

AN OUTLINE HISTORY OF SEAGRASS COMMUNITIES

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ABSTRACT. The primary ecological role played by seagrasses results from their ability to modify the physical environment. Trapping and binding of nutrient-enriched sediments encourages deposit and suspension-feeding invertebrates. Leaves provide a substrate and shelter for flourishing populations of bacteria, algae, protozoans, coelenterates, molluscs, bryozoans, and echinoderms which in turn contribute CaCO₃ to the sediment, forming strata with a good preservation potential. The seagrass community is best developed in tropical and subtropical regions, especially where alternative nutrient sources are limited.

The geological history of seagrass communities is traced with the aid of foraminifera. Gradual encroachment of seagrasses into the sublittoral of the late Cretaceous or early Caenozoic was followed in the Miocene by a rapid dispersal of *Thalassia* and associated biota, arriving for the first time in the Caribbean and mid Pacific.

FEW palaeoecologists would doubt that marine vegetation has played a significant role in the ecosystems of the past. Unfortunately, this role must remain largely enigmatic because of the general lack of non-calcified plant material in the fossil record. The basis for this paper was laid in 1970 when the writer examined recent seagrass associated biota (especially foraminifera) around the Caribbean. It was evident from these studies (e.g. Brasier 1973, 1975a, 1975b, 1975c) and from the considerable work of others, that seagrasses exert great influence over both sedimentation and ecology in shallow-water habitats. Their first appearance in the sublittoral might therefore have been marked by a significant change in community structure, and hence of biofacies. The intention of this paper is to examine briefly the present-day ecological role of seagrasses and then to trace their geographic dispersal through time, leading to an assessment of their probable palaeoecological and evolutionary significance.

SEAGRASS ECOLOGY

Adaptive features. Seagrasses ('eel', 'turtle', 'widgeon', or 'manatee' grass) are the only group of angiosperms known to have successfully invaded the sea. Their means of attachment to the substrate, propagation, and nutrient absorption (*s.l.*) differ considerably from those of marine algae. It is for these reasons that the group has a more marked effect upon water movement, sedimentation, fauna, and flora. Seagrasses somewhat resemble true grasses in mode of growth but are more closely allied to the freshwater monocotyledons. Den Hartog (1970) has reviewed the main features of the group, noting that it is not yet certain whether marine forms evolved from freshwater forms or vice versa. However, genera adapted to either habitat are known from within the several families so that seagrasses form an ecological rather than a taxonomic group.

Most seagrass genera have adapted to the aquatic medium by the development of hydrophilous pollination (Den Hartog 1970). Certain seagrass fruits also float, thus

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aiding plant dispersal (Opurt and Boral 1964). The principal method of increase is, however, by rhizomatous growth, leaves sprouting at regular intervals along the rhizome. The size and shape of these rhizomes and leaves varies greatly between genera and is well reflected in their ecology. Forms with large strap-like leaves and extensive rhizomatous growth such as *Thalassia*, *Cymodocea*, and *Posidonia* are the ones with most interest for the palaeoecologist for these have the greatest effect on the environment and biota.

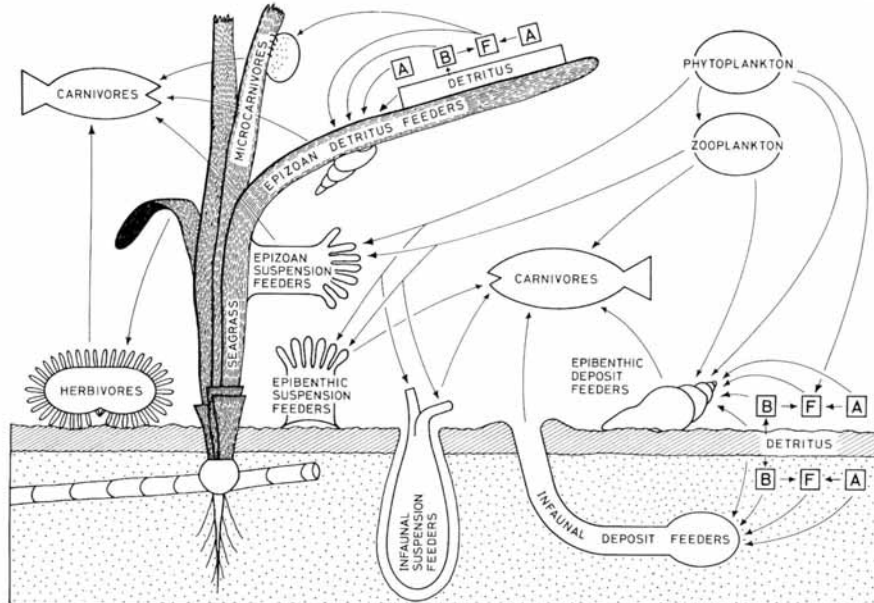
Habitat conditions. Generalizations concerning the physical factors controlling seagrass distribution are difficult to make. Most are found below mean low water and above 12 m depth. Some of the larger forms (e.g. *Thalassia*, *Cymodocea*, *Posidonia*) are tolerant of hypersaline conditions (see Brasier 1975a; Logan and Cebulski 1970). However, differing tolerances of dessication, turbidity, current agitation, sediment thickness, grain size, and humic content are amongst the factors which cause ecological zonation of seagrasses in the sublittoral (e.g. Scoffin 1970; Davies 1970; Thomassin 1971; Pichon 1971). Furthermore, light intensity and periodicity, as well as temperature, may affect the latitudinal distribution of species (see Marmelstein *et al.* 1968).

Influence of seagrass. Seagrass is notable for its ability to influence the character of the sediment substrate. This results from four more or less independent factors. In the first place it supplies biogenic CaCO_3 to the substrate in the form of epibionts and shells from invertebrates and calcareous algae. Secondly, the dense plant growth encourages the sedimentation of suspended particles by reducing current velocities ('baffling') and/or trapping the material on the blades. Thirdly, none of these would be significant were it not for the rhizomes which stabilize the accumulated sediment and bind it together. Fourthly, it may modify the chemical environment. Seagrass photosynthesis and respiration are thought to cause variation in the O_2 and CO_2 content of seawater, which in turn may influence the rate of fixation of CaCO_3 by marine organisms (Davies 1970). Seagrasses can also exert a direct control on the interstitial environment by the reducing action of exudates from plant cells (which probably arise from bacterial action). The role of these factors in sedimentation has already been discussed in some detail by Davies (1970). Their significance is a function of the density of plant growth, the size of the plants, and the width of the leaves, being greatest where all three are maximal.

Seagrasses are, indirectly, important producers of biogenic CaCO_3 because their epibionts are often very dense. Foraminifera and coralline algae may contribute as much as 5100 gm/m² per year (see Land 1970; Patriquin 1972; Brasier 1975a), productivity of both being higher on shallow, turbulent shores. Furthermore, calcareous green algae (e.g. *Penicillus*) which thrive between the blades are copious producers of aragonitic lime mud (Perkins *et al.* 1972). In many areas the net result of these processes is the formation of carbonate banks (see Moulinier and Picard 1952; Scoffin 1970; Davies 1970; Farrow 1971).

SEAGRASS COMMUNITIES

A simplified model of community energetics for tropical seagrass communities is outlined in text-fig. 1, compiled from the extensive literature and the author's observa-



TEXT-FIG. 1. Generalized diagram of the energy flow in a seagrass community. B = bacteria; F = foraminifera and other microherbivores; A = microscopic algae.

tions. A review or synthesis of the ecology of seagrass communities is beyond the scope of this study. The comments below are of necessity generalized, with emphasis on forms likely to be preserved in ancient strata.

Primary producers. Most workers on seagrass communities have commented on the associated algae (e.g. Scoffin 1970; Taylor and Lewis 1970; Davies 1970) which provide shelter for many animals. Calcareous algae are common and include benthic codiaceans and corallines (e.g. *Penicillus*, *Halimeda*, *Goniolithon*, *Lithothamnion*) and encrusting epiphytic corallines (e.g. *Leptoporeolithon* = '*Melobesia*' of many workers). Abundant non calcified algae (e.g. *Laurencia*) may also cause entrapment of sediment, adding to the growth of a seagrass bank.

The primary food source for much of the food web is not seagrass or macro-algae but populations of benthic and epiphytic unicellular algae and bacteria (see Lee *et al.* 1966; Lipps and Valentine 1970) or the accumulated detritus (Taylor and Lewis 1970).

Epizoans. Feeding upon these epiphytic 'blooms' and detritus are a diverse population of epizoans, most significant of which (in terms of numbers and diversity) are the foraminifera. Brasier (1975a) has divided these into primary weed dwellers and secondary weed dwellers, the latter being facultative forms from sediment substrates. Primary weed dwellers include many forms of discoidal shape and sessile habit (e.g. *Sorites*, *Amphisorus*, *Marginopora*, *Cyclogyra*, *Planorbulina*) some of which are

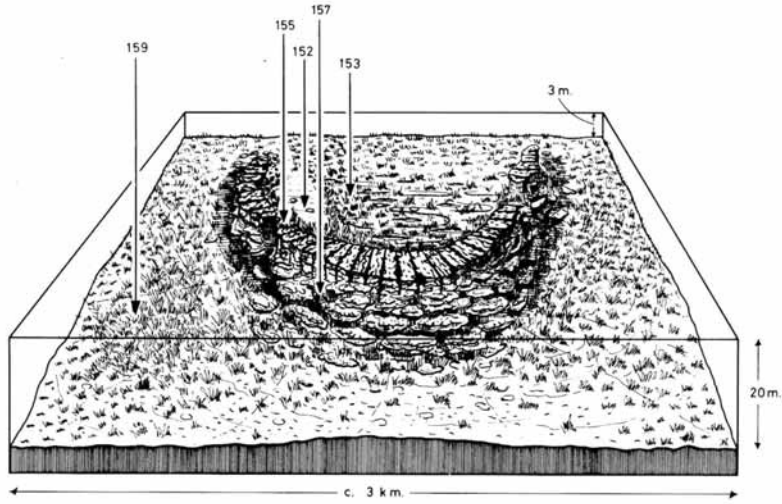
extremely large in size (5 mm+). Morphological criteria for recognizing other kinds of weed-dwelling foraminifera have been discussed by Brasier (1975b). Micro-carnivores may include the paradoxostomatid ostracods (McKenzie 1971; Maddocks 1966). Organisms using the leaves as a firm substrate for suspension feeding include annelids (e.g. *Spirorbis*), bivalves (e.g. *Pteria*, *Barbatia*), coelenterates, bryozoans, and sponges. Detritus feeders (e.g. *Cerithium*) also flourish on the leaves.

Substrate fauna. The lime mud and decaying organic material trapped and bound by dense plant growth are an encouragement to bacteria and these together with microalgae and detritus may form the staple diet of benthic foraminifera (Lee *et al.* 1966; Taylor and Lewis 1970; Lipps and Valentine 1970). Many of these comprise thin-shelled, elongate miliolids of the genus *Cycloforina* (see Brasier 1975b). Foraminifera, algae, and bacteria are in turn a major dietary component of suspension and deposit feeders (Newell 1965; Lipps and Valentine 1970). Gastropods are abundant and diverse (e.g. *Cerithium*, *Strombus*, *Cypraea*, *Olivella*, *Bulla*) and an abundance of small gastropods may be one criterion for the detection of the former presence of seagrass (Moulinier and Picard 1952; Davies 1970). Scleractinian corals may also abound, especially forms tolerant of fluctuating salinity and pH (e.g. *Porites*, *Manicina*, *Siderastrea*).

Dead coral skeletons comprise much of the framework of some seagrass mounds, affording a hard substrate for colonization by epiphytes and epizoans. Echinoids (e.g. *Diadema*, *Tripneustes*, *Lytechinus*, *Toxaneustes*, *Clypeaster*) have adapted to grazing on seagrass leaves and may also be used as palaeoecological indicators (Kier and Grant 1965).

Infauna. Infaunal deposit and suspension-feeding bivalves of seagrass communities are often tolerant of low pH and low oxygen supply (Taylor and Lewis 1970; Taylor 1971) and may increase in diversity with increasing organic content (Thomassin 1971). They include lucinoids, tellinids, and pinnids. The deposit-feeding holothurians, polychaetes, and sipunculids thrive in the nutrient-enriched sediments around seagrass, whilst suspension-feeding crustaceans (e.g. *Neaxius* and *Calianassa*) utilize the organic rich seston (see Farrow 1971; Aller and Dodge 1974). The carnivorous gastropod *Conus* is also found in the seagrass community, attracted by the plentiful food supply and protective canopy (Taylor 1971). Jackson (1972) and Levinton and Bambach (1975) have discussed the molluscan ecology of tropical and temperate seagrass communities.

Diversity. Various studies (e.g. Logan and Cebulski 1970; Taylor 1971; Brasier 1975a, 1975c) have shown that diversity, biomass, standing crop, and productivity are strikingly greater in seagrass communities than in those of surrounding waters. This is essentially because of the wide variety of habitats afforded to the fauna and flora by seagrass. For example, the variety of foraminiferal tests found around Alligator Reef, south of Jamaica, is significantly higher in the vicinity of seagrass (text-fig. 2). A similar temporal example has been described from Abu Dhabi Lagoon (Murray 1970) in which recent colonization by seagrass greatly improved foraminiferal diversity and standing crop. Conversely, annihilation of the backreef seagrass stands of Buccoo Reef, Tobago, by Hurricane Flora in 1963, resulted in a lowering of foraminiferal diversity and standing crop (Dr. S. Radford, pers. comm. 1972). The

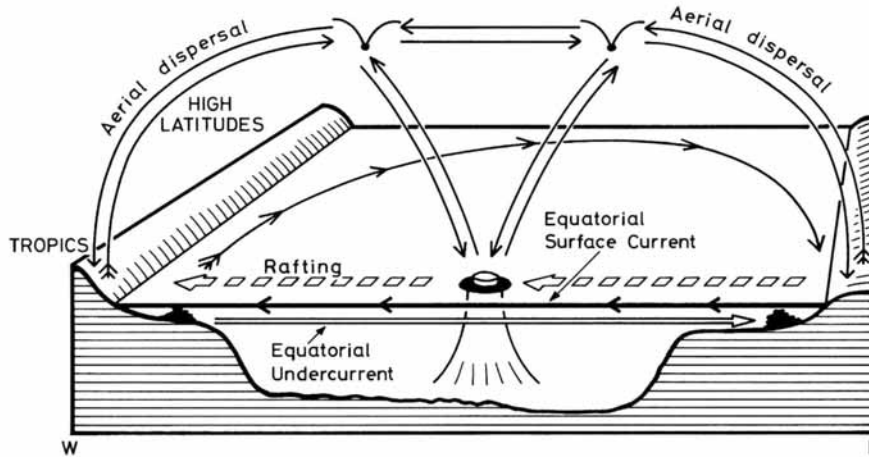


Key	152	153	155	157	159	152	153	155	157	159
Textularia agglutinans										
T. candeiiana										
Bigenerina irregularis										
Valvulina oviedoiiana										
Vertebrulina cassis										
Spiraloculina antillarum										
Cornuspiramia antillarum										
Quinqueloculina agglutinans										
Q. bicostata										
Q. bidentata										
Q. candeiiana										
Q. cuvieriana										
Q. lamarciana										
Q. poeyana										
Q. polygona										
Q. quadrilateralis										
Q. stelligera										
Q. subpoeyana										
Q. tricarinata										
Triloculina carinata										
T. lineolata										
T. oblonga										
T. rotunda										
T. trigonula										
Pyrgo subsphaerica										
Sigmollina arenata										
Schlumbergerina alveoliniformis										
Miliolinella circularis										
Hauerina bradyi										
H. ornatisima										
Articulina mexicana										
A. mucronata										
Archaias angulatus										
Sarites marginalis										
Amphisorus hemprichii										
Peneroplis bradyi										
P. pertusus										
P. proteus										
Monalysidium politum										
Borelis pulchrus										
Bulimina marginata										
Bolivina sp.										
Neonorbina orbicularis										
Discorbis spp. indet.										
D. berthelati										
D. floridana										
D. valvulata										
Valvulinera candeiiana										
Asterigerina carinata										
Siphonina pulchra										
Ammonia beccarii var. tepida										
Rotalinella mira										
R. rosea										
Elphidium discoidale										
E. poeyanum										
Amphistegina gibbosa										
Cibicides lobatulus										
C. pseudoungerianus										
Planorbulina acervalis										
Cymbaloporeta squamosa										
Florilus grateloupi										
DIVERSITY (V value)	11	17	20	4	38					

TEXT-FIG. 2. Distribution of recent foraminiferid tests in samples from Alligator Reef, Jamaica: 152 = unvegetated backreef calcarenite (depth 1 m); 153 = backreef muddy calcarenite from *Thalassia* meadow (1 m); 155 = muddy calcarenite from *Thalassia*-colonized inter-reef channel (2 m); 157 = unvegetated inter-reef *Halimeda* sand (3 m); 159 = carbonate-rich terrigenous muds from *Thalassia* meadow on open shelf (c. 12 m). Sample numbers refer to H.M.S. Fox/U.C.L. Geology Dept. programme, CICAR 1970.

epidemic infection of the temperate seagrass *Zostera* in the 1930s was also accompanied by a lowering of community diversity (see the review by Johnson 1964). Ancient seagrass assemblages might therefore be expected to show increases in diversity compared with neighbouring biofacies.

Community dispersal. Before discussing the distribution of the seagrass community in space and time it is worthwhile to consider the available dispersal mechanisms. Here the concern is primarily the way in which benthonic organisms have crossed wide oceanic barriers such as the tropical Atlantic and the mid Pacific. Some of the possible mechanisms are illustrated in text-fig. 3, none of which can be ruled out on the basis of chance because of the extremely long time period involved.



TEXT-FIG. 3. Diagram of dispersal mechanisms available to tropical shallow-water benthos for crossing ocean barriers in the northern hemisphere. Oceanic islands serve as staging posts. The equatorial surface current (east to west) and undercurrent (west to east) are important. Although dispersal by atmospheric phenomena (e.g. hurricanes) or by birds and marine vertebrates need not be insignificant.

For certain organisms planktonic larvae are the major means of dispersal. Scheltma (1968) has shown that such larvae make it possible for some marine species to breach faunal barriers and colonize new regions. He found that stenothermal tropical larvae are distributed not only throughout the westerly travelling Equatorial Current but also throughout the easterly travelling Equatorial Undercurrent, which runs around the equator. Scheltma concluded that both currents can account for the amphiatlantic distributions of much of the tropical shallow-water benthos between West Africa and South America.

Although these various currents are of value to invertebrates with lengthy planktonic larval stages, those with short ones, such as the foraminifera, stand little chance of reaching their destination. Hence Vaughan (1933) suggested that foraminifera were dispersed by rafting as individuals or small colonies upon seaweed, and Bock (1969) specifically mentioned *Thalassia* as the means of their dispersal throughout

the Caribbean region. But whilst many types of foraminifera can live on anchored seagrass, only those firmly adherent and encrusting forms such as *Planorbulina*, *Sorites*, *Amphisorus*, *Marginopora*, discorbids, cibicidids, and phytal miliolids were found alive and abundant by Brasier (1975c) on grass blades floating on the sea's surface. Forms that are better adapted to a sediment-dwelling niche, such as *Archaias*, were not only rare or absent on floating seagrass but also on populations of floating *Sargassum* and filamentous algae. From this one may expect that rafting on weed, including seagrass, is an unlikely mechanism of dispersal for forms ill-adapted for attachment, although not impossible.

That adherent foraminifera are more widely dispersed is evident from studies of recent forms. Stenothermal 'phytal' foraminifera have a more or less pantropical distribution today, whilst relatively eurythermal phytal forms are almost pandemic (see Brasier 1975a, 1975b). Conversely, typically sediment-dwelling foraminifera of the tropics, such as *Archaias* and the alveolinids, are endemic to certain provinces. Very isolated islands such as Midway Atoll in the mid North Pacific have been colonized by the firmly adherent *Sorites* and *Marginopora* rather than by the loosely adherent or free-lying *Baculogypsina* and *Calcarina*, genera which have not yet made the journey successfully (see Cole 1969).

The pelagic and pseudopelagic dispersal of these organisms is greatly dependent on the current velocity, the length of the journey, and the ecological stresses encountered *en route*. Because of the nature of the oceanic surface currents, migration is also more difficult from west to east in the tropics and from east to west in high latitudes. However, these constraints may be overcome with the aid of very mobile vertebrates (especially turtles, birds, and man) or special atmospheric and oceanic phenomena (e.g. hurricanes). All such journeys may have their chances of success improved by 'staging posts', volcanic and coral islands for example. The role of some of these factors will be considered in special cases below.

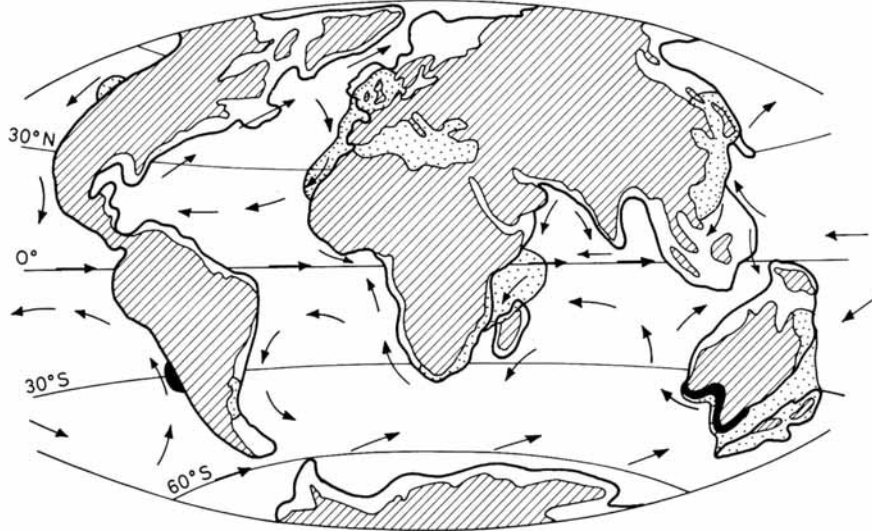
DISTRIBUTION IN TIME AND SPACE

Several lines of evidence can be pursued to indicate the origin and evolution of seagrass and its associated biota. The plant remains themselves are naturally of prime importance but are usually rare and indifferently preserved (see Den Hartog 1970). Unless the reproductive parts have been fossilized, the remains are not easily distinguished from other monocotyledons, causing dissent as to how meaningful many of the so-called fossil seagrasses are. Therefore only those recognized by Den Hartog (1970) are considered here. Unfortunately, the pollen of seagrass lacks exine and is therefore not preserved. Hence less direct methods must be considered.

It is possible to use elements of the rest of the seagrass community such as foraminifera, molluscs, echinoids, and crustaceans as indices of seagrass in earlier seas. Furthermore, Farrow (1971) and others have shown that the sediments which accumulate around seagrass communities are distinctive and, if they escape channelling and other forms of erosion associated with the biotope, they stand a first-class chance of preservation.

A final and most valuable clue to the history of seagrass and its community lies in studies of present-day biogeography, especially that of seagrass, which Den

Hartog (1970) has recently discussed. Examination of those data reveals that seagrass distributions fall generally into three associations: the *Zostera* association (which may be taken to include *Heterozostera*, *Phyllospadix*, *Amphibolis*, and *Posidonia*) is predominantly of temperate water forms with a more or less bipolar distribution (text-figs. 4 and 5); the *Cymodocea* association (including also *Thalassodendron* and *Enhalus*) is mostly tropical but is notably absent from the Neotropics and tropical West Africa (text-fig. 5); the third or *Thalassia* association (including *Halophila*,

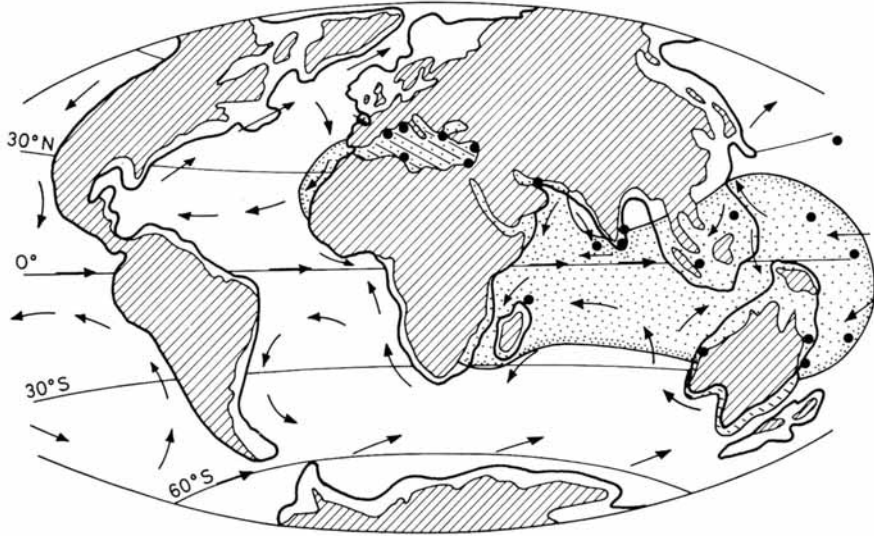


TEXT-FIG. 4. Recent distribution of *Zostera* (*Zostera*) (shown as stipples) and *Heterozostera* (shown in black). Modified from Den Hartog (1970) with ocean surface currents after Sverdrup *et al.* (1942).

Syringodium, and *Halodule*) is also tropical but differs basically in being present in the Neotropics but absent from most of the Mediterranean (text-fig. 6). It should be noted here that seagrasses are, significantly, absent from the coasts of South America excepting the tropical Atlantic region and single records from Chile and Argentina (Den Hartog 1970).

These interesting distributions are remarkably similar to the faunal realms of shallow-water benthic foraminifera. This need be no surprise for they have most probably evolved side by side throughout most of the Cainozoic. The ecological requirements of certain foraminifera have become almost dependent upon seagrass, especially those of the larger soritids ('peneroplids'). Hence *Peneroplis planatus* parallels the *Cymodocea* association in its distribution (text-fig. 4) and is known to live attached to that genus (Blanc-Vernet 1969; Davies 1970). Other living larger foraminifera such as *Alveolinella*, *Calcarina*, *Baculogypsina*, and *Operculina* are further restricted to the Indo-West Pacific. Conversely, *Amphisorus hemprichii* and *Sorites marginalis* appear to parallel the *Thalassia* association in their distribution

(text-fig. 6) and are known to live as epifaunas on *Thalassia* (Bock 1969; Brasier 1975a, 1975c). Phytal microfaunas on *Zostera* are not well known but appear to be dominated by the smaller hyaline forms *Rosalina*, *Discorbis*, *Cibicides*, and *Planorbulina* (J. Scott, pers. comm. 1970). These are equally common on other plants and hard surfaces both in and out of the tropics and therefore do not constitute a specially adapted seagrass faunule. Soritids and other larger tropical foraminifera are usually absent from temperate *Zostera* communities.



TEXT-FIG. 5. Recent distribution of *Posidonia* (dashed lines), the 'Cymodocea association' (stippled), and records of the foraminiferid *Peneroplis planatus* (black circles). Data from Den Hartog (1970) and others.

Whilst other invertebrate groups are similarly associated, the advantages of foraminifera as palaeoecological indices are well known and numerous (e.g. Brasier 1975b). Nevertheless they can only, at best, be an indication of the presence of seagrass and further finds of plants remains themselves or other corroborative evidence should be looked for.

Cretaceous

The oldest seagrass-like fossils are protozosteroids and cymodoceoids (Den Hartog 1970). These have been found as imprints and silicified remains in the upper Cretaceous rocks of Japan and northern Europe (Koriba and Miki 1931, 1960; Oishi 1931; Voigt and Domke 1955). Posidonioids are also known but Den Hartog considered all these Cretaceous forms to be but poorly adapted to marine conditions. Furthermore, the numerous other truly terrestrial angiosperms and cycads found in the Japanese beds must question the validity of referring to the examples as 'seagrasses'. Hence they may have been of little significance to the marine biota of that

time. However, contemporaneous foraminiferal faunas contain a few questionably seagrass-adapted forms such as the peneroplinid *Vandenbroeckia* and meandropsinids such as *Broeckina*, *Edomia*, *Qataria*, and *Pseudedomia*. These all have a distinctive Tethyan (i.e. Mediterranean to Indo-West Pacific) distribution (text-fig. 7), similar to that of the Cretaceous 'alveolinids', but the latter are more likely to have flourished in unvegetated backreef-type sands, as do their descendants. These alveolinids, peneroplinids, and meandropsinids are absent from neotropical strata, and suggest that the Americas were effectively isolated from Africa and Europe in the late Cretaceous (Dilley 1971, 1973).

The present bipolar distribution of the *Zostera* association nevertheless suggests that seagrasses were evolving in Cretaceous times and have since become isolated by continental drift and by the expansion of a more specialized tropical seagrass flora (Den Hartog 1970). The occurrence of the primitive *Heterozostera* both around South Australia and at an isolated locality in Chile (Van Steenis 1962) suggests, like the marsupial evidence (Cox 1973), an archipelagic link between South America and Antarctica in the late Cretaceous. The genus is unrecorded from New Zealand although *Zostera* occurs there.

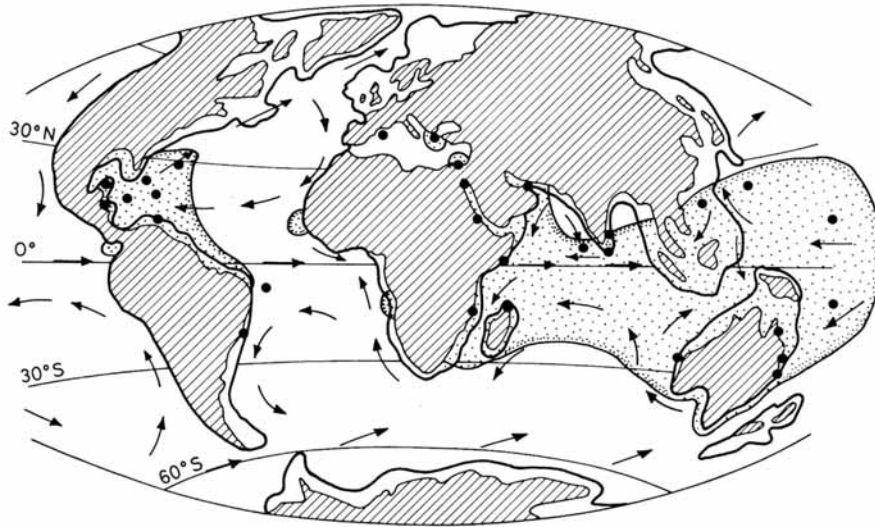
Kennedy and Juignet (1974) have recently described possible seagrass bioherms from the upper Cretaceous of Normandy, although the inferred water depth would seem to be greater than tolerated by seagrasses today.

Palaeocene-Eocene

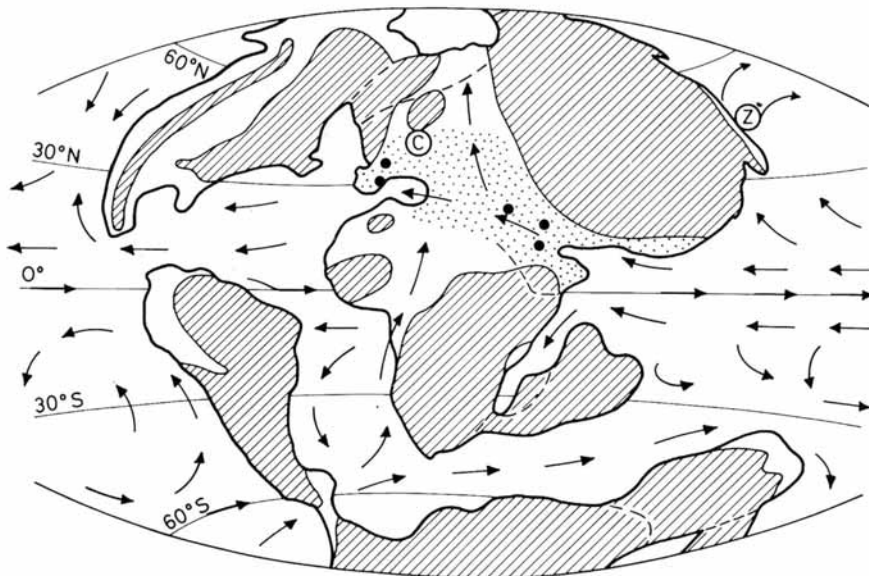
Fossil seagrasses of the *Cymodocea* association are first known from the lower Eocene of the Paris Basin where *Cymodocea* occurred with *Posidonia* (Den Hartog 1970). Significantly their appearance is accompanied more or less contemporaneously by that of the large foraminifer *Orbitolites*, whose living, close relatives *Marginopora* and *Sorites* are unquestionable seagrass dwellers. In the Ypresian limestones of Corbières, southern France, the analogy with recent seagrass sediments is supported by foraminifera (especially *Orbitolites*, *Valvulina*, and thin-shelled miliolids) together with burrowing crustaceans and lithological evidence (Plaziat and Secretan 1971). These fossil seagrass beds even pass laterally into sand blanket calcarenites with the foraminifer *Alveolina* and the crustacean *Calianassa*, much as they do today in the tropics. This *Orbitolites-Alveolina-Calianassa* assemblage has also been described from the Eocene of Somalia (Silvestri 1939).

It is clear from biofacies and lithofacies that some of the later Calcaire Grossier accumulated under similar conditions. Wright and Murray (1972) have further deduced from foraminiferal evidence that seagrass stands (presumably of *Cymodocea* and *Posidonia*) were widespread in the middle and upper Eocene of the English Channel and this is supported by finds of *Posidonia* in the Bracklesham Beds of Selsey Bill, associated with an unusually diverse phytal fauna of miliolids, bryozoa, and molluscs (Curry 1965).

As mentioned above, the alveolinid sand facies of the Eocene occurred also in the late Cretaceous tropical regions, excepting those of the Americas. This provincialism was maintained, but the niche of *Alveolina* may have been occupied in the Eocene of the American region by *Archaias* (as it is today) and also by the extinct *Yaberinella*. It must also be emphasized that *Orbitolites* never reached the Neotropics and that



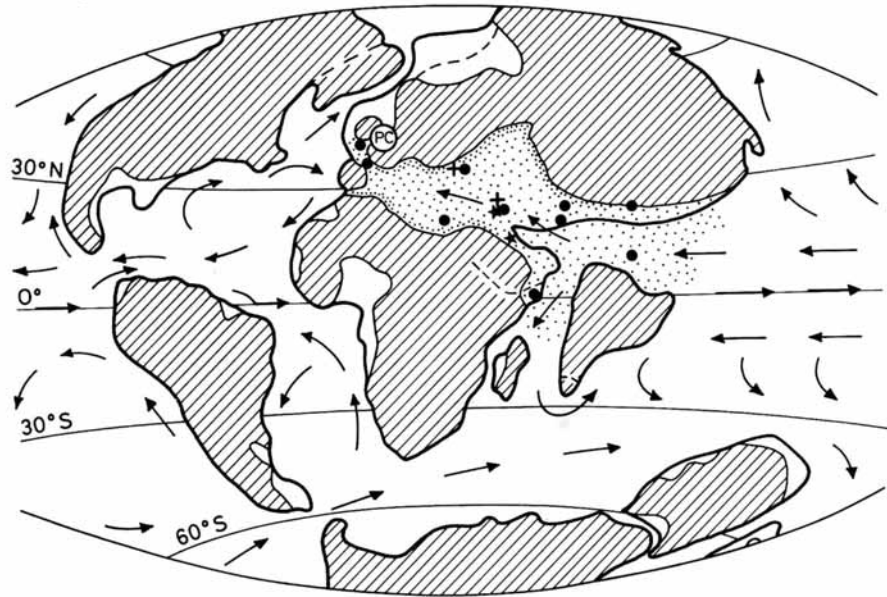
TEXT-FIG. 6. Recent distribution of the 'Thalassia association' (stippled) with records of the foraminiferids *Sorites*, *Amphisorus*, and *Marginopora* (black circles). Data mainly from Den Hartog (1970) and Wright and Murray (1972).



TEXT-FIG. 7. Land, seas, and oceans in late Cretaceous times, with records of fossil cymodoceoids (c) and protozosteroids (z). Black circles show records of possible seagrass-dwelling foraminiferids (peneroplins, meandropsinids, *Praeosorites*). Stipples represent inferred distribution of 'tropical' seagrasses. Palaeogeography and palaeocurrents modified from Cox *et al.* (1973) and Gordon (1973).

the *Cymodocea* association is not in evidence there at present, both facts strongly suggesting that seagrass did not succeed in colonizing this region during the Eocene (see text-fig. 8). None the less, seagrasses are likely to have had a complete Tethyan distribution in the early Eocene because *Orbitolites* occurred at that time as far east as West Pakistan (Nuttall 1925) and has been reported from Tibet and Hyderabad (Davies and Pinfold 1937).

Other foraminifers which might have been seagrass dwellers are *Pseudorbitolites* and '*Taberina*' *daviesi* from the Palaeocene of the Middle East (Henson 1950; Morley-Davies 1971). *Rhipidionina*, a middle Eocene soritid from Istria and the Middle East, and *Saudia*, a dicyclinid from the Palaeocene to middle Eocene of northern Iraq and Arabia, could also be included here.



TEXT-FIG. 8. Land, seas, and oceans in Eocene times, with records of fossil *Posidonia* (P) and *Cymodocea* (C). Symbols show records of possible seagrass-dwelling foraminiferids: black circles = *Orbitolites*; stars = *Saudia*; crosses = *Rhipidionina*. Stipples represent inferred distribution of 'tropical' seagrasses. Palaeogeography and palaeocurrents modified from Cox *et al.* (1973), Gordon (1973), and Ramsay (1973).

It might therefore be concluded that the present-day Mediterranean-Indo-West Pacific distribution of the *Cymodocea* association was initiated at least by early Eocene times and probably during the Palaeocene. The late Cretaceous soritids mentioned above might have heralded the advent of this association of tropical seagrasses for their distribution is remarkably similar, but there are no plant remains to support this speculation.

Oligocene

The extinction of *Orbitolites* and similar forms before the end of the Eocene and their lack of replacement is not easily explained. It was concurrent with the extinction of many other Palaeogene larger foraminifera (Adams 1973) and may perhaps be connected with a contraction of the tropical belt in the Oligocene as shown by palaeoclimatology (Haq 1973). This would have resulted in a scarcity of suitable habitats. Furthermore, *Orbitolites* may have had a life cycle extending over three or four years, as do recent *Marginopora* (Ross 1972) and the consequent lack of adaptability may have rendered it vulnerable to fluctuations of trophic source, habitat, and climate.

It is therefore more difficult to suggest what the distribution of seagrass communities may have been during the Oligocene. *Cymodocea* has been recorded from the Oligocene of Bembridge, Isle of Wight (Chesters *et al.* 1967) which may indicate that this genus maintained its distribution after the demise of its specialized epifauna. No details of stratum, locality of preservation are given, however. The miliolid and rotaliid foraminifera recorded from the Headon Beds of that area were thought by Bhatia (1957) to indicate the presence of vegetation and do in many respects resemble those from recent lagoonal seagrass beds in the tropics (Brasier 1975a). The present distribution of *Cymodocea* suggests hardiness compared with the other tropical genera, which concurs with its presence in the English Oligocene.

Backreef sediments of the tropical Americas during middle and late Oligocene times, contained flourishing 'microfaunas' of *Miogypsina* and *Miogypsinoides*. These large, lenticular, complexly structured foraminifera spread rapidly to other tropical regions, migrating (like the deeper-water *Lepidocyclina*) to the Indo-West Pacific via West Africa and the Mediterranean sea (Adams 1967, 1973). Migration in the opposite direction was apparently difficult at this time. There is, therefore, little to suggest that seagrasses or their biota were able to reach the Neotropics during the Oligocene. None the less, Chesters *et al.* (1967) mention macrofossil records of *Cymodocea* from the Oligocene of Florissant, U.S.A., but unfortunately give no citation. Until there is better evidence this unfigured occurrence may be treated with caution because *Cymodocea* is otherwise unknown around the Americas. The fossil (if a seagrass) would more likely have been of *Thalassia*, *Halophila*, or *Zostera* (?).

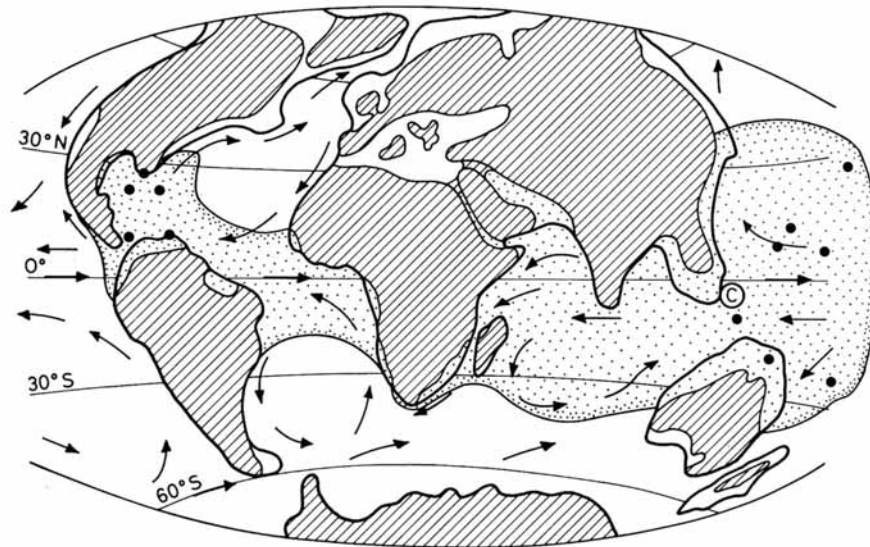
Miocene

At the end of the Oligocene and in the early Miocene, the seas began to withdraw from the Near and Middle East (Savage 1967). This effectively isolated the Mediterranean from the Indo-Pacific province, an event which was further accentuated by the junction of the Betic peninsula of Europe with Africa in the middle Miocene (Berggren 1972).

Somewhat paradoxically it is at the same time that a pantropical expansion of certain shallow-water foraminifera took place, and especially it would appear, of seagrass-dwelling forms. These included *Sorites*, *Amphisorus*, *Marginopora*, and *Peneroplis*, some of which are very similar in appearance to *Orbitolites* (see text-fig. 9). They occur in the lower Miocene limestones of the Caribbean region and appeared at about the same time in the Mediterranean and Indo-West Pacific Region (Adams 1967) and Mid Pacific (Cole 1969) where they still occur today. Equally remarkable

is the fact that the sediment-dwelling *Borelis* became, at the same time, the first alveolinid to reach the Neotropics. *Spiroclypeus* also made a unique appearance outside of the Indo-Pacific realm at this time (Adams 1973) and McKenzie (1967) records that the paradoxostomatid ostracods, which are phytal in habit, appeared and spread very widely in the Miocene. Furthermore, certain coralline algae, otherwise unknown from the Neotropics, arrived in the Caribbean from the Indo-Pacific in middle Miocene times (Brasier and Mather 1975).

This new or improved connection between the tropical Americas and the Indo-West Pacific province in the early Neogene is likely in part to be correlated with the invasion of the Neotropical area by the *Thalassia* association. Although largely



TEXT-FIG. 9. Land, seas, and oceans in Miocene times, with the distribution of fossil *Cymodocea* (C). Black circles show the wide distribution of the seagrass-dwelling foraminiferids *Sorites*, *Amphisorus*, and *Marginopora*. Stipples represent the inferred, almost pantropical, distribution of the *Thalassia* association. Palaeogeography modified from Cox *et al.* (1973), palaeocurrents conjectural.

absent from the Mediterranean it is unique in being present at isolated localities around the west coast of Africa (text-fig. 6). This is consistent with a colonization via the south cape of Africa at a time when the Suez isthmus was closed. Geological evidence can substantiate this. According to Haq (1973) a climatic amelioration of 5–8 °C occurred in the higher latitudes of the southern hemisphere during early and middle Miocene times. The probable net northward movement of the African continent during the Tertiary (Newell 1971) may in combination have made it possible for Indo-West Pacific shallow-water biotas to 'round the cape' and establish along the west coast of Africa. Closure of the Suez isthmus and Persian Gulf

could also have diverted warm Indian Ocean water down the east coast of Africa rather than through the Mediterranean as before, rendering the southern cape more tropical.

That the temperatures were unusually suitable in the early and middle Miocene is supported by otherwise unprecedented records of *Lepidocyclina* and *Miogypsina* from Angola (Lemoine and Douvillé 1904), *Miogypsina* from Brazil (Closs 1966), and *Miogypsinoides* from Nigeria (Adams 1973). The present-day occurrence of the Indo-West Pacific colonist *Borelis*, around the Atol das Rocas, off Brazil (Tinoco 1965) and also around the Cape Verde and Ascension Islands (Adams 1967) suggests that these mid-Atlantic islands served as 'staging-posts' on the westward route. Briggs (1974, pp. 90-111) has pointed out that the (probably) Miocene island of St. Helena, Ascension Islands, has a mixed American Indo-West Pacific fish fauna. The latter, he suggests, arrived on surface currents via the Cape of Good Hope. One may add that one of the two living species of seagrass shared by the Caribbean with the rest of the tropics (*Halodule wrightii*) is the only species extant along the coast of tropical West Africa but is absent from the Pacific and Mediterranean (Den Hartog 1970). Other than this, the Caribbean and Indo-West Pacific share 'twin-species' of *Thalassia*, *Syringodium*, and *Halodule* (ibid.).

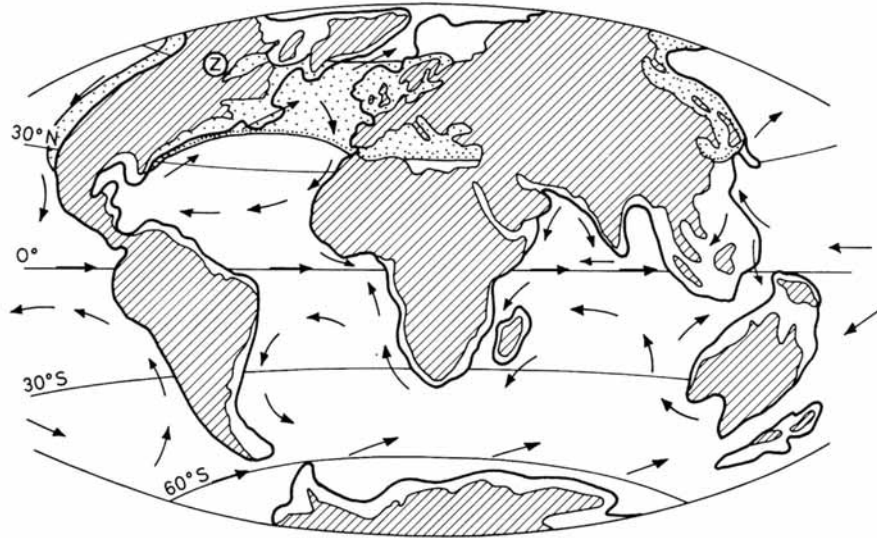
It is reasonable, therefore, to infer that the *Thalassia* association of seagrass, together with other flora and fauna, progressed around the south cape and west coast of Africa during the warmer spell in the early and middle Miocene, to be the first to arrive in the hitherto isolated Neotropical waters. After the onset of cooler late Miocene conditions this southern migration route may have become impassible. Tropical and subtropical faunas certainly show evidence of climatic restriction at this later date (Bandy 1968; Newell 1971).

As shown in text-fig. 6, the *Thalassia* association is widely dispersed at present in the North Pacific, *Halophila* reaching as far as Hawaii and Tuamotu (D. R. Stoddart, written comm. 1974). The seagrass-dwelling foraminifer *Marginopora* first appeared in this region during the Miocene and others have arrived since (Cole 1969). This suggests that this spread of the *Thalassia* association (especially *Halophila*) may also have occurred primarily at that time.

Plio-Pleistocene

Climatic deterioration probably prevented the relatively stenothermal *Thalassia* association from colonizing the higher latitudes of North and South America so that these may have been, as yet, unvegetated by seagrass. Den Hartog (1970) has suggested that colonization of the north Atlantic shores by *Zostera* (*Zosterella*) took place in the Plio-Pleistocene from the north Pacific (see text-fig. 10). This was presumably achieved via the 'arctic' shores of Canada, including Hudson Bay where a relict flora remains. The late Pliocene molluscs of England, Iceland, and New England also share strong north Pacific affinities, which suggests that a two-way migration of biotas took place across North America before the onset of the Pleistocene glaciations (Ekman 1953, p. 122).

Also in the late Pliocene, the Panama isthmus became closed, isolating the Pacific and Atlantic communities. This limited the flow of warm water along the west coasts



TEXT-FIG. 10. Recent distribution of the seagrass *Zostera* (*Zosterella*) and a Pleistocene record (z).

of the tropical Americas which once had flourishing Neotropical faunas. The presently restricted distribution of the *Thalassia* association (text-fig. 6) on the west side of Panama attests to this.

DISCUSSION

Perhaps the major paradox to arise from the foregoing is the suggestion that tropical seagrass communities were expanding their geographic range in the Miocene, when it is generally held that coral-reef communities became more isolated and impoverished at about that time (see Newell 1971). Both changes may largely have been brought about by Alpine earth movements which reached a climax in the Miocene, uplifting many of the Tethyan continental margins. This must have resulted in a concomitant increase in the input of terrestrial material, causing in places greater turbidity and more highly fluctuating levels of nutrients (especially nitrates and phosphates) than occurred before. According to Tappan (1971) and Valentine (1971) such changes would have 'rejuvenated' the coral community ecosystem, causing a reduction in diversity. As the seagrass community is apparently more tolerant of great fluctuations in nutrient levels, acidity, and oxidation, it need not have been adversely affected by the increased 'continentality'.

The east to west dispersal of the *Thalassia* association across the Atlantic in the Miocene could well help to explain the unusual migratory behaviour of *Chelonia mydas*, the seagrass-eating green turtle. Carr and Coleman (1974) recently accounted for its yearly migration from Brazil to the Ascension Islands as a product of seafloor spreading. They have suggested that the breeding grounds on the Mid-Atlantic

Ridge gradually spread further and further away from the South American feeding grounds, starting at least in the early Caenozoic. As a result *C. mydas* now swims WNW.-ESE. against the prevailing equatorial current for nearly eight weeks. It breeds around the Ascension Islands, lays eggs from which juveniles hatch and drift back with the current to Brazil. For this behavioural pattern to develop they imply that the home breeding grounds of South America became inexplicably unsuitable at some stage. Whilst remaining good for feeding, only the mid-ocean volcanic islands provided suitable beaches for egg laying.

Bearing in mind the extremely conservative breeding behaviour of past and present amphibians and primitive reptiles, one wonders how *Chelonia* evolved the above-mentioned exploratory breeding behaviour whilst retaining conservative feeding behaviour. The reverse seems to be more in keeping with present evidence. Firstly, *Chelonia* is not recorded before the Miocene (Carr and Coleman 1974). Secondly, other evidence indicates that seagrass (the food source) did not reach the Americas from the Indo-West Pacific until the Miocene. Thirdly, no such behaviour is known in green turtles from the Indian Ocean (which would have been inherited if they had American origins). It is therefore more likely that *Chelonia* arrived in the Atlantic like many other organisms, via the Cape of Good Hope during Miocene times. It would have found the new American feeding grounds by passively drifting across the equatorial Atlantic, colonizing the Ascension Islands on route. At breeding time instinctive behaviour still leads them eastwards to the Ascension Islands, their original base (Brasier 1974).

One should now consider why it was not possible for the Eocene *Cymodocea* community to cross the Atlantic from east to west in a similar way. Paradoxically, the Atlantic is thought to have been narrower in the Eocene (Smith *et al.* 1973). The answer may therefore lie in the complex and conflicting evidence for palaeocurrents, especially that for the Atlantic's North Equatorial Current which is the one which could have acted as the requisite agent. Interestingly, this is thought to have been weaker than the Equatorial Undercurrent and Counter Current in the Eocene (Ramsay 1973). A warm current from the Indian Ocean into the Mediterranean may also have pertained at that time, produced by north-east trade winds which then had a more northerly sphere of influence (Schwarzbach 1963). The deflection of this current by closure of the eastern end of the Mediterranean may then have helped to extend the tropical zone to the southern cape of Africa, as previously discussed. The closure of the western end of the Mediterranean in the middle Miocene could also have improved the return of the north Atlantic water down the west coast of Europe and North Africa to form a cooler branch of the North Equatorial Current. This cooler water effectively isolated the Mediterranean from the Neotropics and West Africa, as indicated by fossil faunas (Ekman 1953; Berggren 1972).

A final point arises out of the foregoing observations: that the nature of ocean surface currents and the availability of migration routes can be more important than geographical proximity in controlling the similarity of shallow-water benthos. Reconstruction of past continental configurations by analysis of faunal and floral similarity should therefore be viewed with some caution (see Jell 1974).

SOME PALAEOECOLOGICAL IMPLICATIONS

The gradual encroachment of seagrasses into the sublittoral in late Cretaceous and Tertiary times may be surmised from recent studies to have been a significant ecological event. The resultant eutrophication of sediment substrates would have encouraged the development of deposit-feeding organisms, especially prosobranch gastropods and miliolid foraminifera. These two groups have certainly diversified greatly since the Mesozoic. Seagrasses also provide shelter for coralline algae, which likewise have diversified in the Cenozoic (Wray 1971).

One may further suggest that those organisms feeding on herbivores and detritus feeders, such as teleosts and rays, have benefited from the innovation. The archaic turtles could have survived their marine reptile contemporaries after the Mesozoic because of their gastropod and seagrass diet. Mosasaurs were probably used to a cephalopod diet—hence were ill-adapted to exploit such a trophic innovation (see Nicol 1961).

The more rapid encroachment of seagrasses into Neotropical waters in the Miocene must also have been a significant event. At a time when land barriers were making biotic exchange with the rest of the Tethyan tropics increasingly difficult, seagrasses could have aided the dispersal of sessile organisms across the Atlantic and probably to islands in the mid North Pacific. Such relatively sudden innovations are thought to cause rejuvenation of the ecosystem, threatening specialized tropical organisms with extinction (Tappan 1971). The forms most likely to suffer in the Miocene of the Neotropics were those endemics adapted to lower nutrient levels or to coarser and less stable substrates. Hence it may be no coincidence that the specialized, sediment (?) dwelling Neotropical foraminifera *Miogypsina* and *Lepidocyclina* became extinct in their own province during the middle Miocene and not long after in other regions. Their extremely large size, structure, and palaeoecology suggests that they cultured symbiotic algae, which often indicates a relatively low but steady external food supply. If the food supply was increased and trophic stability was upset by the rejuvenation of continental margins and oceanic islands, together with the encroachment of seagrasses, these foraminifera would have had difficulty in adapting, especially if they had long life cycles (see Tappan 1971; Valentine 1971). Other endemics, such as scleractinian corals, seem to have suffered in a like manner (see Newell 1971).

Unfortunately, it is not yet possible to say to what extent the above speculations are justified but they point to some interesting lines for future research.

CONCLUSIONS

The distributions of Recent and fossil seagrasses are similar to the distributions of Recent and fossil seagrass-dwelling foraminifera. The latter may therefore be used as indices (only) of the geographical dispersal of seagrass communities through time. The suggested dispersal patterns are biased towards tropical seagrass communities because tropical foraminifera indices are more distinctive than temperate ones and are therefore more reliable.

Seagrass communities were probably present in the shallow sublittoral waters of the Tethys in late Cretaceous times and almost certainly in Eocene times.

The gradual encroachment of seagrasses into the sublittoral in late Cretaceous to early Tertiary times can be surmised from recent studies to have resulted in three significant modifications of the ecosystem: (i) increase in habitat diversity; (ii) eutrophication of sediment substrates; (iii) additional means of dispersal for sessile organisms (i.e. rafting).

The more or less contemporaneous radiation of deposit feeding and epiphytic gastropods and miliolid foraminifera (including soritids) in the late Cretaceous and Tertiary could be attributed in part to these factors, particularly in tropical waters.

A more rapid colonization of the relatively isolated Neotropical and mid-Pacific sublittoral waters by seagrass communities seems to have occurred during the Miocene. Seagrasses, epibionts, and associated faunas (including the green turtle *Chelonia*) were probably dispersed by oceanic surface currents from the Indian Ocean via the Cape of Good Hope and the islands of the Mid-Atlantic Ridge. Earth movements may also have aided dispersal at this time by the provision of broader shelves and new islands.

The Miocene earth movements and seagrass dispersal could likewise have contributed to the extinction of specialized endemic faunas such as *Lepidocyclina* and *Miogypsina*.

The ecological effects were and are most marked in tropical carbonate environments where the influence of land masses ('continentality') is low and alternative sources of organic and inorganic nutrients are few.

The similarity of fossil assemblages is not always a reliable indication of their former (or present) geographical proximity. Caution should therefore be exercised in applying techniques of similarity analysis to continental reconstructions.

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