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Paleoenvironmental Significance of *Celleporaria* (Bryozoa) from Modern and Tertiary Cool-water Carbonates of Southern Australia

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ABSTRACT

Certain members of the bryozoan genus *Celleporaria* form large, erect colonies of hollow branches (~10–30 cm tall and 1–3 cm diameter). These are common and conspicuous in Pleistocene and Cenozoic neritic strata of the southern margin of Australia. Most of these basins are characterized by decimeter-scale cycles through subtidal, heterozoan, cool-water, carbonate sediments. Several intervals are further characterized by pervasive celleporarid bryozoan thickets (10–30 cm thick), individual units of which can be traced for many tens of kilometers.

Study of modern, live celleporarid bryozoans from the continental shelf of the Great Australian Bight (GAB), Pleistocene celleporarid mounds stranded below the shelf break of the Australian margin, and Miocene celleporarid thickets from the Murray and Torquay Basins indicates that *Celleporaria* thickets form under specific environmental conditions: i.e., low-energy or sub-swell wave-base settings, mud-silt substrate, medium-high mesotrophy, and moderate sedimentation rate. These conditions, however, are not site specific. They are manifested here in two different environmental settings: (1) a deep-water (>200 m), upwelling nutrient source, below the shelf break during extreme sea-level low stands; and (2) shallow-water (<50 m), terrestrial nutrient source, in embayments, far inland from the shelf break during relative high stands of sea-level.

The celleporarid growth habit (species specific—not an ecomorph) allows their populations to proliferate in spatially restricted, transitional, geologically short-lived environments where most other bryozoans cannot cope. Their environmental sensitivity means that *Celleporaria* have great potential for paleoenvironmental analysis of Cenozoic carbonate Tethyan sediments.

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INTRODUCTION

Large colonies of the Bryozoa *Celleporaria* (commonly misidentified as *Cellepora*) are characteristic and distinguishing components of many Tertiary limestones distributed along the southern margin of Australia (Fig. 1). These large, multilaminar, hollow-cylindrical bryozoans, with branches reaching 3 cm in diameter (Figs. 2, 3), commonly form thickets or biostromes up to 30 cm in height. Despite their characteristic morphology, abundance, and routine documentation in the field, the paleoecology and paleoenvironmental significance of *Celleporaria* are not well understood. Discovery of living and non-living colonies of *Celleporaria* with this distinctive growth habit found off the southwestern Australian shelf (Fig. 1, label "I") provides insight into their modern ecology, and helps to evaluate the paleoenvironmental significance of those within the onshore Tertiary limestones. These findings also may have significance for the Cenozoic Tethyan forms found in southern Europe and northern Africa (Spjeldnaes and Moissette, 1997).

The primary goal of this paper lies in identifying the environmental parameters that control the distribution of the large, multilaminar, hollow-cylindrical *Celleporaria*. This paper documents (1) growth habit characteristics of *Celleporaria*, (2) distribution of *Celleporaria* in modern shelf environments, (3) distribution of Miocene *Celleporaria*-rich limestones in the Murray and Torquay basins of southeastern Australia, and (4) the significance of *Celleporaria* with respect to specific environmental parameters governing their distribution.

CELLEPORARIA (LEPRALIELLIDAE, CHEILOSTOMATA)

Taxonomy

Celleporaria is a common and diverse genus with a global distribution of over 120 fossil and living described species. Species of *Celleporaria*, as a whole, exhibit many different colonial growth forms and have broad ecological preferences and tolerances. The traditional growth-form descriptor "celliporiform" (Canu and Bassler, 1920) refers to their massive, multilaminar, pustulose nature, and encompasses a variety of colony shapes ranging from encrusting, to massive, nodular, and erect branching (the "nodular-arborescent" form of Bone and James, 1993). The morphological plasticity and complexity of ontogenetic variation among celleporarid

zooids make their taxonomy challenging. Detailed taxonomic study is not, however, a goal of this paper (see Appendix).

This paper is concerned with a limited group of erect, multilaminate, hollow-branching celleporarids (Fig. 2) with the following growth habit characteristics (nomenclature of Hageman et al., 1998): an erect, rigid contiguous colony, originally cemented to a fistulose sponge substrate (mature colonies may resume upright growth after having been toppled or partially degenerated). Branches are thick (macroserial), but undifferentiated (nonmaculate, without specialized regions on the colony for excurrent feeding chimneys). Branches consist of multiple layers of zooids (multilaminate) formed by an irregular, pustulose arrangement of zooids growing directly on top of each other (frontal-budding). Branches are cylindrical, but hollow, as a result of growth around an ephemeral organic substrate. Branch segments are straight, with frequent bifurcations in more than one plane. Branches anastomose and fuse, forming a three-dimensional box-work in mature colonies (Fig. 3A, 3D); however, branches never bud laterally, but are always continuous with a hollow growing edge. Structural support is achieved by the stacking of thin-walled zooecia, instead of by the more common process within various bryozoan taxa of secreting a thickened extra-zooidal skeleton. The modern taxa relevant to this paper are illustrated in Fig. 4, and briefly described in the Appendix.

Within this paper, as a matter of convenience, the name *Celleporaria* refers only to the closely related species group (e.g., *Celleporaria oculata*, *C. fusca*, *C. gambierensis*, and a number of undescribed species) that exhibits a specific erect, hollow-branching growth habit. Most Australian fossil specimens of this group are designated as *Celleporaria gambierensis*, although there are clear differences among Eocene, Oligo–Miocene, and Quaternary forms. These specimens are similar to, but different than *C. palmata*, which forms thickets in the Pliocene of the Mediterranean (Spjeldnaes and Moissette, 1997).

Frontal Budding

Most cheilostomatid bryozoans grow new zooids only along a proximal perimeter of the colony (growing edge or front). However, several groups of bryozoans have developed the ability to form new individuals by budding them from the surface of the colony. This evolutionary breakthrough (derived independently in several clades) allows colonies to grow in a fundamentally different manner than their ancestors (Banta, 1972; Rider and Cowen, 1977; Lidgard and Jackson, 1989). *Celleporaria* is even more specialized because its frontally budded zooids do not originate from a single parent zooid (Lidgard, 1985). This results in a rather haphazard, pustulose arrangement of actively feeding zooids at multiple levels (newly budded and partially overgrown) at the surface (Fig. 4). Frontal budding allows for rapid occupation of

three-dimensional space. The thin zooecial walls, which display minimal secondary thickening, combined with the pustulose growth (Fig. 2B–C) result in a volumetrically large, structurally competent, colony form with a minimal investment in skeletal resources.

Celleporarid colonies grow by frontal budding and overgrowth of otherwise viable zooids on their surface. Instead of producing several generations of polypides in an individual zooecium before abandoning the zooecium, *Celleporaria* occupy more space with their available resources. Although antecedent layers of zooids lose contact with their exterior environment when they are overgrown, communication pores connect them with the rest of the colony (Lidgard, 1985). This pathway (funiculus) allows for nutrient regression during periods of environmental stress (Cummings, 1975).

Thus, specialized budding and growth have allowed species of *Celleporaria* to grow into some of the largest bryozoan colonies ever reported. For example, on jetty piles in the Gulf of St. Vincent and Spencer Gulf of South Australia, modern *Celleporaria* grow into heads up to one meter in diameter (12 years of observed growth from clean piles; Gowlett-Holmes, pers. comm., 2002), similar to modern bryozoan reefs described from New Zealand (Bradstock and Gordon, 1983). They also grow as 20–50 cm diameter caps and domes in the Oligo–Miocene limestones from the Murray Basin, South Australia.

Colony Growth Habit

Celleporaria grow in three-dimensional anastomosing box-works (Fig. 3A, 3D). This is an uncommon growth habit for bryozoans, but also is observed in some modern forms such as erect schizoporellids (Chenal du Teychan, Bassin d'Archechon, France, ~8 m water depth), *Parasmittina fistulata* from Western Australia (8 km SSE of Cape Bellefin from within 3-m-deep sandy bottom channels with *Posidonia* and *Laurencia*), and *Parasmittina solenasmioides* and *Thalamoporella novaehollandiae* from Cox's Peninsula near Palmerston, Northern Territory, Australia. All of these sites are in relatively protected settings.

This three-dimensional anastomosing box-work growth allows for colonies to escape from their primary substrate, with subsequent generations structurally supported above the substrate by earlier ones (i.e., self-supporting framework). This allows for growth in a setting surrounded by fine, unconsolidated sediment with continuous accumulation. An interpretation of an environment with significant sediment supply is also supported for *Celleporaria* by the abundance of unusually large and abundant spatulate avicularia (Fig. 4B–D), which are believed to be used to clean fine sediment from the colony surface (Rider and Cowen, 1977). Presence of large spatulate avicularia appears to be an inducible characteristic, because otherwise apparently conspecific colonies may or may not display large avicularia on their surface,

suggesting presence or absence at different times during a single colony's developmental history.

CELLEPORARIA FROM THE SOUTHERN AUSTRALIAN MARGIN (QUATERNARY)

Materials and Methods

The distribution of Quaternary (living and relict) erect branching *Celleporaria* was investigated from the southern Australian continental shelf (Fig. 1, label "I"). Sea-floor samples were collected using an epibenthic sled (15 cm gape). Live material was sorted on ship, with representative collections preserved in 70% EtOH. Bulk sediment samples were washed and sieved in the laboratory. Every celleporarid specimen (living or dead) was removed and closely examined for each of the 139 bulk sediment samples from the Great Australian Bight (GAB) (Figs. 1 and 5). A less-detailed survey was made of celleporarids from all 218 bulk sediment samples from the Lincoln and Lacepede Shelves (Fig. 1, label "II"). The volume of original bulk sediment samples was not standardized, but was sufficient to characterize presence/absence of *Celleporaria* at each sample station (0 to ~40 specimens per sample).

Geographic and Environmental Distribution within Region I: The Great Australian Bight and Southwestern Australia

A survey of zooecial characteristics for *all* celleporarid bryozoan specimens regardless of growth habit (e.g., encrusting, massive, and erect) from the GAB sample sites (Figs. 1 and 5), suggests that the hollow-erect, branching growth habit is taxonomically determinate (i.e., a colony form generated by a species that does not grow in any other growth habit). That is, these unusual growth habits are not the result of some common bryozoan that exhibits widespread ecophenotypic plasticity. Only certain species of *Celleporaria* (differentiated by zooecial characteristics) were restricted to a hollow-erect, branching growth-form similar to those of the southern Australian Tertiary basins. Unlike most of the other dozen or so celleporarid species present in the GAB study area, these specific taxa were never found as encrusting, or as poorly developed solid erect branching growth forms. All of these specimens from the GAB (living, dead, relict) were found in varying abundance as isolated, non-fused colonies, suggesting that they were not growing in thickets or mounds on the shelf.

Live, hollow-erect branching *Celleporaria* colonies (fragments 7–10 cm) were recovered from seven sample sites (Figs. 5 and 6). Each of the seven *Celleporaria* colonies was found growing on single digits of *Oceanapia* sp.—a living, pink, fistulose sponge (Fig. 2A). In some cases, the

sponge extended beyond the branch of the mature celleporarid. In other cases, the bryozoan had outgrown the sponge, but retained a hollow central cavity for structural stability. Similar growth habits have been described for recent Mediterranean celleporarids on sponges, gorgonians, and serpulid worm tubes (Pouyet, 1973; Moissette and Pouyet, 1991).

Most of these live colonies were sampled between a water depth of 140 to 160 m (Figs. 5A and 6), although several were recovered from shallower sites (GAB-130 and GAB-135) at ~100 m. These depths are near but below the level of local swell wave base (~130 m). The swell wave base is the water depth below which a hydrodynamic condition exists where sediment is not regularly reworked by waves (swells) generated by distant storms on the open ocean (James et al., 1992; James et al., 1997). No live colonies were recovered from the shallow, wave-swept, inner to middle shelf.

Non-living hollow-erect branching *Celleporaria* colonies were recovered from 16 localities (Figs. 5–6). It is difficult to determine the absolute age of non-living bryozoan skeletons on this shelf based on appearance alone. In general however, relict specimens (long dead or exhumed) are identified as those that are highly abraded, encrusted, and stained (usually gray rather than the brown staining of shoreward samples). Relict specimens were collected from outer-shelf to upper-slope environments in depths ranging from ~180 to 350 meters. Dead, but apparently not relict, colonies are locally abundant and have a similar to slightly shallower depth distribution to those of the living colonies (~90–170 m; Figs. 5A and 6).

Geographic and Environmental Distribution within Region II: Shelf Edge of Central Southern Australia

Comprehensive examination of *Celleporaria* specimens was not possible throughout the Otway, Bonney, Lacepede, and Lincoln Shelves due to sample availability, but relevant information can be obtained from published summaries of sediment distributions (James et al., 1992; Boreen et al., 1993; James et al., 1997, 2001). The distribution of hollow, cylindrical *Celleporaria* on the shelf in these regions is similar to that described here for the GAB, except for the thickets (mounds?) of *Celleporaria* described off of the shelf edge at ~250–450 m (James et al., 1992; Boreen et al., 1993; James et al., 1997). Specimens from these thickets yielded Late Pleistocene ages (13,760 to 21,210 ybp) through C¹⁴ dating (James et al., 1992; Bone and James, 1993; Boreen et al., 1993; James et al., 1997). These correspond to “Facies CC-Coral-Celleporaria Facies” of James et al. (2001, fig. 10) from the GAB; “Facies 5: Shelf edge bryocoral biostrome” of James et al. (1997) of the Lincoln Shelf; and parts of “Facies 4A and 9: Robust bryozoan muddy sand” of James et al. (1992) and Boreen et al. (1993) from the

Lacepede Shelf and Otway Shelf, respectively. Biogenic sediment in these *Celleporaria* thickets is multigenerational, representing accumulation from the late Pleistocene to Recent (James et al., 1997; James et al., 2001). The following provides a generalized description of the sediments from *Celleporaria* thicket facies across the shelf by volume: >50% bryozoans (conspicuous large *Celleporaria*, moderate to low diversity of other erect branching and fenestrate forms, delicate and articulated branching and articulated zooidal forms); ~10% benthic foraminifera; ~5% planktic foraminifera; ~10% mollusks, mainly gastropods and scaphopods; ~10% other bioclasts including abundant ostracodes; ~15% calcareous mud plus siliceous sponge spicules; locally abundant ahermatypic scleractinian and stylasterine corals growing on substrates of relict *Celleporaria* (James et al., 1992; Boreen et al., 1993; James et al., 1997; James et al., 2001).

Similarly, isolated biogenic mounds and mound complexes are observed across the western region of the southern margin of the GAB, in water depths of 200–350 m, located just below the shelf margin break Feary and James, 1995; Hine et al., 2000; Bone and James, 2002). These mounds have been dated (C^{14}) at 14,000–26,000 ybp (James et al., 2000). Although not currently active (draped by several meters of carbonate mud), the mounds had up to 20–40 m of relief on the sea floor as imaged on seismic profiles (Hine et al., 2000, fig. 2). Mounds with such relief are unknown from Tertiary limestones exposed on shore.

Associated Bryozoan Species Richness at the Shelf Edge

The modern shelf of southern Australia is characterized by abundant and diverse bryozoan fauna. It is not uncommon to recover more than 70 bryozoan species from a small sediment sample of the mid- to outer-shelf (Hageman et al., 1996; Bock and Hageman, unpublished data). These high-diversity settings are in water depths well below maximum swell wave base. The outer shelf has higher nutrient richness, but nutrient levels are still toward the oligotrophic side of the spectrum (Li et al., 1996a, 1996b).

It is difficult to estimate the species richness within the shelf-edge Pleistocene thickets/mounds at the time of their formation because the relict *Celleporaria* skeletons are covered with many bryozoans (encrusting and erect) that may have lived among the growing thickets, or may have colonized the skeletons post mortem. In addition, a portion (significance unknown) of the coarse- to very-coarse grained bioclasts, representing a diversity of bryozoans, could be expected to have originated in more shallow water and transported off the shelf onto and filling the thickets (James et al., 2000; James et al., 2001). Although *Celleporaria* are volumetrically dominant, Bone and James (2002) reported a diverse bryozoan fauna (> 70 genera) associated with buried Pleistocene mounds below the GAB shelf.

DISCUSSION OF GREAT AUSTRALIAN BIGHT *CELLEPORARIA*

The patterns observed from the GAB, Lacedpede, and Lincoln Shelves raise several questions. Why are modern, live *Celleporaria* colonies rare, and found as isolated colonies, but generally restricted to a depth range of 140 to 165 m? Why are Late Pleistocene, relict *Celleporaria* colonies found in abundant thickets at much greater water depth and why are most deep-water GAB *Celleporaria* (180–350 m) relict forms? Why are many recently dead *Celleporaria* bioclasts found in moderately shallow water depths (90–165 m)? These questions can be addressed by evaluating the environmental parameters that control the distribution of Quaternary *Celleporaria* in this setting.

The approach taken here was to develop a history of the area based on the correlation of (1) oxygen isotope data (Chappell and Shackleton, 1986), (2) foraminiferal proxies for environments (Table 1), and (3) sedimentological data (James et al., 1992, 1997). These data were used to develop a paleoenvironmental history of the region regarding (1) sea level, (2) ocean currents, and (3) nutrient levels (Table 2). These events can be summarized as a late Pleistocene, glacially driven, sea level low-stand resulting in a mixed water column with more variable nutrient levels, at times eutrophic. The Holocene is represented by a transgression to an interglacial sea level high-stand, resulting in a more stratified water column, with more stable, oligotrophic nutrient levels.

Subsequent to establishing this paleoenvironmental history, the distribution of *Celleporaria* was plotted in both time (using C^{14} age dates) and space within this proposed paleoenvironmental model (Table 2). Several physical and biological parameters are of ecological importance to *Celleporaria* in this environmental model, and are discussed below.

Swell Wave Base

The distribution of modern and late Pleistocene *Celleporaria* on the modern southern Australian shelf is strikingly correlated with swell wave base water depths (~ 130 m in this setting, Fig. 7A). The swell wave base here is unusually deep relative to the world average, resulting from the close proximity of the exceptionally high seas derived from the extensive fetch of the circum-Antarctic Southern Ocean.

Using a sea level curve for the Pleistocene at this setting (Fig. 8) derived from oxygen isotope data (Chappell and Shackleton, 1986) and the known (modern) water depth from which each

specimen was collected, actual water depths during the Pleistocene can be estimated for any specimen (i.e., water depth at which relict colonies originally grew). Three C^{14} dates for relict celleporarid specimens found in thickets off of the Lincoln Shelf are 21,210 ybp, 19,250 ybp, and 14,400 ybp (James et al., 1997). At each of these times, sea level was much lower than it is today. Thus, a 14,400 year old specimen collected in situ from 250 to 300 meters water depth would have grown in a setting with sea level 90 meters lower than today. Therefore, the original water depth in which the colony grew would have been between 160–200 m (Fig. 8). The same calculations can be made for the other two dated, relict specimens. These late Pleistocene mounds initially formed in water depths of 160 to 229 m (Fig. 8). Note that this is deeper than present day swell wave base, but likely reflects a deeper swell wave base than would be expected from a narrow shelf setting (Hageman et al., 1996). The fact that some live *Celleporaria* and many recently dead bioclasts were found in shallower water (90–140 m) may also reflect the fact that maximum swell wave depth is a function of the shelf physiography (width and slope), shape of the coast line, and magnitude and fetch of storms (Hageman et al., 1996).

Nutrients

The movement and exchange of large-scale water masses of variable physical properties (temperature, salinity, and nutrients) are well-documented oceanographic phenomena (Schahinger, 1987; James et al., 1997). However, during high sea level stands, the incursion of stratified water masses from deep ocean onto the shelf are more commonly associated with poorly circulated, rather than nutrient-rich, water masses (Caron and Holmwood, 1983). Upwelling and mixing of water masses on the southern Australian shelf are generally associated with outer shelf during lower sea level stands (Almond et al., 1993; James et al., 2000).

Relict *Celleporaria* mounds are positioned in the place of present-day upwelling currents, just off of the shelf break (Lewis, 1981; Schahinger, 1987; Wells and Okada, 1996). This setting is presently mesotrophic (Li et al., 1996a, 1996b) and would likely have been even more nutrient-rich during the Pleistocene low sea level stand due to increased upwelling and mixing (Tables 1 and 2, Fig. 7B) (Caron and Homewood, 1983; Almond et al., 1993). Although *Celleporaria* abundance is apparently not the equivalent of a true eutrophic apex taxon, their presence as thickets and mounds is correlative to times of higher nutrient conditions. Celleporarid growth strategy is apparently one of efficient, opportunistic utilization of resources when resources are present (r-mode).

The contrast between late Pleistocene and modern conditions on the shelf is enhanced by the fact that hypersaline, nutrient-poor waters develop on the present-day inner shelf of the GAB

and produce unproductive down-welling zones (Hine et al., 2000; James et al., 2000). More sample localities across the continental shelf have evidence of dead *Celleporaria* (sub-recent to relict?), in excess of the number of sample localities with living colonies (Fig. 6). This distribution may reflect a time of more widespread, higher productivity relative to present conditions after/during sea level rise, but before establishment of hypersaline, nutrient-barren, down-welling currents (James et al., 2001).

Sedimentation Rate

Growth-habit characteristics of *Celleporaria* are well suited for life in unconsolidated sediment. Their potential for rapid growth from a self-constructed foundation and specialized avicularia for shedding sediment suggest that *Celleporaria* can survive in environments of relatively continuous sedimentation (i.e., during thicket formation in the late Pleistocene). James et al. (2000) documented surprisingly high sedimentation rates during the Pleistocene, with wave abrasion transporting sediment off the shelf, resulting in Quaternary sediment wedges hosting *Celleporaria* rich mounds. Concomitant bryozoans in these settings are frequently found using *Celleporaria* as a substrate.

Summary of *Celleporaria* and the Quaternary History of the Southern Australian Margin

During the late Pleistocene, approximately 28,000–13,000 ybp, sea level was low (Figs. 7B and 8). *Celleporaria* formed mounds and thickets in upwelling zones just below the shelf edge across much of the southern margin (Fig. 7B).

Sea level rise during the late Pleistocene transgression (~12,000 ybp) may have occurred in relatively rapid pulses (Hanebuth et al., 2000), which would account for a rapid shutdown in thicket formation. Evidence for repeated formation of upper-slope *Celleporaria* mounds throughout the Pleistocene can be observed in ODP seismic and core data (James et al., 2000).

As sea level rose, *Celleporaria* migrated onto the shelf, presumably remaining below maximum swell wave base. Abundant, dead *Celleporaria* skeletons are scattered on the mid- to outer shelf (Figs. 5, 6, and 7A), which may reflect a time of more favorable, higher nutrient levels on the shelf.

On the modern mid- to outer shelf, the establishment of an oligotrophic nutrient regime (Figs. 7A and Table 2) and regional down-welling of high-saline, low-nutrient water limit the development of *Celleporaria*. Development of *Celleporaria* thickets on the shelf may be possible only in absence of these conditions.

This distribution through space and time allows for development of a predictive model for environmental distributions of *Celleporaria*.

MIOCENE *CELLEPORARIA* THICKETS OF SOUTHERN AUSTRALIA (TERRESTRIAL NUTRIENTS SOURCES?)

Most of the Cenozoic basins along the southern margin of Australia contain *Celleporaria*-bearing limestones. Several basins possess limestones and marls with an abundance of *Celleporaria* so profuse that they form decimeter-scale thickets, or bafflestones. These *Celleporaria*-rich units are conspicuous in that they share characteristics among basins, including lithological composition, associated fauna, and meter-scale packaging. Assuming an actualistic application of uniformitarianism, the factors that control the distribution of Quaternary *Celleporaria* outlined above can be used to interpret the paleoenvironments of these Tertiary basins. However, one is immediately struck by how far inland many of these occurrences are from the continental shelf break. These great distances (exceeding 300 km) raise questions for upwelling as the sole control for nutrient levels on epeiric carbonate ramps (Lukasik et al., 2000).

Murray Basin, South Australia

Setting and Materials

The western Murray Basin (Fig. 1) was the site of a large, shallow inland sea measuring 450,000 km² throughout the early Neogene (Ludbrook, 1957, 1958, 1961). The thin (<150 m) sequence of Early to Middle Miocene fossiliferous silty limestones and calcareous clays represent generally low-energy deposition on a vast epeiric ramp: a very low-angle to flat-topped platform of several 100's of kilometers extent (Lukasik et al., 2000). Rocks are exposed along the River Murray in South Australia for nearly 180 km, offering detailed lithostratigraphic correlation of units (Lukasik and James, 1998).

Fauna of the Oligo–Miocene Murray Basin sediments were surveyed from dozens of measured sections outlined in Lukasik and James (1998). The majority and best-developed *Celleporaria*-rich strata are contained within the Miocene Glenforslan Formation, although less-well-developed *celleporariid*-bearing units occur within the overlying Cadell and Bryant Creek formations. A type-reference section of these units (6.4 km S of Morgan) was analyzed in detail for this study (Figs. 1 and 9A, label “III”) (Ludbrook, 1958; Lukasik and James, 1998, section 9). Stratigraphic bulk samples collected every 0.5 m from the Glenforslan through Bryant Creek

formations were washed and picked for Bryozoa. These strata of the Morgan Group (Lukasik and James, 1998) comprise a 22–25 m upward-shallowing depositional cycle (Fig. 10A) of basal cellarid bryozoan and serpulid worm tube grainstones passing rapidly upward into fossiliferous floatstones and rudstones possessing an abundant and diverse bryozoan fauna, including *Celleporaria* (Glenforslan Formation). Diversity within these *Celleporaria*-rich limestones decreases as they are intercalated with muddy, molluscan floatstones of the Cadell Formation (maximum low-stand). These molluscan floatstones are in turn overlain by transgressive, interbedded clays and molluscan—*Marginopora* rudstones of the Bryant Creek Formation (Lukasik and James, 2000).

Paleoenvironmental Distribution of Murray Basin *Celleporaria*

The interpretation of this sequence is one of an offshore to nearshore gradation of facies deposited under progressively higher trophic resources and turbidity in shallowing waters (Lukasik et al., 2000). The *Celleporaria* limestones of the Glenforslan Formation represent deposition under low-energy, sunlit conditions of a low to high mesotrophic regime. As these units built towards the relatively high mesotrophic to eutrophic units of the overlying Cadell Formation, they became progressively less diverse in bryozoans while becoming more abundant in infaunal molluscs and the large photosymbiont-bearing foraminifer *Marginopora* (Fig. 10A). It is in these upper Glenforslan Formation beds, where the *Celleporaria* limestones are intercalated with the muddier, molluscan Cadell Formation facies, that *Celleporaria* form bafflestones created by thickets of a three-dimensional box-work structure correlatable across an outcrop distance of 70 km.

Terrestrially Derived Nutrient Model for Murray Basin *Celleporaria*

Celleporaria beds of the Miocene Murray Basin (Fig. 3C) are found ~300 km inland from the shelf edge (Figs. 1 and 9A). In addition, the basin is partially barred from the continental shelf by a series of granitic islands/shoals approximately 120 km inboard of the shelf edge. In this setting, *Celleporaria* developed mostly during a regression prior to a low stand (Fig. 10A). Water depth of this setting is estimated to be several tens of meters. It would seem virtually impossible to call upon upwelling of ocean waters to provide increased nutrients to this setting. Instead, it is likely that the increase in nutrients was derived from terrestrial sources brought into the system by rivers from the surrounding terrestrial highlands.

Thus, these celleporarid limestones occurred at approximately 20 m water depth within the transition between slightly deeper (~50 m), more oligotrophic carbonate deposition and very shallow (few meters deep) subtidal sea grasses to sand flats (Lukasik et al., 2000).

Other Tertiary *Celleporaria*-Rich Units of Southern Australia

Cyclic, sub-meter-scale hard bands of *Celleporaria* alternating with clays or marls occur in many of the Cenozoic basins along the southern margin of Australia (Fig. 3A). In other units through the Tertiary, concentrations of *Celleporaria* can be observed as incipient beds in cycles of the same scale. Colonies are near their life position (not a lag) and represent early stages of incomplete thicket development.

Well-developed, cyclic *Celleporaria* beds are documented in the Early Miocene “*Cellepora*” Beds of the Torquay Group of the Otway Basin in Victoria, Australia (Raggatt and Crespin, 1955; Reeckmann, 1979; Abele, et al., 1988; Webb, 1995; Boreen and James, 1995; Van der Linden, 1997). These cyclic units are of the same scale as those recognized by Li et al. (2003) in the Upper Oligocene Jan Juc Formation and Puebla Clay Formation, which are stratigraphically immediately below the “*Cellepora*” Beds Member, and are likely associated with fourth order Milankovitch cycles (Li et al., 2003).

Testing the Model: Nutrient Source for Torquay “*Cellepora*” Beds?

Two potential sources of nutrients that are required for *Celleporaria* thickets to develop have been established: (1) upwelling from deep water and (2) terrestrial runoff source in shallow water. The Torquay “*Cellepora*” Beds can be used as a test case to evaluate paleoecological reconstructions based on the ecological criteria derived from the modern southern Australian shelf and Miocene Murray Basin for deep- versus shallow-water *celleporarid* thicket formation. An understanding of the temporal succession of environments involved in the (apparently) continuous deposition of the Puebla Formation and units above (Fig. 10B) will provide more information for paleoenvironmental interpretation than will the characteristics of the Puebla Formation alone. Therefore, the transition from the underlying Puebla Clay into the “*Cellepora*” Beds, and finally into the overlying Zeally and Yellow Bluffs limestones, is presented here.

The traditional interpretation of the sequence is of an overall regression starting with the Puebla Clay (30 m thick) deposited in deep water on the outer to middle shelf below storm wave base (Reeckmann, 1979; Abele et al., 1988; Webb, 1995; Boreen and James, 1995). Foraminifera indicate that the depositional environment of the Puebla Clay was a variable low-oxygen, high-nutrient setting (Li et al., 2003). The interpretation for the depositional setting for the “*Cellepora*” Beds (25 m thick) has varied from shallow marine, inner shelf, 40–60 m (Reeckmann, 1979; M. Warne, unpub. data in Webb, 1995; Beatty et al., 1998), to deep marine, >100 m (Boreen and James, 1995). The deep-water interpretation used the Pleistocene deepwater *celleporarid* thickets off the southern Australian shelf edge as an analog. The overlying Zeally Limestone (25 m thick) is a cross-bedded, bryozoan grainstone with abundant fragments of echinoids, brachiopods, pectinids, and quartz grains (Webb, 1995; Boreen and James, 1995). The Zeally

Limestone has been interpreted as having been deposited in a shallow-water, high-energy, inner-shelf environment (Webb, 1995; Boreen and James, 1995).

This interpretation of an overall regression during deposition of the Puebla Formation from outer-shelf deep water to inner-shelf shallow water presents a problem for interpretation of nutrient supply. If the source is upwelling from a deep ocean, the current must cross 120 km of the continental shelf from the shelf break into the Torquay sub-basin during the relative sea level low stand (Fig. 9B).

An alternative interpretation, proposed here, is that the Puebla Clay was deposited in relatively shallow water in a protected (Stach, 1936) inner-shelf setting, rather than mid-outer shelf. The Puebla Clay was deposited under moderately high sedimentation rate, with some terrestrial input (Fig. 10B). As sea level fell, the "*Cellepora*" beds formed in a setting just below swell wave base, but close enough to the shore to raise the nutrient level to high mesotrophic levels from terrestrial runoff sources. Evidence for a relatively shallow-water inner shelf during deposition of the Puebla Clay, at the beginning of an overall third order regression, is supported by the following evidence.

Flora and Fauna

The Puebla Clay, which directly overlies an erosional unconformity with the Jan Juc Formation, is a gray, clayey, calcareous silt (Webb, 1995) with stringer beds of fragmented (but not abraded) bioclasts (lags of storm wash?) dominated by molluscs. For this study, a survey was made of a single 250-mg bulk sample, collected ~20 m above the base of the formation at Jan Juc Beach, Victoria. The sediment was washed and sieved. The greater than 0.5 mm size fraction includes the following key taxa indicative of near-shore, calm-water, moderately high sedimentation rates: (1) common, well-preserved, encrusting coralline red algae (melebisoid), with a morphology suggesting an epiphytic habit on other shallow-water algae or sea-grass hosts (Abbott and Hollenberg, 1976); (2) common, semi-infaunal bivalve *Pinna* typical of current-dominated, shallow-water unconsolidated silts to sands (Kauffman, 1969), which is found invariably with sea grasses in modern southern Australian waters, and common epifaunal pectinids and ostreids; (3) Common bivalve genera *Tellina* and *Nuclenia*, which are known to be rapid burrowers in unconsolidated silt and sand (Kauffman, 1969; Darragh, 1985; Ludbrook and Gowlett-Holmes, 1989); and (4) a classic bryozoan sand fauna (Cook, 1966), including abundant free-living (*Otionella* and *Selenaria*) and rooted (*Cellaria* and *Melicerita*) forms. Although these taxa are abundant, overall bryozoan diversity is very low. These sand-fauna bryozoans are adapted to conditions of unconsolidated silt and sand under moderate sedimentation rates, as described from the Rhone delta by Lagaij and Gautier (1965). Free-

living forms can dig out and large rooted and articulated forms can slough sediment. The other bryozoan taxa present (very delicate erect branching cyclostomes) indicate a calm-water setting (Stach, 1936).

Other taxa compatible with, but not restricted to, this environment include: (1) abundant turrellid gastropods and scaphopods, which prefer higher nutrient settings, and predatory/scavenger volute and naticid gastropods; (2) a relatively high number of infaunal foraminifera, which also indicate eutrophic conditions (Li et al., 2003); (3) abundant (~75% of specimen count) large, benthic (agglutinated, hyaline, and miliolid) foraminifera (Li et al., 2003); and (4) abundant, well preserved internodes of isidid (articulated branching) octocoral, which indicate calm water in unconsolidated silt (Bayer, 1956).

Other studies that have supported a shallow-water interpretation of this sequence include: (1) calcareous nannofossils (coccolithophores) of genera that are common in the near shore (*Helicosphaera*, *Pontosphaera*, *Lanternithus*, and *Zygrhablithus*), some of which (*Braarudosphaera* and *Micrantholithus*) are extremely rare in open ocean deposits (Siesser, 1979); (2) spicules from nearshore (e.g., Didemnidae ascidians are more abundant in the Puebla Clay than in other Torquay Group strata); and (3) ostracodes in the “*Cellepora*” Beds, which suggest an inner-shelf water depth of 40 m (M. Warne, unpub. data in Webb, 1995).

Petrology and Sedimentology

The presence of glauconite in the Puebla Clay has been interpreted as evidence for slow deposition in deep water (Boreen and James, 1995). However, material examined here suggests that the glauconitic grains are detrital, with no examples of authigenic glauconite within skeletal void space. Glauconite in the Puebla Clay may have been reworked from glauconite-rich Eocene or Oligocene units during post-Jan Juc erosion. An enigmatic bed of “septarian limestone” in the upper Puebla Clay (Boreen and James, 1995; Webb, 1995) forms a prominent hard band, ~9 m from the base of the unit. It actually is a calcite-cemented quartz sandstone, with a likely nearshore source (Reeckmann, 1979). In addition, well-rounded, fine- to coarse-grained quartz sand is present in the Puebla Clay sample analyzed for this study. They are also reported from the “*Cellepora*” Beds and overlying Zeally Limestone (Webb, 1995; Boreen and James, 1995).

Comparison of the “*Cellepora*” Beds at Torquay to Paleoenvironmental Conditions of Similar Australian and Tethyan Settings

Paleoenvironmental interpretations for the Torquay “*Cellepora*” Beds can be made by comparing characteristics of their depositional environment with conditions described among several *Celleporaria* thicket-bearing, shallow-marine settings through the Cenozoic. The Middle

Miocene nearshore, shallow, semi-restricted eutrophic to high-mesotrophic environment with fluctuating oxygen levels (facies M-2 and M-3) of the Murray Basin described by Lukasik et al. (2000, fig. 5, table 3) provide a paleoenvironmental standard to which the Puebla Clay can be compared (Figs. 10, 11). The faunal compositions of the two units are comparable, with the primary difference being that the degree of fragmentation is greater in the Puebla Clay. Virtually all molluscs in the Puebla Clay are fractured, but rarely abraded or encrusted. This suggests that these are storm lags of sediment washed into deeper, otherwise quiet, shallow water. The geometry of the Murray Basin differs from the setting of the Torquay *celleporarid* thickets in that the Murray Basin is a relatively flat basin, which results in a broad coastal plain. The Torquay and Rhodes settings (see below) had nearby uplands, such that sub-wave-base water depths would have been relatively close to the shoreline and would have received clastic, bioclastic, and nutrient input from adjacent littoral and terrestrial settings.

Celleporaria thickets from the Pliocene on the island of Rhodes (Kolymia Limestone) have an associated fauna that indicates a water depth of 30–50 m (Spjeldnaes and Moissette, 1997). They are found in a transgressive sequence (Figs. 10 and 11), ranging from silty marl at the base to a *Celleporaria* thicket to a marl with a more diverse, erect bryozoan fauna on top that rapidly deepens to marine clays above (Spjeldnaes and Moissette, 1997). Isolated fragments of articulated coralline algae and ostreids as well as coarse (littoral) sediment are associated with the marl and *Celleporaria* bed, indicating a near-shore environment (Spjeldnaes and Moissette, 1997). The units of the Puebla Formation compare to those of the Kolymia Limestone (Figs. 10, 11). The Kolymia Limestone in Rhodes apparently represents a single, relatively rapid transgression, whereas the Torquay section represents a longer interval over a slower sea level change, with multiple smaller cycles within it.

The Torquay Basin and Rhodes Island (Fig. 11) share the characteristic of having relatively sharp, steep edges (i.e., close adjacent uplands) (Webb, 1995; Spjeldnaes and Moissette, 1997). In contrast, the Murray Basin is a broad, flat epeiric ramp (Lukasik et al., 2000). These geometries affect distance to shore line versus water depth. Therefore, the Torquay Basin and Rhodes Island are able to have low-level, sub-swell-wave base conditions (~30–80 m) relatively close to the shoreline.

Although comparable facies are not present in the Puebla Formation, the environmental settings described by Gammon et al. (2000) for shallow, warm-water sponge beds with high nutrient sources derived from the continent are perhaps comparable. The Eocene spiculites were probably at a higher trophic level and contained more silica than the depositional environment of

the Puebla Formation, but the shallow, quiet-water, protected embayments are potentially analogous.

In the Eocene of the St. Vincent Basin, South Australia, the Blanche Point Formation is a nearshore, spiculitic unit (James and Bone, 2000; McGowran and Li, 1997). The Tuketja Member, the lowest member of the Blanche Point Formation, has conspicuous, though not bedded, *Celleporaria*. This is also interpreted as deposition in a relatively protected, shallow-water environment, with high nutrient content (James and Bone, 2000; McGowran and Li, 1997). This setting fits into the context of the proposed model, as does the bryozoan-rich, middle Eocene Norseman Limestone paleodrainge channels adjacent to the Bremer Basin (Clarke et al., 1996).

Implications for Interpretation of Sea Level Curves in Australian Cenozoic

The available data suggest that a reevaluation of the environmental depositional setting of the Torquay "Cellepora" Beds and associated units of the Puebla Formation is appropriate. If additional evidence supports near-shore, shallow, quiet water in a protected embayment (rather than deep, outer-shelf, sub-storm wave bases), this would call for a reinterpretation of the correlation of these units with global sea level curves such as Haq et al. (1988).

Similar cyclic beds are also known from the Miocene of the Gippsland Basin (Gallagher and Holdgate, 1996), Middle Miocene of Tasmania (Hageman, unpub. data), and the Eocene of the Ecula Basin (James and Bone, 1994). Incipient beds of *Celleporaria* bands are also known from the Gambier Limestone, and the St. Vincent Basin.

SUMMARY

Because *Celleporaria* have specific physical and biological conditions under which they thrive, they potentially are important paleoenvironmental indicators for depositional environments throughout the Cenozoic of southern Australia. These conditions, however, can be found under different circumstances in different environments (e.g., below swell-wave base in upwelling environments, or in shallow, calm water with terrestrial nutrient source; Fig. 11). Other nutrient sources proposed in the literature (e.g., longshore currents and freshwater seeps) have not been explored here.

Hollow-branched *Celleporaria* are epibionts on fistulose sponges. They have growth habit characteristics that allow them to exploit conditions of moderate sedimentation rates in high nutrient settings, below maximum wave depth. Their rapid growth through frontal budding allows formation of large, robust branches in a three-dimensional box-work. Nutrients can be derived from oceanic upwelling or terrestrial runoff (i.e., an environmental condition, not a specific geographic province). Bryozoan faunas that are diverse in oligotrophic conditions in these regions do not thrive at these times.

Deep-water and shallow-water *Celleporaria* thickets share the following characteristics (regardless of absolute water depth): (1) mesotrophic nutrient regime (intolerant of eutrophic or oligotrophic); (2) substrate of silt or clay with moderately high sedimentation rate; and (3) relatively quiet water, near or below swell wave-base, but below fair-weather wave base.

Deep water and shallow water *Celleporaria* thickets have these same physical conditions, but found in different environments: (1) nutrient source was from upwelling deep-sea currents for deep-water thickets (it is presently unclear how far onto the shelf these may have extended), whereas shallow-water thickets derive their nutrients from terrestrial runoff; (2) water depth for deep thickets was greater than 160 m, and was likely a function of regional storm intensity and fetch, whereas water depth for shallow-water thickets was likely between 20–40 m, depending on the width of the shelf/ramp and the degree of hydrodynamic protection (islands, embayment); (3) deep-water thickets are associated with overall very low sea level stands, whereas shallow-water thickets occurred toward the end of regressive sequences, or early in transgressive sequences (i.e., just below or above a high stand at the depth of storm-wave base), and (4) associated silt- and clay-sized particles are carbonate in deep water thickets, whereas shallow-water thickets contain terrestrially derived siliciclastic sediment.

Both deep-water and shallow-water *Celleporaria* thickets provide clues to their position within third order sea level cycles. They represent transitions from maximum low and high stands, respectively (when other environmental requisites are met). Within these settings, *Celleporaria* thickets appear to be sensitive to 4th order cycles in sea level. Undoubtedly, further documentation of the successional, environmental distribution of *Celleporaria* in Cenozoic sediments of southern Australia will provide broader insights into the history of many Cenozoic depositional systems.

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APPENDIX

Samples (living and benthic sediment) were collected from four voyages of the RV *Franklin* (1989, 1991, 1994, 1995), which sampled sediments across transects of the continental shelf and upper slope (30–600 m) from a region from eastern South Australia to the southwest shelf off Western Australia (Fig. 5). Data for this study are concentrated on material collected from the Southwest Shelf and Great Australian Bight (142 samples). Sediment samples collected with a Blay's pipe dredge on South Australian cruises (1989, 1991, 1994) are used to characterize these regions. Fossil material was collected from a variety of Cenozoic formations across southern Australia.

Taxonomy of *Celleporaria* (Lepraliellidae, Cheilostomata) Sturt 1832, p. 253, t. 3, f. 1. (as *Eschara celleporacea*)

The taxonomy of celleporarid bryozoans is especially problematic. Members of this genus display a great deal of plasticity in their morphologic expression. In addition, key morphological features such as aperture shape and development of avicularia can be observed only during different times of the development of a zooid (ontogeny). Careful scanning electron microscopy of multiple colonies is required for accurate species identification. The literature is filled with species names derived from incomplete study of the group. There are at least two and possibly as many as seven modern species, under the name *Celleporaria oculata* (typically used for living, southern Australian specimens with this growth habit). A complete systematic revision of the Australian members of the genus *Celleporaria* is beyond the scope and goals of this paper, however, relevant taxa are illustrated and briefly discussed here to provide for communication purposes within this paper (Fig. 5).

Most fossil specimens of this group are assigned to the name *Celleporaria gambierensis*, although there are clear differences among Eocene, Oligo-Miocene and Modern forms. These are similar to, but different than *C. palmata*, which forms thickets in the Pliocene of the Mediterranean (Spjeldnaes and Moissette, 1997).

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FIGURES & TABLES

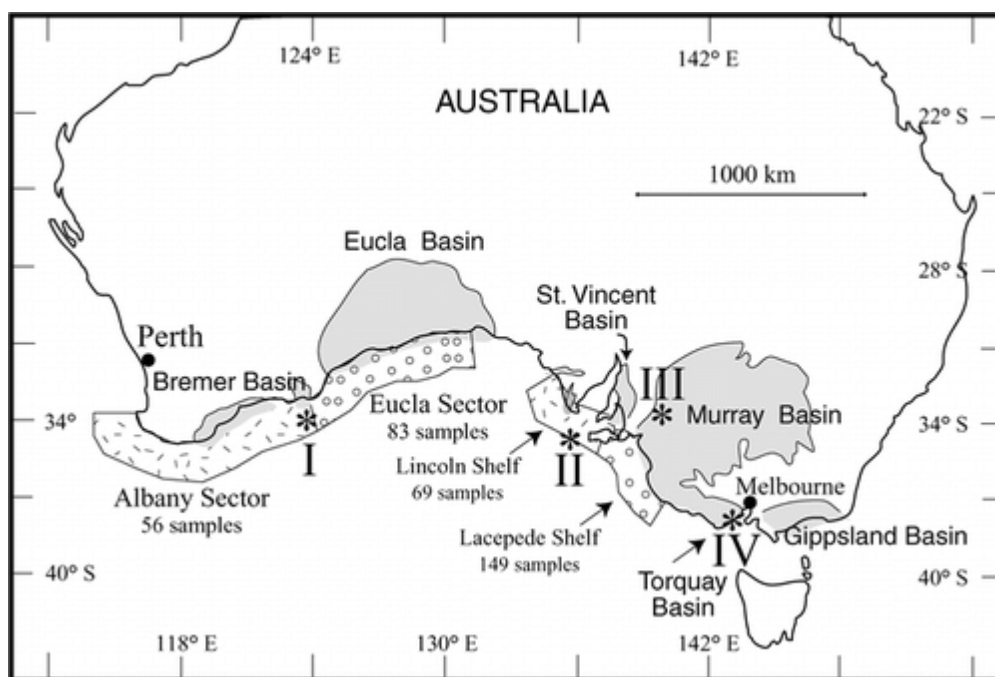


FIGURE 1—Southern Australian Cool-water Province; sampled shelves and Cenozoic Basins. Asterisks labeled I, II, III, and IV indicate the locations of samples in this study used to develop idealized models for *Celleporaria* thicket formation. These positions correspond to labels I, II, III, and IV in Figs. 7, 9, 10, and 11. Fill patterns on the shelf designate field areas (e.g., Albany sector (Fig. 5A) and Eucla sector (Fig. 5B) of the GAB)

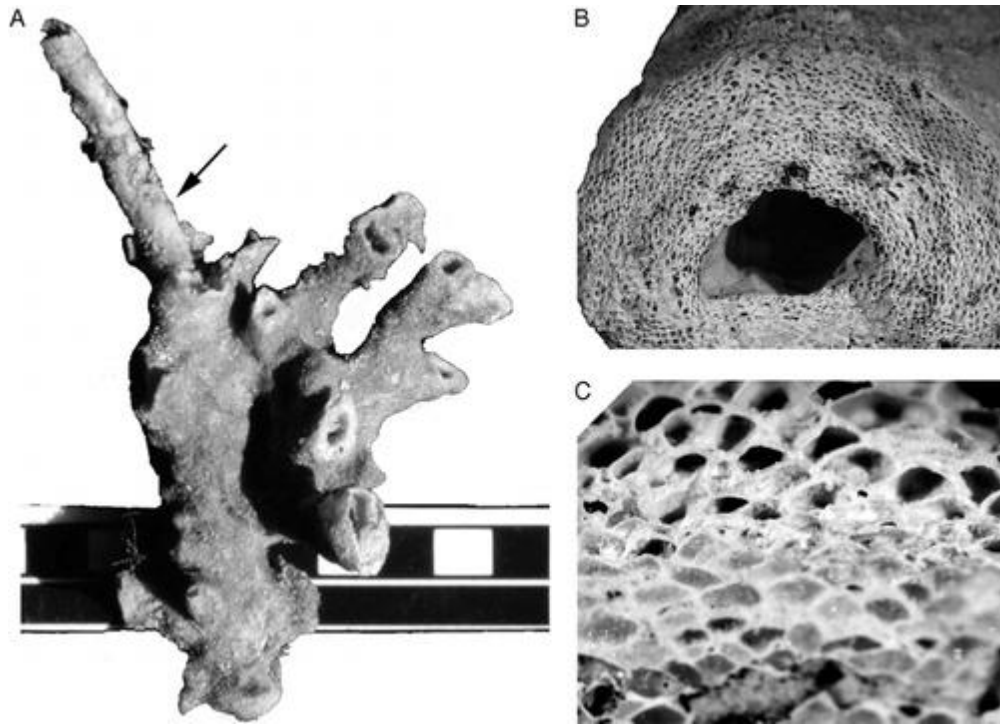


FIGURE 2—(A) Live *Celleporaria* sp. from GAB (Site GAB-119). Arrow indicates sponge (*Oceanapia* sp.) extending beyond end of colony. Other branches display hollow tubes that have grown beyond the sponge (scale in cm). (B) Middle Miocene *Celleporaria* sp. (Gippsland Basin) illustrating multilaminar, frontally budded zooids and hollow branch (frame width 2.3 cm). (C) Close up of specimen (B) illustrating multilaminar, frontally budded zooids and varying degrees of void-filling calcite cement within zooecial (frame width 0.65 cm)

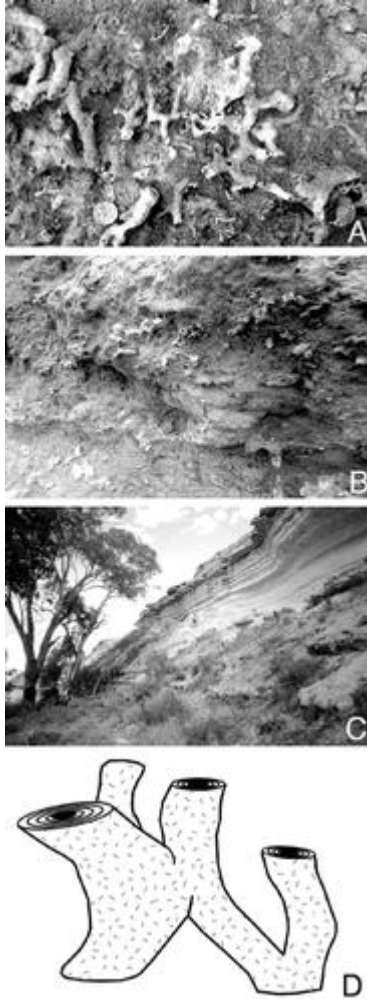


FIGURE 3—(A–B) *Celleporaria* thickets from “*Cellepora*” beds of Puebla Formation, Torquay, Victoria, Australia; label “IV” (Middle Miocene) on Fig. 1. (A) Top view of a bed with anastomosing box-work colonies weathered in relief; coin=2 cm. (B) Lateral view of a *Celleporaria* thicket or bed, approximately 30 cm thick; hammer head=15 cm. (C) Sub-meter scale cyclic beds (long arrows) of the Glenforslan Formation of the Morgan Group, Morgan Bend in Murray Basin, South Australia; label “III” on Fig. 1. Short arrows highlight beds of *Celleporaria* thickets that form ledges. Overall regressive to transgressive sequence centered on dark recessive bed, upper right. (D) Idealized sketch of the three-dimensional, anastomosing, fused growth habit of *Celleporaria*

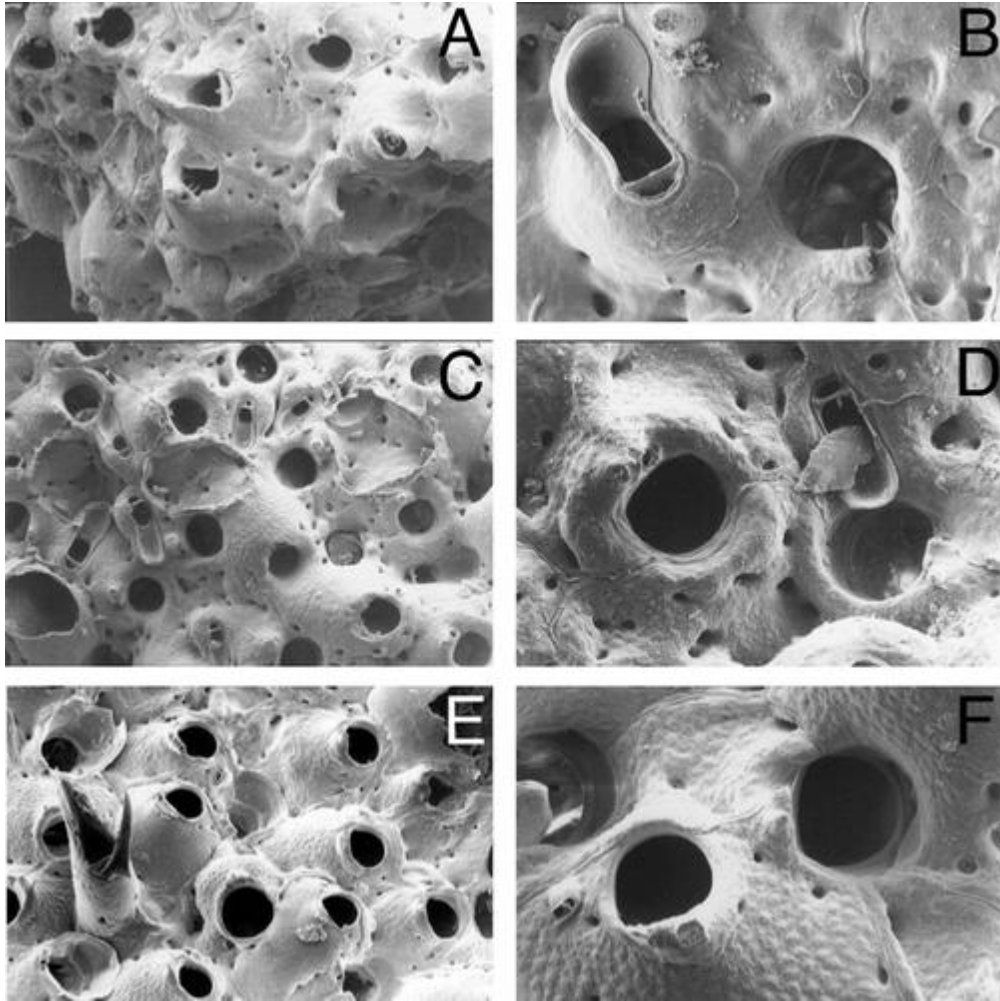


FIGURE 4—Three species(?) (A–B; C–D; E–F) of modern *Celleporaria* from the GAB (A, C, E—47x; B, D, F—125x). Taxonomic concepts for species within the genus are unclear due to the high degree of variability both within and among colonies, including irregular orientation of zooids emplaced at variable levels on the colony surface; variability of vicarious avicularia from spatulate (B), to sharply lancellate (E), and avicularia elevated on pedestals (A) to below the overall colony surface (D); variable appearance of brood chambers (E, F); and variable thickening of frontal walls and surface texture; (B) is a thick wall and (F) is a thin wall.

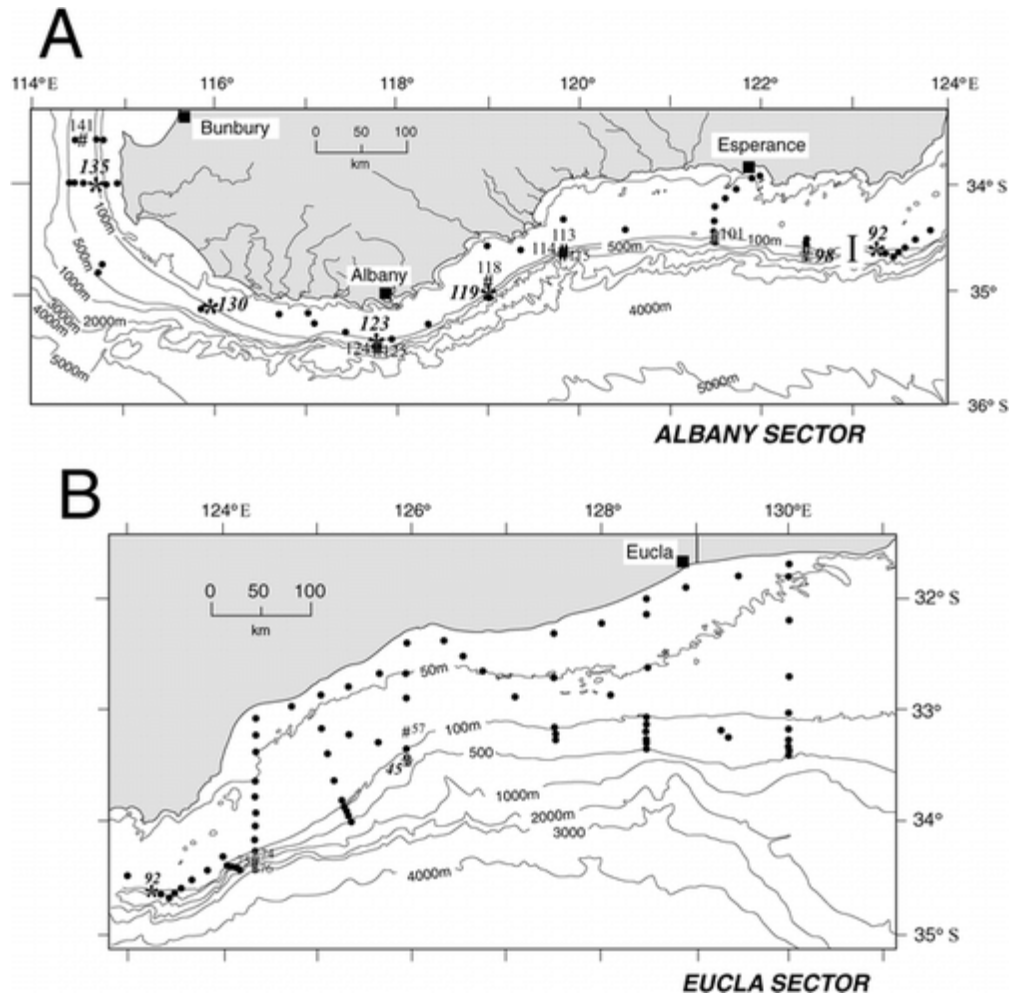


FIGURE 5—Great Australian Bight (GAB) sample localities. Numbers are designated GAB sample sites (Y. Bone, unpublished data); those in large italic fonts and labeled with “*” designate live samples of *Celleporaria*; those in smaller fonts and labeled with “#” designate where dead and/or relict samples of *Celleporaria* were collected, unnumbered sites, designated with “•”, are sites where no hollow-branched *Celleporaria* were found. (A) Albany Sector. (B) Eucla Sector

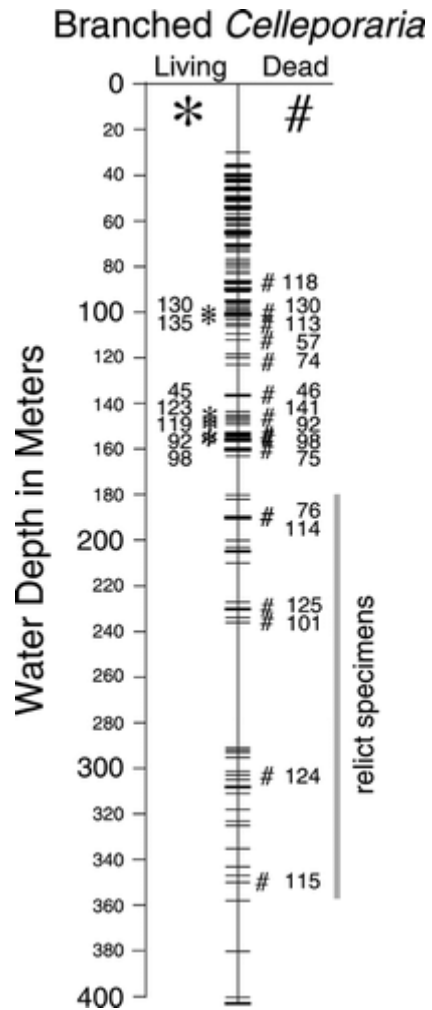


FIGURE 6—Water-depth distribution of GAB sample localities; each crossbar corresponds to a sample site in Fig. 5. Samples with living *Celleporaria* are labeled by sample number and “*” in the left column. Samples with non-living *Celleporaria* are labeled by sample number and “#” in the right column. Sites with no hollow-branched *Celleporaria* are designated by unlabeled crossbars

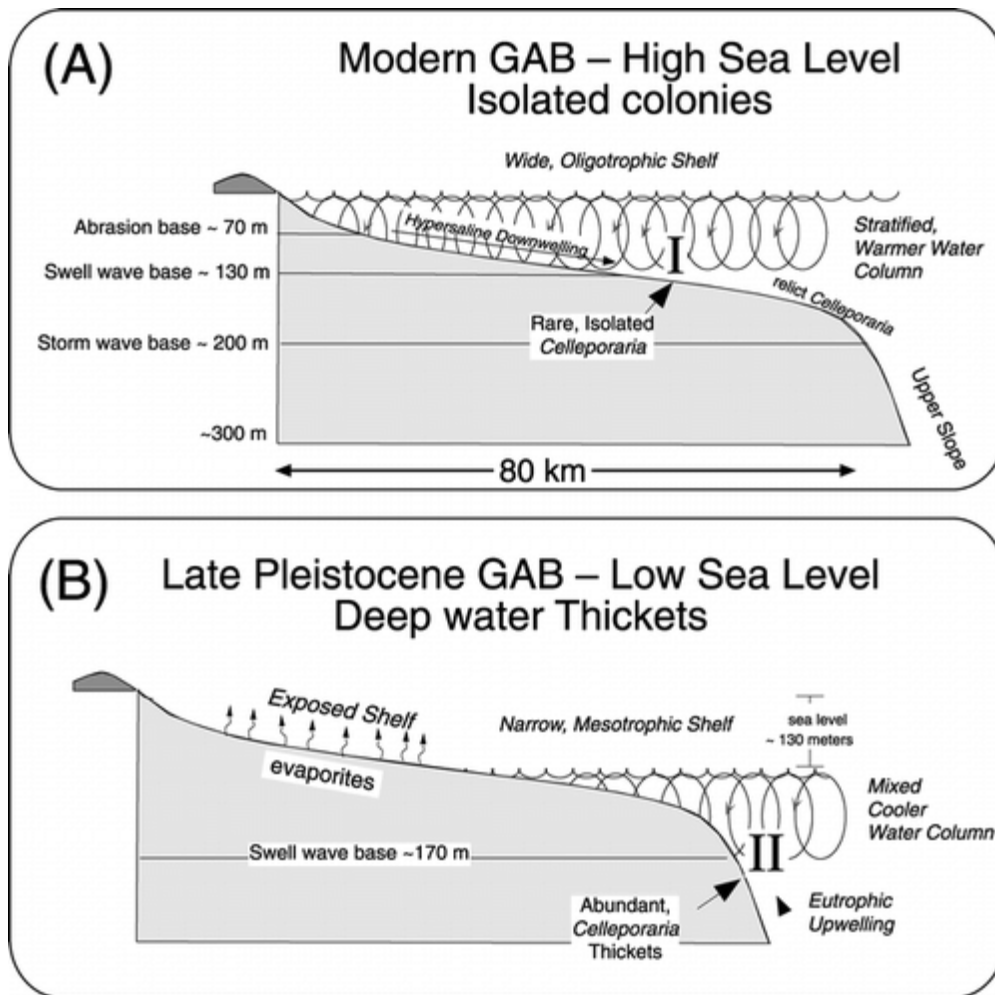


FIGURE 7—Generalized diagrams of the GAB, southern Australian shelf profiles (continent to left, Southern Ocean to right). Labels I and II correspond to the geographic location of *Celleporaria* thickets denoted by labeled asterisks on Fig. 1. (A) Profiles of high, modern and (B) low, late Pleistocene sea level stands illustrate differences in environmental parameters and location of *Celleporaria* growth

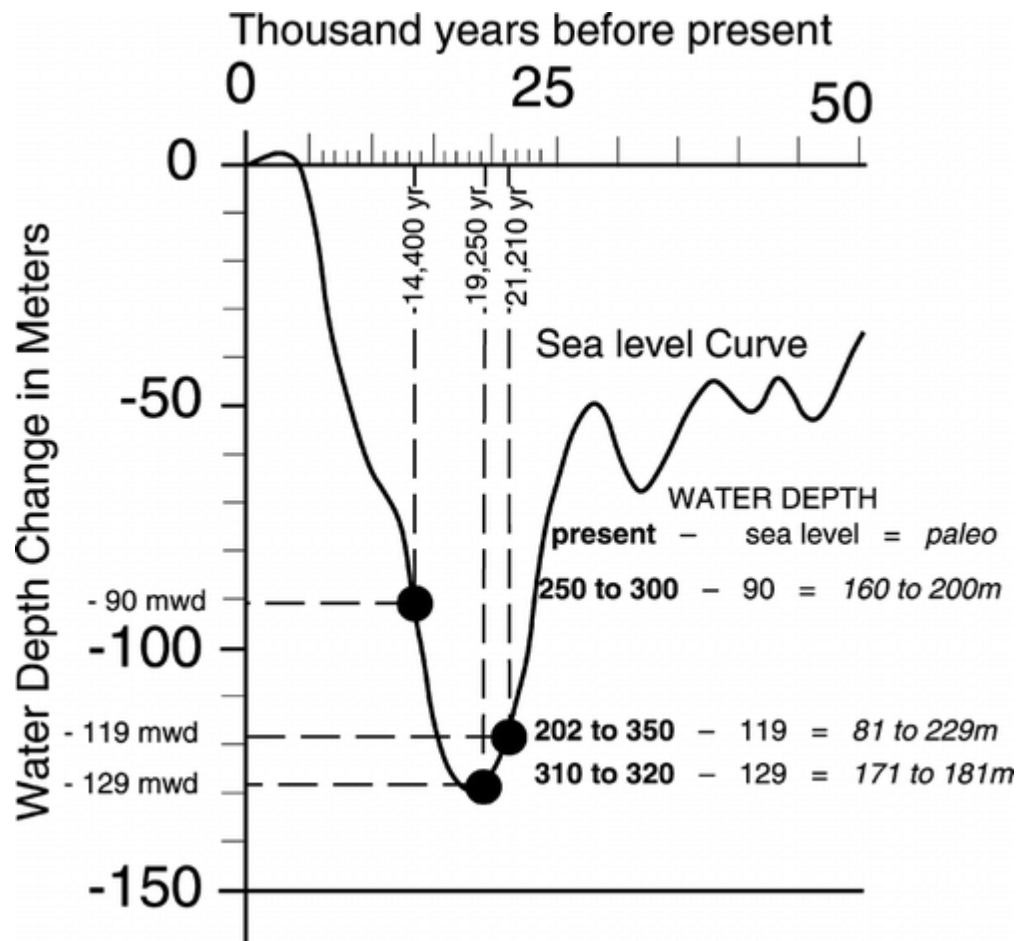


FIGURE 8—Curves used to estimate water depth at the shelf margin during the late Pleistocene. Sea level curve derived from Oxygen isotope data (after Chappell and Shackleton, 1986). Carbon⁻¹⁴ dates of relict bioclasts (James et al., 1997) 14,400 ybp, 19,250 ybp, and 21,210 ybp correspond to drops in sea level of 90 m, 119, m and 129 m, respectively. Thus, late Pleistocene relict bioclasts collected from modern water depths of 200–350 m would have lived in water depths corresponding to 81–229 m water depth

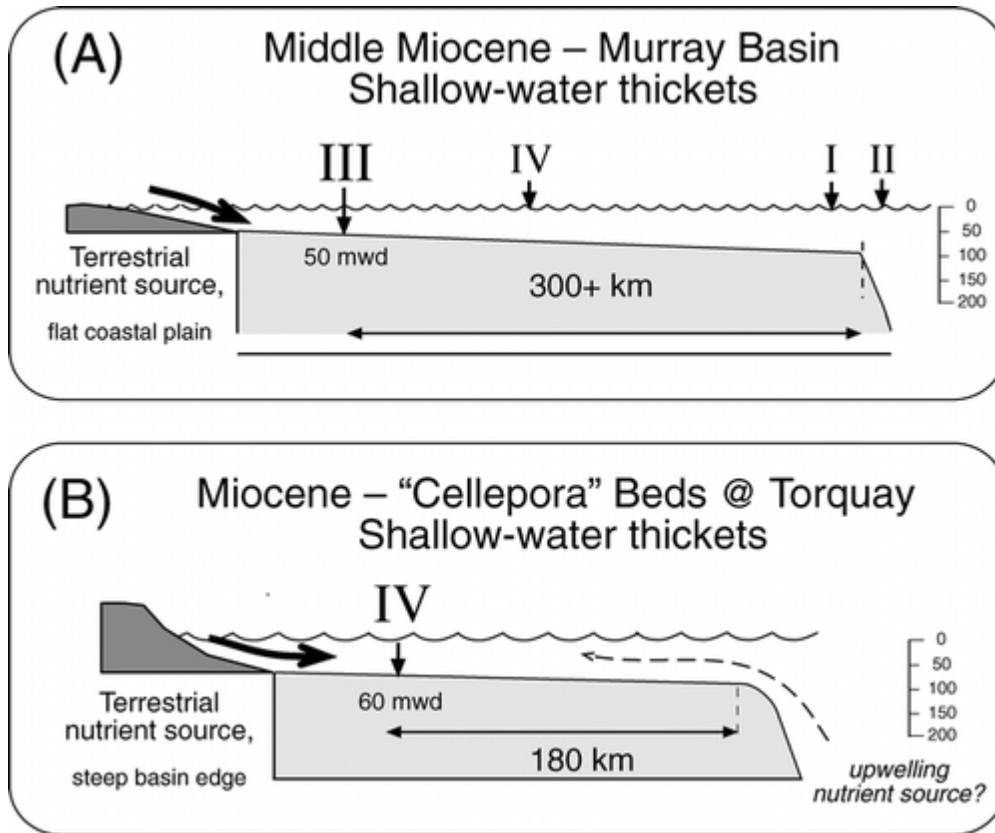


FIGURE 9—Generalized reconstructions (at different scales) of the Miocene southern Australian margin (continent to left, Southern Ocean to right). Labels I–IV correspond to the relative geographic location of *Celleporaria* thickets denoted by labeled asterisks on Fig. 1. Arrows propose the source of nutrients in each setting. (A) Profile of Middle Miocene Murray Basin, South Australia. (B) Early Miocene of Torquay Basin, Victoria

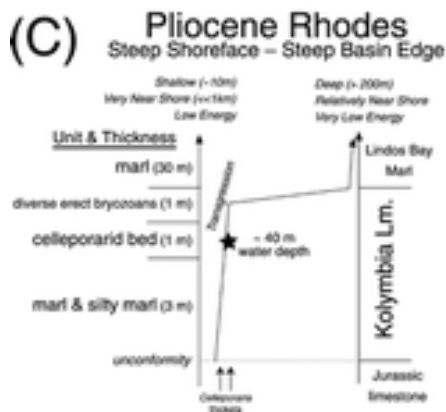
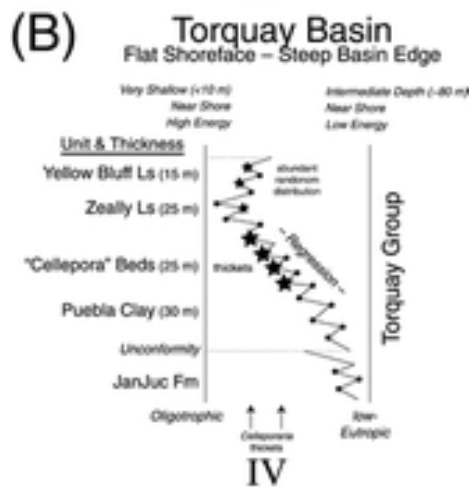
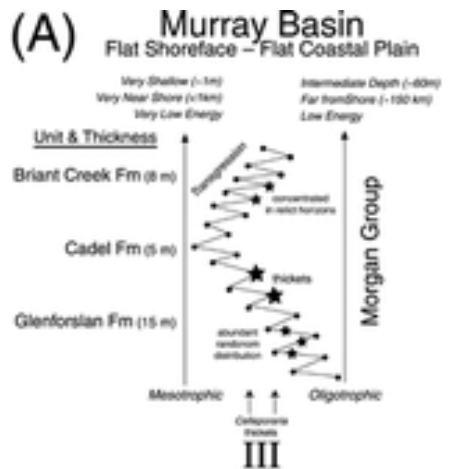


FIGURE 10— Generalized stratigraphy, relative sea level, and trophic resource curves. In all settings, Celleporaria thickets form at a transition to mesotrophic nutrient levels in sub-wave-base conditions. Roman numerals III–IV refer to geographic positions on Figs. 1, 7, 9 and 11. (A) Ledge-forming cycles of Celleporaria in the upper Glensforlan Limestone of the Middle Miocene, Morgan Group from the Murray Basin, South Australia (after Lukasik et al., 2000). (B) Type section for the Early Miocene Puebla Formation, of the Torquay Basin, Victoria. (C) Section of Late Pliocene Kolymbia Limestone, island of Rhodes, Greece (after Spjeldnaes and Moissette, 1997)

	II Late Pleistocene		III Glenforlan Fm. Murray Basin		IV Puebla Fm. Torquay Basin		Kolymbia Ls Rhodes
Nutrient Source	mesotrophic ocean upwelling	mesotrophic terrestrial	mesotrophic terrestrial	mesotrophic terrestrial (+ upwelling?)	mesotrophic terrestrial (+ upwelling?)	mesotrophic terrestrial (+ upwelling?)	mesotrophic terrestrial (+ upwelling?)
Water Depth	below swell wave base (subject to storms) greater than 250 m	below swell wave base (subject to storms) less than 50 m	below swell wave base (subject to storms)	below swell wave base (subject to storms) 40 to 60 m	below swell wave base (subject to storms) 30 to 40 m	below swell wave base (subject to storms)	below swell wave base (subject to storms) 30 to 40 m
Sedimentation	rate = med. to high carbonate silt	rate = med. to high carbonate silt	rate = med. to high carbonate silt	rate = med. to high marl and clay	rate = med. to high marl, clay & boulders from shoreface	rate = med. to high marl, clay & boulders from shoreface	rate = med. to high marl, clay & boulders from shoreface
Sea Level	During extreme low stand	regression prior to local low-stand	regression prior to local low-stand	transgression near high-stand	transgression after low-stand	transgression after low-stand	transgression after low-stand
Environment	below shelf break	shallow epicric ramp 300 km inland from shelf break relatively far from shore, flat coastal plain	shallow epicric ramp 180 km inland from shelf break close to shore, steep basin edge	inner shelf (wide)	inner shelf (narrow) very close to shore, steep basin edge	inner shelf (narrow) very close to shore, steep basin edge	inner shelf (narrow) very close to shore, steep basin edge
References	James et al., 1993 James et al., 1997 Boreen and James, 1995 original data herein	Lukasik & James, 1998 Lukasik et al., 2000 Ludbrook, 1957, 1958 original data herein	Reeckman, 1979 Abello et al., 1988 Boreen and James, 1995 Webb, 1995 Li et al., 2003 original data herein	Spjeldnaes and Moissette, 1997			

FIGURE 11— Comparison of environmental parameters for one deep and three shallow *Celleporaria* thickets. Roman numerals II–IV refer to geographic positions on Figs. 1, 7, 9, and 10

FORAMINIFERAL PROXIES environmental parameters are correlated with relative abundance and/or diversity of key groups	MIXED WATER COLUMN unstable nutrient supply; trophic level low to high; at times eutrophic generally low (oligotrophic)	STRATIFIED WATER COLUMN stable nutrient supply trophic levels partitioned by water column strata
(1) Diversity of Plankton (Lipps, 1987)	—	HIGH diversity
(2) Key Planktic Foram Taxa	ABUNDANT generalists	—
(2a) Generalist species (e.g., <i>Globigerinoides ruber</i>) (Lipps, 1979)	—	DIVERSE & COMMON opportunists
(2b) Opportunist species (e.g., <i>Globigerinoides bulloides</i> and <i>G. falcovensis</i>) (Lipps, 1987)	—	LARGE value
(2c) "ruber ratio" (<i>Gg. bulloides</i> + <i>Gg. falcovensis</i>) <i>Gg. ruber</i>	—	ABUNDANT epifauna
(3) Benthic Foraminifera (Corliss, 1985; Corliss and Chen, 1988)	—	—
(3a) Epifaunal <i>Cibicides</i> sp., <i>Oridorsalis umbonatus</i>	ABUNDANT infauna	—
(3b) Infaunal <i>Uvigerina bifurcata</i> , <i>Bolivina grandispira</i> , <i>Gavelinella barboviana</i>	LARGE value (Shallower Water Depth* and/or High Productivity†)	— (Deeper Water Depth and/or Lower Productivity†)
(3c) Epifaunal/Infaunal	—	More abundant
(4) Planktic vs. Benthic	—	High value
(4a) Planktic forms	—	—
(4b) Benthic forms	—	—
(4c) Planktic/Benthic	—	—

— Conditions opposite from the other column.

* Bolvinsky and Wright (1976).

† Berger and Diester-Haus (1988).

TABLE 1—Neritic ecological conditions characterized by the diversity and abundance of key foraminiferal taxa

	Low sea level	High sea level
Timing of conditions on southern Australian Shelf ^a	22,000 to 12,500 ybp $\delta^{18}\text{O}$ Isotope stage 2 Previous Glacial	12,500 to present $\delta^{18}\text{O}$ Isotope stage 1 Current Interglacial
Shelf width	narrow	very wide
Storm wave base	increased (~180 m)	decreased (~140 m)
Currents	more vigorous upwelling	local downwelling & upwelling
Productivity	variable, at times eutrophic	mediated oligotrophic
Water column	mixed	stratified
Temperature	cool	warm
Subtropical Convergence Zone	off-shelf	on-shelf
<i>Celleporaria</i> distribution	thickets at shelf edge	rare isolated colonies mid-outer shelf

^a Based on foraminiferal proxies summarized in Table 1 (Almond et al., 1993) and sedimentological data from James et al. (1992) and James et al. (1997).

TABLE 2—Summary of physical conditions on the southern Australian shelf margin during times of high and low sea level (after Caron and Holmwood, 1983 and Almond et al., 1993). Shelf edge *Celleporaria* thickets flourished during times low sea level stands among upwelling of cool nutrient-rich, mixed waters*