / Backreef)</td>
<td>Argilliers</td>
<td>Sediment, varies from c200m - 600m thick - complex alterations of pure,</td>
<td>Diceratids, Stromatolites,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>bioclastic and agglomerated limestones, largely stratified and benthic</td>
<td>Oncolites, Ostracods,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>organism rich. Subject to frequent but changeable water emersion.</td>
<td>Foraminifers, Bivalves, and</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Sponges</td>
</tr>
</tbody>
</table>

Table 3.9 Languedoc reef sections.

These facies can be seen and recognised in the Montagne de la Serrane which shows the Jurassic reefal sections (see Figures 3.13 and 3.14).
Fig. 3.12 Stylized cartoon cross - section of Portlandian Languedoc showing palaeogeographical associations and examples of sites from all four main facies. (After diagram from French tourist board leaflet.)
3.4.2.4 Results / discussion

The information given in this report can be used in a number of ways. At the local scale, it can be used to aid in the study of the reef system by allowing the reef to be subdivided into facies zones (see Figure 3.14). This gives information on the ecological distribution of the algae:

It can be seen that the majority of the algae prefer the sheltered lagoonal setting which will suit most of the Dasycladales which can be easily broken in more energetic settings, and the Cyanobacteria which would not cope with more energetic conditions. The fragile calcispheres however prefer the basinal conditions which are very low energy.

The barrier setting suited the Dasyclade Neoteutloporella socialis which was a more robust calcareous alga which formed strong "bushes". These bushes acted as baffles and led to a small accumulation of the other forms of algae which could endure the more favourable conditions found in the shelter the bush produced.

In modern day settings (such as the Bahamas), a similar scenario is observable – the algae (of different types with coralline algae being a large factor nowadays) will still mostly inhabit more sheltered conditions, with some specialized, stronger algae forming "algal ridges" at the higher energy conditions, creating a form of barrier. These modern reefs show that today, Dasycladalean algae normally live in warmer water conditions in shallow seas of generally normal to slightly higher salinity (there can be some difference in algal genera / species with different substrates).

The petrography of the sedimentary facies within the area is interesting and discussed below. Representative thin sections of the facies are numbered e.g. ARG 17, and are currently archived in the sedimentary rock store of the Cardiff University School of Earth, Ocean and Planetary Sciences.

**Biosparite / bioclastic shelly grainstone** (e.g. ARG17) – shows the energy input to the system – no micrite between the relatively well-rounded grains indicates winnowing away of the finer material by currents.
**Superficial ooids** (e.g. ARG19) – show a changing environment with calmer conditions following slightly higher energy ones (oolitic fabric forming around nuclei of largish angular fragments).

**Recrystallization of cement** (e.g. ARG19) – The cement appears to have been recrystallized. This can be seen in the serrated edges of the large cement grains which can be seen running into cracks and into the outer space area which is composed of smaller grains / crystals. This could be part of:

**General diagenetic alteration of the lithologies** –

1. Diagenesis – much alteration of grains (e.g. calcite to dolomite). Possible obliteration of evidence.
2. Veining – calcite veining is common.
3. Micritization (microbial) – the replacement of carbonate grain margins by micrite due to microbial action.

The palaeontological information can also be used on a larger scale (regional to global).

The algae can be used as part of a larger distribution analysis and environmental description tool. Areas can be used either in comparison or contrast for larger scale work with offset against the individual local peculiarities of the respective sites.

Languedoc, as stated previously, is at the end of a northern Tethyan margin barrier reef complex in the Tithonian, which straddles S.E. France roughly latitudinally (Séguret et al 1997). It is importantly placed in terms of palaeophycologically oriented interest and study.

### 3.4.2.5 Conclusions / summary

The Languedoc area, in the late Jurassic, was the site of a large carbonate reef. This reef was home to a large family of fauna and flora across the different localized habitats and was present mainly due to these organisms. One of the main contributors were the various forms of calcareous algae which were important in forming the main
barrier section and the lagoonal deposits behind, which is typical throughout reefs of a similar age.

The sedimentology and phycology of the area in the Tithonian is summarised in Table 3.10:

<table>
<thead>
<tr>
<th>Example area</th>
<th>Main sedimentology</th>
<th>Phycology</th>
<th>Reef setting</th>
</tr>
</thead>
<tbody>
<tr>
<td>La Cadière</td>
<td>Micritic limestone</td>
<td>N/A except calcispheres</td>
<td>Basin</td>
</tr>
<tr>
<td>Rieutord</td>
<td>Bioclastic / crystalline limestone</td>
<td>Cyanobacteria e.g. Cayeuxia &amp; Baccinella irregularis</td>
<td>Foreslope</td>
</tr>
<tr>
<td>Roc Blanc / La Table</td>
<td>Bioclastic limestone &amp;</td>
<td>Neoteuthoporella socialis &amp; some Cayeuxia</td>
<td>Barrier</td>
</tr>
<tr>
<td></td>
<td>“Calcaires graveleux”</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Argilliers</td>
<td>Bioclastic limestone</td>
<td>Many and numerous Dasycladales &amp;</td>
<td>Lagoon</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Cyanobacteria e.g. Campbelliella striata,</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Clypeina jurassica &amp; Cayeuxia</td>
<td></td>
</tr>
</tbody>
</table>

Table 3.10 Languedoc facies and algae summary.

This information can be used to give the summary diagram Figure 3.15 which shows algal assemblage distribution over the reef sections.
Fig. 3.1 | Possible model of algal community distribution over time.

- La Cadire
- Les Olliers
- Niria
- Roc Blanc
- Argillers
- Table

Sites:
- Very common
- Rare
- Occurrence

No recorded occurrence

- Cacilella sociabilis
- C. tenuissima
- C. intermedia
- Calcareostrangulum
- C. multiforme
- C. laminata
- C. polycystis
- C. phloxina
- C. mixta
- C. sp.
- Calcisphaera
3.4.3 Lusitanian Basin, Portugal

3.4.3.1 Introduction

The Lusitanian basin in mid Portugal is an alpine-orogenically inverted Jurassic / Cretaceous basin showing a marine to terrestrial synrift succession (Leinfelder 1993). Portugal during the Mesozoic was positioned in an area of transition between the Boreal and Mesogeian (Tethyan remnants forming the proto-Mediterranean) provinces (Ramalho 1971a) – see Figure 3.16.

![Diagram of Kimmeridgian palaeogeography showing position of Lusitanian Basin. (From Leinfelder 1992)](image)

The Mesozoic Lusitanian Basin formed from the North Atlantic rifting, and the Upper Jurassic reactivation of rifting faults lead to massive calcareous and siliciclastic sediment deposition in all possible depositional environments (Wilson 1979, Leinfelder 1987), with great bathymetric and therefore facies differentiation (Leinfelder 1994). The basin was bounded on three sides by basement, but the basin seems to have had a permanent connection with the Proto-Atlantic in the SW (Lisbon – Sintra area) (Fürsich 1981).
Overall in the Jurassic, more than 5000 metres of marine and continental sediments were deposited (Fürsich 1981).

The shallow Upper Jurassic carbonate sediments are exposed in the southern part of the basin, around the Lisbon area and were formed on isolated structural or halokinetic uplifts (Leinfelder 1993) (see Figure 3.17). This area was home to species of calcareous algae, which can be found at some of the outcrops.

The collection of samples came from three main areas:

1. W. Serra d’Arrabida - S. of Lisbon - Cabo Espichel & Casais da Serra

2. Sintra – Cascais - W. of Lisbon - Murches

3. Alenquer - NE. of Lisbon - Carapinha & Montejunto

These sites can be seen on Figures 3.18 and 3.19, with photographic detail of the more important areas of Cabo Espichel and Murches shown in Figures 3.20, 3.21 and 3.22.
Fig 3.17 Geological map of Southwest Portugal. After Carta geológica de Portugal, 1968
Fig. 3.18 Site locations and Malm outcrops of the Lusitanian Basin.
View E
Units 39 to Cretaceous

Units 40 to Jurassic / Cretaceous boundary

Upper unit 40 (CE5)
Notebook = 20cm

Fig. 3.20 Cabo d'Espichel, Praia de Lagosteiros site photographs and sample locations.
3.4.3.2 Other work done on sites

Most of the sites visited for this work (or at least the general area in which they are located) have had previous geological investigation. The following is a relevant synthesis of this preceding work. See Figures 3.18 to 3.22 for locations and site photographs.

Cabo Espichel

Rimalho, 1971a

A study of this area as part of his thesis: the stratigraphic work was used as a basis for this and other work on this site (see log Figure 3.23). As a general note, the beds here dip to the north changing from c60° at the Cap to c25° at the Jurassic / Cretaceous boundary at Praia dos Lagosteiros.

Fürsich and Schmidt-Kittler, 1980

Upper Kimmeridgian to Upper Portlandian succession of neritic carbonates with intercalations of clastics (marls to conglomerates). There are various facies types:

- Very shallow subtidal nodular biomicrites.
- Coral biostromes.
- Intertidal algal laminites.
- Prodelta silts and marls.
- Fluvial conglomerates.
- Alluvial red beds.

They surmised the environment was a very protected but very shallow inner shelf separated from the sea by a series of diapir ridges (swells or island chains) – “N-S elongated diapir highs – which due to salt movements started to form in central Portugal in the Middle Jurassic and became very active in the Upper Jurassic” – they assume the occurrence of similar diapirs to the West.

Cabo Espichel is at the western end of the Serra da Arrábida (the northern part of a c30km long east – west striking antcline), which during the Upper Jurassic was near the eastern margin of a sedimentary trough. It has c570 metres of exposed Upper Kimmeridgian and Portlandian beds dipping 40° to 60° northwards.
Fig. 3.23. Log of Cap d'Espichel indicating stratigraphic sample locations. Stratigraphy from Ramalho, 1971d.
There is trace fossil evidence of suspension and deposit feeders / scavengers (Skolithos and Cruziana facies) which indicates shallow shelf / intertidal environments. They also say “The abundance of algal remains indicates that the environment was generally very shallow marine, with water depths of mostly less than 20m”.

They record the following lithologies:

- Nodular biomicrites – the predominant lithology consisting of two types – the most abundant of bioclastic wackestones with a high amount of peloids (Dasycladalean debris); the less abundant bioclastic packstones and grainstones.
- Biomicrites – only a few horizons – more exposed, shallower?
- Birds-eye and laminated fenestral micrites – low energy, well protected lagoon.
- Marls and marly silts – shallow, quiet, lower salinity environment.

Overall the sequence was said to be a more or less marginally marine series of environments from fully marine to terrestrial (Fürsich and Schmidt-Kittler, 1980). Water depth was shallow - <20 metres and frequently a lot less.

Montejunto

Wilson, 1979

Upper Oxfordian strata indicative of the period of generally marine conditions found throughout most of the Lusitanian Basin at this time. The Montejunto beds themselves are 350 metres thick and show open marine conditions with some oolitic horizons.

Leinfelder and Wilson, 1989

The Upper Oxfordian deepwater ammonitic lime mudstones to the west and southwest of Montejunto grade northeastwards into a shallow water carbonate buildup. There is a transition slope between these environments characterised by bioclastic wackestones.

Ellis, Wilson and Leinfelder, 1990

The shallow water carbonate buildup is fault controlled (located to the east is a WNW-ESE trending normal fault). The age of the buildup is known to be of the Bifurcatus to Planula zones of the Upper Oxfordian for the sediments to the
southwest, however the age of the shallow water shelf carbonates to the north of the anticline is less certain.

**Ota** (including the area of Alenquer which contains the other site of Carapinha)

Leinfelder, Erbenich and Ramalho, 1988

The Ota limestone was supposed to be a relic of a Bahama-like shallow water platform, characterised by wide lagoonal to tidal areas and a high-energy reefal and debris zone.

Ellis, Wilson and Leinfelder, 1990

The Ota buildup is c5 km S-SE of Montejunto. The exposed area is 6 km long by 2 km wide by up to 160 metres thick. The age has been determined via Dasycladalean associations (Clypeina jurassica, Campbelliella striata and some foraminifera) as Upper Kimmeridgian. The facies zonation is indicative of an aggradational shelf carbonate buildup:

- The western margin is a high energy reefal barrier zone – coral framestones and algal bindstones and intra- to bioclastic grainstones.
- The eastern margin is composed of back reef sands, tidal limestones and lagoonal, low energy, lime mudstones and wackestones as well as some oncolitic channel lag deposits.

It is surmised that this represents a fairly small Bahamian-like carbonate bank.

Leinfelder, 1992

In this paper, the palaeontological and sedimentological discrepancies are resolved tectonically:

Upper Jurassic reefs rich in microbial crusts are generally indicative of deeper or shallow but protected settings, while Upper Jurassic high energy reefs which lack microbial crusts, appear to be bioclastic piles with minor framestone patches.

Ota is an exception as it looks like a modern high-energy coral-melobesiod algal reef. The explanation can be surmised as shown in Table 3.11:
<table>
<thead>
<tr>
<th>Modern reefs</th>
<th>Ota</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Physical and bio-generation of debris compensated for by:</em></td>
<td><em>Lack of fast growing corals therefore – existence of a steep by-pass margin accounted for equilibrium sediment balance</em></td>
</tr>
<tr>
<td>• Stabilisation of loose debris by binding organisms, chiefly melobesiod algae.</td>
<td>• Along the steep margin additional gravitational export was possible.</td>
</tr>
<tr>
<td>• Accelerated coral growth in order to keep pace with sedimentation.</td>
<td>• The steepness of the margin kept the reef tract narrow, so that it could be well winnowed by a longshore current system along the east side of the basin.</td>
</tr>
<tr>
<td>• Export of surplus material into back reef and fore reef areas through wave action.</td>
<td>• The remaining loose debris could, to a large extent, be stabilised by the available algal-like and microbial builders (thrombolic-peloidal crusts, <em>Bacinella, Lithocodium, Thaumatoporella, Tubiphytes</em>).</td>
</tr>
</tbody>
</table>

Table 3.11 Ota reef comparison with modern reefs. After Leinfelder (1992).

**Leinfelder, 1993**

The Ota limestone is representative of a narrow reef-rimmed platform situated on a basement horst which is located near the eastern edge of the Lusitanian Basin. The “aggradational geometry of the [Ota] platform with perfect facies zonation is thought to be due to the existence of a steep, tectonic bypass margin…”

**Leinfelder, 1994**

On the Ota “reef”, microbial crusts “anticipated the stabilising role of coralline red algae in Cenozoic and modern high-energy reefs”.

**Murches**

**Ramalho, 1971a**

Logged the sequence of mostly well exposed beds which dip at 50-55° in a southerly direction.

**Leinfelder, 1994**

(On the Sintra area) There are low diversity coral reefs present on the environment of the prevalence of deeper settings on a distally steepened ramp.

The algae found can be stratigraphically designated as shown in Figure 3.24, and the facies present at the sites are summarized and corresponded in Figure 3.25.
Fig. 3.24 Charts of algal stratigraphical distribution in the Lusitanian Basin, Portugal.
Fig. 3.25 Portugal sites summary facies chart  
(After Wilson 1979 and Ellis et al 1990)
3.4.3.3 Discussion

Most of these Jurassic sites in Portugal are Mid to Upper Malm; only one is Lower Malm, so it shall be looked at first.

Montejunto

The Oxfordian material studied is from the Montejunto area which during this time period, was generally marine in nature. Northern Montejunto shows a shallow water environment of deposition with associated flora and fauna (Wilson 1979). The whole buildup was a probable aggradational carbonate shelf with the slope composed of bioclastic *Tubiphytes* wackestones, and coral biostromes (Ellis et al 1990, Leinfelder and Wilson 1989). This is shown in Figure 3.26.

![Montejunto idealized cross section](image)

Fig. 3.26 Montejunto idealized cross section. (From Leinfelder and Wilson 1989)

Mid – Upper Malm

Ota

The Ota reef shelf is a 6km by 2km by 160 metre high energy reefal rimmed aggradational shelf c5km S – SE of Montejunto (Leinfelder and Wilson 1989, Leinfelder 1992 and Ellis et al 1990) as shown in Figure 3.27. It is unusual in that most Upper Jurassic reefs with microbial binding are not found in high energy settings (Leinfelder 1992).
Chapter 3 Fieldwork

Fig. 3.27 Ota idealized cross section. (From Leinfelder and Wilson 1989)

The Ota limestone is a relic part of an Upper Jurassic Bahamian style platform with wide lagoons and high-energy reefal areas (Leinfelder et al 1988).

The high energy reef was subject to high erosion rates, but the debris was rapidly bound by sediment encrusting organisms. Sediment balance on such a reef setting in the Upper Jurassic would not normally be achieved, and bioclastics usually occur, hence the unusual occurrence found here is due to the physical reef setting; Ota reef was characterised by a very steep by-pass margin, which resulted in higher than usual debris export rates (Leinfelder 1992) – see Figure 3.28:

Fig. 3.28 Ota reef. (From Leinfelder 1992)
Sintra

The sediments of the Sintra area were first described in detail by Ramalho (1971a). The sediments appear to be indicative of a developing ramp: shales to marly limestones to coral and oncolitic limestones (Leinfelder 1987). The sequence also shows evidence of debris flows – see Figure 3.29 for palaeoreconstructions:

![Diagram of Sintra sediments and landforms]

Fig. 3.29 Sintra palaeoreconstructions. (From Ellis et al 1990)
Arrabida

The Arrabida peninsula (Estremadura region) is best typified by the Western end location of Cabo Espichel.

The Upper Kimmeridgian to Upper Portlandian rocks consist of a complete succession of shallow marine carbonates with some intercalations of marls and conglomerates. These sediments were deposited on a very protected, very shallow inner shelf partitioned from open sea conditions by offshore diapir ridges (Fürsich and Schmidt-Kittler 1980) – see Figure 3.30 for palaeoreconstructions.

Fig. 3.30 Cabo Espichel environmental reconstruction. A: facies distribution; B: palaeogeographic framework. Facies scale 20 cm unless otherwise stated. (Adjusted from Fürsich and Schmidt-Kittler 1980) Facies settings: 1 alluvial plain and crevasse splays 2 river channel 3 pro-delta 4 nodular limestones 5 coral biostromes 6 intertidal micrites 7 marly sandstones 8 marls and marly silts.

Overall setting

The Portuguese Upper Jurassic is dominated by the carbonate facies found within the Lusitanian Basin (together with some contemporaneous siliciclastics – the mixture of carbonate and siliciclastic sediments characterised by rapid facies transitions, reflects the integrated effects of sea-level change, basin structure and
configuration, climate, local currents and the adaptation of reef biotas (Leinfelder 1994).

This carbonate sediment infill includes much shallow-water environment facies which would be of a nature suited to the development of benthic green calcareous algae: “shallow water carbonates were episodically widespread throughout the basin and mixed calcareous – clastic sequences were common” (Leinfelder 1987).

The evolution of the (mid and southern part of the) basin can be seen in the palaeogeographic reconstruction and cross-sections.

The emphasis on the investigation of the area was one of palaeophyto geography; not only within the basin but also in comparison to other similar, W. European sites.

### 3.4.3.4 Conclusions

The Jurassic carbonates of the Lusitanian Basin are shallow water bioclastically dominated facies intrinsically linked with interspersions of siliciclastic input.

The individual areas provide interesting insights into different settings, which were part of the overall basin organisation. These elements also counter the general trends of similar settings throughout the rest of the Tethyan deposits (e.g. Ota reef).

Palaeophycologically, the shallow marine carbonate setting and palaeotropical temperature basis, means that it was endowed with a rich and varied algal flora (see raw data tables in Appendix A3). These algae included varieties that appear to be indicative of a tropical water-mass – e.g. *Salpingoporella annulata*, *Clypeina jurassica* and *Campbelliella striata*. All of the algae have been used to define the localized marine environments (e.g. palaeoreconstruction of water depth etc.) and they can be used to identify the regional setting of the SW Iberian peninsula during the Upper Jurassic. Palaeoreconstructions through the Upper Jurassic can be seen in Figure 3.31.

The Lusitanian Basin was a marginally situated basin that was in the type of area (latitudinally) to be indicative of the palaeo-equatorial zone.
### Chapter 3 Fieldwork

<table>
<thead>
<tr>
<th></th>
<th>Montejunto Basinal</th>
<th>Shallow water</th>
<th>Ota</th>
<th>Villa Franca</th>
<th>Barreiro</th>
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<td>Braided rivers</td>
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</table>

### Fig. 3.3 Lusitanian Basin palaeogeographic facies reconstructions
3.4.4 Algal comparison between the upper Malm sites of southern England, mid and southern France and mid Portugal.

![Map of Algae sites comparison locations.](image)

**Fig. 3.32 Algae sites comparison locations.**

### 3.4.4.1 Introduction

The four sites of this work are the main algal outcrops of importance in western Europe in the Upper Jurassic (see Figure 3.32) and the three main ones have been visited and sampled. This work also incorporates all known published algal finds in these areas (as used in the database for this thesis). The algal distribution across these four areas is summarized in Figure 3.33 and Table 3.12. The importance of these sites is due to several factors:

- Relative latitudinal positioning
- Maximum algal diversity of the regions
- Good stratigraphical / sedimentological constraints
Fig: 3.22 Algae found in Upper Jurassic Fieldwork localities.

Green text = Chlorella; Red text = Rhodophyta; Blue text = Cyanophyta and Microrganisatac.
<table>
<thead>
<tr>
<th>Non-Dasyycladales</th>
<th>Las</th>
<th>Lang</th>
<th>Jur</th>
<th>Port</th>
<th>Dasyycladales</th>
<th>Las</th>
<th>Lang</th>
<th>Jur</th>
<th>Port</th>
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<td>Petrascula bugesica</td>
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<td>Lang = Langweid. southern France</td>
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<td>Petrascula barfuriformis</td>
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<td>Jur = French Jura, mid Eastern France</td>
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<td>Petrascula guemelbi</td>
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<td>Petrascula piai</td>
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</tbody>
</table>

| = occurrence |
| ? = questionable |
| ?? = very questionable |

Table 3.12 Algae present at comparison localities
3.4.4.2 Discussion

Upper Malm carbonate areas on the Northern Tethyan margin are similar in style to each other. It can be seen that any environmentally determined change can be seen in the palaeophytogeography of the areas.

It is obvious from Figure 3.33 and Table 3.12 that the northern extreme – Portland – is devoid of Dasycladales. It is inhabited by a sole red algal species – Solenopora ‘portlandica’.

After this, the way forward is to assess palaeoenvironmental differences via Dasycladales (and other ‘algal’) associations differences between the other sites, in order to determine any ‘pattern’. Importantly this should be done between the relatively northerly Jura (with a possibly mid / transitional setting) compared to the more southerly and presumably more tropical Languedoc and Lusitanian Basin.

Some algae are ubiquitous (and abundant) across this southern European region. This includes the fossil assemblage of Clypeina jurassica, Campbelliella striata and Salpingoporella annulata, which is said to be indicative of the upper Malm and has true stratigraphic value (Flügel 1982).

Other algae seem to have occurred at only one or two of the areas. Due to the sedimentological similarities of the regions, the reasoning for this limited dissemination could reasonably be argued to be through temperature zonation of the water masses with differential latitudinal positions.
However, a problem arises from this justification – can those algae, that are observed from only one or two areas, be significant markers of temperatures? – i.e. how do you define and interpret temperature indicative species (or even Genera) from the distribution seen?

One factor that can alter the distribution of algae away from the ‘simplified’ latitudinal banding is that of currents – the circulation of water masses in a direction other than latitudinally will cause a local disturbance in the latitudinal alignment of the temperature regimes. This can be seen today in certain areas (see Figure 3.34 and Table 3.13) and these modern currents have an effect upon the present-day distribution of benthic green calcareous algae.

Fig. 3.34 Map of modern currents that affect algal distribution (Red: warm water; Blue: cold water) and sea surface temperatures of 20°C or higher (in Orange).
<table>
<thead>
<tr>
<th>Temperature (algae effect)</th>
<th>Area</th>
<th>Current</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cold (no algae)</td>
<td>California</td>
<td>Humboldt</td>
</tr>
<tr>
<td></td>
<td>West S. America (with one</td>
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<td></td>
<td>exception in mid Chile)</td>
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<tr>
<td>Warm (extended algae range)</td>
<td>Portugal</td>
<td>Canary</td>
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<td></td>
<td>East S. Africa</td>
<td>Agulhas</td>
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<tr>
<td></td>
<td>Bermuda &amp; N. Carolinas</td>
<td>Gulf Stream</td>
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<td></td>
<td>Brazil</td>
<td>Brazil</td>
</tr>
</tbody>
</table>

Table 3.13 Modern currents of importance.

There would seem to be a single effect by currents upon the Malm algal distribution at the selected sites as shown in Figure 3.35:

The only current which could have had an effect was a warm current by Portugal, which was in a warm area already and so would seem to only alter the local algal population via increasing the latitudinal setting of the warmer isotherms in the general area of flow direction.

Naturally, it is possible to tie in areas other than those directly involved in the authors fieldwork; the Dinaric platform of Slovenia (NW part of the former Yugoslavia - see Figure 3.36) has been shown by Strohmenger et al (1991) to have had a similar setting as the Jura platform at the same time-period (with correlatable stratigraphy being present in both areas). This helps to connect the eastern part of Europe with the western which is well studied here.
This area has algal similarities with the Jura and Languedoc areas (see Table 3.14).

<table>
<thead>
<tr>
<th>Upper Malm algae present at the Dinarides</th>
<th>Common with other southern European sites</th>
</tr>
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<tbody>
<tr>
<td>Desychtideas</td>
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</tr>
<tr>
<td>Campbelliella straita</td>
<td>*</td>
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<tr>
<td>Clypeina calciformis</td>
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<tr>
<td>Clypeina cavimana</td>
<td></td>
</tr>
<tr>
<td>Clypeina hampshorotensis</td>
<td></td>
</tr>
<tr>
<td>Clypeina jurassica</td>
<td>*</td>
</tr>
<tr>
<td>Clypeina parvula</td>
<td>*</td>
</tr>
<tr>
<td>Cylindroporella amica</td>
<td></td>
</tr>
<tr>
<td>Cylindroporella eilenbergeri</td>
<td>*</td>
</tr>
<tr>
<td>Graphoporella minima</td>
<td></td>
</tr>
<tr>
<td>Heteroporella amici</td>
<td></td>
</tr>
<tr>
<td>Linoporella caprosta</td>
<td>*</td>
</tr>
<tr>
<td>Linoporella kapekensis</td>
<td></td>
</tr>
<tr>
<td>Linoporella? swilagens</td>
<td></td>
</tr>
<tr>
<td>Macroporella selli</td>
<td></td>
</tr>
<tr>
<td>Petrascula bursiformis</td>
<td>*</td>
</tr>
<tr>
<td>Pianella annulata</td>
<td>*</td>
</tr>
<tr>
<td>Pianella gigantea</td>
<td></td>
</tr>
<tr>
<td>Pianella grudii</td>
<td></td>
</tr>
<tr>
<td>Pianella pygmaea</td>
<td></td>
</tr>
<tr>
<td>Pseudoclypeina cincti</td>
<td></td>
</tr>
<tr>
<td>Pseudoclypeina farinaccior</td>
<td></td>
</tr>
<tr>
<td>Salpingoporella annulata</td>
<td>*</td>
</tr>
<tr>
<td>Salpingoporella grudii</td>
<td>*</td>
</tr>
<tr>
<td>Salpingoporella pygmaea</td>
<td>*</td>
</tr>
<tr>
<td>Salpingoporella selli</td>
<td></td>
</tr>
<tr>
<td>Teutisporella galliformis</td>
<td></td>
</tr>
<tr>
<td>Teutisporella obsolete</td>
<td></td>
</tr>
<tr>
<td>Vaginella strata</td>
<td>*</td>
</tr>
<tr>
<td>Microproblematica</td>
<td></td>
</tr>
<tr>
<td>Cladocystis mirabilis</td>
<td>*</td>
</tr>
<tr>
<td>Thamnotoporella parallelepistiforma</td>
<td>*</td>
</tr>
</tbody>
</table>


Table 3.14 Jurassic algae present at the Dinarides and other European localities.
Chapter 4 Localised environment unsuitability and
taphonomic effect on the scarcity of benthic calcareous algae
in the English Bathonian.

4.1 Introduction

The Cotswolds area of England includes a large expanse of Bathonian (mid Jurassic) limestone – mainly the Great Oolite Group, the major formation of which is the ~40m thick White Limestone Formation (Palmer, 1979).

Most people working on the Cotswold limestone note its similarity to the sediments and fauna to be found at present at the Bahamas (Elliott 1973, 1981, Palmer and Jenkyns 1975, Palmer 1979). This is to say that ooid formation along with the invertebrate forms found in the Great Oolite are Jurassic analogues of the sediments and faunal associations on present-day oolite shoals. However, the difference is apparent when a comparison of the flora is attempted – benthic marine algae of the tropical and subtropical western Atlantic comprise 1058 species (Wynne 1986) of which 58 species secrete a calcareous covering most likely sufficient to preserve them in the fossil record either as relatively complete skeletons or as significant sediment. Yet, calcareous algae are extremely rare in Cotswold limestone formations (Palmer 1979, Elliott 1982) which leads to a fundamental question - why are calcareous green algae so rare / almost non-existent in the Mid Jurassic limestones of mid-West England while the modern-day Bahamian and other analogues contain them as a fundamental component?

This was an important question for Graham Elliott, who, in a number of papers, tried to formulate an answer. His main explanation first appeared in 1975 – namely, that as time progressed, Dasycladales gradually spread out from a centre of the Tethys Ocean into the marginal waters of lower temperature. His hypothesis was that by the Mid Jurassic, Dasycladales had not evolved the tolerance for the lower temperatures found in mid England at that time. A lower than required temperature would have a “disadvantageous effect” on the intensity of calcification in aragonite-forming algae (Berger and Kaever 1992). The rarity of higher latitude, mid Jurassic green calcareous algae, is not restricted to southern England, there is a similar lack of
Chlorophyta in northern France (Elliott 1984); this rarity appears to be an original scarcity of algae rather than via post-lithification processes obliterating evidence of existence (Elliott 1982). Algal distribution can be seen in Table 4.1 and Figure 4.1. This tolerance theory pervades Elliott’s further work on the subject, but it cannot be proved and was eventually abandoned by Elliott (1986). However, it remains relevant here to consider this hypothesis that he developed because it brings into focus topics of environment and preservation that are central to interpretation of temperature limits in marine calcareous algae. The theory may be doubtful as there is evidence for an increasing temperature curve in the appropriate region at the time stated (Berger and Kaever 1992), however this does not necessarily disprove Elliott because he simply made the point that dasyclads needed warmer temperature then than now. The higher temperature referred to could still have been too low.

4.2 Background

Elliott’s temperature tolerance evolution theory has a foundation in the temperature controlled zonation of benthic life-forms within the modern oceanic realm. The surface water isotherms of 10, 15, 20 and 25°C have been said to “definitely limit the extension of particular floras of marine algae” (Satchell 1920).

The sedimentological evidence of the White Limestone Formation of the Great Oolite of the Cotswolds suggests that the environmental conditions of the area were similar to Florida Bay and the Bahamas in that there is evidence of possible reduced diurnal tidal activity (Palmer 1979), which is a result of wide shallow shelves with restricted circulation (e.g. Florida Bay – Ginsburg 1972) and a corresponding (seasonal) fluctuation in salinity. This is similar to the mid Jurassic situation in the Hebrides (Hudson 1970) – here there is sedimentological evidence of a variable salinity intertidal lagoon (similar to Florida Bay) and areas of intergrowths of Cayeuxia and “other thin tubes” which are similar / identical ancient analogues to the modern Scytonema and Schizothrix head intergrowths (as found on the Florida reef tract which separates the bay from the open ocean and restricts circulation of the marine waters).

All the sedimentological evidence shows striking similarities between the modern Bahamian environment and the Jurassic Cotswolds, so why the algal
<table>
<thead>
<tr>
<th>Reference</th>
<th>Eastern US</th>
<th>New England</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hudson 1970</td>
<td>Erie, Lake</td>
<td>Erie, Lake</td>
<td>Erie, Lake</td>
</tr>
<tr>
<td>Eliot 1975</td>
<td>Maine, Acadia</td>
<td>Maine, Acadia</td>
<td>Maine, Acadia</td>
</tr>
<tr>
<td>Hudson 1970</td>
<td>Maine, Acadia</td>
<td>Maine, Acadia</td>
<td>Maine, Acadia</td>
</tr>
<tr>
<td>Credle 1948</td>
<td>Maine, Acadia</td>
<td>Maine, Acadia</td>
<td>Maine, Acadia</td>
</tr>
<tr>
<td>Whiting 1985</td>
<td>Maine, Acadia</td>
<td>Maine, Acadia</td>
<td>Maine, Acadia</td>
</tr>
<tr>
<td>Fishkill 1969</td>
<td>Maine, Acadia</td>
<td>Maine, Acadia</td>
<td>Maine, Acadia</td>
</tr>
<tr>
<td>Foggia 1979</td>
<td>Maine, Acadia</td>
<td>Maine, Acadia</td>
<td>Maine, Acadia</td>
</tr>
<tr>
<td>Foggia 1979</td>
<td>Maine, Acadia</td>
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<td>Foggia 1979</td>
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<td>Foggia 1979</td>
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</tr>
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<td>Foggia 1979</td>
<td>Maine, Acadia</td>
<td>Maine, Acadia</td>
<td>Maine, Acadia</td>
</tr>
</tbody>
</table>
Fig. 4.1. Bathonian NW Europe algal distribution map. Data from Table 4.1.
paucity in the latter? In the modern day, Dasycladales are less obvious and more
discrete than the calcareous Halimedaceans, but some of the latter tend to
disaggregate into unidentifiable grains compared to the Dasycladales (Wray 1977)
and therefore would be more difficult to discern in the fossil record. An example of
modern Halimedacean disintegration of the calcareous skeleton upon death is that of
Penicillus – studied in the Florida Bay. Upon dying, disaggregation was so utterly
complete that the recent sediment formed from the skeletal fragments was not
distinguishable as being parts of the skeleton of Penicillus (Stockman et al 1967).

It is in this vein that there are more problems with Graham Elliott’s theory –
when comparing modern fossil analogues he states that in modern Halimeda, the
species living on the margins of their “zone of tolerance” are as heavily calcified as
the non-marginals (Elliott 1986), and therefore would be just as representative in the
fossil record. However, in the marginal areas, the species present are actually shown
to be either very weakly or even not at all calcified, and do not contribute to the
sediment at all, even though they are locally abundant in numbers (James et al 1999,
Milliman 1977, Betzler et al 1997) unlike their more tropical cousins which are
(1997) state that due to aragonite undersaturation of waters such as the Mediterranean,
the chances are high for rapid dissolution of poorly calcified algal skeletons. Of
course, dissolution is also common in the tropics, however in these settings the
outlines of aragonitic skeletons are preserved by micritic envelopes which are a minor
occurrence in temperate carbonates. So there is reason to doubt that calcareous algae
growing in the Cotswolds in the mid Jurassic would leave much trace of their
existence even if abundant. This notion is broached by Elliott (1982) – remarking
upon the aragonitic micrite in the lime mud coming from the breakdown of algae such
as Penicillus and Rhipocephalus, he says they would “…only survive recognisably (if
at all) as very rare impressions”. He then says “A possibility therefore exists of
abundant Middle Jurassic Udotaceans…which would contribute to the sediment but
not normally leave recognisable fossil debris”. Elliott goes on to state that there is still
an absence of Mesozoic representatives of algae such as Halimeda which he expects
to find in the sediments. There is also another factor which needs to be taken into
account, namely the fact that the bottom conditions of an area show a strong influence
upon both the character and the distribution of any benthic communities living there (Newell et al 1959). It is noted that the few algal remains found in the mid Jurassic limestones show signs of transportation, and that these algae are the more robust forms that would be difficult to abrade / destroy by transportational erosion (Elliott 1975). In his paper of 1982, Elliott states that the seafloor environment was probably mobile sediment, which is unsuitable for Dasyclad habituation. This ooidal environment which has a mobile sediment would prove difficult for algae to inhabit. It is also interesting to note that one of the factors thought to be important for ooid formation (despite the areas having an overabundance of $\text{Ca}^{2+}$ and $\text{HCO}_3^-$) is “few organisms which remove carbonate from the water” (Flügel 1982) which would seem to preclude calcareous algae from the area of ooid generation.

4.3 Elliott critique

G.F. Elliott examined the English Mid Jurassic lithologies in the Cotswolds and found that the occurrence of Dasycladales in the carbonates is “extremely rare in comparison with those from equivalent rocks in Alpine Europe and Asia” (Elliott 1975). The few algae in British localities show signs of transportation (Elliott 1975) and are themselves only the kind of algae that would survive the energy of transportation. These algae are however the exception rather than the rule – Elliott (1982) took 2000 reconnaissance thin sections of the appropriate lithologies and found no trace of algal remains. This scarcity is also to be found in northern France and appears to be original in nature and not due to post-lithification processes (Elliott 1984). The low diversity of the algal remains can be accepted if a marginal environment of habitation is considered as being the case for the locality (Elliott 1986).

The crux of the problem that Elliott faced was that the sedimentological (and most of the faunal) record of the area studied were indicative of a Bahamian style climate (Elliott 1975, 1982), but there were little remains of dasycladeans which he thought to be a major constituent and well preserved within the modern Bahamian ooid shoal setting.
Elliott varied slightly in his main explanations:

A: 1975 - possible limited opportunity for immigration;
    1982 - immigration was possible.

B: Low temperature tolerance of the algae at that time (1975, 1982, 1983, 1984);
    1986 - revises his opinion and states that it is not due to temperature tolerance
    (but gives no reason - says due to “latest evidence” but does not state or refer
    to latest evidence).

Elliott (1986) states that “...marginal species are as heavily calcified as the
others...” and would therefore be evident in Cotswolds lithologies if they inhabited
the area. This is an assumption which first appeared in his 1982 paper: “...in the
modern Mediterranean the abundant Dasycladus and Acetabularia will leave little
fossil trace, whereas the accompanying Halimeda will leave recognisable debris for
fossilisation”. While this latter statement is true, the previous statement is not
completely accurate.

In this work it will be shown that:

- There is indeed no evidence to support a theory of different temperature tolerances
  of modern and Jurassic calcareous green algae.

- The generalised climate assumptions may have been correct, but the localised
  sedimentological conditions are not suitable for algal habitation – in both the
  Jurassic and in the modern day. (Comparison of dissimilar environments.)

- Processes in effect, act to obliterate evidence of algal occurrence and form a bias
  against algal preservation in the lithologies formed. (Calcification + micrite mud
  formation / disaggregation.)

4.4 Comparison of Cotswolds and Bahama Banks

The distribution of Bathonian calcareous algae across NW Europe and
particularly in the Cotswolds, shows minor differences between the spread of
Dasycladales and that of Halimedaceae – Figures 4.1 and 4.2. Modern varieties of
these groups are found together today in the same environments, and are found in
modern analogues of the Bathonian Cotswold setting, i.e. the Bahamas (Figure 4.3).
**Legend**

- **Site Location**: Circle
- **Dip**: Arrow
- **Great Coke Formation**: Pink

**Fig. 4.2 Breadham dolomite sites in the Great Coke Formation of the Callovian**

<table>
<thead>
<tr>
<th>Layer</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>H</td>
<td>Solenoporaria jurassica</td>
</tr>
<tr>
<td>G</td>
<td>Abdnocodium sp.</td>
</tr>
<tr>
<td>F</td>
<td>Pycnoptilum obtatum</td>
</tr>
<tr>
<td>E</td>
<td>Pycnoptilum convolvulans</td>
</tr>
<tr>
<td>D</td>
<td>Stictoporella striatula</td>
</tr>
<tr>
<td>C</td>
<td>Sartothella dubia</td>
</tr>
<tr>
<td>B</td>
<td>Dunbariellia conlentis</td>
</tr>
<tr>
<td>A</td>
<td>Clyndipteropora cf. abyssorum</td>
</tr>
</tbody>
</table>

Geological map after Richardson et al. 1984 and 1986.
Fig. 4.3 Calcareaous chlorophyte and oolite distribution in the modern Bahamas.
The Bahamian ooidal territory can be subdivided into individual banks/ooid accumulations which allows more detailed analysis. One of the best studied areas is that of Joulters Key, a 400km² micritized ooidal sand flat with mobile ooidal fringes (Figure 4.4), which is located on the northern point of Andros Island. This area, together with similar areas such as the Bight of Abaco and Key Largo, are characterised by large, well developed oolite accumulations within the overall general carbonate setting. The information derived can be seen in Table 4.2 which shows that the modern calcareous algae only thrive in certain areas of the oolite shoal, and that after death fragmentation of the thalli leads to perceived decreased abundance due to the nature of the fragments hindering identification.

4.5 Discussion

Joulters Key, as already stated, is a good area for closer examination of a Bahamian ooid shoal. The shoal sediments are “primarily non-skeletal sands, formed within the shoal with mud weight percentage rarely exceeding 10%” (Harris 1979). The sediments can be differentiated as in Table 4.3. These environments grade into one another across the bank, from the active sands into the algae and sea grass stabilised sand flat (Major et al 1996). Ooid formation occurs in the active area with dynamic morphology, however they can accumulate in conditions quite different from those in which they were formed, and it is clear that the large sand flat region of the bank is not a present-day site of ooid formation (Harris 1979). This arrangement is standard across the other individual shoals in the Bahamas, e.g. Lily Bank, Frasers Hog Cay etc, where seaward of the shoal there is a mixture of superficial ooid, aggregate, peloidal, pelleted sand while platformward there is a seagrass and algae covered muddy peloidal sand and lime mud sediment, which has important implications for fossilisation potential of the algae. These oolite shoals are significant because they are the modern representatives of the sedimentary regime which was more widespread in the extensive Mesozoic shelf seas (Elliott 1973). Of all the Bahamian facies, and in contrast to the others, the mobile oolite sands are relatively devoid of plant and animal life due to the fact that so few species can cope with the demands of a constantly moving substrate (Newell 1959, Palmer 1979). This situation appears also to have been true in the Bathonian White Limestone of the Cotswolds
<table>
<thead>
<tr>
<th>Reason for</th>
<th>Per cent of time mud in the foreshore</th>
<th>Per cent of time salinity of estuary</th>
<th>Per cent of time salinity of branch point of estuary</th>
<th>Per cent of time salinity of branch point of estuary</th>
</tr>
</thead>
<tbody>
<tr>
<td>Poor</td>
<td>2</td>
<td>10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Medium</td>
<td>3</td>
<td>13</td>
<td>13</td>
<td>13</td>
</tr>
<tr>
<td>Good</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 4.1: Generalizedpedo shell/merganser information from U.S. Fish & Wildlife Service, 1980. Notes: Key: 1 = High, 2 = Medium, 3 = Low, 4 = None.
### Fig. 4.4. Joulters Key map.

<table>
<thead>
<tr>
<th>Setting</th>
<th>Sorting</th>
<th>Shoal location</th>
<th>Constituents</th>
<th>Local environment</th>
<th>Probable Cotswold equivalents</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mobile Fringe</td>
<td>Well sorted ooid sand</td>
<td>Active, high energy shoal crest</td>
<td>80-90% ooids. ~5% skeletal fragments.</td>
<td>Active</td>
<td>Bladon Member</td>
</tr>
<tr>
<td>Shelf and Sand Flat channels</td>
<td>Poorly sorted ooid sand</td>
<td>Seaward margin and bankward of shoal</td>
<td>60-80% ooids. ~5% skeletal fragments.</td>
<td>Less agitated environment than the well-sorted.</td>
<td>Bladon Member?</td>
</tr>
<tr>
<td>Sand Flat</td>
<td>Poorly sorted ooid sand and mud</td>
<td>Bankward and between washover bars of well sorted ooid</td>
<td>30-70% ooids. 5-20% skeletal fragments. Up to 20% carbonate mud.</td>
<td>Less agitated environment than the well-sorted.</td>
<td>Ardley Member</td>
</tr>
</tbody>
</table>

Table 4.3. Joulters Key ooid shoal sedimentology.

After Harris (1979)

After information from Major et al 1996
(Palmer 1979). It is obvious that those areas in the Cotswolds which have produced some algae are away from the harsh ooid informing environment – permitting a more abundant flora and the "local development of algal shoals" (Harland and Torrens 1982) in the areas similar to the sand flat setting which have a "varied sedentary epifauna" indicating a stable sea bottom (Palmer 1979).

Calcareous Chlorophyta growing in areas of Bahamian ooid shoals such as the sand flat contribute to the sedimentary accumulation depending on the amount by which they calcify; heavy calcifiers such as *Halimeda* (Halimedaceae) and *Cymopolia* (Dasycladaceae) supply whole or fragmented segments, compared to the light calcifiers, such as *Penicillus, Rhipocephalus, Udotea* (Halimedaceae) and *Neomeris* (Dasycladaceae) which disintegrate into fine debris / lime mud (Ginsburg 1972). This appears similar to the situation in the Bathonian with heavy calcifiers such as *Dobunniella* leaving larger fragments, while any other algae appears probably to have left only skeletally-unrecognisable lime mud. The lime mud contribution from calcareous algae can be considerable; on the Little Bahama Bank, in the Bight of Abaco, there is an accumulation of calcareous muddy sand from such algae as *Penicillus, Rhipocephalus* and *Halimeda* of 120mm/10^3^ years from a coverage of 22 plants / m^2^ per crop and growth rates of *Penicillus* alone of 6-12 crops per year (Neumann and Land 1975). Other less conspicuous algae also contribute greatly due to complete disaggregation, at a local level, such the heavily calcified (74% CaCO_3 dry weight) *Acetabularia antillana*. This alga produces about 720gm/m^2^ of skeletal aragonite in the less than 10μm size range per standing crop at Rodriguez Bank (Marszalek 1975) which is comparable to an accumulation rate of 1cm per 16 years based on one standing crop (whereas in real life there would be 3-5 times the crops and subsequent accumulation) from this alga alone. This is more than 200 times *Penicillus* production in Florida Bay, more than 25 times *Penicillus* production in the inner reef tract of the Florida Keys and 7-10 times the general production rate of *Halimeda* and *Penicillus* together (Marszalek 1975). However this alga is only an important contributor locally, and in general most Acetabulariae are weakly calcified varieties.

It is assumed that the micrite found in the Bathonian White Limestone Formation could have formed, as today, via the breakdown of calcareous algae.
(Palmer 1979) and that even without much recognisable algal debris relative
abundance of algae as well as environmental indications can be obtained from the
Cotswolds micrite; the Ardley Member of the White Limestone Formation is
composed of shallowing upward sequences, and a corresponding increase of micrite
upwards, due to a postulated reduction in current winnowing and increase in
“aragonite needle-producing green algae” abundance as the conditions turned
increasing sheltered and lagoonal (Palmer 1979).

However, as a final point, it is noticed in the Bahamas that while calcareous
algae make an immensely important sediment contribution and a successful binding /
stabilising agent for the back reef environments, they do not grow in dense enough
groups to be of any use as an effective sediment trap (Scoffin 1970).

4.6 Conclusions

- From the information provided, it can be shown that the environment of the
Bathonian Cotswolds and surrounding areas across NW Europe was similar to
modern day Bahamas, but on a larger scale. The outcrops of this environment that are
preserved in the Cotswolds are those recognised in the modern analogue as being of
low suitability for algal habitation. The few preserved flora are accepted as being
sufficiently calcified for some fragments to survive intact, while those possibly living
in the adjacent, more hospitable regions, disaggregated into the small particles which
make up the lime mud accumulations that are found. There appears to be no
sedimentary evidence of climatic unsuitability of the area for algal tolerance, quite
possibly the contrary, however the algae found here are at the edge of the distribution
limits of these groups and so may indeed show some climatic suppression. It may be
that this reasoning was behind Elliott's change of mind (1986) and his abandoning of
his idea that Dasycladales needed warmer temperatures in the Jurassic.
Ch.5 Extant Algae Environmental Distribution

5.1 Introduction / aim

In order to interpret fossil algal distributions (in the case of this work, Jurassic) we need to know the distributions of similar modern algae.

The specific aim here is to document the present day global distribution of calcareous marine algae with respect to temperature to create a comparative database with which to calibrate and assess the spatial distribution of Jurassic algae.

A number of taxonomically diverse algal groups are calcified and geologically long-ranging (Wray, 1977). Extant benthic marine calcareous algae include Dasycladales and Halimedaaceae, (both members of the Chlorophyta), and Corallinaceae (Rhodophyta). The Chlorophyte algae are particularly relevant to this study because they show distinct latitudinal ranges (evidently strongly controlled in their distribution by temperature) and have Jurassic representatives. The Corallinales are mentioned in comparison because as a group they are unbounded and ubiquitous in global distribution and are the most common and abundant modern variety of benthic marine calcareous algae. However, it should be noted that, they have no certain Jurassic representatives (Aguirre et al, 2000).

5.2 Methods

To collate published data on the present-day global distribution of marine benthic calcareous green algae, I reviewed literature (101 sources in total including some important collation works, e.g. Hillis-Colinvaux, 1980, on Halimeda and Berger and Kaever, 1992, on Dasycladales) to produce databases from which plots were made onto present day global maps (see Methods chapter). Some problems were encountered. Some works did not specify species (the genus was mentioned only); sometimes there was only a general locality; there were some misidentifications and some name changes were made over time (this is particularly true of some Halimeda species); and in some papers, there was a lack of much work to identify the algae at
all (except if by algal specialists). Efforts were made to identify the algae as closely as possible. However, in some cases identification was only possible to the genus level.

5.3 Results

The results are shown in Appendices BI and BII and they are plotted in Figures 5.1 to 5.16.

Algae, location and temperature databases.

The databases of the modern green calcareous algae found globally can be found in Appendix BII.

Data plots (e.g. algae, locations and temperature).

The maps of the modern green calcareous algae databases are shown in Figures 5.1 to 5.16 (5.1 – 5.8 = genera of calcified Dasycladales; 5.9 is a summary of all the Dasycladales; 5.10 – 5.14 = genera of calcified Halimedaaceae; 5.15 is a summary of all the Halimedaaceae; 5.16 is a summary of all the calcareous Chlorophyta). Environmental parameters in the modern ocean are shown in Figures 5.17 to 5.23.

Summary

A plot of all the modern calcareous Chlorophyta against temperature is shown in Figure 5.24. This figure was derived from the observation of the number of localities of extant Dasycladales and Halimedaaceae within the boundaries of the major 5°C isocryme bandings overlaid on their distribution plot. These numbers were noted for the overlays of both isocrymal and annual average temperature maps. This figure shows the predeliction of these algae for warm waters, but also shows that they are not restricted to them with some occurrences being located in cooler water realms. The extremes of latitude and their relevant isocrymal temperature of the individual genera of the modern day calcareous Chlorophyta are summarised in Table 5.2.
Fig. 6.2. DASyclADES: Modern Aequiuraria distribution.
5.3.1 Descriptive factors used in distribution analyses

Factors that are used in distribution analyses are summarised in Table 5.1 and illustrated in Figures 5.17 to 5.23.

- **Isozyme temperature**
  - Line of equal coldness
  - Coldest month temperature
  - Isotherm of greatest cooling
  = Line of equal coldness of the coldest months temperature

- **Surface annual average temperature**
  - Surface water annual average water temperature isotherms
  - Isotherm = a line on a map connecting points having equal or constant temperature

- **Insolation**
  - Incoming solar radiation
  - Dependant on the angle of incidence
  - Measured in Jm⁻²yr⁻¹

- **Currents**
  - Cold = decrease temperature; warm = increase temperature
  - They deflect isozymes / isotherms if the current is at an angle to latitude
  - Due to atmospheric circulation via the coriolis effect of the Earth's spin

- **Biogeography of shelf sea faunas**
  - General animal based watermass temperature groupings
  - To depths of 200m; follow broadly latitudinal bands of temperature change, becoming more diverse as they approach the equator
  - Tropical fauna boundary – 20°C isotherm for coldest month (isozyrne)
  - Warm temperate 13-20°C isozyme boundaries (but N. Atlantic lowest average temperature 10°C)

- **Geographic distribution of marine algae**
  - General algae based watermass temperature groupings

- **Phyographic regions**
  - General algae based watermass temperature groupings

- ** Reasons for differences**
  - A – fauna v algae:
    - Different calcification ability
    - Not as sensitive as algae- therefore difficult to assign zones based on taxa
    - Live in more wide-ranging environments
    - Diversity and abundance differences due to greater depth distribution
    - Taking different algae into account
  - B – algae v algae:
    - Taking different physiological features (e.g. currents) into account
    - Accuracy difficulties
    - Terms are 'arbitrary' and therefore there are different ideas as to what is a defining factor for each zone

Table 5.1 Descriptive factors used in distribution analyses (Figs. 5.17 to 5.23).
Fig. 5.17: Isocyanine data after temperature maps in Ocean circulation 1989.
Fig. 5.18 Surface annual average isotherms in °C.
Fig. 5.21 Biogeography of shelf seas lagoons

After Cox and Moore (1993)

Cold Temperate
Warm Temperate
Tropical
Warm Temperate
Cold Temperate
Arctic

+ Antarctic
5.3.2 Modern green calcareous algae distribution results

**DASYCLADALES**

*Acetabularia* (Figure 5.1)

This genus has an abundant worldwide distribution within areas expected to be inhabited. There are also areas on the periphery of this ‘accepted’ region which bear host to communities of this taxon. These areas include water masses of a temperature lower than expected for such a taxon, but this may be countered by the degree of calcification of the vegetation at these sites compared with the more ‘tropical’ regions.

**Extremities**

N. Mediterranean Sea (c45°N) / mid Japan (37°30’N) to mid New Zealand (c41°S).

**Isocrymes**

All occurrences are within the 10°C isocryme.

Most occurrences are >20°C even >25°C.

**Surface annual average**

All occurrences are within the 15°C annual average isotherm.

Most occurrences are >25°C.

**Insolation**

All are > 155 Jm⁻²yr⁻¹

Most are > 200 Jm⁻²yr⁻¹

**Currents**


Cold: Canary to Canary Islands.

**Biogeography of shelf sea faunas**

Most are tropical but some are warm temperate right up to the cold temperate boundary in both northern and southern hemispheres.

**Geographic distribution of marine algae**

Most are tropical but some are warm temperate right up to the cold temperate boundary in both northern and southern hemispheres.
Phytographic regions

Most are tropical but some are warm temperate right up to the cold temperate boundary in both northern and southern hemispheres.

Summation

A well spread alga both longitudinally and latitudinally. The alga appears to have started to spread out from the ‘tropical’ zone and into the warm-temperate area. This move of some colonies into these outer, more environmentally inclement areas is shown as a sparse distribution and in these areas is also physically demonstrated with a decrease in the plants extent of calcification.

Acicularia (Figure 5.2)

This genus is restricted to the Atlantic Ocean – mainly the Caribbean, but with extremities of its range at Bermuda and southeast Brazil. Therefore it would appear that the distribution of this genus is severely restricted to the more tropical region.

Extremities

Bermuda (c33°N) to mid Brazil (c23°S)

Isocrymes

All occurrences are within the 15°C isocryme.

Most occurrences are >20°C (all except one in Bermuda).

Surface annual average

All occurrences are within the 20°C annual average isotherm.

Most occurrences are >25°C isotherm (all except one in Bermuda – 20-25°C).

Insolation

All are > 180 Jm⁻²·yr⁻¹

Most are > 205 Jm⁻²·yr⁻¹ (exceptions are the two extremes)

Currents

Warm: Gulf Stream to Bermuda and Brazil to mid Brazil.

Biogeography of shelf sea faunas

Most are tropical, the two extremes are on the boundaries between tropical and warm temperate.
Geographic distribution of marine algae

All are tropical except for Bermuda in the warm temperate zone (and Brazil on the boundary).

Phytographic regions

Most are tropical, Bermuda and mid Brazil are warm temperate, and the Bahamas and S. Florida examples are on the boundary of the two zones.

Summation

Confined both longitudinally and latitudinally to warmer realms, this alga is of little importance overall and of limited importance locally. It does however add weight to the predominantly tropical nature of the calcareous algae of the present day.

Bornetella (Figure 5.3)

Distribution of this alga is relatively sparsely spread across the Indian and western Pacific realms within waters that would easily fall into a warmer-water zone.

Extremities

Ryuku Islands (c26°N) to Reunion (c21°S)

Isocrymes

All occurrences are (> and) within the 20°C isocryme – the Ryuku Islands reference is on the isocryme.

Surface annual average

Most occurrences are (> and) within the 25°C isocryme with the exceptions of the Ryuku Islands and New Caledonia which are 20 – 25°C isotherms.

Insolation

All are > 180 Jm⁻² yr⁻¹

Most are > 205 Jm⁻² yr⁻¹

Currents

Warm: Kuro to Ryuku Islands and Indian South Equatorial to Reunion and Mauritius.

Biogeography of shelf sea faunas

All the occurrences are tropical except for the Ryuku Islands which are warm temperate.
Geographic distribution of marine algae

All occurrences are in the 'tropical zone' (the Ryuku Islands are just within the boundary).

Phytographic regions

All occurrences are in the 'tropical zone' (the Ryuku Islands are just within the boundary).

Summation

While its longitudinal distribution is opposite to *Acicularia, Bornetellias* latitudinal distribution is even slightly more restricted to the tropical region of the globe.

*Chalmasia* (Figure 5.4)

Similar to *Acicularia* in its spread, or rather lack of, this rare alga is purely Caribbean.

Extremities

Florida (c26°N) to Martinique (c15°N).

Isocrymes

Found in 20+°C isocrymes.

Surface annual average

Found in 25+°C isotherms.

Insolation

>205 Jm⁻²yr⁻¹

Currents

Purely bathed in warm water from the Florida and Caribbean currents.

Biogeography of shelf sea faunas

Tropical up to the boundary of the warm temperate and tropical zones.

Geographic distribution of marine algae

Tropical.

Phytographic regions

Tropical up to the boundary of the warm temperate and tropical zones.
Summation
Very rare and unabundant alga restricted to the two ends of the Caribbean, its
distribution is purely tropical.

Cymopolia (Figure 5.5)
Broadly ‘tropical’ in dispersal, with most abundance in the Caribbean, this
genus is found more northerly of the equator than it is southerly, and is bordering on
the more extreme latitudes in the North.
Extremities
S. Spain (c36 ½ ° N) to Java (c7 ½ °S).
Isocrymes
All occurrences are within the 15°C isocryme.
Most occurrences are within the 20°C isocryme.
Surface annual average
All occurrences are within the 15°C isotherm.
Most occurrences are within the 25°C isotherm.
Insolation
All are > 155 Jm⁻² yr⁻¹
Most are > 205 Jm⁻² yr⁻¹
Currents
Warm: Gulf Stream to Bermuda and Kuro to Ryuku Islands and S. Japan.
Cold: Canary to Canary Islands.
Biogeography of shelf sea faunas
The majority are tropical but a large percentage are warm temperate (c25%).
Geographic distribution of marine algae
The majority are tropical but a small percentage are warm temperate.
Phytographic regions
The majority are tropical but a small percentage are warm temperate.
Summation
A curious distribution with regard to the hemispheres – almost all are found in
the northern hemisphere, up to reasonable latitudes of c40°N, with very few edging
south of the equator. However, if the northern hemisphere is looked at alone, it
displays a typical distribution for calcareous Dasycladaceae. The hemisphere mismatch may be due to the factors of available habitation sites and a combination of modern and ancient migration pathways.

*Halicoryne* (Figure 5.6)

Rare, scattered occurrences of algae in the western Pacific comprise the entire distribution of this taxon.

**Extremities**

Ryuku Islands (c26°N) to New Caledonia (c21°S).

**Isocrymes**

All occurrences are on / within the 20°C isocryme.

Most occurrences are > 25°C isocryme.

**Surface annual average**

All occurrences are within the 20°C isotherm.

Most occurrences are > 28°C isotherm.

**Insolation**

All are > 180 Jm⁻²yr⁻¹

Most are > 205 Jm⁻²yr⁻¹

**Currents**

Warm: Kuro to Ryuku Islands.

**Biogeography of shelf sea faunas**

All are tropical except for the Ryuku Islands which are warm temperate.

**Geographic distribution of marine algae**

All are tropical.

**Phytographic regions**

All are tropical.

**Summation**

Very uncommon and with few sites, this alga is spread latitudinally across the ‘tropical’ zone.
Neomeris (Figure 5.7)

This abundant, world-wide disseminated alga shows a warm-water affinity with no excursions into water of a more temperate nature.

Extremities

Bermuda (c33°N) to S. Africa (c32°S).

Isocrymes

All occurrences are within the 15°C isocryme (15°C N - 20°C S except mid Chile which is 15-20°C S).

Most occurrences are within the 20°C isocryme.

Surface annual average

All occurrences are within the 20°C isotherm (except for mid Chile which is 15-20°C).

Most occurrences are within the 25°C isotherm.

Insolation

Almost all are &gt; 180 Jm² yr⁻¹ (except S. Japan)

Most are &gt; 205 Jm² yr⁻¹

Currents

Warm: Gulf Stream to Bermuda, Agulhas to E. South Africa, Indian S.

Equatorial to Reunion and Mauritius, and Kuro to Ryuku Islands and S. Japan.

N.B. mid Chile location (Berger and Kaever, 1992) is against the cold Peru (Humboldt) current.

Biogeography of shelf sea faunas

Most are tropical, but with a few warm temperate (Japan, Ryuku, and Chile).

Geographic distribution of marine algae

Most are tropical, but with a few warm temperate.

Phytographic regions

Most are tropical, but with a few warm temperate (Bermuda and Chile).

Summation

Broadly tropical, with some extension into warm temperate waters via warm current bathing etc, there is seemingly an inconsistency with the Chilean site.
Polypysa (Figure 5.8)

Similar to Acetabularia in distribution, but with less abundance, this alga is found in most suitable areas and also in outlying peripheral regions.

Extremities

Mid Italy (c42°N) to SW Australia (c34°S).

Isocrymes

All occurrences are within the 10°C isocryme.
Most occurrences are within the 20°C isocryme.

Surface annual average

All occurrences are within the 15°C isotherm.
Most occurrences are within the 25°C isotherm.

Insolation

All are > 155 Jm^-2 yr^-1
Most are > 205 Jm^-2 yr^-1

Currents

Warm: Gulf Stream to Bermuda, Brazil to mid Brazil, Indian S. Equatorial to Mauritius, W. Australian to W. Australia and Kuro to Ryuku Islands and the Japanese mainland.
Cold: Canary to Canary Islands and California to Revalligedlio Islands.

Biogeography of shelf sea faunas

Most are tropical but large numbers are warm temperate, but mostly in the northern Hemisphere.

Geographic distribution of marine algae

Most are tropical but large numbers are warm temperate, but mostly in the northern Hemisphere.

Phytographic regions

Most are tropical but large numbers are warm temperate, but mostly in the northern Hemisphere.

Summation

A well distributed alga displaying ‘classic distribution patterns’ of excursions into non tropical waters, and again with a bias to the northern hemisphere.
All Dasycladaceae (Figure 5.9)

An abundant, worldwide dispersal of this previously supreme and now waning algal family is found in areas covering up to c40-45° either side of the equator – double the official value of the term ‘tropical’ which is applied to members of this family.

Isoeptymes

All occurrences are within the 10°C isocryme.
Most occurrences are within the 20°C isocryme.
Probable limit of calcification: 15°C.

Surface annual average

All occurrences are within the 15°C isotherm.
Most occurrences are within the 25°C isotherm.
Probable limit of calcification: 20°C.

Insolation

All are > 130-155 Jm⁻² yr⁻¹ one New Zealand extreme.
Most are > 180 Jm⁻² yr⁻¹

Currents

Warm: Gulf Stream, Agulhas, Tasman, Brazil, W. Australian and Kuro.
Cold: Canary and California.

Biogeography of shelf sea faunas

Most tropical, many in northern hemisphere, few in southern hemisphere warm temperate, New Zealand occurrence in the cold temperate zone.

Geographic distribution of marine algae

Most tropical, many in northern hemisphere, few in southern hemisphere warm temperate.

Phytographic regions

Most tropical, many in northern hemisphere, few in southern hemisphere warm temperate.

Summation

The vast majority of specimens are tropical in distribution and from these are derived the view that ALL must be. However, there are a number of examples that can be found in warm temperate environments (and even to the cold temperate
boundary). These examples are of interest in terms of growth form and particularly calcification. These extremists do grow ‘well’ in suitable local habitats in the colder temperatures. The northern hemisphere bias of numbers found in the extra-tropical regions must be due to the greater amount of locations with suitable conditions being present.

HALIMEDACEAE

Halima (Figure 5.10)

This taxon is the most speciate, successful, abundant and widely dispersed of all the Halimedaceae. It is spread throughout all the oceans spanning the mid-latitudes of the surface of the globe; most plentifully within the tropics, but also in areas of ‘extremes’ i.e. on the edges of ‘tropical’ waters. It is in these places that the plants are adversely affected in terms of calcification.

Extremities

N. Italy (c43 ½ °N) to SW Australia (c34°S)

Isocrymes

All occurrences are within the 10°C isocryme (10°C in the northern hemisphere, 10-15°C in the southern hemisphere).

Most occurrences are within the 20°C isocryme.

Surface annual average

All occurrences are within the 15°C isotherm.

Most occurrences are within the 20 (to 25)°C isotherm.

Insolation

All are > 155 Jm⁻²yr⁻¹ (155 in the northern hemisphere, 180 in the southern hemisphere).

Most are > 205 Jm⁻²yr⁻¹

Currents

Warm: Gulf Stream to Bermuda,Brazil to mid Brazil, Agulhas to E. South Africa, W. Australian to W. Australia and Kuro to Ryuku Islands and mid Japan.

Cold: Canary to Canary Islands.

Biogeography of shelf sea faunas

Most are tropical, some (few) are warm temperate.
Geographic distribution of marine algae

Most are tropical, some (few) are warm temperate (with a skew of these to the northern hemisphere).

Phytophagic regions

Most are tropical, some (few) are warm temperate.

Summary

This is the most abundant alga of the Halimedaceae, even of all the green calcareous algae at the present day. This abundance is not only in number of localities in which it is found (it is almost ubiquitous in tropical waters), but also in the amount of biomass present at these locations. At sites such as the Great Barrier Reef, *Halimeda* forms meadows and draperies (on horizontal and vertical surfaces respectively) where it is unispeciate. In areas such as this, it is responsible for massive sediment contribution in the form of sand sized particles composed of dead thallus segments which form cemented reefs or unbound mounds.

The genus as a whole is composed of many species, and is without doubt the foremost calcareous chlorophytic primary producer of the present day. It seems that with this dominance it has not progressed far into non-tropical waters, and in the occasions where it has (e.g. the Mediterranean Sea and SW Australia) it has suffered with respect to numbers and calcification.

*Penicillus* (Figure 5.11)

Very abundant in the Caribbean, this taxa has a sparse distribution throught the rest of the worlds main oceans, with few plants being found outside of the’tropical’ zone.

Extremities

NW. Mediterranean (c43 ½ °N) to SW Australia (c32°S)

Isocymes

All occurrences are within the 10°C isocryme (10°C in the northern hemisphere, 15°C in the southern hemisphere).

Most occurrences are within the 20°C isocryme.
Surface annual average

All occurrences are within the 20°C isotherm (except one in the Mediterranean at 15°C).

Most occurrences are within the 25°C isotherm.

Insolation

All are > 180 Jm⁻²yr⁻¹

Most are > 205 Jm⁻²yr⁻¹

Currents

Warm: Gulf Stream to Bermuda, W. Australian to W. Australia and Pacific Equatorial countercurrent to Ecuador.

Biogeography of shelf sea faunas

Most are tropical with some (very few) warm temperate.

Geographic distribution of marine algae

Most are tropical with some (very few) warm temperate.

Phytographic regions

Most are tropical with some (very few) warm temperate.

Summation

With its global longitudinal distribution centered around the Caribbean, this genus displays the typical pattern of a tropical alga starting to expand into cooler waters.

*Rhipocephalus* (Figure 5.12)

This alga is found only within the confines of the Caribbean.

Extremities

N. Bahamas (c26 ½°N) to Panama (c9°N).

Isocrymes

All occurrences are within the 20°C isocryme (20°C in the northern hemisphere, 25°C in the southern hemisphere).

Most occurrences are within the 20-25°C isocryme.

Surface annual average

All occurrences are within the 25°C isotherm.
Insolation

All are > 205 Jm\(^{-2}\)yr\(^{-1}\) (some up to 230 Jm\(^{-2}\)yr\(^{-1}\)).

Currents

Purely bathed in warm water from the Florida and Caribbean currents.

Biogeography of shelf sea faunas

Tropical in distribution up to the boundary of the northern warm temperate zone.

Geographic distribution of marine algae

Tropical in distribution up to the boundary of the northern warm temperate zone.

Phytographic regions

Tropical in distribution up to the boundary of the northern warm temperate zone.

Summation

Restricted in distribution both longitudinally and latitudinally, this alga is only tropical in distribution and in the tropical Caribbean can be an important phycological component and local sediment contributor.

*Tydemania* (Figure 5.13)

This very rare alga is found at a few dispersed localities mainly in the Indian western Pacific oceans. It is a deeper-water living species than the other green algae and, with the water temperature of an ocean decreasing with depth, this may help to explain the very tropical nature of its distribution.

Extremities

Ryuku Islands (c26°N) to N. Great Barrier Reef, Australia (c15 ½ °S).

Isocrymes

All occurrences are within the 15°C isocryme (15°C in the northern hemisphere, 20°C in the southern hemisphere).

Most occurrences are within the 25°C isocryme.
Surface annual average

All occurrences are within the 20°C isotherm (20°C in the northern
hemisphere, 25°C in the southern hemisphere).
Most occurrences are within the 28°C isotherm.

Insolation

All are > 155 Jm⁻²yr⁻¹ (155 in the northern hemisphere, 205 in the southern
hemisphere)
Most are > 205 Jm⁻²yr⁻¹

Currents

Warm: Kuro to Ryuku Islands.

Biogeography of shelf sea faunas

All are tropical except the Ryukus in the warm temperate zone.

Geographic distribution of marine algae

All are tropical.

Phytographic regions

All are tropical.

Summation

A rare chlorophyte with a distribution limited to the tropics of the Indo-Pacific
to depths of approximately 65m+.

\textit{Udotea} (Figure 5.14)

Very abundant, especially in the Caribbean, this alga is dispersed across the
globe within ‘tropical’ limits.

Extremities

Bermuda (c33°N) to E. S Africa (c33°S).

Isocrymes

All occurrences are within the 15°C isocryme (15°C in the northern
hemisphere, 20°C in the southern hemisphere).
Most occurrences are within the 20°C isocryme.
Surface annual average
   All occurrences are within the 20°C isotherm.
   Most occurrences are within the 25°C isotherm.

Insolation
   All are > 180 Jm⁻²yr⁻¹ (180 in the northern hemisphere, 205 in the southern hemisphere)
   Most are > 205 Jm⁻²yr⁻¹

Currents
   Warm: Gulf Stream to N. Carolina and Bermuda, and Agulhas to E. S Africa.

Biogeography of shelf sea faunas
   Most are tropical, but a few are warm temperate.

Geographic distribution of marine algae
   Most are tropical, but a few are warm temperate.

Phytographic regions
   Most are tropical, but a few are warm temperate.

Summation
   The second most abundant Halimedaceae, it is generally tropical in nature showing good mid Atlantic and Indian Ocean spread yet limited Pacific distribution.

All Halimedaceae (Figure 5.15)

   This profuse family has a dispersal similar to that of the Dasycladaceae – up to c40° of latitude in both hemispheres – this is almost twice the official value of the term ‘tropical’ which is said to be indicative of this algal families latitudinal extent. Within true ‘tropical’ areas, when members of this family are present, they are found in great multitudes – their modern dominance from their origin in mid to late Mesozoic times being the opposite of the Dasycladacean fate.

Isocrymes
   All occurrences are within the 10°C isocryme.
   Most occurrences are within the 20°C isocryme.
   Probable limit of calcification: 15°C.
Surface annual average

All occurrences are within the 15°C isotherm.
Most occurrences are within the 25°C isotherm.
Probable limit of calcification: 20°C.

Insolation

All are > 155 Jm⁻² yr⁻¹ (155 in the northern hemisphere, 180 in the southern hemisphere)
Most are > 205 Jm⁻² yr⁻¹

Currents

Warm: Gulf Stream, Agulhas, Brazil, W. Australian and Kuro.
Cold: Peru (Humboldt), Canary and California.

Biogeography of shelf sea faunas

Most are tropical, some are warm temperate (c10%).

Geographic distribution of marine algae

Most are tropical, some are warm temperate (<10%).

Phytographic regions

Most are tropical, some are warm temperate (<10%).

Summation

A major component of any shallow shelf carbonate environment in the tropics, these algae are also a reasonable player in 'sub-tropical' areas – more than has been previously recognised.

This family has taken over the role the Dasycladaceae occupied in the geologic past and has occupied the same ecological niche.

All of this information can be summarised in the following diagrams; Figure 5.24 shows the global isocrymal and annual average temperature grouping distribution of modern Dasycladales and Halimedaceae, while Table 5.2 shows the modern calcareous Chlorophyta extreme distributional limit data.
Fig. 5.24 Global temperature distribution of modern calcareous green algae
Table 5.2: Recent skeletal calcareous green algae global distribution results: initial and temperate extreme limits.

<table>
<thead>
<tr>
<th>Location</th>
<th>Initial Elevation (m)</th>
<th>Initial Temperature (°C)</th>
<th>Initial Salinity (%)</th>
<th>Extreme Elevation (m)</th>
<th>Extreme Temperature (°C)</th>
<th>Extreme Salinity (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>South America</td>
<td>Below 31.5</td>
<td>Below 20</td>
<td>Below 35</td>
<td>Below 31.5</td>
<td>Below 20</td>
<td>Below 35</td>
</tr>
<tr>
<td>North America</td>
<td>Below 31.5</td>
<td>Below 20</td>
<td>Below 35</td>
<td>Below 31.5</td>
<td>Below 20</td>
<td>Below 35</td>
</tr>
<tr>
<td>Europe</td>
<td>Below 31.5</td>
<td>Below 20</td>
<td>Below 35</td>
<td>Below 31.5</td>
<td>Below 20</td>
<td>Below 35</td>
</tr>
<tr>
<td>Asia</td>
<td>Below 31.5</td>
<td>Below 20</td>
<td>Below 35</td>
<td>Below 31.5</td>
<td>Below 20</td>
<td>Below 35</td>
</tr>
</tbody>
</table>

References:

1. South America
2. North America
3. Europe
4. Asia

Note: Initial and extreme limits refer to the range of conditions under which calcareous green algae are known to occur.
5.4 Extant algae systematics

5.4.1 Overview

The following is the nomenclature adopted in this study and is as correct and up-to-date as is possible.

5.4.2 Dasycladales

Division Chlorophyta;
Class Chlorophyceae;
Order Dasycladales.

Comprised of two extant families: Dasycladaceae and Acetabulariaceae.

Dasycladaceae Kützing 1843 as Dasycladaceae

This name includes the superfluous family names of:

- Bornetellaceae Pia 1912
- Neomeridaceae Pia 1912
- Polyphysaceae Kützing 1843
- Verticillatae Blackman & Tansley 1902

(Silva, 1980 see paper for references)

This order can be split into families and tribes, the relevant (extant calcareous) ones being shown in Table 5.3:

<table>
<thead>
<tr>
<th>Extant families</th>
<th>Extant tribes</th>
<th>Extant genera</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acetabulariaceae</td>
<td>Acetabulariaceae</td>
<td>Acetabularia Lamouroux 1812</td>
</tr>
<tr>
<td>(Endlicher) Hauck 1885</td>
<td>Decaisne 1842</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Acicularia d'Archiac 1843</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Chalmasia Solms-Laubach 1895</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Polyphysa Lamouroux 1816</td>
</tr>
<tr>
<td></td>
<td>Halicoryneae</td>
<td>Halicoryne Harvey 1859</td>
</tr>
<tr>
<td></td>
<td>Valet 1969</td>
<td></td>
</tr>
<tr>
<td>Dasycladaceae</td>
<td>Dasycladaceae</td>
<td>Cymopolia Lamouroux 1816</td>
</tr>
<tr>
<td>(Kützing 1843) emend.</td>
<td>Pia 1920</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Neomeris Lamouroux 1816</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bornetella Munier-Chalmas 1877</td>
</tr>
</tbody>
</table>

Table 5.3 Extant calcareous Dasycladaceae classification (after Berger and Kaever, 1992).
This systematic classification, as stated in Berger and Kaever (1992), has evolved over the years. An overview of the main points of the systematics of the Dasycladales can be seen below:

- Pia (1927) – Dasycladaeae subdivided into 17 tribes (including Dasycladaeae incertae tribus) with the arrangement of the primary lateral segments and different location of gamete formation being essential suprageneric characteristics.
- Pascher (1931) – Dasycladaeae elevated to an Order.
- Deloffre (1988) – About 180 genera are placed into 5 families; Beresellaceae, Selenonellaceae, Diploporellaceae, Dasycladaeae and Acetabulariaceae. In turn they are subdivided into 30 tribes.
- Berger and Kaever (1992) – Deloffre’s classification is slightly altered with the genera assigned to the Dasycladaeae being split into two new families – Triploporellaceae and a ‘new’ Dasycladaeae.

5.4.3 Halimedaceae

Division Chlorophyta;
Class Chlorophyceae;
Order Bryopsidales;
Family Halimedaceae.

This family contains the largest living green marine algae (*Halimeda*). Six out of twenty four of the Bryopsidales genera are calcified and the extent of calcification varies with age, taxonomy and local environment (Hillis, 1991).

**Halimedaceae** Link 1832 (subfamily Halimedoideae = calcified Halimedaceae)

This name includes the superfluous family names of:

- Caulerpaceae – Kützing 1843 as Caulerpeae
- Codiaceae – Kützing 1843 as Codieae
- Udoteaceae – J. Agardh 1887

(Silva, 1980 and Hillis-Colinvaux, 1984 see papers for references)
5.4.4 Corallinaceae

Corallinaceae
Division Rhodophyta;
Class Rhodophyceae;
Order Corallinales;
Family Corallinaceae.

For the purposes of modern correlation, the most prolific rock / reef building algal group is that of the coralline red algae. The presently regarded modern environmental parameters governing coralline algae are a tropical to subpolar latitudinal distribution, up to 83°N to 73°S (Mu, 1993; Aguirre et al., 2000), and a depth range of 0 – 270m (Aguirre et al., 2000). All of the members of this group are calcified.

There are three family – subfamily groupings with different depth-temperature distributions, see Figure 5.25:

![Diagram](image)

Fig. 5.25 Corallinaceae latitudinal distribution (After Aguirre et al., 2000).

5.5 Definition of temperature as it relates to organisms

Definition of environmental factors, especially temperature are quite complicated due to annual and longer term variations in temperature and in discrimination between air temperature, water temperature, temperature variations with depth and with time etc.
Environmental information (e.g. sea surface temperatures, insolation and current data) was obtained from individual literature sources and atlases (e.g. Ocean Circulation, 1989).

It is important to note that in terms of phycological distribution, the temperature information that is used must be stated in terms of isocrymes. An isocryme can be defined as a line of equal value of the coldest (surface) water temperature experienced at a locality. This value is used instead of the annual average temperature because algae are temperature sensitive and so it is the isocrymal value that is relevant in defining the values of their temperature distribution restrictions.

5.6 Discussion

5.6.1 Global temperature distribution on the Earth’s surface

There is a primary, fundamental connection between the global factors of latitudinal location and local surface temperature due to the angle of incidence of sunlight. Lower latitudes receive sunlight more perpendicularly than the higher latitudes and this results in a lesser amount of reflection and a lesser amount of atmospheric medium to penetrate, all of which results in a greater surface temperature at the lower latitudes. Also, at higher latitude, the surface receives less energy as the sunlight ‘beam’ is spread across a larger surface area (Mather, 1974) e.g. Table 5.4:

<table>
<thead>
<tr>
<th>Latitudinal zone</th>
<th>Solar energy in Kcal / cm² year</th>
</tr>
</thead>
<tbody>
<tr>
<td>Range</td>
<td>Mean</td>
</tr>
<tr>
<td>90-80°N</td>
<td>N/A</td>
</tr>
<tr>
<td>80-70°N</td>
<td>68-72</td>
</tr>
<tr>
<td>70-60°N</td>
<td>68-85</td>
</tr>
<tr>
<td>60-50°N</td>
<td>68-110</td>
</tr>
<tr>
<td>50-40°N</td>
<td>68-140</td>
</tr>
<tr>
<td>40-30°N</td>
<td>90-200</td>
</tr>
<tr>
<td>30-20°N</td>
<td>115-220</td>
</tr>
<tr>
<td>20-10°N</td>
<td>120-220</td>
</tr>
<tr>
<td>10-0°N</td>
<td>120-170</td>
</tr>
<tr>
<td>0-10°S</td>
<td>120-180</td>
</tr>
<tr>
<td>10-20°S</td>
<td>130-190</td>
</tr>
<tr>
<td>20-30°S</td>
<td>120-200</td>
</tr>
<tr>
<td>30-40°S</td>
<td>110-170</td>
</tr>
<tr>
<td>40-50°S</td>
<td>80-135</td>
</tr>
<tr>
<td>50-60°S</td>
<td>65-95</td>
</tr>
<tr>
<td>60-70°S</td>
<td>65-75</td>
</tr>
<tr>
<td>70-80°S</td>
<td>N/A</td>
</tr>
<tr>
<td>80-90°S</td>
<td>N/A</td>
</tr>
</tbody>
</table>

Table 5.4 Insolation change with latitude (after Mather, 1974).
In the marine realm, this relationship which should result in a parallel latitudinal banding of temperatures, is offset by the action of currents (this is further discussed and expanded upon in section 8.4.8.3).

5.6.2 Distribution of particular algal groups with respect to temperature

5.6.2.1 Global zonations

Temperature regimented regions can be defined across the face of the globe and these regions tend to coincide with similar zones defined via floristic occurrences due to particular tolerances to water temperatures exhibited by various algal taxa (N’Yeurt, 1996). It has been stated that the phycological extent of marine species can be positively tied to the surface water isotherms of 10, 15, 20 and 25°C (Setchell, 1920). Disregarding light, the important controls on algal distribution are the annual (short-term) extremes of temperature. However, even this limiting factor cannot draw ‘razor-sharp limits’ as algal flora can be seen to change quite gradually (Michanek, 1979). The problem can be compounded by the phenomenon of ‘spot distribution’ – i.e. when the distribution of a species is founded on the remotest recorded occurrence – which can show:

- How intensely an area is investigated.
- How rich it is in different biotopes.
- To what extent it contains enclaves with local climatic conditions.

(after Michanek, 1979)

It is useful to divide the Earth’s surface into provincial zones. A phytogeographic realm can be used to delineate algal zone boundaries and is a realm of relatively homogenous flora separated from other realms via floristic discontinuities. These realms can be usefully separated via criteria such as presence and absence of calcified green algae (Mu, 1993).

5.6.2.2 Modern calcareous green algae extremes of distribution

The Calcareous Chlorophyta which occur at the highest latitudes define the temperature limits of the group. Relevant factors such as abundance and calcification extent of the modern specimens will have pertinent discussion on the extent of fossil varieties and our use of them in palaeoecological work.
In the North Atlantic, the northernmost occurrence of calcareous green algae is in North Carolina. Along this coastline in areas of high carbonate content south of Cape Hatteras (which is a barrier to temperature and to carbonate sedimentation) *Halimeda* is locally abundant but of minor overall importance (Milliman et al, 1972). In addition two *Udotea* species are found in Onslow Bay (about 100 miles South of Cape Hatteras) (Schneider, 1976). This embayment has suitable substrate and mild enough temperatures for algae of a tropical nature to populate it having been dispersed to this more sub-tropical clime via the Gulf Stream current (Schneider, 1976). The Gulf Stream has a major effect upon the northern Atlantic as it moves warm water from the Caribbean up along the eastern American coastline and across towards the United Kingdom (Gardner, 1989). This warm water is responsible for the North Carolinas milder temperatures as well as for deflecting isotherms of the northern Atlantic up which results in Bermuda having a much more diverse and abundant assemblage of algal taxa than it would otherwise have.

The Mediterranean Sea is another setting where green calcareous algae occur. However, there are uncertainties over their sediment input. *Halimeda* is found in a number of settings, but only forms sediment in certain environments. One example is in the Balearic Islands where *Halimeda* is only found in one restricted bay (Fornells Bay, N. Menorca) and is relatively common within this bay (Fornos and Ahr, 1997) where it is found in association with an *Acetabularia* species. This location is within a temperate, ‘Foramol’ environment (Fornos et al, 1992) and appears to be a local aberration within the regional Foramol trend. Within the bay the algally derived sediment comprises up to 45.9% of the bioclastic debris in the shallower waters. The living plants are less heavily calcified than tropical examples (47-58% CaCO₃ compared with >70% for tropical specimens) (Fornos et al, 1992).

A similar state of affairs occurs in the western Pacific with species of *Acetabularia* being found at up to 37½ °N in Japan (Arasaki et al., 1979). These algae grow in restricted bays on a series of islands bathed in warmer waters brought northwards via the Kuro current – a North Pacific equivalent of the Gulf Stream. This current is presumed by the author to be responsible for allowing the abundant algae found at the Ryuku Islands.
The southern hemisphere also has extremes of algal latitudinal existence which are similar to those in the northern hemisphere. The outlying locations in the southern hemisphere are australasian. New Zealand has a single occurrence (on the warm / cold temperate boundary) of Acetabularia kilneri in Edgecumbe Bay on the Southwest coast of North Island – again within a bay presumably affording local more affable conditions. In Australia, the western coast possesses a strong tropical element (Womersley, 1981) and the southwestern continental margin is the location of the transition from warm-water to cool-water realms (James et al, 1999). This area has Halimeda and Penicillus at their southerly limit while on the southern coast, Dasycladaceae such as Acetabularia are found (Womersley, 1981). The sedimentary characteristics of the SW Australian coast are cool-water with some subtropical attributes and the sedimentary input from these algae decreases southwards from c29°S, where it shows as trace amounts, to a few degrees further south where the algae “…although alive, are poorly calcified and do not form sediment…” (James et al, 1999).

5.6.2.3 Algal environmental restriction specifics
Order Dasycladales.

This order comprises two main families, the Dasycladaceae and the Acetabulariaceae. It is commonly stated that Dasycladales are restricted to warm-water and correspondingly are low-latitude inhabitants (e.g. Beadle, 1988, Berger and Kaever, 1992). Thus the presently regarded modern environment which is attributed to them in the literature is tropical to subtropical shallow sea waters which are described as either within 13°C isocrymes (Elliott, 1977) or in a belt of distribution of c25°N to 35°S (Berger and Kaever, 1992). This is on the most part quite true, however there are extremes which can display a “scattered distribution outside the optimum habitat” (Elliott, 1968). An example of this is Acetabularia at 45°N in the Adriatic Sea compared to Neomeris and Cymopolia found within the 20°C isocryme between latitudes of 33°N and 24°S (Beadle, 1988, Elliott, 1968, Berger and Kaever, 1992). Mediterranean Acetabularia grow best (in laboratory conditions) at 20-22°C with other taxa showing optimal growth at the higher temperatures of 25-27°C. It should however be noticed that cultivation and growth of all species can be achieved
(although not optimally) at any temperature between 20° and 28°C (Berger and Kaever, 1992).

This order plays an important role as they were substantial contributors to limestones in the Mesozoic and early Cenozoic - fossil genera were more numerous, abundant and more important than today in terms of limestone deposition and shallow water habitat construction. They are useful as guide fossils, both for stratigraphical classification and as they are facies dependant they are therefore a facies indicator for waterdepth, temperature, salinity and turbulence.

Family Halimedaceae.

Halimedaceae have essentially the same distribution as the Dasycladaceae (Beadle, 1988). The presently regarded modern environment which is attributed to them is mostly tropical but some genera are subtropical. Their distribution has been delineated by 20°C isotherms or 12°C isotherms (Mu, 1993) or distribution of c45°N to 34°S (Mu, 1993). 25°C + isotherms has also been suggested as the limit (Hillis, 1991), a tropical zone restriction defined by 23°N and S (Hillis, 1959). The vagueness of quantitative data on restriction to the fringes of the temperate latitudes has been argued as being due to limited adaptation to cooler water temperatures (Hillis, 1959). The fact that both calcareous green algal families share the same environment is no real surprise, however it is interesting to see that Halimedaceae (with Halima in particular) has, in an ecological role, replaced the Dasycladaceae as a “rock-former” (Elliott, 1984) during the Cenozoic, and in this role, they have become the largest extant marine chlorophyte (Hillis, 1991). Calcareous Halimedaceae are mostly tropical (in water temperature terms – not latitudinally) with a small percentage occupying subtropical waters (Hillis, 1991, Hillis-Colinvaux, 1980, 1986).

In the case of the most species rich genus, namely Halima, the optimal temperatures are said to be 27-29°C while they easily accommodate a range of 25-29°C (Hillis-Colinvaux, 1980), but this does not seem to be wholly accurate as is shown by the distribution map (Figure 5.10). The only species which is entirely subtropical is H. cuneata, while H tuna inhabits both subtropical and tropical realms (Hillis, 1959). This belief of their “fairly strict tropical range” means that they are used as strong indicators of a tropical environment (Hillis, 1991). This is not strictly
accurate as it is based on fallacy of a purely tropical temperature distribution. Their extreme but fully calcified distributions are found down to the 12°C isocryme in the Mediterranean (Airoldi et al., 1995) and Japan (Gilmartin, 1966). They are also very important sediment producers and reef builders at the present day (and recent past) (Hillis, 1991).

**Family Corallinaceae**

This group of algae, very important in the modern-day, was not plotted as its distribution as an order is universal across the latitudes as the presently regarded modern environment of the corallinaceae is tropical to subpolar, up to 83°N to 73°S (Mu, 1993; Aguirre et al, 2000). This is to say there are no restrictions with temperature on the group as a whole but on a family level a (temperature related) latitudinal and/or depth change results in a different familial association. Their depth range is 0 – 270m (Aguirre et al, 2000) and they are a large family, including 8 subfamilies. They are important at the present-day as carbonate sediment producers (Aguirre et al, 2000) and major reef builders.

5.6.3 Variation of light and temperature with depth

5.6.3.1 Depth

It is important to ascertain the effect of depth upon the distribution of calcareous algae. Obviously, as photosynthetic organisms, the algae must inhabit the photic zone (the uppermost 200m); this continental shelf “shallow sea” area is still open to a large variation and range of habitable depths. The effects caused by depth can be investigated by observation of the differing modern calcareous Chlorophyta at the same locality with increasing depth. There are two paths that need study—taxonomic changes in the population and physiological changes within the same species.

5.6.3.2 Different genera found at different depths at the same locality.

At a single locality, a study of of the vertical zonations of the calcareous Chlorophyta will show the effects of depth. These effects, if any, will be due to changes in the vital parameters associated with depth, namely:
1. Light intensity (and wavelength),
2. Temperature,

At places known for their abundance of calcareous algae it is possible to assess changes with depth; at the Great Barrier Reef in Australia, *Halimeda copiosa* which is important at shallow depths is also found below 50 metres. There is a marked change in species composition at this locality whenever water depth exceeds c50m, but there appears to be no significant change in the biomass (Drew and Abel, 1988).

At Enewetak Atoll in the Pacific Ocean, *Halimeda* is found to at least 140m water depth (Hillis-Colinvaux, 1986). Here the genus is found to be a major component of reef contribution and differs in speciation at various depths:

<table>
<thead>
<tr>
<th>Depth Range</th>
<th>Species Composition</th>
</tr>
</thead>
<tbody>
<tr>
<td>45m depth – cover 30-50% average.</td>
<td></td>
</tr>
<tr>
<td>53-58m depth – cover up to 50%.</td>
<td></td>
</tr>
</tbody>
</table>
| 76m *H. copiosa.*  
61-91m *H. minima*  
and *taenicola.* | 82m depth – cover 10-50% (some areas 80% cover) (c90m coral = <1% cover). |
| 91m *H. macrophysa.*  
96m *H. fragilis.*  
99m *H. distorta.* | 94m depth – cover c40% (locally up to 80%). *H.distorta, copiosa, fragilis* and *macrophysa* are present. |
| 107-120m depth – cover 10-25% (locally up to 40%). *H. lacunalis* or *taenicola,* *?copiosa* and *distorta* are present. |
| 132-140m depth – cover ≤1%. *H. lacunalis* or *taenicola* are present. |

Table 5.5 *Halimeda* depth distributions and cover at Enewetak atoll (after Hillis-Colinvaux, 1986).

It is presently regarded that, with the exception of *H. cryptica* (an Atlantic species) and possibly *H. opuntia,* there is no reasonable evidence that individual *Halimeda* species indicate specific reef depths (Hillis-Colinvaux, 1986). Any sign of this (see Table 5.5) is probably due to localized conditions, not a global trend.

The pattern of biomass distribution for *Halimeda* on the reef wall - abundant to c90m, decreasing to c10-25% cover at 110m, and disappearing somewhat deeper than 140m (Hillis-Colinvaux, 1986) - does not agree with some earlier views that calcareous Halimedaceae are most abundant in relatively shallow, protected lagoons (Wray, 1977), or that the distribution of *Halimeda* “is very similar to that of hermatypic corals” (James and Ginsburg, 1979) (Hillis-Colinvaux, 1986). This latter situation may have arisen as a result of geographical localities. The depth limit of hermatypic corals in the Caribbean is agreed at ending at c70-80m with possible rare extensions to
100m. James and Ginsburg (1979) report that around Belize, this coral depth is true, and similar to the *Halimeda* situation of the majority ending at c75m with some extending to a maximum (*H. cryptica*) of 110m. This is also the case in nearby Jamaica (Colin et al, 1986). An interesting peculiarity comes when comparing the extreme depths of corals and *Halimeda* at the Caribbean localities with those found in the W. Pacific Ocean where corals grow abundantly to nearer 100m and *Halimeda* commonly to 82m with the deepest found at 146m (Funafuti atoll) (James and Ginsburg, 1979). The greater depth limit in the Pacific may be due to a greater light penetration, as open ocean water is always clearer than water close to large land bodies as there is not as much suspended sediment flushed in from rivers, but more likely is a difference in the form of the reef slopes. At depths of 70-100m, Pacific reefs such as Eniwetok slope at an angle of 60° compared with the vertical cliffs found at the same depths in Caribbean sites such as Discovery Bay, Jamaica; the non-vertical slopes allow for a greater accessibility to the weak light found at these depths (Colin et al, 1986). Also, Discovery Bay is North facing and will therefore, due to it being closer to the Tropic of Cancer than the Equator, be naturally darker.

### 5.6.3.3 Deep living algae.

In terms of depth, the terminology used can be described as: shallow means the upper 25m while deep refers to the rest of the vertical range of *Halimeda*. The 25m limit is chosen because it is the uppermost limit of the only known deepwater species - *H. cryptica* (the shallowest reported depth of *H. copiosa* is 10m) (Hillis-Colinvaux, 1986).

At San Salvador Island in the Bahamas (24°10’N, 74°30’W), *Halimeda cryptica, H. copiosa* and *H. gracilis* are found at 120-150m depth (total range of 20m-152m), *H. lacrimosa var globosa* can be found at 91m, *H. tuna f. platydisca* and *H. discoidea* are present at 73m while *H. goreauii, H. tuna f. tuna* and *H. lacrimosa var lacrimosa* can be seen at 61m depth; these are the deepest found living calcareous chlorophyta flora in the Atlantic Ocean (Blair and Norris, 1988).

The deepwater algae are important to carbonate production and incubations have been conducted at c1 to 2% of the typical surface irradiance (the irradiance at the lowest limit of the euphotic zone) (Jensen et al, 1985). *Halimeda copiosa* has been
found to exhibit plasticity in its utricle dimensions (increasing with depth) which has
been associated with decreased light levels, and is thought to be an adaptation to
increase the light capturing capacity of the plants surface (Blair and Norris, 1988).

At depth, the habit of the same species can change; the deeper living versions
are shorter and more sparsely branched: this has been especially noticed in *H.
macrophysa* (Hillis-Colinvaux, 1986).

At Eniwetok atoll, (30°11′N, 162°15′W) a large number of *Halimeda* found
by Gilmartin (1960) occurred primarily between the 41 and 62m stations and many
even deeper (see Figure 5.26). This supports other reports that *Halimeda* is most
common and luxuriantly developed at deeper levels (Gilmartin, 1960). Also at
Enewetak, *Udotea jennisis* is found to at least -138m depth. All five Halimedaceae
genera (*Halimeda, Udotea, Penicillus, Tydemania, and Rhipocephalus*) have broad
bathymetric ranges: e.g. *Halimeda* is intertidal to at least -150m. Depth tolerances
among species are generally broad, but *H. cryptica* appears restricted to deep water
(25m and deeper) (Hillis, 1991).

In Jamaica, species number versus depth at 60m shows Rhodophyta reduced
by c90% from their surface numbers, while Chlorophyta are reduced by c60%
(*Halimeda* showing a reduction of 36%) and reef corals are reduced by c75%
(Goreau, 1963).

At present no *Halimeda* species are known to be purely restricted to deep
water, although a few grow predominantly at a greater depth (e.g *H. minima* and *H.
cryptica*). It is shown that at 90m *Halimeda* provides considerable cover and greatly
exceeded hermatypic coral cover plus *Halimeda* grows considerably deeper than the
corals do (Hillis-Colinvaux, 1986).

*Halimeda* success below 50m is possibly due to:
A. Reduced competition with hermatypic corals for colonization space,
B. Chemical defense against herbivores,
C. Success at capturing and utilizing available light.

*Halimeda* is very effective at absorbing light in the blue spectrum window
(420-550nm), which is the predominant light wavelength below 100m, as well as
Fig. 5.26 Bathymetric distribution of Euphorex calcareus Chlorophylla (after Gillmorin, 1960; Hillis 1991 and Hillis-Collovax, 1986).
growing at irradiances lower than 1% of the surface value (Hillis-Colinvaux, 1986)
which may suggest that C above is of prime importance.

However, Dasycladales have been generally thought to only be found at
depths of 0-10m (Berger and Kaever, 1992). The general depth range may in fact be a
little deeper, but still within the shallow photic zone. Edelstein (1964) found
Dasycladus (a barely calcified to uncalcified Dasycladalean in normal conditions) at
90m depth off the coast of Israel; in this area, surface water temperature is 28°C,
while at 125m it is still 16-17°C (Oren, 1952): the unusually favourable temperature
gradient as well as extremely clear water is presumed to be the reason for this
extraordinarily deep occurrence. Dasycladales have been found relatively deep
elsewhere: Dasycladus vermicularis (little to no calcification) at 35m in the Ionian
Sea; Neomeris at 50m depth in the Antilles; and Acicularia at a depth of 73m in
Florida (De Castro, 1997).

### 5.6.3.4 Changes in temperature with depth.

The reduction in temperature with depth should have an effect upon the
inhabiting flora – see Table 5.6:

<table>
<thead>
<tr>
<th>Surface temp</th>
<th>Additional associated information</th>
</tr>
</thead>
<tbody>
<tr>
<td>29°C</td>
<td></td>
</tr>
<tr>
<td>120m – 25°C</td>
<td>100m = 1% surface illumination</td>
</tr>
<tr>
<td>150m – 24-20°C</td>
<td>150m = c0.1% surface illumination</td>
</tr>
<tr>
<td>250m – 14-11°C</td>
<td><strong>Halimeda</strong> species found at 100m+</td>
</tr>
<tr>
<td>360m – 8-9°C</td>
<td></td>
</tr>
</tbody>
</table>

Table 5.6 Enewetak water temperatures (after Colin et al, 1986).

This temperature – depth relationship across the globe can be seen in Figure
5.27.
5.6.3.5 Comparison of algal genera with depth related versus latitudinally related temperature changes.

The optimal temperature range for growth of most *Halimeda* species is 27-29°C (Hillis-Colinvaux, 1980), but there are restricted *Halimeda* flora (e.g. in the Mediterranean, Bermuda and S. Japan) which shows that particular species have adapted to survive in temperatures of c20°C. Better adapted is *Udotea*: on the N. Carolina outer shelf (Schneider, 1976) *U. cyathiformis* is found at a depth of 23m. At this locality, the surface water temperature range is 6-8°C in winter up to 28°C in the summer months (Hillis-Colinvaux, 1986). Water temperature at the lower depth limit of *Halimeda* species growth range approaches what appears to be the lower tolerance level for the genus (20.6-24.4°C) (Hillis-Colinvaux, 1986).

Thus it can be seen that the depth at which the algae dwell can have an effect due to temperature differences from the surface. However, in Figure 5.27 it is shown that at both low and mid latitudes (areas of calcified green algal occurrence), at the range of depths possible for green calcified algal inhabitation the temperature does not fall below the surface water temperature limit for these algae. Most of the deeper occurrences of the Chlorophyta are within the very warm waters of the low latitudes. All the algal occurrences have been plotted with relation to the surface water temperatures of the locations as the depth related temperature differences are generally within the calcified algal tolerances and those areas with deep dwelling algae also have shallower genera as well.
5.6.3.6 Variation of algal calcification with temperature / depth

Calcification within calcified algae can vary (particularly in the Chlorophyta), especially close to the limits of their distribution. This affects their preservation potential in the fossil record. Most authors do not note the degree of calcification in present-day algae.

Not all Dasycladales and Halimedaceae calcify and those that do, calcify to different extents. 6 – 8% of all the known algal species, and 10% of green algae, develop a calcareous skeleton (Wray 1977 and Berger and Kaever 1992). Upon death, the Halimedaceae have easily disaggregated aragonitic needles in their skeleton (Halimedaceae such as *Pericillus* disaggregate straight to needles, while e.g. *Halimeda* segments first into ‘coarse sand sized’ parts composed of thallus segments and later can be further broken down into finer sediment) and in tropical lagoons these fragments make up 50-60% of all calcareous mud; compared to the Dasycladales whose skeletons disaggregate into isolated calcareous elements in the calcareous muds of lagoons and bays (Stockman et al., 1967; Berger and Kaever 1992).

Within the Dasycladales, ten out of a total of eleven genera are calcified, but to immensely varying amounts (Berger and Kaever, 1992 and Wray, 1977). This variable calcification is shown below (Table 5.7):

<table>
<thead>
<tr>
<th>Genus</th>
<th>Calcification extent</th>
<th>Fossilization potential</th>
<th>Other information</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neomeris</td>
<td>Very strong</td>
<td>Good</td>
<td></td>
</tr>
<tr>
<td>Cymopolia</td>
<td>Very strong</td>
<td>Good</td>
<td></td>
</tr>
<tr>
<td>Acetabularia</td>
<td>Moderate to strong</td>
<td>Good</td>
<td>Tropical and subtropical distribution – genera of heavy or very heavy calcification are cosmopolitan, others are more regional in distribution.</td>
</tr>
<tr>
<td>Polyphysa</td>
<td>Moderate to strong</td>
<td>Good</td>
<td>Tropical and subtropical distribution – genera of heavy or very heavy calcification are cosmopolitan, others are more regional in distribution.</td>
</tr>
<tr>
<td>Chalmasia</td>
<td>Moderate to strong</td>
<td>Good</td>
<td>Tropical and subtropical distribution – genera of heavy or very heavy calcification are cosmopolitan, others are more regional in distribution.</td>
</tr>
<tr>
<td>Halicoryne</td>
<td>Moderate to weak</td>
<td>Moderate</td>
<td>Due to intracellular calcification.</td>
</tr>
<tr>
<td>Acicularia</td>
<td>Moderate to weak</td>
<td>Moderate</td>
<td>Due to intracellular calcification.</td>
</tr>
<tr>
<td>Bornetella</td>
<td>Moderate to weak</td>
<td>Moderate to poor</td>
<td></td>
</tr>
<tr>
<td>Dasycladus</td>
<td>Weak to none</td>
<td>Poor</td>
<td>No use in this study.</td>
</tr>
<tr>
<td>Batophora</td>
<td>Weak to none</td>
<td>Poor</td>
<td>No use in this study.</td>
</tr>
<tr>
<td>Chlorocladus</td>
<td>None</td>
<td>Very poor</td>
<td>No use in this study.</td>
</tr>
</tbody>
</table>

Table 5.7 Dasycladales calcification (after Berger and Kaever, 1992)
This table shows maximum relative calcification - all algae can calcify less than normal in sub-optimal conditions.

5.6.4 Algal biomineralization

Biomineralized organisms were assigned by Lowenstam (1981) to one of two types:

“Organic matrix-mediated” - where crystallization occurs on an organic framework (this is mainly the case with animals).

“Biologically induced” - where there is bulk extracellular and/or intercellular mineral formation without the presence of organic matrices (this was stated as the case for some bacteria and various green and brown algae).

This fundamental distinction between biologically induced and matrix-mediated biomineralization has been questioned (Simkiss, 1986) but this concept continues to be widely used.

Algal calcification has been attributed to the reduction of CO₂ in the seawater during photosynthesis (Lowenstam, 1981).

Simkiss (1986), explains “biologically induced” mineralization as due to carbon dioxide fixation where the primary reaction is:

\[
\text{CO}_2 + 2\text{H}_2\text{A} \rightarrow (\text{CH}_2\text{O}) + \text{H}_2\text{O} + 2\text{A}
\]

(In photosynthesis \text{H}_2\text{A} = \text{water}, and \text{A} = \text{oxygen}, in non-oxygenic photosynthesis \text{H}_2\text{A} = \text{inorganic sulphur compound or an organic compound, and \text{A} = oxidized product.}

The removal of CO₂ from (sea) water containing calcium bicarbonate leads to the precipitation of CaCO₃ (Simkiss, 1986) via:

\[
\text{Ca}^{++} + 2\text{HCO}_3^- \rightleftharpoons \text{CaCO}_3 \downarrow + \text{H}_2\text{O} + \text{CO}_2
\]

(Stark et al, 1969).

Thus, photosynthetic precipitation is caused by the removal of CO₂ and bicarbonate during photosynthesis and leads to a raised pH and CaCO₃ precipitation. This simple chemical action cannot be the sole mechanism of calcification for:
1. calcified algae grow next to uncalcified algae,
2. calcified algae, such as *Halimeda*, have uncalcified joints,
3. there can be algal calcification without the presence of light.

(Jensen et al, 1985).

The first of these problems could be accounted for by the absence in these algae of additional requirements such as diffusion limitation or surface nucleation (Simkiss, 1986). Borowitzka (1989) suggested that most marine macrophytes are most probably uncalcified because CaCO₃ nucleation is inhibited by organic extracellular products. This may be an evolutionary step to increase photosynthetic rate via the loss of a diffusion and light barrier by-product of photosynthesis. This may also be relevant to the second of the above factors.

The problem of calcification without light is more enigmatic. Most algae are adversely affected by the loss of light, e.g. in the Dasycladales, *Acetabularia acetabulum* mainly calcifies in very well lit localities – however in laboratory cultures, they tend not to calcify. This may in part be due to the light wavelength (DeCastro, 1997). The problem of amount of light, while intrinsically linked with depth (as is temperature), needs further investigation to elucidate this problem.

The evolution of calcification in algae is polyphyletic and very diverse (Pentecost, 1991) down to the genus level. The style and form of calcification is varied amongst the Chlorophyta. All calcareous green algae deposit CaCO₃ extracellularly, but in *Halimeda*, calcification is within the intercellular space, while in other Halimedaceae (such as *Udotea*, *Penicillus* and *Rhipocephalus*) it is in an organic ‘sheath’ overlying the cell wall (Borowitzka, 1986). The process itself, can differ; in *Halimeda*, alkalinization during CO₂ removal favours the precipitation of aragonite (this is the same with *Cymopolia*, *Neomeris* and some *Udotea* species) whereas the process is different in *Acetabularia*, *Rhipocephalus* and *Penicillus* (Pentecost, 1991).

The calcification, as stated, is dependant upon photosynthetic CO₂ (or HCO₃⁻) uptake and in seawater (normal 35% salinity) this is:
\[
\begin{align*}
\text{CO}_2 + \text{H}_2\text{O} & \leftrightarrow \text{H}^+ + \text{HCO}_3^- \leftrightarrow \text{H}^+ + \text{CO}_3^{2-} \\
6.00 & \quad 10.89 \\
(pK_1) & \quad (pK_2)
\end{align*}
\]
(Borowitzka, 1986)

It is likely that, for at least some of the Chlorophyta, there is another mechanism other than CO$_2$ uptake in operation (Borowitzka, 1986). In *Halimeda* the segments decrease their growth rate with age, but become progressively more calcified, even though the rate of calcification is decreased from the rate of younger sections (Borowitzka and Larkum, 1976 and 1977). It appears that after the initial calcification in the pilose layer, these CaCO$_3$ crystals act as crystallization nuclei for more precipitation of calcium carbonate; this is supported by high calcification rates in plants that are light starved or even dead (Borowitzka and Larkum, 1976).

This calcification occurrence can be related to environmental factors, as calcified algae are not found in waters that are not hypercalcified with respect to CaCO$_3$ minerals (Pentecost, 1991; Stanley and Hardie, 1998) – i.e. 9-10 times oversaturated (as found in warm marine waters) in contrast with the normal two times oversaturation (Riding, pers. comm.). As well, in all the algae that have been studied for calcification, the calcification occurs in association with organic matter, primarily polysaccharide (Pentecost, 1991).

Coralline algae, in contrast, have a different calcification process that is unique to them; it is a two stage process involving a tangential calcite deposition followed by a radial calcite deposition (Bosence, 1991). Coralline algae are at present the most consistently and heavily calcified group of red algae with high Mg-calcite precipitated within most walls (Bosence, 1991). This heavy calcification of corallines is the only example of calcification being an apparent advantage in the algae as it affords some protection against grazers (Borowitzka, 1989). It is also this well controlled, heavy intracellular (inside the cell-wall) site of CaCO$_3$ nucleation (which is unique amongst the benthic algae to the Rhodophyta) that may be the reason behind their wide environmental distribution (Riding, in press a).

There is evidence that the calcification process in algae is more sensitive to adverse environmental conditions than to photosynthesis (Goreau, 1963). One such
factor which appears to affect chlorophyte calcification (as well as photosynthesis)
rate is pH. In *Halimeda tuna*, the effect of altering pH can be seen to change the rates
as follows:

At pH 6.3 - high photosynthesis rate and very low calcification rate.
At pH 6.5-8.2 - a direct relationship between photosynthesis and calcification
rates.
At pH >8.5 - calcification rate is enhanced and the photosynthesis rate is
inhibited.

In summary, the extent of calcification has been seen to vary with such factors as
age of the individual, taxonomy and the environment (Hillis, 1991).

CaCO₃ coating of parts of the algal thallus can be of different types. In
Dasycladales for example, calcification can be either internal or external (DeCastro
1997); the CaCO₃ ‘body’ formed by this process is known as a skeleton (see Figure
5.28). DeCastro (1997) states:

“...the skeleton can be continuous or discontinuous, uniform or not, both in longitudinal and
transversal directions; its thickness can change from a thin calcareous film which partially or totally
coats the thallus surface, to a massive body in which the thallus elements are completely embedded.”

Fig. 5.28 Different degrees of calcification in Dasycladales skeletons (from Berger and Kaever 1992).

- Complete calcification of the space between the laterals; b – Thick sleeve-like calcification and
  incrustation of the main axis and laterals; c – Moderate sleeve-like calcification without incrustation of
  main axis and laterals; d – Weak sleeve-like calcification with prominent lime formation at the level of
  the verticils; e – Roll-shaped calcification restricted to the verticils gives rise to annular or perannular
  sediments; f – Calcification restricted to a more or less thin coating enclosing the gametangia.
The skeleton of all calcareous algae may consist of magnesium calcite or aragonite, see Table 5.8, with additional accessoriel elements. The amount of magnesium present in the skeleton is dependant upon the temperature, which allows palaeoecological references to be made (Berger and Kaever 1992).

<table>
<thead>
<tr>
<th>ARAGONITIC CALCAREOUS ALGAE</th>
<th>CALCITIC CALCAREOUS ALGAE</th>
</tr>
</thead>
<tbody>
<tr>
<td>E.G.</td>
<td>E.G.</td>
</tr>
<tr>
<td><em>HALIMEDA</em> (Halimedaceae)</td>
<td><em>LITHOTHAMNIUM</em> (Crustose Corallinaceae)</td>
</tr>
<tr>
<td><em>ACETABULARIA</em> (Dasycladales)</td>
<td><em>LITHOPHYLLUM</em> (Crustose Corallinaceae)</td>
</tr>
<tr>
<td><em>GALAXAURA</em> (Chaetangiaceae)</td>
<td><em>CORALLINA</em> (Articulated Corallinaceae)</td>
</tr>
<tr>
<td><em>PENICILLUS</em> (Halimedaceae)</td>
<td><em>AMPHIROA</em> (Articulated Corallinaceae)</td>
</tr>
<tr>
<td><em>LIGORA</em> (Nemaliaceae)</td>
<td><em>BOSSEA</em> (Articulated Corallinaceae)</td>
</tr>
<tr>
<td><strong>c 1% Mg carbonate</strong></td>
<td><strong>7 to 30% Mg carbonate</strong></td>
</tr>
</tbody>
</table>

Table 5.8 Mg amounts in different forms of algal calcite (info. from Chave 1954).

This relationship of magnesium and temperature in calcitic algal skeletons can be shown thus in Figure 5.29:

![Fig. 5.29 Relationship between water temperature and Mg content in calcareous algae (Chave 1954).](image)

Use of magnesium as a palaeothermometer is, of course, dependant on the calcite of the skeleton being well-preserved. Fossil algae species show substitution of original crystalline characters by diagenetic processes (normally recrystallization – polymorphic transformation) (DeCastro 1997).
5.6.4.1 Calcification change with latitudinally related temperature change.

Calcified green algae are restricted latitudinally due to water temperature decline with increasing latitude. As the latitude increases, the number of taxa found decreases and it is possible to see some 'stress-environment' phenomena, therefore, aragonitic calcification appears temperature dependant (Elliott, 1984). It is an obvious thought that calcification (a process associated with temperature) would be adversely affected as the organisms habitat is situated progressively polewards of the equator. Elliott (1977 and 1984) states that this situation is not the case unless decalcification is already characteristic of the taxon. This may have some validity with Dasyycladales (e.g. Acetabularia mediterranea in the Mediterranean Sea is only partially and thinly calcified after two or three years growth, which is probably an adaptation to the seasonal growth environment (Elliott, 1984)), however it is definitely not the case with the Halimedaceae. This, the dominant group of modern calcareous chlorophytes, is well calcified under normal conditions and does not normally show de-calcifying tendencies. Conditions in some marginal regions which are home to Halimeda are seasonally similar to those in the tropics, but not for the whole year, for example, part of the Mediterranean falls within the 24°C isotherm, but the corresponding isocryme is only 12 or 13°C. It is interesting to note that Mediterranean examples appear to be as heavily calcified as is typical for most Halimeda spp. However, Penicillus has a species in the Mediterranean and this is a 'reduced' variety which may be a response to the sub-optimal conditions encountered (Elliott, 1984). Having said this, when located in other marginal habitats (e.g. the Lacapede Shelf, SW Australia), Halimeda grows with a marked decrease in calcification, to the extreme of being totally uncalcified (James et al, 1999). This change from fully calcified to being uncalcified (although not a common occurrence) seems to occur over a short latitudinal distance of a few degrees, so it may have appeared, without a full global distribution map, that there was no period of calcification change. There does not appear to be any recognisable difference between the marginal environments which produce fully calcified and non-calcified Halimeda (the Mediterranean and SW Australia respectively), and the reasons for the calcification variation are unknown. The sharp, small extent of variably calcified algae would probably not be preserved in the fossil record.
5.6.4.2 Calcification change with depth related temperature change.

Dasycladales calcify less with increasing water depth. It is reasonable to assume that decreasing light quantity and quality and/or lower water temperature are responsible for this (Berger and Kaever, 1992).

Halimedaceae have a more complicated relationship as shown in Table 5.9:

<table>
<thead>
<tr>
<th>% CaCO₃</th>
<th>Halimeda. sp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Decrease with depth</td>
<td>simulans</td>
</tr>
<tr>
<td>Decrease with depth</td>
<td>goreauii</td>
</tr>
<tr>
<td>Same with depth</td>
<td>tuna</td>
</tr>
<tr>
<td>Increase with depth</td>
<td>discoidea</td>
</tr>
<tr>
<td>Increase with depth</td>
<td>gracilis</td>
</tr>
<tr>
<td>Increase with depth</td>
<td>opuntia</td>
</tr>
<tr>
<td>Increase with depth</td>
<td>copiosa</td>
</tr>
</tbody>
</table>

Table 5.9 Calcification changes in some Halimeda species with depth (Hillis, 1991).

On the Great Barrier Reef, an unusually large and heavily calcified form of H. gracilis, a species normally a minor, fragile component of shallower meadows, is found below 50m water depth (Drew and Abel, 1988). This is not unusual as Halimeda is exceptional among the calcareous Chlorophyta in that some species can be more heavily calcified in deep than in shallow water, although this may be recognition of a relative increase due to a decreased amount of organic matter rather than an increased calcification (Goreau, 1963). This effect is the opposite of that seen in other calcareous Halimedaceans, such as Penicillus, Udotea and Rhipocephalus, which are invariably less calcified in deeper water. The possible reason for this greater than normal calcification of deep Halimeda forms is Halimeda’s ability to calcify more rapidly in darkness than in light (Goreau, 1963). It is worth noting that the other calcareous Halimedaceae, namely Tydemania, is purely a deep water dweller – it possesses an ecological adaptive advantage to low-light levels (in that its entire thallus is potentially photosynthetic) (Gilmartin, 1966).

However, it is not just a greater relative calcification of the deeper dwelling algae that separates them from the shallower water versions of their species; the algae existing under reduced light conditions often do not have the same morphological structure of the same species growing in shallower water (Gilmartin, 1960). The most characteristic change is an attenuated form associated with lighter pigmentation (etiolation). One species in which this change was particularly noticed (at Enewetak Atoll) was Halimeda monile - at shallower levels this species was characteristically
short, with heavily calcified forms rising by a short caulescent base from a heavy holdfast with numerous “branches”. With an increase in depth, the “branches” became fewer in number, smaller in relative size and more lightly calcified, while the plant in general became taller and more spindly. The pigmentation can be found to grade from dark green in the shallow water to light green at depth (Gilmartin, 1960). This lighter calcification contradicts Goreau’s statement of increasing calcification with depth, due to species differentiation of response, see above Table 5.9 for further examples.

These morphological changes are occurring at depth, not because of temperature change but due to decreased light levels. Temperature changes across latitudes at the surface waters do not herald adaptive morphological alterations.

5.6.5 Relationship of temperature and calcification regarding algae.

Thus it is readily noticed that temperature difference (regardless of whether it is vertically / depth or latitudinally induced) has an effect upon the calcification ability of algae. A problem arises when that effect is quantified – a latitudinally induced temperature loss tends to lead to a lessening of the calcification extent after crossing a minimum threshold value until the flora is left uncalcified at the extreme occurrences. However a depth induced temperature loss can, in some plants, produce an increase in overall calcification, or similarly to latitudinal change, may in other plants produce a calcification decrease.

In chemical terms, increasing heat shifts the equilibrium of the calcification equation further to the CaCO₃ end and away from the CO₂, hence more CaCO₃ is formed in the water (and this leads to more precipitation). Also, increasing pressure (in this case produced via depth) will suppress CaCO₃ production and increase CO₂ in the water, which should result in less calcification with increasing depth. However at a maximum algal inhabitable depth (light controlled) of 150m, there is no real pressure related influence. Of course, this does not take into account any organic influences on CaCO₃ precipitation. Overall, the depth problem may just be a situation of chemical physics – in an area of overall high CaCO₃ solution, it could be possible for precipitation from the water column to be easier at the more reduced temperatures found at relatively greater depth.
The general temperature related restriction of the distribution of
Dasycladaceae to the more ‘tropical’ / warm-water areas has been related to their
calcification being due to the removal of CO₂ from the water during photosynthetic
activity. Because CaCO₃ solubility increases with decreasing temperature and rising
partial pressure of CO₂, the result is that it is most easily precipitated in warm waters
(Beadle, 1988). In this respect low temperature has a “disadvantageous effect on the

5.7 Conclusions

The results show that the modern latitudinal distribution of the calcareous
Chlorophyta is that both the Dasycladales and the Halimedaceae are similar in their
distribution and that this extends well outside of the tropics into the warm-temperate
realm (up to the boundary with cold-temperate areas).

The overall temperature limit of distribution of these groups can be
summarized in Table 5.10:

<table>
<thead>
<tr>
<th>Chlorophyta</th>
<th>Isocrymes (°C)</th>
<th>Calcified</th>
<th>Non-calcified</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dasycladaceae</td>
<td></td>
<td>12</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>e.g. New Zealand (Berger and Kaever, 1992)</td>
<td>e.g. Mediterranean (Cinelli, 1979)</td>
<td></td>
</tr>
<tr>
<td>Halimedaceae</td>
<td>12</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>e.g. Mediterranean (Airoldi et al, 1995) and Japan (Gilmartin, 1966)</td>
<td>Limit variable dependant on local area, e.g. non-calcified in area of 15°C (SW Australia – James et al, 1999), but calcified in area of 12°C (Japan - Gilmartin, 1966)</td>
<td></td>
</tr>
</tbody>
</table>

Table 5.10 Modern calcareous green algae isocrymal distribution limits.

The limit of 12°C isocrymal, is the best value for the overall useful limit of
these floras as this appears globally standard in occurrence, is more prevalent in
observational analysis and is going to be the limit of fossil occurrences as
calcification is needed for preservation to occur. The extremes of latitude and
abundance of occurrences can be seen in Figures 5.30 and 5.31. Figure 5.32 shows the
calcified limit of distribution (with the superimposed factor of carbonate shelf extent
which is the reason for the algal limit in Brazil being at such a low latitudinal point).

The effect of depth is linked to, but not as important as temperature. Depth of
calcified green algae is limited and as such is minor in the temperature change. Depth
does start to have an effect upon the light availability and this produces a change in
which genera and species are found and can have effects upon their morphology.
Fig. 5.30 Calcareous Chlorophyta latitudinal ranges. (Latitudinal range expresses either N or S further extent.)

Degrees of latitude

Ecuador

Tropic 23.5°

Acetabularia

Polyphya

Cymopolia

Neomeris

Aiculicaria

Borneoflora

Halicorine

Chalmasia

Halmeda

Penicillus

Udotea

Tydemania

Rhipocephalus

Calcareous green algae genera

Halmedaceae

Dasycladales
but in fact reduced numbers from their original co-ordinates. Prediction of the age for the "prodigal" regions previously regarded as "filial" complements distribution. It can be seen that new inductive co-operators.

North - south contrast in numbers is probably due to competitive co-ordination and the resurging amount of applicable habitats. The graphics show the

Fig 5.3.1 Global temperature distribution of Haliimedaceae and Dasyacaridae occurences.

Chapter 5: Extant Algae Environmental Distribution
Chapter 6 Jurassic Algae Palaeobiogeographic Distribution

6.1 Aim

In order to obtain palaeoenvironmental data on the Jurassic, it is necessary to evaluate the spread of environmentally sensitive indicators – in this case calcareous algae.

The aim is to document the spatial distribution of Jurassic Western European calcareous marine algae by plotting the main groups: Dasycladales, Halimeda, Rhodophyta (mostly Solenoporaceae) and Gymnocodiaceae, as well as Cyanobacteria and Microproblematica commonly assigned to the algae.

This approach has been used, in limited application with particular respect to temperature by Mu (1993) for the Cretaceous (all benthic calcareous algae worldwide), Elliott (1977 and 1978) for the Jurassic (Dasycladales of Europe, N Africa and the Middle East), and Flügel (1985) for the Permian (also Dasycladales worldwide). Benthic calcareous algae provide excellent potential for regional palaeotemperature interpretation in shallow marine limestone sequences due to their temperature limitation, long geological range, and frequent abundance in these environments. The essential requirement is that their present-day temperature limits are reasonably well defined (see Chapter 5).

It is thought that the habitats and environmental requirements of Dasycladaeae and Halimeda have changed little overtime and that from the Jurassic their requirements have essentially not changed (Elliott, 1968, 1978, 1981 and Berger and Kaever, 1992). There has been a suggestion of possible changes in the Dasycladales over time (Elliott 1975, 1982, 1983, 1984) but this idea was later recinded (Elliott 1986) (see Chapter 4 for details and discussion).

6.2 Methodology

The approach to this part of the study was via fieldwork visits (see Chapter 3) and by the use of extensive literature available on the subject. A total of 144 sources in the literature were used in the construction of the fossil databases (see Appendix C).
including some major compilations of algal data such as Bassoulet et al (1978) and
Jaffrezo (1973b) for all of Europe, Bouroullec and Deloffre (1970) for southern
These data were thoroughly checked for systematic attributions (see Chapter 7). These
sources covered all of the Jurassic outcrops of a suitable nature in continental Europe.

This work covers a large number of Jurassic algae (see Table 6.1):

<table>
<thead>
<tr>
<th>Algal type</th>
<th>Number of genera</th>
<th>Number of species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dasycladales</td>
<td>61 (49.6%)</td>
<td>185 (57.9%)</td>
</tr>
<tr>
<td>Halimedaceae</td>
<td>11 (8.9%)</td>
<td>17 (5.3%)</td>
</tr>
<tr>
<td>Rhodophyta</td>
<td>8 (6.5%)</td>
<td>17 (5.3%)</td>
</tr>
<tr>
<td>Gymnocodiaceae</td>
<td>1 (0.8%)</td>
<td>3 (0.9%)</td>
</tr>
<tr>
<td>Cyanobacteria</td>
<td>16 (13%)</td>
<td>57 (17.8%)</td>
</tr>
<tr>
<td>Microproblematica</td>
<td>26 (21.1%)</td>
<td>42 (13.1%)</td>
</tr>
<tr>
<td>Total</td>
<td>123</td>
<td>321</td>
</tr>
</tbody>
</table>

Table 6.1 Jurassic algal numbers used in this work

All of this data makes this work arguably the most complete and up to date
European Jurassic algal compilation presently available.

6.3 Palaeobiogeographical distributions

6.3.1 Jurassic databases.

(See Appendix C)

These databases, which are subdivided as described in Chapter 2, are the basis
for the distribution maps and graphs and provide the raw collated data for the Jurassic
algal study.

6.3.2 Maps

There are two terminations of occurrence to be noted – furthest species extent
and furthest major species extent, the difference being:

- Furthest species extent – the furthest latitudinal extreme occurrence of an alga;
  this may be outside what would be recognised as the usual zone of occurrence
due to local favourable conditions superimposed on the regional trend.
• Furthest major species extent - the furthest latitudinal extreme occurrences of an alga which are in keeping with the edge of an algaly abundant realm and therefore is not necessarily the absolute furthest extreme occurrence.

N.B. It is possible that a site / some sites can be said to satisfy both conditions (i.e. in some cases the two extremes are the same).

The line of points joining the furthest major species extents together is the defining limit of normally calcifying flora (excepting weakly calcified individuals and those in localised conditions overprinting the regional trend). This defining limit has been said to be a temperature controlled one (Setchell, 1920). It will be possible to quantify this limit via direct comparison with the similar modern scenario (see Figure 8.13 in section 8.4.8.1 and Figure 9.2 in section 9.3).

6.3.3 Jurassic algae: palaeogeography

The Jurassic Chlorophyta are the most important algae for comparison with the modern data. This is because not only are the modern calcareous green algae temperature dependant, but also these algae (particularly the Dasycladales) were the most numerous Jurassic algal flora (see Table 6.1 above).

(See Figure 6.19 for a summary of Jurassic Chlorophyte distributions as well as Figures 6.1 to 6.18 for more detailed distribution representation of all Jurassic algae.)

Lower Jurassic

Dasycladaceae (Figure 6.2)

A number of species / genera are situated in the southern European countries (of todays tectonic setting – i.e. Spain, southern France, Italy and Yugoslavia to Greece). The furthest species and furthest major species extents are the same and the line of these occurs through the northeastern edge of Iberia and through mid France to northern Italy. There appears to be no spatial pattern to the abundance distributions in the area South of the limit line.

Halimedaceae (Figure 6.3)

Very poorly represented in the fossil record with a sparse occurrence in southern areas (Italy and Yugoslavia) and therefore there are insufficient datapoints to allow any analysis.
Chapter 6 Jurassic Algal Palaeoecographic Distribution

Fig. 6.4 Lower Jurassic 190MA Cyanobacterial distribution map

Legend

Fig. 6.4 Lower Jurassic 190MA Cyanobacterial distribution map

Map after Timewell 1998

Cambridge Paleomap

20°

11-19

6-10

3-5

1-2

numbers

species

20°N

30°N

45°N

Lower Jurassic 190MA
Map after Timiresev v.11
Cambridge paleomap

Chapter 6 Jurassic Algae Palaeoecological Distribution

John Adams PhD thesis
Fig. 6.15 Upper Jurassic + Cretaceous Gynnoecodiacaeae distribution map

Chapter 6 Jurassic-Neogene Palaeoecological Distribution

John Adams PhD thesis
The line in the west and proceeding to the east.

The line of lithology is discussed in detail in the text but can briefly be explained as most likely being due to current action, with old curvatures depressing.

(Other Smith et al., 1994). The line cut the curved, not the line of lithology due to the curvature of the Earth. The curve of the calcareous external line is from the opening calcrete.

The number of species at the locality with different data points is the elevation of calcification, which points out the paleodepression.

Fig. 6.19 Jurassic Cycadophyte distribution on paleogeographic reconstructions (maps after Thomas and others, 1998) Scale of climate.

a calcification external line
Not enough data points to produce

Upper Jurassic 190Ma
Mid Jurassic 170Ma
Lower Jurassic 150Ma

Halimedaceae
Dasycladaceae

Chapter 6 Jurassic Algae Paleobiogeographic Distribution

John Adams PhD Thesis
Other groups

Calcified Cyanobacteria (Figure 6.4) and Microproblematica (Figure 6.5) are more widely present, occurring in southern areas, but are never seen to be abundant.

Overall

All groups are restricted to areas South of the Dasycladalean northern limit.

Mid Jurassic

Dasycladaceae (Figure 6.7)

A more sparse and dispersed floral arrangement than shown by this group for the Lower Jurassic. A tentative furthest major species extent line is denoted through northwestern Iberia, across northern France and into Belgium. This leaves some occurrences in the English Cotswolds as the furthest species extents – outside of the main setting, they should be localised occurrences with weak calcification in sub-optimal settings and work by Elliott (1982, 1984) seems to support this assumption. The abundance of these algae in the more southerly areas of their distribution range is less than in the previous series of the Jurassic. Also, the location of the sites (which are numerically less), are spread further apart than before.

Halimedaceae (Figure 6.8)

As with the Lower Jurassic, Halimedaceae are poorly represented and few datapoints do not permit an accurate furthest major species extent line to be produced. Nonetheless, the distribution of Halimedaceae shows broad similarities with the Dasycladales of this time period.

Other groups

Rhodophyta (Figure 6.9) are sparsely present but widely distributed in western areas, from Italy in the South to southern England in the North. Calcified Cyanobacteria (Figure 6.10) are less widely recorded than in the Early Jurassic, but do occur further North, in northern France. Microproblematica (Figure 6.11) are sparsely present and again widely distributed.

Overall

Temperature-limited groups such as the Dasycladaleans show expansion northwards in central areas (France and England) compared with the Early Jurassic.
Upper Jurassic

Dasycladaceae (Figure 6.13)

A very large flora is present in the Upper Jurassic and is prevalent across southern and mid Europe. There is a very strong and evident furthest major species extent line in a similar position to that in the Mid Jurassic, namely NW. Iberia, N. France and S. Germany to S. Poland. The furthest species extents are North of this and are justifiably few in number – again it is surmised that their existence is weakly calcified in sub-optimal and in localised conditions and this is overprinted on the regional trend. South of this line there is no evident spatial pattern of abundance variation.

Halimedaeeae (Figure 6.14)

A larger population of Halimedaeeae is recognised in the Upper Jurassic. The furthest major species extent line can be drawn through mid Iberia (diagonally), mid France and Switzerland to S. Poland. This would appear to be the same as the furthest species extent. The Halimedaeeae that were described from NW. Scotland (Hudson J.D., 1970 and Dragastan, 1985, 1987 and 1989a) have been wrongly identified and should be recognised as other groups such as Cyanobacteria (see changes to Dragastan taxonomy in Systematics – Section 7.4). The line is at a ‘lower’ (i.e. more southerly) level than the Dasycladaceae line. This may be erroneous due to lack of data, and in reality (as is the case in the modern day) it could be expected that both groups would have a similar termination level. Alternatively it may be that this line is ‘lower’ than it should be due to minimal calcification of Halimedaeeae at the margins of their territory (such as in the modern day at the Lacapede Shelf, SW Australia (James et al, 1999)) which would result in a lack of fossilization of the algae that were present in the Jurassic.

Other groups

Gymnocodiaceae (Figure 6.15) are widely distributed longitudinally but restricted latitudinally to the central area of mainland Europe. Rhodophyta (Figure 6.16) are widely distributed and moderately abundant across the area of study. Calcified Cyanobacteria (Figure 6.17) are abundant and widely distributed in a latitudinally central zone, falling in occurrence North of this area. Microproblematica (Figure 6.18) are similar in distribution (with interesting northern occurrences – see
Systematics Section 7.5 for discussion).

Overall

Temperature limited marine groups (Chlorophyta and Gymnocodiaceae) are very scarce North of a line passing through central to northern France. Cyanobacteria and Rhodophyta are both better represented across all of Europe.

Figure 6.20 summarises the Jurassic calcareous algae distributions and their extrapolated limits shown in Figures 6.1 to 6.18.

6.3.4 Jurassic algae: diversity and palaeolatitude

The graphs of the Jurassic phycological distribution show some sets of trends:

- They show an increase in diversity from the Tropics to the subtropics – this is in fact a false increase and is due to only Europe being studied in the analysis, in the modern European tectonic setting, there is less landmass in southern Europe than in the northern part, and therefore a lesser amount of field sites / outcrops yielding algae for analysis. In reality (if global Jurassic algal occurrences were used) the trend for this section of the graph should be a slight decrease or be relatively similar / constant. This real pattern is seen in modern-day organisms (Figure 6.21):

![Graph showing latitudinal gradients in richness of various marine taxonomic groups showing decreasing diversity with increasing latitude](image)

Fig. 6.21 Latitudinal gradients in richness of various marine taxonomic groups showing decreasing diversity with increasing latitude (after information in Brown, 1988).
FIG. 6.22 Lower Jurassic European algal diversity / palaeolatitude graph
Fig. 6.24 Lower Jurassic European Haliimedaceae diversity / palaeolatitude graph.
Palaeolatitude

Diversity

Fig. 6.27 Mid Jurassic European algal diversity / palaeolatitude graph
Fig. 6.31 Mid Jurassic European Cyanobacteria diversity / paleoelevation graph
Fig. 6.33 Upper Jurassic European algae diversity / palaeolatitude graph.
Fig. 6.35 Upper Jurassic European Haliimedaceae diversity / palaeolatitude graph
Fig. 6.36 Upper Jurassic-European Cymnocladaceae Diversity / Paleolatitude graph.
Fig. 6.38 Upper Jurassic European Cyanobacteria diversity / palaeolatitude graph.
Fig. 6.39 Upper Jurassic European Micropodoblemata diversiety / paleoecolatude graph
Fig. 6.4.1 Jurassic European Haliimedaceae diversity / palaeolatitude graph

Upper Jurassic □ Mid Jurassic ▼ Lower Jurassic ▲
• There is a steep decline in abundance at a particular point – a sudden termination in occurrences. This would seem to be true in accordance with modern calcareous chlorophyte distributions and abundance. This point is normally (in the modern-day) associated with a water temperature (isocrymal) limit – i.e. is the divide between the usual environment and marginal occurrences.

• Specifically, all the ages of individual groups show two interesting trends:
  1. A dramatic secular increase in diversity in the Upper Jurassic.
  2. A moderate spatial increase in latitudinal extent in the Upper Jurassic.

• There is an interesting set of furthest extent trends through time (see Table 6.2 and discussion below):

<table>
<thead>
<tr>
<th>Algal type</th>
<th>Approximate northern latitude of furthest extent</th>
<th>Discussion</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Lower</td>
<td>Mid</td>
</tr>
<tr>
<td>Dasycladales</td>
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<td>36°</td>
</tr>
<tr>
<td>Halimedaceae</td>
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<td>35°</td>
</tr>
<tr>
<td>Rhodophyta</td>
<td>-</td>
<td>35°</td>
</tr>
<tr>
<td>Gymnocodiaceae</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Cyanobacteria</td>
<td>35°</td>
<td>34°</td>
</tr>
<tr>
<td>Microproblematica</td>
<td>39°</td>
<td>33°</td>
</tr>
</tbody>
</table>

Table 6.2 Algal extent progression through the Jurassic.

The distribution of the main algal groupings in the three subperiods of the Jurassic have been plotted on reconstructions of the tectonic and geographic settings of Europe at the times involved (see Figure 6.20). From this, a series of graphs of the diversity of these algal groupings has been produced. The graphs show a diversity and palaeolatitude trend that can show how the abundance changes with latitude. The trend of the graphs can tell us about the overall environmental response of the groups in question as can be seen in Figure 6.45:
The five generalized cartoon graphs seen in Figure 6.45 show the possible trends that can be seen in the diversity decrease of an organism with a palaeolatitude increase. These trends are:

- Declining rate of decline with increasing latitude;
- Low diversity initially and with a slow, steady decline;
- Increasing rate of decline with increasing latitude;
- General, linear decrease with increasing latitude;
- Rapid decline at a specific latitude.

These five types of trend in the modern day are caused by various factors and so when seen in fossil organism plots they can help indicate ancient occurrences of these factors and help to provide explanations. In light of this, the graphs that comprise Figures 6.22 to 6.44 are discussed below:
Figure 6.22 Lower Jurassic European algae diversity / palaeolatitude graph.
*Description:* All available algae plotted as type for the Lower Jurassic period. For the majority of the algal types (Halimedaceae, Cyanobacteria and Microproblematica) there is not enough data for any pattern to be substantiated, but the Dasycladaceae have a good diversity for this time period. *Interpretation:* This graph shows the European Lower Jurassic calcareous algae against each other in terms of diversity and palaeolatitudinal spread. Their individual interpretations can be seen below for figures 6.23 to 6.26.

Figure 6.23 Lower Jurassic European Dasycladales diversity / palaeolatitude graph.
*Description:* The Dasycladales of the Lower Jurassic have a good diversity, abundance and palaeolatitudinal spread for this period of time. They display a rapid fall in diversity at about the 35° N mark which is also around their maximum occurrence in palaeolatitude. The data trend is a mix of a general, linear decrease in diversity with increasing palaeolatitude and a rapid decline in diversity at a specific palaeolatitude. *Interpretation:* The trend of decline shows a general decline in numbers which is expected with a latitudinal increase and according climate change is encountered, but the change to a sudden decline at a specific latitude is evidence of a limiting latitudinal barrier to their habitation – probably a climatologically induced limit.

Figure 6.24 Lower Jurassic European Halimedaceae diversity / palaeolatitude graph.
*Description:* The Halimedaceae of the Lower Jurassic have a low diversity with their maximum palaeolatitude occurrence being at about 28° N. There is not enough data on this group at this time to tell much from their occurrence in terms of trends. There are not enough data points to produce a representative trend. *Interpretation:* The lack of data points means that no interpretation can be made from this indistinct trend.

Figure 6.25 Lower Jurassic European Cyanobacteria diversity / palaeolatitude graph.
*Description:* The Cyanobacteria of the Lower Jurassic have a low diversity with their maximum palaeolatitude occurrence being at about 35° N. There is not enough data on this group at this time to tell much from their occurrence in terms of trends. The data trend is a partial mix of a general, linear decrease in diversity with increasing palaeolatitude and a rapid decline in diversity at a specific palaeolatitude – mostly the latter. *Interpretation:* The trend of decline begins to show a general decline in
numbers which would be expected with a latitudinal increase and according climate change is encountered, but the change to a rapid decline at a specific latitude shows evidence that a limiting latitudinal barrier to their habitation existed – this was probably a climatologically induced limit.

**Figure 6.26** Lower Jurassic European Microproblematica diversity / palaeolatitude graph. *Description:* The Microproblematica of the Lower Jurassic have a low diversity with their maximum palaeolatitude occurrence being at about 39° N. There is not enough data on this group at this time to tell much from their occurrence in terms of trends. There are not enough data points to produce a representative trend. *Interpretation:* The lack of data points means that no interpretation can be made from this indistinct trend.

**Figure 6.27** Mid Jurassic European algae diversity / palaeolatitude graph. *Description:* All available algae plotted as type for the Mid Jurassic period. The algae have a low to moderate diversity for this time period. *Interpretation:* This graph shows the European Mid Jurassic calcareous algae against each other in terms of diversity and palaeolatitude spread. Their individual interpretations can be seen below for figures 6.28 to 6.32.

**Figure 6.28** Mid Jurassic European Dasycladales diversity / palaeolatitude graph. *Description:* The Dasycladales of the Mid Jurassic have a low diversity for this period of time. They display a fall in diversity at about the 36° N mark which is around their maximum palaeolatitude occurrence. The data trend is one of a rapid decline in diversity at a specific palaeolatitude. *Interpretation:* The trend of a rapid decline in diversity at a specific latitude shows evidence of a limiting latitudinal barrier to algal habitation existed – probably a climatologically induced limit.

**Figure 6.29** Mid Jurassic European Halimedaceae diversity / palaeolatitude graph. *Description:* The Halimedaceae of the Mid Jurassic have a low to moderate diversity with their maximum palaeolatitude occurrence being at about 35° N. There are not enough data points to produce a representative trend. *Interpretation:* The lack of data points means that no interpretation can be made from this indistinct trend.

**Figure 6.30** Mid Jurassic European Rhodophyta diversity / palaeolatitude graph. *Description:* The Rhodophyta of the Mid Jurassic have a low diversity with their maximum palaeolatitude occurrence being at about 35° N. The data trend is a mix of a
general, linear decrease in diversity with increasing palaeolatitude and a rapid decline in diversity at a specific palaeolatitude. **Interpretation:** The trend of decline shows a general decline in numbers which is expected with a latitudinal increase and according climate change is encountered, but the change to a sudden decline at a specific latitude is evidence of a limiting latitudinal barrier to their habitation – probably a climatologically induced limit.

**Figure 6.31** Mid Jurassic European Cyanobacteria diversity / palaeolatitude graph. **Description:** The Cyanobacteria of the Mid Jurassic have a low diversity with their maximum palaeolatitude occurrence being at about 34° N. The data trend is one of a declining rate of decline in diversity with increasing palaeolatitude. **Interpretation:** This trend shows the initial rapid decline in numbers of diversity as a group of organisms reaches the limits of its occurrence, but the declining rate of decline with increasing palaeolatitude is evidence of some of the species in this group starting to adapt to the conditions beyond that coped with by their cousins.

**Figure 6.32** Mid Jurassic European Microproblematica diversity / palaeolatitude graph. **Description:** The Microproblematica of the Mid Jurassic have a moderate diversity with their maximum palaeolatitude occurrence being at about 33° N. The data trend is one of a general, linear decrease in diversity with increasing palaeolatitude. **Interpretation:** The trend of decline shows a general decline in numbers which is expected with a latitudinal increase and according climate change encountered.

**Figure 6.33** Upper Jurassic European algae diversity / palaeolatitude graph. **Description:** All available algae plotted as type for the Upper Jurassic period. The algae range from having a low to a high diversity for this time period, some across many locality occurrences. **Interpretation:** This graph shows the European Upper Jurassic calcareous algae against each other in terms of diversity and palaeolatitudinal spread. Their individual interpretations can be seen below for figures 6.34 to 6.39.

**Figure 6.34** Upper Jurassic European Dasycladales diversity / palaeolatitude graph. **Description:** The Dasycladales of the Upper Jurassic have a very high diversity over many sites with their maximum palaeolatitude occurrence being at about 39° N following a very rapid fall in diversity from 38° N. The data trend is one of a rapid decline in diversity at a specific palaeolatitude. **Interpretation:** The trend of a rapid
decline in diversity at a specific latitude shows evidence of a limiting latitudinal barrier to algal habitation existed – probably a climatologically induced limit.

**Figure 6.35** Upper Jurassic European Halimedaceae diversity / palaeolatitude graph. 
*Description:* The Halimedaceae of the Upper Jurassic have a moderate diversity with their maximum palaeolatitude occurrence being at about 36° N. The data trend is one of a general, linear decrease in diversity with increasing palaeolatitude.

*Interpretation:* The trend of decline shows a general decline in numbers which is expected with a latitudinal increase and according climate change encountered.

**Figure 6.36** Upper Jurassic European Gymnocodiaceae diversity / palaeolatitude graph. 
*Description:* The Gymnocodiaceae of the Upper Jurassic have a low diversity with their maximum palaeolatitude occurrence being at about 34° N with most less than 30.5° N. There are not enough data points to produce a representative trend.

*Interpretation:* The lack of data points means that no interpretation can be made from this indistinct trend.

**Figure 6.37** Upper Jurassic European Rhodophyta diversity / palaeolatitude graph. 
*Description:* The Rhodophyta of the Upper Jurassic have a low diversity but cover many sites with their maximum palaeolatitude occurrence being at about 40° N. The data trend is a mix of a general, linear decrease in diversity with increasing palaeolatitude and a rapid decline in diversity at a specific palaeolatitude.

*Interpretation:* The trend of decline shows a general decline in numbers which is expected with a latitudinal increase and according climate change is encountered, but the change to a sudden decline at a specific latitude is evidence of a limiting latitudinal barrier to their habitation – probably a climatologically induced limit.

**Figure 6.38** Upper Jurassic European Cyanobacteria diversity / palaeolatitude graph. 
*Description:* The Cyanobacteria of the Upper Jurassic have a very high diversity with their maximum palaeolatitude occurrence being at about 42° N after a drop in diversity at about 33° N. The data trend is one of a declining rate of decline in diversity with increasing palaeolatitude. *Interpretation:* The trend of decline shows a general decline in numbers which is expected with a latitudinal increase and according climate change encountered.

**Figure 6.39** Upper Jurassic European Microproblematica diversity / palaeolatitude graph. 
*Description:* The Microproblematica of the Upper Jurassic have a moderate
diversity with their maximum palaeolatitude occurrence being at about 42° N after a
drop in diversity across about 30 to 35° N. The data trend is one of a rapid decline in
diversity at a specific palaeolatitude followed by a declining rate of decline in
diversity with increasing palaeolatitude. *Interpretation:* This trend shows the initial
rapid decline in numbers of diversity as a group of organisms reaches the limits of its
occurrence, but the declining rate of decline with increasing palaeolatitude is evidence
of some of the species in this group starting to adapt to the conditions beyond that
coped with by their cousins.

**Figure 6.40** Jurassic European Dasycladales diversity / palaeolatitude graph.
*Description:* Through the Jurassic the Dasycladales have continually progressed
northwards in their palaeolatitudinal extent, but they appeared to suffer in the Mid
Jurassic in terms of diversity as they did so before rapidly expanding in diversity in
the Upper Jurassic. *Interpretation:* With time all organisms expand their sphere of
occurrence on the globe as far as they can, so the increase in palaeolatitudinal extent
is expected, but the diversity drop in the Mid Jurassic could show either a time of
trouble for the Dasycladales in terms of adverse environmental conditions or a
preservational / evidence bias for this time period.

**Figure 6.41** Jurassic European Halimedaceae diversity / palaeolatitude graph.
*Description:* Through the Jurassic the Halimedaceae have also continually progressed
northwards in their palaeolatitudinal extent, but do not show any hindrance in Mid
Jurassic diversity expansion as the Dasycladales did. *Interpretation:* With time
Halimedaceae have expanded their sphere of occurrence on the globe also, but the
lack of a diversity drop in the Mid Jurassic like that of the Dasycladales is unexpected
as any problems affecting the Dasycladales is expected to have a similar effect on the
Halimedaceae.

**Figure 6.42** Jurassic European Rhodophyta diversity / palaeolatitude graph.
*Description:* The Rhodophyta were not observed in the Lower but have increased in
their palaeolatitudinal extent northwards, as well as diversity through the Mid to
Upper Jurassic. *Interpretation:* This is a standard increase in diversity and extent with
time and is typical of a radiating fauna.

**Figure 6.43** Jurassic European Cyanobacteria diversity / palaeolatitude graph.
*Description:* Through the Jurassic the Cyanobacteria have progressed northwards in
their palaeolatitudinal extent, but appear to have suffered in the Mid Jurassic in terms of diversity similarly to the Dasycladales before expanding in diversity in the Upper Jurassic. Interpretation: Similar to the Dasycladales in the pattern of their diversity trend over time with a diversity drop in the Mid Jurassic, the Cyanobacteria also seem to have suffered a climatological shock at this period. Their palaeolatitudinal extent increase is normal in relation to all the other algal groups.

Figure 6.44 Jurassic European Microproblematica diversity / palaeolatitude graph.
Description: Through the Jurassic the Microproblematica have progressed northwards in their palaeolatitudinal extent, but appear to have suffered in the Mid Jurassic in terms of diversity similarly to the Dasycladales and Cyanobacteria before also expanding in diversity in the Upper Jurassic. Interpretation: The Microproblematica trends are in direct correlation with the Dasycladales and Cyanobacteria which gives weight to the supposition of a climatological affect at this time and indicate a similar response.

6.4 Discussion

6.4.1 Interpretation of Jurassic distributions

The Chlorophyta (as can be seen in Table 6.2 above) seem to show an increase in the latitudinal extent of their habitation with time. This appears to have similarities with the temperature tolerance change of Dasycladales theories of Elliott (1975, 1982, 1983 and 1984). This theory, that through time the Dasycladales (originally restricted to the warm tropical Tethyan area) gradually became able to tolerate more cool-water, marginal environments, was recinded by Elliott (1986) with no reason. There is no direct, verifiable evidence of changing temperature tolerance, and the reasoning for this argument is still unclear to this day (see Chapter 4 for details). Possible palaeotemperatures for this area are postulated and can be seen in Chapter 9 (Synthesis). The non-chlorophyte types show a rough similarity to the calcareous greens, but with either a lack of data for the earlier Jurassic, or a Mid Jurassic fluctuation; - this may be as a result of Liassic salinity peculiarities (see Synthesis, Chapter 9) or other factors, associated with the northern European areas, which would have acted as a restrictive buffer but which had been removed by the Upper Jurassic.
Estimation of Jurassic isocrymal limits can be made via comparison of phycological major extent / termination and the isocryme values of the modern day. The use of both Dasycladales and Halimedaaceae should help to ensure a more precise and supported value.

The modern, normally calcified, major species extent / termination occurs at c12°C (see Figure 5.32).

This is to say in the modern day, the 12°C isocryme is the furthest point at which normally calcifying versions of calcareous Chlorophyta are found (excepting localized aberrations due to non-temperature related factors). Assuming no temperature relationship changes from the Jurassic to recent, this is the temperature selected to signify the last major species occurrence lines on the Jurassic palaeoreconstructions.

6.4.1.1 Algal occurrence limit offset to latitude

The lines of the furthest major species extents appear to be a latitudinally influenced line oblique to the lines of latitude in the palaeoreconstructions of Smith et al (1994). In the modern seas the distribution of calcareous algae, in the absence of cold or warm currents, “parallels” latitude. The data for the Jurassic algal distribution extent, summarised in Figure 6.20 show a distinct and consistant disparity with palaeolatitude.

Possible reasons for this disparity are:
1. A false representation due to data inaccuracies.
2. A true representation of an isotherm banding offset from pure latitudinal setting via natural factors.

The first of these two possibilities has two related elements –
1. The limited existence of suitably natured Jurassic outcrops for data collection. This relates to the extent of which Jurassic material is revealed for study and the preservational bias on distribution studies.
2. The existence of suitable environments at the time of deposition. This is important as the Jurassic outcrops have to be compatible with the desired organisms – e.g.
for Chlorophyta the lithology and palaeoenvironment needed was a shallow, low-energy marine limestone.

The required combination of factors limits the extent of area upon which distributional analysis can be undertaken. However, such conditions are met by a number of sites in all time periods (particularly the Upper Jurassic) and the sites are sufficiently well distributed (latitudinally and longitudinally) within Europe to be useful and in the authors opinion provide an accurate representation (Figure 6.46).

![Map of Europe with superimposed data showing Jurassic outcrops across Europe - all stages, all facies.](image)

The remaining possibility is that of a true representation of palaeo-conditions. This is to say that the oblique distribution limit line is an actual palaeodistribution line that was originally offset from pure latitude.

The limit is skewed across the whole of Europe – too large to be associated with the coastal skewing you get at the edges of a land mass – such a large offset is normally associated with water current movement offsetting the latitudinal
temperature banding. In the modern day global setting there are a number of currents that restrict or promote temperature movement from the latitudinal, e.g.:  
  Warm currents: Gulf Stream, Kuro and Agulhas  
  Cold currents: Humboldt and Canary  

There has been some work done involving such factors as currents in the Mesozoic by workers such as Vogt and Tucholke (1986). Such work appears to support the theory of current offset with cold currents repressing the western part of Europe (above Iberia) and warm currents promoting the more eastern areas of Europe (see the Jurassic palaeoreconstruction section in Chapter 9 [Synthesis]).

6.4.1.2 Jurassic calcareous algae distribution analysis

Of all the algal types researched in this study of Jurassic phycology, the most important for this study are the Dasycladales. Their importance is realised through the analysis of the records of their distribution. Through the Jurassic period, the Dasycladales show a general trend of being a prevalent organism in the lower latitudes, at a certain point they have a major decline in occurrence to the point of termination of their distribution. This severely limited dissemination has similarities with modern day calcareous Chlorophyta.

The decrease of a marine organisms’ diversity (its taxonomic richness) across a latitudinal gradient is associated with the seawater temperature acting in a threshold manner (Rosen, 1975 & 1981). Associated with this is the fact that a progressive isocrymal decrease generally occurs with a greater range of annual temperatures which instills a more unstable environmental situation, which may be as relevant or even more so than the isocrymal situation in the control of diversity (Rosen, 1975). Diversity meant here is the taxonomic richness and is important as there is a significant difference between the diversity and latitudinal spread of an algal type and the causative agents governing the two.

6.4.2 Previous work

Marginal Tethyan flora (proposed by Elliott, 1977 and 1984 for the middle Jurassic of southern England) is characterized by the presence of aragonitic green
algae with low diversity and few individuals and can be used to delineate the boundary of the Tethyan Realm. This concept of marginal flora, which are few in numbers and species, show similar features to the living descendants found in warm seas marginal to the tropics, like the Mediterranean (Mu, 1993).

Dasycladaceae

During the Lower and Mid Jurassic, Dasycladaceae are not of substantial importance due to ‘suboptimal’ ecological conditions (Berger and Kaever, 1992). It is the late Jurassic that shows the initiation of a time-period of flourishing diversity and frequency for the Dasycladaceae (Berger and Kaever, 1992). This flourishing was due to more favourable habitats and conditions. It is said that there are no substantial differences between the Jurassic and modern day in this regard (Elliott, 1978 and Berger and Kaever, 1992).

Modern Dasycladaceae are “less obvious and more discrete” than the Halimedaceae but do not “disaggregate into unidentifiable grains” as the Halimedaceae do (Wray, 1977).

Halimedaceae

The post-mortem disaggregation of certain Halimedaceae (e.g. *Penicillus*) is so unmitigated as to form sediment which can not be attributed to the skeletal structure of the plant (Stockman et al, 1967). The tendency to disintegrate gives some explanation as to the limited fossil Halimedaceae record, as the microscopic identifying details have been obliterated or are poorly preserved (Hillis-Colinvaux, 1986). Thus, there is a limited amount of data for phycological palaeoreconstruction of these algae due to the fossil record and this may also affect the validity of any work that is done; the distribution that has been extracted from the limited data has been one of a “longitudinally far-ranging Tethyan pattern” (Hillis-Colinvaux, 1986). There is however, due to the preservational instabilities of this group, no way of knowing the extent of such flora along the Tethyan shallow shelf areas, although the temperature requirements of such flora are said not to have changed (Elliott, 1981 and Hillis-Colinvaux, 1986).

An attempt to elucidate water temperatures from the Jurassic algal distribution information together with the modern algae data can be seen in Table 6.3.
<table>
<thead>
<tr>
<th>Chapter 6: Jurassic Algae Palaeobiogeographic Distribution</th>
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<td><strong>Table 6.3: Green algae results table</strong> (2021 edition and Halimedaaceae)</td>
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<td><em>Stramenopila</em> sp.</td>
<td><em>Stramenopila</em> sp.</td>
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<tr>
<td><em>Chlorophyta</em> sp.</td>
<td><em>Chlorophyta</em> sp.</td>
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<tr>
<td><em>Eustigmatophyceae</em> sp.</td>
<td><em>Eustigmatophyceae</em> sp.</td>
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<tr>
<td><em>Chlorophyceae</em> sp.</td>
<td><em>Chlorophyceae</em> sp.</td>
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<tr>
<td><em>Phaeophyta</em> sp.</td>
<td><em>Phaeophyta</em> sp.</td>
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<tr>
<td><em>Rhodophyta</em> sp.</td>
<td><em>Rhodophyta</em> sp.</td>
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<td><em>Bryophyta</em> sp.</td>
<td><em>Bryophyta</em> sp.</td>
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<td><em>Rhodophyta</em> sp.</td>
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<tr>
<td><em>Bryophyta</em> sp.</td>
<td><em>Bryophyta</em> sp.</td>
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Chapter 7 Systematics of Jurassic calcareous algae

7.1 Aim

The aim is to systematically overview the Jurassic algae and investigate certain Jurassic Microproblematica.

7.2 Jurassic algal systematics

Unless otherwise stated (e.g. Section 7.4 - Changes to Dragastan taxonomy) the systematic assignment of these algae is acknowledged by the author to be correct (see Tables 7.1 and 7.2). Some of the more important algae found by the author during fieldwork are documented here and can be seen in Plates 7.1 to 7.5:

Dasycladales
(In database comprises 61 genera and 185 species)

These algae were the dominant form in the fieldwork samples and some of the most common and interesting ones are listed here and shown in following plates:

- *Campbelliella striata* (see Plate 7.1)
- *Clupeina jurassica* (see Plate 7.2)
- *Salpingoporella annulata* (see Plate 7.2)
- **Neoteutoporella socialis** (see Plate 7.3)
- *Likanella bartheli* (see Plate 7.3)

* These three Dasycladales together are associated with stratigraphic correlation of Upper Malm lithologies (Flügel, 1982).

** This dasycladale is unusual as it appears to like the more turbulent waters of the reef barrier (in Languedoc) as opposed to the quieter back-reef lagoon which is the normal preserve of the Dasycladales. This alga displays subsequent greater skeletal support and growth into large ‘bushes’.
### Table 7.1 Jurassic calcareous Dasycladales in Western Europe.

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<tr>
<th>GENUS</th>
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<td>Acicularella</td>
<td>americana; elongata; elongata aquitanica; elongata elongata; jurassica; sp.</td>
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<td>scheypnuphi</td>
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<tr>
<td>Clypeina</td>
<td>bavarica; calciformis; catinula; (?) delphica; durandelgai; hanabaeneis; inopinae; jurassica; parvula; (?) solkanii; sp.; zumeae</td>
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<td>jurassica</td>
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<td>quercfoliopora</td>
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<td>Dinarella</td>
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<td>Diplopora?</td>
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<td>ellenbergeri</td>
</tr>
<tr>
<td>Zergatella</td>
<td>sp.i.</td>
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</tbody>
</table>

Chapter 7 Systematics of Jurassic calcareous algae

John Adams PhD thesis
### GENUS

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<tr>
<th>Species</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arabiocodium</td>
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</tr>
<tr>
<td>Dehnelia</td>
<td>corinensis</td>
</tr>
<tr>
<td>Halimoda (Bojastria)</td>
<td>hochstetteri lusiaea</td>
</tr>
<tr>
<td>Juracea</td>
<td>bifurcata</td>
</tr>
<tr>
<td>Lechhamptonella</td>
<td>lilewellyae</td>
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<tr>
<td>Pulsarophorum</td>
<td>convolvaris</td>
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<tr>
<td>Pseudocodium (changed to Pulsarophorum)</td>
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<td>Tebyesicodium</td>
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<tr>
<td>Liophyllum?</td>
<td>lusiaea</td>
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<tr>
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<tr>
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<tr>
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<td>(cf.) lusiaea; sp.</td>
</tr>
<tr>
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<tr>
<td>Rubiaea</td>
<td>bartheli</td>
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<tr>
<td>Rodletzella</td>
<td>jurassica</td>
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<tr>
<td>Thamnophorella</td>
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<td>Verminecrella</td>
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</tr>
<tr>
<td>Archicella</td>
<td>radiata</td>
</tr>
<tr>
<td>Bicellate</td>
<td>gnedsae; jurassica; semilunata</td>
</tr>
<tr>
<td>Cymatia</td>
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<tr>
<td>Nugellia</td>
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<tr>
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<tr>
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<tr>
<td>Michileanema</td>
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| Table 7.2 Jurassic Non-Dasyycladean calcareous algae in Western Europe. Guide to colours: |
|-----------------|-----------------|
| Halimiaceae | Rhodophyta Microproblematica | Cyanobacteria | Gymnocodiaceae |

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</tr>
<tr>
<td>Paraolcina</td>
<td>getica; richteri</td>
</tr>
<tr>
<td>Pseudolophoctodum</td>
<td>spongiosa</td>
</tr>
<tr>
<td>Riodaria</td>
<td>atumanav; carpotheca; diamae; lusiaeniensis; monsica; piaga; pumila; tadeuzii; theodori</td>
</tr>
<tr>
<td>Scotlandella</td>
<td>alpina; nodosa</td>
</tr>
<tr>
<td>Symplasma (Girvina)</td>
<td>jurassica (minuta)</td>
</tr>
</tbody>
</table>

**drogastan; leptophallus; sp.**
Plate 7.1 Dasycladales
All scale bars are 1 mm

A - Campbelliella striata (Carozzi, 1954 emend. Berrier, 1974); two nested oblique and two nested transverse sections; Argilliers, Languedoc; Tithonian (ARG 13).
B - Campbelliella striata (Carozzi, 1954 emend. Berrier, 1974); transverse, longitudinal and oblique sections; Argilliers, Languedoc; Tithonian (ARG 18).
C - Campbelliella striata (Carozzi, 1954 emend. Berrier, 1974); two nested oblique sections; Argilliers, Languedoc; Tithonian (ARG 17).
D - Campbelliella striata (Carozzi, 1954 emend. Berrier, 1974); three nested oblique sections; Argilliers, Languedoc; Tithonian (ARG 17).
E - Campbelliella striata (Carozzi, 1954 emend. Berrier, 1974); three nested oblique sections; Argilliers, Languedoc; Tithonian (ARG 17).
F - Campbelliella striata (Carozzi, 1954 emend. Berrier, 1974); two nested longitudinal sections; Argilliers, Languedoc; Tithonian (ARG 18).
Plate 7.2 Dasycladales
All scale bars are 1mm

A - Clypeina jurassica (Favre & Richard, 1927);
multiple transverse sections (broken); Argilliers, Languedoc; Tithonian (ARG 15).
B - Clypeina jurassica (Favre & Richard, 1927);
transverse sections (broken); Argilliers, Languedoc; Tithonian (ARG 4).
C - Clypeina jurassica (Favre & Richard, 1927);
oblique crown and (broken) transverse sections; Cerin, Jura; Kimmeridgian (CER 2).
D - Clypeina jurassica (Favre & Richard, 1927);
oblique section; Ferrières-les-Verrières, Languedoc; Tithonian (FLV 5).
E - Clypeina jurassica (Favre & Richard, 1927); partial transverse crown section; and
Salpingoporella annulata (Carozzi, 1953); transverse section; Cerin, Jura; Kimmeridgian (CER 2).
F - Salpingoporella annulata (Carozzi, 1953);
oblique section; Pont-de-Lemme, Jura; Kimmeridgian to Portlandian (PDL 4).
Plate 7.3 Dasycladales (A, B & C), Halimedaeeae (D & E) and Rhodophyta (F).
All scale bars are 1mm

A - Neoteutiporella socialis (Praturlon, 1963);
longitudinal section; La Table, Languedoc; Tithonian (TAB 1).
B - Neoteutiporella socialis (Praturlon, 1963);
oblique sections; La Table, Languedoc; Tithonian (TAB 1).
C - Likanella bartheli (Berrier, 1971); two broken transverse sections; and
Permiculculus sp. (Elliott, 1955); oblique section; Cabo Espichel, Portugal; Ur Portlandian A (CE 16).
D - Arabicoadium sp. (Elliott, 1957);
slightly oblique transverse section; Ferrières-les-Verreries, Languedoc; Tithonian (FLV 1).
E - Arabicoadium sp. (Elliott, 1957);
transverse section; Ferrières-les-Verreries, Languedoc; Tithonian (FLV 1).
F - Solenoporella jurassica (Rothpletz, 1908);
(longitudinal) section; Carapinha, Portugal; Upper Kimmeridgian (CAR 5).
Plate 7.4 Cyanobacteria
All scale bars are 1 mm

A - Cayeuxia sp. (Follo, 1938); longitudinal section; Argilliers, Languedoc; Tithonian (ARG 10).
B - Cayeuxia sp. (Follo, 1938); oblique section; Argilliers, Languedoc; Tithonian (ARG 18).
C - Cayeuxia sp. (Follo, 1938); (Bernier, 1971); longitudinal section; Argilliers, Languedoc; Tithonian (ARG 8).
D - Cayeuxia sp. (Follo, 1938); oblique section; Argilliers, Languedoc; Tithonian (ARG 9).
E - Cayeuxia sp. (Follo, 1938); slightly oblique longitudinal section; Cluse de la Balme, Jura, Kimmeridgian (CDB 1).
F - Cayeuxia sp. (Follo, 1938); transverse section; Cluse de la Balme, Jura, Kimmeridgian (CDB 1).
Plate 7.5 Microproblematica
All scale bars are 1mm

A - Thaumatoporella parvovesiculifera ([Raineri] Sartoni & Crescenti, 1962); longitudinal section; Argilliers, Languedoc; Tithonian (ARG 10).
B - Thaumatoporella parvovesiculifera ([Raineri] Sartoni & Crescenti, 1962); longitudinal section; (J unidentified alga; oblique); Argilliers, Languedoc; Tithonian (ARG 18).
C - Baccinella irregularis (Radocic, 1959); longitudinal section; Ferrières-les-Veieres, Languedoc; Tithonian (FLV 1).
D - Lithocodium aggregatum (Elliott, 1956) and Baccinella irregularis (Radocic, 1959); longitudinal section; Ferrières-les-Veieres, Languedoc; Tithonian (FLV 1).
E - Baccinella irregularis (Radocic, 1959) and Lithocodium aggregatum (Elliott, 1956); transverse section; Ferrières-les-Veieres, Languedoc; Tithonian (FLV 1).
Halimaceae
(In database comprises 11 genera and 17 species)

- *Arabicodium / Boueina / Halimeda* (see Plate 7.3)
  
  Living *Halimeda* is thought of as being the extant descendant of a lineage of morphologically similar fossil forms (Flügel, 1988). These fossils are:

  *Boueina* Toula 1883 – Upper Triassic to Upper Cretaceous
  *Arabicodium* Elliott 1957 – Mid Jurassic to Early Tertiary
  *Leckhamptonella* – Mid Jurassic (Aalenian)
  
  (*Halimeda* Lamouroux 1812 – Lower Cretaceous to Recent)

  The different stratigraphic occurrences of the algae has been taken by Bassoulet et al. (1983) as evidence of taxonomic distinction. This difference based on age has been adopted due to the differences in modern *Halimeda* being partly based on variable criteria such as dimensional data (Flügel, 1988).

Cyanobacteria
(In database comprises 16 genera and 57 species)

These organisms were numerous and prevalent at all the sites visited across a large range of environments. The most common were Cayeuxiid forms:

- *Cayeuxia* sp. (see Plate 7.4)

Rhodophyta
(In database comprises 8 genera and 17 species)

- *Solenopora / Solenoporella* (see Section 7.3.7) (see Plate 7.3)
7.3 Microproblematica

Microproblematica (also called incertae sedis) are those micro-organisms whose affinities are very much open to question. A number of such organisms have previously been ‘dumped’ into the all-consuming mixed bag of “algae”, but have not been adequately defined or indeed detailed enough to ensure that they are indeed of phyleological origin. This has been noted by algal workers: “algae are used as a dustbin for all bioclast material that cannot otherwise be identified.” (Adams and Mackenzie, 1998), “…the group has served as a ‘wastebasket’ for various unidentifiable biotic and non-biotic constituents presumed to be algae.” (Wray, 1977 [in Babcock, 1986])

The constant relegation of problematica to the realm of calcareous algae has led to the formation of one of the largest fossil taxonomic ‘dumps’ (Babcock, 1986). This problem may have decreased the value of true algae as palaeoenvironmental indicators by making algal classifications suspect via the introduction of non-algal forms (Babcock, 1986).

A number of Problematica have been encountered in this study, and will be discussed here. These organisms can be subjectively put under three groupings:

1. unknown affinity;

2. dubious affinity;

3. problematic situation arises from ‘splitting’ and ‘lumping’ of genera through dubious features.

These organisms can be seen in Table 7.3:
<table>
<thead>
<tr>
<th>Grouping</th>
<th>Taxon</th>
<th>Other information</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unknown</td>
<td><em>Aeoliscus</em> cf. <em>inconstans</em> and cf. <em>tinnininformis</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Alexandrella stricta</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Algites magnus</em> and <em>subtilis</em></td>
<td><em>Algites</em> – &quot;poorly understood but of algal origin&quot; Seward</td>
</tr>
<tr>
<td></td>
<td><em>Bacillariocodium calcarceus</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Consinocodium japonicum</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Enigma parvissima</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Hikocodium fertilis</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Hormathonema</em> sp.</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Koskinobullina socialis</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Marinella lugoni</em></td>
<td>Red alga?</td>
</tr>
<tr>
<td></td>
<td><em>Mercierella dacica</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Otternstella jaffrezoii</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Pycnoporida</em> lobatum</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Rajkella bartheli</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Thaumatoporella parvovesculifera</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Tubiphytes (Shanovella) morrenensis</em></td>
<td>Cyanobacterium, Sponge or Rhodophyte?</td>
</tr>
<tr>
<td></td>
<td><em>Verrniporella neoconica</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Verticillodemes clavaeformis</em></td>
<td></td>
</tr>
<tr>
<td>Dubious affinity</td>
<td><em>Baccinella irregularis</em></td>
<td>Foraminifer / microbial?</td>
</tr>
<tr>
<td></td>
<td><em>Baccinella</em> – <em>Lithocodium</em></td>
<td>Foraminifer / microbial?</td>
</tr>
<tr>
<td></td>
<td><em>Cladocoropsis mirabilis</em></td>
<td>Hydrozoan / sponge?</td>
</tr>
<tr>
<td></td>
<td><em>Cylindrites mosellensis</em></td>
<td>Trace fossil?</td>
</tr>
<tr>
<td></td>
<td><em>Eotheix alpina</em></td>
<td>Crinoid?</td>
</tr>
<tr>
<td></td>
<td><em>Globochaete alpina</em> and <em>spinosa</em></td>
<td>Crinoid?</td>
</tr>
<tr>
<td></td>
<td><em>Lithocodium aggregatum</em> and <em>morikawai</em></td>
<td>Foraminifera?</td>
</tr>
<tr>
<td></td>
<td><em>Lithophyllum masovi</em></td>
<td>Red alga. Real coralline?</td>
</tr>
<tr>
<td></td>
<td><em>Pseudolithocodium carpathicum</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Rothpletzella jurassica</em></td>
<td></td>
</tr>
<tr>
<td>Splitting / lumping</td>
<td><em>Garwoodia bardosi, fissa, flagell, maxima, polytomica, simplex, and toomeyi.</em></td>
<td>No cross partitions like greens, tubes are like Cyanobacteria but are too big</td>
</tr>
<tr>
<td></td>
<td><em>Rivularia atanasivi, lissaviensis, and moesica.</em></td>
<td>Cyanobacteria-modern name based on non-preservation of soft parts</td>
</tr>
</tbody>
</table>

Table 7.3 Jurassic microproportionatica. Red text = those investigated in this report.

Features of algae which can contribute to problems of affinity include:

1. Algae are a diverse group in terms of morphology, ecology, physiology and fossilization potential.
2. They are classified in several different divisions across two of the five kingdoms of organisms.
3. Some diagnostic morphological features of modern algae are not fossilized.
4. They are and have always been significant components of shallow carbonate seas and so are 'expected' in such deposits.
5. Modern algae (and most likely fossil forms) exhibit ecophenotypy (morphologic plasticity under varying ecologic conditions).

(After Babcock, 1986)

There appears to be a problematic criteria assignment when it comes to algal classification which needs to be remedied in order to allow a more accurate assignment of the Problematica to their correct affinity (whether algal or not). Criteria for recognition must derive from algal morphology in general and the morphology of Recent calcareous algae in particular (Riding, 1977).

7.3.1 Algites Seward

This name attributed by Seward (1894) to certain forms is a 'name given to all things poorly understood but of algal origin' (Emberger, 1968 translated) and was originally used for organisms in the Cretaceous of Ecclesbourne near Hastings, England. Their problem of designation to a more relevant taxon is due to their lack of reproductive organs and inner thallus structure (Teslenko, 1991); they are now considered to be the imprints of non-mineralized algal thalli of either the Phaeophyta (brown algae) or Rhodophyta (red algae). These non-calcified impressions were described from the Jurassic of Crimea (Teslenko, 1982) with a questionable non-assignment of taxonomy.

7.3.2 Thaumatoparella parvovesiculifera Sartoni & Crescenti

Type species – Gyroporella parvovesiculifera Raineri 1922

↓

Thaumatoparella parvovesiculifera (Raineri) Sartoni & Crescenti 1962

This genus has been assigned to either the Chlorophyta (De Castro, 1991, Barattolo, 1991) or the Rhodophyta (Bouroullec and Deloffre, 1970 and Ramalho, 1971 as Solenoporaceae, Flügel, 1979 as problematic red algae). It is a thin micrite-walled polygonal and ellipsoidal to spherical microfossil with indistinct wall perforations (Boudagher-Fadel et al., 2001) which commonly occurs as concentrically arranged layers or forming bridges over larger sparitic fenestrae and
may have smaller bodies enclosed within (Boudagher-Fadel et al. 2001, Leinfelder et al. 1993) (see Plate 7.5). The ‘thallus’ may also grow over each other without direct contact. The alga has been described as a crustose or encrusting thallus composed of a single-cell layer of large, polygonal-prismatic cells (Johnson, 1969).

Not only is the question of Chlorophyte verses rhodophyte unsettled (originally the alga was described as a dasycladalean), but also with regard to rhodophyte affinity, there is debate, some assignments having been made to the Solenoporaceae (Elliott, 1957 [as Polygonella incrustata] Bouroullec and Deloffre, 1970, Ramalho, 1971). Johnson (1969) has said that the shape and large cell sizes involved point towards the Solenoporaceae rather than the Corallinaceae. There is no evidence found of fossilized sporangia or conceptacles which would act to settle arguments, however, such structures may not have been present or could have been outside of the preserved thallus parts, as is the case in some extant algae.

An encrusting character is not typical of Dasycladaleans and the single-cell layer of thallial components leads this author to favour a Rhodophyte assignment rather than the original Chlorophyte one. I have noticed some superficial similarities to the coralline alga Lithoporella. Lithoporella melobesioides (Foslie), subfamily Mastophoroidae, family Corallinaceae; described as ‘primigenous filaments composed of palisade cells’ (Woelkerling, 1988) (see Plate 7.6). T. parvovesiculifera has cell sizes of 64-104μm (height) and 26-33μm (width) (Johnson, 1969), and, compared to this, L. melobesioides is at the small end of the T. parvovesiculifera range. It is interesting to note that L. melobesioides does possess gametangial conceptacles (Woelkerling, 1988). Weynschenck (1950) mistook T. parvovesiculifera for L. melobesioides in the European Jurassic and this form was recorded by Elliott (1957) as Polygonella incrustata.

Despite the ‘age problem’ T. parvovesiculifera appears ‘coralline-like’ and as such may be an example of the coralline lineage extending further back in time than presently considered. Such an extension back in time could help link extant corallines (Lower Cretaceous to Recent) and ‘ancestral corallines’ (Palaeozoic) (see Brooke and Riding, 1998 and Riding et al, 1998).
Plate 7.6 Modern Lithoporella melobesioideae and Upper Jurassic Thaumatoporella parvovesiculifera showing similarities suggesting a possible coralline affinity of T. parvovesiculifera.
7.3.3 Jurassic Corallines

There are seven species (within four genera) that have been assigned to the Corallinaceae in the Jurassic (Aguirre et al, 2000), namely:

*Lithoporella elliotti* Emberger
*Lithoporella melobesioides* Foslie
*Lithothamnium ellitianum* Howe & Goldman
*Lithothamnium jurassicum* Gümbel
*Lithophyllum maslovi* Dragastan
*Lithophyllum turinosensis* Endo
*Archaolithothamnium somensis* Endo

However, these are doubtful in age attribution and taxonomic circumscription (Aguirre et al, 2000). It has been stated that all reported Jurassic Corallinaceae are based on misidentifications (improper taxonomic determinations) and that this group only appeared in the Early Cretaceous (Moussavian, 1991, 1992). However, this may be incorrect (see above - 7.3.2).

7.3.4 *Marinella lugeoni* Pfender

This organism commonly occurs in Upper Jurassic and Cretaceous shallow water limestones globally and is known until the Oligocene in Alpine Europe (Leinfelder and Werner, 1993). It was first described from the Late Jurassic of Spain (Pfender, 1939) — although the age in that paper is incorrectly stated as early Jurassic, (Leinfelder and Werner, 1993). In areas (such as the Lusitanian Basin, Portugal) *Marinella* is a common component of shallow water limestones, occurring as “sub-spherical algal nodules up to six centimetre in diameter” (Leinfelder and Werner, 1993) or as fragments.

There has been a long debate over the systematic assignment of *M. lugeoni*, from a cyanophytic origin (Pfender, 1939) to Chlorophyte (Codiacean = Halimedacean) (Bouroullec and Deloffre, 1968) and also a Rhodophyte attribution (Johnson, 1969 as a red alga of uncertain affinities, Flügel, 1979 as a problematic red alga, and Leinfelder, 1986 as an early form of ‘Lithothamnoid’ coralline alga derived from the Solenoporaceae in the course of the Jurassic) see Table 7.4.
<table>
<thead>
<tr>
<th>Authors or Taxa</th>
<th>Order</th>
<th>Family</th>
<th>Suborder</th>
<th>Class</th>
<th>Division</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pfender 1939</td>
<td>Incertae sedis</td>
<td>Cyanophyta</td>
<td>Chlorophyta</td>
<td>Rhodophyta</td>
<td></td>
</tr>
<tr>
<td>Pia, Andrusov (fide Pfender 1939)</td>
<td>? Cyanophyceae</td>
<td></td>
<td>Red alga</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Johnson 1961, 1964</td>
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<td>Codiaeae</td>
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<td>Johnson &amp; Kafka 1965</td>
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<td>Codiaeae</td>
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<td>Imaitzumi 1965</td>
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<td>Codiaeae</td>
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<tr>
<td>Beckmann &amp; Beckmann 1966</td>
<td></td>
<td>? Codiaeae</td>
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<tr>
<td>Bourouillec &amp; Deloffre 1968</td>
<td></td>
<td>Codiaeae</td>
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<td></td>
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<tr>
<td>Johnson 1969</td>
<td></td>
<td></td>
<td>Red alga of uncertain affinity</td>
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<tr>
<td>Radoicic 1970</td>
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<td>Codiaeae</td>
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<tr>
<td>Bolliger &amp; Burri 1970</td>
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<td>Rhodophyta</td>
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<td>Golonka 1970</td>
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<td></td>
<td>Rhodophyta, most probably corallinae family</td>
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<tr>
<td>Masse &amp; Poignant 1971</td>
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<td>Codiaeae</td>
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<td>Ramalho 1971</td>
<td></td>
<td>Codiaeae</td>
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<td>Rey 1972</td>
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<td>Codiaeae</td>
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<tr>
<td>Srivastava 1973</td>
<td></td>
<td>? Rhodophyta</td>
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<td></td>
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<td>Jaffrez 1974</td>
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<td>Codiaeae</td>
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<tr>
<td>Poignant 1978</td>
<td>Incertae sedis</td>
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<tr>
<td>Lauverjat &amp; Poignant 1978</td>
<td>Incertae sedis</td>
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<td>Canerot 1979</td>
<td>Incertae sedis</td>
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<tr>
<td>Flügel 1979</td>
<td></td>
<td></td>
<td>Problematic red alga</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Golleston in Masse 1979</td>
<td></td>
<td>Schizophytoides</td>
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</tr>
<tr>
<td>Tappan 1980</td>
<td></td>
<td>Udoteaceae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cherchi, Gupta &amp; Schroeder 1984</td>
<td>Incertae sedis</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Barattolo &amp; Del Re 1985</td>
<td></td>
<td>(problematic) cyanobacterium</td>
<td>Solenoporaceae resemblance to Melobesiidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Höfling 1985</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Werner 1986</td>
<td></td>
<td>Red alga</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leinfelder 1986</td>
<td></td>
<td>Corallinae</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Reiniger 1987</td>
<td></td>
<td></td>
<td>Problematic red alga</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 7.4 Systematic assignments of *Marinella lugeoni* (from Leinfelder and Werner, 1993 and references therein).

A red algal affinity was discussed by Pfender (1939) and supported by Imaitzumi (1965) and Golonka (1970) on the basis of features attributing it to the Corallinaeaceae (i.e. possible conceptacles and horizontal walls) (Leinfelder, 1986). A lack of thallus differentiation suggests a relationship with solenoporaceans, but a greater affinity with corallinaeans is shown (see Table 7.5 below). There is the possibility that both *Marinella* and corallinaeans are derived from a common ancestor (Leinfelder and Werner, 1993).
<table>
<thead>
<tr>
<th></th>
<th><strong>Marinella</strong></th>
<th><strong>Corallinaeans</strong></th>
<th><strong>Solenoporaceae</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>General outline</strong></td>
<td>Nodular rarely crustose</td>
<td>Nodular (inarticulate C.)</td>
<td>Nodular crustose</td>
</tr>
<tr>
<td><strong>Growth form</strong></td>
<td>Spheroidal, digitiform,</td>
<td>Spheroidal, digitiform,</td>
<td>Spheroidal, crusts,</td>
</tr>
<tr>
<td></td>
<td>rarely cushion-like</td>
<td>crusts</td>
<td>rarely digitiform</td>
</tr>
<tr>
<td><strong>Banding</strong></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><strong>Diameter of cells</strong></td>
<td>5-15μm</td>
<td>5-20μm</td>
<td>20-100μm</td>
</tr>
<tr>
<td><strong>Differentiation of hypo-</strong></td>
<td>-</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td><strong>perithallus</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Epithallus</strong></td>
<td>Outer rim of thin walled</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>cells (?) epithallus</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Dominant direction of</strong></td>
<td>Radial filaments</td>
<td>Tangential cell rows or</td>
<td>Tangential cell rows</td>
</tr>
<tr>
<td><strong>cell growth</strong></td>
<td></td>
<td>radial filaments</td>
<td>or radial filaments</td>
</tr>
<tr>
<td><strong>Dissolution of tissue</strong></td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td><strong>resulting in cavities or</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>enlarged cells</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Conceptacles / sporangia</strong></td>
<td>(+)</td>
<td>+</td>
<td>?</td>
</tr>
<tr>
<td><strong>Megacells / heterocysts</strong></td>
<td>?</td>
<td>+</td>
<td>-</td>
</tr>
</tbody>
</table>

Table 7.5 Thallus relationships of *Marinella lungeoni* to Rhodophyta (from Leinfelder and Werner, 1993).

### 7.3.5 Shamovella (Tubiphytes) Rauser-Chernousova

**Nomenclature / systematics**

An earlier generic name, *Shamovella*, hitherto thought to be invalid, was found to be validly published. *Shamovella obscura* (Maslov) Riding comb. nov. = *Tubiphytes obscurus* Maslov. *Tubiphytes* is a taxonomic rather than a nomenclatural synonym of *Shamovella*. A new combination, *Shamovella obscura*, was made (Riding, 1993).

"*Shamovella* gen. nov. is a name given to a calcareous alga in form of irregularly undulating tubes, with a lumen which possibly may be evidence of its being an encrustation. Viewed externally the tubes are porcelain-white; in thin-sections they are dark-grey, fine grained, multi banded ... , or uniformly solid and with fine filamentous texture..." Rauser-Černousova (1950) translated by Elias (1959) (Riding, 1993).

It should be noted that although *Shamovella* is the correct name to use (both *Shamovella* and *Tubiphytes* are valid names, but *Shamovella* is the senior synonym),

The link between *Shamovella* and *Tubiphytes* was first clearly established by Elias (1959) (Riding, 1993). Although *Nigriporella* is a junior synonym of *Tubiphytes* this does not invalidate the family name (for taxonomic description see Rigby, 1958) (Riding and Guo, 1992):
Family Nigriporellidae Rigby, 1958

Genus *Tubiphytes* Maslov 1956

1951 *Shamovella* Rauser-Chernousova

1956 *Tubiphytes* Maslov (junior synonym)

1958 *Nigriporella* Rigby (junior synonym)

Seven species of *Tubiphytes* have been described (Riding and Guo, 1992), and combinations in *Shamovella* can be made for all these other species hitherto correctly ascribed to *Tubiphytes* (Riding, 1993).

**Environment**

This organism was a prominent Mesozoic (as well as late Palaeozoic) organism in shallow-water reef and shelf margin carbonates (Senobari-Daryan and Flügel, 1991; Barattolo, 1991). It was also capable of colonizing temperate water, greater depths and more cryptic reefal environments than those of known algal forms (Riding and Guo, 1992; Riding and Barkham, 1999). It occurred in the roles of framebuilder (baffler) or encruster (binder) (Senobari-Daryan and Flügel, 1991). Its fossilization and calcification is said to have needed CaCO$_3$ saturated seawater, making it an indicator of tropical environments (Wang et al. 1994) but Riding and Barkham (1999), suggest a temperate water occurrence for this organism in the Lower Permian.

**Affinity**

Newell et al. (1953) favoured a hydrocoralline (hydrozoan) affinity for the fossil that Rauser-Chernousova (1951) named *Shamovella* while Maslov (1956), named the same organism *Tubiphytes* and placed it in algae incertae sedis with a tentative suggestion of cyanobacterial (Schizophyta) affinity (Barattolo, 1991).

Rigby (1958) described the same fossil as a new genus, *Nigriporella*, which he placed in a new hydrozoan family, the Nigriporellidae. Konishi (1959) recognised this as a synonym of *Tubiphytes* but also favoured it as being a hydrozoan. Flügel (1966), regarded *Tubiphytes* as a microproblematicum with the possibility of a comparison with rhodophytes.
After this there tends to be a divergence into three opinions regarding its affinity:

1. Sponge/animal
2. Rhodophyte alga
3. Cyanobacterium or cyanobacterial-chlorophyte consortium.

(Riding and Guo, 1992)

Dragastan (1969) favoured interrelations among *Nubecularia*-like foraminifers, cyanophyceans, and sediment (as did Leinfelder et al., 1993 - symbiotic intergrowth of a nubeculinellid foraminifer (*Nodophthalmidium* or, more likely *Nubeculina*) and a typical dense, microbial envelope), whereas Bernier (1984) thought *Tubiphytes morronensis* Crescenti, and probably also the whole genus of *Tubiphytes*, to be a foraminifer (*Nubeculariidae*). Schmid (1995) considered *Tubiphytes* to be a miliolid foraminifer endosymbiotic with algae, instead of microbes with potential symbionts of Dinophyceans, Rhodophyceans and Cyanobacteria.

Due to its occurrence in temperate water environments (Riding and Barkham, 1999) its depth penetration and its capability of living in cryptic reef environments, it is unlikely to be either a cyanobacterium or a green alga. A foraminiferal affinity cannot be ruled out, but is inconsistent with the morphology and organisation of most *Tubiphytes*, although Riding and Guo (1992) state that (in the Permian) *Tubiphytes* ability to encrust and subsequently incorporate foraminifers may cause a foraminiferal affinity confusion. The presence of an integral canal system would be consistent with hydrozoan or sponge affinities, but the absence of other skeletal cavities does not favour a hydrozoan affinity (Riding and Guo, 1992). It has been suggested that *Tubiphytes* appears to include characteristics of sponges, foraminifers, algae, fungi and bacteria (Senowbari-Daryan and Flügel, 1991).

It seems likely that taxonomically different organisms have been described under the name *Tubiphytes* (Senowbari-Daryan and Flügel, 1991) (see difference between Palaeozoic and Mesozoic forms shown below and Table 7.6).
<table>
<thead>
<tr>
<th>Date</th>
<th>Author</th>
<th>Interpretations</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>1951</td>
<td>Rauser - Chernousova</td>
<td>o</td>
<td>Informal taxonomy. Proposed name <em>Shamovella</em>.</td>
</tr>
<tr>
<td>1953</td>
<td>Newell et al.</td>
<td>o</td>
<td>First descriptions of form in Permian Reef Complex.</td>
</tr>
<tr>
<td>1955</td>
<td>Newell</td>
<td>o</td>
<td></td>
</tr>
<tr>
<td>1956</td>
<td>Maslov</td>
<td>o, x</td>
<td>Proposed name <em>Tubiphytes</em> with <em>T. obscurus</em> as type.</td>
</tr>
<tr>
<td>1958</td>
<td>Rigby</td>
<td>x</td>
<td>Proposed name <em>Nigriporella</em>.</td>
</tr>
<tr>
<td>1959</td>
<td>Elias</td>
<td>o</td>
<td>Linked <em>Shamovella</em> and <em>Tubiphytes</em>.</td>
</tr>
<tr>
<td>1959</td>
<td>Konishi</td>
<td>o</td>
<td>Recognised synonymy of <em>Nigriporella</em> and <em>Tubiphytes</em>.</td>
</tr>
<tr>
<td>1965</td>
<td>Cronis and Toomey</td>
<td>o, x</td>
<td></td>
</tr>
<tr>
<td>1966</td>
<td>Flügel</td>
<td>o</td>
<td></td>
</tr>
<tr>
<td>1969</td>
<td>Toomey</td>
<td>o</td>
<td></td>
</tr>
<tr>
<td>1969</td>
<td>Dragastan</td>
<td>o</td>
<td>Interrelationship of <em>Nubecularia</em> – like foraminifer and cyanobacteria.</td>
</tr>
<tr>
<td>1972</td>
<td>Homann</td>
<td>o, x</td>
<td></td>
</tr>
<tr>
<td>1974</td>
<td>Babcock</td>
<td>x</td>
<td>Problematica of zoologic affinities.</td>
</tr>
<tr>
<td>1977</td>
<td>Babcock</td>
<td>x</td>
<td>Problematica of zoologic affinities.</td>
</tr>
<tr>
<td>1980</td>
<td>Flügel and Flügel-Kahler</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>1981</td>
<td>Flügel</td>
<td>o, o</td>
<td>Consortium hypothesis.</td>
</tr>
<tr>
<td>1983</td>
<td>Flügel</td>
<td>o, o</td>
<td>Consortium hypothesis.</td>
</tr>
<tr>
<td>1984</td>
<td>Bernier</td>
<td>o</td>
<td><em>Nubeculariidae</em> foraminifer.</td>
</tr>
<tr>
<td>1986</td>
<td>Babcock</td>
<td>x</td>
<td>Problematicum.</td>
</tr>
<tr>
<td>1992</td>
<td>Riding and Guo</td>
<td>o</td>
<td></td>
</tr>
<tr>
<td>1993</td>
<td>Leinfelder et al.</td>
<td>o</td>
<td>Symbiotic <em>nubeculariid</em> foraminifer and microbial envelope.</td>
</tr>
<tr>
<td>1993</td>
<td>Riding</td>
<td>N/A</td>
<td>Revalidation of <em>Shamovella</em> (<em>Tubiphytes</em> being a taxonomic synonym).</td>
</tr>
<tr>
<td>1995</td>
<td>Schmid</td>
<td>o</td>
<td>Milolid foraminifer with endosymbiotic algae (dinophyceans, rhodophyceans or cyanobacteria).</td>
</tr>
</tbody>
</table>

Table 7.6 *Shamovella* / *Tubiphytes* affinity history. x = taxonomic opinion, o = formal taxonomic placement. (After Babcock, 1986 see paper for references)

Difference between Palaeozoic and Mesozoic forms

Jurassic specimens attributed to *Tubiphytes* are not equivalent to the true *Tubiphytes* of the Permian. *Tubiphytes morronensis* Crescenti and other similar tubiphytoid morphotypes found in the Jurassic show clear structural differences with
respect to the Permian Tubiphytes obscurus Maslov (1956) and related Late Paleozoic forms (Moussavian 1992).

The Permian Tubiphytes has distinct growth zones, coarsely meshed ‘tissue’, and shows irregularly formed (angular to rounded) and often bubble-shaped ‘pores’, becoming enlarged towards the center. The Jurassic Tubiphytes consist of undifferentiated to finely filamentous structures reminiscent of cyanophyte associations. In many cases, the cavities clearly represent invertebrate fragments (foraminifers, sponge spicules).

Overall Shamovella / Tubiphytes conclusions

There is no evidence to suggest that Tubiphytes is either a cyanobacterium, alga or consortium of cyanobacteria and algae. Its environmental distribution is consistent with an invertebrate affinity and its overall skeletal structure and organization suggest it to be a hydrozoan or sponge, although a foraminiferal affinity cannot be ruled out (Riding and Guo, 1992). Overall, the two most likely affinities appear to be that T. morronensis is either a sponge (Riding and Guo, 1992) or a symbiont-bearing miliolid foraminifer with a two-fold test (Schmid and Leinfelder, 1996). A decision between these two interpretations is impossible at present. In general, it seems that Tubiphytes richly deserves its taxonomic assignment as a problematicum (Babcock, 1986).

7.3.6 Bacinella irregularis Radoicic / Lithocodium aggregatum Elliott

Environment

Bacinella irregularis

This organism is not recorded with any reliability from northern Europe (Banner et al, 1990) and seems to inhabit a similar environment to Lithocodium aggregatum (see below).

Lithocodium aggregatum

This organism was widespread in Mesozoic shallow marine carbonates. It occurs with Bacinella, Thaumatoporella and other calcareous microbial crusts. Like other microencrusters, it is nearly always found autochthonous and is of
palaeoecological value (Leinfelder et al, 1993), indicating a shallow marine, reefal to lagoonal environment with normal salinity and moderate to elevated water energy (Schmid and Leinfelder, 1996). As an encruster, it is indicative of a setting with a low background sedimentation rate (Schmid and Leinfelder, 1996).

*Lithocodium* is typical of lagoonal low-energy, oncoid environments and debris-rich, high-energy reefs. It is commonly found in colonies – specimens or generations overgrow each other which leads to flat to domal crustose colonies as well as pure nodules and oncoids. They may have contributed to reef formation, partly acting as a binder but more as a constructor (Schmid and Leinfelder, 1996).

The non-reefal examples are found with a micritic matrix which suggests low palaeocurrent velocities (probably not exceeding c10 cm/sec) as well as the warm, fully marine, well oxygenated, calcium carbonate rich, mid-shelf sea (c15-60m depth) setting otherwise indicated (Schmid and Leinfelder, 1996).

*Lithocodium aggregatum* does not yet appear to have been found in northern Europe (Banner et al, 1990).

*Lithocodium* and *Baccinella irregularis* in combination

These are common in micritic, calcareous, apparently well oxygenated, marine sediments of Mesozoic age in the Tethys (Banner et al, 1990), and the two genera flourished mainly in the outer parts of lagoons and in shelf margin facies (Barattolo, 1991).

**Affinity and nomenclature / systematics**

The affinity of these organisms is complex due to the ‘interrelationship’ of them both – they have been ascribed as individual organisms, parts of one organism, or two commensal organisms.

*Lithocodium aggregatum* was first described from the Cretaceous of Iraq by Elliott (1956) as a codiacean and later regarded as being of uncertain affinity (Elliott, 1963).

Elliott (1955 and 1956), Johnson (1969) and Dragstan (1980) assigned *Lithocodium* to the Codioceae (encrusting or nodose) (Barattolo, 1991). Johnson (1969) thought *Bacinella* was a cyanophycean. Both organisms together as one, have
been described as codiacean green algae by Elliott (1956a), Praturlon (1964),

*Bacinella* Radoičić and *Lithocodium* Elliott, according to Segonzac and
Marin, (1972), respectively represent older and younger parts of the same thallus
(Barattolo, 1991).

Schäfer and Senowbari-Daryan (1983) suggested a filamentous cyanophyte
affinity for *Bacinella irregularis* and Codiaceae for *Lithocodium* (Leinfelder, 1986).
Other possibilities have included *Bacinella irregularis* as a hydrozoan (Turnsek and
Buser, 1966), as a stromatoporoid (Masse and Poignant, 1970), or as a lichen
(Segonzac and Marin, 1972). *Lithocodium* as either a hydrozoan or a stromatoporoid
(Leinfelder, 1986) and *Lithocodium – Bacinella* as one organism. In the latter case, it
has been suggested that *Lithocodium – Bacinella* represent either different ecological
varieties (Elliott, 1963, supported by Bouroullec and Deloffre, 1968 and Ramalho,
1971) or different parts of the same thallus, *Bacinella* as the young (earlier
ontogenetic) stage and *Lithocodium* as the cortical layer (Segonzac and Marin 1972),
or Banner et al (1990) interpret *Bacinella* as medulla and *Lithocodium* as cortical
layer of a codiacean alga.

*Bacinella* and *Lithocodium* occur both isolated and together (see Plate 7.5),
and when found together they need not necessarily overgrow each other but often
occur separated within one sample or crust. Schäfer and Senowbari-Daryan (1983),
Maurin et al. (1985), and Camoin and Maurin (1988) assume *Bacinella* to be a
Cyanobacterial structure (Leinfelder et al, 1993).

*Lithocodium aggregatum* Elliott (with its synonyms, *Bacinella irregularis*
Radoičić and *Pseudolithocodium carpathicum* Mišik) were assigned to a new
subfamily Lithocodioidea of the family Codiaceae (Banner et al, 1990).

According to Schmid and Leinfelder, (1996), *Lithocodium aggregatum* is a
loftusiacean foraminifer (order Lituolida, Superfamily Loftusiacea). It is not identical
to *Bacinella*, although phrenoteca-like structures crossing parts of the chambers
partly resemble *Bacinella*. Therefore *Lithocodium* and *Bacinella* are not parts of
one organism. The phrenoteca-like structures may cross chambers or even alveoli of
*Lithocodium* in various places and at various angles. They are irregular, thin, dense
partitions which may be interconnected and hence appear in a mesh-like,  
‘bacinelliform’ fashion. Phrenotheca are facultative structures of unknown function  
which occur in some fusulinids (Schmid and Leinfelder, 1996).

Bubble-like structures, formerly interpreted as sporangia in *Lithocodium* are  
identified as the telamminid foraminifer *Troglotella incrustans* Wernli and Fookes  
*laevis*), possibly living as a parasite or more likely a symbiont in the *Lithocodium*  
tissue (Schmid and Leinfelder, 1996). Schmid and Leinfelder suggest that a  
commensal relationship existed, with *Troglotella* feeding on the carbohydrates  
synthesized by *Lithocodium* symbionts. A coelobitic life style for the foraminifer  
within the cavity of *Lithocodium* is presumed (Leinfelder et al, 1993).

All species other than type species *L. aggregatum* are invalid as are  
*Pseudolithocodium carpathicum* and *Baccinellacodium calcareus* (Schmid and  
Leinfelder, 1996).

**Lithocodium / Baccinella: conclusions**

*Lithocodium aggregatum* (Elliott) is a loftusiid foraminifer with an encrusting  
life habit, not a codiacean alga (Schmid and Leinfelder, 1996). *Baccinella irregularis*  
is still enigmatic.

The reinterpretation of *Lithocodium* as a loftusiid foraminifer is an example of  
microproblematica having been attributed to the algae just to avoid dealing with a  
problem (Schmid and Leinfelder, 1996).

### 7.3.7 Solenopora jurassica

Nicholson in Brown, 1894 (see Plate 7.3)

This organism, first described from the Bathonian of Chedworth in  
Gloucestershire (Harland and Torrens, 1982), is most likely to be a red alga. This  
affinity is not really open to question (see below), - what is problematic is the  
nomenclatural affinity. It has become clear that *Solenopora* (Dybowski, 1877), first  
described from the Late Ordovician, is in fact a chaetetid sponge (Riding, in press b)  
as originally stated by Dybowski (1877) before *Solenopora* was reinterpreted as a  
red alga (Brown, 1894). Brown (1894) misidentified the *Solenopora jurassica*  
material (in the Jurassic) as *Solenopora*. This was recognised by Rothpletz (1908)
who accordingly named *Solenopora jurassica* as *Solenoporella jurassica*. Rothpletz (1908) noted that this organism was different from true *Solenopora* and so constructed the genus *Solenoporella*. This differentiation was based on the incorrect reason of a lack of cell connecting pores (which are common in corallines, but confusingly also not found in true *Solenopora*) (Riding, pers. comm.), but the overall division was the correct action. The name of *Solenoporella* has been largely ignored in publications and instead the incorrect name of *Solenopora* is still applied to *S. jurassica*. The change of name may have an effect upon the nomenclature of the family Solenoporaceae (Rhodophyta) which was erected by Pia (1927) alongside the Corallinaceae and Squamariaceae.

I state above that the affinity of *S. jurassica* as a red alga is unopposed, the only problem is one of affinity within the Rhodophyta. The Solenoporaceae is a heterogeneous group (Brooke and Riding, 1998). Some affinity has been made with the corallines (Brown, 1894), however, the cells of *S. jurassica* are too large for it to be a normal coralline alga, so it has been suggested that it may be an ancestral coralline (Riding, pers. comm.). Corallines are are only properly known from the early Cretaceous onwards (see 7.3.3 Jurassic corallines), but appear also to have Ordovician and Silurian representatives (Brooke and Riding, 1998). If this is true, then the Jurassic *S. jurassica* cannot be an ‘ancestral’ coralline but more of a periodically successful ‘branch’ from the coralline lineage. This ‘branching’ from a core Rhodophyte lineage has consequences for other problematic Rhodophyta (e.g. *Marinella lugeoni* – see 7.3.4).

**7.4 Changes to Dragastan taxonomy**

Some Jurassic algae have been plotted in this work in a different group to that assigned by the author of the references (in this case Dragastan O.). This change has been made due to the belief held by the author that they have been misassigned.

The nine genera concerned (covering 31 species) – see Table 7.7 - were all included in the Codiaceae (Chlorophyta) as it was believed that they showed siphonous characteristics of an ordered nature. “...calcereous nodular thalli composed of
tubular filaments, more or less packed and branched...” “Porostromata” (Mancinelli and Ferrandes, 2001).

This assignment is dubious and I believe incorrect. The majority of the genera have, in this work, been put into the Cyanophyta with some consigned to the Microproblematica (Incertae sedis) while others have been left tentatively in the Codiaeae (Halimedaceae).

This reassignment is necessary due to the original assignments being a relic of the time when all algae with a well defined thallus, composed of radiating and often branching tubes (e.g. the Cayeuxiids) were attributed to the Codiaeae (or Udoteaceae of the order Caulerpales). However, modern representatives such as Halimeda exhibit a highly differentiated thallus composed of medullary and cortical filaments arranged at a distinct angle to each other. It is for this reason that many of the classical ‘bush-like’ fossil Codiaeae (e.g. Cayeuxia and Ortonella) are now grouped within the Cyanobacteria (Rivulariaceae) (Leinfelder and Werner, 1993).

The proposed reassignments are shown in Table 7.7:

<table>
<thead>
<tr>
<th>Genus</th>
<th>Number of species</th>
<th>Now assigned as</th>
<th>Dragastan references</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bacinellacodium</td>
<td>1</td>
<td>Microproblematica</td>
<td>1985</td>
</tr>
<tr>
<td>Bevocastria</td>
<td>3</td>
<td>? Halimedaceae (no affective change)</td>
<td>1985, 1989a</td>
</tr>
<tr>
<td>Bicajiella</td>
<td>1</td>
<td>Cyanobacteria</td>
<td>1988</td>
</tr>
<tr>
<td>Bicasia</td>
<td>3</td>
<td>Cyanobacteria</td>
<td>1988</td>
</tr>
<tr>
<td>Carpathocodium</td>
<td>1</td>
<td>? Halimedaceae (no affective change)</td>
<td>1985</td>
</tr>
<tr>
<td>Fagetiella</td>
<td>1</td>
<td>Cyanobacteria</td>
<td>1988</td>
</tr>
<tr>
<td>Garwoodia</td>
<td>7</td>
<td>Microproblematica</td>
<td>1985, 1987, 1989a</td>
</tr>
<tr>
<td>Hedstroemia</td>
<td>14</td>
<td>Cyanobacteria</td>
<td>1985, 1989a</td>
</tr>
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<td>1988</td>
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<td>Cyanobacteria</td>
<td>1989a</td>
</tr>
<tr>
<td>Scotlandella</td>
<td>2</td>
<td>Cyanobacteria</td>
<td>1985</td>
</tr>
<tr>
<td>Tethysicodium</td>
<td>1</td>
<td>? Halimedaceae (no affective change)</td>
<td>1985</td>
</tr>
</tbody>
</table>

Table 7.7 Dragastan algal affinity reassignments.
7.4.1 *Cay euxia* Frollo / *Rivularia* (Roth) Agardh

*Cay euxia* is a common Jurassic calcified cyanobacterium (see Plate 7.4) that, together with Palaeozoic *Botomaella* and *Hed stroemia*, resemble extant rivulariaceans:

Hed stroemia group –
*Hedstroemia* (Rothpletz) - resembles recent calcareous Rivulariacean cyanobacteria.
*Botomaella* (Korde) - resembles recent calcareous Rivulariacean cyanobacteria.
*Cay euxia* (Frollo) - resembles recent calcareous Rivulariacean cyanobacteria.
*Ortonella* (Garwood) – resembles some species of *Scytonema* (cyanobacteria).

(after information in Riding, 1991)

Dragastan (1988a) uses the name *Rivularia* instead of *Cay euxia* for this Jurassic fossil – while comparison between these two organisms is correct, it would be best to use the fossil names to “distinguish these calcified skeletons from extant cyanobacteria whose diagnoses are based on details of soft organic tissues and not on hard parts.” (Riding, 1991). Dragastan also oversubdivides the taxonomy of these fossils based on the angles of divergence of the branches of tubes (Dragastan, 1985, 1988a&b, 1989)

7.5 Conclusions and plot assignment

The present-day calcified cyanobacteria are found in CaCO₃ supersaturated freshwater. When comparison is made with the fossil marine varieties, it would be expected that a similar supersaturated water requirement would be evident via a restriction to the ‘tropical’ areas. For the Jurassic, the distribution of calcified cyanobacteria can be seen to become confusing with time during the Jurassic. Figure 7.1 shows the distribution and main limit of Cyanobacteria during the three stages of the Jurassic. The Lower Jurassic shows some similarity with chlorophyte limits but with a retardation of the limit in the western part of Europe. The cause of this increased limit is not known for sure and may be a fossil bias limitation for it is not seen in the other stages. Mid Jurassic distribution is very similar to the Dasycladales, but in both algaes’ cases there are limited data to extend the limit into the eastern part of Europe. The Upper Jurassic is a very interesting scenario; as with all of the algal
**Chapter 7 Systematics of Jurassic calcareous algae**

**Upper Jurassic 150Ma**

It is difficult to establish a distribution limit for the Cyanobacteria in the Upper Jurassic; there appears to be a vague similarity with the Chlorophyta (as before) including some extensions of 'extra-limit' occurrences through the area of the United Kingdom. This may be evidence that at this time there were localized conditions overprinted on the regional trend which allowed for algal habitation in these certain areas outside of that considered normal.

**Mid Jurassic 170Ma**

In the Mid Jurassic, the Cyanobacteria can be seen to be very similar to the Dasyycladales in their distribution. The western offset from the Dasyycladales seen in the Lower Jurassic has disappeared.

**Lower Jurassic 190Ma**

The Lower Jurassic Cyanobacteria can be seen to display a tolerance similar to the Jurassic Dasyycladales. The retardation of the limit in the West may be a result of fossil bias or factor such as palaeocurrent action.

---

**Legend**

<table>
<thead>
<tr>
<th>Species numbers</th>
<th>Algal types</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-2</td>
<td>Dasyycladales</td>
</tr>
<tr>
<td>6-10</td>
<td>Halimedaaceae</td>
</tr>
<tr>
<td>11-19</td>
<td>Cyanobacteria</td>
</tr>
<tr>
<td>20+</td>
<td></td>
</tr>
</tbody>
</table>

Map after Timescale v3.11
Cambridge paleomap services ltd 1998

Fig 7.1 Jurassic Cyanobacteria distribution limits compared to Chlorophyta.
types, the Upper Jurassic has the most information and good definition for the furthest
major species limits for the Chlorophyta (with some ‘extra-limit’ occurrences). The
Cyanobacteria, however, have a moderate (but not insignificant) number of
occurrences outside (North) of the area of the normal limit for calcareous algae. It is
not possible to draw a major limit for the Upper Jurassic Cyanobacteria for producing
a line similar to the Chlorophyta would leave these other occurrences outside of the
‘normal’ limit and there are too many of these occurrences for this to be acceptable.
The alternative, to include all / most of these occurrences as in the normal extent
would bulge the limit northwards in an unbelievable manner which bears no relation
to the situation shown by other calcareous algal forms. It may be that at this time, a
‘corridor’ of localized conditions was formed which is interfering with the regional
trend and thereby masking it. Alternatively, these calcified cyanobacteria in the
‘northern’ areas may be due to marginal marine environments. These marginal
settings include hypersaline and fresh / brackish waters, which calcified cyanobacteria
are known to inhabit, and this may help to explain the odd northern occurrences.

Overall, it can be seen that Jurassic marine Cyanobacteria appear to show an
affinity for warmer water areas as is expected with extrapolations from the modern
scenario (see above), however, there seems to be (as with other algae) localized
situations which change the regional trend in closely outlying areas.

When plotted on the Jurassic maps, all the above taxa are assigned to the
Microproblematica. This is because it allows categorically correct usage of the maps
even if the assignment of the Microproblematica is not agreed by other workers. The
Microproblematica distribution does not produce any surprising or unexplained
spread outside of the ranges of the more easily assigned algal taxa (with the exception
of the Upper Jurassic Scottish occurrences – see Figure 7.2).

Having been plotted as Microproblematica for the benefit of using the maps, it
is the belief of this author that the assignment of the selected microproblematica
above should be that shown in Table 7.8.
Few species spread mostly across 'southern European' sites. These organisms appear to be bounded by the same limitations as the Dasycladales. Their more southerly limit in the West may be a fossil bias relict.

Few species spread across southern and mid 'European' sites. The distribution of these Microproblematica mirrors that of the Dasycladales.

A large flora spread throughout modern Europe, whose limit fits between the two chlorophyte limits, and with a few sites in western Scotland - this is further North than Chlorophyta are found and may indicate a Cyanobacterial or zoological rather than algal affinity.
<table>
<thead>
<tr>
<th>Microproblematica</th>
<th>Assignment</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Tubiphytes</em>&lt;br&gt;(Shamovella)</td>
<td>A possible poriferan or symbiont-bearing miliolid foraminifer.</td>
<td>Riding and Guo, 1992 and Schmid and Leinfelder, 1996</td>
</tr>
<tr>
<td><em>Baccinella irregularis / Lithocodium aggregatum</em></td>
<td><em>Lithocodium aggregatum</em> is a Loftusiid foraminifer, usually with a commensal relationship with <em>Troglotella incrustans</em> (telaminid foraminifer). <em>Baccinella irregularis</em> is still enigmatic but is a different organism.</td>
<td>Schmid and Leinfelder, 1996</td>
</tr>
<tr>
<td>Jurassic Corallines</td>
<td>Coralline, part of a link of modern corallines and Palaeozoic ‘ancestral corallines’.</td>
<td></td>
</tr>
<tr>
<td><em>Marinella lugeoni</em></td>
<td>A red alga, neither Corallinaceae or Solenoporaceae but somewhere in between.</td>
<td>Leinfelder and Werner, 1993</td>
</tr>
<tr>
<td><em>Thaumatoporella parvovesiculifera</em></td>
<td>A possible Coralline red alga</td>
<td></td>
</tr>
<tr>
<td><em>Algites</em></td>
<td>Non-calcified algal impressions.</td>
<td>Teslenko, 1982</td>
</tr>
<tr>
<td><em>Solenopora jurassica</em></td>
<td>Should be called <em>Solenoporella jurassica</em> and is possibly an offshoot from an ancestral coralline lineage</td>
<td></td>
</tr>
<tr>
<td><em>Cayeuxia / Rivularia</em></td>
<td>Nomenclature should call this fossil <em>Cayeuxia</em>.</td>
<td></td>
</tr>
</tbody>
</table>

Table 7.8 My considered assignment of selected microproblematica.
Ch. 8 Other Palaeoclimatic Indicators

There are other registers of palaeoclimatic information that can be used to elucidate Jurassic sea surface temperature. These other indicators offer an analytical tool for palaeoenvironmental reconstruction that can give both qualitative and in some cases quantitative analysis. They are useful in combination to give an overview of all data reconstruction, and in isolation as a tool for screening / verifying other data.

8.1 Aims

1. To document non-algal palaeoclimatic information for the Jurassic in western Europe.
2. To compare the authors algal work with these other results on Jurassic palaeoclimate.

8.2 Alternative palaeoclimatic markers

Other indicators include:

1. Other organisms.
   - Foraminifera
   - Ammonites
   - Belemnites
   - Corals
   - Ostracodes
   - Sponges
   - Biodiversity
2. Temperature sensitive deposits.
3. Oxygen isotope values.
4. General Circulation Models (GCMs).
8.2.1 Other organisms distribution analysis.

There have been a number of organisms, in the geological past, that have been used to define biogeographic zones. In the Jurassic, the three faunas that are generally referred to for the marine realm are foraminifers, ammonites, and belemnites. It is from faunas such as the ammonites that the division of the northern "Boreal" area and the southern "Tethyan" regions has been deduced (Arkell, 1956).

From studies of general invertebrate assemblages it can be seen that important geographic differences in the distribution of marine Jurassic faunas only become apparent in the Upper Jurassic.

Foraminifers

A useful text on the foraminifera is that of Gordon (1970). In this work he states: "Faunal realms or provinces similar to those established for some other groups of invertebrate animals [ammonites and belemnites] in the Jurassic do not seem to be appropriate for the foraminifera." That is to say that foraminifers cannot delineate provinces, only faunal assemblages roughly within the provinces defined by other fauna. There tends to be an intermingling of the assemblages at the boundary of the Tethyan and Boreal realms which in itself shows signs of fluctuating over time (Figure 8.1).

![European faunal distribution in the Kimmeridgian on a modern plate setting and geography.](image)

Fig. 8.1. European faunal distribution in the Kimmeridgian on a modern plate setting and geography.

(after Gordon, 1970)
If the Tethys seaway was situated roughly along the Jurassic tropical belt, the
distribution of the foraminifers could be attributed (at least partly) to latitudinal
(temperature) factors. This situation would have the Tethyan faunas representing
tropical assemblages and the shelf faunas to the north and south of the Tethys
denoting subtropical to temperate conditions.

While the Tethyan area was a zone of relatively warm conditions, it must be
noted that the climatic gradation from the equator to the poles was more gradual in the
Jurassic than at present. With paleotemperature data indicating an equatorial-polar
difference of 15°C (or at most 20°C) in mean annual temperature, this means that
although water temperature was as significant a biogeographic control in the Jurassic
as it is today, its influence was not as acute because of the greater uniformity of
climate over the Earth (Gordon 1970). This is to say that the Jurassic climate was less
variable than the modern day and therefore cold-intolerant biota appear to have
extended over a greater latitudinal range (Hallam 1994).

Ammonites

Ammonites have traditionally been a source of information pertaining to
Mesozoic biogeography. The major ammonite zones were globally influenced by the
temperature of the water with the latitudinal zonation being duplicated in the Northern
and Southern hemispheres (Craig, 1961). Ammonite data have been used to show that
temperate faunas in Greenland mean that there were no ice caps in the Jurassic world,
and that in the Lower Jurassic and Bajocian, temperate and equatorial faunas spread
northwards while in the Early Callovian, the boreal fauna spread southwards from the
Arctic ocean towards the Mediterranean (Arkell, 1956).

Belemnites

As well as being used in a similar biogeographic manner to ammonites,
belemnites also provide isotopic data which is used for quantitative temperature
analysis (see 8.2.3).

A traditional interpretation is that, since the boundary between the Tethyan –
Boreal realms (for both ammonites and belemnites) roughly follows latitude, the
Boreal Realm must signify a cooler climate (Hallam, 1998). There are, however, a
number of arguments against this (Doyle, 1987). Unlike at the present day, when
diversity is reduced significantly towards the poles in virtually all groups of
organisms, belemnite diversity appears to increase northwards from the Boreal-
Atlantic to the Arctic Province. Also, Arctic endemic belemnites are not strictly
confined latitudinally, but extend down the western side of North America as far as
Mexico, where they are mixed with Tethyan ammonites (Doyle, 1987). Evidently the
Tethyan-Boreal divide is not truly temperature-related and other, palaeogeographic,
factors must have been important (Hallam, 1998).

Latitudinal temperature gradients were not the overall control on the
development of Boreal and Tethyan belemnite realms, instead the Boreal-Atlantic
area (European Archipelago) was an effective barrier to the migration of Tethyan
belemnites to the Arctic and vice-versa. "... presence of fluctuating environmental conditions
around the "European Archipelago" is seen as sufficient to restrict the movement of certain
stenotopic belemnite genera, ..." (Doyle, 1987).

Coral

Another group of organisms that provides some interesting distributions is that
of hermatypic corals. Hermatypic corals are those scleractinian "stony" corals that are
reef-building in nature. Present day forms occur in 'warm-water' conditions due to the
fact that they are zooxanthellate (i.e. their endodermal tissues contain symbiotic
unicellular algae (Rosen 1975)). These dinoflagellate algae in the modern day are
restricted in distribution due to certain parameters:

- Salinity – c36%
- Temperature – 18-29°C (stenothermal)
- Depth – less than c70m (provides for a minimum level of illumination for
  zooxanthellae to photosynthesise)

(After Beauvais 1973 and Rosen 1981)

Although reef corals are limited to the tropics today by temperature, their
development is patchy in tropical areas of constant temperature, indicating that other
factors must also be important (Hallam, 1969).

Insalaco (1996) reported an attempt to "... assess the potential value of Mesozoic
sclerochronology as a tool for palaeoenvironmental and palaeoclimatic interpretations." That work
found no noticable systematic palaeolatitudinal changes in the nature of the growth
banding or the growth rate. This may be due to a more equable Jurassic climate than
at present, and this possibility was put forward as a potential reason for the lack of
any decrease in regional average temperature (and solar radiation) which would result in a decrease in growth rate with increasing palaeolatitude revealed in the data. The spread of coral reefs as far north as Scotland, which lay at approximately 43°N in the Mid Jurassic, contrasts strongly with the present-day limits of reef growth which lie approximately 35° N and S of the Equator (Rosen, 1981). Therefore the lack of large variations in growth rates between the regions (all of which lie within a broad mid-latitude climatic belt) might be accounted for by the small differences in palaeolatitude between the localities, and equable palaeoclimate.

During the Kimmeridgian, however, the northern limit of coral reefs seems to have migrated southwards across Europe, possibly indicating the advent of colder waters (Arkell, 1956; Craig, 1961). The extent of the North Tethys coral reefs dramatically expanded through the Jurassic, from rare early Jurassic occurrences due to the effects of the end Triassic extinction event, to a moderate distribution in the Mid Jurassic because of poor habitat availability, and a great abundance in the late Jurassic with increasing habitat availability (Leinfelder, 1994b). This increase through the Jurassic mirrors the effects of the general Jurassic sea level rise which was governed by the initial breakup of Pangea (Leinfelder, 1994b).

The Upper Jurassic hermatypic coral distribution across Europe is shown in Figure 8.2. This seems to show a general distribution across all the Jurassic outcrops of Europe. The modern global coral zone is within the latitudes that are taken to mark tropical – subtropical areas and can be seen in Figure 8.3. The Jurassic coral reefs are associated with large sponge-dominated reefs across Europe (see sponges below) and also formed small patch reefs on the northern fringes (Crame, 2002). The northern, higher latitude presence of coral reefs and reef corals in the Tithonian has been surmised as indicative of the presence of large tropical current gyres (Beauvais, 1973; Hallam, 1975; and Crame, 2002). Jurassic high-latitude coral reefs (e.g. Scotland) – see Figure 8.2 - are a problem in their distribution compared to the algae. It is unknown if these are true reefs or isolated associations of colonial corals, but are still used as evidence for an equilibrated, balanced climate (at least in the late Jurassic) possibly brought about by the high sea level leading to buffered temperatures (and also reduced circulation) (Leinfelder, 1994b).
Ostracodes

The development of marine ostracode palaeobiogeography in Central and Western Europe parallels a suggested cooling trend. During the Oxfordian, Kimmeridgian and Tithonian, the growing diversification of ostracode palaeobiogeography and an increase in the degree of endemism has been observed (Schudack, 1999) (see Figure 8.4). From the Kimmeridgian into the Tithonian there is also a gradual southerly migration of many species from the subboreally influenced areas in the northwest towards the margin of the Tethys in the southeast. The genus *Cytherelloidea*, an indicator of relatively warm water temperatures, shifts its northern boundary of occurrence towards the south during the Kimmeridgian and Tithonian (see Figure 8.5) - living species of *Cytherelloidea* are bounded by latitudes of 40°S and 37°N – surface water monthly mean temperatures never drop below 10°C (Schudack, 1999).

A suggested increase in the influx of cold boreal waters into central Europe at the beginning of the Tithonian, leading to slightly colder temperatures in the shallow seas would explain the cooling trend and subsequent retreat of the ostracode species. However the slight cooling trend of water temperatures in the Late Jurassic opposes the trend observed by palaeobotanists (see 8.2.2).

Sponges

In the Jurassic, sponges were at their most diverse (being of hexactinellid, hyalosponge and less commonly, lithistid groups), and during the Late Jurassic they were the major reef builders (Ghiold, 1991) (today that role is occupied by the corals). During the Upper Jurassic, a zone of large sponge reefs was present through central and southern Spain, SE France, Switzerland, SW Germany, Central Poland and E Romania and was, at peak growth, at 150m depth (Ghiold, 1991) which is much deeper than the depth range of Dasycladales. Ghiold (1991), states that in this reef setting:

“Lithistids were common in the early stages of the reef’s formation, but their dominance decreased dramatically as the number of hyalosponges increased later. The changes may have come from gradual shifts in the climate, perhaps in sea temperature.”
Fig. 8.4. Ostracode palaeobiogeography of Late Jurassic in Central and Western Europe. (From Schudack, 1999) Lines = boundaries between subprovinces, arrows = exchange areas.
Fig. 8.5. Southward migration of the Thermomorphic ostracode Cymellidionda. (From Schudack, 1999)
Biodiversity

The use of biodiversity in palaeontological studies has begun to advance recently (e.g. Markwick, 2002 for terrestrial fauna), and it has been said by Ostrom (1970) that 'latitudinal species diversity (richness) gradients might provide a better tool for retrodicting palaeoclimate than comparison of an individual fossil with the climate of its living relative'.

Crame (2002) has looked into the Tithonian latitudinal gradients of bivalve faunas and recorded (on a much smaller magnitude than that of the present day) the steep fall in values at the temperate / tropical boundary. This drop in diversity, locates the tropical / temperate divide in the northern hemisphere as 36°N (compared to todays 23°N). He has also shown a similar profile in Tithonian gastropods which points towards the edge of the Tithonian tropics being marked by a sharp decline in diversity – as is the case today.

8.2.2 Temperature sensitive deposits

There are certain 'deposits' that, if found in an area, could be used to indicate relative climatic situations present at that site at the time of their occurrence. It has been said that certain sedimentary facies on their own provide ambiguous but, qualitative Mesozoic climate (and climate change) information, as well as providing important criteria for the testing and refinement of palaeoclimate models (Sellwood and Price 1994).

The deposits which are of use can be seen in Table 8.1:
<table>
<thead>
<tr>
<th>Regime</th>
<th>‘Deposit’</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry to wet and cool (cool temperate to cold)</td>
<td>Tillite</td>
<td>Boulder clay glacial deposit</td>
</tr>
<tr>
<td>Cool and dry (cold)</td>
<td>Dropstone</td>
<td>Glacially transported material deposited in a marine setting (ice over sea)</td>
</tr>
<tr>
<td>Cool and dry (cold)</td>
<td>Glendonite</td>
<td>Ikaitite pseudomorphs (low-temperature polymorph of calcium carbonate [CaCO₃·6H₂O] crystallises at 0°C)</td>
</tr>
<tr>
<td>Dry and warm (arid)</td>
<td>Evaporite</td>
<td>Mineral crystallisation where evaporation exceeds rainfall and rate of water inflow</td>
</tr>
<tr>
<td>Dry and warm (arid)</td>
<td>Calcrete</td>
<td>Nodular to massive carbonate soil</td>
</tr>
<tr>
<td>Dry and warm (arid)</td>
<td>Aeolianite</td>
<td>Wind blown sand dunes</td>
</tr>
<tr>
<td>Warm to cool and wet (tropical)</td>
<td>Coal</td>
<td>Vegetation deposited in areas of terrestrial humidity (precipitation exceeds evaporation)</td>
</tr>
<tr>
<td>Warm and wet (tropical)</td>
<td>Laterite</td>
<td>(also ferriferites) soil of humid tropical climates with a long dry season</td>
</tr>
<tr>
<td>Warm and wet (tropical)</td>
<td>Bauxite</td>
<td>Al-rich laterite plus karstic infills from such sources</td>
</tr>
<tr>
<td>Warm temperate</td>
<td>Kaolinite</td>
<td>Intensive leaching conditions in acid soils in a climate of high temperatures and precipitation</td>
</tr>
<tr>
<td>Warm temperate</td>
<td>Crocodiles</td>
<td>Reptilian vertebrates requiring warm, partially aqueous areas</td>
</tr>
<tr>
<td>Warm temperate</td>
<td>Palms and Mangroves</td>
<td>Frost intolerant plants.</td>
</tr>
</tbody>
</table>

Table. 8.1. Temperature sensitive deposits. (after Scotese 2000)

Such deposits have been used by Scotese (2000) in the Paleomap project, and give rise to maps from which the climatic scenario at the time may be deduced (Figure 8.6).

From these maps, a chronology of temperature change can be derived (see Figure 8.7):

Fig. 8.7. Mesozoic temperature curve. (after Scotese, 2000 and Gradstein et al, 1994)

This temperature curve throws up an interesting scenario; the curve is an average global temperature (which means it is no use for differentiating temperature
controlled zones on the face of the Earth), and is at a constantly higher temperature in the Mesozoic than is the case for the present day (normally about 9.5°C higher than present). However, at the end of the Jurassic (and into the early Cretaceous) there is an abrupt and large decrease in the global average temperature. This drop (in the region of 6°C) is at the time where most organisms, including the calcareous algae, show an increase in their distribution, which is the opposite of what would be expected with a worldwide temperature decrease. The cause of the decrease in the temperature shown on the graph is not known; it appears that the graph has been plotted from almost exclusively terrestrially based data of temperature sensitive deposits (Scotese, 2000) and therefore is difficult to compare to the other data obtained in this work.

There are a few other temperature sensitive deposits that deserve mention here:

The mere occurrence of tropical-style or "Bahamian-type" carbonates can be used as a rough proxy for general temperature-mass approximations in the past.

Most of the shallow shelf Mesozoic carbonates are found in the palaeosubtropics (5-35°N and S) with 99% of occurrences occurring within 45° of the equator (Hallam, 1994). It is interesting to note that the carbonate belt does not expand poleward during warmer intervals, thereby showing that temperature alone is not the limiting factor. However year-round light refraction falls off markedly at about 35° from the equator, the present poleward limit of Bahamian-type environments, and this depositional system relies, either directly or indirectly, on algal fixation of CaCO3. Therefore light penetration appears to be the latitude-limiting factor influencing carbonate distribution (Hallam, 1994).

The remains of land plants and pollen can help provide information on the terrestrial zonation of the Earth in the past, and this can be tentatively linked to the marine realm.

Pollen remains from the southern North Sea region indicate subtropical temperatures in the Late Callovian to Early Oxfordian (Abbink et al, 2001). The plant remains present a problem in the Jurassic - Vakhrameev (1991) shows evidence that
the subtropical forest belt of the former USSR and Asia advanced 15-20° northwards during the Early – Middle Oxfordian indicating a warming period. This form of evidence is usually regarded as reasonably indisputable for indicating temperature change, however, as previously stated (Ostracode section of 8.2.1) this change in terrestrial pattern is in direct opposition to an apparent cooling trend shown in the marine realm.

8.2.3 Oxygen isotopes

Using oxygen isotope ratios in skeletal material to interpret palaeotemperatures was instigated by Urey (1947) and Epstein et al (1953) and is now extensively used and documented (e.g. Marshall 1992, Hudson and Anderson 1989). The premise of the method is that the ratio of δ¹⁶O and δ¹⁸O oxygen isotopes in calcium carbonate is temperature dependent and this ratio can be preserved and recorded when precipitated into a carbonate from solution.

The possibilities for inaccuracy arise mainly from the three assumptions needed for isotopic analysis:
1. Isotopic composition of seawater is assumed to have been the same as at present.
2. Organisms have secreted CaCO₃ in isotopic equilibrium with seawater.
3. Isotopic exchange subsequent to precipitation of the CaCO₃ is negligible.

(Hallam, 1975)

There are problems that can occur, for instance when the lithology has been affected by post-depositional isotopic exchange by diagenesis - serious doubt has been cast on the adequacy of oxygen isotope measurements obtained from Jurassic marine shells because of the problems of meteoric diagenesis (Hallam 1994). The oxygen isotopic composition of Mesozoic and older seawater is a greatly debated subject, one side disputes that an original marine isotope signal can be preserved in such old calcites, while those accepting the possibility of signal preservation, disagree as to the causes of the observed δ¹⁸O depletion in the course of the Phanerozoic (Podlaha et al, 1998). The possible explanations range from changing isotopic composition of past seawater to progressively warmer and / or more stratified ancient
oceans. However the problem with isotope signals remains as the oxygen isotopic composition of carbonates does becomes progressively more depleted in $\delta^{18}O$ with increasing age of the rocks as well as the advancing diagenetic recrystallization of carbonate results in $\delta^{18}O$ depletion (Veizer et al, 1999).

There is a dispersion of stable isotope values of several permil for any given time period; is this an inherent feature of the low-Mg calcitic belemnite rostra, as in the modern brachiopods? If so is it due to palaeoenvironment parameters or hypothesized species specific isotopic fractionation? Due to the belemnites being extinct, we do not know if isotopic fractionation was associated with rostra secretion and therefore, cannot know how much of the observed scatter could be due to this factor. It is suggested that the most likely scenario is that the $\delta^{18}O$ temporal trend and the spread of values reflect the temperature and / or salinity variations of belemnite habitats (Podlaha et al, 1998).

Another problem is the action of “vital effects” – the original values of the isotopes can vary according to a variety of influences apart from temperature, which can be controlled by the organism itself.

From the multitude of fossil types, one of the best for isotopic composition analysis appears to be belemnites (others are used e.g. ammonite aptchi). This is because the most commonly preserved part of a belemnite, the rostrum, is composed of stable, megascopic, radially arranged calcite which can show visually any alteration (Bowen 1961a). The other fossil types that are regularly used for isotopic analysis include foraminifers and brachiopods.

In addition, the pH of seawater can have an influence on isotopic analysis. For example, reconstructions based on foraminifer $\delta^{18}O$ may underestimate sea surface temperatures, as shown on mid Cretaceous material being $\sim 2 - 3.5°C$ higher than previously thought (Zeebe, 2001). The scenario is that higher CO$_2$ in the atmosphere will reduce the pH of the oceans which would increase the fractionation between the shell calcite and the water which would result in isotopically heavier shells and therefore erroneously interpreted lower temperatures (Zeebe, 2001).

Relevant isotopically derived palaeotemperatures can be found in the literature (e.g. Price and Sellwood 1994, Bowen 1961a&b etc.) see Figure 8.8. and Table 8.2. Much local data is presented and from this is hypothesised general situations, e.g.
Recent reconstructions show postulated palaeocontinental areas which show the proximity to land of the isotopic samples (which may be a factor in their values).

Fig. 6.2. Oxygen isotope data from European Jurassic European palaeocontinental images. Information from: Brand (1986), Bowern (1961), Hesseldao et al. (2000), Patterson (1999), Pickard et al. (1996), Price and Seilwood (1996).
<table>
<thead>
<tr>
<th>Broad age (Malm)</th>
<th>Stage setting</th>
<th>Location</th>
<th>(Av.) Temperature °C</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Jurassic</td>
<td>Tithonian</td>
<td>Vidin (Plešivec), Bulgaria</td>
<td>23.6</td>
<td>Teis et al (1975)</td>
</tr>
<tr>
<td>Kimeridgian to Tithonian</td>
<td>Cala Fornells, SW Mallorca</td>
<td>14.7</td>
<td>Price and Sellwood (1994)</td>
<td></td>
</tr>
<tr>
<td>Lower Kimeridgian</td>
<td>Hundertwasser, Near Streichen, Württemberg, Schwarzwald, Germany</td>
<td>21.0</td>
<td>Bowen (1961a &amp; b)</td>
<td></td>
</tr>
<tr>
<td>Upper Oxfordian</td>
<td>Rodoch near Perte à Bovay, Kanton du Vaud (Prealps), Switzerland</td>
<td>26.7</td>
<td>Bowen (1961b)</td>
<td></td>
</tr>
<tr>
<td>Upper Oxfordian</td>
<td>Brauneck near Aarau, Kanton Aargau, Switzerland</td>
<td>24.4</td>
<td>Bowen (1961b)</td>
<td></td>
</tr>
<tr>
<td>Oxfordian</td>
<td>Huntingdon, Britain</td>
<td>21.4</td>
<td>Bowen (1961b)</td>
<td></td>
</tr>
<tr>
<td>Oxfordian</td>
<td>Calvert pit, SW Oxford, Britain</td>
<td>23.9</td>
<td>Bowen (1961b)</td>
<td></td>
</tr>
<tr>
<td>Oxfordian</td>
<td>Arc, Doubs, France</td>
<td>23.1</td>
<td>Bowen (1961b)</td>
<td></td>
</tr>
<tr>
<td>Oxfordian</td>
<td>Pagny, France</td>
<td>19.0</td>
<td>Picard et al (1998)</td>
<td></td>
</tr>
<tr>
<td>Upper Jurassic (Dogger)</td>
<td>Mid Jurassic</td>
<td>Lubaczow near Lwów, SE Poland</td>
<td>27.7</td>
<td>Bowen (1961a &amp; b)</td>
</tr>
<tr>
<td>Callovian</td>
<td>Skye, Scotland</td>
<td>16.5</td>
<td>Price and Sellwood (1994)</td>
<td></td>
</tr>
<tr>
<td>Callovian</td>
<td>Łukow, Poland</td>
<td>12.5</td>
<td>Brand (1986)</td>
<td></td>
</tr>
<tr>
<td>Callovian</td>
<td>Dijon, France</td>
<td>24.0</td>
<td>Picard et al (1998)</td>
<td></td>
</tr>
<tr>
<td>Mid Callovian</td>
<td>Mihaylovgrad (Gaganica), Bulgaria</td>
<td>25.8</td>
<td>Teis et al (1975)</td>
<td></td>
</tr>
<tr>
<td>Upper Bajocian</td>
<td>Vidin (Belotinci), Bulgaria</td>
<td>20.1</td>
<td>Teis et al (1975)</td>
<td></td>
</tr>
<tr>
<td>Bajocian</td>
<td>Eigg, Inner Hebrides, Scotland</td>
<td>23.0</td>
<td>Patterson (1999)</td>
<td></td>
</tr>
<tr>
<td>Bajocian</td>
<td>Vanvey, France</td>
<td>27.3</td>
<td>Picard et al (1998)</td>
<td></td>
</tr>
<tr>
<td>Bajocian</td>
<td>Bessent Park, N of Bayeux, Normandy, France</td>
<td>20.7</td>
<td>Bowen (1961b)</td>
<td></td>
</tr>
<tr>
<td>Upper Bajocian</td>
<td>Vidin (Belotinci), Bulgaria</td>
<td>16.0</td>
<td>Teis et al (1975)</td>
<td></td>
</tr>
<tr>
<td>Bajocian</td>
<td>1Km N of Sully, Normandy, France</td>
<td>20.5</td>
<td>Bowen (1961b)</td>
<td></td>
</tr>
<tr>
<td>Bajocian</td>
<td>Coulouges-sur-l’Auise, France</td>
<td>21.4</td>
<td>Bowen (1961b)</td>
<td></td>
</tr>
<tr>
<td>Mid Bajocian</td>
<td>Etropol, Bulgaria</td>
<td>34.8</td>
<td>Teis et al (1975)</td>
<td></td>
</tr>
<tr>
<td>Lower Bajocian</td>
<td>Teteven, Bulgaria</td>
<td>30.1</td>
<td>Teis et al (1975)</td>
<td></td>
</tr>
<tr>
<td>Aalenian to Bajocian</td>
<td>Guerschoten, Alsace, France</td>
<td>20.1</td>
<td>Bowen (1961b)</td>
<td></td>
</tr>
<tr>
<td>Lower Jurassic (Lias)</td>
<td>Upper Liassic</td>
<td>Whirby, Yorkshire, Britain</td>
<td>31.7</td>
<td>Bowen (1961b)</td>
</tr>
<tr>
<td>Upper Toarcian</td>
<td>Teteven (Polaten), Bulgaria</td>
<td>33.2</td>
<td>Teis et al (1975)</td>
<td></td>
</tr>
<tr>
<td>Upper Toarcian</td>
<td>Sofia (Bov), Bulgaria</td>
<td>37.8</td>
<td>Teis et al (1975)</td>
<td></td>
</tr>
<tr>
<td>Toarcian</td>
<td>Northampton, Britain</td>
<td>26.3</td>
<td>Bowen (1961b)</td>
<td></td>
</tr>
<tr>
<td>Toarcian</td>
<td>Thoars, Deux Sèvres, France</td>
<td>24.9</td>
<td>Bowen (1961b)</td>
<td></td>
</tr>
<tr>
<td>Toarcian?</td>
<td>Sulz, Fricktal, Kanton Aargau, Switzerland</td>
<td>27.3</td>
<td>Bowen (1961b)</td>
<td></td>
</tr>
<tr>
<td>Toarcian?</td>
<td>Le Tabousset, at the Hongrin river, Kanton du Vaud (Prealps), Switzerland</td>
<td>23.4</td>
<td>Bowen (1961b)</td>
<td></td>
</tr>
<tr>
<td>Toarcian?</td>
<td>Les Puys, W of Tremettaz, Alpes Fribourgeoises, Kanton de Freibourg, Switzerland</td>
<td>23.5</td>
<td>Bowen (1961b)</td>
<td></td>
</tr>
<tr>
<td>Lower Toarcian</td>
<td>Teteven, Bulgaria</td>
<td>31.5</td>
<td>Teis et al (1975)</td>
<td></td>
</tr>
<tr>
<td>Upper Pleinsbachian</td>
<td>Sofia (Zimevica), Bulgaria</td>
<td>29.5</td>
<td>Teis et al (1975)</td>
<td></td>
</tr>
<tr>
<td>Upper Pleinsbachian</td>
<td>Sofia (Bukorovci), Bulgaria</td>
<td>20.6</td>
<td>Teis et al (1975)</td>
<td></td>
</tr>
<tr>
<td>Upper Pleinsbachian</td>
<td>Aytos (Transak), Bulgaria</td>
<td>28.1</td>
<td>Teis et al (1975)</td>
<td></td>
</tr>
<tr>
<td>Upper Pleinsbachian</td>
<td>Sofia (Ginci), Bulgaria</td>
<td>27.7</td>
<td>Teis et al (1975)</td>
<td></td>
</tr>
<tr>
<td>Pleinsbachian</td>
<td>St. Vincent Herlanges, Vendee, France</td>
<td>24.5</td>
<td>Bowen (1961b)</td>
<td></td>
</tr>
<tr>
<td>Lower Pleinsbachian</td>
<td>Sofia (Berende-Izvor), Bulgaria</td>
<td>23.1</td>
<td>Teis et al (1975)</td>
<td></td>
</tr>
<tr>
<td>Sinemurian/ Pleinsbachian</td>
<td>Wine Haven, Robin Hood’s Bay, N. Yorkshire</td>
<td>17.5</td>
<td>Hesselbo et al (2000)</td>
<td></td>
</tr>
</tbody>
</table>

Table 8.2 European Jurassic isotope temperatures.
"... in the Jurassic the earth had larger tropical and semitropical belts than at present, with an equatorial region running through the U.S.A. and Europe..." (Bowen 1961b). This data is uncritically stated in order to show all the data; critically reassessed data is used in palaeotemperature reconstructions (see section 8.4.8.1).

There is another use of oxygen isotopes in palaeotemperature reconstructions; the differences found between them can be used to reconstruct whether the carbonate is of a temperate / cool-water or tropical / warm-water environment. This has been shown in the modern day for the Lacapede Shelf in Australia (Rahimpour-Bonab et al, 1997). The study of suitable organisms (azooxanthellate corals, coralline algae and bryozoans) has shown that the isotopic ratios for similar organisms are different from one environment to another, and that diverse organisms living in the same environment may have dissimilar isotopic values due to either metabolic processes or fractionation during calcification (Rahimpour-Bonab et al, 1997). Using the following palaeotemperature equations it is said that $\delta^{18}O_{calc}$ decreases by 1% with every 4°C increase in temperature:

Calcite: \[ T(°C) = 16.9 - 4.38 (\delta c - \delta w) + 0.10 (\delta c - \delta w)^2 \]

Aragonite: \[ T(°C) = 20.6 - 4.34 (\delta^{18}O_{arg} - \delta w) \]

(Rahimpour-Bonab et al, 1997)

A potentially useful geochemical indicator has been put forward in Sr/Ca ratios (in coral aragonite), with an inverse relationship between temperature and the uptake of strontium relative to calcium (DeVilliers et al, 1994). There is however, a significant spatial and depth variability in Sr/Ca ratios (estimated at <0.2°C for corals in tropical oligotrophic waters and possibly greater in upwelling areas). Also, the two most likely ‘pitfalls’ of Sr/Ca thermometry are:

1. The effect of biogenic cycling of Sr versus Ca in the ocean surface.
2. The effect of a variable extension rate on Sr incorporation in coral aragonite.

(DeVilliers et al, 1994)

This is in addition to the poor preservation potential of Jurassic aragonite.
8.2.4 General Circulation Models

"The hard geological data – the evidence of what the world climate pattern actually was – is necessarily incomplete geographically, temporally, and with regard to important atmospheric parameters (e.g. clouds)." (Allen et al 1994).

This statement suggests the need to develop suitable General Circulation Models (GCMs). There are at present a number of, as yet, insufficiently detailed and complex models that are presently being used. These models "...currently suffer from inadequate or inappropriate parameterizations, over simplistic algorithms, primitive coupled atmosphere-ocean systems, and technological limitations on computing power." (Allen et al 1994). The accuracy of the models is limited by the influences of model boundary condition uncertainties and internal errors (Valdes 1994). The most significant unknowns that affect the model output, and provide model errors, are: palaeogeography, palaeo-orography, sea surface temperatures and ocean heat flux (Sellwood et al, 2000) as well as fundamental problems arising from the incompleteness of the geological record (Price et al, 1997).

A major problem encountered with these models is the modelling of sea surface temperatures (SST) – in general, it is specified using a "...simple, zonally symmetric profile ranging from 27°C in the tropics to 0°C at the poles." (Valdes 1994). This is still, best based on the sparse and potentially unreliable oxygen isotope values (Valdes 1994, Sellwood and Price 1994) especially from planktonic foraminifers arguably the best indicator of ambient sea surface temperatures (Price et al, 1997). It has been said that the errors inherent in supplying the SST field represent a serious limitation to the palaeoclimate modeling of pre-Pleistocene periods (Chandler et al, 1992).

The models are based upon palaeogeographical reconstructions and this can give rise to some lack of resolution, however, this is a minor point compared to other ‘boundary conditions’ as the resolution of the models is only about 4° (Valdes 1994). This is definitely true of the latest Valdes model – a variation [with a new convective scheme] on the UGAMP [Uk university Global Atmospheric Modelling Programme] model.

GCM simulations require data both to specify boundary conditions (e.g. palaeogeography, atmospheric CO₂, ocean temperature) and to evaluate results, but each of these parameters must be kept independent to avoid circularity (Price et al,
1997).

In the modelling of the Late Jurassic, the greenhouse conditions mean it is free of polar ice caps. This may be in part due to the zonally uniform SST of $27^\circ$X cos (latitude) and no change in this with seasons. The distribution of climatically sensitive facies (climate proxies) suggest the UGAMP model is “doing reasonably well” in simulating Kimmeridgian climates (see Figure 8.9) (Sellwood et al, 2000) especially precipitation and mean annual average temperature (Price et al, 1997). These models lead to the derivation of maps such as Figures 8.10 and 8.11 which show the atmospheric trends which are likely to have been present in the Upper Jurassic and which can be compared to the marine data.

Fig. 8.10. GCM map of 2 metre altitude European isocrymes (lines of equal coldest value) in $^\circ$C in the Kimmeridgian. (After maps of Valdes et al, 1999 and Smith et al, 1994).
8.3 Results

This section gathers together what the other indicators actually show about European Jurassic climate and the comparison of these results with the authors algal indications.

8.3.1 Jurassic European climate interpretation from other indicators

Lower Jurassic (Liassic) (Hettangian, Sinemurian, Pliensbachian and Toarcian)

During this time ammonites are seen to spread northwards and the temperature sensitive deposits show the boundary between the supposed warm temperate and tropical boundary (probably the terrestrial border) is to be found in the area of the modern-day English Channel. Overall, the trend appears to show a slight warming.

Mid Jurassic (Dogger) (Aalenian, Bajocian, Bathonian and Callovian)

The small amount of evidence for this time series shows that in the Callovian, the ‘boreal’ area spread southwards; therefore, while the climate was initially similar to the Lower Jurassic, there was a slight cooling trend towards the end.

Upper Jurassic (Malm) (Oxfordian, Kimmeridgian and Portlandian)

This time series has the most climatic evidence of all the Jurassic series. Ammonite, belemnite and foraminifer data show that in the Kimmeridgian, the mid European area was the transition between the ‘Boreal’ and ‘Tethyan’ areas. For the same time, coral reefs (a good indicator at the present day) appear to have migrated southwards, possibly a sign of an influx of colder waters from the ‘Boreal’ area. During all three stages of this series, the ostracode data show a similar southward migration and signs of cooling. However this cooling trend in these marine organisms in the Oxfordian, is opposed by an apparent warming trend in terrestrial flora. Also problematic, the temperature sensitive deposits show a similar setting to the Lower Jurassic – the warm temperate and tropical boundary is to be found in the area of what is now the English Channel. However, continental drift has moved this area slightly North of its previous position which indicates a warming similar to that shown in the plants. Having stated this, the overall setting indicates a cooling trend similar to that shown in the marine realm (see Figure 8.7). A possible explanation for this is the difference between the terrestrial and the marine realms and the great influence
terrestrially related deposits have on the temperature sensitive deposit maps. Overall, in the marine realm (as this is directly relevant to this work) it appears that there was an influx of cooler waters from the ‘Boreal’ area which had the effect of repressing the boundary towards the South.

8.4 Discussion and conclusions

8.4.1 Algae versus foraminifers

The work by Gordon (1970) appears to show a trend for foraminifera (Figure 8.1) which is similar to that of the Halimedaceae for the time period. This trend is of a slightly more ‘southerly’ nature than that shown by the Dasy cladaceae (Figure 6.20).

8.4.2 Algae versus hermatypic corals

The Upper Jurassic zooxanthellate corals are distributed across the whole of Europe (as shown by Beauvais 1973) and occur in areas far in excess of the northerly limit of the algal flora. However there appears to be a slight decrease in the number of localities in the northern European areas and this may tentatively be compared with the decrease in genera numbers with (the decreasing temperature associated with) increasing latitude found in the modern day (Rosen 1981). However, this comparison is speculative due to the fact that the number of localities and number of genera found at those individual localities have only a limited connection. It can be seen that the corals appear to be the only organisms that show a significant change to the scenario produced by the algal flora. This conflict is further discussed in Section 8.4.11.

8.4.3 Algae versus ammonites and belemnites

The most prevalent and preserved fauna of the Jurassic time period is that of the Cephalopods. These animals, represented by both ammonites and belemnites, were numerous and diverse in nature and their genera have been assigned to water-masses, namely Tethyan for the warm-water varieties and Boreal for their cool-water counterparts. This assignment of genera appears to be quite subjective as correlation with living counterparts is impossible as there are no extant genera of these animals. The two orders’ watersheds shows some parallel latitudinal distribution with the algal
limits and with each other (the general orientation is slightly at odds with the algal limit due possibly to the different factors which act upon the nektonic cephalopods and the benthic algae).

8.4.4 Algae versus ostracodes

The ostracode pattern of distribution (northern limit) for the Upper Jurassic (Schudack, 1999) is similar to the Dasycladales limit proposed by the author, if the subboreal ostracodes are excluded. These subboreal ostracodes seem to live in the areas outside of the Dasycladales limit.

8.4.5 Algae versus sponges

The Jurassic sponge reefs are not directly comparable with the algal maps. The reefs are contained within the limit of the algae, but existed at a depth quite far below that of algal habitation (although not as deep as modern sponges live) and so would experience a different temperature environment than the ‘surface’ dwelling algae.

8.4.6 Algae versus biodiversity

The results of the biodiversity trends are a good match for those found with the algae, both showing a similar trend. The postulated transition between the temperate and tropical waters at 36°N palaeolatitude (Crame 2002) found from the biodiversity data is, for the mid European area, at a similar palaeolatitude as the algal distribution limit.

8.4.7 Algae versus temperature sensitive deposits

The obvious feature of the temperature sensitive deposits is that most of them are terrestrially related and as such should reflect a larger temperature range than that of the buffered marine environment. However, if anything, the opposite seems to be the case for both the Upper and Lower Jurassic. The deposits used by Scotese (2000) and the climatic zones to which they are assigned appear to be both reasonable and correct. This means that their distribution and the global zonings derived from them are also reasonable. They indicate that the whole of the main body of Europe, in both the Upper and Lower Jurassic, was on the northern edge of the tropical zone, with the
boundary with the warm temperate zone situated within the area of the English
Channel and northern German coast. This boundary is similar to the northern
distribution limit of the Dasycladaceae. However, the question remains why terrestrial
conditions show a more equable climate than the marine realm.

8.4.8 Algae versus isotope palaeotemperatures

This element of the comparisons is different in as much as the isotopic
information would hopefully give quantifiable evidence to add to the derived
information. This is to say, if the derived Jurassic palaeotemperatures gave a
reasonable structured pattern these values could be applied to the calculated
temperature zones to put qualitative figures on the boundary delineations.

However, the isotopic values for the Jurassic sub-periods show no structured
pattern in their distribution. The values should decrease steadily with a roughly
latitudinally oriented increase, but even allowing for a small error in the figures there
is no way the values obtained could possibly show such a pattern. In two of the sub-
periods, the temperature values are mixed in relation to their distribution from each
other and no apparently reasonable figures can be discerned. The only possible
exception to this is the Mid Jurassic period if some SE European figures are discarded
and then this would leave us with a Dasycladaceae distribution limit for this time of
about 20°C. It would therefore appear that all the isotopic data for the Jurassic cannot
be relied upon to give a figure for algal distribution limits. The reasons for this are:

- Possible diageneric alteration of the calcium carbonate leading to spurious results;
- Limited distribution of applicable specimens leading to aberrant samples being
  regarded as ‘normal’;
- Limited knowledge of non-extant faunas:
  1. Unknown fractionation rate of Belemnites;
  2. Unknown growing period of Belemnites (e.g. seasonal or annual which affects
     which sea temperatures are recorded).
- Regional water temperature variation (‘error’ bars on temperature range figures)
  can be greater than the total range shown on the isotopically derived figures.

It is for this reason that the isotope data is reassessed (see Figure 8.12 and method
below).
Chapter 8 Other Indicators

John Adams PhD thesis

Page 8.12 Assessed oxygen isotope derived Jurassic European palaeotemperatures that lie in with algal temperature scheme.

Isotope selection methodology see section 8.4.8.1.

This diagram Smith et al. (1994) reconstructions of Jurassic Europe were used instead of TimeTrek as in most algal distributions as these reconstructions show postulated palaeocoastlines which shows the proximity and of the isotopic samples (which may be a factor in their values).

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8.4.8.1 Selected isotope methodology

Modern algal temperature value differences (isocrymal to annual average) for the palaeolatitudes of relevance are just under 5°C (determined from a comparison of Figures 5.17 and 5.18), therefore the summer increase in temperature (i.e. the difference between isocryme and maximum) can be stated as c10°C and this change in values based on algae in the Jurassic yields temperatures equivalent to the isotopically derived values. This produces the possibility that the isotopic palaeotemperature values (especially for those creatures used which have no extant versions, e.g. belemnites) may be showing summer maximum temperatures due to seasonal growth instead of average temperatures from year-round growth (see Section 8.4.11).

The method of selection and the usage of the ‘selected’ isotopes was as follows:

1. Convert the prime data (summer °C) to isocryme values via minusing 10°C (which is the relevant amount for the conversion at the palaeolatitudes concerned).
2. Insert the 12°C algally derived isocryme onto the map.
3. Look for obvious isotope inconsistencies and remove them.
4. Produce other palaeoisocrymes from the remaining points (taking into account the number of isotope location points, the dashing/solid nature of the lines according to the amount of support for the lines and the extent of the isocrymal lines spatially, due to the previous point). It should be noted that the isocrymes are accordingly contoured by eye. Another point to be noted is that in reality the palaeoisocrymes cannot go through the land areas, but they do on the maps as it makes them easier to see and follow across the Jurassic European landscape of many islands.

See Figure 8.13 for a diagrammatic representation of the above process producing an isotopic result assessment and palaeoisocryme formation.

The isotope values in Europe can be locally far ranging which means that they must contain certain aberrations – this may be evidence that at least some of them are incorrect, or there may be localized overprinting on a regional trend which could
Fig 9.13 Palaeosol development and palaeosol chronology formation

Unless otherwise stated the palaeosol sites are after Smith et al (1994) and the palaeosol chronology reconstruction maps are after Timetek Vol 11 Cambridge palaeo map services Ltd (1998).

The method of selection and the usage of the "selected" isopoles was as follows:

1. Convert the palaeo data (summer 1°C) to isopole values (6°C) that is the relevant amount for the conversion of the palaeosalinity concerns.

2. Map the 12°C isotherm derived isopole onto the map.

3. Look for obvious isopole inconsistencies and remove them.

4. Reduce other palaeosol signals from the isopole layers, taking into account the number of isopole location points, the clarity and/or nature of the lines and the extent of the isopole charts, due to the previous point. It should be noted that the isopoles are accurately contoured by eye. Another point to note is that in reality the palaeosol charts cannot go through the land areas, but they do on the maps as it makes them easier to see and follow across the Jurassic European landscape of many islands.

The Iso1 - Lower Jurassic isotope, Iso2 = Mid Jurassic isotope, Iso3 = Upper Jurassic isotope, Black line = digital derived 12°C isopole.

Isopole 1 = interpolated isopole - well inferred, Isopole 2 = interpolated isopole - possibly inferred.

The slight differences of the palaeosalinity charts to the isotope figures can be allowed by isopole errors ranges and the possibility of current offset. The lines go through the palaeo land areas for ease of viewing only.
account for some seemingly spurious temperatures. It has been said that the Jurassic
isotope determinations could be used to delineate palaeotemperature trends where
they roughly conform with similar trends from other sources (Frakes, 1986) (see
Figure 8.12 for selected isotope values).

Salinity affecting algal distribution is a possible influence in the Lower
Jurassic – salinity restricts algae and affects O2 isotopes (reduced salinity leads to
more negative isotopic values being produced which results in higher isotopically
stated temperatures ), however a condition of abnormal salinity cannot be true for all
of Europe and not for all of the Jurassic.

The algally derived isocrymal temperature maps also make the Jurassic high
palaeolatitude corals assignment as hermatypic (zooxanthellate) highly questionable
(see Section 8.4.11 for further discussion).

Evidence of palaeocurrents can be found in the literature and this is shown
transposed to my maps in section 8.4.8.3.2.. It is possible to interpret the angle of
offset of the isocrymes from the palaeolatitude as being (at least partially) the result of
these currents actions. The similar scenario is seen in todays ocean (see section
8.4.8.3.1). The Jurassic currents may also affect the linear nature of the isocrymes as
they have been depicted, but there is insufficient data to predict how much the
currents would disrupt them.

The currents and the palaeobathymetric geography of the late Kimmeridgian
can be seen in Figure 8.14 and shows a further reason why, in this late point of the
Jurassic, the French shelf was such an algal rich area.

8.4.8.2 Gradients (isocrymes)
8.4.8.2.1 Modern gradients (Figure 5.17)

Ocean temperature gradients are variable across the globe due especially to the
action of currents; warm currents close the gradients (make them steeper), cold
currents open them (make them shallower). There is also an effect on the gradients
causd by whether the seas / oceans are restricted– e.g. Red Sea, Mediterranean /
Black Sea or whether they are open– e.g. Pacific Ocean, Indian Ocean, Atlantic
Ocean.
After Schwartzman (1993) and Abbink et al. (2001)

Figure 6.14 North Atlantic Palaeoecological Model of the Krombichl

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Oxygen poor - anoxic water current

Oxygen saturated water current

---

NNE

SSW

Tethys

French Shelf

English Shelf

Warm Water

Cool Water

High Latitude

Mid Latitude

200m

50m

100m

---

15-20°C

20-30°C
The figures for these different factors can be deduced from the modern maps (Figure 5.17) and the relevant facts are shown in Table 8.3:

<table>
<thead>
<tr>
<th>Modern ocean</th>
<th>1°C =</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red Sea</td>
<td>0.4° of latitude</td>
</tr>
<tr>
<td>Mediterranean</td>
<td>2° of latitude</td>
</tr>
<tr>
<td>Pacific cold current</td>
<td>5° of latitude</td>
</tr>
<tr>
<td>Pacific warm current</td>
<td>0.98° of latitude</td>
</tr>
<tr>
<td>Average North Pacific</td>
<td>2.5° of latitude</td>
</tr>
<tr>
<td>Average South Pacific</td>
<td>1.666666666° of latitude</td>
</tr>
<tr>
<td>Average North Atlantic</td>
<td>2.2° of latitude</td>
</tr>
<tr>
<td>Average South Atlantic</td>
<td>3.333333333° of latitude</td>
</tr>
</tbody>
</table>

Table 8.3. Modern ocean surface water gradient features.

**8.4.8.2.2 Jurassic gradients** (as shown in Figure 9.2 without offset for currents)

The Lower and Mid Jurassic are similar both to each other and to the modern open ocean scenario (e.g. the Atlantic Ocean) affected by currents acting upon it.

The Upper Jurassic has palaeoisocrymes that are much closer together (therefore giving a steeper gradient). A possible reason for this could be that there has been a change in the oceanic conditions, e.g. the formation of warm currents or restricted seas. Also, the palaeoisocrymes were more latitudinal in their orientation than previously observed in the Jurassic. This could have been due to factors such as either an increased or decreased effect from palaeocurrents. It should be noted that a lower number of palaeoisocrymes can be inferred from the isotopic data available for the Upper Jurassic than were surmisable for the Lower and Mid Jurassic.

The Jurassic European gradients can be worked out similarly to the modern ones and can be seen in Table 8.4:

<table>
<thead>
<tr>
<th>Isocrymes</th>
<th>Lower Jurassic</th>
<th>Mid Jurassic</th>
<th>Upper Jurassic</th>
</tr>
</thead>
<tbody>
<tr>
<td>8-10°C</td>
<td>X</td>
<td>1°C = 4.8° of latitude</td>
<td>X</td>
</tr>
<tr>
<td>10-12°C</td>
<td>1°C = 4.05° of latitude</td>
<td>1°C = 4.8° of latitude</td>
<td>1°C = 2.4° of latitude</td>
</tr>
<tr>
<td>12-14°C</td>
<td>1°C = 4.05° of latitude</td>
<td>1°C = 4.05° of latitude</td>
<td>1°C = 0.8° of latitude</td>
</tr>
<tr>
<td>14-16°C</td>
<td>1°C = 2.4° of latitude</td>
<td>1°C = 4.8° of latitude</td>
<td>1°C = 1.6° of latitude</td>
</tr>
<tr>
<td>16-18°C</td>
<td>1°C = 2.4° of latitude</td>
<td>1°C = 3.2° of latitude</td>
<td>1°C = 1.6° of latitude</td>
</tr>
<tr>
<td>18-20°C</td>
<td>1°C = 3.2° of latitude</td>
<td>1°C = 3.2° of latitude</td>
<td>1°C = 2.4° of latitude</td>
</tr>
<tr>
<td>20-22°C</td>
<td>1°C = 2.4° of latitude</td>
<td>1°C = 3.2° of latitude</td>
<td>X</td>
</tr>
<tr>
<td>22-24°C</td>
<td>X</td>
<td>1°C = 2.4° of latitude</td>
<td>X</td>
</tr>
</tbody>
</table>

Table 8.4. Jurassic European Tethyan surface water gradients.
The data in Table 8.4 above can be combined with the modern data in Table 8.3 (seen diagramatically as Figure 8.15 below) in order to give possible reasons for the Jurassic gradients observed. This can be seen in Table 8.5.

![Diagram of isocrymes and gradient features](image)

Fig. 8.15. Graphical representation of modern ocean surface water gradient features.

<table>
<thead>
<tr>
<th>Isocrymes</th>
<th>Lower Jurassic</th>
<th>Mid Jurassic</th>
<th>Upper Jurassic</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1°C = Poss. expl.</td>
<td>1°C = Poss. expl.</td>
<td>1°C = Poss. expl.</td>
</tr>
<tr>
<td>8-10°C</td>
<td>X N/A</td>
<td>4.8° of latitude</td>
<td>Cold current X N/A</td>
</tr>
<tr>
<td>10-12°C</td>
<td>4.05° of latitude</td>
<td>Cold current</td>
<td>2.4° of latitude</td>
</tr>
<tr>
<td>12-14°C</td>
<td>4.05° of latitude</td>
<td>Cold current?</td>
<td>0.8° of latitude</td>
</tr>
<tr>
<td>14-16°C</td>
<td>2.4° of latitude</td>
<td>Average open</td>
<td>1.6° of latitude</td>
</tr>
<tr>
<td>16-18°C</td>
<td>2.4° of latitude</td>
<td>Average open</td>
<td>1.6° of latitude</td>
</tr>
<tr>
<td>18-20°C</td>
<td>3.2° of latitude</td>
<td>Average open</td>
<td>2.4° of latitude</td>
</tr>
<tr>
<td>20-22°C</td>
<td>3.2° of latitude</td>
<td>Average open</td>
<td>X N/A</td>
</tr>
<tr>
<td>22-24°C</td>
<td>X N/A</td>
<td>2.4° of latitude</td>
<td>Average open</td>
</tr>
</tbody>
</table>

Table 8.5. Jurassic European Tethyan surface water gradients with possible explanations derived from modern ocean scenarios.

### 8.4.8.3 Currents

#### 8.4.8.3.1 Modern currents

Current movement (both cold and warm) has the effect of altering the temperature banding away from a latitudinal orientation. These currents set up a cyclical, conveyor belt of global seawater which results in warm water flowing to cold water / low latitude water flowing to high latitudes. Therefore warm water is transported from the Equator towards the poles while cold waters take the opposite
journey. This circular movement is very obvious in the modern oceans as shown in Figure 8.16.

8.4.8.3.2 Jurassic currents

The palaeocurrent data for the Jurassic of Europe can be seen in Figure 8.17; it shows the following trends:

- In the Lower Jurassic there is no palaeocurrent data available.
- In the Mid Jurassic there is evidence of warm and cold palaeocurrents meeting on the western edge of Europe (both flowing into the Proto-Atlantic). The cold palaeocurrent from more northerly areas acts to depress the palaeoisocryme in this area. There are also some warm palaeocurrents that can be inferred in the eastern part of Europe which have the effect of pushing the palaeoisocryme northwards. This dual effect is the most plausible reason as to why the palaeoisocrymes are at an angle to the palaeolatitude.
- In the Upper Jurassic there is an even distribution of both warm and cold palaeocurrents across Upper Jurassic Europe and the palaeoisocrymes, which were oriented more latitudinally than previously, are probably like this due to a change in effect from the palaeocurrents.

8.4.9 Algae versus General Circulation Models

The trouble with GCMs (such as Valdes et al 1999) is that they are primarily atmospherically based and while they can take the marine interface into account in their calculations they can shed little light on the effects in the marine realm itself. Another problem is that GCMs can tend to be too general in their results – the global answer leads to inherent “fuzziness” when individual areas are highlighted. For example, the Valdes et al model (1999) is a good example in that their result for the four seasons of the time period 150 Ma (Upper Jurassic) (Figure 8.10) lies within the lower 20°Cs for the entire European area.
Fig. 8.17 Jurassic European palaeoenvironmental reconstruction. 

- Warm uncertainty
- Cold uncertainty
- Cold
- Warm

Upper Jurassic 150 Ma
Mid Jurassic 170 Ma
Lower Jurassic 190 Ma

No palaeocurrent data

Boundaries of ammonite provinces

* *
8.4.10 Overall indicator conclusions

Overall comparison and evaluation of the other palaeoclimate indicators can be surmised as:

Foraminifera: these appear to be a good indicator of palaeotemperature delineated boundary positioning and show a similar overall pattern as the calcareous green algae.

Coral: the zooxanthellate coral indications appear to be inconclusive in palaeotemperature assignment which is surprising as they are considered to be the most important factor in determining water-mass definition in the modern oceans. They produce the only definite problem in cooler water temperature assignments in the European Jurassic.

Ammonites and belemnites: these organisms show similar, almost parallel correlation to algal distribution and each other – however as there are no extant forms of these organisms there could be understandable problems with their interpretation.

Ostracodes: these organisms, like foraminifera, show a similar pattern to the calcareous Chlorophyta and seem to be a good indicator of the movement of water masses of different temperatures.

Deposits: the deposits show a land based zonation which is roughly similar to algal patterns but surprisingly this terrestrial climate is shown as having been more equable than the marine world is shown to have been.

Sponges: these organisms are not very useful for direct comparison with the algae due to depth differences but they do provide more evidence of the extent of the latitudinal distribution of the Tethyan realm.

Biodiversity: this form of analysis is very good for elucidation of major latitudinally related markers which effect species diversity (e.g. temperature).

Isotopes: this indicator of palaeotemperature has severe problems and cannot be relied upon on its own to give precise data for this time period.

GCMs: these models are not precise enough and are limited by problems of inherent supposition, but they do show promise for the future.
From the results of the above palaeotemperature indicators it can be seen that there is a reasonable argument for the algal work being correct (at the very least being useful as supporting evidence), with the best support for it being the two most accepted indicators of foraminifera and sensitive deposits as well as the lesser used ostracodes.

It should be noted that the GCMs may be improved by incorporating algally derived information which may serve to improve precision.

It was a desired aim to obtain Jurassic derived quantitative data for the environmental conditions (i.e. actual palaeotemperature figures). This data could be used in association with an overprint of modern values onto similar Jurassic floral (and possibly other factors) isotherms / isocrymes. The overprinting of modern values is dependant on the lack of change in environmental conditions from the Jurassic to the present. The assignment of possible palaeotemperature figures for the stages of the Jurassic which were derived from the temperature limit of the modern Chlorophyta assigned to the Jurassic Chlorophyta limits and with relevant isotopic figures included, can be seen in Figures 8.13 and 9.2.

8.4.11 Temperature interpretation of Jurassic European marine environments

Results from the fossil algae studied in this work, together with the evidence from other sources such as palaeocurrent data, enable the suggestion of the authors version of the marine palaeoenvironmental conditions during the three series of the Jurassic.

The present-day line of termination for calcified Dasycladales is pertinent to the of c12°C isocryme temperature. Assuming no difference in the algal limits and tolerances between the Jurassic and the modern day (a supposition assumed by the work of Elliott, 1978 and 1986), then this value can be ascribed to the same line determined in the series of the Jurassic.

A problem appears to arise when this value is compared to the isotopically derived water temperature values in the same area. The isotope values are around twice the algally derived values; this presents a number of possibilities which should be explored. The first possibility is that the isotope values are inaccurate, but they are generally similar to each other which appears to show consistency in the
determination of these temperature values. An alternative possibility is that the 
temperature limit of the algae has changed with time – but the palaeolatitudinal value
(just over c30°N) equivalent of the modern day is similar to the derived algal
temperatures, therefore, if this scenario is true, there has to have been a massive
Jurassic temperature increase (even in the ‘cooler’ Upper Jurassic period). This idea
ties into the abandoned Elliott temperature tolerance work, but such a massive
temperature increase is not evident in other temperature-sensitive indicators.

The algal termination line appears to be relevant and seemingly correct as it is
in close proximity over all three series of the Jurassic, as would be expected with the
age differences.

There is evidence in the Cretaceous of the modern Mediterranean area of
cooling which means that high temperatures (producing chlorozoan associations)
were reduced (to produce a foramol association). In the early Senonian (Upper
Cretaceous) of northwestern Sardinia, it is seen that sediments dominated by
molluscs, with variable amounts of red algae, bryozoa and echinoid assemblages (a
rhodalgal association typical of anomalous tropical or transitional areas - more
generically considered foramol-type deposits) replaced sediments including
hermatypic corals, green algae and variable amounts of non-skeletal grains
(chlorozoan / chloralgal association). These latter components were mostly dominant
in Jurassic to early Cretaceous times and the change is consistent with a change
(conditions of stress), during the early Senonian, of the parameters within the marine
environment (Carannante et al 1995). Therefore in the Jurassic the temperatures were
relatively high which supports the overall isotope trend.

There is an uncertainty over whether Belemnites laid down their skeletal
calcite in a summer growing season or if they were capable of steady growth
throughout the year. Two geological members in Svalbard seem compatible with
belemnites recording summer temperatures (Ditchfield, 1997).

What if only summer temperatures are recorded (not isocrymes as the algae
are representing)? This would mean belemnites show seasonal calcite deposition
(summer values are equal to the warmest isotherm as opposed to coldest). In a
supporting way, modern foraminifera (which are meant to be exemplary for isotopic palaeotemperature analysis, especially in the Cenozoic) show seasonality in their isotope values. Significant seasonal variability of both δ\(^{13}\)C and δ\(^{18}\)O occurs in many planktonic foraminifera species and species occur in their highest abundances during their preferred thermal and food source conditions. Isotopic signatures deposited during a high-flux time of year may skew the annual isotopic record. Equilibrium or disequilibrium may not be a temporally consistent phenomenon for a species but may be seasonally influenced by varying hydrographic conditions (Sautter and Thunell, 1991). Maximum temperature variations occur in the subtropical regions with minimal fluctuations in tropical and moderate variations in polar regions. In the Atlantic Ocean, the approximate seasonal surface-water temperature ranges are less than 2°C in low latitudes (0-20°N), 8-9°C between latitudes 30-45°N and 5-6°C between 50-60°N latitude. The seasonal δ\(^{18}\)O trend in living species off of Bermuda, ranges in surface temperature from 27.6 to 19.4°C. The oxygen isotopic compositions of living planktonic foraminifera therefore, vary as a function of changing surface-water temperature (Williams et al, 1981).

Frakes (1986) suggested, due to possible alteration effects, that δ\(^{18}\)O results (from molluscs) are best considered as representing maximum temperatures.

The possibility of summer only isotope results leads to the conclusion of seasonality in the climate at the palaeolatitudes of Europe during the Jurassic. This seasonality can be supported by some algal evidence – Wright (1985) has shown that the red alga Solenopora jurassica in the Bathonian of Gloustershire displays regularly alternating banding of perithallial cells which reflect seasonally induced changes. The different bands are the result of differential preservation and diagenetic replacement due to original differences in the magnesium content of the thallus calcite (more Mg in the summer due to a more rapid summer growth).

However, we are left with the problem of the Upper Jurassic hermatypic corals in places such as eastern Scotland - see Figure 8.18 (although this problem is not just in the Upper Jurassic – see Figure 8.19). Is it possible that they could have survived cooler temperatures then (i.e. has their temperature tolerance decreased over time?); the normal modern range of hermatypic corals is 18 to 29°C. There is no known,
Fig. 8.19 Jurassic British coal distribution (after Negus, 1983) and relative palaeolatitude.

Lower Jurassic

Mid Jurassic

Upper Jurassic
reasonable, evidence for a decrease in tolerance to colder temperatures. Therefore, this leads us to the main question that naturally arises, namely – are the high latitude Jurassic corals really hermatypic? In modern northern hemisphere latitudinal distribution, hermatypes are found up to c35° (the Honshu Island reefs of Japan), and ahermatypes are thus unrestricted (Teichert, 1958). The use of the terms hermatypic and ahermatypic can be confusing as they are defined by two features, one of which is not actually mutually exclusive:

1. Presence of symbiotic zooxanthellate algae (present in hermatypics and not in ahermatypics).
2. Ability (and tendency) to build ‘reefs’ (supposed to be indicative of hermatypics and not of ahermatypics, but actually is not the case – see below).

Jurassic (and other fossil) hermatypic taxa are thus described because they are believed to have possessed zooxanthellae like those of the modern day (although this is not always so in the Recent – Bertling, 1993). Modern ahermatypic, cold-water, corals have been found to build large reef-like structures and colonial skeletons which are (without observable zooxanthellae) externally similar to many hermatypic corals (Teichert, 1958 and Stanley, 2001).

It is an interesting point that there are no known cold-water (ahermatypic) corals for the Jurassic (Leinfelder, 2001). All the coral specimens found have been attributed to the hermatypic corals, even though it is impossible to know for sure if the coral was hermatypic as the intracellular zooxanthellae are never preserved in the fossils (Teichert, 1958 and Stanley, 2001). This leads to the usage of the ‘reef coral’ application in order to verify the corals trophic status – but this is not really a valid assumption as it has “no consistent palaeoecological or sedimentological meaning” for use as evidence of algal symbiosis (Rosen, 2000). It is true, however, that the symbiosis of corals with zooxanthellae leads to more rapid calcification and associated attainment of much larger skeleton sizes and broader ranges of colonial organisations and shapes (Rosen, 2000 and Stanley, 2001), due to the derivation of carbon compounds from the zooxanthellae (Rosen, 2000).

There have been investigations into indirect methods of hermatypic inference (independent of reef-based evidence). This has ranged from the mere use of size of
solitary corals (Page et al, 1984) to the extraction of soluble organic compounds and the distinction of their differences in modern corals (Gautret et al, 1997) and applied to fossils (see Stanley, 2001). The following synthesis (Table 8.6) of indirect methods (Rosen 2000) is characteristic of the array of inferences normally used:

<table>
<thead>
<tr>
<th>1</th>
<th>Stable isotope signatures</th>
<th>Those characteristic of living hermatypic corals = symbiosis in fossil.</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>Comparative morphology</td>
<td>Those morphologies found only in living hermatypic corals = symbiosis in fossil.</td>
</tr>
<tr>
<td>3</td>
<td>Assemblage characteristics</td>
<td>Those characteristics of living hermatypic corals = symbiosis in fossil.</td>
</tr>
<tr>
<td>4</td>
<td>Ecological functional morphology</td>
<td>Adaptation in poorly lit water for symbiotes = symbiosis in fossil.</td>
</tr>
<tr>
<td>5</td>
<td>Taxonomic uniformitarianism</td>
<td>Species and genera that are zooxanthellate today = zooxanthellate in the past.</td>
</tr>
</tbody>
</table>

Table 8.6. Indirect methods used to infer coral hermatyp in fossils (after Rosen, 2000).

In the above table (Table 8.6), numbers 3 and 4 have been tried for the mid European (Switzerland and S. France) Jurassic corals (but there is little doubt about these corals anyway as they were in tropical areas). Numbers 1 and 5 are probably the most reliable of the methods, but cannot always be applied (Rosen, 2000).

The use of growth rates in shallow-water ‘reefs’ could be used for reef type differentiation (as hermatypes are much faster growers – see above). However, work done (Insalaco, 1996 and Insalaco et al 1997) indicates that there is no apparent trend to the data which would help to differentiate, but the main graph (Insalaco, 1996) is drawn strangely and can be seen redrawn in Figure 8.20, where there does seem to be a trend towards showing that those low growth rate corals expanding to high latitude Britain could be ahermatypic compared to those higher rate corals restricted in France to southern Britain (probably hermatypic). There is some support for this in terms of dominance of Thamnasteria concinna in the higher latitudes of the Late Jurassic (Bertling, 1993) - see Figure 8.21.
Fig. 9.6: 20 shallow water Late Jurassic reefs growth rates (redrawn from Indacio 1996).

Paleolatitude (N)

Thamnophisera concilia

I. sastrata explanata

Britain

Northern France

Growth Rate (mm/yr)
Fig. 8.21 High latitude dominance of Thamnasteria concinna in the Late Jurassic

This shows the kind of picture expected in a modern ahermatypic corals’ dominance. Overall, this work puts the high palaeolatitude corals in waters of a temperature that is too low for the equivalent modern hermatypic species to survive (see Figure 8.18 for the Upper Jurassic); this leads to their assignment as hermatypic (zooxanthellate) corals as being regarded by the author as highly questionable.

An extra question which can be posed is why is the algal distributional extent repressed in the Lower Jurassic? The extent of algae (particularly the Chlorophyta) and their abundance, is limited in the Lias and this, due to the age, may be part of a situation passed on from the end Triassic. Palaeontological evidence shows that the Rhaetic (end Triassic) was a time of transgression of a shallow hypersaline sea in the northwestern part of Europe (Britain across to Germany) (Hallam and El Shaarawy, 1982). This event can be seen in South Wales via the non development of the ‘carbonate factory’, drowned out by the transgression (Wright, V.P., pers. comm.).

The Rhaetic hypersalinity has been estimated palaeontologically to be about 25-30% (compared with ‘normal’ salinity of c35%) and has been estimated as lasting, with fluctuations, for about a million years (Hallam and El Shaarawy, 1982). Interestingly, there is evidence for other episodes of hypersaline conditions in northern Europe occurring in the Jurassic. NE England in the lower Toarcian (upper Lias) shows, based on isotopic analyses of belemnites, that the surface waters were less saline than normal by a similar ∼5% difference (Sælen et al., 1996), while later, there is evidence in the Bathonian of western Scotland of hypersaline conditions (Hudson, J.D., 1970). These episodes of shallow stratified brackish waters would, if algae were to be present
in such areas, be a major barrier to calcified marine algae habitation. It is well known
that in the modern day, with very few exceptions (such as the few *Halimeda
incrassata* and *Acetabularia crenulata* and *farlowii* in the Texan Laguna Madre where
seasonal salinity ranges from 20 to 80% (Berger and Kaever, 1992 and Kaldy, 1996)),
that algae such as the calcareous Chlorophyta (especially Dasycladales) are very
sensitive to and intolerant of altered and fluctuating salinity (Berger and Kaever,
1992). The existence of reduced salinity may help explain some of the apparently
erroneous isotopically derived palaeotemperatures (see Table 8.7) in these areas at the
relevant times, for, as has been previously stated, salinity affects the results especially
reduced salinity can produce higher than true derived temperatures.

<table>
<thead>
<tr>
<th>Broad age</th>
<th>Stage setting</th>
<th>Location</th>
<th>Measured temperature °C</th>
<th>Algal temperature zone °C corrected to summer temperature</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mid Jurassic</td>
<td>Bathonian</td>
<td>Eigg, Inner Hebrides, Scotland</td>
<td>23.0</td>
<td>17</td>
<td>Patterson (1999)</td>
</tr>
<tr>
<td>(Dogger)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lower Jurassic (Lias)</td>
<td>Upper Lias</td>
<td>Whitby, Yorkshire, Britain</td>
<td>31.7</td>
<td>&lt;18</td>
<td>Bowen (1961b)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Toarcian</td>
<td></td>
<td>Northampton, Britain</td>
<td>26.3</td>
<td>19</td>
<td>Bowen (1961b)</td>
</tr>
</tbody>
</table>

Table 8.7 European Jurassic isotope temperatures that appear to be erroneously too warm possibly due to reduced salinity conditions.
Ch. 9 Synthesis

From this work, the following syntheses can be deduced:

9.1 Present-day calcareous green algae

The biogeography of the present-day calcified Chlorophyta reflect surface water temperatures.

9.1.1 Dasycladales

This order is a minor constituent in today's oceanic realm (Wray, 1977) and is not normally considered in most texts on the subject of sediment contribution / shallow water structures. Dasycladeans are commonly regarded as 'tropical' (Berger and Kaever, 1992). This is not altogether accurate; while these organisms are most abundant and diverse in 'tropical areas', they are also found well outside this realm, although to a lesser extent (see Section 5.6.2.3). The main factor determining their distribution is temperature – particularly isocrymes, because the dasycladeans are very susceptible to low temperatures (Berger and Kaever, 1992). Temperature in the marine realm is not solely dependent on latitude. At the present-day, the isocrymal limit of calcareous forms of the order Dasycladales is 12°C (see Section 5.7). Of the normally calcareous forms, some may survive uncalcified in waters down to isocrymes of 10°C. This variation is matched in calcification extent shown between the different genera (see Section 5.6.3.6).

9.1.2 Halimedaceae

The family Halimedaceae is the major calcareous chlorophyte group and primary producer of calcareous sediment in the modern shallow ocean (Hillis-Colinvaux, 1980). Again, the distribution of these organisms, like the Dasycladeales, has been stated as 'tropical' and they have been hailed as indicators of the tropical realm both at the present-day and as fossil temperature indicators (Elliot, 1981, Hillis, 1991). As with the Dasycladeales in their actual distribution, this 'tropical' nature is true for many species of Halimedaceae but not for all, and some inhabit areas well into temperate zones. The isocrymal limit of most Halimedaceae is identical to
the Dasycladales at 12°C. However, it is not possible to give a temperature limit to non-calcifying halimedaceans as this appears to depend upon local factors which overprint the influence of temperature. Nonetheless, the non-calcifying occurrences appear to be rare and can be assigned to the unusual rather than the normal.

Calcification of dasycladaleans and halimedaceans can also be affected by depth – the Halimedaceae inhabit a greater depth range than the Dasycladales: 150m normally, compared with 20m normally for the Dasycladales (to a 90m extreme). The nature of the change in calcification with depth is different in different species – most reduce calcification while some appear to increase it (although this may actually be more a result of decreasing organic matter).

9.2 Jurassic algae

The three series of the Jurassic indicate the different distributions of the calcareous algae found within them. Although Halimedaceae are important calcified Chlorophyta at the present-day, during the Jurassic the Dasycladales were more important green algae. It is also relevant to note that the habitat of calcified Cyanobacteria has changed – in the Jurassic they occurred in marine as well as freshwater, whereas nowadays they are virtually entirely freshwater in environment.

9.2.1 Lower Jurassic (Lias)

During this time period, the Dasycladales were moderately abundant within the limits of their distribution in southern Europe. The other calcareous algae that were present show a sparse occurrence in these localities.

9.2.2 Mid Jurassic (Dogger)

Dasycladales continued to be more abundant than other calcareous algae – although their occurrences had decreased in number (this may just be a preservational feature). Their latitudinal distribution had increased, with a ‘corridor’ of occurrences northward through eastern France into mid England. Other calcified algae show only a slight increase in latitudinal distribution compared to the Early Jurassic.
9.2.3 Upper Jurassic (Malm)

In the Upper Jurassic, calcareous algae show an explosion in both abundance and diversity. This is partially due to a greater number of algally-suitable localities being preserved and partially due to an actual increase in algal abundance (observed in the field by sheer numbers of species found in the algal settings).

The Dasycladales were once again the dominant calcareous algae. They were present in large numbers at a large number of sites across mid and southern Europe (with a few more northerly extremes). The Halimedaceae were still relatively sparse in comparison with the Dasycladales but were more numerous in localities than previously.

In the Upper Jurassic, where there are sufficient datapoints to form a reasonable limit as opposed to the Lower or Mid Jurassic, it can be seen that the Halimedaceae appear to terminate further southwards than the Dasycladales. In contrast, the modern situation shows an almost shared termination limit – the Dasycladales occur only marginally more poleward than the Halimedaceae. This more restricted distribution for Halimedaceae is equivalent to a c3°C isocrymal higher temperature (see Section 6.3.3). This may be an indication of a slight change in the tolerance of Halimedaceae from the Jurassic to the present, or just a lack of evidence of fossil Halimedaceae up to the area of the Dasycladales termination line (either due to preservational bias or perhaps because this was a region of variable / non calcification of Halimedaceae).

Calcified algae that occupied a significant number of localities north of the Dasycladales (taken as representative of the then chlorophyte assemblage) limit, include the Rhodophyta (this is consistent with the modern situation), Cyanobacteria (due to the change from marine to the modern day setting of freshwater, it is unknown if this is extreme or not; however the northernmost finds may be reflecting marginal marine – evaporite / brackish - conditions) and Microproblematica (which, due to their questionable nature, cannot be assessed for temperature significances).

See Figure 9.1 for Jurassic chlorophyte termination line comparisons.
Halimedaceae

Upper Jurassic 150 Ma

Mid Jurassic 170 Ma

Lower Jurassic 190 Ma

Dasycladales

There are few Halimedaceae occurrences in the Jurassic. This is evidence in the Upper Jurassic. These series are generally incised. In the Upper Jurassic, Dasycladales are more difficult to determine. Modern halimeda species in the Jurassic - this Halimedaceae present.


Fig. 9.1 Jurassic Chlorophyte distribution on paloeoecosystems.
9.3 Jurassic temperature conclusions

There are, as has been shown, a number of indicators other than calcareous algae that provide an insight into Jurassic palaeoclimates. These indicators, discussed in Chapter 8, vary in their usefulness and reliability and certain ones appear to be useful in giving us more detail to the Jurassic algal distribution data, particularly the oxygen isotope data. Palaeotemperatures inferred from oxygen isotope values (see Figure 8.12) have some similarities with temperatures inferred from algal distributions which allows for their use in forming the palaeoisocrymes. Of the other available palaeoclimate indicators, foraminifers and ostracodes appear to be most useful in marine reconstruction with limits approximating algal frontiers; also, biodiversity gradients appear useful in delineating the temperate / tropical boundary.

The derivation of the temperature limit of 12°C isocrymal for modern calcified Chlorophyta has enabled this temperature to be applied to the Jurassic. This isocryme, together with selected isotopic values (adjusted to isocrymal values, and chosen from all the isotopic palaeotemperature work for their accord and likelihood to be an accurate portrayal) has resulted in marine surface water isocrymal reconstructions for the three stages of the European Jurassic (Figure 9.2).
Fig. 9.2 Jurassic European regional palaeotemperature reconstruction.

Upper Jurassic 150 Ma

Mid Jurassic 170 Ma

Lower Jurassic 190 Ma
9.4 Suggestions for further work

The following are suggestions for further work possibilities brought up by this study:

**Continuance of the spatial distribution plots for both modern and fossil calcareous algal finds.**

Such databases are never completed, they need continual updating as new finds are discovered. Also, better definition of the transition of water masses and concentration on data associated with distributional limits are most important.

**Documenting numerical abundance of both fossil and modern calcareous algae.**

This would involve the production of different datasets, ones based on the relative abundance of individual genera / species at the different localities. This would allow for comparison of localities of different latitudes in terms of actual taxonomic abundances as well as species distributions. This may only be possible for the modern data set as preservational incompleteness of the fossil record makes this more difficult to do for fossil data, although it would be useful to try.

**Extending similar work to other areas in the world for the Jurassic.**

Ultimately, the best case scenario would be a global distribution of all calcareous algae for the Jurassic, however, merely a similar study on adjacent areas such as eastern Tethys would be interesting for its comparison with this studies work.

**Similar work for other time periods of interest.**

Studies of other periods with abundant algae would be of great interest (such as the Permian as an algally interesting time, or the Palaeocene for direct comparative purposes), and this could lead to the possibility of doing this work in the same geographical area and note the algal evolution over a time period longer than just a system such as the Jurassic. The interesting time periods for Dasycladales appear to be the Permian and Palaeocene (Flügel 1985, Barattolo 1991, Génot 1991 and Berger and Kaever 1991) – their highpoints, and possibly also the Triassic (Flügel 1979, 1985, 1991). The Palaeocene seems to be of interest for the Halimedaceae (Génot 1991 and Barattolo 1991) and more recent (while they appeared in the Upper Triassic they only developed, in a massive explosion of numbers, at the Pliocene / Recent - Flügel 1991).
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Appendices

A  Fieldwork raw data / Jura / Ain
   // Languedoc
   /// Portugal

B  Modern Algae / List of genera and species of modern green calcareous algae
   // Databases

C  Jurassic Algae  Databases
Appendix

A

Fieldwork raw data
Appendix

AI

Jura / Ain
## Sites

<table>
<thead>
<tr>
<th><strong>Place</strong></th>
<th><strong>Modern Latitude and longitude</strong></th>
<th><strong>Description</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Pont de la Chaux</td>
<td>46°39' N, 5°55.5'E</td>
<td>Forest road cutting, D40 between Pont de la Chaux and Châtelneuf, c28m long by max. 2.5m high. Three lithologies: 4m+ of micritic limestone with calcite veining, overlain by c1m of crinoidal limestone and then c65cm+ of very weathered and broken up lagoonal type rock with oolite. The beds were dipping 007°/10°N.</td>
</tr>
<tr>
<td>Pont de Lemme</td>
<td>46°36' N, 5°57'E</td>
<td>Rail cutting and rock exposure behind houses on East side of main road, c25m high? and 75m long? Weathered oo-biosparite?</td>
</tr>
<tr>
<td>Vouglands Dam</td>
<td>46°24' N, 5°41'E</td>
<td>Dam / reservoir side road section.</td>
</tr>
<tr>
<td>Molinges</td>
<td>46°21'N to 46°20'N, 5°46'E</td>
<td>Road sections – D63 – 10 to 15 foot tall by c50 foot long. Broken, weathered, lot of micrite, some brachiopods, corals and oyster beds. Bedding 317°/10°SE but variable + some faulting. D100 – c100m long by, arced from 8 foot to 30 foot high. Very weathered and cracked, massive oolite shoal (with occasional small oncolite) changing to micrite with crinoids and gastropods.</td>
</tr>
<tr>
<td>Echallon – Oyonnax</td>
<td>46°14' N, 5°42'E</td>
<td>Roadside cutting on D13 (near 958 spotheight). Section c8 foot tall by 25 foot long. Overgrown, weathered and fractured. Oncitic?</td>
</tr>
<tr>
<td>Echallon (Le Caquet)</td>
<td>46°12' N, 5°44'E</td>
<td>Road / track cutting. Initially overgrown exposures of fractured micritic limestone, track drops down sequence to scree slope of cutting of oo-onc rock (very fractured). Initial exposures c300 yards by 10 foot high ; cutting face c10m high by 50m long.</td>
</tr>
<tr>
<td>Mares Quarry</td>
<td>46°11' N, 5°43'E</td>
<td>Working quarry / mine + road above. Road (to Plagne) above entrance – roadside cuttings c30 foot high. Lithology light cream to white limestone, partially chalky with ooids and oncoids + bioclastics (largely gastropods). Uf Kimmeridgian to Tithonian. Entrance – bedding vast and fractured, appears horizontal (maybe dip slightly to the South). From the mine – rock pile of massive chunks of colonial coral.</td>
</tr>
<tr>
<td>Virieu-Martin</td>
<td>45°57' N, 5°48'E</td>
<td>Roadside cutting on track between Gignez and Brénaz (D123). Possible lagoonal rocks. Outcrop is overgrown, c1.5 to 2m tall by &gt;1km long. Horizontal bedding.</td>
</tr>
<tr>
<td>Location</td>
<td>Latitude</td>
<td>Longitude</td>
</tr>
<tr>
<td>---------------</td>
<td>-----------</td>
<td>-----------</td>
</tr>
<tr>
<td>Landaise</td>
<td>45°52'N</td>
<td>5°48'E</td>
</tr>
<tr>
<td>Armix</td>
<td>45°52'N</td>
<td>5°35'E</td>
</tr>
<tr>
<td>Cerin</td>
<td>45°47'N</td>
<td>5°33'E</td>
</tr>
<tr>
<td>Le Rocheret</td>
<td>45°35'N</td>
<td>5°44'E</td>
</tr>
<tr>
<td>St. Didier</td>
<td>45°34'N</td>
<td>5°45'E</td>
</tr>
<tr>
<td>Cluse de la Balme</td>
<td>45°33'N</td>
<td>5°44.5'E</td>
</tr>
</tbody>
</table>
## Sites

<table>
<thead>
<tr>
<th>Image</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><img src="image1.jpg" alt="Image" /></td>
<td>View SW of river L’Ain part of Lac Vouglans. To the south of the barrage.</td>
</tr>
<tr>
<td><img src="image2.jpg" alt="Image" /></td>
<td>View WNW of beds at Landaise. Beds are approximately 1.5 – 2 metres high.</td>
</tr>
<tr>
<td><img src="image3.jpg" alt="Image" /></td>
<td>Entrance to Mares Quarry. Gate is four foot high. View W.</td>
</tr>
<tr>
<td><img src="image4.jpg" alt="Image" /></td>
<td>View S of Pont-de-llemme rock face and old cutting. Metre rule for scale (leaning on vehicle).</td>
</tr>
<tr>
<td><img src="image5.jpg" alt="Image" /></td>
<td>Cluse de la balme small disused quarry. View S. Metre rule for scale.</td>
</tr>
<tr>
<td><img src="image6.jpg" alt="Image" /></td>
<td>View N of beds at St. Didier. Metre rule for scale.</td>
</tr>
<tr>
<td><img src="image7.jpg" alt="Image" /></td>
<td>View N in Le Rocheret Quarry. Industrial vehicle is about four metres high for scale.</td>
</tr>
</tbody>
</table>
## Lithologies

<table>
<thead>
<tr>
<th>Name</th>
<th>Description</th>
<th>Best example sample number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oolite</td>
<td>Well cemented ooidal limestone.</td>
<td>Mo5</td>
</tr>
<tr>
<td>Micrite</td>
<td>Limestone composed of mostly micrite matrix – chemical precipitate?</td>
<td>Cer3</td>
</tr>
<tr>
<td>Reef limestone</td>
<td>Bioclastic “reef rock” limestone with biologic components e.g. shells etc.</td>
<td>Mo1</td>
</tr>
<tr>
<td>Oncolite grainstone</td>
<td>Limestone composed mainly of oncoidal material with a general sparite matrix.</td>
<td>Oy1</td>
</tr>
<tr>
<td>Bioclastic grainstone</td>
<td>Similar to reefal limestone but with a more homogenous nature – less “rubbly”.</td>
<td>Ech1/3</td>
</tr>
</tbody>
</table>
## Previous algae found

<table>
<thead>
<tr>
<th>Site</th>
<th>Age</th>
<th>Algal species</th>
</tr>
</thead>
</table>
| Pont-de-la-Chaux| Kimmeridgian to Portlandian | *Thaumatoporella parvovesiculifera*  
|                 |                         | *Likanelia bartheli*  
|                 |                         | *Salpingoporella annulata*  
|                 |                         | *Cayeuia piae*  
|                 |                         | *Cayeuia moldavica*  
|                 |                         | *Vaginella striata*  
|                 |                         | *Cylindroporella lemmensis*  
|                 |                         | *Cylindroporella sugdeni*  
|                 |                         | *Acicularia americana*  
|                 |                         | *Acicularia elongata*  |
| Pont-de-Lemme   | Kimmeridgian to Portlandian | *Clypeina jurassica*  
|                 |                         | *Likanelia bartheli*  
|                 |                         | *Cylindroporella lemmensis*  |
| Vougans Dam     | Kimmeridgian to Portlandian | *Clypeina jurassica*  
|                 |                         | *Salpingoporella annulata*  
|                 |                         | *Campbelliella striata*  
|                 |                         | *Montenegroflorifera*  
|                 |                         | *Likanelia bartheli*  
|                 |                         | *Acicularia sp.*  
|                 |                         | *Acicularia elongata*  
|                 |                         | *Cayeuia sp.*  
|                 |                         | *Thaumatoporella parvovesiculifera*  |
| Molinges        | Kimmeridgian to Portlandian | *Thaumatoporella parvovesiculifera*  
|                 |                         | *Parachaetetes jurassica*  
|                 |                         | *Solenopora jurassica*  
|                 |                         | *Bacinella irregularis*  
|                 |                         | *Macroporella sp.*  
|                 |                         | *Salpingoporella annulata*  
|                 |                         | *Salpingoporella pygmaea*  
|                 |                         | *Salpingoporella jurassica*  
|                 |                         | *Cayeuia sp.*  
|                 |                         | *Petrascula bursiformis*  |
| Echallon         | Kimmeridgian to Portlandian | *Clypeina jurassica*  
|                 |                         | *Thaumatoporella parvovesiculifera*  
|                 |                         | *Solenopora jurassica*  
|                 |                         | *Bacinella irregularis*  
|                 |                         | *Salpingoporella annulata*  
|                 |                         | *Cayeuia sp.*  
|                 |                         | *Cladocoropsis mirabilis*  
|                 |                         | *Lithocodium aggregatum*  |
| Mares Quarry    | Kimmeridgian to Portlandian | *Campbelliella striata*  
<p>|                 |                         | <em>Salpingoporella pygmaea</em>  |</p>
<table>
<thead>
<tr>
<th>Location</th>
<th>Age</th>
<th>Fossil assemblage</th>
</tr>
</thead>
</table>
| Virieu-Martin      | Kimmeridgian to Portlandian | Petrascula bursiformis  
Macroporella sp.  
Cayeuxia piae  
Petrascula annulata  
Gyroporella sp.  |
| Landaize           | Kimmeridgian to Portlandian | Clypeina jurassica  
Thaumatoporella parvovesiculifera  
Campbelliella striata  
Salpingoporella annulata  
Salpingoporella sp.  
Cayeuxia sp.  
Cylindroporella sp.  
Vaginella striata |
| Armix              | Kimmeridgian to Portlandian | Petrascula piai  
Petrascula ? bugesiaca  
Montenegrella florifera  
Clypeina ? aff. solkani  
Terquemella concava  
Likanella Bartheli  
Cayeuxia piae |
| Cerin              | Kimmeridgian       | Clypeina jurassica  
Thaumatoporella parvovesiculifera  
Campbelliella striata  
Salpingoporella annulata  
Lithocodium - Bacinella |
| Cluse-de-la-Balme  | Kimmeridgian       | Clypeina jurassica  
Thaumatoporella parvovesiculifera  
Likanella Bartheli  
Bacinella irregularis  
Campbelliella striata  
Salpingoporella annulata  
Cayeuxia sp. |

## Hand Specimens

<table>
<thead>
<tr>
<th>Sample</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>MQ1</td>
<td>White, (mostly recrystallized) bioclastic, well cemented limestone with some small ooids, bivalves and gastropods</td>
</tr>
<tr>
<td>MQ2</td>
<td>Grey / white, fine grained, well cemented limestone – bioclastic (corals); very similar to MQ1</td>
</tr>
<tr>
<td>MQ3</td>
<td>Pieces of colonial coral (interconnecting branches) – little matrix (weathered out), very fragile</td>
</tr>
<tr>
<td>St.D1</td>
<td>Creamy, massive, well cemented, fine grained limestone</td>
</tr>
<tr>
<td>ROC1</td>
<td>Yellow, very well cemented, mixture of clastic and micritic limestone with some calcite veins and some possible stylolites</td>
</tr>
<tr>
<td>ROC2</td>
<td>Light grey, very well cemented limestone – mixture of clastic limestone in a micritic background</td>
</tr>
<tr>
<td>CER1</td>
<td>Creamy grey micritic? Homogenous limestone with echinoid fossil</td>
</tr>
<tr>
<td>CER2</td>
<td>Creamy yellow, very well cemented, bioclastic limestone</td>
</tr>
<tr>
<td>CER3</td>
<td>Light grey, massive limestone – well cemented, with crinoid ossicles in – possibly a micritic limestone with some clastic input</td>
</tr>
<tr>
<td>VM1</td>
<td>Grey, apparently clastic, well cemented limestone with stylolites</td>
</tr>
<tr>
<td>VM2</td>
<td>Same as VM1</td>
</tr>
<tr>
<td>VM3</td>
<td>Same as VM1</td>
</tr>
<tr>
<td>ARM1</td>
<td>Oncoidal / bioclastic?, medium grey, well cemented limestone with stylolites</td>
</tr>
<tr>
<td>ARM2</td>
<td>Yellow, bioclastic? very well cemented, limestone</td>
</tr>
<tr>
<td>ARM3</td>
<td>Yellow, bioclastic? very well cemented, limestone with calcite veins</td>
</tr>
<tr>
<td>CDB1</td>
<td>Yellowy-white, very well cemented, oncoidal clastic limestone with occasional stylolites</td>
</tr>
<tr>
<td>CDB2</td>
<td>Light brown / grey, well cemented, bioclastic? limestone</td>
</tr>
<tr>
<td>PC1</td>
<td>Light brown, very well cemented, bioclastic limestone</td>
</tr>
<tr>
<td>PC2</td>
<td>Creamy, well cemented, oncoidal limestone with bioclastic input</td>
</tr>
<tr>
<td>PC3</td>
<td>Light brown, well cemented, bioclastic limestone</td>
</tr>
<tr>
<td>PC4</td>
<td>Light brown / grey, very well cemented, clastic limestone – some cracks, some biotic input and some ooids</td>
</tr>
<tr>
<td>LAN1</td>
<td>Dark grey, very well cemented, limestone – clastic micrite?</td>
</tr>
<tr>
<td>LAN2</td>
<td>Similar to LAN1</td>
</tr>
<tr>
<td>LAN3</td>
<td>Bioclastic, grey, very well cemented limestone</td>
</tr>
<tr>
<td>OY1</td>
<td>Light brown, very well cemented, oncoidal limestone with lots of calcite veins</td>
</tr>
<tr>
<td>OY2</td>
<td>White, very well cemented, calcite veined pisoliths / ooids</td>
</tr>
<tr>
<td>OY3</td>
<td>Grey / brown, very well cemented oncoidal limestone</td>
</tr>
<tr>
<td>MO1</td>
<td>Grey bioclastic limestone, very cracked “reef rock”? very well cemented with possible corals and bivalves</td>
</tr>
<tr>
<td>MO2</td>
<td>Light grey to dark grey, very well cemented clastic limestone</td>
</tr>
<tr>
<td>MO3</td>
<td>Similar to MO2, but bioclastic?</td>
</tr>
<tr>
<td>MO4</td>
<td>Similar to MO2</td>
</tr>
<tr>
<td>MO5</td>
<td>White oolite – well cemented</td>
</tr>
<tr>
<td>MO6</td>
<td>Oolitic / oncoidal mix – white, well cemented limestone with echinoid spines</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>and bivalves</td>
<td></td>
</tr>
<tr>
<td>MO7</td>
<td>Similar to MO6</td>
</tr>
<tr>
<td>PDL1</td>
<td>Grey / brown micrite, very well cemented</td>
</tr>
<tr>
<td>PDL2</td>
<td>Dark grey limestone – micrite? Rock very fractured but well cemented</td>
</tr>
<tr>
<td>PDL3</td>
<td>Brown (bio?)clastic? well cemented limestone</td>
</tr>
<tr>
<td>PDL4</td>
<td>Light brown, bioclastic, well cemented limestone</td>
</tr>
<tr>
<td>PDL5</td>
<td>Similar to PDL4</td>
</tr>
<tr>
<td>PDL6</td>
<td>Similar to PDL4</td>
</tr>
<tr>
<td>PDL7</td>
<td>Similar to PDL4</td>
</tr>
<tr>
<td>ECH1</td>
<td>Light brown bioclastic, well cemented limestone</td>
</tr>
<tr>
<td>ECH2</td>
<td>Similar to ECH1</td>
</tr>
<tr>
<td>ECH3</td>
<td>Similar to ECH1 but white and less well cemented</td>
</tr>
<tr>
<td>ECH4</td>
<td>Similar to ECH3</td>
</tr>
<tr>
<td>VO1</td>
<td>White, well cemented bioclastic limestone</td>
</tr>
<tr>
<td>VO2</td>
<td>Similar to VO1</td>
</tr>
<tr>
<td>VO3</td>
<td>Similar to VO1 but slightly more oolitic</td>
</tr>
<tr>
<td>VO4</td>
<td>Similar to VO1 but slightly more oolitic</td>
</tr>
</tbody>
</table>

Sites: CDB= Cluse de la Balme; STD= St. Didier; LE ROC= Le Rocheret; CER= Cerin; ARM= Armix; LAND= Landaize; V-M= Virieu-Martin; MQ= Mares Quarry; ECH= Echallon; OY= Oyonnax; MOL= Molinges; V DAM= Vougans Dam; PDL= Pont de Lemme; PDLC= Pont de la Chaux.
## Macrofossils

<table>
<thead>
<tr>
<th>Sample number</th>
<th>Fossil type</th>
<th>Preservation state</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cer1</td>
<td>Small cidaroid echinoid.</td>
<td>Poor, very broken / partial and flat. Very little left.</td>
</tr>
<tr>
<td>Cer2</td>
<td>Crinoid ossicles (2 types-possibly <em>Pentacrinites</em> and other).</td>
<td>Weathered – reasonable.</td>
</tr>
<tr>
<td>MQ1</td>
<td>Bivalves and Gastropods.</td>
<td>Reasonable.</td>
</tr>
<tr>
<td>MQ2</td>
<td>Corals.</td>
<td>Good.</td>
</tr>
<tr>
<td>MQ3</td>
<td>Colonial coral.</td>
<td>Very weathered.</td>
</tr>
<tr>
<td>Mo1</td>
<td>Coral / sponge and bivalves.</td>
<td>Reasonable to good.</td>
</tr>
<tr>
<td>Mo6</td>
<td>Echinoid spines and bivalves.</td>
<td>Reasonable.</td>
</tr>
<tr>
<td>Land (no specific number)</td>
<td>Possible <em>Thalassinoides</em> burrows.</td>
<td>Weathered.</td>
</tr>
<tr>
<td>Mo (no specific number)</td>
<td>Brachiopods, oysters and small gastropods.</td>
<td>Good.</td>
</tr>
<tr>
<td>MQ (no specific number)</td>
<td>Diceratid bivalves and brachiopods.</td>
<td>Reasonable.</td>
</tr>
<tr>
<td>Pdlc (no specific number)</td>
<td>Crinoids.</td>
<td>Reasonable.</td>
</tr>
</tbody>
</table>
### Thin sections

<table>
<thead>
<tr>
<th>Thin section number</th>
<th>Description</th>
<th>Algae found</th>
<th>Other microfossils</th>
</tr>
</thead>
<tbody>
<tr>
<td>OY1</td>
<td>Dark grey cracked micrite.</td>
<td><strong>Clypeina jurassica</strong></td>
<td></td>
</tr>
<tr>
<td>OY2</td>
<td>Oncoid / clastic mix with bioclasts and a sparite matrix. Some recrystallized calcite infill.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>OY3.1</td>
<td>Oncoid / clastic mix in a recrystallized calcitic infill. Poor slide.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>OY3.2</td>
<td>Poor slide. Same as OY3.1 except with more bioclasts.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MO1.1</td>
<td>Dark grey micrite-like limestone with bioclasts including bivalves and a possible sponge - crystalline veins / cracks.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MO1.2</td>
<td>Same as MO1.1.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MO2</td>
<td>Dark micrite with many bioclasts (sponge, echinoid spines, foraminifera and bivalve fragments) and crystalline calcitic veins.</td>
<td><strong>Salpingoporella annulata?</strong></td>
<td><strong>Foraminifer, Echinoid spine, Sponge</strong></td>
</tr>
<tr>
<td>MO3</td>
<td>Poor slide. Bioclastic (including bivalves and echinoid spines) limestone with a micrite matrix.</td>
<td><strong>Pseudoepimastopora? Macroporella?</strong></td>
<td><strong>Echinoid spine</strong></td>
</tr>
<tr>
<td>MO4</td>
<td>Poor slide. Same as MO3.</td>
<td><strong>Cayeuxia?</strong></td>
<td></td>
</tr>
<tr>
<td>MO6</td>
<td>Clast supported ooidal limestone with occasional bivalve fragments. Bad slide.</td>
<td></td>
<td><strong>Foraminifer</strong></td>
</tr>
<tr>
<td>VO1.1a</td>
<td>Bio / pseudo-ooidal reefrock mess with bivalve fragments.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>VO1.1b</td>
<td>Very poor slide. Same as VO1.1a.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>VO1.2</td>
<td>Bio / pseudo-oosparite.</td>
<td></td>
<td><strong>Eggerella cf. meentzeni</strong></td>
</tr>
<tr>
<td>VO2.1</td>
<td>Very poor slide. Clastic mess. Reef rock ?</td>
<td></td>
<td></td>
</tr>
<tr>
<td>VO3</td>
<td>Messy biosparite. Bad slide.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Code</td>
<td>Description</td>
<td>Facies</td>
<td></td>
</tr>
<tr>
<td>-------</td>
<td>-----------------------------------------------------------------------------</td>
<td>-----------------------------------------------------------------------------------------</td>
<td></td>
</tr>
<tr>
<td>PDL1</td>
<td>Dark grey micrite with, at the edges, layers of bioclasts / ooids.</td>
<td>Evenly bioclastic with significant amount of bioclasts.</td>
<td></td>
</tr>
<tr>
<td>PDL2</td>
<td>Small pieces of clastic mess.</td>
<td>Small pieces of clastic mess.</td>
<td></td>
</tr>
<tr>
<td>PDL3</td>
<td>Poor slide. Small ooids and a recrystallized matrix.</td>
<td>Poor slide. Small ooids and a recrystallized matrix.</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Salpingoporella annulata?</em></td>
<td><em>Salpingoporella annulata?</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Littuola cf. nautiloidea</td>
<td>Miliolid? Eggerella cf. meentzeni, Trocholina alpina, Lenticulina sp.?</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Miliolid? Trocholina alpina</td>
<td>Miliolid? Trocholina alpina</td>
<td></td>
</tr>
<tr>
<td>PDL6</td>
<td>Bioclastic limestone with a recrystallized matrix.</td>
<td>Bioclastic limestone with a recrystallized matrix.</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Clypeina jurassica,</em> Likanella bartheli</td>
<td><em>Clypeina jurassica,</em> Likanella bartheli</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Trocholina elongata, Trocholina alpina, Miliolid?</td>
<td>Trocholina elongata, Trocholina alpina, Miliolid?</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cayeuxia</td>
<td>Cayeuxia</td>
<td></td>
</tr>
<tr>
<td>PC1</td>
<td>Oosparite with occasional bioclasts of gastropod and bivalve.</td>
<td>Oosparite with occasional bioclasts of gastropod and bivalve.</td>
<td></td>
</tr>
<tr>
<td>PC2</td>
<td>Oncloid and clastic mash with some ooids, crystalline calcitic infill of gaps.</td>
<td>Oncloid and clastic mash with some ooids, crystalline calcitic infill of gaps.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Echinoid spine</td>
<td>Echinoid spine</td>
<td></td>
</tr>
<tr>
<td>PC3</td>
<td>Oosparite and bivalve fragments (<em>Ostrea</em>?). Crystalline calcite infill of gaps.</td>
<td>Oosparite and bivalve fragments (<em>Ostrea</em>?). Crystalline calcite infill of gaps.</td>
<td></td>
</tr>
<tr>
<td>PC4.1</td>
<td>Clastic mess – reef rock?</td>
<td>Clastic mess – reef rock?</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Cayeuxia</em> ?</td>
<td><em>Cayeuxia</em> ?</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sponge?</td>
<td>Sponge?</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Halimedacean?</td>
<td>Halimedacean?</td>
<td></td>
</tr>
<tr>
<td>ECH1</td>
<td>Algal bioclastic limestone – recrystallized matrix / infill.</td>
<td>Algal bioclastic limestone – recrystallized matrix / infill.</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Campbelliella striata</em></td>
<td><em>Campbelliella striata</em></td>
<td></td>
</tr>
<tr>
<td>VM1</td>
<td>Dark micrite with some bioclasts – bivalves?</td>
<td>Dark micrite with some bioclasts – bivalves?</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Miliolid?</td>
<td>Miliolid?</td>
<td></td>
</tr>
<tr>
<td>VM2</td>
<td>Same as VM1.</td>
<td>Campbelliella striata, Gyroporella / Macroporella sp. (uncertain), Likanella bartheli?</td>
<td>Eggerella cf. meentzeni</td>
</tr>
<tr>
<td>----</td>
<td>-------------</td>
<td>------------------------------------------------------------------------------------</td>
<td>------------------------</td>
</tr>
<tr>
<td>VM3</td>
<td>Calcite veined bioclastic micrite (gastropods, bivalve fragments, foram and algae).</td>
<td>Clypeina jurassica</td>
<td>Miliolid?</td>
</tr>
<tr>
<td>LAN1</td>
<td>Algal bioclastic limestone – recrystallized matrix / infill.</td>
<td>Campbelliella striata, Clypeina jurassica, Cylindroporella / Salpingoporella sp.</td>
<td>Unrecognised foraminifer</td>
</tr>
<tr>
<td>LAN2</td>
<td>Algal bioclastic limestone – recrystallized matrix / infill.</td>
<td>Clypeina jurassica</td>
<td>Eggerella cf. meentzeni, Unrecognised foraminifer</td>
</tr>
<tr>
<td>ARM1</td>
<td>Bioclastic limestone with large bivalves.</td>
<td></td>
<td>Sponge? Trocholina elongata, Lituola nautiloidea</td>
</tr>
<tr>
<td>ARM2</td>
<td>Same as ARM1 except with more small bioclasts, gastropods, complete bivalves and a micritic matrix.</td>
<td>Varioparietes sp?, Cayeuxia</td>
<td></td>
</tr>
<tr>
<td>CER2</td>
<td>Poor slide. Bioclastic limestone with a recrystallized matrix / infill.</td>
<td>Clypeina jurassica, Pseudoepimastopora ?, Campbelliella striata, Cayeuxia, Salpingoporella annulata?</td>
<td>Gastropod</td>
</tr>
<tr>
<td>CER3</td>
<td>Dark micrite with some bioclasts.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CDB1</td>
<td>Reef rock mess – bioclastic / clastic mix with bivalve and gastropod fragments and a recrystallized matrix.</td>
<td>Cayeuxia, Campbelliella striata, Baccinella irregularis?, Salpingoporella pygmae</td>
<td>Eggerella cf. meentzeni</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-------</td>
<td>----------------------------------------------------------------</td>
<td>----------------------------------------------------------------</td>
<td>----------------------------------------------------------------</td>
</tr>
<tr>
<td>CDB2</td>
<td>Matrix supported biosparite – mix of small clastic and bioclastic bits.</td>
<td>Miliolid? Trocholina elongata, Haurania sp.</td>
<td></td>
</tr>
<tr>
<td>ROC1</td>
<td>Poor slide. Reef rock mess.</td>
<td>Miliolid? Trocholina alpina, Lenticulina sp.? protopeneroplis</td>
<td></td>
</tr>
<tr>
<td>ROC2</td>
<td>Bioclastic limestone with a recrystallized matrix supported structure.</td>
<td>Salpingoporella annulata ?</td>
<td>Sponge? Miliolid? Trocholina alpina Foraminifera</td>
</tr>
<tr>
<td>STD1</td>
<td>Bioclastic biosparite.</td>
<td>Salpingoporella pygmae ?</td>
<td>Miliolid? Trocholina elongata, Protopeneroplis striata</td>
</tr>
</tbody>
</table>

Other hand specimens proved difficult to thin section due to the friable nature of the limestone, causing break-up of the sample at rocksaw and / or thin sectioning processes. (these specimens were: MQ1, MQ2, MQ3, MO5, MO7, ECH2, ECH3, ECH4, CER1)

Sites : CDB= Cluse de la Balme; STD= St. Didier; LE ROC= Le Rocheret; CER= Cerin; ARM= Armix; LAND= Landaize; V-M= Virieu-Martin; MQ= Mares Quarry; ECH= Echallon; OY= Oyonnax; MOL= Molinges; V DAM= Vougians Dam; PDL= Pont de Lemme; PDLC= Pont de la Chaux.
Appendix

AII

Languedoc
Sites

Argilliers
- low (1-1.5m tall) roadside exposure – extensive and complete.
- variable hydrodynamism – lagoonal back reef + some “beach rocks” (sub-emersion).

La Table
- barrier reef facies (Neoteutoporella socialis bushes + corals + sponges + diceratids).
- poor patchy exposure mostly vegetation covered (forestry track).

Roc Blanc / Mtn de la Serrane
- lower MSE – barrier facies (like La Table – sponges + corals) to lagoonal facies
  (change at 3rd hair pin on track) by fingered / lensed contact. “Calcaires graveleux”- reworked by storms: also black pebbles – possible karstic infill from palaeosols.
- Roc Blanc- partly dolomitized.

Rieutord
- forereef facies.
- old train track + cuttings.

Les Prats / La Maline
- slope of Eastern side of Rocher de la Barre.
- karstic surface and covered with “patine”.
- large corals.
- barrier facies.

Rocher de la Barre
- karstic.
- barrier to lagoonal facies.

Le Méjanel
- external platform / basin.

Les Oliviers
- very low outcrop (c0.3m) along private roadway.
- two layers- micrite and shelly.
- join of slope and basin?

La Cadière
- basinal deposits.
- well bedded, fine, homogenous limestone.

Coupe du Coutah / Pont du Hasard
- well bedded (horizontal) basinal limestones in dry gorge.

Ferrières – les – Verreries
- barrier facies.
- massive clastic limestone + “calcaire graveleux”.
- diceratids + branching coral.
## Lithology descriptions

<table>
<thead>
<tr>
<th>Lithology</th>
<th>Description</th>
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<tr>
<td>Bioclastic Limestone</td>
<td>White – creamy coloured, limestone composed of a mixture of biotic input with areas of varying amounts of intraclasts and micritic infill.</td>
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<tr>
<td>&quot;Calcaires Graveleux&quot;</td>
<td>&quot;Calcareous Gravel&quot; – a limestone grit whose individual pebbles can be composed of most any calcareous sedimentary construct – oolith, pseudo oolith, intraclast, oncoid, bioclast, etc. Normally the grit is bound together by cement or algal binding.</td>
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<tr>
<td>Calcirudite</td>
<td>Large, coarse crystal composite limestone with some evidence of bioclastic input. Large crystals may be partly a secondary feature.</td>
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<td>Submicrite</td>
<td>Pelagic style limestone – homogeneous, very small grains with occasional (rare) broken fragments of bioclastic input and some veining. Dark grey in colour.</td>
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<tr>
<td>Thin laminar</td>
<td>Pelagic style laminates in distinct beds of almost pure, homogeneous limestone similar to submicrite.</td>
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<tr>
<td>Dolomite</td>
<td>Normally totally replaced limestone with calcareous veining.</td>
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# Algae previously reported in the area

<table>
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<tr>
<th>Algae</th>
<th>Age</th>
<th>Author</th>
<th>Other information</th>
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### Languedoc algae found in this study

*Frequency in particular slide:*

- **V.r.** = very rare
- **R.** = rare
- **F.** = fair occurrence
- **C.** = common
- **V.c.** = very common

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### Other Microfossils

*Frequency in particular slide:*

- **V.r** = very rare
- **R.** = rare
- **F.** = fair occurrence
- **C.** = common
- **V.c** = very common

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</tbody>
</table>

Identification after Bodeur 1992 (unpublished)
## Notable macrofossils

<table>
<thead>
<tr>
<th>Fossil</th>
<th>Condition</th>
<th>Hand specimen number</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cidaroid echinoid</td>
<td>Good</td>
<td>N/A – area of FLV 1-2</td>
<td>In possession of Y. Bodeur at Nantes University- unusually complete (rare here)</td>
</tr>
<tr>
<td>Corals</td>
<td>Good</td>
<td>MSE 1</td>
<td>Mostly cast</td>
</tr>
<tr>
<td>Bivalve shell</td>
<td>V. poor</td>
<td>OL 2</td>
<td>V. weathered</td>
</tr>
<tr>
<td>Echinoid spine</td>
<td>Poor</td>
<td>OL 2</td>
<td>Small, oblique fracture</td>
</tr>
<tr>
<td>Belemnite rostrum</td>
<td>Fair</td>
<td>RIE 5</td>
<td></td>
</tr>
<tr>
<td>NUMBER</td>
<td>AGE</td>
<td>DESCRIPTION</td>
<td></td>
</tr>
<tr>
<td>--------</td>
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<td></td>
</tr>
<tr>
<td>MEJ 1</td>
<td>Tithonian</td>
<td>Light grey homogenous micrite, conchoidal fractures, occasional purple staining.</td>
<td></td>
</tr>
<tr>
<td>RDB 1</td>
<td>Tithonian</td>
<td>Light grey / white clastic (c1-2mm), well cemented limestone with a possible gastropod.</td>
<td></td>
</tr>
<tr>
<td>RDB 2</td>
<td>Tithonian</td>
<td>Light grey clastic, well cemented limestone with different sized clasts (1-5mm).</td>
<td></td>
</tr>
<tr>
<td>RDB 3</td>
<td>Tithonian</td>
<td>Oncoidal and bioclastic light grey well cemented limestone with calcite veins.</td>
<td></td>
</tr>
<tr>
<td>RDB 4</td>
<td>Tithonian</td>
<td>Buff coloured calcite veined limestone with rounded clasts – pseudo-oncoids? Well cemented with some calcite infilling.</td>
<td></td>
</tr>
<tr>
<td>PR/M 1</td>
<td>Tithonian</td>
<td>White well cemented mash of grains.</td>
<td></td>
</tr>
<tr>
<td>PR/M 2</td>
<td>Tithonian</td>
<td>Light grey / brown crystalline limestone with coral?</td>
<td></td>
</tr>
<tr>
<td>PR/M 3</td>
<td>Tithonian</td>
<td>White, well cemented semi-crystalline clastic limestone with possible bivalve fragment.</td>
<td></td>
</tr>
<tr>
<td>FLV 1</td>
<td>Tithonian</td>
<td>Buff / light grey bioclastic limestone with a well cemented micrite matrix.</td>
<td></td>
</tr>
<tr>
<td>FLV 2</td>
<td>Tithonian</td>
<td>Buff / light grey bioclastic limestone with a well cemented micrite matrix. Has a dendritic pattern on a cracked surface.</td>
<td></td>
</tr>
<tr>
<td>FLV 3</td>
<td>Tithonian</td>
<td>Well cemented light grey bioclastic (bivalves?) limestone with possible corals and a dendritic pattern.</td>
<td></td>
</tr>
<tr>
<td>FLV 4</td>
<td>Tithonian</td>
<td>Light grey oncotic / pisolithic limestone with calcite veining and well cemented calcite vug filling as well.</td>
<td></td>
</tr>
<tr>
<td>FLV 5</td>
<td>Tithonian</td>
<td>Cream coloured massive (micritic) homogenous limestone with small calcite veins.</td>
<td></td>
</tr>
<tr>
<td>FLV 6</td>
<td>Tithonian</td>
<td>Light grey calcite veined limestone</td>
<td></td>
</tr>
<tr>
<td>MSE 1</td>
<td>Tithonian</td>
<td>Light brown / white micrite with many corals</td>
<td></td>
</tr>
<tr>
<td>MSE 2</td>
<td>Tithonian</td>
<td>White generally massive limestone with some bioclasts?</td>
<td></td>
</tr>
<tr>
<td>MSE 3</td>
<td>Tithonian</td>
<td>Buff bioclastic / oncotic mix, well cemented limestone.</td>
<td></td>
</tr>
<tr>
<td>MSE 4</td>
<td>Tithonian</td>
<td>White micrite with angular black pebbles / fragments / intraclasts.</td>
<td></td>
</tr>
<tr>
<td>MSE 5</td>
<td>Tithonian</td>
<td>Partly crystalline, well cemented light brown / white oncrite.</td>
<td></td>
</tr>
<tr>
<td>MSE 6</td>
<td>Tithonian</td>
<td>Creamy white oncrite – pseudo-ons 4mm-2cm (most c5mm), well cemented with some calcite veining.</td>
<td></td>
</tr>
<tr>
<td>ARG 1</td>
<td>Tithonian</td>
<td>White (bio?)clastic limestone with many calcite veins, well cemented.</td>
<td></td>
</tr>
<tr>
<td>ARG 2</td>
<td>Tithonian</td>
<td>White (bio?)clastic limestone with many calcite veins, well cemented.</td>
<td></td>
</tr>
<tr>
<td>ARG 3</td>
<td>Tithonian</td>
<td>White (bio?)clastic / oncoidal limestone with many calcite veins, well cemented.</td>
<td></td>
</tr>
<tr>
<td>ARG 4</td>
<td>Tithonian</td>
<td>White, well cemented bioclastic limestone (partly recrystallized).</td>
<td></td>
</tr>
<tr>
<td>ARG 5</td>
<td>Tithonian</td>
<td>Medium grey reasonably homogenous, well cemented,</td>
<td></td>
</tr>
<tr>
<td>ARG 6</td>
<td>Tithonian</td>
<td>partly recrystallized limestone.</td>
<td></td>
</tr>
<tr>
<td>ARG 7</td>
<td>Tithonian</td>
<td>Bioclastic / oncoidal light grey / white, well cemented limestone.</td>
<td></td>
</tr>
<tr>
<td>ARG 8</td>
<td>Tithonian</td>
<td>Buff clastic limestone, well cemented and heavily veined / recrystallized.</td>
<td></td>
</tr>
<tr>
<td>ARG 9</td>
<td>Tithonian</td>
<td>White bioclastic, partly recrystallized well cemented limestone.</td>
<td></td>
</tr>
<tr>
<td>ARG 10</td>
<td>Tithonian</td>
<td>White bioclastic limestone, well cemented and calcite veined with possible corals.</td>
<td></td>
</tr>
<tr>
<td>ARG 11</td>
<td>Tithonian</td>
<td>Very bioclastic well cemented white limestone with a light grey matrix. Some recrystallized vug infill.</td>
<td></td>
</tr>
<tr>
<td>ARG 12</td>
<td>Tithonian</td>
<td>Very bioclastic well cemented white limestone with a light grey matrix, partly recrystallized.</td>
<td></td>
</tr>
<tr>
<td>ARG 13</td>
<td>Tithonian</td>
<td>Oncoidal / bioclastic, well cemented white limestone.</td>
<td></td>
</tr>
<tr>
<td>ARG 14</td>
<td>Tithonian</td>
<td>Light grey bioclastic limestone, well cemented.</td>
<td></td>
</tr>
<tr>
<td>ARG 15</td>
<td>Tithonian</td>
<td>Light grey very bioclastic limestone, well cemented.</td>
<td></td>
</tr>
<tr>
<td>ARG 16</td>
<td>Tithonian</td>
<td>Light grey micrite + (bio?)clasts. Well cemented with some calcite veining.</td>
<td></td>
</tr>
<tr>
<td>ARG 17</td>
<td>Tithonian</td>
<td>Light grey, well cemented bioclastic limestone.</td>
<td></td>
</tr>
<tr>
<td>ARG 18</td>
<td>Tithonian</td>
<td>Light grey, well cemented bioclastic limestone.</td>
<td></td>
</tr>
<tr>
<td>ARG 19</td>
<td>Tithonian</td>
<td>Light grey, well cemented bioclastic limestone with some calcite veining.</td>
<td></td>
</tr>
<tr>
<td>ARG 20</td>
<td>Tithonian</td>
<td>Light grey / light brown, well cemented bioclastic limestone with some calcite veining and some calcite crystal infill.</td>
<td></td>
</tr>
<tr>
<td>ARG 21</td>
<td>Tithonian</td>
<td>Light grey / light brown, small bioclasts in limestone. Very well cemented with some calcite veining.</td>
<td></td>
</tr>
<tr>
<td>ARG 22</td>
<td>Tithonian</td>
<td>Light grey, bioclastic limestone. Well cemented with some calcite veining.</td>
<td></td>
</tr>
<tr>
<td>ARG 23</td>
<td>Tithonian</td>
<td>White, bioclastic limestone. Well cemented with some calcite veining.</td>
<td></td>
</tr>
<tr>
<td>ARG 24</td>
<td>Tithonian</td>
<td>White, bioclastic limestone. Well cemented with some calcite veining and some calcite crystal infill.</td>
<td></td>
</tr>
<tr>
<td>ARG 25</td>
<td>Tithonian</td>
<td>Yellow / white bioclastic limestone, well cemented.</td>
<td></td>
</tr>
<tr>
<td>TAB 1</td>
<td>Tithonian</td>
<td>Creamy grey / white limestone – well cemented micrite with large biota (including Neoteutoporella socialis).</td>
<td></td>
</tr>
<tr>
<td>TAB 2</td>
<td>Tithonian</td>
<td>Creamy limestone of small clasts with coral and patches of micrite.</td>
<td></td>
</tr>
<tr>
<td>TAB 3</td>
<td>Tithonian</td>
<td>Buff coloured small clasts of limestone with bushes of Neoteutoporella socialis, corals and calcite veins.</td>
<td></td>
</tr>
<tr>
<td>CAD 1</td>
<td>Tithonian</td>
<td>Moderately cemented, medium grey micrite? With calcite vug fills.</td>
<td></td>
</tr>
<tr>
<td>CAD 2</td>
<td>Tithonian</td>
<td>Medium grey micrite with lighter grey subangular intraclasts (also micrite) 1mm-2cm.</td>
<td></td>
</tr>
<tr>
<td>CAD 3</td>
<td>Tithonian</td>
<td>Very dark grey shaley limestone – micrite and some dark clasts and calcite veins.</td>
<td></td>
</tr>
<tr>
<td>CAD 4</td>
<td>Tithonian</td>
<td>Very dark grey homogenous micrite.</td>
<td></td>
</tr>
<tr>
<td>Sample</td>
<td>Age</td>
<td>Description</td>
<td></td>
</tr>
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<td>-----------------------------------------------------------------------------</td>
<td></td>
</tr>
<tr>
<td>CAD 5</td>
<td>Tithonian</td>
<td>Dark grey micrite with some (dark) intraclasts.</td>
<td></td>
</tr>
<tr>
<td>CAD 6</td>
<td>Tithonian</td>
<td>Dark grey homogenous micritic limestone? A few major calcite veins.</td>
<td></td>
</tr>
<tr>
<td>CAD 7</td>
<td>Tithonian</td>
<td>Dark grey homogenous micrite. Some calcite veins.</td>
<td></td>
</tr>
<tr>
<td>CAD 8</td>
<td>Tithonian</td>
<td>Medium grey homogenous micrite with some intraclasts and conchoidal fractures.</td>
<td></td>
</tr>
<tr>
<td>CAD 9</td>
<td>Tithonian</td>
<td>Medium grey homogenous micrite with calcite veining.</td>
<td></td>
</tr>
<tr>
<td>RIE 1</td>
<td>Tithonian</td>
<td>Pebble conglomerate (1mm-2cm) with good crystalline space-filling calcite cement.</td>
<td></td>
</tr>
<tr>
<td>RIE 2</td>
<td>Tithonian</td>
<td>Light grey / buff veined crystalline? Limestone with bioclastic fragments.</td>
<td></td>
</tr>
<tr>
<td>RIE 3</td>
<td>Tithonian</td>
<td>Light grey relatively massive limestone with signs of coral.</td>
<td></td>
</tr>
<tr>
<td>RIE 4</td>
<td>Tithonian</td>
<td>Tan / grey micrite with some calcite veining.</td>
<td></td>
</tr>
<tr>
<td>RIE 5</td>
<td>Tithonian</td>
<td>Well cemented, light grey bioclastic limestone grains plus part of a Belemnite rostrum.</td>
<td></td>
</tr>
<tr>
<td>RIE 6</td>
<td>Tithonian</td>
<td>Grey crystalline limestone with evidence of bioclasts.</td>
<td></td>
</tr>
<tr>
<td>RIE 7</td>
<td>Tithonian</td>
<td>Crystalline? Limestone with bioclastic fragments. Light grey in colour with corals.</td>
<td></td>
</tr>
<tr>
<td>RIE 8</td>
<td>Tithonian</td>
<td>Medium grey micrite with calcite veins.</td>
<td></td>
</tr>
<tr>
<td>RIE 9</td>
<td>Tithonian</td>
<td>Homogenous buff / grey micrite.</td>
<td></td>
</tr>
<tr>
<td>OL 1</td>
<td>Tithonian</td>
<td>Light grey, calcite veined homogenous micrite.</td>
<td></td>
</tr>
<tr>
<td>OL 2</td>
<td>Tithonian</td>
<td>Mixture of OL1 and a buff bioclastic limestone. Relatively well cemented with remains of an echinoid spine.</td>
<td></td>
</tr>
<tr>
<td>C/P 1</td>
<td>Tithonian</td>
<td>Dark grey homogenous micrite.</td>
<td></td>
</tr>
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</table>
### THIN SECTIONS

<table>
<thead>
<tr>
<th>NUMBER</th>
<th>AGE</th>
<th>DESCRIPTION</th>
</tr>
</thead>
<tbody>
<tr>
<td>MEJ 1</td>
<td>Tithonian</td>
<td>Reasonably dark micrite with some possible layering and some fine calcite veining.</td>
</tr>
<tr>
<td>RDB 1</td>
<td>Tithonian</td>
<td>Rounded grains with calcitic vug infill and foraminifers.</td>
</tr>
<tr>
<td>RDB 2</td>
<td>Tithonian</td>
<td>Rounded grains with masses of foraminifers.</td>
</tr>
<tr>
<td>RDB 3</td>
<td>Tithonian</td>
<td>Sub-angular to sub-rounded grains and larger masses – algally enveloped bioclasts? Lots of foraminifers.</td>
</tr>
<tr>
<td>RDB 4</td>
<td>Tithonian</td>
<td>Rounded grains with some foraminifers.</td>
</tr>
<tr>
<td>PR/M 1</td>
<td>Tithonian</td>
<td>MISSING / DESTROYED</td>
</tr>
<tr>
<td>PR/M 2</td>
<td>Tithonian</td>
<td>Calcitic infill and bivalve fragments.</td>
</tr>
<tr>
<td>PR/M 3</td>
<td>Tithonian</td>
<td>Jumble of angular and rounded grains of many types. Possible algae?</td>
</tr>
<tr>
<td>FLV 1</td>
<td>Tithonian</td>
<td>Rounded grains in micritic matrix, foraminifers, possible algae, coarse crystalline calcite in vein, coral fragment and bivalve fragments.</td>
</tr>
<tr>
<td>FLV 2</td>
<td>Tithonian</td>
<td>Small rounded grains with foraminifers and Thaumatoporella parvovesiculifera – reef rock.</td>
</tr>
<tr>
<td>FLV 3</td>
<td>Tithonian</td>
<td>Background grains merged, corals, foraminifers, bivalve fragments.</td>
</tr>
<tr>
<td>FLV 4</td>
<td>Tithonian</td>
<td>Rounded grains – some ooidal, foraminifers.</td>
</tr>
<tr>
<td>FLV 5</td>
<td>Tithonian</td>
<td>Dark micrite with subrounded grains inset, possible partial Clypeina jurassica, calcite veining.</td>
</tr>
<tr>
<td>FLV 6</td>
<td>Tithonian</td>
<td>Ooids, possible partial algae-centered bioclasts.</td>
</tr>
<tr>
<td>MSE 1</td>
<td>Tithonian</td>
<td>Calcitic infill? Plus Cayeuxia.</td>
</tr>
<tr>
<td>MSE 2</td>
<td>Tithonian</td>
<td>Recrystallized reef rock with big shells and coral / sponge fragments.</td>
</tr>
<tr>
<td>MSE 3</td>
<td>Tithonian</td>
<td>Large grains – sub-rounded, bioclastic, Campbelliella striata, Cayeuxia, foraminifers and some calcitic infill – possible partially changed to dolomite?</td>
</tr>
<tr>
<td>MSE 4</td>
<td>Tithonian</td>
<td>Micrite with intraclasts.</td>
</tr>
<tr>
<td>MSE 5</td>
<td>Tithonian</td>
<td>Rounded grains with some larger grains – algally bound bioclasts? Calcitic infill of some areas. Clypeina jurassica, Cayeuxia, foraminifers.</td>
</tr>
<tr>
<td>MSE 6</td>
<td>Tithonian</td>
<td>Large algally bound bioclasts / oncocids, foraminifers, possible algae, gastropod, large scale crystallization between grains.</td>
</tr>
<tr>
<td>ARG 1</td>
<td>Tithonian</td>
<td>Well-rounded grainstone with calcite veins, foraminifers, Cayeuxia, partial Clypeina jurassicas, gastropod.</td>
</tr>
<tr>
<td>ARG 2</td>
<td>Tithonian</td>
<td>Pseudo-oids and areas of matrix, calcite veined.</td>
</tr>
<tr>
<td>ARG 3</td>
<td>Tithonian</td>
<td>Bioclastic, matrix supported, well-rounded grains, lots of pieces of Clypeina jurassica, foraminifers.</td>
</tr>
<tr>
<td>ARG 4</td>
<td>Tithonian</td>
<td>Bioclastic, matrix supported, well-rounded grains, lots of pieces of Clypeina jurassica, foraminifers, bivalve fragments, Apophoratella?</td>
</tr>
<tr>
<td>ARG 5</td>
<td>Tithonian</td>
<td>“Clotted micrite” with foraminifers and possible Cayeuxia.</td>
</tr>
</tbody>
</table>
ARG 6  Tithonian  Bioclastic, foraminifers, bivalve fragments, *Cayeuxia*, *Clypeina jurassica*.

ARG 7  Tithonian  Rounded to sub-rounded matrix supported grains, *Cayeuxia*, foraminifers, echinoid spine, possible *Thaumatoporella parvovesiculifera*, some drusy mosaic cement.

ARG 8  Tithonian  Rounded, bioclastic matrix supported grains, *Cayeuxia*, *Campbelliella striata*, *Clypeina jurassica*, foraminifers, and reworking of cyanobacterial matter.

ARG 9  Tithonian  Sub-rounded grains, some bound together, drusy mosaic cement, *Cayeuxia, Campbelliella striata, Clypeina jurassica*, foraminifers and a possible chaetid sponge.

ARG 10  Tithonian  Rounded matrix supported grains, with some drusy mosaic cement and *Cayeuxia, Campbelliella striata*.

ARG 11  Tithonian  Drusy mosaic cement binding *Cayeuxia*, large limestone clumps and foraminifers.

ARG 12  Tithonian  Sub-rounded to sub-angular grains with some large clumps, bivalve fragments, crustacean coprolites, *Campbelliella striata*, and drusy mosaic cement.

ARG 13  Tithonian  Rounded to sub-rounded grains with foraminifers, *Cayeuxia*, small calcite veining, lots of *Campbelliella striata* and drusy mosaic cement.

ARG 14  Tithonian  Sub-angular micritic lumps in a sparry cement with foraminifers, *Cayeuxia*, and *Campbelliella striata*.

ARG 15  Tithonian  Clumps of rounded grains in a micrite matrix (micrite meniscus fabric between grains), foraminifers, *Cayeuxia, Campbelliella striata, Clypeina jurassica*.


ARG 17  Tithonian  Biosparite / bioclastic shelly grainstone – lots of *Campbelliella striata*, and foraminifers, *Clypeina jurassica*.

ARG 18  Tithonian  Bioclastic, lots of *Campbelliella striata, Cayeuxia*, plus encrusting algae – eg *Thaumatoporella parvovesiculifera*.


ARG 20  Tithonian  Rounded grains and calcite veins, foraminifers, *Cayeuxia*, bivalve fragments, *Campbelliella striata*.

ARG 21  Tithonian  Sub-rounded grains, grain supported, some size layering, a few calcite veins, *Cayeuxia*.

ARG 22  Tithonian  Sub-rounded grains, some clumps, some algal layered grains, some size layering, large vug with calcite infill, sparse *Cayeuxia* and foraminifer.
ARG 23 Tithonian Sub-angular grains with calcite infill between, gastropod, foraminifers, *Cayeuxia* and *Campbelliella striata*.

ARG 24 Tithonian Sub-angular grains with calcite infill between, foraminifers, *Cayeuxia* and *Campbelliella striata*.

ARG 25 Tithonian Sub-rounded grains, *Cayeuxia*, *Clypeina jurassica* and space filling calcite.

TAB 1 Tithonian *Neoteutoporella socialis* bush, some small sub-rounded grains, foram.

TAB 2 Tithonian *Cayeuxia*? Sub-rounded to rounded grains, bivalve fragments and some calcitic infill.

TAB 3 Tithonian *Neoteutoporella socialis* bush? Mainly very small sub-rounded bioclastic grains, foraminifers, *Montenegroella*?

CAD 1 Tithonian Recrystallized limestone.

CAD 2 Tithonian Dark micritic limestone with some limestone clasts. Fine limestone veins.

CAD 3 Tithonian MISSING / DESTROYED

CAD 4 Tithonian MISSING / DESTROYED

CAD 5 Tithonian Dark micrite with some very small bioclastic pieces (indistinguishable), few fine calcite veins, stylolites.

CAD 6 Tithonian Dark micrite with some very small bioclastic pieces (indistinguishable), many fine calcite veins.

CAD 7 Tithonian MISSING / DESTROYED

CAD 8 Tithonian Dark micrite with some very small bioclastic pieces (indistinguishable), fine calcite veins, and one large calcite vein (large calcite crystals).

CAD 9 Tithonian Dark micrite with some very small bioclastic pieces (indistinguishable), fine calcite veins.

RIE 1 Tithonian Calcite grains with calcite overgrowths – secondary crystallization and vug filling.

RIE 2 Tithonian Mixed grains in a micritic matrix with calcite crystal growths, foraminifers, *Cayeuxia*? Partial echinoid spine.

RIE 3 Tithonian Mixed grains, *Cayeuxia*? Echinoid spine, foraminifers and bryozoan.

RIE 4 Tithonian Jumble of angular grains and bioclastic fragments, coral.

RIE 5 Tithonian Jumble, partly recrystallized? *Cayeuxia*? *Thaumatoporella parvovesiculifera* / *Pseudoepimastopora*? Possible echinoid spine fragments?

RIE 6 Tithonian Mixture of sub-rounded grains and bioclasts, micritic matrix, calcite crystalline infill, partial oblique *Neoteutoporella socialis*?

RIE 7 Tithonian Sub-rounded grains and bioclasts, micritic matrix, foraminifers, calcite crystalline infill.

RIE 8 Tithonian Dark mass of grains, calcite veining, echinoid spine, foraminifers.

RIE 9 Tithsonian Dark mass of grains.
<p>| | | |</p>
<table>
<thead>
<tr>
<th></th>
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</thead>
<tbody>
<tr>
<td>OL 1</td>
<td>Tithonian</td>
<td>Dark micrite, two possible foraminifera.</td>
</tr>
<tr>
<td>OL 2</td>
<td>Tithonian</td>
<td>Small bioclastic fragments (indefinable) in dark micrite.</td>
</tr>
<tr>
<td>C/P 1</td>
<td>Tithonian</td>
<td>Very fine laminated, reasonably dark homogenous micrite.</td>
</tr>
</tbody>
</table>
Appendix

AIII

Portugal
## Sites

<table>
<thead>
<tr>
<th>Site</th>
<th>Location (Longitude / Latitude)</th>
<th>Description</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cabo Espichel</td>
<td>9°13’W / 38°25’N</td>
<td>Cliff sections at western end of Serra d’Arrabida (end of N 379). Massive beds at c40° dip. Cliffs are c130 metres high and c 180-320 metres along section.</td>
<td>Upper Kimmeridgian to Upper Portlandian.</td>
</tr>
<tr>
<td>Casais da Serra</td>
<td>9°1.5’W / 38°28’N</td>
<td>Road section on N 379 at edge of geological reserve of Serra d’Arrabida. 1 km south of town. Cutting c30 metres long and c1.8 metres high.</td>
<td>Kimmeridgian to Portlandian.</td>
</tr>
<tr>
<td>Murches</td>
<td>9°27’W / 38°44’N</td>
<td>Roadside cutting on road between Malveira da serra and Murches, c 150 metres long and c4 metres high.</td>
<td>Portlandian B to Purbeck.</td>
</tr>
<tr>
<td>Carapinha</td>
<td>9°0.5’W / 39°4.5’N</td>
<td>Large working horseshoe-shaped quarry at Carapinha.</td>
<td>Kimmeridgian to Portlandian.</td>
</tr>
<tr>
<td>Montejunto</td>
<td>9°3.5’W / 39°11.5’N + 39°3.5’W / 39°11’N</td>
<td>Road cutting of the road up the north side of the Montejunto anticline from Pragancaw to military installation.</td>
<td>Oxfordian.</td>
</tr>
</tbody>
</table>
Main limestone lithologies

<table>
<thead>
<tr>
<th>Lithology</th>
<th>Description</th>
<th>Best example sample number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mudstone</td>
<td>Very fine-grained limestone mud with some bioclasts or abiotic grains.</td>
<td>CE4</td>
</tr>
<tr>
<td>Floatstone / rudstone</td>
<td>Composed chiefly of (pseudo) ooids and oncoids.</td>
<td>MUR4</td>
</tr>
<tr>
<td>Bioclastic/micritic wackestone</td>
<td>The dominant lithology, normally very heavily bioclastic in nature.</td>
<td>CE15</td>
</tr>
<tr>
<td>“Reef rock” bindstone / framestone</td>
<td>Rare lithology; example of main reef binding / compositional rock.</td>
<td>CDS2</td>
</tr>
</tbody>
</table>
Hand specimens

<table>
<thead>
<tr>
<th>Name / code</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>CE1</td>
<td>Light grey / brown wackestone. Possible dendrites on the outside.</td>
</tr>
<tr>
<td>CE2</td>
<td>Light grey wackestone. Few bioclasts – bivalve etc.</td>
</tr>
<tr>
<td>CE3</td>
<td>Dark grey nodular (?) limestone with some possible clastics.</td>
</tr>
<tr>
<td>CE4</td>
<td>Buff coloured wackestone limestone with bioclastic “shelly” layer at top.</td>
</tr>
<tr>
<td>CE5</td>
<td>Light grey micrite with occasional bioclasts.</td>
</tr>
<tr>
<td>CE6</td>
<td>Medium grey biomicritic wackestone.</td>
</tr>
<tr>
<td>CE7</td>
<td>Light grey, partly recrystallized poor biowackestone.</td>
</tr>
<tr>
<td>CE8</td>
<td>Medium grey biowackestone.</td>
</tr>
<tr>
<td>CE9</td>
<td>Medium / light grey wackestone – bioclastic.</td>
</tr>
<tr>
<td>CE10</td>
<td>Medium grey, biomicritic algal wackestone – stuffed full of Vaginella striata.</td>
</tr>
<tr>
<td>CE11</td>
<td>Very dark grey micritic (?) limestone.</td>
</tr>
<tr>
<td>CE12</td>
<td>Light grey micritic limestone – some diagenetic (?) calcite veins (few).</td>
</tr>
<tr>
<td>CE13</td>
<td>Medium grey micritic (?) limestone – possible few bioclasts.</td>
</tr>
<tr>
<td>CE14</td>
<td>Medium to dark grey biowackestone – full of Vaginella striata.</td>
</tr>
<tr>
<td>CE15</td>
<td>Medium grey biowackestone – possibly algal.</td>
</tr>
<tr>
<td>CE16</td>
<td>Medium grey nodular biomicritic limestone with calcite veins.</td>
</tr>
<tr>
<td>CE17</td>
<td>Buff coloured micritic limestone – possibly nodular.</td>
</tr>
<tr>
<td>CDS1</td>
<td>Buff colour wackestone with bivalve fragments and patches of recrystallization.</td>
</tr>
<tr>
<td>CDS2</td>
<td>Buff coloured biowackestone.</td>
</tr>
<tr>
<td>CDS3</td>
<td>Dark buff bioclastic wackestone with echinoid spines and bivalves.</td>
</tr>
<tr>
<td>MUR1</td>
<td>Black marl mudstone.</td>
</tr>
<tr>
<td>MUR2</td>
<td>Black marl mudstone with possible intraclasts (?).</td>
</tr>
<tr>
<td>MUR3</td>
<td>Very dark grey floatstone – matrix supported mudstone with large clasts.</td>
</tr>
<tr>
<td>MUR4</td>
<td>Very dark grey marl wackestone including some bioclasts.</td>
</tr>
<tr>
<td>MUR5</td>
<td>Black wackestone marl.</td>
</tr>
<tr>
<td>MUR6</td>
<td>Black marl mudstone with a few intraclasts.</td>
</tr>
<tr>
<td>MUR7</td>
<td>Black marl mudstone.</td>
</tr>
<tr>
<td>CAR1</td>
<td>White / buff bioclastic wackestone – possibly algae present (?).</td>
</tr>
<tr>
<td>CAR2</td>
<td>Buff very bioclastic packestone with oncoids (?).</td>
</tr>
<tr>
<td>CAR3</td>
<td>Crystallized vein of calcite / dolomite crystals – very coarse and well formed.</td>
</tr>
<tr>
<td>CAR4</td>
<td>Dark grey wackestone oncolite.</td>
</tr>
<tr>
<td>CAR5</td>
<td>Microbial reef rock with Solenopora (ella).</td>
</tr>
<tr>
<td>CAR6</td>
<td>Microbial reef rock.</td>
</tr>
<tr>
<td>CAR7</td>
<td>Microbial reef rock (thrombolite?).</td>
</tr>
<tr>
<td>CAR8</td>
<td>Microbial reef rock and possible Solenopora (ella).</td>
</tr>
<tr>
<td>CAR9</td>
<td>Buff coloured oolitic / oncolitic packestone / grainstone.</td>
</tr>
<tr>
<td>MON1</td>
<td>Microbial reef rock.</td>
</tr>
<tr>
<td>MON2</td>
<td>Light grey clastic wackestone.</td>
</tr>
<tr>
<td>MON3</td>
<td>Light grey homogenous micrite mudstone.</td>
</tr>
<tr>
<td>MON4</td>
<td>Light grey homogenous micrite mudstone and calcite vein.</td>
</tr>
</tbody>
</table>
## Algae previously found

<table>
<thead>
<tr>
<th>Site locality</th>
<th>Algae</th>
<th>Age of strata</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cabo Espichel</td>
<td><em>Clypeina jurassica</em></td>
<td>Mid Portlandian (rare)</td>
<td>Ramalho 1971a &amp; 1968</td>
</tr>
<tr>
<td></td>
<td><em>Vaginella striata</em></td>
<td>Upper Portlandian A &amp; Lower Portlandian B</td>
<td>Ramalho 1971a &amp; 1968</td>
</tr>
<tr>
<td></td>
<td><em>Terquehella (?) triangularis</em></td>
<td>Portlandian B</td>
<td>Ramalho 1971a</td>
</tr>
<tr>
<td></td>
<td><em>Salpingoporella annulata</em></td>
<td>Portlandian B</td>
<td>Ramalho 1971a &amp; 1968</td>
</tr>
<tr>
<td></td>
<td><em>Permocacculus sp.</em></td>
<td>Upper Portlandian A &amp; Portlandian B</td>
<td>Ramalho 1971a</td>
</tr>
<tr>
<td></td>
<td><em>Cylindroporella cf. arabica</em></td>
<td>Portlandian B</td>
<td>Ramalho 1971a</td>
</tr>
<tr>
<td></td>
<td><em>Actinoporella podolica</em></td>
<td>Portlandian B (rare)</td>
<td>Ramalho 1971a</td>
</tr>
<tr>
<td></td>
<td><em>Thaumatoporella parvovesiculifera</em></td>
<td>Mid Portlandian A</td>
<td>Ramalho 1971a</td>
</tr>
<tr>
<td>Murches</td>
<td><em>Permocacculus sp.</em></td>
<td>Portlandian B &amp; Purbeckian</td>
<td>Ramalho 1971a</td>
</tr>
<tr>
<td></td>
<td><em>Terquehella (?) triangularis</em></td>
<td>Upper Portlandian B</td>
<td>Ramalho 1971a</td>
</tr>
<tr>
<td></td>
<td><em>Salpingoporella annulata</em></td>
<td>Upper Portlandian B &amp; Purbeckian</td>
<td>Ramalho 1971a</td>
</tr>
<tr>
<td></td>
<td><em>Thaumatoporella parvovesiculifera</em></td>
<td>Upper Portlandian B &amp; Purbeckian</td>
<td>Ramalho 1971a</td>
</tr>
<tr>
<td></td>
<td><em>Cylindroporella cf. arabica</em></td>
<td>Portlandian B &amp; Upper Purbeckian</td>
<td>Ramalho 1971a</td>
</tr>
<tr>
<td>Montejunto</td>
<td><em>Cylindroporella lusitanica</em></td>
<td>Upper Oxfordian</td>
<td>Ramalho 1971b</td>
</tr>
</tbody>
</table>
### Thin sections

<table>
<thead>
<tr>
<th>Sample</th>
<th>Lithology</th>
<th>Algae</th>
<th>Foraminifera</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>CE2</td>
<td>Biomericrite wackestone.</td>
<td>N/A</td>
<td>N/A</td>
<td>Biofragments.</td>
</tr>
<tr>
<td>CE5</td>
<td>Mudstone / wackestone.</td>
<td><em>Permocactus sp?</em> <em>Salpingoporella annulata?</em> <em>Zergatella sp? Or Cylindroporella cf arabica.</em></td>
<td><em>Anchiospiralina lusitanica</em> <em>Kurnubia palastiniensis</em> <em>Pseudocyclammina gr. parvula-mulischens</em> Miliolid.</td>
<td>N/A</td>
</tr>
<tr>
<td>CE7</td>
<td>Biomericrite wackestone with large calcite veins.</td>
<td><em>Cylindroporella cf arabica / lusitanica?</em> <em>Permocactus sp.</em></td>
<td>Miliolid.</td>
<td></td>
</tr>
<tr>
<td>CE10</td>
<td>Wackestone with calcite veins.</td>
<td><em>Campbelliella striata.</em> <em>Salpingoporella annulata.</em> <em>Pemocactus sp? Clypeina jurassica? Or Actinoporella podolica.</em></td>
<td><em>Anchiospiralina lusitanica.</em></td>
<td>N/A</td>
</tr>
<tr>
<td>Code</td>
<td>Description</td>
<td>Lenticulariaceae</td>
<td>Anchiocyclammina</td>
<td>Finds</td>
</tr>
<tr>
<td>------</td>
<td>-------------------------------------------------</td>
<td>--------------------------</td>
<td>--------------------------</td>
<td>------------------------------------</td>
</tr>
<tr>
<td>CE11</td>
<td>Biomicritic wackestone.</td>
<td><em>Salpingoporella</em></td>
<td><em>Anchiocyclammina</em></td>
<td>Bivalve fragments. Gastropods.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>annulata</td>
<td><em>lusitanica</em> cf mayni</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Terquevella</em> (?)</td>
<td><em>Miliolids</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>triangularis</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Cylindroporellula</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>cf arabica</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>triangularis?</em></td>
<td><em>Barkenia</em> sp?</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Miliolids</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>triangularis</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Baccinella</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>irregularis</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>UNKNOWN algae?</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CE14</td>
<td>Bioclastic wackestone.</td>
<td><em>Salpingoporella</em></td>
<td><em>Rectocyclammina</em></td>
<td>Bioclastic fragments.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>annulata</td>
<td><em>chouberti</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Vaginella striata</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CE15</td>
<td>Very biomicritic wackestone (algal biomicrite).</td>
<td><em>Salpingoporella</em></td>
<td><em>Anchiocyclammina</em></td>
<td>Bivalve fragments. Gastropod.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>annulata</td>
<td><em>lusitanica</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Cylindroporellula</em></td>
<td><em>Miliolids</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>cf arabica</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Vaginella striata</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Actinoporella</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>podolica</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CE16</td>
<td>Biomicritic wackestone with calcite veins.</td>
<td><em>Vaginella striata</em></td>
<td>N/A</td>
<td>Bivalve fragments.</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Cylindroporellula</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>cf arabica</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Lithocodium</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>aggregatum</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CE17</td>
<td>Wackestone with small calcite veins.</td>
<td>N/A</td>
<td><em>Anchiocyclammina</em></td>
<td>N/A</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>lusitanica</em></td>
<td></td>
</tr>
<tr>
<td>CDS1</td>
<td>Wackestone.</td>
<td>N/A</td>
<td><em>Pfenderina</em> sp.</td>
<td>Gastropods.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>*Trocholina alpina-</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>elongata</em></td>
<td></td>
</tr>
<tr>
<td>CDS2</td>
<td>Bindstone.</td>
<td>N/A</td>
<td><em>Pfenderina</em> sp.</td>
<td>N/A</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>*Trocholina alpina-</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>elongata</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Pseudocyclammina</em></td>
<td></td>
</tr>
<tr>
<td>CDS3</td>
<td>Wackestone.</td>
<td>N/A</td>
<td><em>Pfenderina</em> sp.</td>
<td>Indeterminate bioclasts.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Kurnubia</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>palastiniensis</em></td>
<td></td>
</tr>
<tr>
<td>MUR1</td>
<td>Slightly fabricated grain / packstone.</td>
<td><em>Terquevella</em> (?)</td>
<td><em>Trocholina alpina</em></td>
<td>N/A</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>triangularis</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Permocalculus</em> sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MUR2</td>
<td>Slightly oolitic / oncoticic mudstone / wackestone.</td>
<td><em>Baccinella</em></td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>irregularis</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MUR3</td>
<td>Floatstone with some pseudo-oids.</td>
<td><em>Salpingoporella</em></td>
<td><em>Reophax</em> sp.</td>
<td>Chaetid sponge.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>annulata</td>
<td><em>Rectocyclammina</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>chouberti</em></td>
<td></td>
</tr>
<tr>
<td>MUR4</td>
<td>Floatstone / rudstone with pseudo-oids / oncoids.</td>
<td>N/A</td>
<td>N/A</td>
<td>Recrystallized echinoid spines.</td>
</tr>
<tr>
<td></td>
<td>Description</td>
<td>Species</td>
<td>Identification</td>
<td>Comment</td>
</tr>
<tr>
<td>-------</td>
<td>------------------------------------------------------------------------------</td>
<td>----------------------------------------</td>
<td>----------------</td>
<td>-----------------------------</td>
</tr>
<tr>
<td>MUR5</td>
<td>Ooid / oncoid and mudstone alternates with calcite veins.</td>
<td><em>Permoculus sp.?</em></td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>MUR6</td>
<td>Grain / packstone with calcite veins.</td>
<td><em>Permoculus sp.</em></td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>MUR7</td>
<td>Abiotic mudstone with small calcite veinules.</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>CAR2</td>
<td>Calcite veined packstone.</td>
<td><em>Baccinella irregularis.</em></td>
<td>Rectocycalaminna chouberti. Unidentified foram.</td>
<td>N/A</td>
</tr>
<tr>
<td>CAR3</td>
<td>No thin section made.</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>CAR4</td>
<td>Rudstone.</td>
<td><em>Baccinella irregularis.</em></td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>CAR5</td>
<td>Bindstone / framestone.</td>
<td>Very large <em>Solenopora.</em></td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>CAR6</td>
<td>Semi-bioclastic packstone?</td>
<td>N/A</td>
<td>Chaetid sponge.</td>
<td>N/A</td>
</tr>
<tr>
<td>CAR7</td>
<td>Bindstone.</td>
<td><em>Baccinella irregularis.</em></td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>CAR8</td>
<td>Packstone / bindstone.</td>
<td>N/A</td>
<td>Unidentified foram. Echinoid spine. Bivalve fragment.</td>
<td>N/A</td>
</tr>
<tr>
<td>CAR9</td>
<td>Oosparite wackestone including pseudo-oolids.</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>MON1</td>
<td>Reef rock – framestone?</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>MON3</td>
<td>Grainstone.</td>
<td>N/A</td>
<td>Echinoid spine.</td>
<td>N/A</td>
</tr>
<tr>
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<td>Grainstone.</td>
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## Algae previously found from logs in Ramalho (1971d)

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| CE3                     | Permocalculus sp.  
                          | *Terquebillia triangularis* |
| CE4                     | Permocalculus sp.  
                          | *Terquebillia triangularis* |
|                         | Indeterminate Dasycladales |
| CE5                     | Permocalculus sp.  
                          | *Cylindroporella cf arabica* |
|                         | Indeterminate Dasycladales |
| CE6                     | Indeterminate Dasycladales |
| CE7                     | Indeterminate Dasycladales |
| CE8                     | Permocalculus sp.  
                          | *Salpingoporella annulata* |
| CE9                     | Permocalculus sp.  
                          | *Cylindroporella cf arabica* |
|                         | Indeterminate Dasycladales |
| CE10                    | Permocalculus sp.  
                          | *Cylindroporella cf arabica* |
|                         | *Zergatella sp1* |
| CE11                    | Permocalculus sp.  
                          | *Vaginella striata* |
|                         | Indeterminate Dasycladales |
| CE12                    | *Vaginella striata*  
                          | *Salpingoporella annulata* |
|                         | Indeterminate Dasycladales |
| CE13                    | Permocalculus sp.  
                          | *Vaginella striata* |
|                         | *Zergatella sp1* |
| CE14                    | Permocalculus sp.  
                          | *Vaginella striata* |
|                         | Indeterminate Dasycladales |
| CE15                    | *Vaginella striata*  
                          | *Salpingoporella annulata* |
|                         | Indeterminate Dasycladales |
| CE16                    | *Vaginella striata*  
                          | Indeterminate Dasycladales |
| CE17                    | *Clypeina jurrassic*  
                          | *Vaginella striata* |
|                         | *Murches* |
| MUR1                    | Indeterminate Dasycladales |
| MUR3                    | Permocalculus sp.  
                          | *Cylindroporella cf arabica* |
|                         | *Terquebillia triangularis* |
|                         | *Salpingoporella annulata* |
|                         | Indeterminate Dasycladales |
| MUR4                    | Permocalculus sp.  
                          | *Terquebillia triangularis* |
|                         | Indeterminate Dasycladales |
| MUR5                    | Permocalculus sp.  
                          | Indeterminate Dasycladales |
| MUR6                    | Permocalculus sp.  
                          | *Thaumatoporella parvovesiculifera* |
Appendix

B

Modern algae
Appendix

BI

List of genera and species of modern green calcareous algae
### BI List of genera and species of modern green calcareous algae

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<td>U. palmata</td>
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<td>U. verticillosa</td>
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<td>U. wilsonii</td>
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</table>
Appendix

BII

Modern algae databases
Modern benthic calcareous algae database

DASYCLADALES
  
  * Acetabularia
    * acetabulum

  - Mediterranean coast, France, (Génot 1991)
  - Tarragona, NE Spain, (Cinelli 1979)
  - Palma, Mallorca, (Cinelli 1979)
  - Bay of Fortells, N. Menorca, Balearic Islands, (Fornos et al 1992), water °C 12.7-27.5, as Acetabularia mediterranea
  - Perpignan, S. France, (Cinelli 1979)
  - Marseille, S. France, (Cinelli 1979)
  - Nice, S. France, (Cinelli 1979)
  - N. Corsica, (Cinelli 1979)
  - Genoa, Italy, (Cinelli 1979)
  - (10km south of) Livorno, NW Italy, 43°30'N / 10°20'E, (Airoldi et al 1995)
  - NW Italian coast, (Cinelli 1979)
  - NW, NE and S Sardinia, (Cinelli 1979)
  - NW and NE Sicily, (Cinelli 1979)
  - Mid Eastern Italy, (Cinelli 1979)
  - Naples, Italy, (Cinelli 1979)
  - Istria, Yugoslavia, (Cinelli 1979)
  - Dubrovnik, Yugoslavia, (Cinelli 1979)
  - Malta, (Cinelli 1979)
  - Pantelleria (Island), (Cinelli 1979)
  - Lesbos, Rhodes and Argolikos kolpos, Greece, (Cinelli 1979)
  - N. Libya, (Cinelli 1979)
  - N. Tunisia, (Cinelli 1979)
  - N. Algeria, (Cinelli 1979)
  - Lanzarote, Canary islands, (Berger and Kaever 1992)
  - Balearics, SW France, N Tunisia, mid Adriatic, Lesbos, Malta, Crete and Rhodes, Mediterranean sea, (Berger and Kaever 1992)
  - Sri Lanka, (Silva et al 1996)
    * antillana
    * calcicus

see Chlamasia antillana

- SW and mid Japan, (Arasaki et al, 1979)
- Normalup Inlet, Australia, 35°5'S / 116°43'E, (Womersley 1981)
- S. St. Vincent Gulf, S. Australia, (Womersley 1981)
- Coffin Bay, S. Australia, (Womersley 1981)
- Fremantle to around N. Australia, (Womersley 1981)
- Hopeless Reach, Shark Bay, Australia, 25°45'S / 113°45'E, (Kendrick et al 1990)
- Gladstone Inlet, Shark Bay, Australia, 25°55'S / 114°10'E, (Kendrick et al 1990)
- Hamelin Pool, Shark Bay, Australia, 26°07'S / 114°07'E, (Kendrick et al 1990)
- Jamaica, (Taylor 1960)
- Virgin Islands, (Taylor 1960)
- Palma, Mallorca, (Cinelli 1979)
- Mediterranean, (Berger and Kaever 1992)
- Guanica (SW) and Cabo Rojo (SW), Puerto Rico, (Almadovar and Ballantine 1983)
- N Venezuela, (Berger and Kaever 1992)
- West Indies, (Berger and Kaever 1992)
- Mid Red Sea, (Berger and Kaever 1992)
- Mid Southern Australia (Bight), (Berger and Kaever 1992)
- Mascarene Islands, (Berger and Kaever 1992)
- Tonga and Tongatapu, Polynesia, (Berger and Kaever 1992)
- S Japan, (Berger and Kaever 1992)
- Cape York, Deception Bay, E Australia, (Berger and Kaever 1992)
- E Philippines, (Berger and Kaever 1992)
- Torres Strait, NE Australia, (Berger and Kaever 1992)
- Brazil, (Berger and Kaever 1992)
- South China Sea, (Berger and Kaever 1992)
- Andaman Islands, (Silva et al 1996)
- Nicobar Islands, (Silva et al 1996)
- Australia, (Silva et al 1996)
- Bahrain, (Silva et al 1996)
- Bangladesh, (Silva et al 1996)
- India, (Silva et al 1996)
- Kenya, (Silva et al 1996)
- Kuwait, (Silva et al 1996)
- Mauritius, (Silva et al 1996)
- Mozambique, (Silva et al 1996)
- Saudi Arabia, (Silva et al 1996)
- S Africa, (Silva et al 1996)

*clavata*
- Okinawan and Amami Islands, Japan, (Arasaki et al, 1979)
- Comoro Islands, (Silva et al 1996)
- Kenya, (Silva et al 1996)
- Mauritius, (Silva et al 1996)
- Seychelles, (Silva et al 1996)
- Tanzania, (Silva et al 1996)
- Thailand, (Silva et al 1996)

*crenulata*
- Lower Laguna Madre, Texas, (Kaldy, 1996) (Berger and Kaever, 1992)
- Barranquilla, Colombia, (Génét 1991)
- New Providence, Bahamas, (Britton & Millspaugh 1962)
- Rose Island, Bahamas, (Britton & Millspaugh 1962)
- Andros Island, Bahamas, (Britton & Millspaugh 1962) (Newell et al 1959)
- Great Bahama, (Britton & Millspaugh 1962)
- Green Cay, Bahamas, (Britton & Millspaugh 1962)
- Exuma chain, Bahamas, (Britton & Millspaugh 1962)
- Cat Island, Bahamas, (Britton & Millspaugh 1962)
- Watling’s Island (San Salvador), Bahamas, (Britton & Millspaugh 1962) (Marshall 1980)
- Mariguanua, Bahamas, (Britton & Millspaugh 1962)
- Caicos Islands, Bahamas, (Britton & Millspaugh 1962)
- Great Ragged Island, Bahamas, (Britton & Millspaugh 1962)
- Harrington Sound, Mullet Bay, Fairylands and Stovel Bay, Bermuda, (Taylor and Bernatowicz 1969)
- Walsingham region, Bermuda, (Britten 1965), as Acetabulum crenulatum
- Barbados, (Britton & Millspaugh 1962) (Taylor 1960)
- Santo Domingo (Antilles), (Britton & Millspaugh 1962)
- NW Andros Island, Bahamas, (Hardie 1977) (Garrett 1977)
- Joulters Key, Bahamas, (Harris 1979)
- Ferry Reach, NE Bermuda, (Moore 1969)
- Texas, (Taylor 1960)
- Bahamas, (Taylor 1960)
- Cuba, (Taylor 1960)
- Jamaica, (Taylor 1960)
- Hispaniola, (Taylor 1960)
- Puerto Rico, (Taylor 1960)
- Guanica (SW), La Parguera (SW), Cabo Rojo (SW), San Juan to Luquillo (NE), Fajardo (E) and Guayama (SE), Puerto Rico, (Almodóvar and Ballantine 1983)
- Virgin Islands, (Taylor 1960)
- St. Martin, (Taylor 1960)
- Barbuda, (Taylor 1960)
- Guadeloupe, (Taylor 1960)
- British Honduras, (Taylor 1960)
- Colombia, (Taylor 1960)
- Spanish Water, SE Curacao, The Netherlands Antilles, 12°5’N / 68°51’W, (Kuenen and Debrot 1995), water °C 26-29 annual range
- Netherlands Antilles, (Taylor 1960)
- Venezuela, (Taylor 1960)
- Fitches Creek Bay (N) and Seaforths (W), Antigua, Lesser Antilles, (Price and John 1979)
- Bimini Bay, Bahamas, (Newell et al 1959)
- Mud Key, SW Florida, (81°45’W / 24°42’N), (Dawes et al 1967)
- Florida and Florida Keys, (Berger and Kaever 1992)
- Dry Tortugas, (Berger and Kaever 1992)
- Texas, (Berger and Kaever 1992)
- Yucatan, Gulf of Mexico, (Berger and Kaever 1992)
- West Indies, (Berger and Kaever 1992)
- Malaysia, (Berger and Kaever 1992)
- Andaman Islands, (Silva et al 1996) crenulata var. monodisca
- Andaman Islands, (Silva et al 1996)
- Nicobar Islands, (Silva et al 1996)
- Sri Lanka, (Silva et al 1996) dentata
- Okinawan and Amami Islands, Japan, (Arasaki et al, 1979)
- Celebes and Flores, Sunda Islands, (Berger and Kaever 1992)
- Ryuku Islands, (Berger and Kaever 1992)
- New Caledonia, Melanesia, (Berger and Kaever 1992)
- E Philippines, (Berger and Kaever 1992)
- Solor and Rotti, Indonesia, (Silva et al 1996) exigua
- Okinawan Islands, Japan, (Arasaki et al, 1979)
- Flores and Rotti, Indonesia, (Silva et al 1996)
- Kenya, (Silva et al 1996)
- Seychelles including Mahé Islands, (Silva et al 1996)
- Thailand, (Silva et al 1996) farlowii.
- Salomon Islands, (Berger and Kaever 1992) haemmerlingi
- Kilmeri
- Mid Great Barrier Reef, E Australia, (Berger and Kaever 1992)
- New Caledonia, Melanesia, (Berger and Kaever 1992)
- Edgecumbe Bay, SW North Island, New Zealand, (Berger and Kaever 1992)
- India, (Silva et al 1996)
- Andaman Islands, (Silva et al 1996) major
- Thailand, (Berger and Kaever 1992)
- Taiwan, (Berger and Kaever 1992)
- N New Guinea, (Berger and Kaever 1992)
- E Java, (Berger and Kaever 1992)
- E Philippines, (Berger and Kaever 1992)
- Horn and Thursday Islands, Torres Strait, NE Australia, (Berger and Kaever 1992)
- Melanesia, (Berger and Kaever 1992)
- Bari bi
- Okinawan Islands, Japan, (Arasaki et al, 1979)
- Palma, Mallorca, (Cinelli 1979)
- N. Algeria, (Cinelli 1979)
- Naples, Italy, (Cinelli 1979)
- Capo Passero, SE Sicily, (Cinelli 1979)
- Malta, (Cinelli 1979)
- Alexandria, Egypt, (Cinelli 1979)
- Suez, Egypt, (Cinelli 1979)
- Haifa, Israel, (Cinelli 1979)
- Aldabra Islands, (Silva et al 1996)
- Diego Garcia Atoll, (Silva et al 1996)
- India, (Silva et al 1996)
- Indonesia, (Silva et al 1996)
- Kenya, (Silva et al 1996)
• Mauritius, (Silva et al 1996)
• Mozambique, (Silva et al 1996)
• Pakistan, (Silva et al 1996)
• Reunion, (Silva et al 1996)
• Seychelles including Mahe Island, (Silva et al 1996)
• Singapore, (Silva et al 1996)
• Somalia, (Silva et al 1996)
• S Africa, (Silva et al 1996)
• Tanzania, (Silva et al 1996)
• Thailand, (Silva et al 1996)

**Peniculus**

*see Polyphysa peniculus*

*Polyphysoides*

• Atwood Cay, Bahamas, (Britton & Millsbaugh 1962)
• Caicos Islands, Bahamas, (Britton & Millsbaugh 1962)
• Castle Island, Bahamas, (Britton & Millsbaugh 1962)
• Guadeloupe, (Britton & Millsbaugh 1962)
• Jamaica, (Britton & Millsbaugh 1962)

*Polyphysoides f. deltoideum*

• Bermuda, (Taylor 1960)
• Bahamas, (Taylor 1960)
• Jamaica, (Taylor 1960)
• Guadeloupe, (Taylor 1960)
• Barbados, (Taylor 1960)

**Pusilla**

*see Polyphysa pusilla*

*ryukyuensis*

• Okinawan and Amami, Islands, Japan, (Arasaki et al, 1979)
• Ryuku Islands, (Berger and Kaever 1992)
• E Philippines, (Berger and Kaever 1992)

*schenkii*

• Key Largo, Florida, (Genot 1991)
• S. Florida, (Woelkerling 1976)
• Mayaguez (W), Puerto Rico, (Almodovar and Ballantine 1983)

*sp.*

• Bight of Abaco, Little Bahama Bank, (Neumann and Land 1975)
• Sombrero Island, 18°36'N / 63°25'W, (Ogden et al 1985)
• Robin Bay, SE St. Croix, Virgin Islands, (Adey et al 1977)
• Waikiki fringing reef, off Oahu Island, Hawaii, (Sorokin 1995)
• North Sound, Grand Cayman Island, (Roberts 1977)
Modern benthic calcareous algae database

DASYCLADALES

*Acicularia*

schenckii

- Rose Island, Bahamas, (Britton & Millspaugh 1962)
- American Virgin Islands, (Britton & Millspaugh 1962)
- Virgin Islands, (Taylor 1960)
- Barbados, (Britton & Millspaugh 1962) (Taylor 1960)
- Hungry Bay, Bermuda, (Britten 1965)
- Mangrove Lake, SSE Bermuda, (Moore 1969)
- Jamaica, (Britton & Millspaugh 1962) (Taylor 1960)
- Porto Rico, (Britton & Millspaugh 1962)
- Puerto Rico, (Taylor 1960)
- Cabo Frio, Brazil, (Britton & Millspaugh 1962)
- Brazil, (Taylor 1960) (Berger and Kaever 1992)
- Florida, (Taylor 1960)
- Bahamas, (Taylor 1960)
- Hispaniola, (Taylor 1960)
- Martinique, (Taylor 1960)
- Guadeloupe, (Taylor 1960)
- Dums point (NE), Antigua, Lesser Antilles, (Price and John 1979)
- Carribbean and Gulf of Cariaco, Venezuela, (Berger and Kaever 1992)
- Dry Tortugas, (Berger and Kaever 1992)
Modern benthic calcareous algae database

DASYCLADALES

_ Bornetella _
_capitata_

- Tonga, Polynesia, (Berger and Kaefer 1992)
- Ryuku Islands, (Berger and Kaefer 1992)
- New Caledonia, Melanesia, (Berger and Kaefer 1992)
- Andaman Islands, (Silva et al 1996)
- Comoro Islands, (Silva et al 1996)
- Indonesia, (Silva et al 1996)
- Mauritius, (Silva et al 1996)
- Reunion, (Silva et al 1996)
- Somalia, (Silva et al 1996)

_ nitida _

- Port Blair, South Point, Andaman Islands, (Baluswami et al 1982)
- Palawan, Philippines, (Génot 1991)
- Malayan Archipelago, (Berger and Kaefer 1992)
- Mascarene Islands, (Berger and Kaefer 1992)
- Tonga, Polynesia, (Berger and Kaefer 1992)
- New Caledonia, Melanesia, (Berger and Kaefer 1992)
- New Guinea, (Berger and Kaefer 1992)

_ nitida var. minor _

- Mauritius, (Silva et al 1996)

_ oligospora _

- Cauda, Vietnam, (Génot 1991)
- Malayan Archipelago, (Berger and Kaefer 1992)
- Sunda Islands, (Berger and Kaefer 1992)
- New Caledonia and New Hebrides, Melanesia, (Berger and Kaefer 1992)
- Philippines, (Berger and Kaefer 1992)
- SW Java, (Berger and Kaefer 1992)
- Java, Sumbu and Sumba, Indonesia, (Silva et al 1996)
- Madagascar, (Silva et al 1996)
- Singapore, (Silva et al 1996)
- Tanzania, (Silva et al 1996)

_ sphaerica _

- Oahu, Hawaii, (Génot 1991)
- Hawaiian Islands, (Berger and Kaefer 1992)
- Malayan Archipelago, (Berger and Kaefer 1992)
- Ryuku Islands, (Berger and Kaefer 1992)
- New Caledonia, Melanesia, (Berger and Kaefer 1992)
- NE New Guinea, (Berger and Kaefer 1992)
- Philippines, (Berger and Kaefer 1992)
- Vietnam, South China Sea, (Berger and Kaefer 1992)
- Madagascar, (Silva et al 1996)
- Mauritius, (Silva et al 1996)
- Reunion, (Silva et al 1996)
- Singapore, (Silva et al 1996)
Modern benthic calcareous algae database

**DASYCLADALES**

*Chalmisia*

*antillana*

- Florida, (Taylor 1960)
- S. Florida, (Woelkerling 1976)
- Florida Keys, (Berger and Kaever 1992)
- Lake Surprise, Florida Bay side of Key Largo, (Marszalek 1975), as Acetabularia antillana
- Rodriguez Key, Marszalek (1975), as Acetabularia antillana
- Tavernier Bank, Marszalek (1975), as Acetabularia antillana
- Blackwater Sound, Florida Bay shoreline, (Marszalek 1975), as Acetabularia antillana
Modern benthic calcareous algae database

**DASYCLADALES**

*Cymopodia*

- Rincon and Asabela, NW Puerto Rico, (Liddle, 1979)
- Andros Island, Bahamas, (Genot 1991) (Britton & Millspaugh 1962)
- New Providence, Bahamas, (Britton & Millspaugh 1962)
- Berry Islands, Bahamas, (Britton & Millspaugh 1962)
- Mariguanas, Bahamas, (Britton & Millspaugh 1962)
- S. Florida, (Woelkerling 1976)
- Haiti, (Britton & Millspaugh 1962) (S) (Diaz-Piffer 1969)
- Porto Rico, (Britton & Millspaugh 1962)
- Puerto Rico, (Taylor 1960) (Diaz-Piffer 1969)
- Ponce (S), Guayana (S), Cabo Rojo (SW), Rincon (W), Aguatilla to Guajataca (NW), Arecibo (N) and Vieques and Culebra Islands (E), Puerto Rico, (Almadovar and Ballantine 1983)
- Mexico, (Britton & Millspaugh 1962) (Taylor, 1960)
- S Gulf of Mexico, Mexico, (Diaz-Piffer 1969)
- Gulf of Mexico, (Berger and Kaever 1992)
- Canary Islands, (Britton & Millspaugh 1962) (Berger and Kaever 1992)
- Spain, (Britton & Millspaugh 1962)
- Joulters Key, Bahamas, (Harris 1979)
- St. Georges Harbour, St. Davids Island, Smiths Island sides of Mullet Bay, S St. Georges Island, Richardson's Cove, Red Hole of Hamilton Harbour and Riddell's Bay, Bermuda, (Taylor and Bernatowicz 1969)
- Bahamas, (Taylor 1960)
- Caicos Islands, (Taylor 1960)
- Hispaniola, (Taylor 1960)
- Wetherell point (NW), Antigua, Lesser Antilles, (Price and John 1979)
- Great Abaco, Bahamas, (Diaz-Piffer 1969)
- N Dominican Republic, (Diaz-Piffer 1969)
- Anguiller, (Diaz-Piffer 1969)
- Antigua, (Diaz-Piffer 1969)
- Martinique, (Diaz-Piffer 1969)
- Offshore Caracas, Venezuela, (Diaz-Piffer 1969)
- Curacao, Lesser Antilles, (Diaz-Piffer 1969)
- Content Keys, SW Florida, (81°30'W / 24°47'N), (Dawes et al 1967)
- Tanger, Morocco, (Berger and Kaever 1992)
- Cadiz, SW Spain, (Berger and Kaever 1992)
- Caribbean, (Berger and Kaever 1992)

*van bosseae*

- Sunda Islands, (Berger and Kaever 1992)
- S Japan, (Berger and Kaever 1992)
- Ryuku Islands, (Berger and Kaever 1992)
- Mid to N Melanesia, (Berger and Kaever 1992)
- NE Philippines, (Berger and Kaever 1992)
- Malay Archipelago, (Berger and Kaever 1992)
- SW Java, (Berger and Kaever 1992)
- Indonesia, (Silva et al 1996)
Modern benthic calcareous algae database

DASYCLADALES
Halicoryne
spicata

- Flores, Sunda Islands, Indonesia, (Berger and Kaever 1992) (Silva et al 1996)
- New Caledonia, Melanesia, (Berger and Kaever 1992)

wrighthii

- Ryuku Islands, (Berger and Kaever 1992)
- Philippines, (Berger and Kaever 1992)
- Bali, Indonesia, (Silva et al 1996)
Modern benthic calcareous algae database

DASYCLADALES

Neomeris annulata

- Carrie Bow Bay, Belize Barrier Reef, 16°48'N / 88°05'W, (Littler et al 1983)
- Rose Island, Bahamas, (Genot 1991) (Britton & Millspaugh 1962)
- New Providence, Bahamas, (Britton & Millspaugh 1962)
- Berry Islands, Bahamas, (Britton & Millspaugh 1962)
- Great Bahama, (Britton & Millspaugh 1962)
- North Cat Cay, Bahamas, (Britton & Millspaugh 1962)
- Mariguna, Bahamas, (Britton & Millspaugh 1962)
- Caicos Islands, Bahamas, (Britton & Millspaugh 1962)
- Castle Island, Bahamas, (Britton & Millspaugh 1962)
- Great Ragged Island, Bahamas, (Britton & Millspaugh 1962)
- Mauritius, (Britton & Millspaugh 1962) (Silva et al 1996)
- Madagascar, (Britton & Millspaugh 1962) (Silva et al 1996)
- Sombrero Island, 18°36’N / 63°25’W, (Ogden et al 1985)
- San Salvador, Bahamas, (Marshall 1980)
- Boiler Bay, NE St. Croix, Virgin Islands, (Adey et al 1977)
- Robin Bay, SE St. Croix, Virgin Islands, (Adey et al 1977)
- St. Davids Island, Patet Island, St. Georges Island, Shelly Bay, Fairylands (N Hamilton Island), Tuckers Town (S Hamilton Island), Harrington Sound, Richardsons Cove, St. Catherines Beach, Coney Island and Mylands Bay, Bermuda, (Taylor and Bernatowicz 1969)
- White’s Island in Hamilton Harbour and Harrington Sound, Bermuda, (Britten 1965)
- S. Florida, (Woolkerling 1976)
- Bahamas, (Taylor 1960)
- Jamaica, (Taylor 1960) (Diaz-Pifferer 1969)
- Hispaniola, (Taylor 1960)
- Puerto Rico, (Taylor 1960) (Diaz-Pifferer 1969)
- Guayanilla (S), Guanica (SW), La Parguera (SW), Cabo Rojo (SW), Mayaguez (W), Aguadilla to Guajataca (NW), Vieques and Culebra Islands (E) and Humacao to Yabucoa, Puerto Rico, (Almadovar and Ballantine 1983)
- Virgin Islands, (Taylor 1960)
- Nevis, (Taylor 1960)
- Guadeloupe, (Taylor 1960) (Diaz-Pifferer 1969)
- Martinique, (Taylor 1960)
- Barbados, (Taylor 1960) (Diaz-Pifferer 1969)
- Trinidad, (Taylor 1960)
- Wetherell Point (NW), Antigua, Lesser Antilles, (Price and John 1979)
- Eleuthera, Bahamas, (Diaz-Pifferer 1969)
- Sanana Cay, Bahamas, (Diaz-Pifferer 1969)
- Cuba, (Diaz-Pifferer 1969)
- Haiti, (Diaz-Pifferer 1969)
- N Dominican Republic, (Diaz-Pifferer 1969)
- Anguilla, (Diaz-Pifferer 1969)
- Curacao, Lesser Antilles, (Diaz-Pifferer 1969)
- Cabo Orange area, N Brazil, (Diaz-Pifferer 1969)
- Mud Key, SW Florida, (81°45'W / 24°42'N), (Dawes et al 1967)
- Cape Verde Islands, (Berger and Kaeber 1992)
- Dry Tortugas, (Berger and Kaeber 1992)
- West Indies, (Berger and Kaeber 1992)
- Sunda Islands, (Berger and Kaeber 1992)
- W Madagascar, (Berger and Kaeber 1992)
- Mascarene Islands, (Berger and Kaeber 1992)
- Hawaiian Islands, (Berger and Kaeber 1992)
- Samoa and Tonga, Polynesia, (Berger and Kaeber 1992)
- Yonaguni-Jima Island, East China Sea, (Berger and Kaever 1992)
- Ryuku Islands, (Berger and Kaever 1992)
- Mid W Chile, (c30°S), (Berger and Kaever 1992)
- New Caledonia, Melanesia, (Berger and Kaever 1992)
- N New Guinea, (Berger and Kaever 1992)
- E Philippines, (Berger and Kaever 1992)
- South China Sea, (Berger and Kaever 1992)
- Malay Archipelago, (Berger and Kaever 1992)
- Aldabra Islands, (Silva et al 1996)
- Chagos Archipelago, (Silva et al 1996)
- Comoro Islands, (Silva et al 1996)
- India, (Silva et al 1996)
- Indonesia, (Silva et al 1996)
- Laccadive Islands, (Silva et al 1996)
- Maldive, (Silva et al 1996)
- Reunion, (Silva et al 1996)
- Seychelles, (Silva et al 1996)
- Singapore, (Silva et al 1996)
- Tanzania, (Silva et al 1996)
- Guam, 13°23'N / 144°55'E, (Meyer et al 1994)

*bilimbata*
- New Caledonia, Melanesia, (Berger and Kaever 1992)
- Palawan Island, Philippines, (Berger and Kaever 1992)
- Seychelles, (Silva et al 1996)
- cokeri
- New Providence, Bahamas, (Britton & Millspaugh 1962)
- Berry Islands, Bahamas, (Britton & Millspaugh 1962)
- Great Bahama, (Britton & Millspaugh 1962)
- Gun Cay, Bahamas, (Britton & Millspaugh 1962)
- Current town, Eleuthera, Bahamas, (Britton & Millspaugh 1962)
- Exuma chain, Bahamas, (Britton & Millspaugh 1962)
- Atwood Cay, Bahamas, (Britton & Millspaugh 1962)
- Castle Island, Bahamas, (Britton & Millspaugh 1962)
- Great Ragged Island, Bahamas, (Britton & Millspaugh 1962)
- San Salvador, Bahamas, (Marshall 1980)
- Bahamas, (Taylor 1960)
- West Indies, (Berger and Kaever 1992)

*dumetosa*
- Cuba, (Taylor 1960)
- Jamaica, (Taylor 1960)
- Virgin Islands, (Taylor 1960)
- West Indies, (Berger and Kaever 1992)
- Malayan Archipelago, (Berger and Kaever 1992)
- W Madagascar, (Berger and Kaever 1992)
- Madagascar, (Silva et al 1996)
- Tonga and Tongatapu, Polynesia, (Berger and Kaever 1992)
- N Melanesia, (Berger and Kaever 1992)
- N New Guinea, (Berger and Kaever 1992)
- Malaysia, (Berger and Kaever 1992)
- Andaman Islands, (Silva et al 1996)
- India, (Silva et al 1996)
- Indonesia, (Silva et al 1996)
- Kenya, (Silva et al 1996)
- Mozambique, (Silva et al 1996)
- Nicobar Islands, (Silva et al 1996)
- Singapore, (Silva et al 1996)
- S Africa, (Silva et al 1996)
- Tanzania, (Silva et al 1996)

*mucosa*
- Atwood Cay, Bahamas, (Britton & Millspaugh 1962)
- Caicos Islands, Bahamas, (Britton & Millspaugh 1962)
- Great Ragged Island, Bahamas, (Britton & Millspaugh 1962)
- San Salvador, Bahamas, (Marshall 1980)
Bahamas, (Taylor 1960)
- Cuba, (Taylor 1960)
- Netherlands Antilles, (Taylor 1960)
- Hodge Point (N) and Crawle Bay (SE), Antigua, Lesser Antilles, (Price and John 1979)
- Cape Verde Islands, (Berger and Kaefer 1992)
- West Indies, (Berger and Kaefer 1992)
- Ryuku Islands, (Berger and Kaefer 1992)
- New Caledonia, Melanesia, (Berger and Kaefer 1992)
- Marshall Islands, Micronesia, (Berger and Kaefer 1992)
- Diego Garcia Atoll, (Silva et al. 1996)
- Maldives, (Silva et al. 1996)
- Bight of Abaco, Little Bahama Bank, (Neumann and Land 1975)
- Hawaii, (Harney 2000)
- Sunda Islands, (Berger and Kaefer 1992)
- Mascarene Islands, (Berger and Kaefer 1992)
- Reunion, (Silva et al. 1996)
- Hawaiian Islands, (Berger and Kaefer 1992)
- Society Islands and Tonga, Polynesia, (Berger and Kaefer 1992)
- Ryuku Islands, (Berger and Kaefer 1992)
- N Melanesia, (Berger and Kaefer 1992)
- N New Guinea, (Berger and Kaefer 1992)
- Marshall Islands, Micronesia, (Berger and Kaefer 1992)
- NE Philippines, (Berger and Kaefer 1992)
- South China sea, (Berger and Kaefer 1992)
- Malay Archipelago, (Berger and Kaefer 1992)
- SW Java, (Berger and Kaefer 1992)
- Aldabra Islands, (Silva et al. 1996)
- Indonesia, (Silva et al. 1996)
- Kenya, (Silva et al. 1996)
- Laccadive, (Silva et al. 1996)
- Mozambique, (Silva et al. 1996)
- Seychelles, (Silva et al. 1996)
- Singapore, (Silva et al. 1996)
- S Africa, (Silva et al. 1996)
- Tanzania, (Silva et al. 1996)
- Rotuma Island, (N) Fiji Island Group, 12°30'S / 177°05'E, (N'Yeurt 1996)
- Sikka, Flores, Indonesia, (N'Yeurt 1996)
Modern benthic calcareous algae database

DASYCLADALES

*Polypysa*

- clavata
- exigua
- myriospora

- Salvador, E Brazil, (Berger and Kaever 1992)
- parvula

- SW and mid Japan, and Okinawan and Amami Islands, Japan (Arasaki et al, 1979), as *Acetabularia mobii*
- Mid and SW Japan, (Berger and Kaever 1992)
- Ryuku Islands, (Berger and Kaever 1992)
- Canary Islands, (Berger and Kaever 1992)
- Malta and mid W Italy, Mediterranean, (Berger and Kaever 1992)
- Revillagigedo Islands, S of Baha, Mexico, (Berger and Kaever 1992)
- Macassar, Celebes, (N’Yeurt 1996)
- Celebes, Sunda Islands, (Berger and Kaever 1992)
- Karachi, Pakistan, (Berger and Kaever 1992)
- Mid Red Sea, (Berger and Kaever 1992)
- Mascarene Islands, (Berger and Kaever 1992)
- E Africa (Kenya), (Berger and Kaever 1992)
- Hawaiian Islands, (Berger and Kaever 1992)
- E Phillipines, (Berger and Kaever 1992)
- Rotuma Island, (N Fiji Island Group, 12°30'S / 177°05'E, (N’Yeurt 1996)
- Fiji, (N’Yeurt 1996)
- Tuvalu, (N’Yeurt 1996)
- Tahiti, (N’Yeurt 1996)

- penicula

- Hopeless Reach, Shark Bay, Australia, 25°45'S / 113°45'E, (Kendrick et al 1990)
- Gladstone Inlet, Shark Bay, Australia, 25°55'S / 114°10'E, (Kendrick et al 1990)
- Hamelin Pool, Shark Bay, Australia, 26°07'S / 114°07'E, (Kendrick et al 1990)
- Guanica (SW), Puerto Rico, (Almadovar and Ballantine 1983)
- Colombia, (Taylor 1960), as *Acetabularia penicula*

- Mid Southern (Bight) and SW Australia, (Berger and Kaever 1992)
- New Caledonia, Micronesia, (Berger and Kaever 1992)
- Australia, (Silva et al 1996), as *Acetabularia penicula*

- polysoides

- Canary Islands, (Berger and Kaever 1992)
- Bermuda, (Berger and Kaever 1992)
- West Indies, (Berger and Kaever 1992)

- pusilla

- Mariquana, Bahamas, (Britton & Millspaugh 1962), as *Acetabularia pusilla*
- Castle Island, Bahamas, (Britton & Millspaugh 1962), as *Acetabularia pusilla*
- Montego Bay, Jamaica, (Britton & Millspaugh 1962), as *Acetabularia pusilla*
- Florida, (Taylor 1960), as *Acetabularia pusilla*, (Berger and Kaever 1992)
- S. Florida, (Woelkerling 1976), as *Acetabularia pusilla*
- Bahamas, (Taylor 1960), as *Acetabularia pusilla*
- Jamaica, (Taylor 1960), as *Acetabularia pusilla*
- Fanneys Cove (NE), Antigua, Lesser Antilles, (Price and John 1979), as *Acetabularia pusilla*
- Belize and Puerto Rico, (Berger and Kaever 1992)
- Yucatan, (Berger and Kaever 1992)
- West Indies, (Berger and Kaever 1992)
- Aldabra Islands, (Silva et al 1996), as *Acetabularia peniculus*
- Seychelles, (Silva et al 1996), as *Acetabularia peniculus*
Modern benthic calcareous algae database

HALIMEDACEAE

*Halimeda*

*bikinensis*
- Bikini Atoll, Namu Islands, Marshall Islands, (Hillis-Colinaux 1980)
- Saya de Malha, (Hillis-Colinaux 1980) (Silva et al 1996)
- Craigados Carajos, (Silva et al 1996)
- Bali, Indonesia, (Silva et al 1996)
- Fiji, (N'Yeur 1996)
- Rotuma Island, (N) Fiji Island Group, 12°30'S / 177°05'E, (N'Yeur 1996)

*borneensis*

- Celand Station no 10, E coast of Pulau Gaya, N Borneo, (Hillis-Colinaux 1980)

*copiosa*
- Carrie Bow Bay, Belize Barrier Reef, 16°48'N / 88°05'W, (Littler et al 1983)
- San Salvador, Bahamas, (Hillis 1991)
- Dixon Hill, NE San Salvador, Bahamas, 24°8.3'N / 74°26.2'W, (Blair and Norris 1988)
- Green Cay, NW San Salvador, Bahamas, 24°8.5'N / 74°31.2'W, (Blair and Norris 1988)
- Cockburn Town, W San Salvador, Bahamas, 24°3.2'N / 74°32.6'W, (Blair and Norris 1988)
- Fernandez Bay, SW San Salvador, Bahamas, 24°0.9'N / 74°33.4'W, (Blair and Norris 1988)
- French Bay, S San Salvador, Bahamas, 23°56.7'N / 74°31.3'W, (Blair and Norris 1988)
- Davies Reef, Great Barrier Reef, Australia, (Hillis 1991)
- Runaway Bay, East Palissadoes, Little Bay, Maria Buena Bay, Port Royal Cays, South East Cay, Orange Bay, Mangrove Point and Discovery Bay, Jamaica, (Goreau and Graham 1967)
- Glory be Reef, Ocho Rios, mid N shore Jamaica, (77°0'W / 18°24'N), (Hillis-Colinaux 1980)
- Maria Buena and Runaway Bay, Parish of St. Ann, Jamaica, (Hillis-Colinaux 1980)
- Offshore La Parguera, Puerto Rico, (Ballantine 1982)
- Pandora Cay, Great Detached Reef, Blackwood Channel, Quoin Island, Hibernia, Lizard Island, Cooktown Ribbon Reefs, Bowl Reef, Swains Reefs and Finders Reefs, Great Barrier Reef, Australia, (Drew and Abel 1988)
- Ribbon Reefs 2.5 and 7 off Cooktown, Great Barrier Reef, Australia, (Marshall and Davies 1988)
- John Brewer Reef, Central Great Barrier Reef, Australia, NE of Townsville, (Delaney et al 1996)
- Big Bank / North Bank, Great Barrier Reef, Australia, NE of Cooktown, (Delaney et al 1996)
- Grand Cayman Island, (Johns and Moore 1988)
- La Parguera (SW), Puerto Rico, (Alamador and Ballantine 1983)
- Knoll 2, île du Coin and île Grande Coquillage, Perros Buhno, Chagos Archipelago, (Drew 1995)
- Île de la Passe, île Maupou and île du Sel, Salomon Atoll, Chagos Archipelago, (Drew 1995)
- Seychelles and Anohl, (Drew 1995), (Silva et al 1996)
- Coral Sea, (Drew 1995)
- Aldabra Islands, (Silva et al 1996)
- Sumba, Indonesia, (Silva et al 1996)
- Madagascar, (Silva et al 1996)
- Maldive, (Silva et al 1996)
- Staniard Rock, off Andros Island, Bahamas, 24°51.7'N / 77°52.3'W, (Littler et al 1988)

*copiosa f. elongata*

- Pandora Cay, Great Detached Reef, Blackwood Channel, Quoin Island, Hibernia, Creech Reef, Waterwitch, Lizard Island, Cooktown Ribbon Reefs, Bowl Reef and Swains Reefs, Great Barrier Reef, Australia, (Drew and Abel 1988)
- John Brewer Reef, Central Great Barrier Reef, Australia, NE of Townsville, (Delaney et al 1996), *as Halimeda hederacea*
- Big Bank / North Bank, Great Barrier Reef, Australia, NE of Cooktown, (Delaney et al 1996), *as Halimeda hederacea*
- Funanamu, Ellice Islands, (Hillis-Colinaux 1980)
- Piscadera Bay, Curacao, (Hillis-Colinaux 1980)

*cryptica*
- Maria Buena Bay, Jamaica, (McConnell and Hills-Colinaux 1967) (Hillis-Colinaux 1980)
- Glory be Reef, Ocho Rios, mid N shore Jamaica, (77°0'W / 18°24'N), (Hillis-Colinaux 1980)
- Cardiff Hall Beach, Runaway Bay, Parish of St. Ann, Jamaica, (Hillis-Colinaux 1980)
- Offshore La Parguera and Margarita Reef, Puerto Rico, (Ballantine 1982)
- Grand Cayman Island, (Johns and Moore 1988)
- Dixon Hill, NE San Salvador, Bahamas, 24°8.3'N / 74°26.2'W, (Blair and Norris 1988)
- Green Cay, NW San Salvador, Bahamas, 24°8.5'N / 74°31.2'W, (Blair and Norris 1988)
• Cockburn Town, W San Salvador, Bahamas, 24°32.3'N / 74°32.6'W, (Blair and Norris 1988)
• Fernandez Bay, SW San Salvador, Bahamas, 24°0.9'N / 74°33.4'W, (Blair and Norris 1988)
• French Bay, S San Salvador, Bahamas, 23°56.7'N / 74°31.3'W, (Blair and Norris 1988)
• La Parguera (SW), Puerto Rico, (Almadovar and Ballantine 1983)
  cryptica var. acerifolia
• Offshore Salinas, Puerto Rico, (Ballantine 1982)  cuneata
• East London to Beira, E. South Africa, (Branch and Branch, 1983)
• S Africa, (Silva et al 1996)
• Recherche Archipelago, 34°06'S / 123°11'E, (Womersley 1981)
• Inhaca Island, E. Africa, (Hillis-Colinvaux 1980)
• Natal Bay, Durban, S Africa, (Hillis-Colinvaux 1980)
• Durban, S. Africa, (N'Yeurt 1996)
• Okah, Gujarat state, India, (Hillis-Colinvaux 1980)
• India, (Silva et al 1996)
• Andaman Islands, (Silva et al 1996)
• Australia, (Silva et al 1996)
• Chagos Archipelago, (Silva et al 1996)
• Indonesia, (Silva et al 1996)
• Kenya, (Silva et al 1996)
• Madagascar, (Silva et al 1996)
• Mozambique, (Silva et al 1996)
• Nicobar Islands, (Silva et al 1996)
• Pakistan, (Silva et al 1996)
• Reunion, (Silva et al 1996)
• Somalia, (Silva et al 1996)
• Tanzania, (Silva et al 1996)
• Taiwan, (N'Yeurt 1996)
• Fiji, (N'Yeurt 1996)
• Rotuma Island, (N) Fiji Island Group, 12°30'S / 177°05'E, (N'Yeurt 1996)  cylindracea
• Lizard Island, Great Barrier Reef, Australia, (Borowitzka and Larkum 1977)
• Blackwood Channel and Swains Reef, Great Barrier Reef, Australia, (Drew and Abel 1988)
• Knoll 2 and Ile du Coin, Peros Badians, Chagos Archipelago, (Drew 1995)
• Kayangel Atoll, Palau, (Drew 1995)
• Coral Sea, (Drew 1995)
• Perville, Nosii-Be, Madagascar, (Hillis-Colinvaux 1980)
• Madagascar, (Silva et al 1996)
• Amirante Islands, (Silva et al 1996)
• Cargados Carajos, (Silva et al 1996)
• Chagos Archipelago, (Silva et al 1996)
• Djibouti, (Silva et al 1996)
• Rotti and Sawo, Indonesia, (Silva et al 1996)
• Mozambique, (Silva et al 1996)
• Saya de Malha bank, (Silva et al 1996)
• Coetivy Reef, Seychelles, (Silva et al 1996)
• Somalia, (Silva et al 1996)
• Snark Banks, Noumea, SW New Caledonia, (Garrigue 1991)  discoidea
• Carrie Bow Bay, Belize Barrier Reef, 16°48'N / 88°05'W, (Littler et al 1983)
• Heron and Lizard Islands, Great Barrier Reef, Australia, (Borowitzka and Larkum 1977)
• Biscayne Bay, Florida, (McConnell and Hillis-Colinvaux 1967)
• Cayo Enrique Reef (off La Parguera) and Cabo Rojo (Pitohuya), Puerto Rico, (Stark et al 1969)
• Vera Cruz, Mexico, (Kaldy, 1996)
• Flower Gardens (coral bank c17km SSE of Galveston), (Kaldy, 1996)
• Kenyan coast, (Coppejans and Verellen 1991) (Silva et al 1996)
• Coral Reef Patch Reef, 1.5km east of Old Rhodes Key, Florida, (Wiman and McKendree 1975)
• Enewetak Atoll, Marshall Islands, (Hillis 1991) (Drew 1995)
• Great Bahama, (Britton & Millsbaugh 1962)
• Florida, (Britton & Millsbaugh 1962) (Hillis-Colinvaux 1980)
• S. Florida, (Woelkerling 1976)
• Cuba, (Britton & Millsbaugh 1962)
• Porto Rico, (Britton & Millsbaugh 1962)
- Guayanilla (S), Guanica (SW), La Parguera (SW), Cabo Rojo (SW), Mayaguez (W), Rincon (W), Aguadilla to Guajataca (NW), Arecibo (N), San Juan to Luquillo (NE), Fajardo (E), Vieques and Culebra Islands (E), Humacao to Yucucao (SE) and Guayama (SE), Puerto Rico, (Almadovar and Ballantine 1983)
- Lower California, (Britton & Millspaugh 1962)
- Hawaii, (Britton & Millspaugh 1962)
- Philippines, (Britton & Millspaugh 1962)
- Sombrero Island, 18°36'N 63°25'W, (Ogden et al 1985)
- Guanica and Cabo Rojo, Puerto Rico, (Ballantine 1982)
- Pandora Cay, Great Detached Reef, Blackwood Channel, Quoin Island, Hibernia, Waterwitch, Lizard Island, Cooktown Ribbon Reefs, Bowl Reef and Swains Reefs, Great Barrier Reef, Australia, (Drew and Abel 1988)
- Ribbon Reefs 2.5 and 7, off Cooktown, Great Barrier Reef, Australia, (Marshall and Davies 1988)
- Hawaii, (Harney 2000)
- Grand Cayman Island, (Johns and Moore 1988)
- Green Cay, NW San Salvador, Bahamas, 24°8.5'N / 74°31.2'W, (Blair and Norris 1988)
- French Bay, S San Salvador, Bahamas, 23°56.7'N / 74°31.3'W, (Blair and Norris 1988)
- Hodge Point (N), Reeds Beach (E) and Wetherell Point (NW), Antigua, Lesser Antilles, (Price and John 1979)
- Tanegashima (30°35'N) and Yaku (30°21'N), Osumi Islands, Japan, (Tsuda and Kamura 1991)
- Amamioshima, Amami Islands, Japan, (28°20'N), (Tsuda and Kamura 1991)
- Izena (26°56'N) and Okinawa (26°12'N), Okinawa Islands, Japan, (Tsuda and Kamura 1991)
- Miyako, Sakishima Islands, Japan, (24°47'N), (Tsuda and Kamura 1991)
- Taketomi, Yaeyama Islands, Sakishima Islands, Japan, (24°20'N), (Tsuda and Kamura 1991)
- Taiwan, (Tsuda and Kamura 1991)
- Mainland Japan, (Tsuda and Kamura 1991)
- Off Cape Sable, SW Florida, (81°28'W / 25°07'N), (Dawes et al 1967)
- S of Cape Sable, SW Florida, (81°12'W / 25°01'N), (Dawes et al 1967)
- Mouth – Florida Bay, SW Florida, (81°17'W / 24°55'N), and (81°28'W / 24°55'N), (Dawes et al 1967)
- Content Keys, SW Florida, (81°30'W / 24°47'N), (Dawes et al 1967)
- Mud Key, SW Florida, (81°45'W / 24°42'N), (Dawes et al 1967)
- Sawyer Key, SW Florida, (81°35'W / 24°47'N), (Dawes et al 1967)
- Bambari Knoll, Knoll 2 and 3, Ile du Coin and Ile Grande Coquillage, Peros Bahnos, Chagos Archipelago, (Drew 1995)
- Ile de la Passe, Salomon Atoll, Chagos Archipelago, (Drew 1995)
- La Reunion, (Drew 1995) (Silva et al 1996)
- Nicobar group, (Drew 1995) (Silva et al 1996)
- Angria bank, (Drew 1995)
- Ryuku Islands, (Drew 1995)
- Kayangel Atoll, Palau, (Drew 1995)
- Glory be Reef Ocho Rios, mid N shore Jamaica, (77°0'W / 18°24'N), (Hillis-Colinvaux 1980)
- Tiahura Reef, NW Moorea Island, Society Islands, French Polynesia, 17°30'S / 149°50'W, (Payri 1988)
- N Moorea Island, French Polynesia, (Payri 1995)
- Amirante Islands, (Silva et al 1996)
- Andaman Islands, (Silva et al 1996)
- Bangladesh, (Silva et al 1996)
- Chagos Archipelago, (Silva et al 1996)
- Djibouti, (Silva et al 1996)
- India, (Silva et al 1996)
- Indonesia, (Silva et al 1996)
- Madagascar, (Silva et al 1996)
- Maldives, (Silva et al 1996)
- Mauritius, (Silva et al 1996)
- Mozambique, (Silva et al 1996)
- Singapore, (Silva et al 1996)
- Somalia, (Silva et al 1996)
- Sri Lanka, (Silva et al 1996)
- Thailand, (Silva et al 1996)
- Tanzania, (Silva et al 1996)
- Rotuma Island, (N) Fiji Island Group, 12°30'S / 177°05'E, (N’Yeurt 1996)
- Snark Banks, Noumea, SW New Caledonia (Garrigue 1991)
- Corralejo (Fuerteventura), Canary Islands, (Ballesteros et al 1992)
- Cape Verde Islands, (Ballesteros et al 1992)
- Seychelles, (Dolgushina et al 1995)
- Guam, 13°25'N / 144°55'E, (Meyer et al 1994)
- Agat Bay, Guam, (Paul and Alstyn 1988)

*discoides var. platyloba*

- Florida, (Taylor 1960)
- Bahamas, (Taylor 1960)
- Cuba, (Taylor 1960)
- Jamaica, (Taylor 1960)
- Puerto Rico, (Taylor 1960)
- Virgin Islands, (Taylor 1960)
- Guadeloupe, (Taylor 1960)
- Martinique, (Taylor 1960)
- Panama, (Taylor 1960)
- Colombia, (Taylor 1960)
- Venezuela, (Taylor 1960)
- Brazil, (Taylor 1960)
- Trinidad, (Taylor 1960)

**distorta**
- Blackwood Channel, Quoin Island, Hibernia, Lizard Island, Cooktown Ribbon Reefs and Flinders Reefs, Great Barrier Reef, Australia, (Drew and Abel 1988)
- Okinawa, Japan, (26°12'N), (Tsuda and Kamura 1991)
- Taketomi, Yaeyama Islands, Sakishima Islands, Japan, (24°20'N), (Tsuda and Kamura 1991)
- Coral Sea, (Drew 1995)
- Ryukyu Islands, (Drew 1995)
- Lagoon of Ats Atoll, near Ponape, Caroline Islands, (Hillis-Colinvaux 1980)

**favulosa**
- Rose Island, Bahamas, (Britton & Millsophaugh 1962)
- Cave Cays, Exuma chain, Bahamas, (Britton & Millsophaugh 1962) (Hillis-Colinvaux 1980)
- Bahamas, (Taylor 1960)

**fragilis**
- Pass between Alembel and Lojwa Islets, Eniwetak Atoll, (Hillis-Colinvaux 1980)
- Great Detached Reef, Quoin Island, Hibernia, Waterwitch, Lizard Island, Cooktown Ribbon Reefs, Bowl Reef, Swains Reef and Flinders Reefs, Great Barrier Reef, Australia, (Drew and Abel 1988)
- Ribbon Reefs 2.5 and 7 off Cooktown, Great Barrier Reef, Australia, (Marshall and Davies 1988)
- Hateruma, Yaeyama Islands, Sakishima Islands, Japan, (24°03'N), (Tsuda and Kamura 1991)
- Ryukyu Islands, (Drew 1995)
- Coral Sea, (Drew 1995)
- Cargados Carajos, (Silva et al 1996)
- Madagascar, (Silva et al 1996)
- Maldives, (Silva et al 1996)
- Zanzibar, Tanzania, (Silva et al 1996)

**gigas / xishoensis**
- Angria bank, (Drew 1995)
- Coral Sea, (Drew 1995)
- Guam, 13°25'N / 144°55'E, (Meyer et al 1994)

** goreauii**
- Carrie Bow Bay, Belize Barrier Reef, 16°48'N / 88°05'W, (Litteret al 1983)
- Runaway Bay, Jamaica, (McConnell and Hillis-Colinvaux 1967)
- Corsair Patch Reef, 1.5km east of Old Rhodes Key, Florida, (Wiman and McKendree 1975)
- Ocho Rios, N Jamaica, 18°24'N / 77°0'W, (Hillis-Colinvaux 1980)
- Puerto Rico, (Ballantine 1982)
- Guanica (SW), La Parguera (SW) and Mona and Desecheo Islands (W), Puerto Rico, (Almadovar and Ballantine 1983)
- Grand Cayman Island, (Johns and Moore 1988)
- Cockburn town, W San Salvador, Bahamas, 24°43.2'N / 74°32.6'W, (Blair and Norris 1988)
- French Bay, S San Salvador, Bahamas, 23°56.7'N / 74°31.3'W, (Blair and Norris 1988)
- **goreauii f. compacta**
- **Cardiff Hall Beach, St. Ann Parish, Jamaica, (Hillis-Colinvaux 1980)**
- **goreauii f. goreauii**
- **Cardiff Hall Beach, St. Ann Parish, Jamaica, (Hillis-Colinvaux 1980)**
- **gracilis**
- **Cardiff Hall Beach, St. Ann Parish, Jamaica, (Hillis-Colinvaux 1980)**
- **gracilis**
- **S. Water Island, St. Thomas, Virgin Islands, (McConnell and Hillis-Colinvaux 1967)**
- **Flower Gardens (coral bank c17km SSE of Galveston), (Kaldy, 1996)**
- **Kenyan coast, (Coppejans and Verellen 1991) (Silva et al 1996)**
- **Touros and Rio do Fogo Beach, state of Rio Grande do Norte, Brazil, 35°09'W - 35°28'W / 4°57'S - 5°17'S, (Testa, 1997), water °C 26.5-28.5**
- **Offshore Margarita Reef and Media Luna Reef, Puerto Rico, (Ballantine 1982)**
- **Great Detached Reef, Blackwood Channel, Quoin Island, Hibernia, Lizard Island, Cooktown Ribbon Reefs, Bowl Reef and Swains Reef, Great Barrier Reef, Australia, (Drew and Abel 1988)**
- **Ribbon Reefs 2.5 and 7 off Cooktown, Great Barrier Reef, Australia, (Marshall and Davies 1988)**
- **Dixon Hill, NE San Salvador, Bahamas, 24°8.3'N / 74°26.2'W, (Blair and Norris 1988)**
- **Green Cay, NW San Salvador, Bahamas, 24°8.5'N / 74°31.2'W, (Blair and Norris 1988)**
• Jamaica, (Taylor 1960)
• Puerto Rico, (Taylor 1960)
• Virgin Islands, (Taylor 1960)
• Guadeloupe, (Taylor 1960)
• Martinique, (Taylor 1960)
• Panama, (Taylor 1960)
• Colombia, (Taylor 1960)
• Venezuela, (Taylor 1960)
• Brazil, (Taylor 1960)
• Trinidad, (Taylor 1960)

*distorsia*

• Blackwood Channel, Quoin Island, Hibernia, Lizard Island, Cooktown Ribbon Reefs and Flinders Reefs, Great Barrier Reef, Australia, (Drew and Abell 1988)
• Enewetak Atoll, Marshall Islands, (Hillis-Colinvaux 1980) (Drew 1995)
• Okinawa, Japan, (26°12'N), (Tsuda and Kamura 1991)
• Taketomi, Yaeyama Islands, Sakishima Islands, Japan, (24°20'N), (Tsuda and Kamura 1991)
• Coral Sea, (Drew 1995)
• Ryukyu Islands, (Drew 1995)
• Lagoon of Ats Atoll, near Ponape, Caroline Islands, (Hillis-Colinvaux 1980)

*favolosa*

• Rose Island, Bahamas, (Britton & Millspaugh 1962)
• Cave Cays, Exuma chain, Bahamas, (Britton & Millspaugh 1962) (Hillis-Colinvaux 1980)
• Bahamas, (Taylor 1960)

*fragilis*

• Pass between Alembel and Loja Islets, Enewetat Atoll, (Hillis-Colinvaux 1980)
• Great Detached Reef, Quoin Island, Hibernia, Waterwitch, Lizard Island, Cooktown Ribbon Reefs, Bowl Reef, Swains Reef and Flinders Reefs, Great Barrier Reef, Australia, (Drew and Abell 1988)
• Ribbon Reefs 2.5 and 7 off Cooktown, Great Barrier Reef, Australia, (Marshall and Davies 1988)
• Hateruma, Yaeyama Islands, Sakishima Islands, Japan, (24°03'N), (Tsuda and Kamura 1991)
• Ryukyu Islands, (Drew 1995)
• Coral Sea, (Drew 1995)
• Cargados Carajos, (Silva et al 1996)
• Madagascar, (Silva et al 1996)
• Maldives, (Silva et al 1996)
• Zanzibar, Tanzania, (Silva et al 1996)

*gigas / xishaensis*

• Angria bank, (Drew 1995)
• Coral Sea, (Drew 1995)
• Guam, 13°25'N / 144°55'E, (Meyer et al 1994)

*goreauui*

• Carrie Bow Bay, Belize Barrier Reef, 16°48'N / 88°05'W, (Littler et al 1983)
• Runaway Bay, Jamaica, (McConnell and Hillis-Colinvaux1967)
• Coral reefs, 1.5km east of Old Rhodes Key, Florida, (Wiman and McKendree 1975)
• Ocho Rios, N Jamaica, 18°24'N / 77°0'W, (Hillis-Colinvaux 1980)
• Puerto Rico, (Ballantine 1982)
• Guanica (SW), La Parguera (SW) and Mona and Desecheo Islands (W), Puerto Rico, (Almadovar and Ballantine 1983)
• Grand Cayman Island, (Johns and Moore 1988)
• Cockburn town, W San Salvador, Bahamas, 24°3.2'N / 74°32.6'W, (Blair and Norris 1988)
• French Bay, S San Salvador, Bahamas, 23°56.7'N / 74°31.3'W, (Blair and Norris 1988)

* goreauui f. compacta *

• Cardiff Hall Beach, St. Ann Parish, Jamaica, (Hillis-Colinvaux 1980)
• goreauui f. goreauui

• Cardiff Hall Beach, St. Ann Parish, Jamaica, (Hillis-Colinvaux 1980)

* gracilis *

• S. Water Island, St. Thomas, Virgin Islands, (McConnell and Hillis-Colinvaux1967)
• Flower Gardens (coral bank c17km SSE of Galveston), (Kaldy, 1996)
• Kenyan coast, (Coppejans and Verellen 1991) (Silva et al 1996)
• Tours and Rio do Fogo Beach, state of Rio Grande do Norte, Brazil, 35°09'W - 35°28'W / 4°57'S - 5°17'S, (Testa, 1997), water 26.5-28.5
• Offshore Margarita Reef and Media Luna Reef, Puerto Rico, (Ballantine 1982)
• Great Detached Reef, Blackwood Channel, Quoin Island, Hibernia, Lizard Island, Cooktown Ribbon Reefs, Bowl Reef and Swains Reef, Great Barrier Reef, Australia, (Drew and Abell 1988)
• Ribbon Reefs 2.5 and 7 off Cooktown, Great Barrier Reef, Australia, (Marshall and Davies 1988)
• Dixon Hill, NE San Salvador, Bahamas, 24°8.3'N / 74°26.2'W, (Blair and Norris 1988)
• Green Cay, NW San Salvador, Bahamas, 24°8.5'N / 74°31.2'W, (Blair and Norris 1988)
Cockburn Town, W San Salvador, Bahamas, 24°3.2'N / 74°32.6'W, (Blair and Norris 1988)
Fernandez Bay, SW San Salvador, Bahamas, 24°0.9'N / 74°33.4'W, (Blair and Norris 1988)
French Bay, S San Salvador, Bahamas, 23°56.7'N / 74°31.3'W, (Blair and Norris 1988)
S. Florida, (Woolferting 1976)
La Parguera (SW), Puerto Rico, (Almadovar and Ballantine 1983)
Ile Touquet and Ile Grande Coquillage, Peros Bahnos, Chagos Archipelago, (Drew 1995)
Ile Boddam, Salomon Atoll, Chagos Archipelago, (Drew 1995)
Chagos Archipelago, (Silva et al 1996)
Lakshadweep Archipelago, (Drew 1995)
Seychelles and Atolls, (Drew 1995) (Silva et al 1996)
Kayangel Atoll, Palau, (Drew 1995)
Saya de Malha, (Hillis-Colinvaux 1980) (Silva et al 1996)
Pulau stupai, N edge of Sanding Islands, Mentawei Islands, W of Sumatra, (Hillis-Colinvaux 1980)
Mentawai Islands, Indonesia, (Silva et al 1996)
Aladbra Islands, (Silva et al 1996)
Amirante Islands, (Silva et al 1996)
Andaman Islands, (Silva et al 1996)
Comoro Islands, (Silva et al 1996)
India, (Silva et al 1996)
Laccadive Islands, (Silva et al 1996)
Nicolau Islands, (Silva et al 1996)
Singapore, (Silva et al 1996)
Sri Lanka, (Silva et al 1996)

gracilis var. opuntioides

hederacea
see copiosa f. elongata as hederacea is misnamed / a synonym (Hillis Colinvaux 1969)
hummi
see offshore La Parguera, offshore Salinas, Ballena Bay and Guanica, Puerto Rico, (Ballantine 1982)
Guanica (SW) and La Parguera (SW), Puerto Rico, (Almadovar and Ballantine 1983)
incrassata

St. Davids Island, Ireland Island, Whites Bay and Stovel Bay, Bermuda, (Taylor and Bernatowicz 1969)
Punta Arenas, Puerto Rico, (McConnell and Hillis-Colinvaux 1967)
Port Isabel, lower Laguna Madre, Texas, 26°08'N / 97°14.5'W, (Kaldy, 1996)
Kayan coast, (Coppejans and Verellen 1991) (Silva et al 1996)
Right of Abaco, Little Bahama Bank, (Neumann and Land 1975)
Cormor Patch Reef, 15km east of Old Rhodes Key, Florida, (Wiman and McKendree 1975)
Dirk Hartog Island, Shark Bay, Australia, 26°05'S / 113°10'E, (Kendrick et al 1990)
N. Jamaica, (Hillis 1991)
Ocho Rios, N Jamaica, 18°24'N / 77°0'W, (Hillis-Colinvaux 1980)
Joulers Key, Bahamas, (Harris 1979)
Andros Island, Bahamas, (Newell et al 1959)
Bimini, Bahamas, (Newell et al 1959)
San Salvador, Bahamas, (Marshall 1980)
Matheson Hammock, Sands Key and between boca chita and Sands Key, biscayne Bay, Florida, (Macintyre and Reid 1995)
Boiler Bay, NE St. Croix, Virgin Islands, (Adey et al 1977) (Conner and Adey 1977)
Bahia Fosforente and cabo rojo, Puerto Rico, (Ballantine 1982), as tridens
Great Detached Reef, Blackwood Channel, Quoin Island, Hibernia, Waterwitch, Lizard Island, Cooktown Ribbon Reefs, Bowl Reef and Swains Reef, Great Barrier Reef, Australia, (Drew and Abel 1988)
Nonsuch (E) and Falmouth (S) Bays, Antigua, (Mulier 1988)
Grand Cayman Island, (Johns and Moore 1988)
Amamioshima, Amami Islands, Japan, (28°20'N), (Tsuda and Kamura 1991)
Yoron, Amami Islands, Japan, (27°02'N), (Tsuda and Kamura 1991)
Okinawa, Japan, (26°12'N), (Tsuda and Kamura 1991)
Miyako, Sakishima Islands, Japan, (24°47'N), (Tsuda and Kamura 1991)
Yonaguni, Yaeyama Islands, Sakishima Islands, Japan, (24°27'N), (Tsuda and Kamura 1991)
Taiwan, (Tsuda and Kamura 1991)
S. Florida, (Woolferting 1976)
Off Cape Sable, SW Florida, (81°20'W / 25°13'N) and (81°28'W / 25°07'N), (Dawes et al 1967)
Mouth – Florida Bay, SW Florida, (81°17'W / 24°55'N), (81°28'W / 24°55'N) and (81°19'W / 24°58'N), (Dawes et al 1967)
• Content Keys, SW Florida, (81°29'W / 24°48'N) and (81°30'W / 24°47'N), (Dawes et al 1967)
• Mud Key, SW Florida, (81°45'W / 24°42'N), (Dawes et al 1967)
• Ponce (S), Guayanilla (S), La Parguera (SW), Cabo Rojo (SW), Mona and Desecheo Islands (W), Arecibo (N), San Juan to Luquillo (NE), Fajardo (E), Vieques and Culebra Islands (E), Humacao to Yabucoa (SE) and Guayama (SE), Puerto Rico, (Almadovar and Ballantine 1983)
• Knoll 2, Peros Banhos, Chagos Archipelago, (Drew 1995)
• Chagos Archipelago, (Silva et al 1996)
• Kayangel Atoll, Palau, (Drew 1995)
• Ryukyu Islands, (Drew 1995)
• Spaanse Baai, SE coast Curacao, (Hillis-Colinvaux 1980)
• Spaanse Water, SE Curacao, The Netherlands Antilles, 12°5'S / 68°51'W, (Kuenen and Debrot 1995), water°C 26-29 annual range
• Amirante Islands, (Silva et al 1996)
• Andaman Islands, (Silva et al 1996)
• Australia, (Silva et al 1996)
• Cargados Carajos, (Silva et al 1996)
• (Keeling) Cocos Islands, (Silva et al 1996)
• Diego Garcia Atoll, (Silva et al 1996)
• Indonesia, (Silva et al 1996)
• Laccadive Islands, (Silva et al 1996)
• Madagascar, (Silva et al 1996)
• Maldives, (Silva et al 1996)
• Mauritius, (Silva et al 1996)
• Nicobar Islands, (Silva et al 1996)
• Saya de Malha bank, (Silva et al 1996)
• Seychelles, (Silva et al 1996) (Dolgushina et al 1995)
• Somalia, (Silva et al 1996)
• Zanzibar, Tanzania, (Silva et al 1996)
• Thailand, (Silva et al 1996)
• Guam, 13°25'N / 144°55'E, (Meyer et al 1994)
• Sainte-Marie Bay and Snark Banks, Noumea, SW New Caledonia (Garrigue 1991)

_Incrassata f. gracilis_

• Bermuda, (Taylor 1960)
• Florida, (Taylor 1960)
• Mexico, (Taylor 1960)
• Bahamas, (Taylor 1960)
• Caicos Islands, (Taylor 1960)
• Anguilla Islands, (Taylor 1960)
• Cuba, (Taylor 1960)
• Jamaica, (Taylor 1960)
• Hispaniola, (Taylor 1960)
• Puerto Rico, (Taylor 1960)
• Virgin Islands, (Taylor 1960)
• St. Martin, (Taylor 1960)
• St. Barthlemy, (Taylor 1960)
• Guadeloupe, (Taylor 1960)
• Dominica, (Taylor 1960)
• Martinique, (Taylor 1960)
• Barbados, (Taylor 1960)
• Grenada, (Taylor 1960)
• British Honduras, (Taylor 1960)
• Panama, (Taylor 1960)
• Netherlands Antilles, (Taylor 1960)
• Sawyer Key, SW Florida, (81°35'W / 24°47'N), (Dawes et al 1967)

_Incrassata f. ovata_

• N Moorea Island, French Polynesia, (Payri 1995)
• Tiahura Reef, NW Moorea Island, Society Islands, French Polynesia, 17°30'S / 149°50'W, (Payri 1988)

_Incrassata f. tripartita_

• Bermuda, (Taylor 1960)
• Florida, (Taylor 1960)
• Mexico, (Taylor 1960)
• Bahamas, (Taylor 1960)
• Caicos Islands, (Taylor 1960)
• Anguilla Islands, (Taylor 1960)
• Cuba, (Taylor 1960)
- Jamaica, (Taylor 1960)
- Hispaniola, (Taylor 1960)
- Puerto Rico, (Taylor 1960)
- Virgin Islands, (Taylor 1960)
- St. Martin, (Taylor 1960)
- St. Barthelemy, (Taylor 1960)
- Guadeloupe, (Taylor 1960)
- Dominica, (Taylor 1960)
- Martinique, (Taylor 1960)
- Barbados, (Taylor 1960)
- Grenada, (Taylor 1960)
- British Honduras, (Taylor 1960)
- Panama, (Taylor 1960)
- Netherlands Antilles, (Taylor 1960)
- Content Keys, SW Florida, (81°30'W / 24°47'N), (Dawes et al 1967)
- Sawyer Key, SW Florida, (81°35'W / 24°47'N), (Dawes et al 1967) irregular

- Antilles, W. I., (Hillis-Colinvaux 1980)
  - lacrimalosa

- Corsair Reef Patch, 1.5km east of Old Rhodes Key, Florida, (Wiman and McKendree 1975)
- Exuma chain, Bahamas, (Britton & Millsapagh 1962)
- Mariguana, Bahamas, (Britton & Millsapagh 1962) (Hillis-Colinvaux 1980)
- Great Ragged Island, Bahamas, (Britton & Millsapagh 1962)
- Cuba, (Britton & Millsapagh 1962) (Taylor 1960)
- San Salvador, Bahamas, (Marshall 1980)
- Bahamas, (Taylor 1960)
- Sawyer Key, SW Florida, (81°35'W / 24°47'N), (Dawes et al 1967)
- Content Key, Florida, (Hillis-Colinvaux 1980)
- Madagascar, (Silva et al 1996)
- Anguilla Island, Cay Sal Banks, Bahamas, 23°29'N / 79°29'W, (Little et al 1988)
- Dixon Hill, NE San Salvador, Bahamas, 23°48.3'N / 74°26.2'W, (Blair and Norris 1988)
- Cockburn Town, W San Salvador, Bahamas, 24°3.2'N / 74°32.6'W, (Blair and Norris 1988)
- French Bay, S San Salvador, Bahamas, 23°56.7'N / 74°31.3'W, (Blair and Norris 1988)
  - lacrimalosa var. lacrimalosa

- Fernandez Bay, SW San Salvador, Bahamas, 24°0.9'N / 74°33.4'W, (Blair and Norris 1988)
  - lacunalis

- Blackwood Channel, Quoin Island, Hibernia and Flinders Reefs, Great Barrier Reef, Australia, (Drew and Abel 1988)
- Knoll 2 and Ille Touquet, Peros Bahnos, Chagos Archipelago, (Drew 1995)
- Kayangel Atoll, Palau, (Drew 1995)
- Coral Sea, (Drew 1995)
- Aldabra Islands, (Silva et al 1996)
- Chagos Archipelago, (Silva et al 1996)
- Mozambique, (Silva et al 1996)
- S Africa, (Silva et al 1996)
  - lacunalis f. lacunalis

- Enyu Island, Bikini Atoll, Marshall Islands, (Hillis-Colinvaux 1980)
  - lacunalis f. lata

- Enewetak Atoll, Marshall Islands, (Hillis-Colinvaux 1980)
- Between Alemvel and Lojwa Islets, Enewetak Atoll, Marshall Islands, (Hillis-Colinvaux 1980)
  - macroloba

- Guam, 13°25'N / 144°55'E (Hudson, 1985) (Meyer et al 1994)
- Agat Bay and Western Shoals, Apra Harbour, Guam, (Paul and Alstyne 1988)
- Heron and Lizard Islands, Great Barrier Reef, Australia, (Borowiczka and Larkum 1977)
- Kenyan coast, (Coppens and Veerlen 1991) (Silva et al 1996)
- Gazi Bay, Kenya, (Coppens and et al 1992)
- Malindi, Kenya, (Hillis-Colinvaux 1980)
- Wistari Reef (near Heron Island), Great Barrier Reef, Australia, 23°35'S / 151°54'E, (Noble, 1986)
- Amamiso Island (28°20'N), Kakeroma (28°03'N) and Yoron (27°02'N), Amami Islands, Japan, (Tsuda and Kamura 1991)
- Kume, Okinawa Islands, Japan, (26°20'N), (Tsuda and Kamura 1991)
- Miyako, Sakishima Islands, Japan, (24°47'N), (Tsuda and Kamura 1991)
- Ishigaki (24°30'N), Taketomi (24°20'N), Irionomote (24°20'N) and Yonaguni (24°27'N), Yaeyama Islands, Sakishima Islands, Japan, (Tsuda and Kamura 1991)
- Taiwan, (Tsuda and Kamura 1991)
- Seychelles and Atolls, (Drew 1995)
• Seychelles including Mahe Island, (Silva et al 1996)
• Ryukyu Islands, (Drew 1995)
• Nuka Alofa, Tonga, (Hillis-Colinvaux 1980)
• Aldabra Islands, (Silva et al 1996)
• Andaman Islands, (Silva et al 1996)
• Australia, (Silva et al 1996)
• Comoro Islands, (Silva et al 1996)
• Djibouti, (Silva et al 1996)
• India, (Silva et al 1996)
• Indonesia, (Silva et al 1996)
• Laccadive Islands, (Silva et al 1996)
• Madagascar, (Silva et al 1996)
• Malaysia, (Silva et al 1996)
• Nicobar Islands, (Silva et al 1996)
• Somalia, (Silva et al 1996)
• Sri Lanka, (Silva et al 1996)
• Tanzania, (Silva et al 1996)
• Thailand, (Silva et al 1996)
• Yemen, (Silva et al 1996)
• Sainte-Marie Bay and Snark Banks, Noumea, SW New Caledonia (Garrigue 1991)
• Tiahura Reef, NW Moorea Island, Society Islands, French Polynesia, 17°30'S / 149°50'W, (Naim 1988)

macrophylla

• Kenyan coast, (Coppejans and Verellen 1991) (Silva et al 1996)
• Enewetak Atoll, Marshall Islands, (Hillis-Colinvaux 1980) (Drew 1995)
• Matsuku, Fiji Islands, (Hillis-Colinvaux 1980) (N'Yeurt 1996)
• Pulau Stupai, N of Sanding Island, Mentawai Islands, W of Sumatra, (Hillis-Colinvaux 1980)
• Aldabra Islands, (Silva et al 1996)
• Sumatra and Timor, Indonesia, (Silva et al 1996)
• Snark Banks, Noumea, SW New Caledonia (Garrigue 1991)
• Rotuma Island, (N) Fiji Island Group, 12°30'S / 177°05'E, (N'Yeurt 1996)

magnidiscia

• Green Island, Great Barrier Reef, Australia, 4°15'S / 155°0'E, (Noble, 1986)
• Wistari Reef (near Heron Island), Great Barrier Reef, Australia, 23°35'S / 151°54'E, (Noble, 1986)
• SW lagoon, Noumea, New Caledonia, (Noble, 1986)

melanesica

• Isle Lifou, Loyalty Islands, region of Luengoni, New Caledonia, (Hillis-Colinvaux 1980)

micronesica

• Kenyan coast, (Coppejans and Verellen 1991) (Silva et al 1996)
• Pandora Cay, Great Detached Reef, Blackwood Channel and Flinders Reefs, Great Barrier Reef, Australia, (Drew and Abel 1988)
• Enewetak Atoll, Marshall Islands, (Hillis-Colinvaux 1980) (Drew 1995)
• Okinawa, Japan, (26°12'N), (Tsuda and Kamura 1991)
• Taketomi (24°20'N) and Hateruma (24°03'N), Yaeyama Islands, Sakishima Islands, Japan, (Tsuda and Kamura 1991)
• Knoll 2, Ile Poule, Ile du Coin and Ile Touquet, Peros Bahnos, Chagos Archipelago, (Drew 1995)
• Coral Sea, (Drew 1995)
• Ryuku Islands, (Drew 1995)
• Kayangel Atoll, Palau, (Drew 1995)
• Atolls, near Panape Island, E Caroline Islands, (Hillis-Colinvaux 1980) (N'Yeurt 1996)
• South Pagi Island, W of Sumatra, (Hillis-Colinvaux 1980) (Silva et al 1996)
• Aldabra Islands, (Silva et al 1996)
• Chagos Archipelago, (Silva et al 1996)
• Sumatra and Sumba, Indonesia, (Silva et al 1996)
• Madagascar, (Silva et al 1996)
• Maldives, (Silva et al 1996) (N'Yeurt 1996)
• Tahiti (N'Yeurt 1996)
• Rotuma Island, (N) Fiji Island Group, 12°30'S / 177°05'E, (N'Yeurt 1996)
• John Brewer Reef, Central Great Barrier Reef, Australia, NE of Townsville, (Delaney et al 1996)

minima

• Flinders Reefs, Great Barrier Reef, Australia, (Drew and Abel 1988)
• Enewetak Atoll, Marshall Islands, (Hillis-Colinvaux 1980) (Drew 1995)
• Enewetak Islet, Enewetak Atoll, (Hillis-Colinvaux 1980)
• Ile Anglaise, Salomon Atoll, Chagos Archipelago, (Drew 1995)
• Kayangel Atoll, Palau, (Drew 1995)
• Coral Sea, (Drew 1995)
• Bikini lagoon, Bikini Atoll, Marshall Islands, (Hillis-Colinvaux 1980)
• Chagos Archipelago, (Silva et al 1996)
• Sumba, Indonesia, (Silva et al 1996)
• Tiahura Reef, NW Moorea Island, Society Islands, French Polynesia, 17°30'S / 149°50'W, (Payri 1988)

**monile**
• Carrie Bow Bay, Belize Barrier Reef, 16°48'N / 88°05'W, (Littler et al 1983)
• Pineros Islands, Puerto Rico, (McConnell and Hillis-Colinvaux 1967)
• Guayanilla (S), Guanica (SW), La Parguera (SW), Cabe Rojo (SW), Mayaguez (W), San Juan to Luquillo (NE), Fajardo (E), Vieques and Culebra Islands (E) and Guayama (SE), Puerto Rico, (Almada and Ballantine 1983)
• Eniwetok Atoll, Marshall Islands, (Gilmartin, 1966)
• Corsair Patch Reef, 1.5km east of Old Rhodes Key, Florida, (Wiman and McKendree 1975)
• Rose Island, Bahamas, (Britton & Millsbaugh 1962)
• Cat Island, Bahamas, (Britton & Millsbaugh 1962)
• Watling’s Island, Bahamas, (Britton & Millsbaugh 1962) (Marshall 1980)
• Mariguanu, Bahamas, (Britton & Millsbaugh 1962)
• Caicos Islands, Bahamas, (Britton & Millsbaugh 1962)
• Great ragged Island, Bahamas, (Britton & Millsbaugh 1962)
• Salt Cay, Bahamas, (Britton & Millsbaugh 1962)
• Anguilla isles, Bahamas, (Britton & Millsbaugh 1962)
• Bermuda, (Britton & Millsbaugh 1962)
• Mullet Bay, Baileys Bay, Stovel Bay, Fairylands and Somerset Island, Bermuda, (Taylor and Bernatowicz 1969)
• Florida, (Britton & Millsbaugh 1962)
• S. Florida, (Woelkerling 1976)
• Guadeloupe, (Britton & Millsbaugh 1962)
• Colon, Panama, (Britton & Millsbaugh 1962)
• Rodriguez bank (SW of Key Largo), Florida Keys Reef tract, (Ginsburg 1972)
• Ocho Rios, N Jamaica, (18°24'N / 77°0'W), (Hillis-Colinvaux 1980)
• Glory be Reef, Ocho Rios, mid N shore Jamaica, (77°0'W / 18°24'N), (Hillis-Colinvaux 1980)
• Richardson’s Cove, NE Bermuda, (Moore 1969)
• Boiler Bay, NE St. Croix, Virgin Islands, (Adey et al 1977)
• Bahia de Jobos, Guanica and Bahia Fosforescente, Puerto Rico, (Ballantine 1982)
• Nonsuch (E) and Falmouth (S) Bays, Antigua, (Multer 1988)
• Morris Bay (SSW), Fitches creek Bay (N) and Hodge Point (N), Antigua, Lesser Antilles, (Price and John 1979)
• Grand Cayman Island, (Jones and Moore 1988)
• Mud Key, SW Florida, (81°45'W / 24°42'N), (Dawes et al 1967)
• S Woman Key, SW Florida, (81°55'W / 24°27'N), (Dawes et al 1967)

**monile f. cylindrica**
• Bermuda, (Taylor 1960)
• Florida, (Taylor 1960)
• Bahamas, (Taylor 1960)
• Caicos Islands, (Taylor 1960)
• Anguilla Islands, (Taylor 1960)
• Cuba, (Taylor 1960)
• Cayman Islands, (Taylor 1960)
• Jamaica, (Taylor 1960)
• Hispaniola, (Taylor 1960)
• Puerto Rico, (Taylor 1960)
• Virgin Islands, (Taylor 1960)
• Guadeloupe, (Taylor 1960)
• British Honduras, (Taylor 1960)
• Panama, (Taylor 1960)
• Netherlands Antilles, (Taylor 1960)
• Venezuela, (Taylor 1960)

**monile f. robusta**
• Bermuda, (Taylor 1960)
• Florida, (Taylor 1960)
• Bahamas, (Taylor 1960)
• Caicos Islands, (Taylor 1960)
• Anguilla Islands, (Taylor 1960)
• Cuba, (Taylor 1960)
• Cayman Islands, (Taylor 1960)
• Jamaica, (Taylor 1960)
• Hispaniola, (Taylor 1960)
• Puerto Rico, (Taylor 1960)
• Virgin Islands, (Taylor 1960)
- Guadeloupe, (Taylor 1960)
- British Honduras, (Taylor 1960)
- Panama, (Taylor 1960)
- Netherlands Antilles, (Taylor 1960)
- Venezuela, (Taylor 1960)
  \textit{nervosa}
- Red Sea, (Hillis-Colinvaux 1980)
  \textit{opuntia}
- Marquesas Keys – Quick sands area, Florida Keys, 24°35'N / 82°30'W, (Hudson, 1985)
- Marquesas Keys, Florida (29km/18mi W of Key west), (Hudson 1984)
- Carrie Bow Bay, Belize Barrier Reef, 16°48'N / 88°05'W, (Littler et al 1983)
- Cayo Enrique Reef (off La Parguera), Puerto Rico, (Stark et al 1969)
- Vera Cruz, Mexico, (Kaldy, 1996)
- Kenyan coast, (Coppejans and Verellen 1991) (Silva et al 1996)
- Gazi Bay, Kenya, (Coppejans et al 1992)
- Corsair Patch Reef, 1.5km east of Old Rhodes Key, Florida, (Wirman and McKendree 1975)
- Davies Reef, Great Barrier Reef, Australia, (Hillis 1991)
- New Providence, Bahamas, (Britton & Millsapgh 1962)
- Rose Island, Bahamas, (Britton & Millsapgh 1962)
- Berry Islands, Bahamas, (Britton & Millsapgh 1962)
- South Cat Cay, Bahamas, (Britton & Millsapgh 1962)
- Gun Cay, Bahamas, Britton & Millsapgh (1962)
- Exuma chain, Bahamas, (Britton & Millsapgh 1962)
- Watling's Island (San Salvador), Bahamas, (Britton & Millsapgh 1962) (Marshall 1980)
- Mariguanu, Bahamas, (Britton & Millsapgh 1962)
- Anguilla Isles, Bahamas, (Britton & Millsapgh 1962)
- Florida, (Britton & Millsapgh 1962)
- S. Florida, (Woelkerling 1976)
- Barbados, (Britton & Millsapgh 1962)
- Colon, Panama, (Britton & Millsapgh 1962)
- Jamaica, (Britton & Millsapgh 1962)
- Rodriguez bank (SW of Key Largo), Florida Keys Reef tract, (Ginsburg 1972)
- N side of Marathon– Florida Keys and Crane Point Hammock, SW Florida Bay, (Delgado and LaPointe 1994)
- Ocho Rios, N Jamaica, (18°24'N / 77°00'W), (Hillis-Colinvaux 1980)
- Glory be Reef, Ocho Rios, mid N shore Jamaica, (77°00'W / 18°24'N), (Hillis-Colinvaux 1980)
- Bath, SE Barbados, (James et al 1977)
- Between boca chita and Sands Key, Biscayne Bay, Florida, (Macintyre and Reid 1995)
- Boiler Bay, NE St. Croix, Virgin Islands, (Adey et al 1977) (Conner and Adey 1977)
- Bahia de Jobos, Baha Fosforescente and Cabo Rojo, Puerto Rico, (Ballantine 1982)
- Great Detached Reef, Quon Island, Hibernia, Lizard Island, Swains Reef and Flinders Reefs, Great Barrier Reef, Australia, (Drew and Abel 1988)
- John Brewer Reef, Central Great Barrier Reef, Australia, NE of Townsville, (Delaney et al 1996)
- Hawaii, (Harney 2000)
- Waikiki fringing Reef, off Oahu Island, Hawaii, (Sorokin 1995)
- Grand Cayman Island, (Johns and Moore 1988)
- Beggar Point (N), Morris Bay (SSW), Half moon Bay / Soldier Point (E), Dums Point (NE), Seaforths (W), Hodge Point (N), Exchange Bay (E), Deep Bay (WNW), Antigua, Lesser Antilles, (Price and John 1979)
- Andros Island, Bahamas, (Newell et al 1959)
- Bimini, Bahamas, (Newell et al 1959)
- Mage, Osumi Islands, Japan, (30°45'N), (Tsuda and Kamura 1991)
- Anamioshima (28°20'N) and Yoron (27°02'N), Amami Islands, Japan, (Tsuda and Kamura 1991)
- Izena (26°56'N) and Okinawa (26°12'N), Okinawa Islands, Japan, (Tsuda and Kamura 1991)
- Ikema (24°56'N) and Miyako (24°47'N), Miyako Islands, Sakishima Islands, Japan, (Tsuda and Kamura 1991)
- Ishigaki (24°30'N), Taketomi (24°20'N), Iriomote (24°20'N) and Yonaguni (24°27'N), Yaeyama Islands, Sakishima Islands, Japan, (Tsuda and Kamura 1991)
- Taiwan, (Tsuda and Kamura 1991)
- Off Cape Sable, SW Florida, (81°28'W / 25°07'N), (Dawes et al 1967)
- South of Cape Sable, SW Florida, (81°12'W / 25°01'N), (Dawes et al 1967)
- Mouth – Florida Bay, SW Florida, (81°17'W / 24°55'N) and (81°19'W / 24°58'N), (Dawes et al 1967)
- Content Keys, SW Florida, (81°29'W / 24°48'N) and (81°30'W / 24°47'N), (Dawes et al 1967)
- Sawyer Key, SW Florida, (81°35'W / 24°47'N), (Dawes et al 1967)
- W Cape Sable, SW Florida, (81°16'W / 25°07'N), (Dawes et al 1967)
- Ponce (S), Guayanilla (S), Guanica (SW), La Parguera (SW), Cabo Rojo (SW), Mona and Descecheos Islands (W), San Juan to Luquillo (NE), Fajardo (E), Vieques and Culebra Islands (E), Humacao to Yabucoa (SE) and Guayama (SE), Puerto Rico, (Almadovar and Ballantine 1983)
- Bamburi Knoll, Knoll 2, Ile Poule, Ile du Coin and Ile Touquet, Peros Banhos, Chagos Archipelago, (Drew 1995)
- Ile Mapou, Ile Takamaka and Ile Anglaise, Salomon Atoll, Chagos Archipelago, (Drew 1995)
- La Reunion, (Drew 1995) (Silva et al 1996)
- Mauritius, (Drew 1995)
- Mauritius including Agalega Islands, (Silva et al 1996)
- Nicobar group, (Drew 1995) (Silva et al 1996)
- Lakshadweep Archipelago, (Drew 1995)
- Seychelles and Atolls, (Drew 1995)
- Seychelles including Mahe Island, (Silva et al 1996)
- Coral Sea, (Drew 1995)
- Ryuku Islands, (Drew 1995)
- Kayangel Atoll, Palau, (Drew 1995)
- Aldabra Islands, (Silva et al 1996)
- Amirante Islands, (Silva et al 1996)
- Andaman Islands, (Silva et al 1996)
- Bangladesh, (Silva et al 1996)
- Coco group, Burma, (Silva et al 1996)
- Cargados Carajos, (Silva et al 1996)
- Chagos Archipelago including Egmont Atoll, (Silva et al 1996)
- Comoro Islands, (Silva et al 1996)
- Diego Garcia Atoll, (Silva et al 1996)
- Djibouti, (Silva et al 1996)
- India, (Silva et al 1996)
- Indonesia, (Silva et al 1996)
- Laccadive Islands, (Silva et al 1996)
- Madagascar, (Silva et al 1996)
- Malaysia, (Silva et al 1996)
- Maldives, (Silva et al 1996)
- Mozambique, (Silva et al 1996)
- Rodriguez Island, (Silva et al 1996)
- Saya de Malha bank, (Silva et al 1996)
- Singapore, (Silva et al 1996)
- Somalia, (Silva et al 1996)
- Sri Lanka, (Silva et al 1996)
- Tanzania, (Silva et al 1996)
- Thailand, (Silva et al 1996)
- Spanish Water, SE Curacao, The Netherlands Antilles, 12°5’N / 68°51’W, (Kuenen and Debrot 1995), water°C 26-29 annual range
- Miskito Channel, Nicaraguaan Rise, SW Caribbean, c16°0’S / 81°40’W, (Hine et al 1988)
- Morrocoy National Park, Venezuela, 10°52’N / 69°16’W, (Bitter 1993)
- Pago Bay, Agat Bay and Western Shoals, Apra Harbour, Guam, (Paul and Alstyne 1988)
- Pohnpei (= Ponape), E Caroline Islands, (Paul and Alstyne 1988)

opuntia f. cordata

- Florida, (Taylor 1960)
- Mexico, (Taylor 1960)
- Bahamas, (Taylor 1960)
- Caicos Islands, (Taylor 1960)
- Anguila Islands, (Taylor 1960)
- Cuba, (Taylor 1960)
- Cayman Islands, (Taylor 1960)
- Jamaica, (Taylor 1960)
- Hispaniola, (Taylor 1960)
- Puerto Rico, (Taylor 1960)
- Virgin Islands, (Taylor 1960)
- Tortola Islands, (Taylor 1960)
- St. Barthelemy, (Taylor 1960)
- Guadeloupe, (Taylor 1960)
- Martinique, (Taylor 1960)
- Barbados, (Taylor 1960)
- Grenada, (Taylor 1960)
- British Honduras, (Taylor 1960)
- Old Providence Island, (Taylor 1960)
- Costa Rica, (Taylor 1960)
- Canal zone, Panama, (Taylor 1960)
- Colombia, (Taylor 1960)
• Netherlands Antilles, (Taylor 1960)
• Islas las Aves, (Taylor 1960)
• Venezuela, (Taylor 1960)
• Trinidad, (Taylor 1960)
• Tobago, (Taylor 1960)
• Brazil, (Taylor 1960)
• Morris Bay (SSW) and Dumps Point (NE), Antigua, Lesser Antilles, (Price and John 1979)
• Content Keys, SW Florida, (81°29' W / 24°48'N), (Dawes et al 1967)

  opuntia var. hederacea

• N Moorea Island, French Polynesia, (Payri 1995)
• Tahiti, (N’Yeurt 1996)
• Fiji, (N’Yeurt 1996)
• Ribbon Reefs 2.5 and 7 off Cooktown, Great Barrier Reef, Australia, (Marshall and Davies 1988)
• Rotuma Island, (N) Fiji Island Group, 12°30'S / 177°05'E, (N’Yeurt 1996)

  opuntia f. opuntia

• Enewetak Atoll, Marshall Islands, (Hillis 1991)
• N Moorea Island, French Polynesia, (Payri 1995)
• Rotuma Island, (N) Fiji Island Group, 12°30'S / 177°05'E, (N’Yeurt 1996)

  opuntia f. triloba

• Florida, (Taylor 1960)
• Mexico, (Taylor 1960)
• Bahamas, (Taylor 1960)
• Caicos Islands, (Taylor 1960)
• Anguila Islands, (Taylor 1960)
• Cuba, (Taylor 1960)
• Cayman Islands, (Taylor 1960)
• Jamaica, (Taylor 1960)
• Hispaniola, (Taylor 1960)
• Puerto Rico, (Taylor 1960)
• Virgin Islands, (Taylor 1960)
• Tortola Islands, (Taylor 1960)
• St. Barthelemy, (Taylor 1960)
• Guadeloupe, (Taylor 1960)
• Martinique, (Taylor 1960)
• Barbados, (Taylor 1960)
• Grenada, (Taylor 1960)
• British Honduras, (Taylor 1960)
• Old Providence Island, (Taylor 1960)
• Costa Rica, (Taylor 1960)
• Canal zone, Panama, (Taylor 1960)
• Colombia, (Taylor 1960)
• Netherlands Antilles, (Taylor 1960)
• Islas las Aves, (Taylor 1960)
• Venezuela, (Taylor 1960)
• Trinidad, (Taylor 1960)
• Tobago, (Taylor 1960)
• Brazil, (Taylor 1960)
• Mamora Reef / Isaac Point (SE), Antigua, Lesser Antilles, (Price and John 1979)
• Mouth – Florida Bay, SW Florida, (81°28' W / 24°55'N), (Dawes et al 1967)
• Mud Key, SW Florida, (81°45'W / 24°42'N), (Dawes et al 1967)

  opuntia f. minor

• Florida, (Taylor 1960)
• Mexico, (Taylor 1960)
• Bahamas, (Taylor 1960)
• Caicos Islands, (Taylor 1960)
• Anguila Islands, (Taylor 1960)
• Cuba, (Taylor 1960)
• Cayman Islands, (Taylor 1960)
• Jamaica, (Taylor 1960)
• Hispaniola, (Taylor 1960)
• Puerto Rico, (Taylor 1960)
• Virgin Islands, (Taylor 1960)
• Tortola Islands, (Taylor 1960)
• St. Barthelemy, (Taylor 1960)
• Guadeloupe, (Taylor 1960)
• Martinique, (Taylor 1960)
- Barbados, (Taylor 1960)
- Grenada, (Taylor 1960)
- British Honduras, (Taylor 1960)
- Old Providence Island, (Taylor 1960)
- Costa Rica, (Taylor 1960)
- Canal zone, Panama, (Taylor 1960)
- Colombia, (Taylor 1960)
- Netherlands Antilles, (Taylor 1960)
- Islas las Aves, (Taylor 1960)
- Venezuela, (Taylor 1960)
- Trinidad, (Taylor 1960)
- Tobago, (Taylor 1960)
- Brazil, (Taylor 1960)

  *papryacea*

- Red Sea, (Hillis-Colinvaux 1980)
- SE Arabian coast, (Silva et al 1996)
- Singapore, (Silva et al 1996)
- Somalia, (Silva et al 1996)
- Yemen, (Silva et al 1996)

  *pelata*

- Nicobar Islands, (Silva et al 1996)

  *rectangularis*

- Australia, (Hillis-Colinvaux 1980) (Silva et al 1996)
- renchii (including batanensis)
- Kenyan coast, (Coppejans and Verellen 1991) (Silva et al 1996)
- Diani, Kenya, (Hillis-Colinvaux 1980)
- Mage (30°45'N) and Yaku (30°21'N), Osumi Islands, Japan, (Tsuda and Kamura 1991)
- Amamioshima, Amami Islands, Japan, (28°20'N), (Tsuda and Kamura 1991)
- Okinawa, Japan, (26°12'N), (Tsuda and Kamura 1991)
- Taiwan, (Tsuda and Kamura 1991)
- Ryuku Islands, (Drew 1995)
- Johannes Island, Comoro Islands, (Hillis-Colinvaux 1980)
- Comoro Islands, (Silva et al 1996)
- Madagascar, (Silva et al 1996)
- Mozambique, (Silva et al 1996)
- Somalia, (Silva et al 1996)
- Tanzania, (Silva et al 1996)
- Yemen, (Silva et al 1996)

  *scabra*

- Biscayne Bay, Florida, (McConnell and Hillis-Colinvaux 1967)
- Florida, (Taylor 1960)
- S. Florida, (Woelkerling 1976)
- Sands Key, Florida, (Hillis-Colinvaux 1980)
- New Providence, Bahamas, (Britton & Millsapugh 1962)
- Rose Island, Bahamas, (Britton & Millsapugh 1962)
- Berry Islands, Bahamas, (Britton & Millsapugh 1962)
- Great bahama, (Britton & Millsapugh 1962)
- Bimini, Bahamas, (Britton & Millsapugh 1962) (Newell et al 1959)
- North Cat Cay, Bahamas, (Britton & Millsapugh 1962)
- South Cat Cay, Bahamas, (Britton & Millsapugh 1962)
- Gun Cay, Bahamas, (Britton & Millsapugh 1962)
- Eleuthera, Bahamas, (Britton & Millsapugh 1962)
- Exuma chain, Bahamas, (Britton & Millsapugh 1962)
- Watling's Island, Bahamas, (Britton & Millsapugh 1962)
- Atwood Cay, Bahamas, (Britton & Millsapugh 1962)
- Mariguana, Bahamas, (Britton & Millsapugh 1962)
- Caicos Islands, Bahamas, (Britton & Millsapugh 1962) (Taylor 1960)
- Castle Island, Bahamas, (Britton & Millsapugh 1962)
- Great Ragged Island, Bahamas, (Britton & Millsapugh 1962)
- Anguilla isles, Bahamas, (Britton & Millsapugh 1962) (Taylor 1960)
- Salt Cay, Bahamas, (Britton & Millsapugh 1962) (Taylor 1960)
- Sands Key, Florida, (Britton & Millsapugh 1962)
- Bahamas, (Taylor 1960)
• Cuba, (Taylor 1960)
• Andros Island, Bahamas, (Newell et al 1959)
  *simulans*
• Berry Islands, Bahamas, (Britton & Millspaugh 1962)
• Atwood Cay, Bahamas, (Britton & Millspaugh 1962)
• Mariguanas, Bahamas, (Britton & Millspaugh 1962)
• Caicos Islands, Bahamas, (Britton & Millspaugh 1962) (Taylor 1960)
• Great Ragged Island, Bahamas, (Britton & Millspaugh 1962)
• Culebra Island, Porto Rico, (Britton & Millspaugh 1962)
• Bermuda, (Britton & Millspaugh 1962) (Taylor 1960)
• Tuckers Town, Bermuda, (Britton 1965)
• Florida, (Britton & Millspaugh 1962) (Taylor 1960)
• S. Florida, (Woelkerling 1976)
• Cuba, (Britton & Millspaugh 1962) (Taylor 1960)
• Jamaica, (Britton & Millspaugh 1962) (Taylor 1960)
• Glory be Reef, Ocho Rios, mid N shore Jamaica, (77°0’W / 18°24’N), (Hillis-Colinvaux 1980)
• Sombra, Jamaica, (Hillis-Colinvaux 1980)
• Spanish Cove, Runaway Bay, Jamaica, (Hillis-Colinvaux 1980)
• American Virgin Islands, (Britton & Millspaugh 1962)
• Virgin Islands, (Taylor 1960)
• Colon, Panama, (Britton & Millspaugh 1962)
• Panama, (Taylor 1960)
• Ocho Rios, N Jamaica, (18°24’N / 77°0’W), (Hillis-Colinvaux 1980)
• Joulters Key, Bahamas, (Harris 1979)
• Puerto Rico, (Ballantine 1982) (Taylor 1960)
• Guayanilla (S), Guanica (SW), La Parguera (SW), Cabo Rojo (SW), Mayaguez (W), Vieques and Culebra Islands (E), Humacao to Yabucoa (SE) and Guayanilla (SE), Puerto Rico, (Almadovar and Ballantine 1983)
• Culebra Island, Puerto Rico, (Hillis-Colinvaux 1980)
• Grand Cayman Island, (Johns and Moore 1988)
• Bahamas, (Taylor 1960)
• Hispaniola, (Taylor 1960)
• St. Barthelemy, (Taylor 1960)
• Dominica, (Taylor 1960)
• Martinique, (Taylor 1960)
• British Honduras, (Taylor 1960)
• Old Providence Island, (Taylor 1960)
• Colombia, (Taylor 1960)
• Brazil, (Taylor 1960)
• Beggars Point (N), Morris Bay (SSW), Mamora Reef / Isaac Point (SE) and Half moon Bay / Soldier Point (E), Antigua, Lesser Antilles, (Price and John 1979)
• Kurme (26°20’N), and Okinawa (26°12’N), Okinawa Islands, Japan, (Tsuda and Kamura 1991)
• Miyako, Japan, (24°47’N), (Tsuda and Kamura 1991)
• Taketomi (24°20’N) and Iriomote (24°20’N), Yaeyama Islands, Japan, (Tsuda and Kamura 1991)
• Mud Key, SW Florida, (81°45’W / 24°42’N), (Dawes et al 1967)
• Kayangel Atoll, Palau, (Drew 1995)
• Ryukyu Islands, (Drew 1995)
• Australia, (Silva et al 1996)
• Sumba, Indonesia, (Silva et al 1996)
• Laccadive Islands, (Silva et al 1996)
• Tanzania, (Silva et al 1996)
• Rotuma Island, (N Fiji Island Group, 12°30’S / 177°05’E, (N’Yeurt 1996)
• Seychelles, (Dolgushina et al 1995)
• Elbow Island, Cay Sal Banks, Bahamas, 23°57.5’N / 80°29’W, (Litter et al 1988)
• Tiahura Reef, NW Moorea Island, Society Islands, French Polynesia, 17°30’S / 149°50’W, (Payri 1988)
• Snark Banks, Nounoua, SW New Caledonia, (Garrigue 1991)
  *sp.*
• Frank Sound, Grand Cayman Island, W. Indies, (Jones and Desrochers 1997)
• Turneffe Islands, Belize, 17°20’N / 87°45’W, (Gischler and Lomando, 2000)
• Lighthouse Reef, Belize, 17°20’N / 87°30’W, (Gischler and Lomando, 2000)
• Grovers Reef, Belize, 16°45’N / 87°35’W, (Gischler and Lomando, 2000)
• Rodriguez Key, (Marszalek 1975)
• Perth, Australia, (Womersley 1981)
• Rodriguez bank (SW of Key Largo), Florida Keys Reef tract, (Ginsburg 1972)
• NW Andros Island, Bahamas, (Hardie 1977) (Garrett 1977)
• Bahia Honda Key, South lagoon, Florida, (Bennam and Kohn 1982)
• Bimini Lagoon, Bahamas, (Seocffin 1970)
• E of Recife, E Brazil, 08°03'S / 34°38'W, (Alexandersson and Milliman 1981)
• E of Rio de Janeiro, Brazil, 21°53'S / 40°13'W, (Alexandersson and Milliman 1981)
• Robin Bay Reef, SE St. Croix, Virgin Islands, (Adams et al. 1977)
• North Sound, Grand Cayman Island, (Roberts 1977)
• Ouvea atoll, Loyalty Islands, New Caledonia, c20°30'S / 166°25'E, (Chevillon 1996)
• Chesterfield atoll, New Caledonia, c19°30'S / 158°30'E, (Chevillon 1996)
• Eastern Lagoon, New Caledonia, c21°20'S / 166°0'E, (Chevillon 1996)
• Northern Lagoon, New Caledonia, c19°30'S / 163°30'E, (Chevillon 1996)
• Punta de San Blas, Caribbean coast, Panama, 9°34'N / 78°58'W, (Shulman and Robertson 1996)
• Vulcan sub-basin, between Timor and NW Australia, (Hovland et al. 1994)

**staposa**
- Enjebi Islet, Eniwetok Atoll, (Hillis-Colinvaux 1980)
- Seychelles and Atolls, (Drew 1995) (Silva et al 1996)
- Kayangel Atoll, Palau, (Drew 1995)
- Rongelap Atoll, Naen Island, Marshall Islands, (Hillis-Colinvaux 1980)
- Aldabra Islands, (Silva et al 1996)
- Desroches Island, Amirante Islands, (Silva et al 1996)
- Cargados Carajos, (Silva et al 1996)
- Egmont Atoll, Chagos Archipelago, (Silva et al 1996)
- Kenya, (Silva et al 1996)

**taenicola**
- Great Detached Reef, Hibernia, Lizard Island, Swains Reefs and Flinders Reefs, Great Barrier Reef, Australia, (Drew and Abel 1988)
- Lagoon side of pass between Alembel and Lojwa Islets, Eniwetok Atoll, (Hillis-Colinvaux 1980)
- Kayangel Atoll, Palau, (Drew 1995)
- Coral Sea, (Drew 1995)
- Maldives, (Silva et al 1996)
- Rotuma Island, (N Fiji Island Group, 12°30'S / 177°05'E, (N’Yeurt 1996)
- Seychelles, (Dolgushina et al 1995)
- Tiahura Reef, NW Moorea Island, Society Islands, French Polynesia, 17°30'S / 149°50'W, (Payri 1988)

**tridens**
- New Providence, Bahamas, (Britton & Millspaugh 1962)
- Rose Island, Bahamas, (Britton & Millspaugh 1962)
- Andros Island, Bahamas, (Britton & Millspaugh 1962) (Newell et al 1959)
- Great Bahama, (Britton & Millspaugh 1962)
- North Cat Cay, (Britton & Millspaugh 1962)
- Green Cay, Bahamas, (Britton & Millspaugh 1962)
- Exuma chain, Bahamas, (Britton & Millspaugh 1962)
- Cat Island, Bahamas, (Britton & Millspaugh 1962)
- Watling’s Island, Bahamas, (Britton & Millspaugh 1962)
- Atwood Cay, Bahamas, (Britton & Millspaugh 1962)
- Mariigua, Bahamas, (Britton & Millspaugh 1962)
- Caicos Islands, Bahamas, (Britton & Millspaugh 1962)
- Castle Island, Bahamas, (Britton & Millspaugh 1962)
- Great Ragged Island, Bahamas, (Britton & Millspaugh 1962)
- Salt Cay, Bahamas, (Britton & Millspaugh 1962)
- Anguilla isles, Bahamas, (Britton & Millspaugh 1962)
- Bermuda, (Britton & Millspaugh 1962)
- Florida, (Britton & Millspaugh 1962)
- Guadeloupe, (Britton & Millspaugh 1962)
- Rodriguez bank (SW of Key Largo), Florida Keys Reef tract, (Ginsburg 1972)
- Bimini, Bahamas, (Newell et al 1959)

**tuna**
- Heron and Lizard Islands, Great Barrier Reef, Australia, (Borowitzka and Larkum 1977)
- Heron Reef Flat, S Great Barrier Reef, Australia, 23°26'S / 151°55'E, (Rogers 1996)
- One Tree Island, Great Barrier Reef, Australia, 23°31'S / 152°08'W, (Franklin et al. 1996), water °C 20-27 annual range
- Buena Bay, Jamaica, (McConnell and Hillis-Colinvaux 1967)
- Vera Cruz, Mexico, (Kady, 1996)
- Kenyan coast, (Copepejas and Verellen 1991) (Silva et al 1996)
- Wistari Reef (near Heron Island), Great Barrier Reef, Australia, 23°35'S / 151°54'E, (Noble, 1986)
- N. Rottnest Shelf, SW continental margin, Australia, 32° - 30°S, (James et al 1999), V. poor – not calcified.
- Houtman Abrolhos, SW continental margin, Australia, 29°S, (James et al 1999), V. poor – not calcified.
- Carnarvon Ramp, SW continental margin, Australia, 24°-27°S, (James et al 1999), Not calcified.
- Coral Cay, Bahamas, (Britton & Millsap 1962)
- Mariguanu, Bahamas, (Britton & Millsap 1962)
- Cozumel, Mexico (1985/6) (Cernohous & Taylor 1995)
- St. Davids Island, Shelly & Burton Bays, southern coast of Hamilton Island, Tuckers Town and Port Royal Bay on S of Hamilton Island, Ireland Island + NE Reefs and Whalebone Bay, Bermuda, (Taylor and Bernardowicz 1969)
- Spanish Point, Gibbet Island, Harrington Sound and Achilles Bay, Bermuda, (Britten 1965)
- Florida, (Britton & Millsap 1962)
- S. Florida, (Wrackling 1976)
- Jamaica, (Britton & Millsap 1962)
- Boscobel, Jamaica, (Hillis-Colinvaux 1980)
- Barbados, (Britton & Millsap 1962)
- Mediterranean, (Britton & Millsap 1962)
- Ocho Rios, N Jamaica, 18°24'N / 77°W, (Hillis-Colinvaux 1980)
- San Salvador, Bahamas, (Marshall 1980)
- Sombrero Island, 18°36'N / 63°25'W, (Ogden et al 1985)
- Capo Rosso, Puerto Rico, (Ballantine 1982)
- Ponce (S), Guaynajulu (S), Guanica (SW), La Parguera (SW), Cabo Rojo (SW), Mona and Desecheo Islands (W), Mayaguez (W), Fajardo (E), Vieques and Culebra Islands (E), and Guayama (SE), Puerto Rico, (Almadovar and Ballantine 1983)
- Blackwood Channel, Quoin Island, Waterwitch, Lizard Island, Cooktown Reef, Swains Reefs, Great Barrier Reef, Australia, (Drew and Abel 1988)
- Grand Cayman Island, (Johns and Moore 1988)
- Beggars Point, N, Morris Bay (SSW), Mamora Reef / Isaac Point (SE) and Half moon Bay / Soldier Point (E), Antigua, Lesser Antilles, (Price and John 1979)
- Waikiki fringing reef, off Oahu Island, Hawaii, (Sorokin 1995)
- Okinawa, Japan, 26°12'N, (Tsuda and Kamura 1991)
- Ishigaki, Yaeyama Islands, Japan, 24°30'N, (Tsuda and Kamura 1991)
- Mainland Japan, (Tsuda and Kamura 1991)
- Bamburi Knoll and Ile du Coin, Peros Bhanos, Chagos Archipelago, (Drew 1995)
- Main pass, Ile de la Passe, Ile Mapou, Ile Takamaka, Ile du Sel and Ile Boddam, Salomon Atoll, Chagos Archipelago, (Drew 1995)
- La Reunion, (Drew 1995) (Silva et al 1996)
- Nicobar group, (Drew 1995) (Silva et al 1996)
- Lakshadweep Archipelago, (Drew 1995)
- Angria bank, (Drew 1995)
- Ryuku Islands, (Drew 1995)
- Aldabra Islands, (Silva et al 1996)
- Amirante Islands, (Silva et al 1996)
- Andaman Islands, (Silva et al 1996)
- Cargados Carajos, (Silva et al 1996)
- Chagos archipelago including Egmont Atoll, (Silva et al 1996)
- Diego Garcia Atoll, (Silva et al 1996)
- India, (Silva et al 1996)
- Indonesia, (Silva et al 1996)
- Laccadive Islands, (Silva et al 1996)
- Madagascar, (Silva et al 1996)
- Malaysia, (Silva et al 1996)
- Maldives, (Silva et al 1996)
- Mozambique, (Silva et al 1996)
- Pakistan, (Silva et al 1996)
- Rodriguez Island, (Silva et al 1996)
- Saya de Malha bank, (Silva et al 1996)
- S. Africa, (Silva et al 1996)
- Sri Lanka, (Silva et al 1996)
- Tanzania, (Silva et al 1996)
• Yemen, (Silva et al 1996)
• Bay of Fornells, N Menorca, Balearic Islands, (Fornos et al 1992), water °C 12.7-27.5 annual range
• Elbow Island, Cay Sal Banks, Bahamas, 23°57.5’N / 80°29’W, (Littler et al 1988)
• Tossa de Mar, NE Spain, (Llobet et al 1991)
• (10 km S of) Livorno, NW Italy, 43°30’N / 10°20’E, (Airolidi et al 1995)
• Rotuma Island, (N Fiji Island Group, 12°30’S / 177°05’E, (N’Yeurt 1996)

Tuna f. playdisca
• Haifa Bay, Israel, (Edelstein and Komarovsky 1961)
• French Bay, S San Salvador, Bahamas, 23°56.7’N / 74°31.3’W, (Blair and Norris 1988)
• Bermuda, (Taylor 1960)
• Florida, (Taylor 1960)
• Mexico, (Taylor 1960)
• Bahamas, (Taylor 1960)
• Caicos Islands, (Taylor 1960)
• Anguila Islands, (Taylor 1960)
• Cuba, (Taylor 1960)
• Jamaica, (Taylor 1960)
• Hispaniola, (Taylor 1960)
• Puerto Rico, (Taylor 1960)
• Virgin Islands, (Taylor 1960)
• St. Martin, (Taylor 1960)
• Saba bank, (Taylor 1960)
• Guadeloupe, (Taylor 1960)
• Barbados, (Taylor 1960)
• British Honduras, (Taylor 1960)
• Panama, (Taylor 1960)
• Colombia, (Taylor 1960)
• Brazil, (Taylor 1960)

Tuna f. tuna
• Green Cay, NW San Salvador, Bahamas, 24°8.5’N / 74°31.2’W, (Blair and Norris 1988)
• Cockburn Town, W San Salvador, Bahamas, 24°3.2’N / 74°32.6’W, (Blair and Norris 1988)

Velansquezii
• Kenyan coast, (Coppejans and Verellen 1991) (Silva et al 1996)
• Isema (26°56’N), Kume (26°20’N) and Okinawa (26°12’N), Okinawa Islands, Japan, (Tsuda and Kamura 1991)
• Miyako, Sakishima Islands, Japan, (24°47’N), (Tsuda and Kamura 1991)
• Ishigaki (24°30’N), Kuro (24°14’N) and Yonaguni (24°27’N), Yaeyama Islands, Japan, (Tsuda and Kamura 1991)
• Taiwan, (Tsuda and Kamura 1991)
• Ryuku Islands, (Drew 1995)
• Waha, Ryuku Islands, (Hillis-Colinvaux 1980)
• Luzon Island, Casagian, Sta. Ana, Prov., Philippines, (Hillis-Colinvaux 1980)
• Guam, (Hillis-Colinvaux 1980)
Modern benthic calcareous algae database

HALIMEDACEAE

**Penicillus**

*capitatus*

- Harrington Sound, Bermuda, (Wefer, G. 1980)
- St. Georges Island, Stovel Bay on Hamilton Island, Elys Harbour on the S of Hamilton Island, Harrington Sound, Ireland Island, Mullet Bay, Mangrove lake, Riddell's Bay and Hungry Bay, Bermuda, (Taylor and Bernatowicz 1969)
- Carrie Bow Bay, Belize Barrier Reef, 16°48'N / 88°03'W, (Littler et al 1983)
- Lower Laguna Madre, Texas, (0 calcification?), (Kaldy, 1996)
- Bright of Abaco, Little Bahama Bank, (Neumann and Land 1975)
- N. Jamaica, (Hillis 1991)
- Glory be Reef, Ocho Rios, mid N shore Jamaica, (77°0'W / 18°24'N), (Hillis-Colinvaux 1980)
- New Providence, Bahamas, (Britton & Millsbaugh 1962)
- Rose Island, Bahamas, (Britton & Millsbaugh 1962)
- Berry Islands, Bahamas, (Britton & Millsbaugh 1962)
- Andros Island, Bahamas, (Britton & Millsbaugh 1962) (Newell et al 1959)
- Great Bahama, (Britton & Millsbaugh 1962)
- Garden Cey, Bahamas, (Britton & Millsbaugh 1962)
- Exuma chain, Bahamas, (Britton & Millsbaugh 1962)
- Cat Island, Bahamas, (Britton & Millsbaugh 1962)
- Watling's Island (San Salvador), Bahamas, (Britton & Millsbaugh 1962) (Marshall 1980)
- Atwood Cey, Bahamas, (Britton & Millsbaugh 1962)
- Mariguana, Bahamas, (Britton & Millsbaugh 1962)
- Caicos Islands, Bahamas, (Britton & Millsbaugh 1962)
- Great Ragged Island, Bahamas, (Britton & Millsbaugh 1962)
- Bermuda, (Britton & Millsbaugh 1962)
- Florida, (Britton & Millsbaugh 1962)
- S. Florida, (Woelkerling 1976)
- Guadeloupe, (Britton & Millsbaugh 1962)
- Rodriguez Bank (SW of Key Largo), Florida Keys Reef tract, (Ginsburg 1972)
- N side of Marathon- Florida Keys and Crane Point Hammock, SW Florida Bay, (Delgado and LaPointe 1994)
- Joulers Key, Bahamas, (Harris 1979)
- NE Florida Bay, between Rodriguez and Crane Keys, (Stockman et al 1967)
- Mangrove Lake, SSE Bermuda, (Moore 1969)
- Boiler Bay, NE St. Croix, Virgin Islands, (Adey et al 1977) (Conner and Adey 1977)
- Beggars Point (N), Morris Bay (SSW), Mamora Reef / Isaac Point (SE), Half Moon Bay / Soldier Point (E), Hodge Point (N), and Reeds Beach (E), Antigua, Lesser Antilles, (Price and John 1979)
- Waikiki fringing Reef, off Oahu Island, Hawaii, (Sorokin 1995)
- Bimini, Bahamas, (Newell et al 1959)
- Off Cape Sable, SW Florida, (81°20'W / 25°13'N) and (81°28'W / 25°07'N), (Dawes et al 1967)
- Content Keys, SW Florida, (81°29'W / 24°48'N) and (81°30'W / 24°47'N), (Dawes et al 1967)
- Mud Key, SW Florida, (81°45'W / 24°42'N), (Dawes et al 1967)
- Mouth – Florida Bay, SW Florida, (81°19'W / 24°58'N), (Dawes et al 1967)
- Ponce (S), Guayanilla (S), Guanica (SW), La Parguera (SW), Cabo Rojo (SW), Mona and Desecheo Islands (W), Mayaguez (W), Arecibo (N), San Juan to Luquillo (NE), Fajardo (E), Vieques and Culebra Islands (E), Humacao to Yabucoa (SE) and Guayama (SE), Puerto Rico, (Almadovar and Ballantine 1983)
- Spanish Water, SE Curacao, The Netherlands Antilles, 12°5'N / 58°51'W, (Kuenen and Debrot 1995), water °C 26-29 annual range

*capitatus f. elongatus*

- Bermuda, (Taylor 1960)
- Florida, (Taylor 1960)
- Mexico, (Taylor 1960)
- Bahamas, (Taylor 1960)
- Caicos Islands, (Taylor 1960)
- Cuba, (Taylor 1960)
- Cayman Islands, (Taylor 1960)
- Jamaica, (Taylor 1960)
- Hispaniola, (Taylor 1960)
Puerto Rico, (Taylor 1960)
Virgin Islands, (Taylor 1960)
St. Martin, (Taylor 1960)
St. Barthelemy, (Taylor 1960)
St. Eustatius, (Taylor 1960)
Guadeloupe, (Taylor 1960)
Dominica, (Taylor 1960)
Martinique, (Taylor 1960)
Grenada, (Taylor 1960)
British Honduras, (Taylor 1960)
Old Providence Island, (Taylor 1960)
Canal zone, Panama, (Taylor 1960)
Colombia, (Taylor 1960)
Netherlands Antilles, (Taylor 1960)
Isla las Aves, (Taylor 1960)
Trinidad, (Taylor 1960)
Content Keys, SW Florida, (81°30'W / 24°47'N), (Dawes et al 1967)
Sawyer Key, SW Florida, (81°35'W / 24°47'N), (Dawes et al 1967)*

Bermuda, (Taylor 1960)
Florida, (Taylor 1960)
Mexico, (Taylor 1960)
Bahamas, (Taylor 1960)
Caicos Islands, (Taylor 1960)
Cuba, (Taylor 1960)
Cayman Islands, (Taylor 1960)
Jamaica, (Taylor 1960)
Hispaniola, (Taylor 1960)
Puerto Rico, (Taylor 1960)
Virgin Islands, (Taylor 1960)
St. Martin, (Taylor 1960)
St. Barthelemy, (Taylor 1960)
St. Eustatius, (Taylor 1960)
Guadeloupe, (Taylor 1960)
Dominica, (Taylor 1960)
Martinique, (Taylor 1960)
Grenada, (Taylor 1960)
British Honduras, (Taylor 1960)
Old Providence Island, (Taylor 1960)
Canal zone, Panama, (Taylor 1960)
Colombia, (Taylor 1960)
Netherlands Antilles, (Taylor 1960)
Isla las Aves, (Taylor 1960)
Trinidad, (Taylor 1960)
Sawyer Key, SW Florida, (81°35'W / 24°47'N), (Dawes et al 1967)

Bight of Abaco, Little Bahama Bank, (Neumann and Land 1975)

Long Bank, Bahamas, (Britton & Millsbaugh 1962)
Great Bahama, (Britton & Millsbaugh 1962)
Bimini, Bahamas, (Britton & Millsbaugh 1962) (Newell et al 1959)
Florida, (Britton & Millsbaugh 1962)
S. Florida, (Woolkerling 1976)
Guadeloupe, (Britton & Millsbaugh 1962)
Antilles, (Britton & Millsbaugh 1962)
Rodriguez Bank (SW of Key Largo), Florida Keys Reef tract, (Ginsburg 1972)
N side of Marathon- Florida Keys and Crane Point Hammock, SW Florida Bay, (Delgado and LaPointe 1994)
San Salvador, Bahamas, (Marshall 1980)
Morris Bay (SSW), Reeds Beach (E) and Port Royal Bay (N), Antigua, Lesser Antilles, (Price and John 1979)
Waikiki fringing Reef, off Oahu Island, Hawaii, (Sorokin 1995)
Andros Island, Bahamas, (Newell et al 1959)
Off Cape Sable, SW Florida, (81°28'W / 25°07'N), (Dawes et al 1967)
Mouth – Florida Bay, SW Florida, (81°17'W / 24°55'N) and (81°19'W / 24°58'N), (Dawes et al 1967)
Content Keys, SW Florida, (81°30'W / 24°47'N), (Dawes et al 1967)
Sawyer Key, SW Florida, (81°35'W / 24°47'N), (Dawes et al 1967)*

Bermuda, (Taylor 1960)
• Florida, (Taylor 1960)
• Bahamas, (Taylor 1960)
• Cuba, (Taylor 1960)
• Cayman Islands, (Taylor 1960)
• Jamaica, (Taylor 1960)
• Hispaniola, (Taylor 1960)
• Puerto Rico, (Taylor 1960)
• Virgin Islands, (Taylor 1960)
• Anguilla Islands, (Taylor 1960)
• St. Bartslemy, (Taylor 1960)
• Guadeloupe, (Taylor 1960)
• Grenada, (Taylor 1960)
• British Honduras, (Taylor 1960)
• Old Providence Island, (Taylor 1960)
• Colombia, (Taylor 1960)
• Content Keys, SW Florida, (81°30′W / 24°47′N), (Dawes et al 1967)
• Mud Key, SW Florida, (81°45′W / 24°42′N), (Dawes et al 1967)

/lamourosa laxii

• Carrie Bow Bay, Belize Barrier Reef, 16°48′N / 88°05′W, (Littler et al 1983)
• Bight of Abaco, Little Bahama Bank, (Neumann and Land 1975)
• New Providence, Bahamas, (Britton & Illsighpaugh 1962)
• Rose Island, Bahamas, (Britton & Millsapugh 1962)
• Great Bahama, Bahamas, (Britton & Millsapugh 1962)
• Garden Cay, Bahamas, (Britton & Millsapugh 1962)
• Bimini, Bahamas, (Britton & Millsapugh 1962)
• Green Turtle Cay, Bahamas, (Britton & Millsapugh 1962)
• Exuma chain, Bahamas, (Britton & Millsapugh 1962)
• Watling’s Island, Bahamas, (Britton & Millsapugh 1962)
• Mariguanu, Bahamas, (Britton & Millsapugh 1962)
• Caicos Islands, Bahamas, (Britton & Millsapugh 1962)
• Castle Island, Bahamas, (Britton & Millsapugh 1962)
• Great Ragged Island, Bahamas, (Britton & Millsapugh 1962)
• Florida, (Britton & Millsapugh 1962)
• S. Florida, (Woolkerling 1976)
• Cuba, (Britton & Millsapugh 1962)
• Jamaica, (Britton & Millsapugh 1962)
• Porto Rico, (Britton & Millsapugh 1962)
• Ponce (S), Guayanilla (S), Guanica (SW), Cabo Rojo (SW) and Vieques and Culebra Islands (E), Puerto Rico, (Almadovar and Ballantine 1983)
• American Virgin Islands, (Britton & Millsapugh 1962)
• Off Cape Sable, SW Florida, (81°28′W / 25°07′N), (Dawes et al 1967)
• Content Keys, SW Florida, (81°30′W / 24°47′N), (Dawes et al 1967)
• Mud Key, SW Florida, (81°45′W / 24°42′N), (Dawes et al 1967)
• Sawyer Key, SW Florida, (81°35′W / 24°47′N), (Dawes et al 1967)

/lamourosa laxii var. gracilis

• Florida, (Taylor 1960)
• Mexico, (Taylor 1960)
• Bahamas, (Taylor 1960)
• Caicos Islands, (Taylor 1960)
• Cuba, (Taylor 1960)
• Jamaica, (Taylor 1960)
• Puerto Rico, (Taylor 1960)
• Virgin Islands, (Taylor 1960)
• St. Eustatius, (Taylor 1960)
• Guadeloupe, (Taylor 1960)
• Panama, (Taylor 1960)

/manaarensis

/nodulosus

• Abrolhos or Cliff Head, N of Rottnest Island, Australia, (Walker 1991)
• Dirk Hartog Island, Shark Bay, Australia, 26°02′S / 113°10′E, (Kendrick et al 1990)
• Hopeless Reach, Shark Bay, Australia, 25°45′S / 113°45′E, (Kendrick et al 1990)
• Freycinet Estuary, Shark Bay, Australia, 26°20′S / 113°35′E, (Kendrick et al 1990)
• Gladstone Inlet, Shark Bay, Australia, 25°55′S / 114°10′E, (Kendrick et al 1990)
• Australia, (Silva et al 1996)

/pyriformis
• Carrie Bow Bay, Belize Barrier Reef, 16°48'N / 88°05'W, (Littler et al 1983)
• New Providence, Bahamas, (Britton & Millsapgh 1962)
• Rose Island, Bahamas, (Britton & Millsapgh 1962)
• Berry Islands, Bahamas, (Britton & Millsapgh 1962)
• Andros Island, Bahamas, (Britton & Millsapgh 1962) (Newell et al 1959)
• Great Bahama, (Britton & Millsapgh 1962)
• Bimini Harbour, Bahamas, (Britton & Millsapgh 1962) (Newell et al 1959)
• Exuma chain, Bahamas, (Britton & Millsapgh 1962)
• Cat Island, Bahamas, (Britton & Millsapgh 1962)
• Walts'Island (San Salvador), Bahamas, (Britton & Millsapgh 1962) (Marshall 1980)
• Marigat, Bahamas, (Britton & Millsapgh 1962)
• Caicos Islands, Bahamas, (Britton & Millsapgh 1962)
• Anguilla Islands, Bahamas, (Britton & Millsapgh 1962)
• Bermuda, (Britton & Millsapgh 1962)
• Mullet Bay, Elys Harbour, Harrington Sound, Richardsowns Cove and Coney Island, Bermuda, (Taylor and Bernatowicz 1969)
• Ely's Harbour and Harris Bay, Bermuda, (Britten 1965)
• Florida, (Britton & Millsapgh 1962)
• S. Florida, (Woekertinger 1976)
• Jamaica, (Britton & Millsapgh 1962)
• Guadeloupe, (Britton & Millsapgh 1962)
• NW Andros Island, Bahamas, (Hardie 1977) (Garrett 1977)
• Joutiers Key, Bahamas, (Harris 1979)
• NE Florida Bay, between Rodriguez and Crane Keys, (Stockman et al 1967)
• Off Cape Sable, SW Florida, (81°20'W / 25°13'N), (Dawes et al 1967)
• La Parguera (SW), Fajardo (E) and Vieques and Culebra Islands (E), Puerto Rico, (Almadovar and Ballantine 1983) pyriformis f. explanatus
• Bermuda, (Taylor 1960)
• Florida, (Taylor 1960)
• Bahamas, (Taylor 1960)
• Caicos Islands, (Taylor 1960)
• Cuba, (Taylor 1960)
• Jamaica, (Taylor 1960)
• Hispaniola, (Taylor 1960)
• Virgin Islands, (Taylor 1960)
• Anguilla Islands, (Taylor 1960)
• St. Eustatis, (Taylor 1960)
• Guadeloupe, (Taylor 1960)
• Panama, (Taylor 1960)

• ibogae

• Comoro Islands, (Silva et al 1996)
• India, (Silva et al 1996)
• Timor, Indonesia, (Silva et al 1996)
• Madagascar, (Silva et al 1996)
• Thailand, (Silva et al 1996)

• sp.

• Poreus and Rio do Fogo Beach, state of Rio Grande do Norte, Brazil, 35°09'W - 35°28'W / 4°57'S - 5°17'S, (James et al 1999), water°C 26.5-28.5
• Rodriguez Key, (Marzalek 1975)
• Perth, Australia, (Womersley 1981)
• Rodriguez bank (SW of Key Largo), Florida Keys Reef tract, (Ginsburg 1972)
• Bahia Honda Key, South lagoon, Florida, (Benham and Kohn 1982)
• Bimini lagoon, Bahamas, (Scoffin 1970)
• Robin Bay, SE St. Croix, Virgin Islands, (Adey et al 1977)
• Quoin Island, Hibernia and Lizard Island, Great Barrier Reef, Australia, (Drew and Abel 1988)
• North Sound, Grand Cayman Island, (Roberts 1977)
• SE France, (Elliott 1981)
• Bermuda, (Elliott 1981)
• Florida, (Elliott 1981)
• Jamaica, (Elliott 1981)
• N. Colombia, (Elliott 1981)
• Panama, (Elliott 1981)
• E. Indonesia (Seram?), (Elliott 1981)
• Timor, (Elliott 1981)
• Torres Strait, N. Australia, (Elliott 1981)
• Abrolhos, SW Australia, (Elliott 1981)
Modern benthic calcareous algae database

**HALIMEDACEAE**

*Rhizocephalus*

- oblongus
- *phoenix*
- Carrie Bow Bay, Belize Barrier Reef, 16°48'N / 88°05'W, (Littler et al 1983)
- Bight of Abaco, Little Bahama Bank, (Neumann and Land 1975)
- New Providence, Bahamas, (Britton & Millspaugh 1962)
- Berry Islands, Bahamas, (Britton & Millspaugh 1962)
- Bimini, Bahamas, (Britton & Millspaugh 1962)
- North Cat Cay, Bahamas, (Britton & Millspaugh 1962)
- Florida, (Britton & Millspaugh 1962) (Taylor 1960)
- Cuba, (Britton & Millspaugh 1962) (Taylor 1960)
- San Salvador, Bahamas, (Marshall 1980)
- Bahamas, (Taylor 1960)
- New Providence, Bahamas, (Britton & Millspaugh 1962)
- Berry Islands, Bahamas, (Britton & Millspaugh 1962)
- Andros Island, Bahamas, (Britton & Millspaugh 1962) (Newell et al 1959)
- Bimini, Bahamas, (Britton & Millspaugh 1962) (Newell et al 1959)
- Exuma chain, Bahamas, (Britton & Millspaugh 1962)
- Cat Island, Bahamas, (Britton & Millspaugh 1962)
- Atwood Cay, Bahamas, (Britton & Millspaugh 1962)
- Mariguanas, Bahamas, (Britton & Millspaugh 1962)
- Florida, (Britton & Millspaugh 1962)
- Cuba, (Britton & Millspaugh 1962)
- Jamaica, (Britton & Millspaugh 1962)
- Porto Rico, (Britton & Millspaugh 1962)
- Mona and Desecho Islands (W), Aguadilla to Guajataca (NW) and Humacao to Yabucoa (SE), Puerto Rico, (Almodovar and Ballantine 1983)
- Guadeloupe, (Britton & Millspaugh 1962)
- NW Andros Island, Bahamas, (Hardie 1977)
- Joulter's Key, Bahamas, (Harris 1979)
- Bimini Lagoon, Bahamas, (Garrett 1977)
- San Salvador, Bahamas, (Marshall 1980)
- Port Royal Bay (N), Antigua, Lesser Antilles, (Price and John 1979)
- Off Cape Sable, SW Florida, (81°28'W / 25°07'N), (Dawes et al 1967)
- Content Keys, SW Florida, (81°30'W / 24°47'N), (Dawes et al 1967)
- Mud Key, SW Florida, (81°45'W / 24°42'N), (Dawes et al 1967)
- Smith Shoal, SW Florida, (81°55'W / 24°43'N), (Dawes et al 1967)

*phoenix f. brevifolius*

- Florida, (Taylor 1960)
- Bahamas, (Taylor 1960)
- Cuba, (Taylor 1960)
- Jamaica, (Taylor 1960)
- Hispaniola, (Taylor 1960)
- Puerto Rico, (Taylor 1960)
- Guadeloupe, (Taylor 1960)
- British Honduras, (Taylor 1960)
- Old Providence Island, (Taylor 1960)
- Panama, (Taylor 1960)
- Colombia, (Taylor 1960)

*phoenix f. longifolius*

- Florida, (Taylor 1960)
- Bahamas, (Taylor 1960)
- Cuba, (Taylor 1960)
- Jamaica, (Taylor 1960)
- Hispaniola, (Taylor 1960)
- Puerto Rico, (Taylor 1960)
- Guadeloupe, (Taylor 1960)
- British Honduras, (Taylor 1960)
- Old Providence Island, (Taylor 1960)
- Panama, (Taylor 1960)
- Colombia, (Taylor 1960)

  *sp.*

- Rodriguez Key, (Marszalek 1975)
- Rodriguez bank (SW of Key Largo), Florida Keys Reef tract, (Ginsburg 1972)
- Bimini Lagoon, Bahamas, (Scoffin 1970)
- North Sound, Grand Cayman Island, (Roberts 1977)
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HALIMEDACEAE

Tydemania

expeditionsis

• Maldives, (McConnell and Hillis-Colinvaux1967) (Gilmartin, 1966)
• Bay of Bengal, (Gilmartin, 1966)
• Caroline Islands, (Gilmartin, 1966)
• Philippines, (Gilmartin, 1966)
• Ryukyu Islands (Japan), (Gilmartin, 1966)
• Cooktown Ribbon Reefs. (Drew and Abel 1988)
• Guam, 13°25'N / 144°55'E, (Meyer et al 1994) gardineri

• Chagos Archipelago, (Gilmartin, 1966) mabahithae

• Red Sea, (Gilmartin, 1966)
Modern benthic calcareous algae database

HALIMEDACEAE

Udotea

*abbotiorum*

- Content Keys, Monroe county, Florida, (Littler and Littler 1990)
- NW Tobacco Range, Belize, (Littler and Littler 1990)
- Horn's Bay, Bermuda, (Littler and Littler 1990)
- Santurce, Puerto Rico, (Littler and Littler 1990)
- Panama, (Littler and Littler 1990)
- Colombia, (Littler and Littler 1990)

*argentea*

- Dirk Hartog Island, Shark Bay, Australia, 26°05' S / 113°10' E, (Kendrick et al 1990)
- Hopeless Reach, Shark Bay, Australia, 25°45' S / 113°45' E, (Kendrick et al 1990)
- Freycinet Estuary, Shark Bay, Australia, 26°20' S / 113°35' E, (Kendrick et al 1990)
- St. Joseph Atoll, Amirante Islands, (Silva et al 1996)
- Australia, (Silva et al 1996)
- Cargados Carajos, (Silva et al 1996)
- Madagascar, (Silva et al 1996)
- Mauritius, (Silva et al 1996)
- Seychelles, (Silva et al 1996)
- Singapore, (Silva et al 1996)

*caribaea*

- NW Tobacco Range, Belize, (Littler and Littler 1990)
- Cayo San Felipe, Cuba, (Littler and Littler 1990)

*conglutinata*

- Bimini Harbour, Bahamas, (Littler and Littler 1990)
- Port George Cay, Caicos Islands, Bahamas, (Littler and Littler 1990)
- San Salvador Islands, (Littler and Littler 1990)
- Monito Island, Puerto Rico, (Littler and Littler 1990)
- New Providence, Bahamas, (Britten & Millsbaugh 1962)
- Andros Island, Bahamas, (Britten & Millsbaugh 1962)
- Joulters Cays, Bahamas, (Britten & Millsbaugh 1962)
- North Cat Cay, Bahamas, (Britten & Millsbaugh 1962)
- Bimini, Bahamas, (Britten & Millsbaugh 1962)
- Green Cay, Bahamas, (Britten & Millsbaugh 1962)
- Watling's Island, Bahamas, (Britten & Millsbaugh 1962)
- Mariguanas, Bahamas, (Britten & Millsbaugh 1962)
- Caicos, Bahamas, (Britten & Millsbaugh 1962)
- Castle Island, Bahamas, (Britten & Millsbaugh 1962)
- Bermuda, (Britten & Millsbaugh 1962) (Taylor 1960)
- Nonsuch Island, Charles Island, Castle Island, Pear Rock, mouth of Richardson's Cove + NE Reefs and North Rock, Bermuda, (Taylor and Bernatowicz 1969)
- South Beach in Paget and Harris Bay, Bermuda, (Britten 1965)
- Florida, (Britten & Millsbaugh 1962) (Taylor 1960)
- S. Florida, (Woelkerling 1976)
- American Virgin Islands, (Britten & Millsbaugh 1962)
- Boilier Bay, NE St. Croix, Virgin Islands, (Aday et al 1977)
- Mexico, (Taylor 1960)
- Bahamas, (Taylor 1960)
- Cuba, (Taylor 1960)
- Jamaica, (Taylor 1960)
- Hispaniola, (Taylor 1960)
- Virgin Islands, (Taylor 1960)
- St. Martin, (Taylor 1960)
- St. Eustatus, (Taylor 1960)
- Guadeloupe, (Taylor 1960)
- Grenada, (Taylor 1960)
- Old Providence Island, (Taylor 1960)
- Panama, (Taylor 1960)
- Colombia, (Taylor 1960)
- Brazil, (Taylor 1960)
- Hodge point (N), Antigua, Lesser Antilles, (Price and John 1979)
- Off Cape Sable, SW Florida, (81°20'W / 25°13'N) and (81°28'W / 25°07'N), (Dawes et al 1967)
- S of Cape Sable, SW Florida, (81°12'W / 25°01'N), (Dawes et al 1967)
- Mouth – Florida Bay, SW Florida, (81°17'W / 24°55'N), (81°28'W / 24°55'N) and (81°19'W / 24°58'N), (Dawes et al 1967)
- Content Keys, SW Florida, (81°30’W / 24°47’N), (Dawes et al 1967)
- Mud Key, SW Florida, (81°45’W / 24°42’N), (Dawes et al 1967)
- Smith Shoal, SW Florida, (81°55’W / 24°43’N), (Dawes et al 1967)
- W Cape Sable, SW Florida, (81°16’W / 25°07’N), (Dawes et al 1967)
- W Shark Point, SW Florida, (81°19’W / 25°25’N), (Dawes et al 1967)
- Carrie Bow Bay, Belize Barrier Reef, 16°48’N / 88°05’W, (Littler et al 1983)
- Berry Islands, Bahamas, (Britton & Millsap 1962)
- Bimini, Bahamas, (Britton & Millsap 1962) (Newell et al 1959)
- North Cat Cay, Bahamas, (Britton & Millsap 1962)
- Exuma chain, Bahamas, (Britton & Millsap 1962)
- Caicos Islands, Bahamas, (Britton & Millsap 1962)
- Castle Island, Bahamas, (Britton & Millsap 1962)
- Barbados, (Britton & Millsap 1962) (Taylor 1960)
- Isles des Saintes, Guadeloupe, (Britton & Millsap 1962)
- North Carolina, (Britton & Millsap 1962)
- Colon, Panama, (Britton & Millsap 1962)
- Onslow Bay, Carolinas, (Schneider 1976)
- San Salvador, Bahamas, (Marshall 1980)
- Bermuda, (Taylor 1960)
- North Carolina, (Taylor 1960)
- Florida, (Taylor 1960)
- S. Florida, (Woelkerling 1976)
- Bahamas, (Taylor 1960)
- Cuba, (Taylor 1960)
- Jamaica, (Taylor 1960)
- Virgin Islands, (Taylor 1960)
- Guadeloupe, (Taylor 1960)
- Panama, (Taylor 1960)
- Brazil, (Taylor 1960)
- Trinidad, (Taylor 1960)
- Waikiki fringing Reef, off Oahu Island, Hawaii, (Sorokin 1995)
- Andros Island, Bahamas, (Newell et al 1959)
- Guanica (SW), La Parguera (SW), Cabo Rojo (SW), San Juan to Luquillo (NE) and Vieques and Culebra Islands (E), Puerto Rico, (Almadover and Ballantine 1983)
- cyathiformis var cyathiformis f. cyathiformis
- Mangrove Cay, Andros Island, Bahamas, (Littler and Littler 1990)
- Carrie Bow Cay, Belize, (Littler and Littler 1990)
- Caracol Bay, Caracol Reef, Haiti, (Littler and Littler 1990)
- Iles de Saintes, Guadeloupe, Lesser Antilles, (Littler and Littler 1990)
- Mayaguez, Puerto Rico, (Littler and Littler 1990)
- cyathiformis var cyathiformis f. influndibulum
- Singer Island, Palm Beach county, Florida, (Littler and Littler 1990)
- West Indies, (Littler and Littler 1990)
- Curlew Cay, Belize, (Littler and Littler 1990)
- Medicea Luna Bay, Media Luna Cay, Honduras, (Littler and Littler 1990)
- cyathiformis var cyathiformis f. sublittoralis
- Garden Key, Dry Tortugas, Florida, (Littler and Littler 1990)
- Bush Key, Dry Tortugas, Florida, (Littler and Littler 1990)
- Cave Cays, Exuma chain, Bahamas, (Littler and Littler 1990)
- Tobago Cays, Grenadines, Mayreau, Lesser Antilles, (Littler and Littler 1990)
- Manati, Playa Tortuguero, Puerto Rico, (Littler and Littler 1990)
- cyathiformis var flabellifolia
- Pigsty Reef, San Blas Islands, Panama, (Littler and Littler 1990)
- Carrie Bow Cay, Belize, (Littler and Littler 1990)
- Onslow Bay, Carteret county, North Carolina, (Littler and Littler 1990)
- dizonii
- Curlew Cay, Belize, (Littler and Littler 1990)
- 2.2km E of Lake Worth Inlet, Palm Beach county, Florida, (Littler and Littler 1990)
- Caracol Bay, Caracol Reef, Haiti, (Litter and Litter 1990)
- Galeta Island, Panama, (Litter and Litter 1990)
- E. Flower Garden Banks, Gulf of Mexico, (Litter and Litter 1990)
- Nicaragua, (Litter and Litter 1990)
- Puerto Rico, (Litter and Litter 1990)

**doyi**
- Tobago Cays, Grenadines, Lesser Antilles, (Litter and Litter 1990)
- Caracol Bay, Caracol Reef, Haiti, (Litter and Litter 1990)
- Media Luna Bay, Honduras, (Litter and Litter 1990)
- Puerto Rico, (Litter and Litter 1990)

**fibrosa**
- Carrie Bow Bay, Curlew Cay and Gallows Point, Belize, (Litter and Litter 1990)
- Jamaica, (Litter and Litter 1990)
- Haiti, (Litter and Litter 1990)

**flabellum**
- Carrie Bow Bay, Belize Barrier Reef, 16°48'N / 88°05'W, (Litter et al 1983)
- Bight of Abaco, Little Bahama Bank, (Neumann and Land 1975)
- Lighthouse Reef, Belize, (Litter and Litter 1990)
- Looe Key, Monroe county, Florida, (Litter and Litter 1990)
- Tobago Cays, near Mayreau, Grenadines, Lesser Antilles, (Litter and Litter 1990)
- New Providence, Bahamas, (Britton & Millspaugh 1962)
- Berry Islands, Bahamas, (Britton & Millspaugh 1962)
- Great Bahama, (Britton & Millspaugh 1962)
- Garden Cay, Bahamas, (Britton & Millspaugh 1962)
- Bimini, Bahamas, (Britton & Millspaugh 1962) (Newell et al 1959)
- Exuma chain, Bahamas, (Britton & Millspaugh 1962)
- Watling’s Island (San Salvador), Bahamas, (Britton & Millspaugh 1962) (Marshall 1980)
- Marigua, Bahamas, (Britton & Millspaugh 1962)
- Caicos Islands, Bahamas, (Britton & Millspaugh 1962) (Taylor 1960)
- Great Ragged Island, Bahamas, (Britton & Millspaugh 1962)
- Salt Cay, Bahamas, ( Britton & Millspaugh 1962) (Taylor 1960)
- Bermuda, ( Britton & Millspaugh 1962) (Taylor 1960)
- St David’s Island, Stow Bay, Elys Harbour on Hamilton Island, S Ireland Island, Coney Island, Ferry Reach shore of Hamilton Island, Tucker’s Town Bay and Hungry Bay, Bermuda, (Taylor and Bernatowicz 1969)
- Florida, (Britton & Millspaugh 1962) (Taylor 1960)
- S. Florida, (Woelkerling 1976)
- Guadeloupe, (Britton & Millspaugh 1962) (Taylor 1960)
- Colon, Panama, (Britton & Millspaugh 1962)
- Panama, (Taylor 1960)
- Onslow Bay, Carolinas, (Schneider 1976)
- North Carolina, (Taylor 1960)
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- East Andros Island, Bahamas, (Newell et al 1959)
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Appendix

C

Jurassic algae databases
DATABASE OF BENTHIC CALCAREOUS ALGAE FROM THE EUROPEAN JURASSIC

N.B. Algae may extend outside of the Jurassic – only occurrences in this time period are stated.

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  - Bouroullec, J. and Deloffre, R. 1970

- Cardesse 1, Aquitaine (France)
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  - Bouroullec, J. and Deloffre, R. 1970

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  - Golonka, J. 1970b

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  - Bernier, P. 1968

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- Murches and Espichel, Lusitanian basin (Portugal) Portlandian B. Ramalho, M.M. 1971d

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- Facho, Lusitanian Basin (Portugal) Portlandian. Ramalho, M.M. 1971d

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- Languedoc (France)

- Velebit (Yugoslavia) Lower Lias. Jaffrezio, M. 1973b

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- Pont-de-lévenöl and pont-de-la chaux, Jura méridional, Kimmeridgian – Portlandian. Bernier, P. 1971
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- Alpes sennes (Italy)
- N. Alps (Austria)

**Heteroparella ellenbergeri**

- Languedoc (France)
- Velebit (Yugoslavia)
- Corbières (France)
- S.Pyrenees / Basque country (Spain)
- Canders, région de St. Chinian (France)

**Heteroparella fourcadei**

- St. Jean de Barrou, Corbières (France)

**Heteroparella jaffrezo**

- Jura méridional

**Heteroparella lemmensis**

- Jura (France)
- Puig Campana and Cabezón de oro, Alicante (Spain)
- Jura méridional
- Bijuesca, Sierra del Madero (NW Spain)
- Arroyo Cerezo, Sierra del Madero (NW Spain)

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**Carpathians**

Oxfordian – Kimmeridgian

**Hettangian**

**Sinemurian**

**Lower Lias**

**Sinemurian**

Upper Sinemurian

**Kimmeridgian – Portlandian**

**Upper Kimmeridgian – lower Portlandian**

**Upper Jurassic**

**Upper Kimmeridgian – Portlandian**

**Upper Kimmeridgian**

**Tithonian**

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1989a

Bassoulet, J.P. et al. 1978

Bassoulet, J.P. et al. 1978

Bassoulet, J.P. et al. 1978

Peybernès, B. 1979

Jaffrezo, M. 1979

Jaffrezo, M. and Benest, M. 1975

Bernier, P. 1984

Bassoulet, J.P. et al. 1978

Granier, B. 1986

Bernier, P. 1984

Wnendt-Juber, E. 1990

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**Likanelia** \textit{bartheli}  

- Bavaria (Germany)  
  - Kimmeridgian – Portlandian / Tithonian.  
  \hspace{1cm} Flaviani, A.  
  \hspace{1cm} 1983  
  \hspace{1cm} Bassoulet, J.P. et al.  
  \hspace{1cm} 1978  
  \hspace{1cm} Bernier, P.  
  \hspace{1cm} 1971

- Coupe de la Balme (Belley, Jura, France)  
  - Kimmeridgian.  
  \hspace{1cm} Bernier, P. and Gaillard, C.  
  \hspace{1cm} 1980

- Cluse-des Hôpitaux, Ain, Jura méridional (France)  
  - Portlandian.  
  \hspace{1cm} Bernier, P.  
  \hspace{1cm} 1979a

- Barrage de Vouglans, S. Jura méridional (France)  
  - Bernier, P.  
  \hspace{1cm} 1978

- Jura méridional  
  - Upper Kimmeridgian – Portlandian.  
  \hspace{1cm} Bernier, P.  
  \hspace{1cm} 1984  
  \hspace{1cm} Jaffrezo, M.  
  \hspace{1cm} 1973b  
  \hspace{1cm} Wnendt-Juber, E.  
  \hspace{1cm} 1990

- Noviercas, Aguilon and Cédillas, Sierra del Madero (NW Spain)  
  - Tithonian.  
  \hspace{1cm} Wnendt-Juber, E.  
  \hspace{1cm} 1990

- Jaulin and Arroyo Cerezo, Sierra del Madero (NW Spain)  
  - Kimmeridgian – Portlandian.  
  \hspace{1cm} Bernier, P. and Gaillard, C.  
  \hspace{1cm} 1979

- Vouglans Dam and Cluse de la Balme, Jura (France)  
  - Portlandian.  
  \hspace{1cm} Azema, J. and Jaffrezo, M.  
  \hspace{1cm} 1972

**Likanelia** \textit{sp.}  

- Puig Campana (Province of  
  - Portlandian.  
  \hspace{1cm} Azema, J. and Jaffrezo, M.  
  \hspace{1cm} 1972
Linoporella? buseri
- Julian Alps (Yugoslavia)
- Aurunci Mtn., Lazio (Italy)

Linoporella capriotica
- Capri (Italy)

Linoporella kapelensis
- Mt. Velika Kapela, Dinaric alps (Yugoslavia)

Linoporella lucasi
- Alpes fanes and fosses, Dolomites (Italy)

Linoporella? suilajensis
- Mt. Suilaja, Dalmatia (S. Croatia)
- Medziharjels and Povazsky Chimec, Cachticke Karpaty mtns and

Alicante, Spain
- Ghimbav Massif, E. Carpathians

Upper Oxfordian – Kimmeridgian.
Dragastan, O. 1989a

Lower – middle Lias.
Bassoullet, J.P. et al. 1978

Lower Sinemurian.
Chiocchini et al. 1979

Tithonian.
Bassoullet, J.P. et al. 1978

Jaffrezo, M. 1973b

Portlandian.
Bassoullet, J.P. et al. 1978

Bassoullet, J.P. et al. 1978

Kimmeridgian
Bassoullet, J.P. et al. 1978

Bassoullet, J.P. et al. 1978

Kimmeridgian – Portlandian.

Malm.
Bassoullet, J.P. et al. 1978

Upper Oxfordian.
Bassoullet, J.P. et al. 1978

Tithonian / Portlandian
Sokac, B. and Nikler, L. 1973

Sinemurian
Bassoullet, J.P. et al. 1978

Cros, P. and Lemoine, M. 1966 & 1967

Upper Jurassic.
Sokac, B. and Velic, I. 1976

Kimmeridgian – Tithonian.
Sotak, J. and Misik, M. 1993
Stramberg, W. Carpathians (E. Czech.)

- Astileu, NE of Padurea Criului mtns, N. Apuseni Tithonian. Dragastan, O. 1989a

**Linoparella taurica**
- Crimea (USSR) Kimmeridgian. Jaffrezo, M. 1973b
- Argelliers, Languedoc (France) Portlandian. Jaffrezo, M. 1979

**Lithoparella cayeuaxia**
- Rieutord, Languedoc (France) Upper Portlandian. Jaffrezo, M. 1979

**Lithoparella sp.**
- West of Sesimbra (Portugal) Portlandian. Ramalho, M.M. 1971a
- Aquitaine (France)

Macroparella embergeri
  - Cap d'Espichel (Portugal) Kimmeridgian - Portlandian. Canérrot, J. 1979
- Baysère 1 and Mimizan 1, Aquitaine (France)
- Olmedo (N.W. Sardinia)

Macroparella espichelensis
- Sondage Courtion (Switzerland) Portlandian. Bassoulet, J.P. et al. 1978
- Cap Espichel (Portugal)
- W of Sezimbra (Portugal)
- Jura Mid to Bernier, P.
Macroporella gigantea

- Le Méjanel / Roc Blanc and Cagnasse (Les Oliviers), Languedoc (France)
- Upper Kimmeridgian - upper Portlandian

Macroporella pygmaea

- Le Méjanel / Roc Blanc and Cagnasse, Languedoc (France)
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Macroporella praturloni

- Bicaz gorge, Hagimass mtns, E. Carpathians (Romania)
- Upper Tithonian
- Cachtice Karpaty mtns and Stramberg, W. Carpathians (E. Czech.)
- Upper Kimmeridgian - lower Tithonian

Macroporella retica

- Dolomites (Italy)
- Lower Sinemurian
- Austria
- DACHSTEINKALK. Hettangian - upper Sinemurian
- Alpes méridionales, dolomites, Lombardi (Italy)

Macroporella sellii

- Velebit, Slovenia (N.W. Yugoslavia)
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- S. Italy
- Lower - Mid
- **Aurunci, Ernici, Simbruini and Lepini Mtns., Lazio (Italy)**
  - Jaffrezo, M. 1973b
- **Marsica (Italy)**
  - Callovian lower Kimmeridgian.
  - Jaffrezo, M. 1973b

**Macroparella sp. (?)**

- Southern Latium – Abruzzi (central Apennines, Italy)
  - Mid – upper Lias.
  - Praturlon, A. 1966
- **Macroparella sturi**
  - Préjano (Spain)
  - Mid Sinemurian.
  - Dragastan, O. and Trappe, J. 1986
- **Megaparella sp.**
  - Kotouc and Obecni Lom quarries, Cachticke Karpaty mtns and Stramberg, W. Carpathians (E. Czech.)
  - Upper Tithonian.
  - Sotak, J. and Misik, M. 1993

**Milanovicella momciliana**

- Porches section, central Algarve (Portugal)
  - Portlandian.
  - Granier, B. and Berthou, P-Y. 1994

**Montenegrella florifera**

- Barrage de Vouglands, and Cerin, S. Jura meridional (France)
  - Portlandian.
  - Bernier, P. 1978c
- **Munieria baconica**
  - Southern Upper
  - Praturlon, A.
Myrmekioporella mosana
Neomizziella elongata

Neoteutoporella gallaeformis a

Neoteutoporella socialis a

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*Palaeodasycla barrabei dus*
- Ile de Chios (Greece)  Liassic  Bassoulet, J.P. et al 1978
- Dinarides (Yugoslavia)  Bassoulet, J.P. et al 1978
- Central Appenines (Italy)  Bassoulet, J.P. et al 1978
- Dolomites (Italy)  Sinemurian lower Lotharingian
- Julian Alps (Yugoslavia)  Lower and middle Liassic  Bassoulet, J.P. et al 1978
- Corbières (France)  Lower and middle Liassic  Bassoulet, J.P. et al 1978
- Corbières (France)  Sinemurian lower Lotharingian
- Forage de Gimont 1 (SPG) and carotte number 14 at 1939m and Echantillon de terrain AG282 and Laramendy and Arbaïlles, Aquitaine (France)  Upper Sinemurian  Carozzi, A.V. et al 1972
- Aurunci Mtn., Lazio (Italy)  Upper Sinemurian  Chiocchini et al 1979
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Palaeodasycla mediterraneus
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- Southern Latium – Mid – upper Praturlon, A. Lias.
  Abruzzi (central Sartoni, S. and Apennines, Crescenti, U. Italy) 1959
- Caserta Bassoulet, J.P. (Italy) et al. 1978
- Majorca Bassoulet, J.P. (Spain) et al. 1978
- Andalousia Bassoulet, J.P. (Spain) et al. 1978
- Beotia Bassoulet, J.P. (Greece) et al. 1978
- Marsica Jaffrezo, M. (Italy) 1973b
- Betic Bassoulet, J.P. cordillera et al. 1978 (Spain)
- Epire– Bassoulet, J.P. Lias. et al. 1978
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- Salerno Bassoulet, J.P. (Italy) et al. 1978
- Simi Bassoulet, J.P. (Greece) et al. 1978
- Taurus Bassoulet, J.P. (Turkey) et al. 1978
- Sabina Cros, P. and (Italy) Lemoine, M. 1967
- Velebit Bassoulet, J.P. (Yugoslavia) Sinemurian et al. 1978 –
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| **St. Germain-de-Joux, Jura, France**                         |               | Bernier, P. 1984  |
| **Cluse-des Hôpitaux, Ain, Jura méridional (France)**         |               | Bernier, P. and Gaillard, C. 1979 |
| **Jura méridional**                                          |               |                  |
| **Armix, Jura (France)**                                     |               |                  |

<p>| <strong>Haute Jura (France)</strong>                                      |               |                  |
| <strong>Laufon (France)</strong>                                          |               |                  |
| <strong>Stramberg (Austria)</strong>                                      |               |                  |
| <strong>Geneva (Switzerland)</strong>                                     |               |                  |</p>
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### Pianella **gigantea**

- **Grand Saleve (France)**  
  Sequanian / Portlandian.  
  Jaffrezo, M. 1973b
- **Dinarides (Yugoslavia)**  
  Upper Malm.  
  Jaffrezo, M. 1973b
- **Causses (France)**  
  Lower Portlandian.  
  Jaffrezo, M. 1973b
- **Dijon (France)**  
  Upper Oxfordian.  
  Jaffrezo, M. 1973b
- **Southern Latium – Abruzzi (central Apennines, Italy)**  
  Upper Malm.  
  Praturlon, A. 1966
  Jaffrezo, M. 1973b

### Pianella **grudii**

- **Dinarides (Yugoslavia)**  
  Upper Kimmeridgian.  
  Radoicic, R. 1970
- **Montenegro (Yugoslavia)**  
  Kimmeridgian – Portlandian.  
  Jaffrezo, M. 1973b
- **Calabria (Italy)**  
  Portlandian.  
  Jaffrezo, M. 1973b
- **Marsica (Italy)**  
  Upper Malm.  
  Jaffrezo, M. 1973b
- **Velebit (Yugoslavia)**  
  Middle Kimmeridgian.  
  Jaffrezo, M. 1973b

### Pianella **johnsoni**

- **Salzkammerg**  
  Kimmeridgian  
  Flügel, E. 1979
Pianella *pygmaea*

- Carpathians (Romania) - Lower Portlandian. Jaffrezo, M. 1973b
- Southern Latium - Abruzzi (central Apennines, Italy) - Upper Malm. Praturlon, A. 1966
- Dorgali (Sardinia) - Sartoni, S. 1965
- Monte Plaia and M. Rotondo, Marche-Abruzzi (Italy) - Sartoni, S. 1965
- Salzkammergut (Austria) - Kimmeridgian - Tithonian. Flügel, E. 1979
- Geneva (Switzerland) - Upper Oxfordian - Tithonian. Jaffrezo, M. 1973b
- Carpathians (Romania) - Upper Malm. Jaffrezo, M. 1973b
- Velebit (Yugoslavia) - Mid Malm. Jaffrezo, M. 1973b
- Marsica (Italy) - Upper Tithonian. Jaffrezo, M. 1973b
- Sicily (Italy) - Upper Malm. Jaffrezo, M. 1973b
- Causses (France) - Upper Kimmeridgian - lower Portlandian. Jaffrezo, M. 1973b
- Abruzzes (Italy) - Upper Tithonian. Jaffrezo, M. 1973b
- Bavaria (Germany) - Lower Malm. Jaffrezo, M. 1973b
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**Pseudoepimast jurassica opora**

- Alpes calcaires sept (Austria)
- Mts. Haghimas (Romania)
- Sulzfluh and Salzkammergut (Austria)
- Olvega and Frias, Sierra del Madero (NW Spain)
- Bicaz gorge, Hagimas mtns, E. Carpathians (Romania)
- Kotovc quarry, Stramberg, W. Carpathians (E. Czech.)

**Pseudoepimast sp. opora**

- Mimizan 1 and Antarès 2, Aquitaine (France)

**Pseudotrinocla piae dus**

- Cachticke Karpaty mtns and Stramberg, W. Carpathians (E. Czech.)
- Fagetul Ciucului Massif, E. Carpathians

**Radioiciella barthelii**

- Jura, France

**Radioiciella iailaensis**

- Crimea, U.S.S.R.

**Salpingoporella aff. annulata**

- Maciço Calcário Estremenho (Portugal)

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Kimmeridgian - Portlandian. Bassouillet, J.P. et al. 1978

Oxfordian - Tithonian. Flügel, E. 1979

Kimmeridgian. Wnendt-Juber, E. 1990

Upper Tithonian. Dragastan, O. 1981

Upper Kimmeridgian - Portlandian. Bouroullec, J. and Deloffre, R. 1970

Mid Tithonian. Sotak, J. and Misik, M. 1993

Upper Tithonian. Dragastan, O. 1989a

Kimmeridgian and Portlandian Tithonian. Granier, B. 1989a

Upper Bathonian. Azeredo, A.C. 1999
Salpingoporella annulata (= a. apenninica)

- Southern Latium – Abruzzi (central Apennines, Italy)
- Grand Salève (France)
- Calabria (Italy)
- Dorgali (Sardinia)
- Jura méridional (France)
- Istria (Yugoslavia)
- Le Méjanel / Roc Blanc / Le Luc, Languedoc (France)
- Causses (France)
- Montenegro (Yugoslavia)
- Bavaria (Germany)
- Caserta (Italy)
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- Latium (Italy)  Lias.  Jaffrezo, M.  1973b
- Velebit  Mid Lias.  Jaffrezo, M.  1973b
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- Marsica  Lias.  Jaffrezo, M.  1973b
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- Andalousia  Sinemurian.  Jaffrezo, M.  1973b
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Teutlorella gallaeformis

- External  Upper  Radoicic, R.  1965
  Dinarides, S.  Dogger and  Jaffrezo, M.  1973b
  Herzegovina,  Lower  Malm.
  (Yugoslavia)
- Velebit  Bathonian –  Jaffrezo, M.  1973b
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Teutlorella obsolenta

- Southern  Upper  Praturlon, A.  1966
  Lati um –  Malm.
  Abruzzi  (central
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  Italy)
- Savoie  Lower  Bassoullet, J.P.
  (France)  Kimmeridgian –
  (Switzerland)
- Languedoc  Portlandian /  Bassoullet, J.P.
  (France)  Tithonian.
- Czechoslovakia
- Carpathians  Upper  Bassoullet, J.P.
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- Aude  Kimeridgian –
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- Prealpes  Jaffrezo, M.  1973b
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- Dinarides  Kimeridgian –
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**Trinoclodus perplexus**
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- Pont-de-lémmem and Pont-de-la chaux, Jura méridional (France)
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- Serra da Arrábida, environs de Lisbonne (Portugal)
  Ramalho, M.M.
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- Dorgali (Sardinia)
  Upper Sartoni, S.
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- Le Méjanel / Roc Blanc and Le Luc, Languedoc (France)
  Bernier, P.
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- Grand-Colombier-de-Culoz, Ain (France)
  Bernier, P. and Enay, R. 1972

- Jura and des Grands Causses (France)
  Ramalho, M.M.
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- Calabria (Italy)
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- Cévennes (France)
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- Appenins centro – méridionaux (Italy)
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- Morella (Spain)
  Kimmeridgian.
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- Appenins méridionaux (Italy)
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- Sardinia
  Lower and mid Tithonian.
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- Istria (Yugoslavia)
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- Marche-Abruzzi (Italy)
  Jurassic.
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- Ain (France) Ramalho, M.M. 1968
- Cap d'Espichel (Portugal) Lower Portlandian. Ramalho, M.M. 1971c
- Littoral and Murches, Lusitanian basin (Portugal) Portlandian A. Ramalho, M.M. 1971d
- Tranca and Facho, Lusitanian basin (Portugal) Kimmeridgian – Portlandian A. Ramalho, M.M. 1971d

**Zergabriella embergeri**

- See *Macroporella embergeri* Granier, B. 1989b

**Zergatella sp. 1**

- Littoral, Lusitanian basin (Portugal) Portlandian A. Ramalho, M.M. 1971d
- Facho, Lusitanian basin (Portugal) Portlandian. Ramalho, M.M. 1971d
- Murches, Freixal, Monsanto and Espichel, Portlandian B. Ramalho, M.M. 1971d
Lusitanian basin
(Portugal)
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N.B. Algae may extend outside of the Jurassic – only occurrences in this time period are stated.

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| **Arabicodium anae** | • Brestnishka, Balkan Mtns.
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| **Arabicodium bicazensis** | • Suhard and Bicaz gorges, E.
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| **Arabicodium jurassicum** | • Fagetul Ciuculi Mts., Bicaz valley, E.
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| | • Codaçal and Barinha, Lusitanian basin
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**Bacinella**  
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- Liesberg and  
  Courtelle,  
  Swiss Jura  
- Cagnassee,  
  Languedoc  
  (France)  
- Roe Blanc,  
  Languedoc  
  (France)  
- Stramberg,  
  Slovakia  
  (Czechoslovakia)  

**Bacinellacodium**  
*calcareus*  
- Fagetul  
  Ciucului, E.  
  Carpathians  

**Bevocastria**  
*elliotti*  
- Fagetul  
  Ciucului, E.  
  Carpathians  

**Bevocastria**  
*ellipoidea*  
- Postavaru  
  massif, E.  
  Carpathians  
- Ghimbav  
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  Dimbovicioara  
  basin, E.  
  Carpathians  

**Bevocastria**  
*toomeyi*  
- Cetea and  
  Presaca  
  Ampoiului, S.  
  Apuseni  

**Bicajiella**  
*radiata*  
- Bicajel, Bicaz  
  gorges, E.  
  Carpathians  

**Bicasiella**  
*giuvalae*  
- Giuvala  
  Massif,  
  Dimbovicioara  
  basin, E.  
  Carpathians  
- Vinturarita  
  Massif, S.  
  Carpathians  
- Cetea hill,  
  Trascau mts,  
  S. Apuseni  

Oxfordian.  
Insalaco, E. et al 1997  
Insalaco, E. et al 1997  
Portlandian.  
Bernier, P. 1968  
Bernier, P. 1968  
Bernier, P. 1967  
Tithonian.  
Eliasova, H. 1981  
Tithonian.  
Dragastan, O. 1985  
Tithonian.  
 Dragastan, O. 1985  
Tithonian.  
Dragastan, O. 1989a  
Upper Oxfordian – Kimmeridgian.  
Dragastan, O. 1989a  
Tithonian.  
Dragastan, O. 1985  
Tithonian.  
Dragastan, O. 1988  
Tithonian.  
Dragastan, O. 1988  
Tithonian.  
Dragastan, O. 1988
**Bicasiella jurassica**
- Bicajel and Ghilicos, Bicaz gorges, E. Carpathians
- Saratii valley, Persani mtns
- Vinturarita Massif, S. Carpathians

**Bicasiella semilunata**
- Abruzzi (Italy)
- Velebit Mtn. (Yugoslavia)
- Mts. Ghilecos, E. Carpathians (Romania)
- Bulgaria

**Boueina hochstetteri**
- Olvega, Cedrillas and Losilla, Sierra del Madero (NW Spain)
- Aguilón and Belchite, Sierra del Madero (NW Spain)
- Bicaz gorge, Hagimas mtns, E. Carpathians (Romania)

**Carpathocodiu anae m**
- Renieblas, west Madero, Soria Province (N. Spain)
- Bicaz gorges, E. Carpathians
- Dealul Dreptului, Hateg-Pui, S. Carpathians

**Cayeuxia americana**
- Sulzfluh

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**Dragastan, O.**
- 1988
- Mid and upper Lias.
- Upper Tithonian.
- Kimmeridgian.
- Upper Tithonian.
- Oxfordian.
- Tithonian.
- Oxfordian –

**Bassoulet et al 1983**
- Bassoulet et al 1983
- Bassoulet et al 1983
- Bassoulet et al 1983
- Wndt-Juber, E. 1990
- Wndt-Juber, E. 1990
- Dragastan et al 1987
- Dragastan, O. 1985
- Dragastan, O. 1985
- Flügel, E. 1979
Cayeuxia anae

(Austria)

- East Carpathians (Romania)
- Salzkammergut (Austria)
- Torrecilla, Olvega, Ciria and Villar del Campo, Sierra del Madero (NW Spain)
- Aguilon, Sierra del Madero (NW Spain)
- Biecz gorge, Hagimasa mtns, E. Carpathians (Romania)

mid Tithonian. Malm. Mišik, M. 1979
Kimmeridgian - Tithonian. Flügel, E. 1979
Tithonian. Wnendt-Juber, E. 1990
Upper Tithonian. Dragastan, O. 1981

Cayeuxia (cf.) atanasini

- Maestrazgo (mid E. Spain)
- Frias and Cerdillas, Sierra del Madero (NW Spain)

Portlandian. Canérot, J. 1979
Kimmeridgian. Wnendt-Juber, E. 1990

Cayeuxia austriaca

- Sulzfluh and Salzkammergut (Austria)

Oxfordian – Tithonian. Flügel, E. 1979

Cayeuxia doerflesiana

- Ernstbrunn region (Austria)

Tithonian. Kamptner, E. 1951

Cayeuxia kurdistanensis

- Le Méjanel / Roc Blanc, Languedoc (France)
- Jaén area, Nueva Carteya 1, S.Cordoba, Andalousia (Spain)

Portlandian. Bernier, P. 1968
Upper Sinemurian. Deloffre, R. 1972
- Aquitaine (France)  
  Upper Sinemurian  
  Oxfordian – lower Kimmeridgian.  
  Carozzi, A.V. et al 1972

- Maestrazgo (mid E. Spain)  
  Portlandian.  
  Canérot, J. 1979

- Sulzfluh (Austria)  
  Oxfordian – mid Tithonian.  
  Flügel, E. 1979

- Gimont 1, Aquitaine (France)  
  Upper Oxfordian.  
  Bouroullec, J. and Deloffre, R. 1970

- Coupe du Sudou, Coupe du Mont Sacon and Auch 1, Aquitaine (France)  
  Kimmeridgian.  
  Bouroullec, J. and Deloffre, R. 1970

- Meillon 1, Bordes 1 and Coupe du Col d’Espadres, Aquitaine (France)  
  Portlandian.  
  Bouroullec, J. and Deloffre, R. 1970

- Antarès 2, Aquitaine (France)  
  Portlandian A.  
  Ramalho, M.M. 1971d

- Littoral, Lusitanian Basin (Portugal)  
  Oxfordian – mid Tithonian.  
  Flügel, E. 1979

Cayeuxia *mediterranea*  
- Sulzfluh (Austria)  
  Upper Malm.  
  Praturlon, A. 1966

Cayeuxia *moldavica*  
- Southern Latium – Abruzzi (central Apennines, Italy)  
  Bathonian.  
  Fischer, J.C. 1969

- Martigny, Any -Martin-Rieux,
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| Le Méjanel /
Roc Blanc,
Languedoc
(France) | Portlandian | Bernier, P. | 1967 |
|          |               | Bernier, P. | 1968 |
| E. Carpathians | Upper Jurassic | Frollo, M.M. | 1938 |
| Bicaz valley,
Carpathians | Kimmeridgian –
Portlandian. | Dragastan, O. | 1968a |
| Ostrów and
Celiny,
Swietokrzyskie
Mts.(Poland) | Astartian
(Upper Oxfordian –
Lower Kimmeridgian).
Kimmeridgian –
Tithonian. | Dragastan, O. | 1968a |
| Salzkammergut (Austria) | Kimmeridgian –
Tithonian. | Flügel, E. | 1979 |
| Torrecilla,
Valdegutur,
Olvega,
Bijuesca,
Villar del Campo,
Soria, Ricla
and Alacon,
Sierra del Madero (NW Spain) | Kimmeridgian –
Tithonian. | Wnendt-Juber, E. | 1990 |
| Aguilon,
Sierra del Madero (NW Spain) | Kimmeridgian –
Tithonian. | Wnendt-Juber, E. | 1990 |
| Bicaz gorge,
Hagimas mtns, E.
Carpathians
(Romania) | Lower Tithonian. | Dragastan, O. | 1981 |
|          |               | Dragastan, O. |         |
### Cayeuxia nodosa

- **Rețezat mtns, Fundatura & Ciclovia, S. Carpathians** (Romania)  
  - Mid – upper Purbeck.  
  - Hudson, J.D.  
  - 1981

- **Skye, Eigg and Muck** (Northern Inner Hebrides)  
  - Lower Purbeck.  
  - Pugh, M.E.  
  - 1968

- **St. Alban’s Head, Dorset** (UK)  
  - Mid – upper Lias.  
  - Praturlon, A.  
  - 1966

### Cayeuxia piae

- **Le Méjanel / Roc Blanc, Languedoc** (France)  
  - Portlandian.  
  - Bernier, P.  
  - 1968

- **E. Carpathians**  
  - Upper Jurassic.  
  - Frollo, M.M.  
  - 1938

- **Aurières, Languedoc** (France)  
  - Bathonian.  
  - Bernier, P.  
  - 1967

- **Jaén area, Nueva Carteya 1, S. Cordoba, Andalousia** (Spain)  
  - Upper Sinemurian.  
  - Deloffre, R.  
  - 1972

- **Bicaz valley, Carpathians**  
  - Kimmeridgian – Portlandian.  
  - Dragastan, O.  
  - 1968a

- **Aquitaine** (France)  
  - Upper Sinemurian and Oxfordian – lower Kimmeridgian.  
  - Carozzi, A.V. et al 1972

- **Forage de Gimont 1** (SPG) and carotte number 14 at  
  - Sinemurian.  
  - Carozzi, A.V. et al 1972

  - Bouroulec, J. and Deloffre, R. 1970
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<td>Catalanides and Maestrazgo (mid E. Spain)</td>
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<td>Coupe du Sudou, Coupe du Mont Sacon and Auch 1, Aquitaine (France)</td>
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<td>Meillon 1, Bordes 1 and Coupe du Col d’Espadres, Aquitaine (France)</td>
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<td>Antarès 2, Aquitaine (France)</td>
<td>Portlandian</td>
<td>Bouroullec, J. and Deloffre, R. 1970</td>
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<td>Portlandian A.</td>
<td>Ramalho, M.M.</td>
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<td>Barreiro, Lusitanian basin (Portugal)</td>
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<td>Facho, Lusitanian basin (Portugal)</td>
<td>Upper Oxfordian – Kimmeridgian.</td>
<td>Ramalho, M.M.</td>
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<td>Corfu</td>
<td>Lower Jurassic.</td>
<td>Boudagher-Fadel et al</td>
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<td>Central Appenines (Italy)</td>
<td>Hettangian-Sinemurian.</td>
<td>Boudagher-Fadel et al</td>
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<td>Balearic islands (Spain)</td>
<td>Lower Jurassic.</td>
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<td>Ramalho, M.M.</td>
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<td>Echantillon de terrain PM941 and coupe du Sudou, Aquitaine (France)</td>
<td>Upper Oxfordian.</td>
<td>Azeredo, A.C. and Ramalho, M.</td>
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<td>Cortiçal, Maciço Calcário Estremenho,</td>
<td>Lower Bathonian.</td>
<td>Azeredo, A.</td>
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<td>Lusitanian Basin (Portugal)</td>
<td>1993</td>
<td>Bernier, P. and Gaillard, C.</td>
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<td>Vouglaux Dam and Molinges, S. Jura meridional (France)</td>
<td>Kimmeridgian–Portlandian.</td>
<td>Bernier, P. 1979</td>
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<td>Moesian platform (Romania)</td>
<td>Tithonian.</td>
<td>Dragastan, O. 1981</td>
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<td>Liesberg and Courtelle, Swiss Jura</td>
<td>Oxfordian.</td>
<td>Insalaco, E. et al 1997</td>
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<td>Bois du parc, Burgundy (France)</td>
<td>Lower Purbeck.</td>
<td>Pugh, M.E. 1968</td>
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<td>Isle of Portland, Dorset (UK)</td>
<td>Upper Jurassic.</td>
<td>Jaffrezo, M. 1974</td>
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<td>M. Morrone di Pacentro, Marche-Abruzzi (Italy)</td>
<td>Lower Kimmeridgian.</td>
<td>Carozzi, A.V. et al 1972</td>
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<td>Forage de Bordes 1 and carotte number 7 at 5524.70m, Aquitaine (France)</td>
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<td>Pieniny Cordillera, Pieniny Klippen belt, Slovakia</td>
<td>Lower Malm.</td>
<td>Mišik, M. 1979</td>
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<td>West of Sesimbra (Portugal)</td>
<td>Lower Portlandian.</td>
<td>Ramalho, M.M. 1971a</td>
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<td>Aldealpozo, west Madero, Soria</td>
<td>Oxfordian.</td>
<td>Dragastan et al 1987</td>
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**Cladocoropsis mirabilis**
Province (N. Spain)

- Cap d'Espichel (Portugal)
  Lower Portlandian.
  Ramalho, M.M. 1971c

- Monte Tuttavista (E. Sardinia)
  Portlandian.
  Azéma, J. et al. 1977
<table>
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<th>Genus</th>
<th>Species</th>
<th>Location</th>
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<td>Consinocodium</td>
<td>japonicum</td>
<td>• Salzkammergut (Austria)</td>
<td>Kimmeridgian – Tithonian.</td>
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<td>• Bavaria (Germany)</td>
<td>Upper Jurassic.</td>
<td>Bassoullet et al 1983</td>
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<td>• Meuse (France)</td>
<td>Upper Oxfordian.</td>
<td>Maubeuge, P.L. 1950</td>
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<td>Enigma</td>
<td>parvissima</td>
<td>• Stramberg, Slovakia (Czechoslovakia)</td>
<td>Tithonian.</td>
<td>Eliasova, H. 1981</td>
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<tr>
<td>Eothrix</td>
<td>alpina</td>
<td>• Majorca (Spain)</td>
<td>Tithonian.</td>
<td>Colom, G. 1948</td>
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<td>Fagetiella</td>
<td>angulata</td>
<td>• Fagetul Ciucului Bicaz gorges and Postavaru Massif, E. Carpathians</td>
<td>Tithonian.</td>
<td>Dragastan, O. 1988</td>
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<td>• Vinturarita Massif, S. Carpathians</td>
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<td>Dragastan, O. 1988</td>
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<td>Garwoodia</td>
<td>bardosi</td>
<td>• Ghilcos, E. Carpathians</td>
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<td>Dragastan, O. 1985</td>
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<td>Garwoodia</td>
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<td>Garwoodia</td>
<td>fluegeli</td>
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<td>Dragastan et al 1987</td>
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<td>• Lapos valley, Bardos massif, Bicaz gorges, E. Carpathians</td>
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<td>Garwoodia</td>
<td>maxima</td>
<td>• Bucegi mtns, E. Carpathians</td>
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• Cetea hill, Trascau mtns, S. Apuseni

Dragastan, O. 1989b
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| Garwoodia  | polytomica | • Bicajel, Bicaz gorges, E. Carpathians
         |         | • Vinturalita massif, S. Carpathians                                      | Tithonian.   | Dragastan, O. 1989a |
|            | simplex | • Albioara hill, Padurea Craiului mtns, N. Apuseni                      | Tithonian.   | Dragastan, O. 1989a |
|            | toomeyi | • Postavaru massif, Giuvala massif Dâmbovicioara basin and Bicajel Bicaz gorges, E. Carpathians
<pre><code>     |         | • Mateias massif, S. Carpathians                                        | Tithonian.   | Dragastan, O. 1989a |
</code></pre>
<p>|            |         | • Ghimbav massif, Dâmbovicioara basin, E. Carpathians                    | Kimmeridgian. | Dragastan, O. 1989a |
| Girvanella | jurassica | • Bicaz gorge, Hagimas mtns, E. Carpathians (Romania)                   | Lower Tithonian. | Dragastan, O. 1981 |
|            | minuta  | • Celiny and Sobków, Swietokrzyskie Mts.                                | Astartian (Lower Kimmeridgian). | Golonka, J. 1970b |
|            |         | • S. Tiago dos velhos (Portugal)                                        | Lower Tithonian. | Leinfelder, R.R. and Werner, W. 1993 |
|            |         | • Consolação (Portugal)                                                 | Kimmeridgian. | Leinfelder, R.R. and Werner, W. 1993 |
|            | sp.     | • Bois du parc, Burgundy                                                | Oxfordian.   | Insalaco, E. et al 1997 |
|            |         | • Liesberg and Courtèlle, Swiss Jura                                     | Basal        | Brown, P.R.  |</p>
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<td>Azerêdo, A. 1993</td>
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<td>Bernier, P. 1967</td>
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<td>Maciço Calcário Estremeno (Portugal)</td>
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<td>Azeredo, A.C. 1999</td>
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<td>Sulzfluß and Salzkammergut (Austria)</td>
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<td>Flügel, E. 1979</td>
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<td><em>iliasica</em></td>
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- Franconian Alps, Bavaria (Germany)
- Rarau basin, Romania
- Bucegi Mts. and Barat region (Romania)
- Majorca (Spain)
- Marche-Abruzzi (Italy)
- East Carpathians
- Southern Latium – Abruzzi (central Apennines, Italy)
| **Hedstroemia** | **bifilosa** | **Tithonian.** | Dragastan, O. 1989a |
| **Hedstroemia** | **exiguua** | **Tithonian.** | Dragastan, O. 1989a |
| **Hedstroemia** | **hansi** | **Tithonian.** | Dragastan, O. 1989a |
| **Hedstroemia** | **humili** | **Tithonian.** | Dragastan, O. 1989a |
| **Hedstroemia** | **jurassica** | **Tithonian.** | Dragastan, O. 1989a |
| **Hedstroemia** | **klausi** | **Kimmeridgian – Tithonian.** | Dragastan, O. 1989a |
| **Hedstroemia** | **moldavica** | **Tithonian.** | Dragastan, O. 1985 |
| **Hedströemia** | **orientalis** | Bicajel Bicaz gorges and Postavaru massif, E. Carpathians | Tithonian. | Dragastan, O. 1989a |
| **Hedströemia** | **pilifera** | Cetea hill, Trascau mtns, S. Apuseni | Tithonian. | Dragastan, O. 1989a |
| **Hedströemia** | **racasensis** | Racas, Padurea Craiului mtns, N. Apuseni, Giuvala massif, Dîmbovicioara basin, E. Carpathians | Kimmeridgian – Tithonian. | Dragastan, O. 1989a |
| **Hedströemia** | **ramulosa** | Ghimbav massif, Dîmbovicioara basin, E. Carpathians | Upper Oxfordian – Kimmeridgian. | Dragastan, O. 1989a |
| **Hedströemia** | **solida** | Vinturarita Massif, S. Carpathians | Tithonian. | Dragastan, O. 1989a |
| **Hedströemia** | **teres** | Ghimbav massif, Dîmbovicioara basin, E. Carpathians | Kimmeridgian. | Dragastan, O. 1989a |
| **Hedströemia** | **zonata** | Giuvala massif, Dîmbovicioara basin, E. Carpathians | Tithonian. | Dragastan, O. 1989a |
| **Hedströemia** | **sp.** | Stairhole, Lulworth Cove, Dorset(UK), Dolomites (Italy) | Lower Purbeck. | Pugh, M.E. 1968 |
|  |  |  | Inferior Lias. | Cros, P. and Lemoine, M. 1967 |
**Hikocodium fertilis**
- Bicaz gorge, Haghimias Mtns, E. Carpathians (Romania)
- Lower Tithonian. Dragastan, O. 1981

**Hormathonema sp.**
- Aldealpozo, west Madero, Soria Province (N. Spain)
- Upper Kimmeridgian. Dragastan et al 1987

**Juraella bifurcata**
- Jura méridional
- Upper Oxfordian – upper Kimmeridgian. Bernier, P. 1984

**Koskinobullina socialis**
- N. Spain
- N.W. Sardinia (Italy)
- Valverde and Vale de Ventos, Lusitanian basin (Portugal)
- Upper Bathonian. Azerêdo, A. 1993
- Abrigo, Lusitanian basin (Portugal)
- Upper Bathonian – Callovian. Azerêdo, A. 1993
- Torrecilla, Bijuesca, Soria, Ricla, Aguilon, Jaulin, Losilla and Frías, Sierra del Madero (NW Spain)
- Belchite, Sierra del Madero (NW Spain)
- Arroyo Cerezo, Sierra del Madero (NW Spain)
- Tithonian. Wnendt-Juber, E. 1990
**Leckhamptonella llewellyae**
- Leckhampton, Cheltenham, Gloucestershire, Aalenian, Elliott, G.F. 1982

**Lithocodium aggregatum**
- Southern Latium – Abruzzi (central Apennines, Italy), Upper Malm, Praturlon, A. 1966
- Vale de Travelho, Lusitanian basin (Portugal), Callovian, Azerêdo, A. 1993
- Barinha, Casal Velho and Cabeça Gorda, Lusitanian basin (Portugal), Lower Bathonian, Azerêdo, A. 1993
- Vale de Ventos and Portela das Salgueiras, Lusitanian basin (Portugal), Upper Bathonian, Azerêdo, A. 1993
- M. Rotondo, Marche-Abruzzi (Italy), Upper Malm, Crescenti, U. et al. 1969
- Catalanides and Maestrazgo (mid E. Spain), Upper Kimmeridgian – Portlandian, Canérot, J. 1979
- Salzkammergut (Austria), Upper Kimmeridgian – Tithonian, Flügel, E. 1979
- Olvega and Losilla, Sierra del Madero (NW Spain), Kimmeridgian, Wnendt-Juber, E. 1990
- Littoral, Lusitanian Basin, Upper Kimmeridgian, Ramalho, M.M. 1971d
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<td>Ramalho, M.M.</td>
<td>1971d</td>
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**Lithocodium** *morikawai*  
- Southern Latium – Abruzzi (central Apennines, Italy)  
  Upper Malm.  
  Praturlon, A.  
  1966  
- Sulzfluh and Salzkammergut (Austria)  
  Oxfordian – Tithonian.  
  Flügel, E. 1979  
- Olvega, Bujuesca, Belchite and Frias, Sierra del Madero (NW Spain)  
  Kimmeridgian.  
  Wnendt-Juber, E. 1990

**Lithocodium** *sp.*  
- Bois du parc, Burgundy  
  Oxfordian.  
  Insalaco, E. et al 1997  
- Liesberg and Courtélie, Swiss Jura  
  Dogger.  
  Peybernès, B. 1979  
- Coupe de Cerin (Belley, Jura, France)  
  Kimmeridgian.  
  Bernier, P. and Gaillard, C. 1980
  
- Le Méjanel / Roc Blanc, Languedoc (France)  
  Portlandian.  
  Bernier, P. 1968

**Lithophyllum?** *maslovi*  
- Ota (Portugal)  
  Upper Oxfordian – Kimmeridgian.  
  Leinfelder et al 1988

**Marinella** *lugeoni*  
- Southern periphery of the  
  Kimmeridgian – Oxfordian.  
  Golonka, J. 1970
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<td>Wnendt-Juber, E. 1990</td>
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<td>Maestrazgo and N. Castilla la Nueva (mid E. Spain)</td>
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<td>Wnendt-Juber, E. 1990</td>
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<td>Ricla, Aguilon and Losilla, Sierra del Madero (NW Spain)</td>
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<td>Arroyo Cerezo, Sierra del Madero (NW Spain)</td>
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<td>Murches and Monsanto,</td>
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Lusitanian basin (Portugal)  Portlandian – Purbeck. Ramalho, M.M. 1971d

- Barreiro, Lusitanian basin (Portugal)
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<td>Mercierella</td>
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<td>americana</td>
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<td>aff. ramosus</td>
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<td>Praturlon, A. 1966</td>
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<td>Niteckiella</td>
<td>flabelliformis</td>
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<td>Albioara hill, Padurea Craiului mtns, N. Apuseni</td>
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<td>Dragstan, O. 1988</td>
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<td>Ortonella</td>
<td>lemoineae</td>
<td>Ghilcos, E. Carpathians</td>
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<td>Ortonella</td>
<td>robusta</td>
<td>Fagetul Ciucului, Bicaz gorges and Guivala massif, Dimbovicioa</td>
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<td>Dragstan, O. 1989b</td>
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ra basin, E.
Carpathians
Ortonella *sp.*
- Worbarrow Tout (Dorset)  
- Mupe and Worbarrow bays, Dorset(UK)  
- Alacon, Sierra del Madero (NW Spain)
- Basal Purbeck.  
- Lower Purbeck.  
- Kimmeridgian.  
- Brown, P.R. 1964  
- Pugh, M.E. 1968  
- Wnendt-Juber, E. 1990

Otternstella *jaffrezo*i
- Porches, central Algarve (Portugal)  
- Portlandian.  
- Granier, B. and Berthou, P-Y. 1994

Palaeosiphonit*us* *convolens* m
- Daglingworth quarry, Cirencester, Gloucestershire (UK)  
- Fowlers Hill, Quenington (UK)  
- Upper Bathonian.  
- Elliott, G.F. 1985

Parachaetetes *discoidale*
- Bijuesca, Villar del Campo, Talveila, Aguilon, Belchite and Losilla, Sierra del Madero (NW Spain)  
- Kimmeridgian.  
- Wnendt-Juber, E. 1990

Parachaetetes *jurassica*
- Molinges, Jura (France)  
- Kimmeridgian – Portlandian.  
- Bernier, P. and Gaillard, C. 1979

Parachaetetes *sp.*
- Southern Latium – Abruzzi (central Apennines, Italy)  
- Southern Latium – Abruzzi (central Apennines, Italy)  
- Dogger and Malm  
- Praturlon, A. 1966

Paraortonella *getica*
- Ghilicos, E. Carpathians  
- Tithonian.  
- Dragastan, O. 1985

Paraortonella *richteri*
- Bucegi mtns and Bicaz gorges, E. Carpathians  
- Ghilicos, E.  
- Tithonian.  
- Dragastan, O. 1988  
- Dragastan, O.
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<th><em>Permoiccalus</em></th>
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<td><em>Permoiccalus</em></td>
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<td>Neuberg, Bavaria (Germany)</td>
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<td>Schlangintweit, F. and Ebli, O.</td>
<td>1997</td>
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<td><em>Permoiccalus</em></td>
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<td>West of Sesimbra (Portugal)</td>
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<td>Murches, Espichel and Facho, Lusitanian Basin (Portugal)</td>
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<td>1971d</td>
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<td>1971d</td>
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<td>Monsanto and Barreiro, Lusitanian Basin (Portugal)</td>
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| *Pseudochaetetes* | *champagnensi* | Lomont, Jura (France) | Upper Oxfordian. | Firtion, F. and Schneider E. | 1958 |
**Pseudocodium convolvens**

- Southern Latium – Abruzzi (central Apennines, Italy)

Dogger and Malm. Praturlon, A. 1966

**Pseudohedrostromia spongiosa**

- Giuvala massif, Dimboviciao basin, E. Carpathians

Tithonian. Dragastan, O. 1989a

**Pseudolithocodium carpathicum**

- Aguilon, Belchite and Cerdillas, Sierra del Madero (NW Spain)

Kimmeridgian. Wnendt-Juber, E. 1990

**Pycnoporidium (cf.) lobatum**

- Skye, Eigg and Muck (Northern Inner Hebrides)
- Southern periphery of the Swietokrzyskie Mts. (Poland)
- Salzkammergut (Austria)
- Soria, Sierra del Madero (NW Spain)
- Arroyo Cerezo, Sierra del Madero (NW Spain)

Kimmeridgian – Oxfordian. Golonka, J. 1970a

Mid-Upper Purbeck. Hudson, J.D. 1970


Tithonian. Wnendt-Juber, E. 1990

**Pycnoporidium sp.**

- Skye, Eigg and Muck (Northern Inner Hebrides)

Mid-Upper Purbeck. Hudson, J.D. 1970

**Rajkaella bartheli**

- Neuberg, Bavaria (Germany)


**Rivularia atanasivi**

- Villar del

Oxfordian. Dragastan et al
Campo, west and upper 1987
Madero, Kimmeridgi an.
Soria
Province (N. Spain)

- Bicaz gorges, Tithonian. Dragastan, O.
  E.
  Carpathians 1985
<p>| <strong>Rivularia</strong> | <strong>carpathica</strong> | • Bicaz gorges, E. Carpathians | Tithonian. | Dragastan, O. 1985 |
| <strong>Rivularia</strong> | <strong>dianae</strong> | • Piatra Craiului, E. Carpathians | Tithonian. | Dragastan, O. 1985 |
| <strong>Rivularia</strong> | <strong>lissaviensis</strong> | • Villar del Campo, west Madero, Soria Province (N. Spain) | Oxfordian and upper Kimmeridgian. | Dragastan et al 1987 |
| • Fagetul Ciucului, Bicaz gorges and Piatra Craiului massif, E. Carpathians | Tithonian. | Dragastan, O. 1985 |
| <strong>Rivularia</strong> | <strong>moesica</strong> | • Villar del Campo, west Madero, Soria Province (N. Spain) | Upper Kimmeridgian. | Dragastan et al 1987 |
| • Fagetul Ciucului, E. Carpathians | Tithonian. | Dragastan, O. 1985 |
| <strong>Rivularia</strong> | <strong>piae</strong> | • Bicajel, Bicaz gorges, E. Carpathians | Tithonian. | Dragastan, O. 1988 |
| <strong>Rivularia</strong> | <strong>pumili</strong> | • Giuvala Massif, Dimbovicioara basin, and Bicajel, Bicaz gorges, E. Carpathians | Tithonian. | Dragastan, O. 1988 |
| <strong>Rivularia</strong> | <strong>tadeuszi</strong> | • Bicajel, E. Carpathians | Tithonian. | Dragastan, O. 1985 |
| <strong>Rivularia</strong> | <strong>theodori</strong> | • Saratii valley and Persani mtns, E. Carpathians | Oxfordian. | Dragastan, O. 1985 |
| • Bicaz gorges, E. Carpathians | Tithonian. | Dragastan, O. 1985 |
| <strong>Rothpletzella</strong> | <strong>jurassica</strong> | • Celiny, | Upper | Golonka, J. |
| Scotlandella | alpina | Sobków and Sokolów, Swietokrzyskie Mts. (Poland) | Oxfordian - Kimmeridgian. | 1970b |
| Scotlandella | nodosa | Bicaz gorges, E. Carpathians | Tithonian. | Dragastan, O. 1985 |
| Solenopora | (cf.) condensata | Skye, Scotland | Purbeckian. | Dragastan, O. 1985 |
| Solenopora | jurassica | Marinha, Lusitanian basin (Portugal) | Lower Bathonian. | Azeredo, A. 1993 |
| | | Maciço Calcário Estremenho (Portugal) | | Azeredo, A.C. 1999 |
| | | Talveila, Frias and Casas de Bucar, Sierra del Madero (NW Spain) | Kimmeridgian. | Wnendt-Juber, E. 1990 |
| | | Jaulin, Sierra del Madero (NW Spain) | Tithonian. | Wnendt-Juber, E. 1990 |
| | | Malton, Yorkshire (U.K.) | Upper Oxfordian. | Lemoine, P. 1928 |
| | | Foss cross Quarry Chedworth, Gloucestershire | Mid-Upper Bathonian. | Brown, A. 1894 |
| | | Chémery, Ardennes (France) | Dogger. | Harland, T.L. and Torrens, H.S. 1982 |
| | | Pyrenees (Navarro - Languedoc) | | Wright, V.P. 1985 |
| | | Besancon region | Upper Oxfordian. | Brown, A. 1894 |
| | | | | Lemoine, P. 1928 |
| | | | | | Fischer, J.C. 1969 |
| | | | | | Peybernès, B. 1979 |
| | | | | | Rollet, A. and Rollet, M. 1959 |</p>
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<th>jurassica var. lingoesis</th>
<th>Langres plateau (France)</th>
<th>Lower Bajocian.</th>
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<td>Solenopora</td>
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<td>Praturlon, A. 1966</td>
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<td><strong>Solenopora</strong></td>
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<td><strong>Solanoporella</strong></td>
<td>sp.</td>
<td><strong>Sympleca</strong> (Girvanella)</td>
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<td>Portlandian.</td>
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<td>Basal Purbeck.</td>
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<td>Flügel, E.</td>
<td>1979</td>
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<td><strong>Upper Oxfordian.</strong></td>
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<td>Fremy, P. and Dangeard, L.</td>
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*Note: Meanings and references are based on the order of presentation.*
**Tethysicodium** *wrayi*

- Lisieux region (France)
- Fagetul Ciucului, E. Carpathians
- Vinturarita, S. Carpathians
- Southern Latium – Abruzzi (central Apennines, Italy)
- West of Sesimbra (Portugal)
- Slovenia (N.W. Yugoslavia)
- Coupe de la Balme and Coupe de Cerin, Belley, Jura (France)
- Le Méjanel / Roc Blanc and Cagnasse, Languedoc (France)
- Grand-Colombier-de-Culoz, Ain (France)
- Dinarides, Yugoslavia
- Lumezzane valley, Brescia, Lombardy (Italy)
- Vale de Travelho, Lusitanian

**Thaumatoporella** *parvovesiculifera*

- lower Kimmeridgian.
- Tithonian. Dragastan, O. 1985
- Draganst, O. 1985
- Mid – upper Lias.
- Praturlon, A. 1966
- Boudagher-Fadel et al 2001
- Portlandian.
- Ramalho, M.M. 1971a
- Oxfordian – lower Kimmeridgian.
- Buser, S. and Ogorelec, B. 1981
- Bernier, P. and Gaillard, C. 1980
- Portlandian.
- Bernier, P. 1968
- Bernier, P. and Enay, R. 1972
- Upper Kimmeridgian.
- Cassinis, G. 1971
- Callovian.
- Azeredo, A. 1993
basin (Portugal)
- Penedos Negros, Lusitanian basin (Portugal)
- Mendiga, Cabeça Gorda and Barhina, Lusitanian basin (Portugal)
- Cortiçal, Lusitanian basin (Portugal)
- Valverde, Portela das Salgueiras and Vale de Ventos, Lusitanian basin (Portugal)
- Le Luc, Languedoc (France)
- Jaén area, Nueva Carteya 1, S.Cordoba, Andalousia (Spain)
- Estrons de la Vieille, Corbières (France)
- West Carpathian mountains
- Serra da Arrábida, environs de Lisbonne (Portugal)

Bajocian – Azerêdo, A. 1993
Bathonian. 1993
Lower Bathonian. 1993
Upper Bathonian. 1993
Portlandian. Bernier, P. 1967
Upper Sinemurian. Deloffre, R. 1972
Upper Jurassic. Jaffrezo, M. 1974
Malm. Mišik, M. 1979
Kimmeridgian – Ramalho, M.M. 1968
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<td>Aquitaine (France)</td>
<td>Oxfordian – lower</td>
<td>Carozzi, A.V. et al</td>
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<td>Maciço Calcário Estremenho (Portugal)</td>
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<td>Villar del Campo, west Madero, Soria Province (N. Spain)</td>
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<td>Sulzfluhr and Salzkammergut (Austria)</td>
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<td>Ricla, Alacon, Ejulve and Frias, Sierra del Madero (NW Spain)</td>
<td>Kimmeridgian.</td>
<td>Wnendt-Juber, E.</td>
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- Belchite, Sierra del Madero (NW Spain)  
  Kimmeridgian – Tithonian.  
  Wndt-Juber, E. 1990

- Cardesse 1, Aquitaine (France)  
  Upper Oxfordian – lower Kimmeridgian.  
  Bouroullec, J. and Deloffre, R. 1970

- Bordes 1, Cieutat 1, Meillon 1, Tournay 1, Antares 2 and Baysère 1, Aquitaine (France)  
  Lower Kimmeridgian.  
  Bouroullec, J. and Deloffre, R. 1970

- Monte Tuttavista (E. Sardinia)  
  Portlandian.  
  Azéma, J. et al. 1977

- Molinges, Landaize and Cluse de la Balme, Jura (France)  
  Kimmeridgian – Portlandian.  
  Bernier, P. and Gaillard, C. 1979

- Littoral, Lusitanian basin (Portugal)  
  Upper Kimmeridgian – Portlandian.  
  Ramalho, M.M. 1971d

- Murches, Lusitanian basin (Portugal)  
  Portlandian A – Purbeck.  
  Ramalho, M.M. 1971d

- Monsanto, Lusitanian basin (Portugal)  
  Kimmeridgian.  
  Ramalho, M.M. 1971d

- Barreiro, Lusitanian basin (Portugal)  
  Upper Oxfordian.  
  Ramalho, M.M. 1971d

- Espichel, Lusitanian basin (Portugal)  
  Portlandian A.  
  Ramalho, M.M. 1971d

- Tranca, Lusitanian basin  
  Upper Oxfordian – Kimmeridgian  
  Ramalho, M.M. 1971d

- Corfu Lias. Boudagher-Fadel et al 2001

- Alicante Portlandian. Granier, B. 1986
(Spain) Upper Azéma, J. et al. 1977

- Monte Albo Kimmeridgian. Azéma, J. et al. 1977
(E. Sardinia) Portlandian.

- Monte Tuttavista (E. Sardinia) Oxfordian – Flügel, E. 1979

- Sulzfluh and Salzkammergut (Austria) Tithonian. Dragastan, O. 1989a

- Ghimbav Massif, Dimbocioara Basin, E. Carpathians Tithonian.

- Czorsztyn series – Klippen Belt (Czechoslovakia) Upper Jurassic. Dragastan, O. and Mišik, M. 1975

- West Carpathian mountains Oxfordian. Mišik, M. 1979

**Colour key:**

**Blue** = Cyanobacteria

**Red** = Red

**Green** = Halimedaceae (Udoteaceae)

**Pink** = Incertae sedis / microproblematica

**Yellow** = Gymnocodiaceae