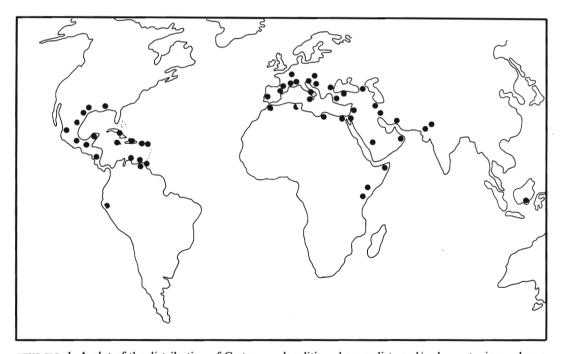
# CRETACEOUS TETHYAN CORAL-RUDIST BIOGEOGRAPHY RELATED TO THE EVOLUTION OF THE ATLANTIC OCEAN

by A. G. COATES

ABSTRACT. The percentage of endemic coral and rudist genera is plotted for each stage of the Cretaceous in the Tethyan realm. From Neocomian to Aptian times only a Mediterranean faunal province is clearly defined by endemic genera. From Albian times a Caribbean province appears and, in general, increases in endemic coral and rudist genera up to the Maestrichtian. The separation and evolution of this province is related to geographic isolation of the Caribbean from the Mediterranean by spreading of the Atlantic Ocean.

It has long been known that a distinct association of organisms, with a high degree of endemism, has characterized the Caribbean, Mediterranean, Middle Eastern, and Himalayan regions throughout Mesozoic and Tertiary time. This region, generally referred to as Tethys, is clearly demonstrated in the Cretaceous by reference to the distribution of hermatypic corals and rudists (text-fig. 1), certain gasteropods



TEXT-FIG. 1. A plot of the distribution of Cretaceous localities where rudists and/or hermatypic corals are dominant elements of the fauna. One circle may represent more than one locality. The localities outline the approximate limits of the Tethyan realm, although the boundaries may have migrated north or south at different times during the Cretaceous.

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(Sohl 1971, p. 1613), and orbitoline foraminifera among others, which typically occur associated in very shallow water biohermal limestone facies.

The great diversity of these faunas and the widespread construction of organic frameworks dominated by hermatypic corals, algae, and rudists (many of which also probably possessed zooxanthellae in their mantles), strongly suggest a tropical realm. With this conclusion as a starting-point an attempt is made to trace the evolution of provinces within this realm during Cretaceous times. I am extremely grateful to Dr. N. F. Sohl for helpful criticism and data on the distribution of Nerinacean gasteropods and rudists and to Dr. E. G. Kauffman for access to his data on endemism of bivalves within the Tethyan Realm (1972).

### DATA AND METHODS USED TO IDENTIFY FAUNAL PROVINCES

The definition of faunal provinces should be based on a comparison of faunas having a consistent and reliable taxonomy. Many groups which are important elements in Cretaceous Tethyan biohermal facies are either undescribed or subject to confused taxonomy. Ostracodes, often extremely abundant in the Caribbean limestone-shale sequences, are not yet described (Hazel 1972, pers. comm.). Many gasteropods need generic revision before intercontinental comparisons may be safely made (N. F. Sohl 1972, pers. comm.), and, particularly in the Caribbean, large non-rudist bivalve faunas remain to be described.

The distributional data for the evolution of Tethyan provinces has been provided by rudists and hermatypic scleractinia which have been the subject of many papers both in the Caribbean and Indo-Mediterranean regions. In general the definition of the rudist genera are taken from the *Treatise on Invertebrate Paleontology* (R. C. Moore, ed.). Those for the scleractinian corals is taken from the author's card file (revising the literature identifications wherever possible). The data for the Caribbean is augmented with the author's identification of genera in the extensive collections of the United States Geological Survey and the Smithsonian Institution.

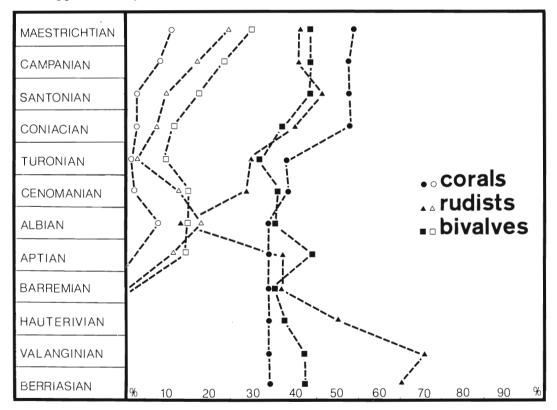
Because an adequate and consistent taxonomy does not exist at the species level the regional comparisons have been made with genera. The percentage of endemic genera has been used as the criterion for provinciality. This is a safe but somewhat crude approach to palaeobiogeography because a statistical technique as, e.g. cluster analysis, using some coefficient of similarity, compares the association of all the taxa in any fauna with another, not just the mutually exclusive ones. This is likely to reveal more subtle and detailed provincial patterns. However, the presence of some endemic taxa is characteristic of major faunal provinces and serves to trace the effect of plate movements on biogeography.

The distribution of known genera of corals (exclusive of ahermatypic cosmopolitan genera) and rudists from the Indo-Mediterranean and Caribbean regions were plotted by stages throughout the Cretaceous. In each of these regions for each stage, the number of endemic genera was expressed as a percentage of the total number of genera occurring within Tethys.

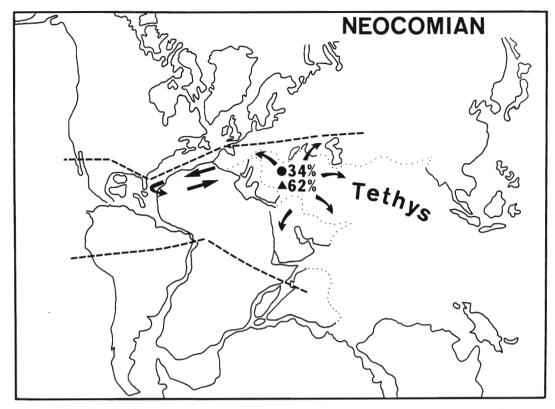
## EVOLUTION OF ENDEMISM WITHIN TETHYS

From the beginning of the Cretaceous the Mediterranean region is characterized by a high proportion of endemic genera (text-figs. 2, 3). This presumably reflects a long, stable history for this region of Tethys going back to Triassic times. On the other hand the Caribbean, from the Neocomian until the Aptian, does not have any endemic genera although corals and rudists are known from many localities. Even allowing that the Mediterranean faunas have been more extensively collected and studied, it seems apparent that it was the only major endemic centre at this time.

In the Aptian-Albian the Caribbean region appears as a distinct province for the first time (text-fig. 2). In general, in the Caribbean, rudists show a consistently higher percentage of endemic genera than corals but both groups follow very similar trends. Endemism in corals and rudists reaches a high point in the Albian but decreases again to a low in the Turonian before steadily increasing to its highest level in the Maestrichtian (text-fig. 2). It is interesting to note that diversity (total number of genera) in both rudists and corals also increases; the number of coral genera rises from approximately 50 in the Albian to over 90 in the Maestrichtian.



TEXT-FIG. 2. Graphs showing per cent of Tethyan endemic genera for each stage in the Cretaceous for the Caribbean province (open symbols) and the Mediterranean province (black symbols). The curve for bivalves is taken from Kauffman (1972).



TEXT-FIG. 3. Map showing distribution of endemic genera in the Neocomian plotted on symposium outline map (Oct. 1971) for the Mid Jurassic. Symbols as for text-fig. 2. Dashed line indicates approximate limits of Tethys.

In the Mediterranean region, from Albian times, endemism also increases and there is an indication, as in the Caribbean, of a recession in the Turonian (text-fig. 2). Unlike the Caribbean, however, this trend levels off in the Campanian-Maestrichtian. At this time there is also clear indication of a Middle Eastern province emerging to the east of the present Mediterranean characterized by endemic rudist genera. This province is not indicated by any endemic corals (text-fig. 4).

# CAUSES OF ENDEMISM

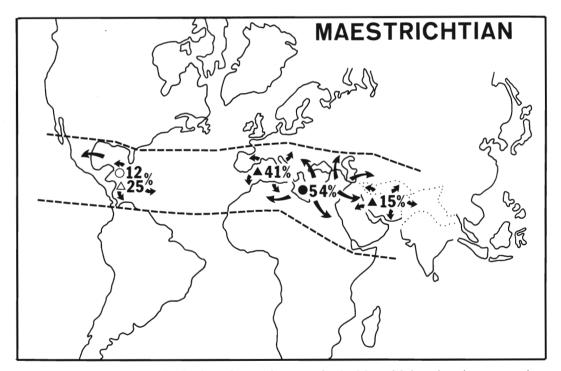
If it is assumed that the Tethyan provincial system in the Cretaceous represents the tropics of the times, then the evolution of biogeographic provinces within it cannot be explained by latitudinal-temperature gradients, which are the major controlling factors in the north-south configuration of most major faunal provinces (Valentine 1967, 1971a; Sohl 1971, p. 1663).

The causes of endemism are therefore to be sought in east-west barriers, such as north-south land masses and cool or deep oceans, both of which are closely controlled by plate tectonic patterns. Valentine (1971b, p. 115) in a discussion of this topic concludes that 'the number of provinces is related to the extent to which

continental masses are fragmented by mid-oceanic ridges and therefore separated by abyssal ocean floors and to the latitudinal gradient'.

The evolution of endemism in the Cretaceous between the Caribbean and Mediterranean provinces (text-figs. 2, 3) is a clear example of the effect of the development of an oceanic ridge system as a migration barrier. If temperature gradients prevent a Tethyan fauna from migrating north or south and are not a factor for province development within the tropics then the inception of a Tethyan Caribbean province in Aptian-Albian times and its increasing degree of endemism up to the Maestrichtian can be related to the spreading of the Atlantic Ocean ridge system isolating it from the Mediterranean province. After the Albian, larval mobility and duration of corals, rudists, and other bivalves (and probably many other taxa) is insufficient to allow these organisms to migrate across the barrier of the widening Atlantic Ocean.

The apparent decrease in endemism during the Cenomanian-Turonian may be due to the fact that very few faunas of this age in the Caribbean are known but it may also reflect changes in the shelf provinces due to major marine transgressive-regressive cycles in Albian-Cenomanian times.



TEXT-FIG. 4. Map showing distribution of endemic genera in the Maestrichtian plotted on symposium outline map (Oct. 1971) for the Tertiary (Palaeocene). Symbols as for text-fig. 3.

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