PRE-MIOCENE SEAGRASS COMMUNITIES
IN THE CARIBBEAN

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ABSTRACT. Fossil seagrasses are rarely found in the geological record. Since their ancient distribution cannot be determined directly, it has to be inferred by examining the components which characterize seagrass communities. In this way it has been suggested that although seagrasses first appeared in the late Cretaceous, they did not reach the Caribbean until the Miocene.

Caribbean larger foraminifera of late Cretaceous to Oligocene age are discussed, and certain species belonging to the genera *Chubbina, Ayalaina, Yaberinella, Cyclorbiculinoides, Cyclorbiculina,* and *Peneroplis* are recognized as probable seagrass-dwellers. A new model for the Caribbean is proposed in which seagrasses first appeared in late Cretaceous times, and became widespread during the Eocene.

THE importance of seagrasses in trapping carbonate sediment and stabilizing ecological niches is well known, and has been carefully documented by a number of authors such as Scoffin (1970), and Brasier (1975). Whilst it is highly desirable that the former distribution of these plants be determined in space and time, this is unfortunately difficult. Seagrasses lack readily fossilizable parts, and their pollen has a thin or absent exine which makes preservation unlikely. Even when preservation has taken place, it is difficult to distinguish between marine grass parts and those from terrestrial or freshwater areas which have subsequently been transported into a marine environment. The ancient distribution of seagrasses therefore has to be determined by indirect approaches based on the biological and sedimentological features, which together characterize present-day seagrass communities.

Although it is generally accepted that seagrasses first appeared during the late Cretaceous, there is no agreement as to how widespread they were at this or subsequent times. Based on sedimentological evidence, Petta and Gerhard (1977) concluded that certain Campanian sediments in Colorado were probably fossilized marine grass banks, analogous to modern *Thalassia* beds. This suggestion later received support from Bretsky (1978) who pointed out that the bivalves present in these sediments were well adapted to living in a seagrass environment. By contrast, Brasier (1975) has given an account, based mainly on palaeontological evidence, whereby seagrasses did not reach the Americas and Caribbean regions before the Miocene. Records of larger foraminifera in the Caribbean seem to be inconsistent with such a hypothesis. Before entering into such a discussion it is first necessary to describe the way in which larger foraminifera can be used to reconstruct seagrass distributions.

FORAMINIFERA AS INDICATORS OF VANISHED SEAGRASSES

The value of using larger foraminifera to indicate previous areas of seagrasses has already been outlined by Brasier (1975) but some of the problems associated with this approach should, perhaps, be re-emphasized.

At the present day, a number of foraminifera are known to spend at least a part of their life, in some geographical areas, as epifaunas on the blades of seagrasses. These include *Peneroplis planatus, Amphisorus hemprichi, Sorites marginalis, Marginopora vertebralis, Archaias angulatus,* and *Cyclorbiculina compressa* (Bock 1969; Davies 1970; Brasier 1975; Steinker and Steinker 1976; pers. obs.). These forms all have a relatively large size, a complex endoskeleton and a discoidal shape, and it would seem highly likely that at least some morphologically similar species have shared a similar style

in the geological past. Thus, in theory, it should be possible to map out the distribution of certain fossil species, and to equate these occurrences with the former distribution of seagrasses.

This approach is limited because it has not yet been demonstrated that these, or any other foraminifera, are *restricted* to living on seagrasses. Living specimens of most of the forms mentioned above have also been reported from sediment samples, although in most cases these sediments were within grass beds, or closely associated with them. Seasonal changes, resulting in changes in the abundance of seagrass, also affect the foraminiferal populations (Bock 1969; Hottinger 1977). Thus although Bock (1969) found sixty-six different benthonic species attached to *Thalassia* blades on the Florida Keys, only ten of these were abundant throughout the year.

Further complications arise because living forms which apparently prefer an epiphytic lifestyle, may have close relatives which are better adapted to different environments. Present-day examples are known where different species of the same genus, living in approximately the same area, apparently prefer different substrates (see, for example, Hottinger 1977). This is a common feature amongst many other groups of animals, and is often referred to as the Volterra-Gause principle. Even microspheric and megalospheric forms of the same species may occupy different environments (Walker 1976).

Other features which might be expected of fossil seagrass communities include highly diverse foraminiferal populations, as these are often associated with present-day marine-vegetated areas (Murray 1970; Steinker and Steinker 1976). By contrast the adjacent unvegetated areas tend to contain a less diverse fauna, a smaller percentage of mud-sized particles (Scoffin 1970), and may be the typical habitats for the spherical to fusiform alveolinids *Borelis* and *Alveolinella*. These two differing facies would be expected to occur as lateral equivalents in the fossil record.

The above discussion suggests that correlating fossil foraminiferal distributions with those of seagrasses will be subject to certain degrees of inaccuracy, ambiguity, and personal bias. Of particular importance is the scale on which such correlations are attempted. Over small areas there can be little hope of identifying seagrass localities using fossil foraminifera, but on a regional scale it should at least be possible to identify those areas which are consistent with the proposal that they contained fossil seagrass communities. This approach will now be applied to the Caribbean region.

RECONSTRUCTING FORAMINIFERAL DISTRIBUTION PATTERNS IN THE CARIBBEAN

Dilley (1973) and Hottinger (1973) have discussed some of the general problems involved in mapping ancient larger foraminiferal distributions, and in the Caribbean such problems are especially acute. Not only must the recorded occurrences be taken into account, but also the state of knowledge across the region. This point can be illustrated by considering Jamaica, which has a well-established Geological Survey and University Geology Department, together with a long history of palaeontological research (Chubb 1975). Despite the many previous studies, and the relatively small size of the island (11 420 km²), four new genera and six new species of larger foraminifera have been described from the Middle Eocene deposits alone over the last ten years (Robinson 1969, 1974a; Eva 1976b). Clearly the faunas are not yet adequately described, and the situation elsewhere in the region is considerably worse. Critical areas such as Nicaragua or Hispaniola have had relatively few detailed investigations, and whilst forms may be equally diverse, published accounts are lacking.

It should also be remembered that marine sediments of Palaeocene and Oligocene age have not always been widely recognized in the region. In the former case this appears to reflect a real gap in the marine record (Khudoley and Meyerhoff 1971). The latter case, however, reflects the confusion that has arisen ever since Eames *et al.* (1960, p. 448) first declared that 'no Oligocene can be recognised in the marine sediments of the western hemisphere'. Although this position has been repeatedly refuted by later workers, a certain amount of confusion still surrounds the recognition of the Oligocene in the Caribbean, and this should be considered when discussing faunal distributions of this age.

Finally it will be noted that the foraminiferal distributions have been plotted onto a present-day map of the Caribbean (text-fig. 1a, b). This approach can only be justified because all present reconstuctions of the Caribbean–Central American region for Cretaceous or early Tertiary times remain highly controversial.
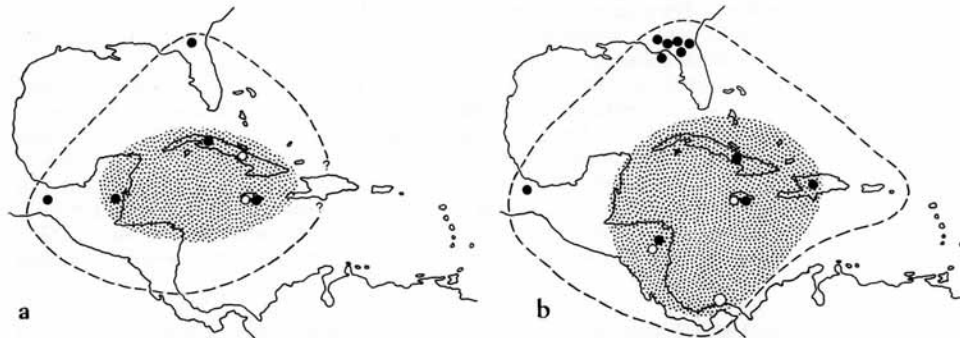
OCCURRENCES OF SELECTED LARGER FORAMINIFERA

Upper Cretaceous. Brasier (1975, p. 690) suggested that the genera *Vandenbroeckia, Broeckia, Edomia, Qateria,* and *Pseudedomia* might have been seagrass-adapted forms, and noted that their distribution was restricted to the Tethyan region. However, a number of similarly constructed porcellaneous forms were present in the Caribbean at this time (Dilley 1973; Robinson 1974c). These included species of the genus *Chubbina* which have an analogous structure to *Pseudedomia*, a lenticular to discoidal shape (Robinson 1968b), and which are known from Jamaica, Mexico, Florida, and Cuba (Hamaoui and Fourcade 1973). Another similar-shaped species is the peneroplid *Ayalaina rutteni* which has a thin-walled delicate test, and has been recorded from Jamaica and Cuba (Robinson 1968b).

These forms seem to be restricted to the northern Caribbean (text-fig. 1a), as opposed to the widespread development of the pseudorbitoids and orbitoids (Dilley 1973; Robinson 1974c). This probably indicates significant large-scale variations in the shallow-water facies of the Caribbean at this time. The greatest recorded faunal diversity in the carbonate shelf environment occurs in Jamaica, Cuba, and Belize; and these areas are tentatively correlated with the distribution of seagrasses (text-fig. 1a).

Palaeocene–Eocene. Marine Palaeocene sediments are poorly represented on the Caribbean islands (Khudoley and Meyerhoff 1971) but carbonate rocks of Eocene age occur across much of the region, and often contain abundant larger foraminifera.

Brasier (1975) placed great emphasis on the distribution of *Orbitolites* in reconstructing his distribution of Eocene seagrasses. The justification for this approach lies in the close structural similarity between *Orbitolites* and living species such as *M. vertebralis*, and *S. marginalis* which attach themselves to marine vegetation. This view was also shared by Hottinger (1973, p. 444) who suggested that *Orbitolites* 'lived probably epiphytic on plants like recent *Sorites*'.

TEXT-FIG. 1. Maps of the Caribbean showing the distributions of selected larger foraminifera for (*a*) late Cretaceous, and (*b*) Eocene times. In (*a*) solid circles represent species of *Chubbina* and open circles *Ayalaina rutteni*; in (*b*) solid circles represent species of *Fabularia* or *Borelis*, whilst open circles depict *Cyclorbiculinoides jamaicensis* or *Yaberinella jamaicensis*. The dashed lines contain the larger imperforate foraminiferal provinces as defined by Robinson (1974c, 1977). Areas that were probably inhabited by seagrasses are shaded. Sources of data are discussed in the text.

Although it is true that *Orbitolites* is unknown in the Caribbean, several closely related forms are present. These include *Cyclorbiculinoides jamaicensis*, which is widely distributed in the Eocene shelf carbonates of Jamaica (Robinson 1974*b*), and which is structurally so similar to *Orbitolites* that it was originally mistaken for it (Robinson 1968*a*). Other large peneropliform to discoidal species present in the shelf carbonates of Jamaica include *Yaberinella jamaicensis*, and a species belonging to a new genus, analogous to *Puteolina*, which has not yet been formally described. The palaeoecological position of *Y. jamaicensis* deserves attention, for although both Hottinger (1973) and Eva (1976*a*) have suggested a restricted back-reef environment for this species, it is now known from such widely spaced areas as Jamaica (Vaughan 1928), Panama (Cole 1952), and Nicaragua (F. Bourgeoise pers. comm. 1975). Whilst much still remains to be learnt about the ways in which larger foraminifera are dispersed, attachment to floating seagrasses is known to be an important and effective method (Bock 1969; Hottinger 1977). The size, shape, and distribution pattern of *Y. jamaicensis* are therefore all consistent with an epiphytic lifestyle.

If the discoidal-shaped species discussed above represent seagrass dwelling forms, we might also expect to find, in laterally equivalent strata, back-reef sediment dwellers similar to the present-day *Borelis*. Brasier (1975, p. 694) took this view, but argued that it was not until the Miocene that *Borelis* became 'the first alveolinid to reach the Neotropics'. This assertion deserves some comment. Cole (1941) and Levin (1957) have both recorded *Borelis* from Eocene deposits in Florida, and the genus has also been reported from Mexico (Butterlin and Bonet 1960), although none of these references is accompanied by unequivocal illustrations. However, the near-spherical alveolinids *Fabularia vaughani*, *F. verseyi*, and *Pseudofabularia matleyi* have been well illustrated, and are widely distributed in the inner shelf carbonates of Jamaica (Robinson 1974*a, b*; Eva 1976*b*). *F. vaughani* has long been known from Florida (Cole and Ponton 1934), and Wessem (1943) and Butterlin (1956) have also recorded the presence of alveolinids in the Eocene limestones of Cuba.

The lithology of the Eocene sediments in Jamaica is also consistent with the view that seagrasses were established by this time. The lower Eocene and lower Middle Eocene shelf deposits are characterized by lenticular bodies of highly fossiliferous limestone, 0·5–2·5 km in diameter, surrounded by well-bedded unfossiliferous quartzo-feldspathic sandstones and siltstones (Robinson 1969; Wright 1974). These sediments appear to be analogous to those which presently accumulate within the Salt River Estuary off St. Croix (Petta and Gerhard 1977). Here carbonate deposition is confined, and largely created and stabilized by, discrete areas covered by seagrasses and their associated faunas. The surrounding areas are carbonate deficient, and consist of terrigenous muds deposited by the Salt River. The younger Eocene shelf sediments in Jamaica consist predominantly of poorly sorted biomicrites, which although not indicative of fossil seagrass beds, are certainly consistent with such possible palaeoenvironments.

The presence of seagrasses in the Caribbean by Eocene times therefore seems quite likely although the extent of its distribution is less certain. Faunas are most diverse in Jamaica, Cuba, and Nicaragua, but the presence of *Y. jamaicensis* in Panama suggests that seagrasses may have been extending southwards. Areas of relative carbonate stabilization are also reflected in the distribution of mangroves, and it seems significant that *Pelliceria* and *Rhizophora* are known from both Jamaica and Panama at this time, but appear to be absent from Florida (Graham 1977). The larger foraminiferal faunas in Florida are clearly impoverished compared with Jamaica (Robinson 1974*c*), suggesting that seagrasses did not reach so far north, or that they were only poorly developed (text-fig. 1*b*).

Oligocene. During the Upper Eocene many larger foraminifera became extinct, leaving several niches vacant, which were not always immediately reoccupied. In the Caribbean this is exemplified by the disappearance of the possible seagrass-dwellers *Y. jamaicensis* and *Cyclorbiculinoides jamaicensis*, and also by probable sediment-dwelling genera such as *Fabularia*, *Pseudofabularia*, and *Keramosphaera*. Although the latter niche appears to have been quickly occupied by species such as *Archais angulatus* (McFarlane 1977; Seiglie *et al.* 1977), and *Fusarchais bermudezi* (Reichel 1952), possible seagrass-dwelling forms are uncommon. They may, however, be represented by species such as

Peneroplis proteus, Puteolina sp., and *Cyclorbiculina* sp., which are known from the islands of the Greater Antilles (McFarlane 1977; Seiglie *et al.* 1977).

Miocene–Recent. Evidence for the presence of seagrasses in the Caribbean during this time has been discussed by Brasier (1975), and need not be further elaborated.

CONCLUSIONS

Although there are a number of difficulties inherent in any attempt to analyse the distribution of fossil foraminifera in the Caribbean, it is clear that even the present evidence is inconsistent with the model proposed by Brasier (1975).

Exactly when seagrasses appeared in the Neotropics in unclear, but the late Cretaceous forms are diverse, and in *Ayalaina rutteni* and species of *Chubbina* there is the suggestion of seagrass-adapted forms. The Eocene deposits of the region are most studied, and their larger foraminifera and sediment type almost certainly indicates the presence of seagrasses by this time.

Present evidence therefore suggests that the establishment of seagrasses in the Caribbean followed similar lines to that in the Tethyan region. Hopefully this proposal will encourage workers to seek further evidence for fossil seagrass communities in the Caribbean. Future work must involve not only studies of foraminiferal distributions, but also detailed sedimentological studies, and searches for fossil remains of the plants themselves.

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