

LARGER FORAMINIFERA AND SEAS THROUGH TIME

by F. C. DILLEY

ABSTRACT. The broad features of larger foraminiferal distribution through their history from Late Palaeozoic times on are outlined on the appropriate Symposium Base Maps, and briefly discussed in the context of such maps. Major postulates in plate tectonics and continental drift theory, viz. the opening of the Atlantic Ocean and the flight of India and Australasia are considered in relation to evidence from this group of organisms.

ALTHOUGH study of distribution patterns of fossil organisms is far from new, the present symposium imposes modern constraints to the topic in a contemporary context. The 17th Inter-University Congress held at Queen Mary College, London, in December 1969 which took as its theme 'Faunal Provinces in Space and Time' provided an earlier opportunity for some of the present contributors to take a hesitant step in this direction, although the theme was as much concerned with the nature and perhaps definition of 'Provinces' for their own sake as with the implications of the patterns discerned in the field of plate tectonics, sea-floor spreading, and continental drift.

The writer explored some aspects of these implications regarding Cretaceous foraminifera on that occasion (Dilley 1971) and here extends this exploration more generally through the history of the larger foraminifera from Late Palaeozoic times on. At the same time and with the aid of the Smith, Briden, and Drewry reconstructions some of the more significant aspects of the distribution data are analysed and discussed in more detail.

Statistical treatment of the data as urged by Professor Sneath is more appropriately reserved for the specific treatment and investigation of individual taxa at genus or species level at carefully defined horizons and by more numerate micropalaeontologists than the writer, but a strong quantitative element is nevertheless implicit in the basis for the patterns here described. This follows from the vast quantity of data relating to the foraminifera as a whole which has become available largely through the widespread activities of the large number of palaeontologists engaged in the exploration side of the oil industry.

The broad outlines of larger foraminiferal distribution have already been deduced on a global scale for the Cretaceous (Dilley 1971, 1972); a circum-global belt of occurrence has thus been demonstrated on a present-day continental arrangement and latitudinal grid.

Before proceeding further, I remind the reader of certain generalities concerning this fossil group:

1. The term 'Larger Foraminifera' is not a taxonomic category but is composed of taxa which fall rather naturally into taxonomic categories at about 'family' level and have been so classified without special reference to their biogeography. In brief, it is not a question of selection of data to support a particular biogeographical

hypothesis. The adjective 'larger' connotes a size normally in excess of 1 mm for the greatest dimension of the test, but the category excludes forms of large size (occasionally even in excess of several millimetres) but simple structure. The chief criterion is complexity of internal morphology which resolves itself ultimately into the capacity to modify the major chamber cavities by secondary septa, partitions, and the like. Large size and relative complexity of structure often go together but not invariably so.

2. Where definitive evidence exists, these forms are established as shelf benthos characteristic of warmer seas. The evidence resides both in direct observation at the present day among extant forms, and by inference from lithological and organic associations in the fossil record.

OUTLINES OF LARGER FORAMINIFERAL DISTRIBUTION

Late Palaeozoic fusulinaceans

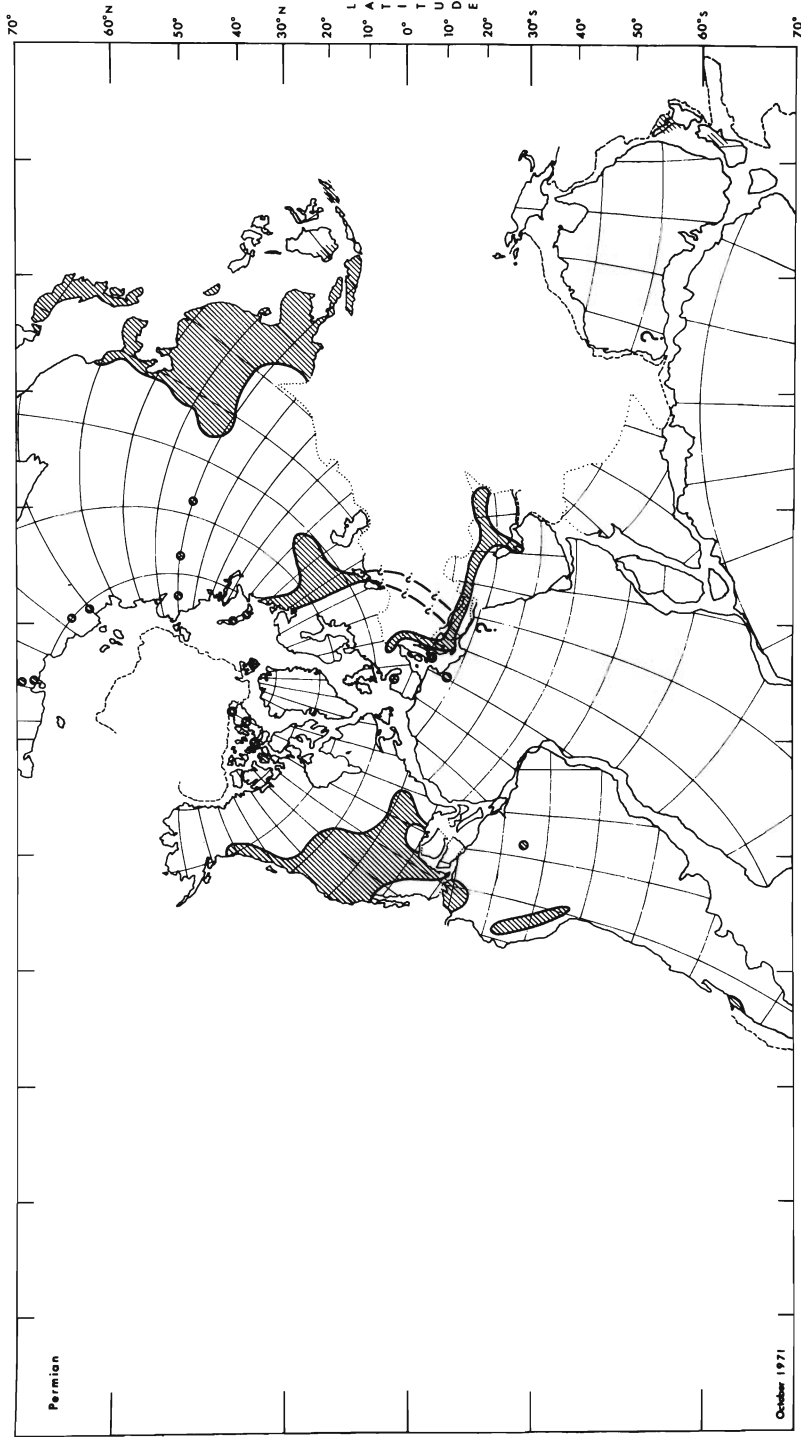
Although it is logical to consider first the distribution of the fusulinaceans as the geologically earliest of the larger foraminiferal groups, the pattern observed (whether on a present-day continental arrangement and latitudinal grid or that of the appropriate symposium map) differs so fundamentally from the broadly constant patterns deduced from Mesozoic and Tertiary periods, that it could well have been left until last.

The distribution data summarized in text-fig. 1 is derived essentially from that presented by Thompson (in Loeblich, Tappan *et al.* 1964) with minor addition only, but plotted on the Symposium Base Map. Occurrences within the Canadian Arctic Islands and in Greenland become more credible on text-fig. 1 than in the present-day arrangement used by Thompson, but those from the extreme north of Asia seem incredibly high latitude by any standard of subsequent record for any larger foraminifera. The reason may lie in a different response by the fusulinaceans to water temperature. Most authorities certainly have inferred Tropical and even reefal associations for the group (Glaessner 1945) but Thompson is less definite and attributes to them an environment in somewhat deeper and more open water than that in which subsequent members of the larger foraminiferal groups flourished.

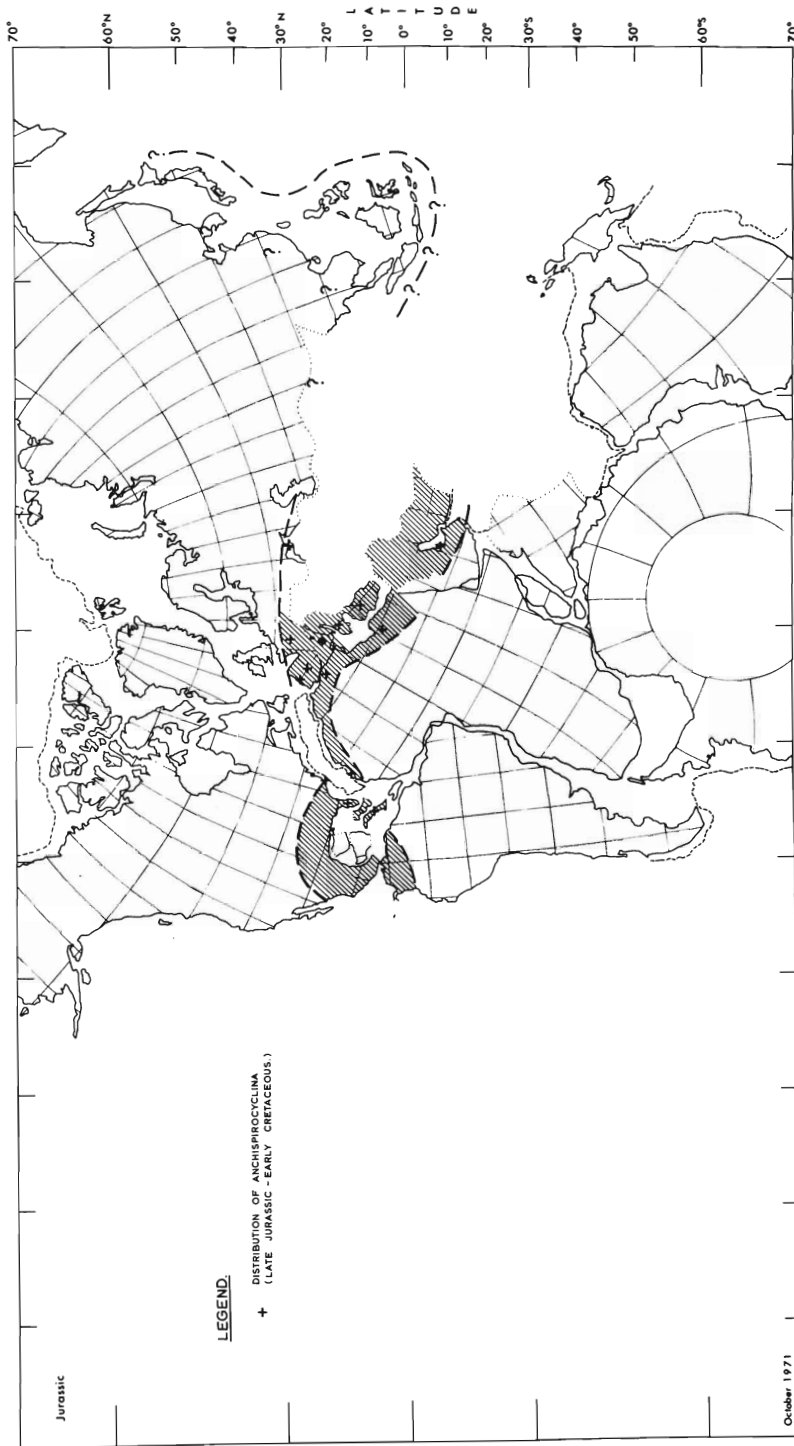
Mesozoic larger foraminifera

Triassic. The Triassic can be dealt with summarily. Records of essentially Lower Jurassic genera (e.g. *Orbitopsella*) are occasionally shown as originating doubtfully in the Late Triassic but there is no reliable evidence for larger foraminifera of this age.

Jurassic. All occurrences within this interval relate to the single superfamily Lituolacea, composed of agglutinating genera with complex chamber walls and chamber cavities modified by partitions or infoldings of the inner layers of the chamber walls. The number of taxa involved is also small by subsequent standards, although this



TEXT-FIG. 1. Distribution of Late Palaeozoic fusulinaceans (slightly modified after Thompson 1964).



TEXT-FIG. 2. Tentative limits of larger foraminifera (*Lituolacea*) in the Jurassic.

situation improves with time. The gross pattern of global distribution (text-fig. 2) involves regions which, as will emerge subsequently, appear 'traditional' for the larger foraminifera throughout their Mesozoic and subsequent history: the central American region, the lands bordering the present Mediterranean, the Middle East and south-west Asia, the East Indies and Japanese Islands. This pattern surely reflects in large part the distribution of shelf-seas within a low-latitude circum-global belt approximately parallel to present-day latitudes, and places broad but definite constraints upon the Mesozoic and Tertiary mapmaker.

Cretaceous. I have dealt with this period in some detail elsewhere (Dilley 1971, 1972) but some additional information has been incorporated in text-fig. 3. Comparison of the Jurassic and Cretaceous Base Maps discloses some important changes: (a) North America has moved some 15° to the north while the southern continents and Europe remain fairly static; (b) Eastern Asia has rotated some 20° to the south; (c) The central Atlantic has opened to perhaps half of its present width.

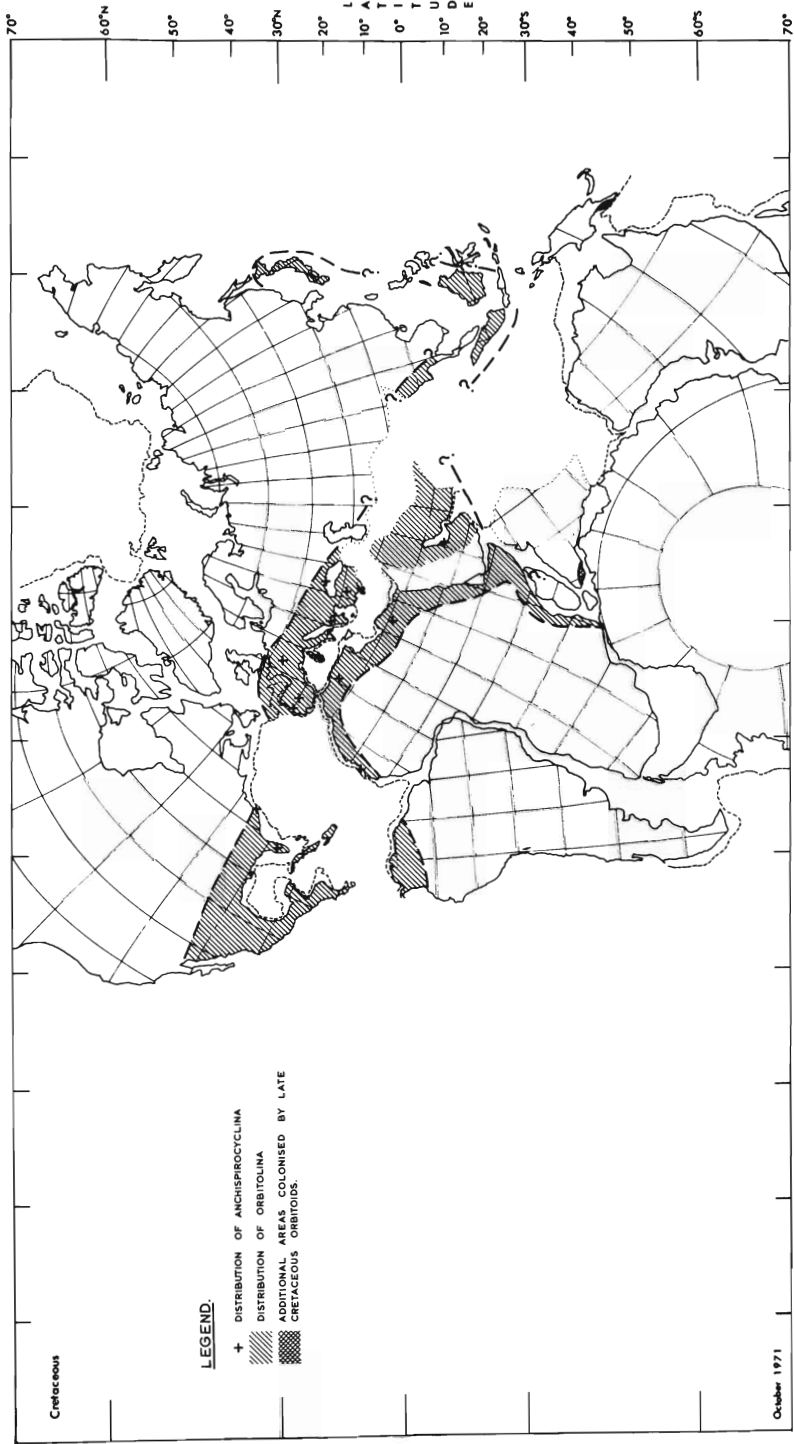
Considering North America first, the distribution of *Anchispirocyclina*, *Choffatella*, and *Orbitolina* in the Early Cretaceous delimits an area little changed from that recognized for Jurassic larger foraminifera. With *Anchispirocyclina* reaching the latitude of Cape Hatteras and *Orbitolina* that of the head of the Gulf of California, a southerly rather than a northerly drift would be more consistent with the evidence here.

In Europe, *Orbitolina* penetrated southern England, which is a little to the north of the northernmost Jurassic records of larger foraminifera. This is not inconsistent with the static condition postulated for the region. In East Africa, *Choffatella* penetrated as far south as Somaliland and *Orbitolina* to southern Tanzania, a considerable extension from Jurassic larger foraminiferal limits. The static arrangement implicit in the Base Map is therefore not reflected in the larger foraminiferal distribution here.

In east Asia, a northerly migration of the larger foraminiferal limits could be expected but with *Orbitolina* ranging only as far as Hokkaido no confirmation of the southerly drift implied by the dextral rotation postulated here is possible.

Larger foraminiferal limits in the Late Cretaceous extend beyond those designated for the Early Cretaceous only in New Guinea, peninsular India, and doubtfully Madagascar. Each of these records relates to orbitoidal forms of the Late Senonian and might perhaps be better interpreted if plotted on the Eocene Map. The Madagascar reference is unaccompanied by figures and I have not as yet been able to confirm the record. The Indian and New Guinea records would be marginally acceptable in their plotted positions but the latitudes seem somewhat high for these forms which generally have clear reefal associations in many areas of their occurrence.

Evidence from the central American region is generally lacking in the interval (Cenomanian-Lower Campanian) when the alveolines and many 'Soritidae', Dicyclinidae, and other families were flourishing in Mediterranean Tethys. The former region is, however, sufficiently explored to suggest that absence of these forms from the Americas is real enough and not due to collecting failure. Certainly



TEXT-FIG. 3. Limits of Cretaceous larger foraminifera.

sediments of appropriate age do occur. A similar condition obtains also along the north-west African coast, i.e. in the Tarfaya and Senegalese Basins, where larger foraminifera are as yet unknown from Cenomanian to Early Senonian times.

Tertiary

An apparent radiation of the larger foraminifera as a whole beyond the 'traditional' regions characterizes the Tertiary (text-fig. 4). The Symposium Base Map indicates: (i) Only minor change in the position of North America; (ii) an appreciable sinistral rotation of Africa and Australia, the latter moving well to the east; (iii) India has completed most of its northerly flights; (iv) the South Atlantic is now well developed.

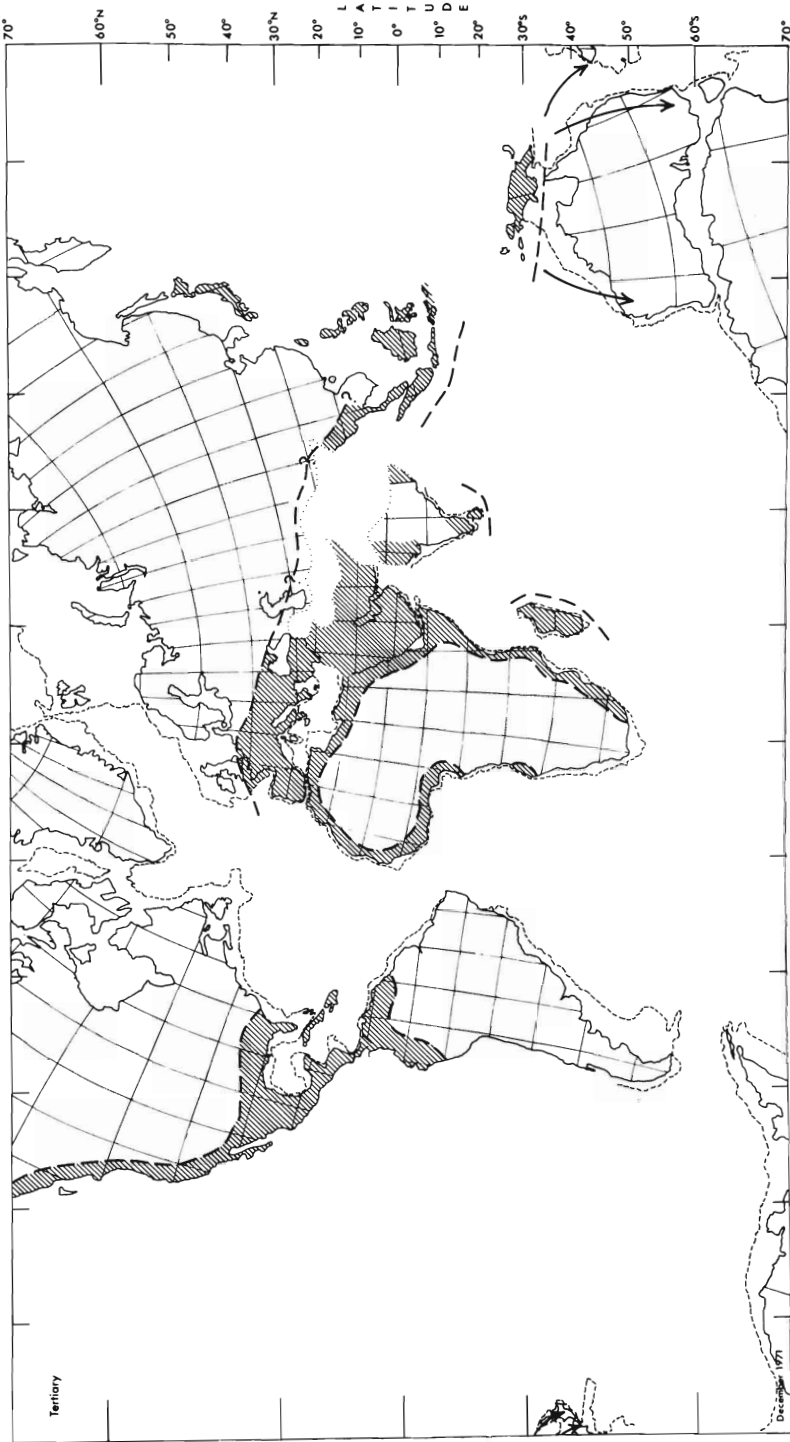
The central American region with its well-documented Late Cretaceous orbitoidal faunas reappears as the focus of American Tertiary larger foraminiferal distribution following the Mid-Cretaceous break in the record. The dispersal of the Discocyclinidae along the Pacific coast to southern Alaska defies interpretation on a purely 'drift' hypothesis. To reach the very high latitude shown on the Base Map (i.e. beyond 70° N.) in the later Eocene must surely imply an anomalously mild oceanic regime along this coast, by comparison elsewhere in the Northern Hemisphere. Thus, Eocene *Nummulites* and *Alveolina* reached only extreme southern Britain, little different here from the northernmost limits of Jurassic and Cretaceous larger foraminiferal types in northern Europe. In the Oligocene and Miocene this area also represented the most northerly occurrence of the group, with *Nummulites* in the Low Countries and Miogypsinids in northern Germany. Larger foraminifera have not been reliably reported from the thick North Sea Tertiary sequences or the Tertiary of Denmark.

The disparity in extent of larger foraminiferal penetration along East and West African coasts observed in the Cretaceous is maintained and even accentuated in the Early Tertiary, but records of *Lepidocyclina* and *Miogypsina* from Angola (Lemoine and Douvillé 1904) in the Miocene tend to modify this situation in the Neogene.

In Australasia, Discocyclinidae reached north-west Australia and the south island of New Zealand, both in Eocene times, while Lepidocyclinidae reached Batesford in South Australia during the Miocene. Miogypsinids also reached New Zealand's north island in the Miocene but there is as yet no record of Palaeogene *Nummulites*. New Guinea, however, which had entered within the 'realm' of the larger foraminifera only in the very Late Cretaceous is firmly within its bounds by Eocene times with a full Pacific suite of larger foraminiferal genera.

OBJECTIVE SUMMARY OF THE DISTRIBUTION PATTERNS

1. A tropical belt of larger foraminifera persisted in much the same areas throughout Mesozoic and Tertiary times.
2. Poleward penetration of a few genera took place at various times beyond the traditional 'homelands' of the group, e.g. Cretaceous *Orbitolina* and Eocene *Discocyclina*.
3. The timing of these penetrations usually implies controls by factors other than



TEXT-FIG. 4. Limits of Tertiary larger foraminifera.

drifting, but the tool is in any event probably too blunt for assessing possible continental shifts of a few degrees of latitude only.

4. Perhaps the most striking feature of the distribution data is the great longitudinal mobility of many genera and species which were at the same time latitudinally restricted. For example *Orbitolina* became abundant and widespread at genus level and one suspects also at species level, the entire length of 'Tethys'. Cretaceous orbitoid genera such as *Orbitoides* and *Omphalocyclus* occur from one 'end' of the 'biome' to the other. Tertiary Lepidocyclinidae such as *Eulepidina* ranged across the Atlantic from the Americas to Europe and Africa and to the Far East. Even among *Nummulites* (a genus which scarcely penetrated the Americas and then only with obviously great difficulty) examples come readily to mind of distinctive species ranging the entire length of the Old World 'biome', e.g. the Oligocene reticulate form *N. intermedius fichteli*. These examples could be extended in number considerably.
5. The fusuline pattern is scarcely reconcilable with the Mesozoic and Tertiary pattern whether on a present-day globe or the symposium reconstruction. With this Late Palaeozoic group there seems to have been virtual ubiquity of distribution given sediments of appropriate age and facies.

THE OPENING OF THE ATLANTIC OCEAN

The North Atlantic

The factor of longitudinal mobility leads inevitably into consideration of the problem of the Atlantic Ocean. Three genera are especially relevant from this point of view in the earlier Cretaceous: *Anchispirocyclus* which ranges from the latest Jurassic into the very early Cretaceous, *Choffatella*, a Neocomian to Albian form, and *Orbitolina* which ranges from Barremian to Late Cenomanian.

Once a path has been cleared through the taxonomy (for a discussion see Maync 1959, Jordan and Applin 1952, Loeblich, Tappan *et al.* 1964), the records of *Anchispirocyclus* plotted on text-figs. 2 and 3 can all be referred to the single (type) species *A. lusitanica* (Egger). The case of *Choffatella* is similar, for although several species have been described, only one has survived detailed specialist taxonomic study, *C. decipiens* Schlumberger. (The recent description of a Late Jurassic species, *C. tingitana*, by Hottinger awaits comparative study and reports from additional localities for further evaluation.) In the case of *Orbitolina* a truly vast quantity of data is available relating to perhaps 30 or more described species from the central American region across Europe and Asia to the northern Japanese island of Hokkaido. 'Dust-bin' species are obviously well represented in the literature and we await a detailed statistical analysis of the entire group in order to assess the influence of the late Early Cretaceous Atlantic on their distribution at species level, for although many notable attempts have been made at morphogenetic analysis, no simple rationalization has emerged. In a detailed quantitative review of American forms, Douglass (1960) distinguished eight species but felt able to assign only one (and that doubtfully) to an Old World species.

This suggests that by Aptian-Albian times a widening proto-Atlantic had already significantly modified the distribution pattern of this highly mobile genus, but the

evidence of *Anchispirocyclus* and *Choffatella* scarcely lends support to this facile assumption. Moreover, the disappearance of larger foraminifera as a whole from the central American region between Late Albian and Early Senonian times warns of possible other controlling factors. It is indeed surprising that the larger litiolids, well established in the central American region through Jurassic and Early Cretaceous times, were unable to generate their continuation into the Late Cretaceous and that the same group in the Old World continued to flourish, producing repeated examples of new genera particularly in European Tethys and south-west Asia, culminating in Maestrichtian times with the 'enormous' complex genus *Loftusia*.

What may eventually prove to be a highly significant find was recently reported by Gupta and Grant (1971) who have recorded *Orbitolina* from Flemish Cap, a locality on the North American continental slope some 400 miles due east of Newfoundland. On a present-day globe the record appears incongruous in relation to the distribution pattern established for the genus and especially so since it appears to be a European species (*O. conoidea* Gras), yet latitudinally it is south of the northernmost occurrences of the genus in Europe. On the Symposium model, the record is much less startling, and possibly even predictable given beds of suitable facies and appropriate age. We can but await further results from drilling off the North American coasts.

The picture changes with the start of the Late Cretaceous. As noted already, larger foraminifera disappear abruptly from the American scene while new families, and new genera within old-established families, appear progressively in the Old World. The Cretaceous alveolines enjoyed great mobility within the Old World, although they were not so widespread as subsequently in the Tertiary when one genus only (*Borelis*) appears to have reached the Americas. Dicyclinidae ranged from western Europe to the Middle East as did also another important sub-family, the Meandropsininae. The picture therefore is of considerable mobility but not across the Atlantic.

Larger foraminifera reappear in the American record in the Senonian, although there appears to be some doubt as to the precise level in European stage terms, and their reappearance takes place within the 'traditional' central American region. Orbitoidal forms are particularly involved in this return and the relationships of Old and New World taxa become important to evaluate. In the past forty years genera have been split and variously regrouped and additional taxa described, not all of which have survived re-evaluation. The biogeographical review of these forms by Vaughan (1933) makes little impact in terms of current classification, but some aspects of the distribution seem to be of general acceptance. First, the Orbitoididae *sensu stricto* (including *Orbitoides* and *Omphalocyclus*) appear in the record effectively synchronously in the Old and New Worlds. Second, the Pseudorbitoididae originate in the central American region and apart from isolated records from Port Moresby in Papua and rather doubtfully from southern India, remain restricted to the New World. A contrast such as this between the mobility patterns observable in two morphologically rather similar, stratigraphically coeval and within certain limits genetically related families, exposes in full measure the pitfalls awaiting the unwary advocate of 'drift' seeking evidence from the distribution of organisms.

The South Atlantic

Consideration of the South Atlantic raises a different set of problems. The Symposium Base Maps imply a post-Cretaceous date before any appreciable opening and a two-thirds open condition by Eocene times.

As with the central Americas, larger foraminifera seem to have vacated the north-west African coasts south of Morocco at the close of the Early Cretaceous, not to return until the Early Tertiary when a fairly diverse suite of Discocyclinidae and Nummulitidae appears in Senegal. Records further south than this are rather sparse and limited in diversity, the extension to the Cameroons accommodating only poorly characterized Nummulitids (not *Nummulites* s. str.) in the Eocene, and Miogypsinidae in the Miocene. The Angola occurrences of Miocene *Lepidocyclina* and *Miogypsina* are not necessarily migrants from the north and may have worked their way around South Africa. Careful taxonomic studies may resolve this problem in due course. Along opposing coasts in South America no record is yet known south of Venezuela.

It is difficult to relate these patterns more or less directly to controls originating from a drifting apart of the two continents in very early Tertiary times. Certainly in the condition of opening indicated by the Eocene Base Map one might have expected a spread of larger foraminifera to latitudes similar to those reached along the East African coast. If the South Atlantic gyre was comparable with that of today, and assuming a northerly origin, a cold Benguela current may well have played an important part in inhibiting the southerly spread of these forms. On the other hand one might expect by the same token that complementary warm currents would carry such forms to higher latitudes along the South American coastal basins, but this apparently is not the case. The available evidence is, however, scanty and important discoveries could yet be made.

THE NORTHWARD FLIGHT OF INDIA

The opening of the North and South Atlantic raised questions of mobility within the 'biome'. The postulated rapid flight of India from a Cretaceous position tucked into the East African coast to its present position attained effectively by Early Tertiary times involves quite different considerations. Unfortunately two major factors operate against investigation of the postulate in terms of larger foraminiferal distribution: (i) The extreme rarity of Cretaceous marine sedimentary basins along the coastal margins of southern India and Ceylon; (ii) The location of the region within the larger foraminiferal 'biome' throughout the postulated shift and the probability of connecting sub-tropical shelf environments at any intermediate stage in the process.

It is not surprising to find that where sediments of suitable facies and appropriate age exist, as for example in the Coromandel region, orbitoid foraminifera of the latest Cretaceous and Discocyclinidae of the Early Tertiary should be on record. The search for further clues here should perhaps be in the offshore areas.

Madagascar may be more significant than India, however, and a possible test of the postulated Cretaceous position would be the discovery of *Orbitolina* in the Aptian-Albian (or possibly also Cenomanian) of the island. Even so, such a

discovery could conceivably be interpreted also simply as an extension of the East African distribution of the genus. Visser has mentioned but not figured a record of *Lepidorbitoides* from the island. If confirmed this would represent the sole record from East Africa of this group and would suggest very definitely a more northerly Late Cretaceous position than obtains today.

AUSTRALIA, NEW ZEALAND, AND NEW GUINEA

I have called attention elsewhere (Dilley 1971) to the problems surrounding the interpretation of larger foraminiferal distributional patterns in Australasia during the Cretaceous. Suffice it here to reiterate that: (i) New Guinea stands apart from the East Indies in its lack of earlier Cretaceous larger foraminifera and is thus linked with Australia and New Zealand in this particular; (ii) its entry fully within the larger foraminiferal 'biome' is initiated in the latest Cretaceous and is already complete by the very early Tertiary. It is clear, however, that many of the larger foraminiferal genera appropriate to the Pacific began to find their way into southerly districts of both Australia and New Zealand from the start of the Tertiary, but whether this is attributable to movement of the plate into lower latitudes, or a radiation of such genera into higher latitudes will be very difficult to resolve. A wider radiation of Eocene Discocyclinidae into high latitudes certainly seems an inescapable conclusion on the evidence from the Pacific Coast of North America and oceanic circulation can scarcely be invoked as a prime cause on present evidence of a cold Alaska current. On the other hand the causation appears not to be a global feature in so far as no general increase of water temperatures is indicated by the evidence from northern Europe and the North Sea Basin. The separation of factors which might be causatory of anomalies in distribution patterns is indeed difficult as Professor Sneath has pointed out.

CONCLUSION

Can we see then any glimmer of the truth about continental drift in larger foraminiferal distribution patterns? Evidently we have in this heterogeneous, stenothermal, benthonic fossil group many forms of proven very high longitudinal mobility, but which nevertheless found the crossing of the Mid-Cretaceous Atlantic (in whatever form it existed) an impossible venture, and this despite the fact that the admittedly few) Early Cretaceous forms seem to have achieved the crossing with little difficulty.

One might be tempted to maintain from this evidence that a crucial stage in the opening of the central Atlantic was reached in Mid-Cretaceous times were it not for the uncomfortable fact that the *entire* group effectively disappeared from the American scene during this interval of time and moreover retreated also in north-west Africa to the 'Mediterranean' region proper.

In the latest Cretaceous, and the Tertiary, although well-developed larger foraminiferal faunas reappear in the central American region, the evidence is strongly indicative of difficulty in making the east to west crossing, as Adams demonstrated at the 1965 meeting of the Palaeontological Association. One cannot but ask oneself

in this context, how or where restricted American families such as the pseudorbitoids can have originated. Certainly, apart from the three-layered ('orbitoidal') groups such as the Lepidocyclinidae, Miogypsinidae, and perhaps also the Discocyclinidae, the mainstream of larger foraminiferal development has always been in Old World Tethys.

My contribution is offered somewhat agnostically. In preparing it, I was very conscious of Professor Westoll's remarks at the 1965 Symposium on Continental Drift, who, despite his averred belief in the reality of drift, commented that 'perhaps more dubious and unconvincing evidence has been published in this field (of distribution of organisms) by enthusiastic drifters than in all the other fields put together'.

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