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SPECULATIONS ON THE PALAEOECOLOGY OF SELECTED LARGER FORAMINIFERA

by

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A comparison between the lithologic and biotic characters of Oligo-Miocene sediments from several stratigraphic sections in Australia and those of modern counterparts has permitted the palaeoecology of some fossil larger foraminifera to be evaluated. Eight larger foraminiferal fossil associations have been recognized, each representing a certain environment. Three of these were typical of sea-grass communities at depths of less than 12 m: the *Lepidocyclina* (*Eulepidina*) *ephippioides* — *Heterostegina borneensis* association in oceanic salinities but in sheltered situations; the *Lepidocyclina* (*Nephrolepidina*) *howchini* — *Cycloclypeus eidae/carpenteri* association in the same salinitites, but in open situations; the *Lepidocyclin* (*Nephrolepidina*) *howchini* — *Marginopora vertebralis* association in metahaline salinities. Two associations were typical of high energy sandy substrates in depths of less than 30 m: the *Operculina complanata* — *Gypsina howchini* association in oceanic salinities and the *Austrotrillina howchini* — *Flosculinella bontangensis* association in metahaline salinities. Three were typical of open situations with oceanic salinities: the *Lepidocyclina* (*Eulepidina*)*badjirraensis* — *Cycloclypeus eidae* association lived in waters deeper than 12 m, and the lower boundary overlapped the *Cycloclypeus eidae* — *Operculina complanata* association, which ranged to near the base of the euphotic zone at depths near 120 m; the *Operculina complanata* — smaller benthonic foraminiferal association was typical of depths near 120 m or greater.

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THE systematics or stratigraphic distribution of foraminifera have been extensively studied; but comparatively little has been published on their ecology or palaeoecology. With foraminifera, as with other fossil groups, it is necessary to study the relationship of living representatives to their environment (e.g. sediments, substrate, fauna, flora and water-mass) before valid conclusions can be made about fossil forms. During the last few years an increasing amount of information has been gathered on modern faunas, but much of this is generalized and the relationships to the physical and chemical regimes are often lightly treated. Sedimentological studies are often good sources of information: e.g. Logan & Cebulski (1970), Logan *et al*. (1970), and Davies (1970) on the sediments from Shark Bay, Western Australia, and Kendall & Skipworth (1969) on the Persian Gulf. Some authors, dealing specifically with foraminiferal faunas, have used generalized techniques such as the planktonic:benthonic ratio (e.g. Grimsdale & Morkhoven, 1955), triangular plots of the percentages of rotalines, miliolines, and textularines in the assemblage (Murray, 1968, 1973), and the Fisher Diversity Index (Fisher, Corbett, & Williams, 1943), all of which have proved very useful; the last requires identification of different species, but the others need only counts of easily identified suborders.

Recent studies have shown that marine waters can be divided into four major types, three of which have been defined as follows: oceanic waters with salinities ranging between 36 and 40% , metahaline between 40 and 56% , and hypersaline from 56 to 70% (Logan & Cebulski, 1970).

Murray (1968, 1973) and Wright & Murray (1972) have summarized previous published data on the distribution of modern foraminifera on a triangular diagram (Fig. 6). Several distinct fields can be recognized for different environments: 'hypersaline' (= metahaline in this study) shelf of the Persian Gulf, 'hypersaline' lagoon, normal marine lagoon, shelf sea of normal salinity, hyposaline and near-shore shelf sea and hyposaline lagoon. They also found that the diversity data (Fisher Diversity Index) sorted into similar fields. Because the smaller benthonic species have not been studied, the diversity indices could not be calculated for this work.

Recently, Greiner (1969) has advanced the hypothesis that distribution of foraminifera may be controlled by their wall-forming processes. He argues that porcellanous forms (milioline) do not need a nucleating surface for calcite precipitation and so require sea water to be supersaturated in calcium carbonate, a condition which is most commonly found in warm, very saline water. Rotaline and other hyaline forms are most abundant where the concentration of calcium carbonate is lower, because calcite is secreted on an organic nucleating surface (these forms would not be able to secrete well-ordered crystals where calcium carbonate is abundant); the tests of agglutinated (textularine) forms contain little or no calcite, a feature which enables them to live in very low concentrations of calcium carbonate. This hypothesis certainly explains the usefulness of the triangular plot method of Murray (1968, 1973) for environmental interpretations. Modern distribution of miliolines and textularines, however, suggests that miliolines can tolerate higher and textularines lower calcium carbonate concentrations than those of oceanic salinities.

Other generalizations can be made on distribution of smaller foraminifera. Miliolines, especially the larger forms, are typical of shallow water; they occur most abundantly in metahaline salinities, with some ranging into oceanic situations. Wright & Murray (1972, p.73) noted that this group is usually associated 'with weeds and rocks or sandy substrates at depths of less than 30 m'. Phleger (1960, pp. 258-59) noted that 'thick-shelled, large species of Elphidium, Streblus and Miliolidae...and...large and robust arenaceous forms such as Textularia' are typical of depths less than 20 m in the nearshore turbulent zone. In the deeper waters of the continental shelf the number of planktonic species increase, and rotalines dominate the assemblages.

Studies on the distribution of modern planktonic foraminifera have shown that they are stratified by depth (Bé, 1960; Douglas & Savin, 1972; Emiliani, 1954, 1971; Frerichs, 1971; Hecht & Savin, 1972; Jones, 1967, 1968). Although the juveniles of some species live in the surface waters and later migrate to deeper levels, others may live at similar levels throughout ontogeny (Bé, 1969). Douglas & Savin (1972) suggested that forms of the Globigerinoides quadrilobatus group are most numerous in the near-surface waters, Globigerina spp. at intermediate depths, and Globoquadrina spp., Globorotalia spp. and other thick-walled genera (e.g. Sphaeroidinella) in deeper waters. Often size increases with depth (Bandy, 1954), or the test wall thickens by addition of secondary calcite deposits (Bé, 1965; Bé & Ericson, 1963). Lee et al.(1965) noted the presence of zooxanthellae in Globigerinoides ruber, and their absence in Globigerina bulloides. They concluded that the former would be restricted to the euphotic zone and the latter to greater depths. This agrees with the vertical distribution recorded by Bé (1960), Bradshaw (1959), and others, as well as data from oxygen isotope palaeotemperature studies (Jones, 1967, 1968; Emiliani, 1954, 1971; Douglas & Savin, 1972). After reviewing the literature, Dietz-Elbrachter (1971) noted that Hastigerina pelagica, H. siphonifera, and Orbulina have also been recorded as having a symbiotic relationship with green algae.

Coralline algae are good depth indicators. Johnson (1961, p. 22) noted that 'algae do not grow at depths greater than light penetrates... very few types of algae extend down to the extreme limit of light'. He concluded that most forms live in strong light, near low-tide level, and the majority of these are restricted to less than 30 m; however some species have been found living at 300 m. Nodular forms are not known below 80 m. Johnson (1961) reported that articulated forms require fairly 'brilliant' light; he considered that brilliant light occurs over depths of less than 30 m.

The enclosing rock can give much information about the environment of deposition: the presence of syngenetic minerals can give information about the redox-potential; the presence or absence of mud and the degree of sorting, rounding, and size of the sedimentary particles can be used to estimate environmental energy; the preserved biota can allow depth to be estimated; palaeotemperatures can be gauged from measurements of oxygen isotopes extracted from calcium carbonate deposited by organisms. The possibility of reworking or post-mortem transportation can also be estimated from the amount of environmental energy. The terminology advocated by Dunham (1962), based on the depositional texture of carbonate sediments, has been used in this work.

This paper is only part of a study of larger foraminiferal faunas from Oligo-Miocene rocks from Western Australia. A brief stratigraphic summary is followed by a discussion of the lithology of the sediments and their depositional environment. Past and present ideas on the environmental distribution of larger foraminifera are reviewed, including some generalizations on certain smaller forms which are important in the faunas studied. From this information an attempt is made to deduce the environmental ranges of large foraminiferal assemblages and the palaeoecology of individual taxa recorded from the rock units.

Thin sections of limestones used for illustration (Plates 1 to 3) prefixed UWA are deposited in the collections of the Geology Department, University of Western Australia, Perth. Two thin sections of limestones collected by staff of the Bureau of Mineral Resources, CR 77 and 7164-0357, are not registered, but are stored in the collections of that organization.

Rock stratigraphy and larger foraminiferal assemblages

The rock-stratigraphic nomenclature for the North West Cape area (Fig. 1) used in this paper is that of Condon _et al_.(1955; 1956) and Quilty (1974) (Figs. 2, 4). An additional unit, the 'Bullara Limestone', is recognized informally and will be described in another paper. The name denotes a sequence of massive, brown to grey, poorly to well cemented bioclastic limestones that unconformably underlie the Trealla Limestone and disconformably overlie lateral equivalents of the Giralia Calcarenite in the subsurface of Rough Range (Fig. 1). The inter-relationships of these units are illustrated in Figure 2. The stratigraphy of Ashmore Reef No. 1 (Fig. 1) has been discussed by Craig (1968, unpublished) and is summarized in Fig. 3. Foster (1970) has described the rock-stratigraphic setting of the Batesford Limestone (Fig. 5).

Eight assemblages of larger foraminifera have been recognized in the North West Cape area, and some of these can be recognized in Ashmore Reef No. 1 Well and in the Batesford Limestone, demonstrating their validity as biological entities. There are at least two successive assemblages in each section; in those from North West Cape (Fig. 4) and Ashmore Reef No. 1 Well (Fig. 3) the associations are in a similar order; those from the Batesford Limestone (Fig. 5) show a similar relationship, but occur in a different order. The assemblages in the descending stratigraphic order found in the North West Cape area are:

(8) *Austrotrillina howchini* — *Flosculinella bontangensis* association. The two nominate species and *Marginopora vertebralis* dominate; rare specimens of *Sorites* sp., *Peneroplis* sp., *Borelis pygmaeus*, *Operculina complanata*, *O. venosa*, *Cycloclypeus* (*Cycloclypeus*) sp. cf. *C. carpenteri*, *Gypsina globulus*, *G. howchini*, *G. mastaelensis*, and *Lepidocyclina* (*Nephrolepidina*) sp. cf. *L. howchini* may also be present.

(7) *Lepidocyclina* (*Nephrolepidina*) *howchini* — *Marginopora vertebralis* association. In addition to the two nominate species, which dominate the assemblages, there are less common forms including *Austrotrillina howchini*, *Borelis pygmaeus*, *Operculina complanata*, *O. venosa*, *Cycloclypeus* (*Cycloclypeus*) sp. cf. *C. carpenteri*, *Miogypsina* (*Lepidosemicyclina*) sp. cf. *M. thecideaeformis*, *Amphistegina quoii*, *Borodina septentrionalis*, *Gypsina globulus*, *G. howchini*, *G. mastaelensis*; *Cycloclypeus* (*Katacycloclypeus*) sp. cf. *C. annulatus* is very rare.

(6) *Lepidocyclina* (*Nephrolepidina*) *howchini* — *Cycloclypeus* (*Cycloclypeus*) *eidae* / *carpenteri* association. This assemblage is dominated by *L.* (*N.*) *howchini* and *C.* (*C.*) *eidae* or *C.* (*C.*) *carpenteri*, with smaller numbers of *Operculina complanata*, *Miogypsina* (*Lepidosemicyclina*) *thecideaeformis*, *Amphistegina quoii*, *Gypsina globulus* and *G. howchini* present, and rare *Heterostegina suborbicularis*, *Miogypsina* (*Miogypsinoides*) *dehaarti*, *Borodina septentrionalis*, *Carpenteria alternata*, and *C. proteiformis*.

(5) *Lepidocyclina* (*Eulepidina*) *badjirraensis* — *Cycloclypeus* (*Cycloclypeus*) *eidae* association. The nominate species characterize this assemblage. In addition less common specimens of *Operculina complanata*, *Amphistegina quoii*, *Gypsina globulus*, *Carpenteria alternata*, and *Lepidocyclina* (*Nephrolepidina*) *howchini* may be present.

(4) *Cycloclypeus* (*Cycloclypeus*) *eidae* — *Operculina complanata* association. The two nominate species dominate the assemblages, with rare specimens of

Gypsina globulus, *Carpenteria alternata*, and juvenile *Lepidocyclina (Eulepidina) badjirraensis*.

(3) *Operculina complanata* -- smaller benthonic foraminiferal association. Rare specimens of juvenile *Cycloclypeus (Cycloclypeus) eidae* and very rare juvenile *Lepidocyclina (Eulepidina) badjirraensis* may be present in faunas dominated by smaller benthonic foraminifera.

(2) *Lepidocyclina (Eulepidina) ephippiodes* -- *Heterostegina borneensis* association. In addition to the two nominate species, *L. (Nephrolepidina) sumatrensis* and *Amphistegina bikiniensis* dominate the assemblages. Rare specimens of *Operculina complanata*, *Gypsina globulus*, and *G. howchini*, and very rare *Austrotrillina* sp. cf. *A. striata*, *Sorites* sp., *Borelis pygmaeus*, and *Halkyardia* sp. cf. *H. minima* may be present.

(1) *Operculina complanata* -- *Gypsina howchini* association. The two nominate species dominate. Rare specimens of *Lacazinella* sp. cf. *L. wichmanni*, probably reworked from the underlying lateral equivalents of the Giralia Calcarenite, are also present.

Lithology of the sediments

North West Cape Area

Mandu Calcarenite. The Mandu Calcarenite consists of poorly sorted bioclastic packstone and quartzose bioclastic wackestone (Pl. 1, Figs. A-D). The sand-size fraction of the wackestone falls within the fine to very fine sand range on the Wentworth Scale; small angular quartz grains dominate, and foraminifera (smaller benthonic and planktonic) are the most common bioclasts. The grainsize of the packstone is coarser, ranging from fine to coarse sand, although individual bioclasts may range to 50 mm. Most of these are angular, but some are subrounded. In the uppermost parts of the formation, the sediments are characterized by skeletal fragments of coralline algae, and encrusting and larger foraminifera, suggesting deposition influenced by the presence of seagrass at depths of less than 12 m (see p.).

The older sediments of the Mandu Calcarenite do not contain this fauna.

'Bullara Limestone'. The 'Bullara Limestone' consists of poorly to moderately well sorted, bioclastic grainstone and packstone (Pl. 1, Figs. E–G), of which the bioclasts are subangular to subrounded and range from medium to coarse sand-size, with some reaching 5 mm. The biota is dominated by shallow-water forms, chiefly coralline algae and foraminifera (encrusting and larger forms become abundant towards the upper parts). Some of the bioclasts are stained black, but no authigenic minerals such as pyrite have been recorded. The packstone contains a much lower mud content than do equivalent sediments of the Mandu Calcarenite.

Tulki Limestone. The cycle of sedimentation that started with the deposition of the Mandu Calcarenite continued with the Tulki Limestone. Bioclastic packstone (Pl. 2, Figs, A,B) which is almost identical with that of the uppermost Mandu Calcarenite predominates, and contains the same biotic association Lepidocyclina (Nephrolepidina) howchini — Cycloclypeus (Cycloclypeus) sp., suggesting that it was deposited under similar conditions. In contrast to the sediments of the underlying Mandu Calcarenite, bioclastic grainstone , probably deposited in channels or banks, is also present, indicating that environments were less uniform.

The lower Tulki Limestone is characterized by a red colour produced by red soil particles and fossils (Pl. 2, Fig. D), derived by subaerial erosion from an adjacent coastline. The derived fauna, identical with that from the uppermost Mandu Calcarenite, suggests that it was being eroded while the Tulki Limestone was being laid down, a suggestion which is supported by the presence of a minor disconformity (see Fig. 3 and Pl. 2, Fig. A) marking the boundary between the two units in the Badjirrajirra Creek area. Further evidence for subaerial exposure is the presence of solution channels in the Mandu Calcarenite, immediately under the disconformity. The absence of the intense recrystallization features that characterize the uppermost Tulki Limestone (Pl. 2, Figs, C, E, F below the regional disconformity separating it from the Trealla Limestone (Fig. 2) suggests that the Mandu Calcarenite was exposed for a short time only. This is supported by the similarity of the planktonic faunas found immediately below the base of the Tulki Limestone and those from the top of this unit at the same locality, where reworked forms have not been recognized.

Trealla Limestone. The sediments of the lower parts of the Trealla Limestone are identical with those from the uppermost Mandu Calcarenite and contain a very similar biota. It is concluded, therefore, that these beds were deposited under comparable conditions. While they were being laid down, a protective barrier to the west may have begun to form by the deposition of the Pilgramunna Formation. This barrier possibly permitted the development of lagoonal facies, in which packstone (Pl. 2, Fig. G) accumulated. Grainstone (Pl. 2, Fig. H) predominates in the upper parts of the Trealla Limestone in the Cape Range area, and elsewhere in the Carnarvon Basin. It was probably laid down under similar conditions to the 'Bullara Limestone'.

Pilgramunna Formation. The Pilgramunna Formation consists of well sorted quartzose bioclastic grainstone (Pl. 3, Fig. B) interbedded with rare bioclastic packstone (Pl. 3, Fig. A). All grains are well rounded and range from medium to coarse sand-size. The bioclasts, which make up only a small volume, are very similar to those found in the lower part of the Trealla Limestone. The coarse grainsize, absence of mud, degree of sorting, and rounding suggest that it was deposited in a high-energy environment. The Pilgramunna Formation is a strongly linear deposit, stretching north-northeast along the west side of Cape Range, and, as has been suggested, may have formed a protective barrier, on the east side of which the Trealla Limestone accumulated. The quartz was probably carried in a direction approximately parallel to the present coast-line by longshore currents, and mixed with bioclastics derived from nearby accumulations of Trealla Limestone.

Ashmore Reef No. 1 Well

The sediments of the 'Cartier Beds' in Ashmore Reef No. 1 Well are almost identical with those from the lower Mandu Calcarenite, except that they are darker (Pl. 3, Fig. C), probably because of the presence of terrigenous clay minerals. Those of the unnamed calcarenite (Pl. 3, Figs D-G) are very similar to the upper Mandu Calcarenite, both lithologically and faunally. These factors suggest that the sediments of both units originated under similar environmental settings to those for the Mandu Calcarenite.

Batesford Limestone

Bowler (1963) and Foster (1970) have described the sedimentology of the Batesford Limestone. Foster (1970) noted that the limestone was composed of skeletal grainstone (Pl. 3, Fig. H), with most bioclasts being fragmented. Both authors concluded that the limestone was deposited in high-energy shallow water.

Ecology of modern larger foraminifera - a review

Relationship of algae to larger foraminifera

It has been known for some time that certain invertebrates are associated with symbiotic algae. Until recently, few algal symbionts had been recorded from the foraminifera. Winter (1907) described them in the soritid *Peneroplis pertusus*. Rhumbler (1909) and Lee *et al.* (1965) recorded a similar association in some planktonic forms. Cushman (1922) reported green algae in the protoplasm of Orbitolites (=Sorites) and Cycloclypeus. In a later paper (Cushman, 1930), he suggested that the families Camerinidae, Peneropliidae, and Alveolinellidae contain representatives that maintain a symbiotic relationship with green algae, similar to hermatypic corals. Doyle & Doyle (1940) recorded zooxanthellae from Orbitolites duplex and noted that they were not evenly distributed through the protoplasm. Grimsdale (1959) speculated that the fossil 'orbitoidal' foraminifera maintained similar relationships, in explanation of the convergent evolution seen in these forms. Boltovskoy (1963) reported analogous relationships in several genera of smaller foraminifera. Lee & Zucker (1969) studied symbiotic algae in the soritid Archaias, noting that they were concentrated under thin window-like chamber walls and appear to enable the host to utilize Ca^{++}-ion more efficiently; these writers also showed that the host was able to ingest other micro-organisms for food. Both Dietz-Elbrachter (1971) and Röttger (1972a, b; 1973) found that Heterostegina depressa was mobile and able to grow and reproduce without food other than that supplied by symbiotic algae. Röttger (1972a) also noted that the symbionts can be passed on to daughter cells during multiple fission; he also related the very high population densities often associated with this species to its relationship with algal symbionts. Ross (1972) recorded zooxanthellae in Marginopora vertebralis and Alveolinella quoyi; he noted that Marginopora was quite mobile and able to ingest other food sources, and also that the algae were concentrated under the thin walls of the lateral chamberlets.

Haynes (1965) has related the evolution of radial wall structure to the presence of zooxanthellae, noting that many near-shore, thin-walled species appear to be hosts to green algae. He also related the evolution.

of chamberlets, annular growth, and structures such as the marginal cord in some larger foraminifera to the acquisition of symbiotic algae, noting (p. 42) that these features enable the organism 'to reduce the tendency to pile up laminae of shell material into a thick mass', which would impede penetration of light. He has suggested (p. 42) that the shape of larger foraminifera 'can be explained as a compromise between hydrodynamic factors and the requirements of metabolism involving symbiosis'. The sphericity of Gypsina is explained as a 'perfect adaptation of high energy reefal conditions'; discoidal tests increase their hydrodynamic stability by the addition of secondary calcite deposits in the form of pillars, thickened septa, and umbilical bosses. These features strengthen the test without altering its shape and at the same time maintain thin outer chamber walls. Haynes found that in water less than 4.6 m deep the rate of photosynthesis in diatoms fell rapidly, probably as a result of damage from increased short-wave radiation. He suggested that the random arrangement of calcite crystals in the walls of porcellaneous forms scattered damaging radiation, permitting photosynthesis in extremely shallow water.

Many tropical shallow seas are low in nutrients (Ryther, 1963; Beers et al., 1968): in such places the presence of algal symbionts would provide the host organism with a ready source of food, even though its depth range is limited to the euphotic zone. Once the need for foraging is removed, a bilateral symmetry is no longer necessary. Radial symmetry permits growth in all directions and produces a habit more suited to sedentary life. There are many examples in biology of sessile forms that have a basic bilateral symmetry on which is superimposed radial symmetry e.g. cirripeds and serpulid worms. It is well known that almost all larger foraminifera pass through bilateral into radial symmetry early in ontogeny, and throughout phylogeny the bilateral condition is gradually reduced.

In conclusion, the test of larger foraminifera is ideally suited to house symbiotic algae, and hence for sedentary life. Indeed, almost all extant forms are now known to have this association and habit. As the tests of extinct and modern forms are similarly constructed, it is almost certain that extinct forms too maintained a similar life style. This provides a logical explanation for the evolutionary trends toward radial symmetry and increasing size and surface area in all groups of larger foraminifera.

Ecology of modern larger foraminifera

Because of the presence of algal symbionts most of the larger foraminifera are restricted to the euphotic zone, which in clear warm waters extends to depths of about 120 m. Some of the simpler forms (those in which bilateral symmetry is still the main habit) are probably able to live in depths beyond the euphotic zone, for their reliance on algal symbionts for food may not be sufficient to restrict the distributions.

The few studies that have been made suggest that the alveolinids are typically found in high-energy, mud-free, metahaline environments in depths of 0 to 6 m. Reiss & Gvirtzman (1966) have recorded *Borelis schlumbergeri* at depths between 1.5 to 20 m, most abundantly below 3 m. Logan (1959) and Davies (1970) have recorded *Alveolinella quoyi* from similar environments in Shark Bay, Western Australia. Jell *et al.*(1965, p. 277) have recorded this species from 'the channel between Heron and Wistari Reefs', from depths ranging from 18 to 30 m in sand, much of which has been derived from the 'reef edge and reef flat' (Maxwell *et al.*, 1961, p. 225). The enrolled test of this species is well suited to high-energy conditions. Greiner

(1969) considered that porcellaneous forms tended to be more typical of metahaline waters for reasons given earlier (p.).

Archaias spp., Marginopora vertebralis, Sorites spp., and Peneroplis spp. typically occur in metahaline conditions as epibionts attached to the leaves of sea grasses (Blanc-Vernet, 1969; Davies, 1970; Grant et al., 1973; Illing, 1952; Lee & Zucker, 1969; Logan, 1959; Murray, 1970, 1973). However, Marginopora vertebralis is also recorded as being attached to a solid substrate, or living loosely on unconsolidated reef detritus (Ross, 1972), or associated with brown algae (Jell et al., 1965). Ross (1972) has also noted that this species tends to increase in size with depth, because reproduction is either delayed or inhibited if it is swept outside its optimum range; in either case the organism continues to grow. Logan (1959) and Davies (1970) recorded this species down to depths of 8 m in metahaline salinities; Ross (1972) recorded it from oceanic waters. The forms appears to be euryhaline, the only environmental restriction, other than depth, being the requirement for a substrate, suitable for attachment, which is also exposed to solar radiation.

Graham & Militante (1959) recorded Heterostegina suborbicularis from the littoral zone down to depths of 32 m in the Philippines. Lutze et al. (1971) found H. depressa in shallow waters near islands in the shallow waters near islands in the Central Basin of the Persian Gulf, at depths ranging from 15 to 35 m, in association with Amphistegina madagascarensis and Operculina ammonoides. Röttger & Berger (1972 p. 89) recorded H. depressa from 'clear, shallow seas of the tropics... [it] lives on firm substrate and epiphytic on algae'. Röttger (1973) and Spindler & Röttger (1973) showed that this species is attached to the substrate by an ectoplasmic sheath, through which the pseudopodia could penetrate, and from which the animal could escape at will. After reviewing the literature to that time, Adams (1965, p. 305) concluded that 'most species [of *Heterostegina*] are commonest atless than 40 fathoms [7 m].' However, most of the records failed to distinguish between living and dead specimens. The evidence of Graham & Militante (1959), Röttger & Berger (1972), and Röttger (1972a, 1973) suggests that *Heterostegina* can live only within the shallower parts of the euphotic zone; for this reason any records below about 50 m are probably of dead specimens that have been redistributed after death. Cole (1957a, p. 751) concluded that *Heterostegina* (in common with *Alveolinella* and *Borelis*) 'requires warm, shallow protected situations'.

There are very few records of *Cycloclypeus* from Recent seas, and only one of living specimens - that of Cushman (1922) from the Philippines; this record probably refers to an earlier publication (Cushman, 1921) in which he recorded *C. guembelianus* from a depth of 44 m in Buton Strait and from 68 m on a hard sandy bottom near Romblon. Adams (1965, p. 305), on reviewing the literature on Recent and fossil occurrences, concluded that *Cycloclypeus* can 'tolerate a wide depth range, but on the whole favour deeper water, from 50 to 200 fathoms [91 to 316 m]'. If *Cycloclypeus* does contain zooxanthellae, as studies on living specimens of this and other genera suggest, it is unlikely that it can live at greater depths than 120 m, and records from deeper waters are probably of dead specimens which have been redistributed after death.

Operculina is probably the earliest and therefore the most primitive form of the nummulitids (Bannink, 1948) and for this reason is probably the least specialized and least reliant on algal symbionts as a food source. Therefore, it would be expected to have a wider environmental range than either Heterostegina or Cycloclypeus, and to live at depths beyond the range of green algae. Cushman (1921) observed that species of Operculina are more typical of fairly shallow water, with some large forms reaching considerable depths. No distinction was made between living and dead specimens, so it is impossible to ascertain the depth range of living forms from his records. Graham & Militante (1969) recorded Operculina from depths of 2 to 32 m in the Philippines. Cole (1957a) and Adams (1965) both considered that this genus tolerates cooler and deeper water than other nummulitids, and Adams noted that some species seem to be more sensitive to depth; O. bartschi (=O. complanata) has been reported abundantly between 30 and 90 m, and O. venosa in depths of less than 50 m. A study of the available literature indicates that the more complanate and evolute forms tend to occur in shallower water than the more compactly coiled, involute species.

The nummulitids all appear to be stenohaline, being restricted to oceanic waters.

There have been few records of Gypsina from Recent seas, and most of these are of G. globulus. This species is most commonly found on sandy substrates (Graham & Militante, 1959), although it has been recorded on muddy bottoms (Blanc-Vernet, 1969). The structure of the test appears to be adapted for high-energy environments (Haynes, 1965). Under such conditions, G. globulus would be readily transported, and its wide depth range seems to support this conclusion. Todd (1965) considered that it is typical of shallow water, and most records, which are from less than 100 m, support this (Brady, 1884; Cushman, 1921; Graham & Militante, 1959). It has been found at much greater depths, down to 582 m by Cushman (1921), but forms from such depths are almost certainly reworked from shallow waters. G. globulus appears to be typical of warm shallow waters near reefs and in lagoons (Cushman, 1921; Cushman et al., 1954; Graham & Militante, 1959; Todd, 1965), but it can survive in cooler water (Nyholm, 1962). G. vesicularis has been reported only from warm shallow waters (Brady, 1884; Cushman et al., 1954). However, some authors (e.g. Nyholm, 1962) failed to distinguish between the two forms, and others (e.g. Todd, 1965) suggested that they are conspecific. Both arguments imply that G. vesicularis may have a similar range to G. globulus. Nyholm (1962) has found Gypsina attached to stones and bottles, and because G. globulus lacks an attachment area, the species was probably G. vesicularis. Adams (1965, p. 306) concluded that Gypsina 'occurs at all depths: no accurate depth zonation is possible at present', but as noted above, it seems to be most abundant in warm shallow seas.

Some smaller forms dominate a few of the fossil assemblages studied, and so are here considered briefly. Amphistegina has a wide range of test shape, from flat and lenticular to inflated and gibbose; there is also a large variation in number of chambers. Whether or not is is possible to differentiate individual species on these characters is open to debate. The test shape is adapted for moderately high-energy conditions (Logan, 1959; Logan & Cebulski, 1970). Amphistegina is stenohaline, being restricted to oceanic salinities (Bandy, 1954; Blanc-Vernet, 1969; Logan, 1959; Logan & Cebulski, 1970; McKee et al., 1959; Seigle, 1970). Houbolt (1957), McKee et al. (1959), and Blanc-Vernet (1969) have recorded dead tests in large numbers in mud-free sands. McKee et al. (1959) recorded A. madagascariensis in reefal areas down to depths of 8 m. Graham & Militante (1959) reported this species from the littoral zone down to 32 m in the Philippines. Blanc-Vernet (1969) found the same form in the Mediterranean Sea, living in areas of sea grasses and coralline algae, in shallow water. She also noted that it was easily transported after death. Lutze et al. (1971) recorded it from depths of 15 to 35 m in the Persian Gulf. A. lessonii appears to prefer deeper waters than A. madagascariensis (Blanc-Vernet, 1969). Bandy (1954) found A. lessonii down to depths of 122 m, and McKee et al. (1959) noted that it is fairly rare at less than 30 m, but abundant to about 65 m. Logan (1959) did not give depth ranges, but recorded it from shallow channels and reaches, and stated that it is also associated with sea-grass areas in the oceanic parts of Shark Bay. Cushman (1950) and Dietz-Elbrachter (1971) listed Amphistegina as one of several species of foraminifera which have algal symbionts. This is supported by its depth distribution, which appears to be less than 100 m. Murray (1973) considered that the principal range is from 5 to 20 m. Rotalia seems to be restricted to shallow high-energy water associated with reefs; Murray (1973) gave the main depth range as 0-40 m. Boltovskoy (1963) has found zooxanthellae in the protoplasm of this genus. Elphidium is another shallow-water form which has been found in association with sea grasses in both oceanic and metahaline areas by Blanc-Vernet (1969) and Logan & Cebulski (1970). Boltovskoy (1963) and Haynes (1965) have both recorded symbiotic algae in association with Elphidium. Very little is known about the modern distribution of Anomalinella, although it is commonly very abundant in some fossil assemblages. Anomalinella appears to be restricted to the Indo-Pacific region (Cushman et al., 1954; Belford, 1966); Brady (1884) found it at depths of 60 m, and Graham & Militante (1959) reported it from 1.4 to 27 m (occurring abundantly between 4.6 and 6.4 m). Recent records of Carpenteria are very few, and only those of C. proteiformis (the modern species which is most similar to fossil species in this study) have been used in this work. Brady (1884) and Cushman (1921) have documented this species from 30 to 1628 m, but Cushman et al. (1954)

found it typical of reef flat or beach areas.

Depositional environments

Some of the methods outlined on p. , such as the triangular diagrams illustrating the ratios of rotaline, milioline, and textularine forms (Fig. 7) and the percentage of planktonic (%P) (Table I) and benthonic (%B) individuals in the faunas from the various sections studied have been employed to reconstruct the environments in which the rock units and faunal associations discussed above were deposited. Tables II and III summarize the main lithologic and biotic criteria of the relevant rock-stratigraphic units.

Mandu Calcarenite

Lower part. Muddy sediments are typical of low energy environments, where sorting and winnowing by current and wave action are minimal. Such environments are typical of lagoonal, back-reef, or some other setting protected by a barrier (for sediments of shallow-water origin), or at levels in deeper water, well below wave-base.

The average %P for the lower Mandu Calcarenite is 36, which according to Phleger (1960) is typical of values found on the outer continental shelf, in depths of 60 to 100 m, where values range from 10 to 50 percent. The presence of globigerine and globorotaline planktonic forms is indicative of such depths (Douglas & Savin, 1972). The absence of coralline algae, larger foraminifera, and other forms known to have a symbiotic relationship with green algae, suggests that these sediments were deposited below the euphotic zone. The fauna plots in the rotaline field of the triangular plot (Fig. 7), which is within the same area as that for faunas from 'shelf seas' (Wright & Murray, 1972, Fig. 6); this indicates that oceanic salinities prevailed at the time of deposition.

In summary, the evidence suggests that the lower Mandu Calcarenite was deposited at depths just below the euphotic zone, that is, probably a little deeper than 120 m. The initial appearance of larger foraminifera at the top of this lower part (which is the first appearance of _Operculina complanata_) implies that depths were approaching, or possibly within, the lower part of the euphotic zone.

Upper part. The presence of a rich shallow-water biota and the absence of deep-water features in the packstone (Pl. 1, Figs B-D) of the upper Mandu Calcarenite indicate that these sediments were deposited in low-energy shallow water. As there is no evidence for any form of barrier (reefal or otherwise) to the west of Cape Range at the time of deposition behind which fine-grained sediments could accumulate, some other mechanism must be invoked to explain the origin of these rocks. Davies (1970) noted that sediments characterized by skeletal fragments of coralline algae, encrusting foraminifera, and bryozoa, and with a high mud content, are typical of sea-grass communities, in which mud produced by skeletal breakdown in high-energy conditions is trapped by a leaf baffle that subsequently decays without leaving any trace. Because the sediments of the topmost beds of the upper Mandu Calcarenite have the same characteristics as those described above, it is concluded that they were deposited as a direct result of the influence of sea grasses. A baffle can also be produced by other organisms such as _Halimeda_ or other large forms. The muddy sediments that contain a shallow-water fauna, with few encrusting foraminifera, rare coralline algae, and abundant large discoidal foraminifera (pl. 1, Fig. B), were probably deposited in depths below the range of sea grasses, under a baffle produced by the large tests of _Lepidocyclina_ (_Eulepidina_) or _Cycloclypeus_.

The %P for the upper Mandu Calcarenite ranges from 3 to 33, with the lowest values at the top. The higher values are typical of depths less than 100 m, and the lower ones of depths less than 60 m (Phleger, 1960). This is supported by the presence of large populations of Globigerinoides, which are most abundant at less than 100 m in modern seas (Bé, 1960; Jones, 1968). Coralline algae are present throughout, but only become abundant in the uppermost beds. The abundance of larger and smaller foraminifera which are known to contain symbiotic algae at the present day (e.g. Cycloclypeus, Operculina, Amphistegina, Anomalinella, Rotalia, etc.) supports the conclusion that deposition took place within the euphotic zone, that is in depths of less than 120 m. The presence of sea-grass communities in the topmost beds indicates very shallow water. Davies (1970) found that sea grasses extend to 12 m but are best developed in depths of less than 7.6 m. Ginsburg (1956, p. 2409) stated that 'turtle grass has no bathymetric limit in the back-reef, the dense carpets are most abundant in water deeper than 6 feet [2 m]'; the back-reef area in Florida Bay is no deeper than 12 m. Lynts (1966) found turtle grass in depths shallower than 2.7 m, but gave no lower limit. Thus the appearance of typical sea-grass deposits in the uppermost Mandu Calcarenite (Pl. 1, Figs. C,D) suggests that it was deposited in depths of less than 12 m.

'Bullara Limestone'

Most of the 'Bullara Limestone' was deposited in a moderately high-energy environment, where most or all of the mud fraction was removed by the action of currents or waves. In such a setting, mixing of faunas from different environments may be expected. The presence of articulated coralline algae and encrusting foraminifera suggests that some of the fauna was derived from adjacent sea-grass communities, and indeed, the presence of packstone (Pl. 1, Fig. G) suggests that sea grasses may have been directly responsible for the accumulation of some of the limestone. Some of the smaller miliolids show evidence of boring by blue-green algae and there are many pellets which show evidence that they may have been produced by the alteration of miliolids or coralline algae as desribed by Kendall & Skipworth (1969). Such blue-green algae are common at 30 m in coastal waters at Woods Hole, USA, and have been found at a depth of 75 m in the Caribbean Sea (Golubić, 1973, p. 470). They are commonly found in conditions of increased salinities (Kendall & Skipworth, 1969; Davies, 1970). The presence of stenohaline forms, typical of oceanic salinities (Amphistegina, Heterostegina and Operculina), suggests that the pellets were derived from a different environment. The presence of Lacazinella and Halkyardia suggests that Eocene rocks were exposed to subaerial erosion at the time of deposition of the 'Bullara Limestone'. Nodular coralline algae are present (Pl. 1, Figs. G,H); these forms are typical of high-energy conditions and are commonly found in areas of mud-free sands at depths of less than 30 m (Johnson, 1961). They may be in situ, and if so, indicate depths within the euphotic zone. The rarity of encrusting and larger foraminifera in the lower parts of the 'Bullara Limestone' suggests that it was deposited farther from sea-grass communities, probably in deeper waters. Planktonic forms are almost completely absent, which is a feature of the very shallow nearshore turbulent zone in depths of less than 20 m (Phleger, 1960). The fauna plots in the field for 'normal marine lagoons' of Wright & Murray (1972) on the triangular diagram (Fig. 7). Thus, it is concluded that the 'Bullara Limestone' was deposited in a shallow high-energy environment, with oceanic salinities, and within the euphotic zone in depths which may have been less than 20 m. The upper parts were laid down in shallower water than the lower.

Tulki Limestone

The bioclastic packstone (Pl. 2, Fig. B) from the Tulki Limestone is similar to that of the uppermost Mandu Calcarenite (Pl. 1, Figs. C,D) and was probably deposited under the same conditions. The packstone from the lower part contains the same Lepidocyclina (Nephrolepidina) howchini - Cycloclypeus (Cycloclypeus) eidae or C. (C.) carpenteri association as that of the uppermost Mandu Calcarenite (Table II). However, as noted on page , much of this appears to have been reworked from the lower unit.

The bioclastic grainstone (Pl. 2, Fig. D) contains the same larger foraminiferal association as the packstone. The mud-free lithology suggests that it was deposited on a current- or wave-swept bottom. The average %P is less than 2, suggesting very shallow water (Phleger, 1960). The fauna plots in the 'hypersaline lagoon' or 'normal marine lagoon' fields of Wright & Murray (1972) (Fig. 7). This suggests that the fauna has been derived from both oceanic and metahaline sea grass communities. The sediments contain well rounded bioclasts, which are fairly well sorted, and may represent sands laid down in very shallow water or even as a beach deposit.

The bioclastic packstone from near the top of the Tulki Limestone contains the Lepidocyclina (Nephrolepidina) howchini - Marginopora vertebralis association, which is a different larger foraminiferal assemblage from that from similar sediments in the lower parts of the unit. However, neither the %P or the triangular plots differ appreciably from those of the top of the Mandu Calcarenite, which suggests little change in overall environmental conditions.

The presence of a large population of reworked forms, some sediments which were probably deposited under a sea-grass baffle, and others deposited on a bank or beach, or in a channel, suggest that the Tulki Limestone was deposited in quite shallow water, probably less than

12 m, with salinities commonly oceanic but occasionally metahaline. The absence of reworked forms at the top of the unit may indicate a slight increase in water depth or a greater distance from shore, but with water depths still less than 12 m.

Trealla Limestone

Lower part. Bioclastic packstone (Pl. 2, Fig. G) from the lower Trealla Limestone is restricted to the Cape Range area, and contains a typical Lepidocyclina (Nepholepidina) carpenteri - Marginopora vertebralis association. The average %P is 2, suggesting depths of less than 20 m (Phleger, 1960). The fauna plots in the 'shelf seas' field of Wright & Murray (1972) (Fig. 7). The presence of stenohaline forms such as Amphistegina, Cycloclypeus, and Operculina indicates oceanic conditions. Both fauna and sediments are similar to those from the top of the Mandu Calcarenite and Tulki Limestone, and are typical of sea-grass areas.

The bioclastic packstone was deposited under a sea-grass baffle, in normal oceanic salinities, in conditions protected by a barrier which was being formed to the west. Depths were probably less than 12 m.

Upper part. The faunas, which contain large populations of miliolines, plot in the milioline field of the triangular diagram (Fig. 7). The presence of textularine forms has caused the plots to fall outside the 'hypersaline lagoon' field of Wright & Murray (1972); this suggests that textularine forms may not be typical of metahaline communities. However, such forms are common throughout the grainstone of the Trealla Limestone (Pl. 2, Fig. H); so some arenaceous forms could presumably survive in these salinities. The absence of planktonic forms may be the result of restricted circulation, and this, together with the rarity of oceanic forms such as Amphistegina, Cycloclypeus, and Operculina, and the presence of boring blue-green algae, suggests metahaline salinities; the boring algae are indicative of depths of less than 75 m (Golubić, 1973); this gives credence to the suggestion made on page that a protective barrier, the Pilgramunna Formation, restricted circulation of sea water, permitting salinities to rise during the deposition of the grainstone of the upper Trealla Limestone. The grainstone also contains nodular algae, and alveolinids (Borelis and Flosculinella), and these, together with the roundness of the bioclasts, indicate accumulation in high-energy conditions within the shallower parts of the euphotic zone. The presence of encrusting and attached forms, Marginopora vertebralis, Sorites spp., Peneroplis spp., and articulated coralline algae, suggests that sea-grass communities were important contributors to the sediment.

Pilgramunna Formation

The fauna from the Pilgramunna Formation is very poor; the bioclasts consist of rounded fragments of foraminifera, other invertebrates, and articulated coralline algae (Pl. 3, Figs, A,B). The larger foraminifera are typical of the Lepidocyclina (Nephrolepidina) howchini - Marginopora vertebralis association, which was probably derived from post-mortem transportation from the packstone of the lower Trealla Limestone. The well sorted quartzose sands appear to have been transported by longshore currents (see p.), from outside the North West Cape area. The Pilgramunna Formation was deposited in high-energy conditions in very shallow water; the carbonate grains were probably derived from nearby sea-grass communities, which now are represented by the deposits forming the lower Trealla Limestone.

Other areas

The palaeoecology of the 'Cartier Beds' and unnamed calcarenites in Ashmore Reef No. 1 Well and the Batesford Limestone in Victoria has been discussed on page .

Conclusions

The changing assemblages of larger foraminifera within the Cape Range and Yardie Groups in the North West Cape area are related to changing environmental conditions. For this reason the presence of a particular faunal assemblage can be used for environmental interpretation, provided sedimentological evidence is taken into account.

The following conclusions can be made (see also Fig. 8):

(1) Operculina complanata - Gyosina howchini association: this is typical of high-energy conditions, indicated by the presence of nodular coralline algae. Depths were probably less than 30 m (see p).

(2) Lepidocyclina (Eulepidina) ephippioides - Heterostegina borneensis association: the abundance of encrusting and attached forms suggests that this assemblage was typical of sea-grass communities at depths of 12 m or less, in sheltered situations.

(3) Operculina complanata - smaller benthonic foraminiferal association: the sediments are typical of low-energy conditions and were probably deposited below wave-base. Larger foraminifera are never abundant, and the prevalence of juveniles suggests that they were swept into water too deep for their survival. This, together with the absence of coralline algae, indicates depths near the base of the euphotic zone, that is, close to 120 m.

(4) Cycloclypeus (Cycloclypeus) eidae - Operculina complanata association: the sediments are typical of low-energy conditions, and in this respect the association is very similar to that of (3). However the presence of large adult specimens of Cycloclypeus suggests that depths were shallower, being within the euphotic zone and, therefore, less than 120 m. The rarity of coralline algae, which were probably transported from shallower

water, may indicate that depths were near the base of the euphotic zone. The upper limit of this association overlaps with (5) below.

(5) *Lepidocyclina* (*Eulepidina*) *badjirraensis* - *Cycloclypeus* (*Cycloclypeus*) *eidae* association: the sediments contain a high proportion of mud, suggesting similar conditions to (3) and (4) above. However, large numbers of the large discoidal foraminifera *Lepidocyclina* (*Eulepidina*) may have provided an effective baffle which could trap fine-grained sediment derived from skeletal breakdown in a fairly high-energy environment. The large tests are found only in the lower parts, and size gradually diminishes towards the top. Ross (1972) recorded an increase in size and age of *Marginopora* with increasing depth of water. The same explanation is advanced here. Coralline algae are quite rare in the lower parts, but become common higher. It is concluded that depths were more shallow than for (4), but greater than 12 m, overlapping with (4) in deeper water.

(6) *Lepidocyclina* (*Nephrolepidina*) *howchini* - *Cycloclypeus* (*Cycloclypeus*) *eidae*/*carpenteri* association: as noted on pages and , the fauna and sediment contain characterics typical of sea-grass communities, implying depths of less than 12 m, and oceanic salinities in open situations.

(7) *Lepidocyclina* (*Nephrolepidina*) *howchini* - *Marginopora vertebralis* association: as noted on page , both sediments and fauna of this zone are typical of sea-grass communities, and therefore were probably deposited in less than 12 m. The presence of *Marginopora vertebralis* differentiates this association from (6). Even though this form is euryhaline in modern seas, and oceanic forms such as *Amphistegina* and *Cycloclypeus* are also present, the last two are much less common than in (6). This may imply that the salinities were metahaline.

(8) *Austrotrillina howchini* - *Flosculinella bontangensis* association: the absence of mud is indicative of fairly high environmental energies, a conclusion which is supported by the presence of alveolinids

(Borelis and Flosculinella) and nodular coralline algae. Miliolines dominate the assemblages, and show evidence of alteration by boring algae. These features indicate depths of less than 30 m (see p), metahaline salinities, and high-energy conditions. Marginopora and Peneroplis could well have been derived from adjacent sea-grass communities.

Palaeoecology of selected larger and other foraminifera

Miliolinaceae

Austrotrillina. No representatives of this genus are extant. In the North West Cape area it is quite rare and is confined to the grainstones of the 'Bullara' and Trealla Limestones. Because these sediments, in particular the latter, were deposited in shallow, metahaline conditions, it is concluded that Austrotrillina was restricted to metahaline salinities, in common with most modern miliolids.

Lacazinella. As noted earlier (p), Lacazinella has probably been reworked from the middle Eocene Giralia Calcarenite. The shape of the test, which is very similar to the alveolinids, suggests that it was adapted for high energy conditions.

Borelis and Flosculinella. Alveolinids in modern seas are confined to warm, shallow, metahaline waters of fairly high energy. Alveolinella, as noted on page , is known to have a symbiotic relationship with green algae, which would confine it to shallow waters. Borelis is found only in the grainstones of the 'Bullara' and Trealla Limestones, and Flosculinella is confined to the upper Trealla Limestone. As noted earlier the Lepidocyclina (Eulepidina) ephippioides - Heterostegina borneensis association may have been derived from different environments, including metahaline ones. However, the Austrotrillina howchini - Flosculinella bontangensis association is typical of metahaline conditions, which implies that Borelis and Flosculinella, in common with Austrotrilline, has similar environmental ranges to modern alveolinids.

Peneroplis, Sorites, and Marginopora. These three genera are represented in Recent seas, and their environmental ranges have already been discussed (pp.). Both Peneroplis and Sorites are confined to the upper 'Bullara' and Trealla Limestones. The upper Trealla Limestone contains a typical metahaline assemblage, and for this reason it is assumed that the two forms have had similar environmental ranges up to the present day.

Marginopora, which is a euryhaline form in modern seas, is attached to a variety of substrates and is confined to warm, shallow water. It has been recorded with a metahaline fauna from the top of the 'Bullara Limestone', which contains a typical lower Tertiary e assemblage. Adams (1970) noted that it is common in Tertiary f sediments, a conclusion which is supported by this study, for Marginopora is very common in the Trealla Limestone. Its presence in both the Lepidocyclina (Nephomolepidina) howchini - Marginopora vertebralis and the Austrotrillina howchini - Flosculinella bontangensis associations indicates that it has maintained a similar environmental range to the present day. Thus, early in its evolution, Marginopora was probably restricted to metahaline environments, in common with its relatives the peneroplids and soritids; and during the time of lower Tertiary f it adapted to oceanic conditions, permitting its survival in a wider range of habitats.

Nummulitidae

Operculina. This genus is found in all the larger foraminiferal associations and so has a very wide distribution. It is very rare in the upper Trealla Limestone, and was probably, therefore, stenohaline, preferring oceanic salinities as it does in the Recent. Its stratigraphic range also implies that it might not have been confined to the euphotic zone, but had a wide depth range.

Heterostegina. Modern species are confined to very shallow sheltered oceanic waters. Amphistegina is present in the upper 'Bullara Limestone' with Heterostegina borneensis, indicating that they both had similar ranges. H. cf. suborbicularis is found only in the Lepidocyclina (Nephrolepidina) howchini-Cycloclypeus (Cycloclypeus) eidae/carpenteri association, where it is extremely rare; this also seems to have had a similar range to modern forms.

Cycloclypeus. In modern seas, Cycloclypeus seems to be restricted to the deeper parts of the euphotic zone. However, in the North West Cape area, it is found in the larger foraminifera assemblages of the uppermost Mandu Calcarenite and Tulki and lower Trealla Limestones. As noted earlier (p), the Cycloclypeus (Cycloclypeus) eidae - Operculina complanata association was probably near the base of the euphotic zone, whereas the associations of Lepidocyclina (Nephrolepidina) howchini - Marginopora vertebralis were typical of depths of less than 12 m. Thus Cycloclypeus may have had a wider environmental range in the past, and today is confined to the deeper parts of its earlier range. The sediments in which both of the associations based on Lepidocyclina (Nephrolepidina) howchini occur are typical of sea-grass communities, and it is postulated that Cycloclypeus was attached to the leaves of such plants, in a similar manner to Heterostegina today. Cycloclypeus is also present in the Batesford Limestone, the fauna of which was derived from a hard substrate (Foster, 1970). This genus may have been able to survive on a wide range of substrates, provided that they were suitable for attachment, and was probably stenohaline, being confined to oceanic waters, as it is today.

Miogypsina

In common with other larger foraminifera, the glassy test wall of *Miogypsina* is well adapted to enclose zooxanthellae. The production of lateral chambers and pillars would provide a strong test that would resist erosion in high energy environments, but at the same time maintain thin lateral walls that allowed easy penetration of light. Hence the production of strengthening features, such as thicker laminae or pillars, might indicate the degree of environmental energy.

M. (*Miogypsinoides*). This subgenus is confined to the *Lepidocyclina* (*Eulepidina*) *badjirraensis* - *Cycloclypeus eidae* and *Lepidocyclina* (*Nephrolepidina*) *howchini* - *Cycloclypeus* associations. Both assemblages are thought to have lived in less than 50 m depth and in oceanic salinities.

M. (*Lepidosemicyclina*). This subgenus is confined to the two associations based on *Lepidocyclina* (*Nephrolepidina*) *howchini* and has not been found in the same sample as *M.* (*Miogypsinoides*). It is thought to have inhabited shallow-water, particularly those of sea-grasses in oceanic salinities.

Amphistegina

Amphistegina is always associated with oceanic forms such as globigerinids, and has maintained a similar stenohaline, shallow-water range throughout its existence.

Gypsina

The spherical shape of *G.* *globulus* is believed to be a sound indicator of high-energy environments. This species is most numerous in the *Lepidocyclina* (*Nephrolepidina*) *howchini* - *Cycloclypeus* (*Cycloclypeus*) *eidae*/*carpenteri* association, which lived in shallow waters of fairly high energy. Because it is found in almost all larger foraminiferal assemblages, it must have had a wide environmental range, as it has today.

G. howchini is very similar morphologically to the modern *G. vesicularis*. It is found in the 'Bullara Limestone' and also in the two associations based on *Lepidocyclina* (*Nephrolepidina*) *howchini*, which suggests that it was associated with sea-grass communities; it is also found in the Batesford Limestone, where it occurs with a fauna derived from a solid substrate. This implies that *G. howchini* was probably stenohaline, living in oceanic conditions, where a suitable substrate onto which it could become attached was available.

G. mastaelensis is very rare in the lower Trealla Limestone, but is more common in the upper. Its morphology indicates that it was an attached form, and the failure to find it attached to another object suggests that it was living on a surface which has subsequently decayed, or that the method of cementation was organic. The association with a fauna known to contain forms that now live on sea grasses might imply that it, too, lived on such plants. Its absence or rarity in oceanic assemblages indicates that it was typical of metahaline environments.

Carpenteria

Carpenteria is most numerous in assemblages of the uppermost Mandu Calcarenite and Tulki Limestone, although it is found to range into the lower Mandu Calcarenite. It was obviously attached to a solid substrate, which may or may not be preserved. In modern times it is most typical of shallow-water conditions, which probably was also true for the past.

Lepidocyclina

Lepidocyclina is most common in assemblages typical of oceanic salinities. It is rare in the grainstone of the upper Trealla Limestone, and specimens are all small and broken, suggesting that it was displaced into an environment in which it could not survive. The thin lateral walls of the chambers and large discoidal test are characters typically developed in forms that maintain a symbiotic relationship with algae. Indeed, its confinement to the shallower water deposits supports this conclusion. In most populations there are specimens, flattened or even concave on one side, that may have been attached. Ross (1972), Röttger (1973), and Spindler & Röttger (1973) have described the mechanism by which Marginopora and Heterostegina are attached to the substrate. According to these authors, neither is cemented to the surface, but is attached by a sheet of rigid ectoplasm which can be absorbed or left behind when the animal needs to move to another locality. A similar mechanism is suggested for Lepidocyclina, which would allow the organism some free movement, and permit its reorientation to light. However, it is apparent that not all specimens of Lepidocyclina were attached, a characteristic it shared with Recent Marginopora. In some forms (those from Ashmore Reef No. 1 Well, core 2 - Pl. 3, Fig. F) the test is almost spherical, with a thick central zone surrounded by a narrow peripheral flange somewhat reminiscent of Gypsina globulus; this sphericity is probably an adaptation to high-energy environments where suitable substrates were absent or attachment was difficult to maintain. Moreover, the degree of pillar development can also be related to the amount of environmental stress, for it provides a strengthening of the test and greater resistance to erosive action, while at the same time it maintains thin lateral walls to the chambers. In lower-energy regimes the test does not need the same protection and so pillars are not developed. In all populations, a wide range of variation is found; some forms have well developed pillars, in others the pillars are weak or absent. A feature of evolutionarily advanced populations is the development of specimens with radiating ridges extending from the central zone to the peripheral flange, which give the test a stellate pattern. These ridges are formed by a local increase in the number of lateral chambers, and at the same time there are fewer in the intervening areas. The effect is to produce strengthened ridges which would provide protection and support for the delicate areas in between, where the thin walls so produced would provide a larger area over which photosynthesis (by the contained zooxanthellae) would take place. This hypothesis explains the function of a feature which is obviously of great evolutionary importance, and has been specifically selected by evolutionary pressure. Such features must have a significant part to play in the evolution of any group of organisms and so require some explanation.

L. (Eulepidina). This subgenus is confined to the upper 'Bullara Limestone' and parts of the upper Mandu Calcarenite. In the former it is associated with species that are found in sea-grass assemblages, under oceanic conditions. Since it is larger than the accompanying specimens of L. (Nephrolepidina), L. (Eulepidina) may not have been attached to sea grasses, but may have lived freely on the bottom mud. However, some specimens figured by other authors (e.g. Yabe & Hanzawa, 1929; Cole, 1957b; Hanzawa, 1957) are very concave on one side, and so may have been attached to some object. In the upper Mandu Calcarenite, L. (Eulepidina) becomes progressively larger towards the base. Ross (1972) has noted that the size of Marginopora increases with depth of water. The same explanation is advanced for the large specimens of L. (Eulepidina), and this is supported by the gradual disappearance of coralline algae towards the base. The size of the embryconch associated with the larger tests also increases, implying the same relationship to depth. Thus, it is concluded that this subgenus was living at depths below the level of sea grasses, but within the euphotic zone. However, during the earlier periods of its stratigraphic range, L. (Eulepidina) may have lived in shallower water. As noted earlier, Cycloclypeus is now found only at the deeper levels of its former depth range, which suggests that towards the end of their biostratigraphic history, some larger foraminifera move progressively to the deeper part of their environmental range, possibly as a response to invasion of similar environments by newly evolving forms, with which they were unable to compete.

L. (*Nephrolepidina*). This subgenus is restricted to the upper 'Bullara Limestone', uppermost Mandu Calcarenite, and Tulki and Trealla Limestones. In the upper Trealla Limestone it is always very small and very rare, suggesting that it was swept into environments where it could not survive. In all the other zones it is associated with sea-grass assemblages. However, the sole population of *L.* (*Nephrolepidina*) that is associated with large specimens of *L.* (*Eulepidina*) is of a different species, which apparently could tolerate deeper water, and may have been attached to the tests of *L.* (*Eulepidina*). *L.* (*Nephrolepidina*) is present in the Batesford Limestone, the fauna of which may have been derived from forms attached to a hard bottom and not sea-grasses. Thus this subgenus probably was able to live on a variety of substrates, but was confined to shallow waters (possibly less than 12 m), similar to the modern distribution of *Marginopora*.

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Table I. Percentages of the various foraminiferal elements found in the rock units of the North West Cape area. (gnst.=grainstone; pkst.=packstone; wkst.=wackestone).

Table II Lithologic and biotic characteristics of the rock units of the North West Cape area. (gnst.=grainstone; pkst.=packstone; wkst.=wackestone).

Table III. Lithologic and biotic characteristics of the Batesford Limestone and the rock units in Ashmore Reef No. 1 Well. (gnst.=grainstone; pkst.=packstone; wkst.=wackestone).

Fig. 1 Locality map showing the areas treated in this paper.

Fig. 2 Diagrammatic east-west cross-section of the North West Cape area, showing the stratigraphic relationships between the Oligo-Miocene rocks.

Fig. 3 Stratigraphic summary of the Oligo-Miocene section in Ashmore Reef No. 1 Well, Bonaparte Gulf Basin. (recry.=recrystallized; pkst.=packstone; wkst.=wackestone).

Fig. 4 Composite stratigraphic sections from three localities in the North West Cape area.

Fig. 5 Stratigraphic summary of the Batesford Limestone, Batesford (modified after Carter, 1964, fig. 15).

Fig. 6 Triangular plot based on Recent faunas from three different environments (modified after Murray, 1973, fig. 102).

Fig. 7 Triangular plots for foraminiferal assemblages from four rock-stratigraphic units in the North West Cape area.

Fig. 8 Diagrammatic reconstruction of the environments occupied by the larger foraminiferal associations discussed in this paper.

Plate 1. Figs. A-D, Mandu Calcarenite; Figs. E-H, 'Bullara Limestone'.

Fig. A Quartzose-bioclastic wackestone. Sample UWA 70543. x 4.5

Fig. B Bioclastic packstone with numerous tests of *Lepidocyclina* (*Eulepidina*) *badjirraensis*. Sample UWA 68313. x 3

Fig. C Bioclastic packstone with *Lepidocyclina* (*Nephrolepidina*) *howchini* and *Amphistegina quoii*. Sample UWA 68324. x 4.5

Fig. D Bioclastic packstone with *Lepidocyclina* (*Nephrolepidina*) *howchini*, *Cycloclypeus eidae/carpenteri*, and *Amphistegina quoii*. Sample UWA 68321. x 4.5

Fig. E Fine grained bioclastic grainstone. Sample UWA 53674. x 4.5

Fig. F. Bioclastic packstone with *Lepidocyclina* (*Nephrolepidina*) *sumatrensis*, *Heterostegina borneensis*, and *Amphistegina bikiniensis*. Sample UWA 70600. x 4.5

Fig. G Bioclastic packstone with *Operculina complanata*, *Gypsina howchini*, and *Amphistegina bikiniensis*. Sample UWA 53675. x 3.5

Fig. H Slightly recrystallized bioclastic grainstone with coralline algal fragments and rounded lithoclasts. Sample UWA 53676. x 4.5

Plate 2. Fig. A, Mandu Calcarenite; Figs. B-F, Tulki Limestone; Figs. G,H, Trealla Limestone.

Fig. A Bioclastic packstone with *Lepidocyclina* (*Nephrolepidina*) *howchini*, *Cycloclypeus eidae/carpenteri*, *Operculina complanata*, and *Amphistegina quoii* overlying a minor disconformity on bioclstic packstones containing a similar fauna; note the truncated fragments of *Halimeda*. Sample UWA 68324. x 4

Fig. B Bioclastic packstone with *Lepidocyclina* (*Nephrolepidina*) *howchini*, *Cycloclypeus eidae*/*carpenteri*, and *Halimeda*. Note the solution channels linking the bioclasts. Sample UWA 70473. x 4.5

Fig. C Recrystallized limestone from immediately below the regional unconformity separating the Tulki and Trealla Limestones. Note the altered specimen of *Lepidocyclina*. Sample UWA 51903. x 6.5

Fig. D Bioclastic grainstone *Lepidocyclina* (*Nephrolepidina*) *howchini* and *Operculina complanata*. Note the presence of reworked fossils with dark infilling and rounded soil fragments (dark lithoclasts). Sample UWA 51893. x 4.5

Fig. E Recrystallized limestone similar to Fig. C above. Sample UWA 68349. x 4.5

Fig. F Recrystallized limestone similar to Figs C and E above. Bioclasts are not identifiable but their outlines have been preserved. Sample 7164-0357. x 4

Fig. G Bioclastic packstone with *Lepidocyclina* (*Nephrolepidina*) *howchini*, *Cycloclypeus* (*Cycloclypeus*) sp., *C.* (*Katacycloclypeus*) sp., and *Amphistegina quoii*. Note the nodular coralline alga infilled with spar. Sample UWA 68342. x 4.5

Fig. H Bioclastic grainstone with *Flosculinella bontangensis*, *Sorites* sp., and numerous smaller miliolines and rounded lithoclasts. Sample UWA 51909. x 4.5

Plate 3. Figs. A-B, Pilgramunna Formation; Figs. C-G, Ashmore Reef No. 1 Well; Fig. H, Batesford Limestone.

Fig. A Quartzose-bioclastic packstone with fragments of coralline algae and foraminifera. Sample UWA 68353. x 4.5

Fig. B Quartzose-bioclastic grainstone with similar bioclasts to Fig. A above. Sample CR 77. x 4.5

Fig. C Bioclastic wackestone from the 'Cartier Beds'. Sample UWA 70610. x 4

Fig. D Bioclastic packstone with *Lepidocyclina* (*Eulepidina*) *badjirraensis*, *Cycloclypeus eidae*, *Operculina complanata*, and *Amphistegina quoii*, from the lower unnamed calcarenite. Compare with Plate 1, Fig. B. Sample UWA 70606. x 4

Fig. E Bioclastic packstone with *Lepidocyclina* (*Nephrolepidina*) *howchini*, *Cycloclypeus eidae/carpenteri*, *Miogypsina* (*Lepidosemicyclina*) *thecideaeformis*, and crustose coralline algae, from the unnamed calcarenite. Sample UWA 70603. x 4

Fig. G Bioclastic packstone with microspheric specimens of *Lepidocyclina* (*Nephrolepidina*) *howchini* from the upper unnamed calcarenite. Sample UWA 72226. x 4.5

Fig. H Bioclastic grainstone with *Lepidocyclina* (*Nephrolepidina*) *howchini*, *Cycloclypeus carpenteri*, *Operculina complanata*, *Gypsina howchini*, and *Amphistegina quoii*. Sample UWA 10653. x 4

Table I

ROCK UNIT	Lithology		%				
			Textularines	Miliolines	Rotalines	Planktonics	Larger Foraminifera
TREALLA LIMESTONE	gnst	mean	9·9	45·3	44·8	0	12·3
		Range	9-12	17-78	11-73	0	4-21
	pkst	mean	6·9	7·4	85·7	2·2	23·7
		Range	2-12	2-27	60-94	0-3	5·45
TULKI LIMESTONE	gnst	mean	13·0	16·8	70·2	1·6	6·7
		Range	4-24	10-27	62-79	1-2	6-8
	pkst	mean	4·7	3·3	92·0	0·7	34·1
		Range	0-12	0-4	84-99	0-3	16-67
MANDU CALCARENITE	pkst	mean	1·0	0·5	98·5	14·6	19·4
		Range	0·6-3	0-3	94-99	3-33	3-42
	pkst/wkst	mean	0·6	0	99·4	35·6	0
		Range	0-7	0	93-100	2-68	0
"BULLARA LIMESTONE"	gnst	mean	0·4	10·4	89·2	0·4	14·4
		Range	< 1	2-19	80-98	< 1	1-20
	pkst/gnst	mean	5·4	28·1	66·5	0	0·8
		Range	5-6	19-38	57-75	0	0-2

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Percentage of the various foraminiferal elements found in the rock units of the North West Cape area.

Table II

ROCK UNIT		LITHOLOGY	KEY PLANKTONIC GENERA	FIELD OF TRANGULAR PLOF (Fig.8)	MAIN FAUNAL ELEMENTS STILL EXTANT	LARGER FORAMINIFERAL ASSOCIATION	FLORA	OTHER FAUNAL ELEMENTS
Pilgramunna Formation		Qtz-bioclastic gnst	none		*Marginopora* *Sorites*	*Lepidocyclina (N.) howchini* - *Marginopora vertebralis*	Articulated Coralline Algae	Corals Bryozoans Echinoids
Trealla Limestone	upper	bioclastic gnst	none	Milioline / Rotaline	*Peneroplis, Sorites, Marginopora Borelis*, encrusting forms.	*Austrotrillina houchini* - *Flosculinella bontangensis*	Nodular + Articulated Coralline algae Boring blue-green algae	Corals Bryozoans, Molluscs, Echinoids
	lower	bioclastic pkst	*Orbulina* *Globinerinoides*	ROTALINE	*Marginopora, Operculina, Cycloclypeus, Gypsina, Amphistegina*, encrusting forms	*Lepidocyclina (N.) howchini* – *Marginopora vertebralis*	Nodular + Articulated Coralline, algae	Corals, Bryozoans, Molluscs, Echinoids
Tulki Limestone	upper	bioclastic pkst	*Praeorbulina* *Globigerinoides*					
	lower	bioclastic pkst/gnst	*Globigerinoides*		*Operculina, Cycloclypeus, Gypsina, Amphistegina, Rotalia*, encrusting forms.	*Lepidocyclina (N.) howchini* – *Cycloclypeus eidae/carpenteri*	Articulated Coralline algae	Bryozoans, Echinoids
Mandu Calcarenite	upper	bioclastic pkst	*Globigerinoides*					
					Operculina, Cycloclypeus, Gypsina Amphistegina, Anomalinella Elphidium	*Lepidocyclina (E.) badjirraensis* - *Cicloclypeus eidae*	none	Bryozoans, Echinoids
			Globorotalia obesa			*Cycloclypeus eidae* - *Operculina complanata*	none	Bryozoans, Echinoids
			Globigerina		*Operculina, Elphidium, Anomalina Gyroidinoides, Eponides*	*Operculina complanata* - Smaller bethonic foraminifera	none	Bryozoans, Echinoids
	lower	bioclastic wkst	*Globorotalia Kugleri* *Globigerina*		Smaller benthonic forms only	none	none	Bryozoans
"Bullara Limestone"	upper	bioclastic gnst	*Globorotalia* *Globigerina*		*Sorites, Borelis, Operculina Heterostegina, Gypsina, Amphistegina, Elphidium*, encrusting f.	*Lepidocyclina (E.) ephippioides* - *Heterostegina borneensis*	Nodular + Articulated Coralline algae Boring blue-green algae	Bryozoans, Molluscs, Echinoids
	lower	bioclastic pkst/gnst	none		*Operculina, Gypsina, Amphistegina, Rotalia, Elphidium*	*Operculina complanata* - *Gypsina howchini*	Nodular + Articulated Coralline algae	Bryozoans, Echinoids

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Lithologic and biotic characteristic of the rock units of the North West Cape area (grainstone, packstone wackstone)

Table III

AREA	ROCK UNIT		LITHOLOGY	KEY PLANKTONIC GENERA	MAIN FAUNAL ELEMENTS STILL EXTANT	LARGER FORAMINIPERAL ASSOCIATION	FLORA	OTHER FAUNAL ELEMENTS
ASHMORE REEF NO.I WELL	Unnamed Calcarenites	upper	bioclastic pkst	none	*Marginopora*, *Operculina*, *Cycloclypeus*, *Gypsina* *Amphistegina*, encrusting forms.	*Lepidocyclina (N.) howchini* – *Marginopora vertebralis*	Crustose + Articulated Coralline algae	Bryozoans
		lower	bioclastic pkst	*Globigerinoides*	*Operculina*, *Cycloclypeus*, *Gypsina*, *Amphistegina*, encrusting forms	*Lepidocyclina (N.) howchini* – *Cycloclypeus eidae/carpenteri* to *Lepidocyclina (E.) badjirraensis* – *Cycloclypeus eidae*	Crustose + Articulated Coralline algae	Echinoids
	"Cartier Beds"	upper	bioclastic pkst / wkst	*Globigerinoides* *Globigerina* *Globorotalia*	*Operculina*, *Cycloclypeus*, *Gypsina*, *Amphistegina*	*Cycl. eidae* – *Operc. complanata* to *Operc. complanata* – Smaller bethonic foraminifera.	none	Bryozoans
		lower			*Amphistegina*, *Elphidium*	none		
BATESFORD	Batesford Limestone		bioclastic gnst	*Globigerinoides* *Praeorbulina*	*Operculina*, *Cycloclypeus* *Gypsina*, *Amphistegina*, encrusting forms.	*Lepidocyclina (N.) howchini* – *Cycloclypeus carpentari* *or* *Operculina complanata* – Smaller benthonic foraminifera	Articulated Coralline Algae	Bryozoans Molluscs Echinoids

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Lithologic and biotic characteristics of the Batesford Limestone and the rock units in Ashmore Reef N° I Well.

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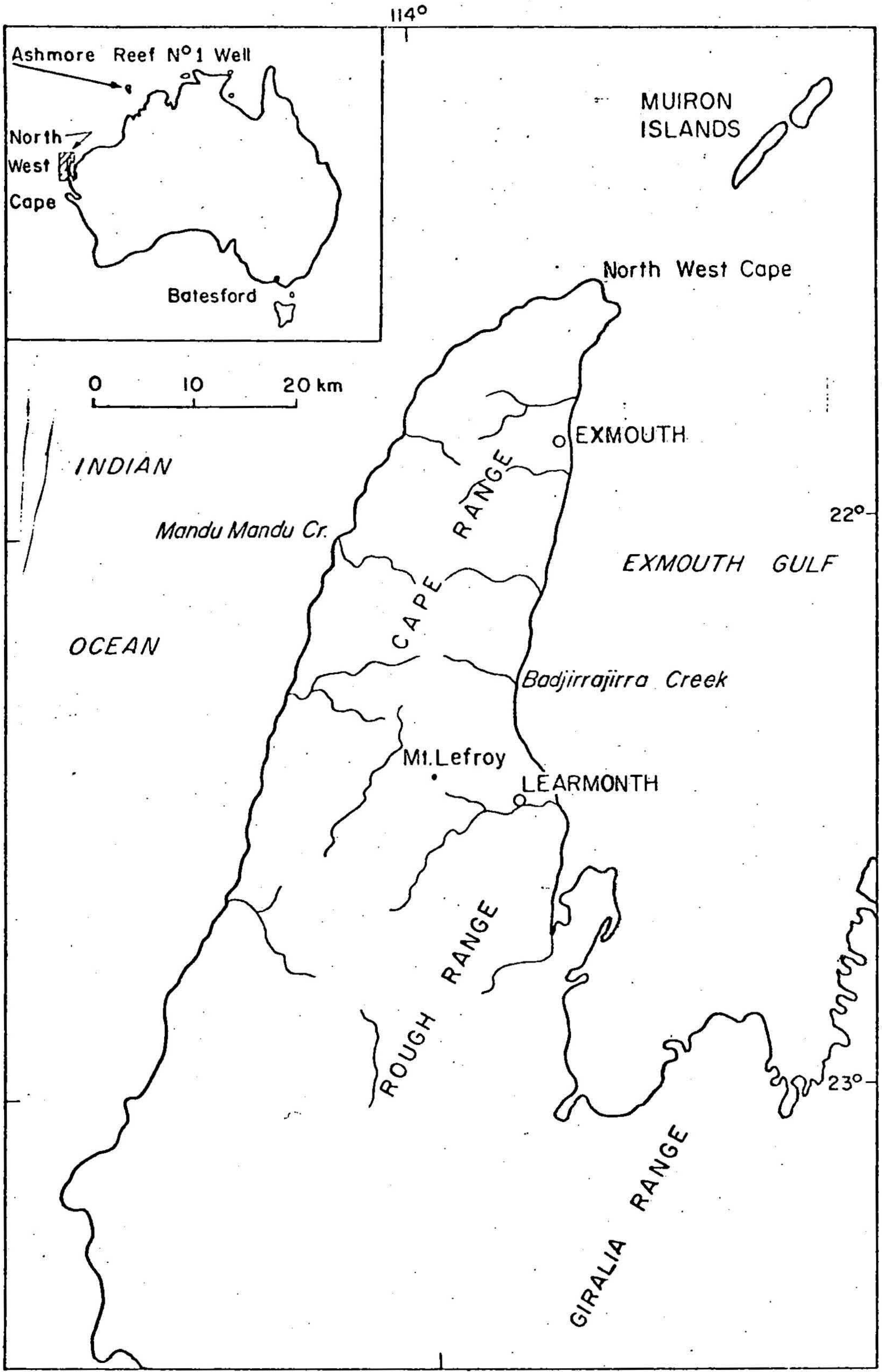

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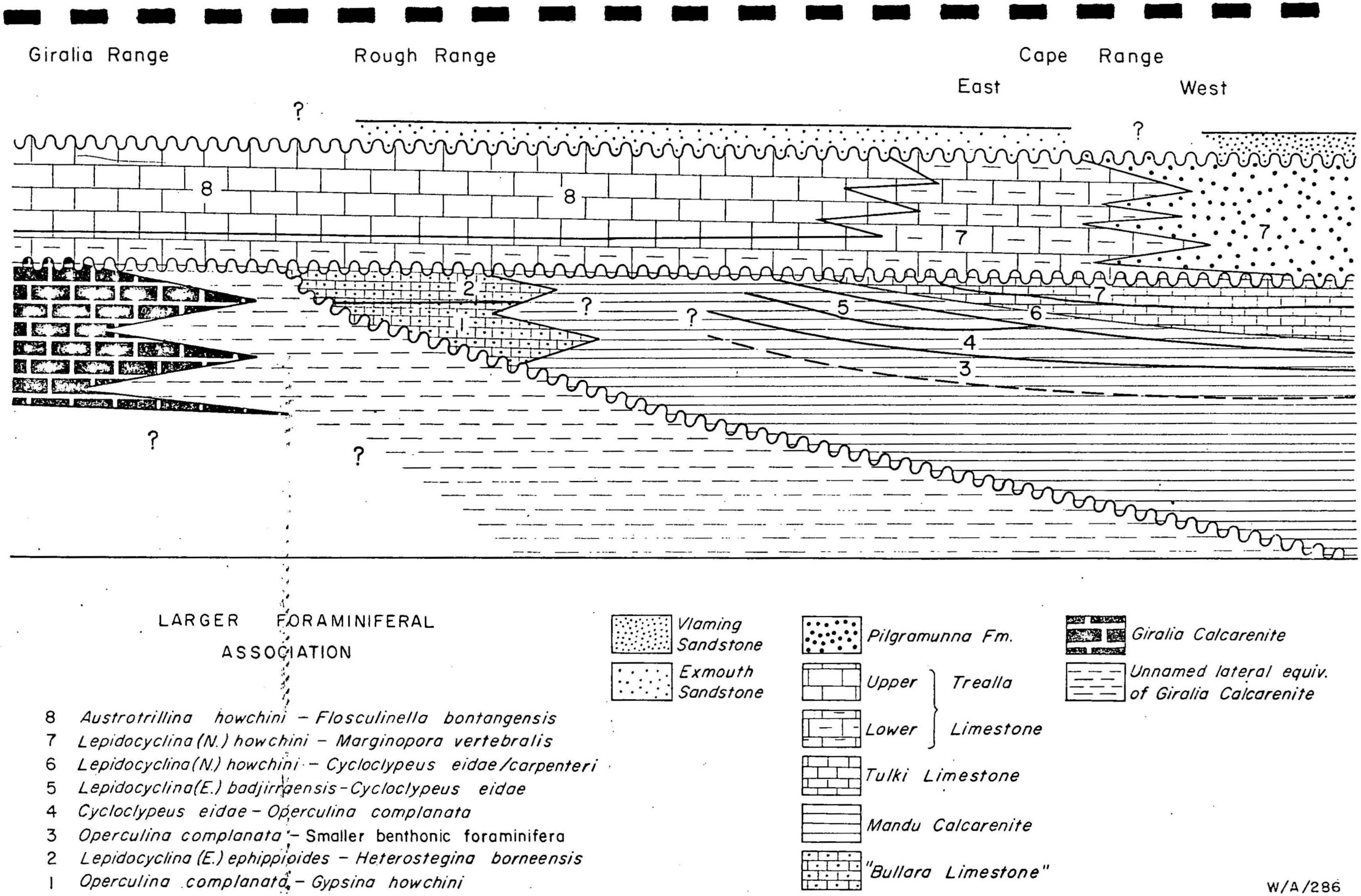
Fig. I Locality map showing the areas treated.



LARGER FORAMINIFERAL ASSOCIATION

8 *Austrotrillina howchini – Flosculinella bontangensis*
7 *Lepidocyclina (N.) howchini – Marginopora vertebralis*
6 *Lepidocyclina (N.) howchini – Cycloclypeus eidae/carpenteri*
5 *Lepidocyclina (E.) badjirraensis – Cycloclypeus eidae*
4 *Cycloclypeus eidae – Operculina complanata*
3 *Operculina complanata* – Smaller benthonic foraminifera
2 *Lepidocyclina (E.) ephippioides – Heterostegina borneensis*
1 *Operculina complanata – Gypsina howchini*

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Fig. 2 Diagrammatic east-west cross-section of the North West Cape area, showing the stratigraphic relationships between the Obligo – Miocene rocks.

Record 1974/195

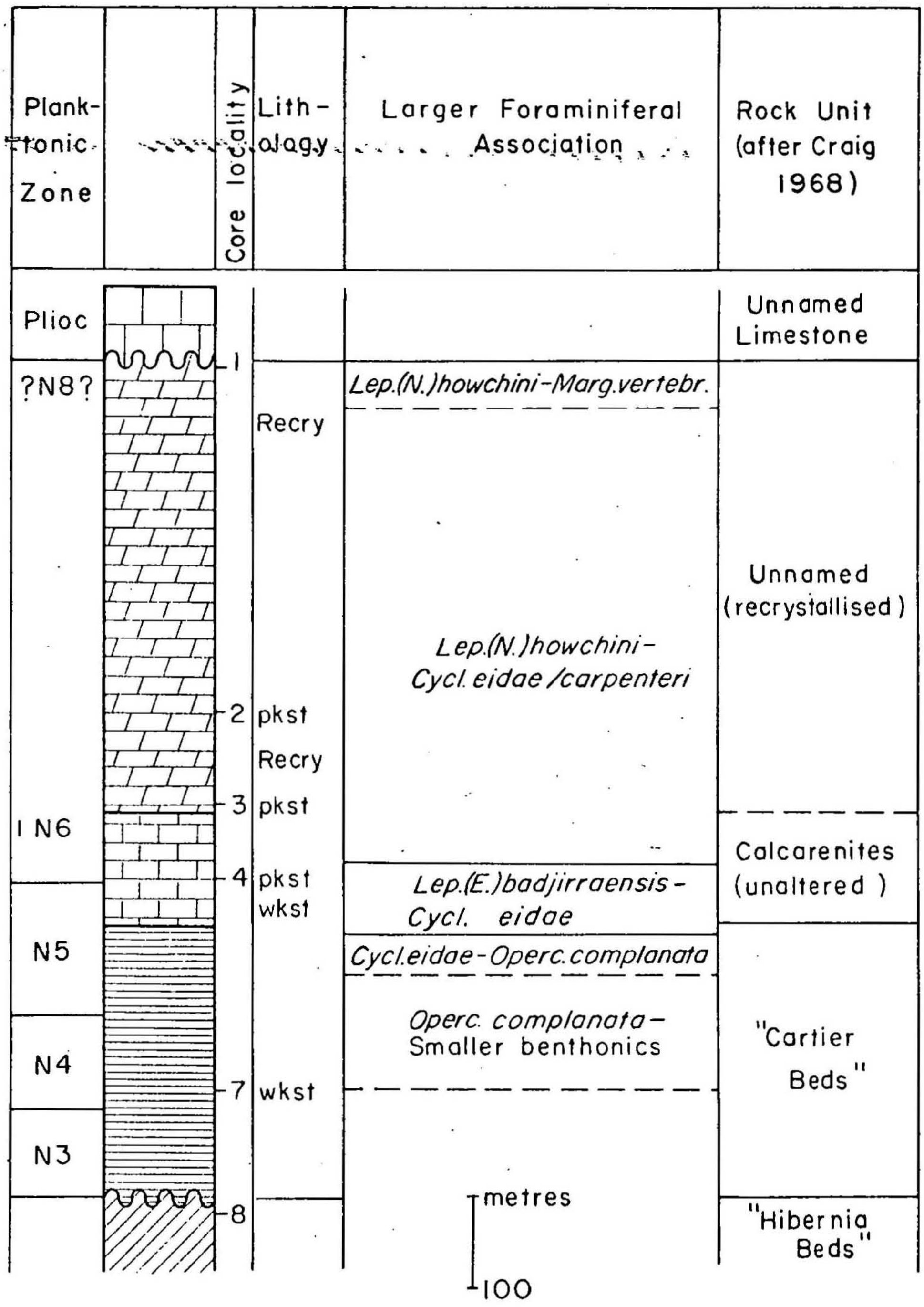

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Fig. 3 Stratigraphic summary of the Obligo-Miocene.
Record 1974/195

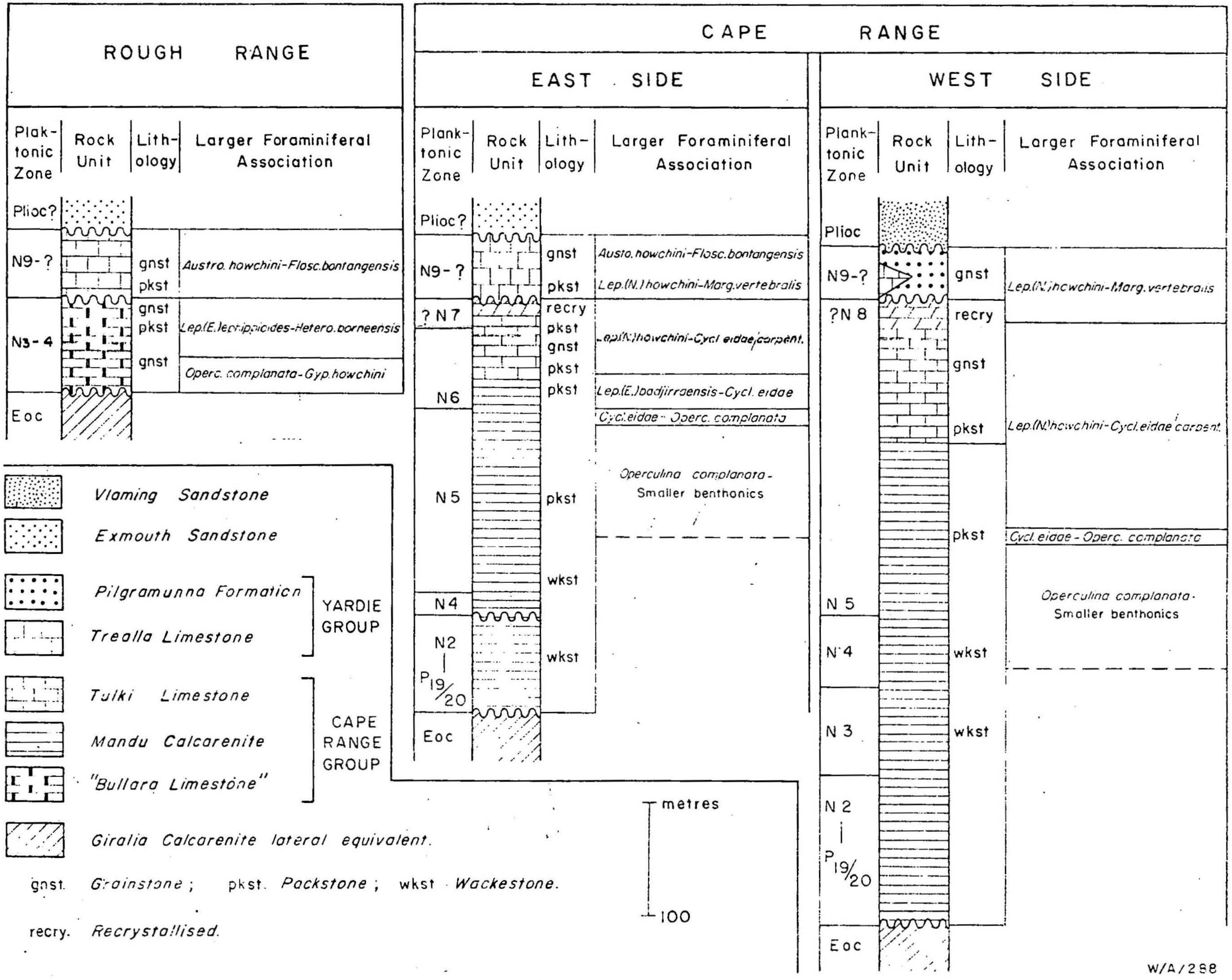

Fig. 4 Composite stratigraphic sections from three localities in the North West Cape area.
Record 1974/195

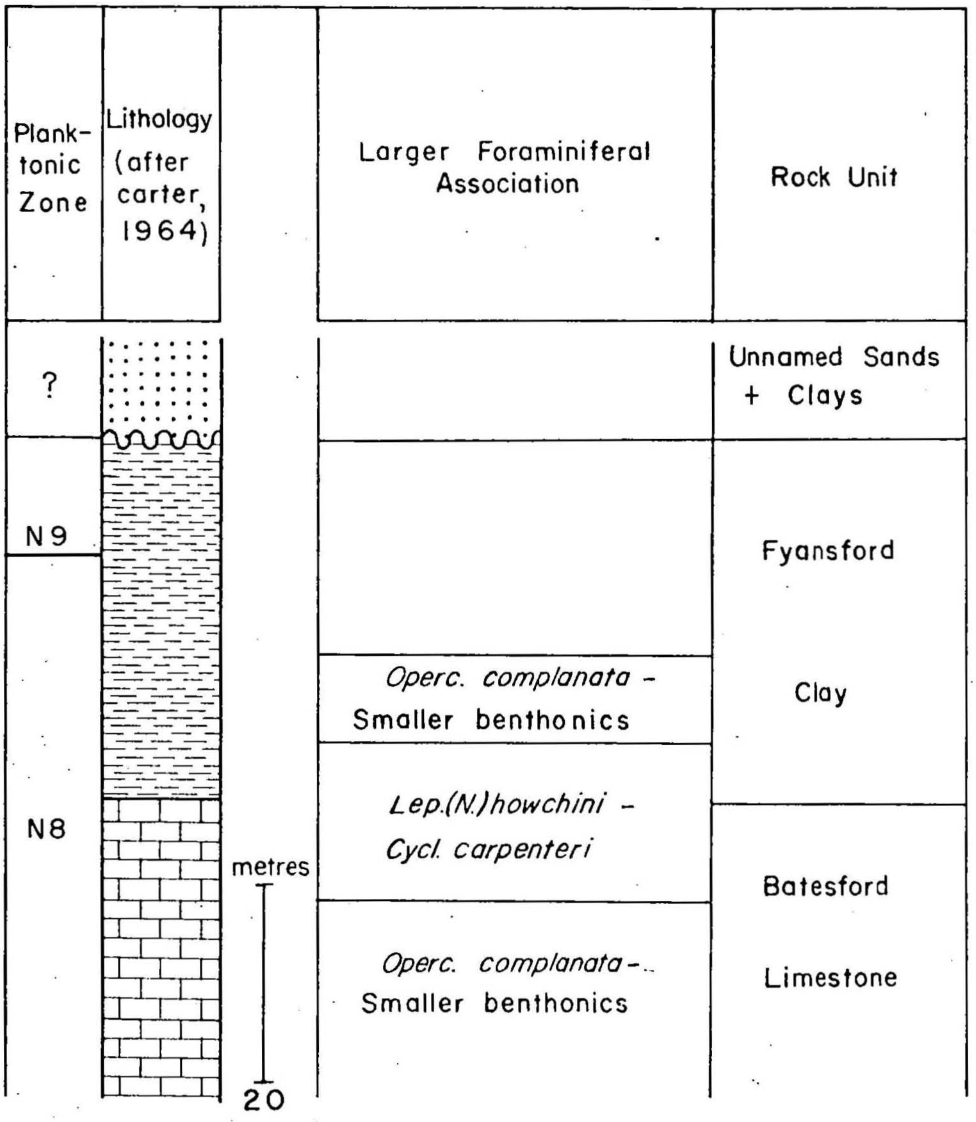

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Fig. 5 Stratigraphic summary of the Batesfor Limestone.
Record 1974/195

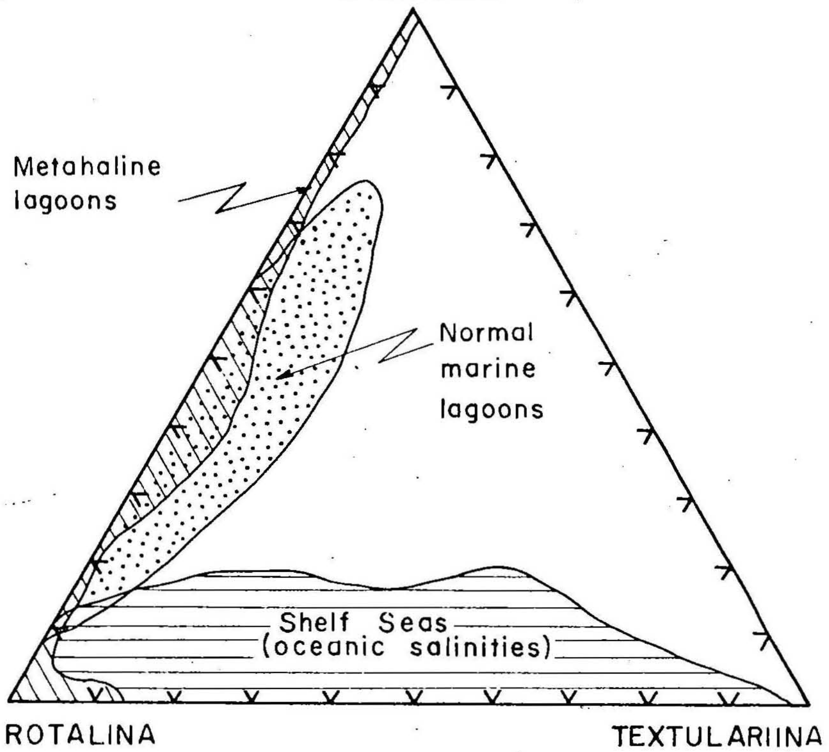

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Fig. 6 Triangular plot based on Recent faunas from three different evironment.

Record 1974/195

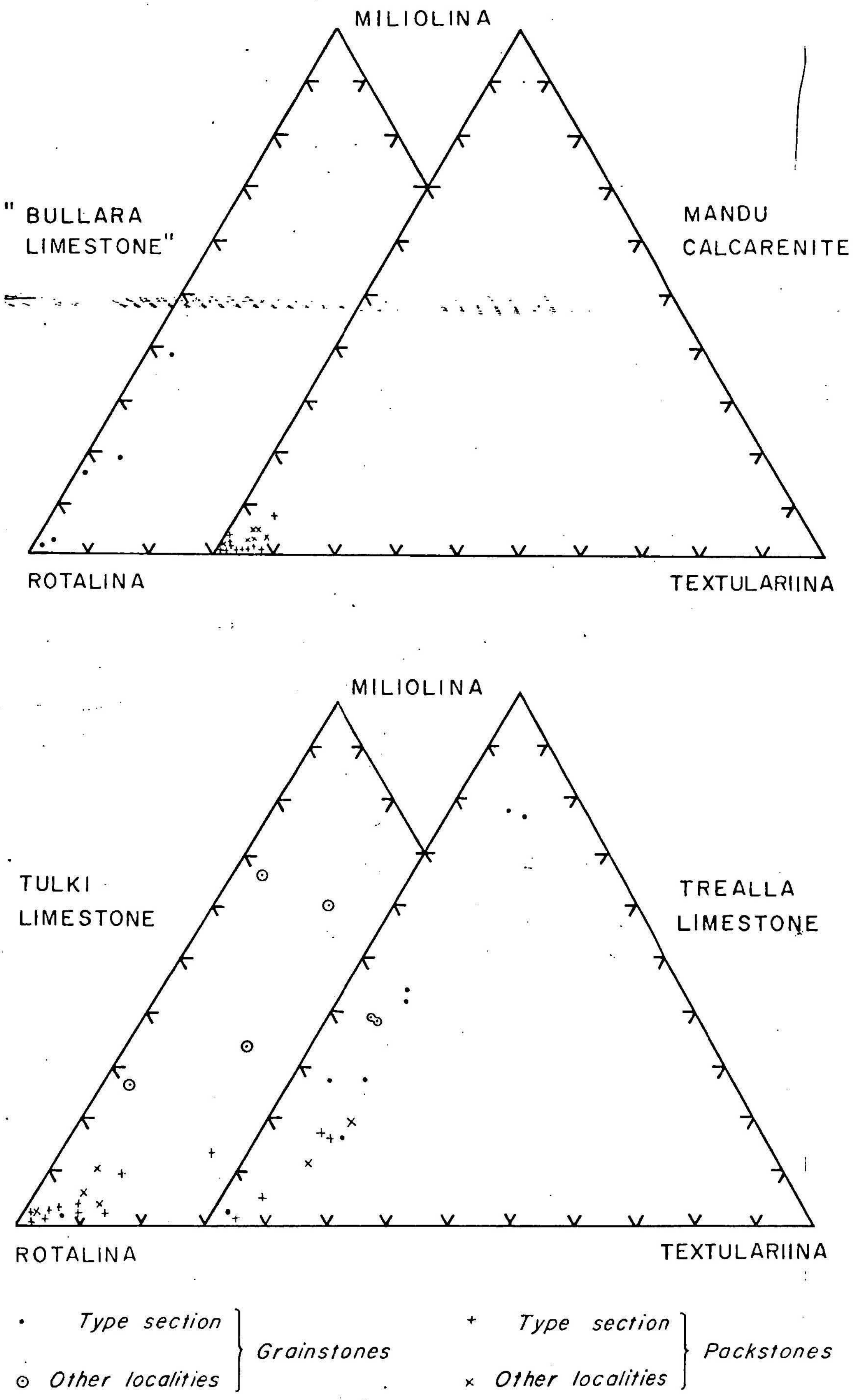

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Fig. 7 Triangular plots for foraminiferal assemblages from four rock-stratigraphic units in the North West Cape area.

Record 1974/195

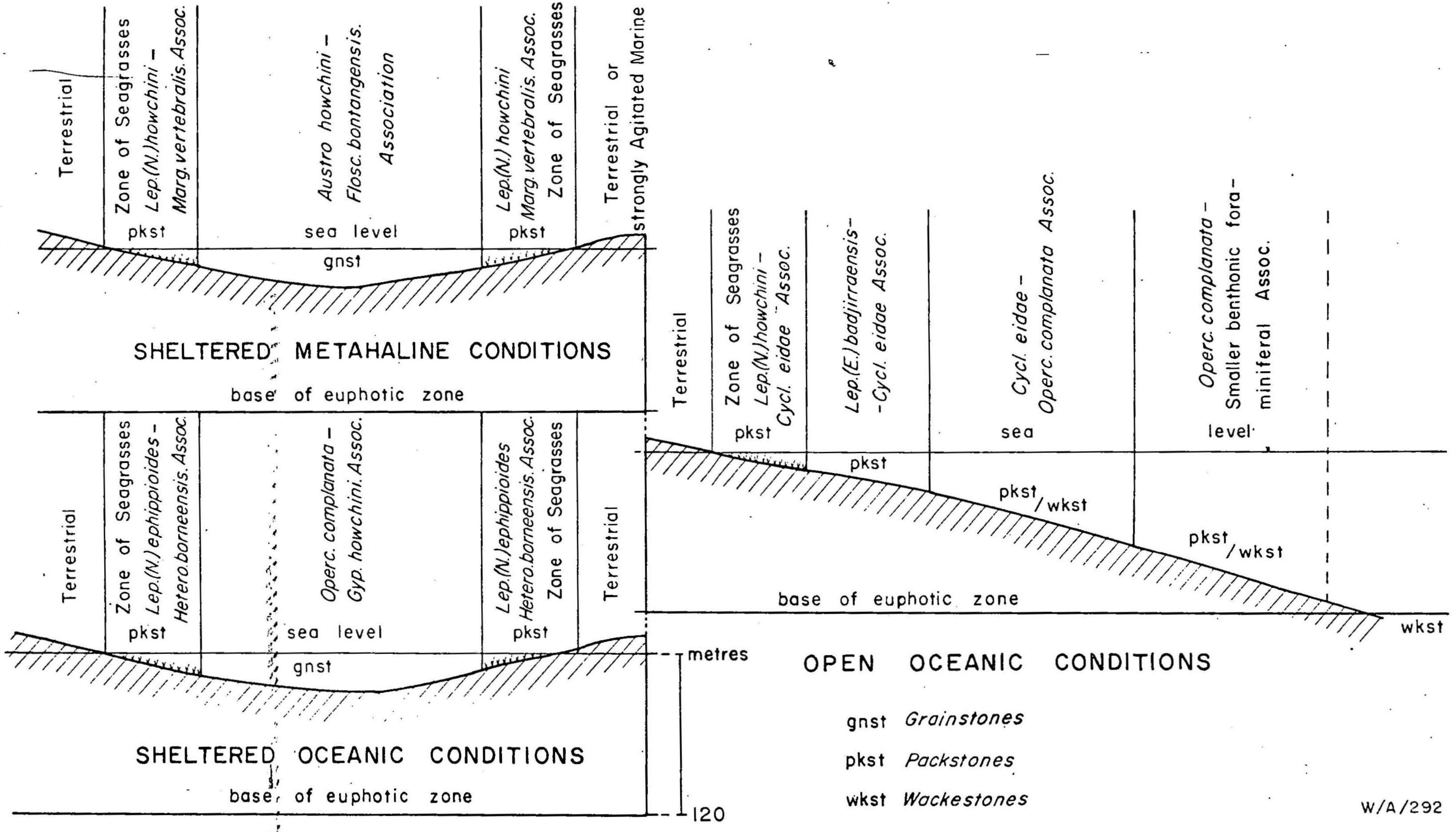

Fig. 8 Diagrammatic reconstruction of the environments occupied by the larger foraminiferal associations.
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Plate 1

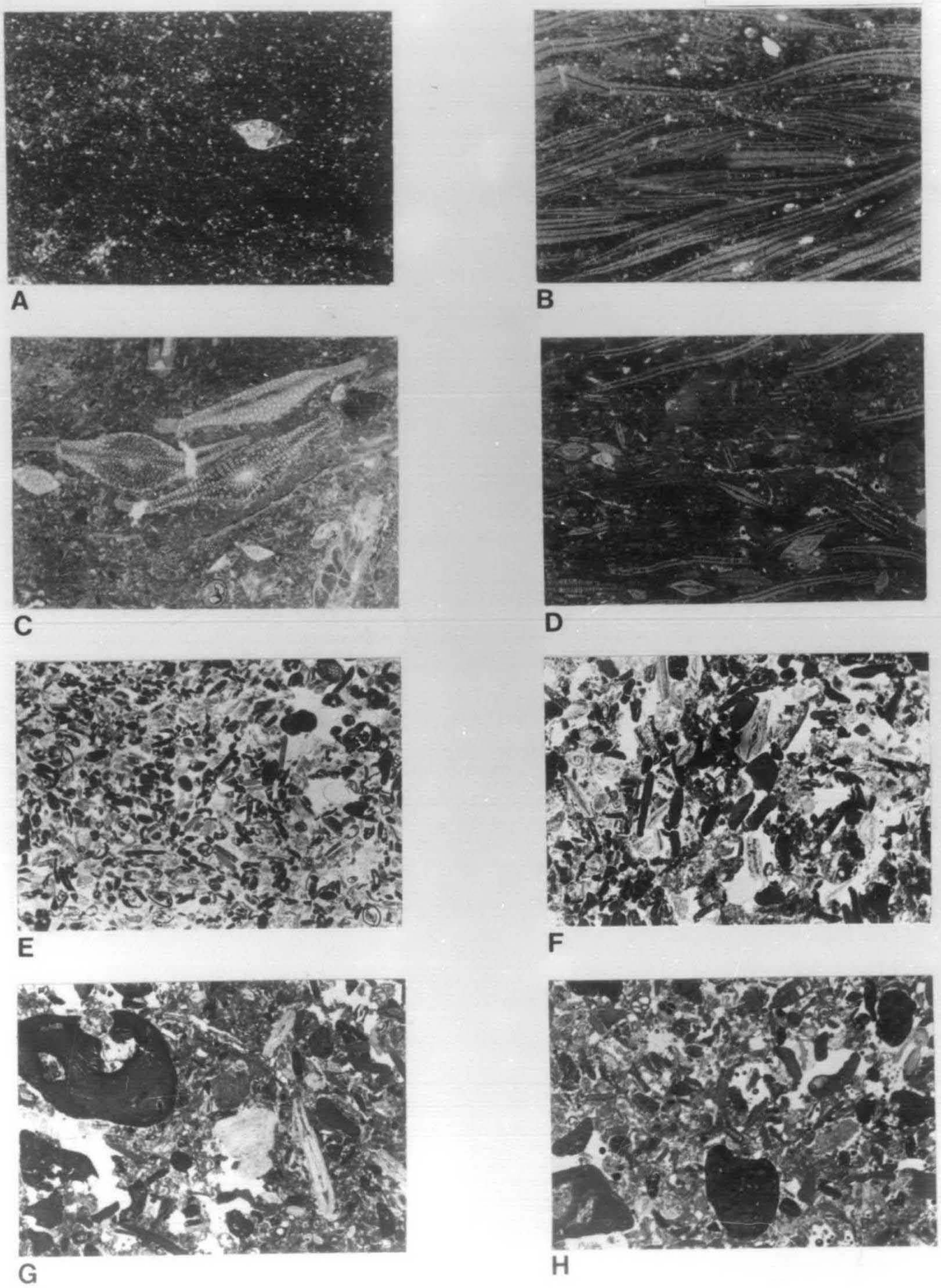

Plate 2

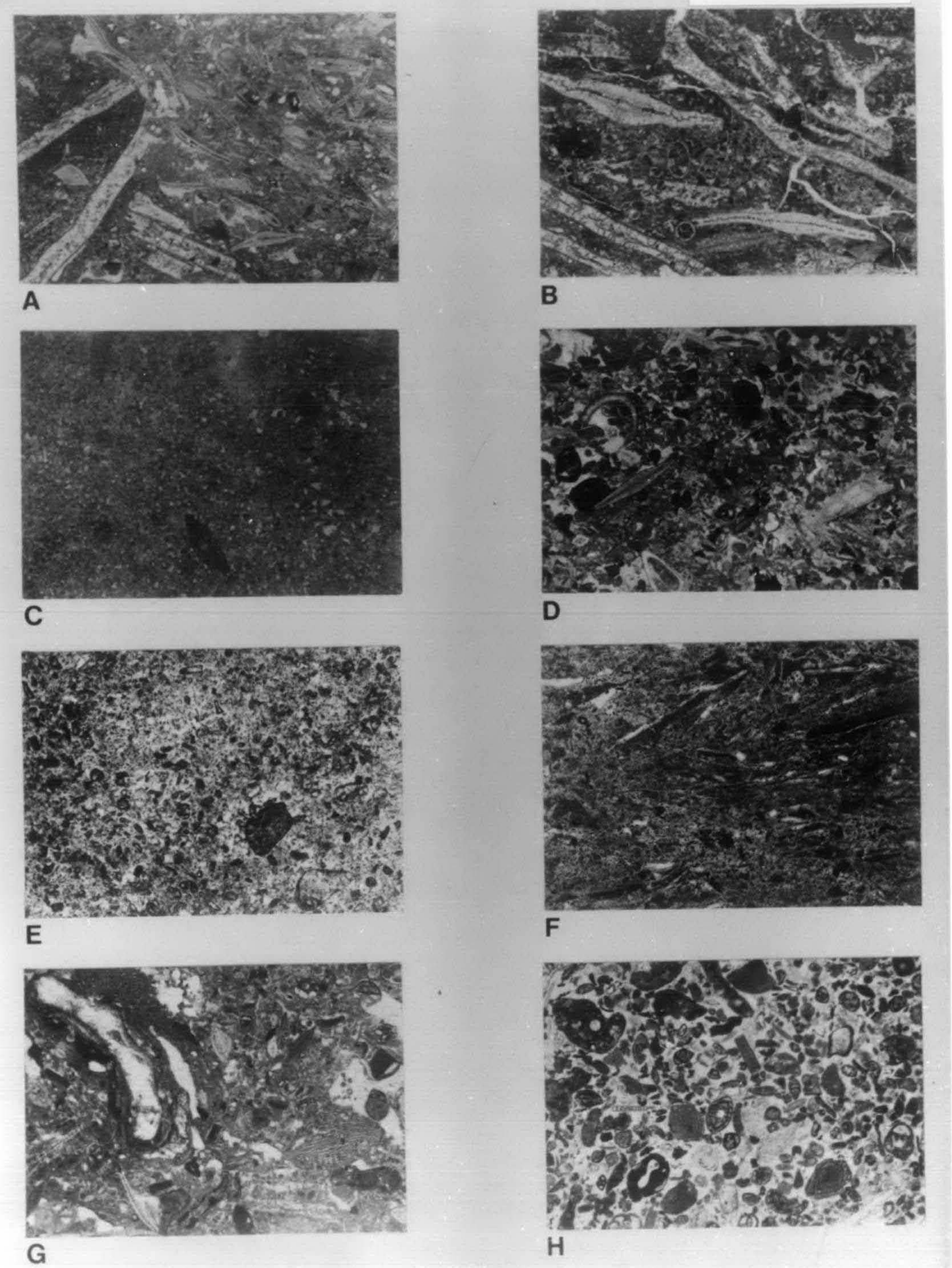

Plate 3